

PROCEEDINGS

23rd International Ornithological Congress

Under the auspices of the
International Ornithological Committee

Organized by the
China Ornithological Society

Beijing, China, 11–17 August 2002

Editorial preface

For the first time since the 20th Congress in Christchurch, New Zealand, in 1990, a substantially complete proceedings of an international ornithological congress are published here in hard copy. Reproduction in CD-Rom format is also envisaged. The present Proceedings appear in two parts of the *Acta Zoologica Sinica*. Ten of twelve plenary lectures, including the two covering the origin of birds from the “Presidential Debate”, were published in 2004 in volume 50, pp. 880–1001. And here, the Official Report of the Congress, comprehensive summaries of all Round Table Discussions (RTDs), and all symposia that were submitted are published in full in a special supplement of the journal; two of the plenaries, submitted in shortened or abstract form and too late for inclusion in the 2004 issue, are added in the supplement.

For the first time since 1990, too, an Official Report is published in sufficient detail to provide a comprehensive record of the Congress and developments in the organizational machinery for future congresses, particularly in the International Ornithological Committee. Here I draw attention to a thorough report on the functioning of the Scientific Planning Committee for this Congress, and to a report from an *ad hoc* Finance Committee set up by incoming President Walter Bock at the the 22nd Congress in Durban to investigate the financial affairs of the International Ornithological Committee and the running of congresses with an eye to their future. It makes important recommendations concerning the need for fund raising and fund servicing by the IOCommittee, the rationalization of financial obligations between the IOCommittee and local organizing committees, and the development of an international federation of ornithological societies and ornithologists. Implementation of the recommendations is likely to prove crucial for the future development of international ornithological congresses.

Of the Round Table Discussions, numbered 1–24, only 20 were actually held. Reports of all those held are included here, one of them (RTD 18) separately in the Official Report of the Congress because it was produced by a Standing Committee, namely the Standing Committee on Ornithological Nomenclature. Under editorial instruction, RTDs were formatted in two sections, the first laying out the issues addressed, and the second detailing the outcomes of the meetings. Conservation-oriented issues are a recurring theme. No less than 13 of the RTDs focused on them, reflecting the emerging pre-eminence of bird conservation in ornithology today, driven by a declining bird fauna globally. Areas of conservation covered by the RTDs ranged from monitoring of environmental contamination and bird pests in agriculture to the impacts of threatening diseases, long-line fishing, loss of migratory stopover sites, the bird trade and climate change. Three were concerned with essentially

Asian issues: the work of the threatened bird program and networks of Birdlife International in Asia, the collapse of vulture populations in southern Asia, and shorebird conservation on the East Asia-Australasian flyway.

Regrettably only 36 of the 39 symposia presented were submitted for publication. Of these, 17 are complete, 9 one paper short, 6 two short, and 1 and 3 comprise one and two papers respectively. The range of subjects covered and the detail of information presented, impossible even 50 years ago, is awesome and reflects well the enormous advances made in all branches of ornithological science in that period, from gene expression, hormonal action and molecular systematics to satellite-tracking of migration, differential functioning of avian right and left eyes, the workings of the syrinx, flight energetics and integration of avian physiology with exogenous life cycle rhythms. Again conservation issues emerge pre-eminently, addressed directly in 11 symposia, of which 7 concern Asia at least in part. To enable ready perception of the content of the symposia, I present here a brief synopsis of each:

S01 — Perspectives in avian acoustic communication: in memory of Louis Baptista (5 papers) ranges from advances in understanding the modes of the remarkable wing sonations in the South American Pipridae to the discovery of triggering and signal mechanisms for vocalization in the brain, and for vocal learning, a phenomenon known in only three orders of birds: Psittaciformes, Apodiformes (Trochilidae) and Passeriformes.

S02 — The role of high quality individuals in populations of long-lived birds (3 papers) uses species studies on different seabird groups to bring out the importance of quality condition in pre-fledging young, particularly mass, for future survival, recruitment and breeding success.

S04 — Influence of birds on ecosystem structure and function (3 papers) deals with the environmental impact of land and freshwater birds at broad, ecosystem scales in different parts of the world (North America, Madagascar and New Zealand), particularly their keystone roles in food harvesting, pollination and seed dispersal.

S06 — Macroscopic and microscopic evolutionary perspectives on feathers (4 papers) focuses on the origin and evolutionary development of feathers from ontogenetic, paleontological and selectional perspectives. It addresses the functional structure of feathers, touches on the origin of flight, and, in its introduction and conclusion, draws attention to many still-unanswered questions.

S07 — Key issues in the conservation of sites important for birds (4 papers) reviews the establishment of Important Birds Areas (IBAs) in developing countries (Asia,

Africa and Mexico), outlining procedures and processes at local, national and international levels, recounting experiences and giving “take-home” messages.

S08 — Effects of global climate change on birds: evidence and predictions (5 papers) addresses the current impact of global climate change on timing of breeding and migration in land-, sea- and shore- birds, highlighting a developing phenological disjunction and focusing on the prediction of effects.

S09 — Photoperiodism: mechanisms and adaptations (2 papers) is concerned with physiological linkages, centering on the endocrine system, from the reception of photoperiodic signal to expression in reproduction and molt. It clarifies complexities in hormonal release and inhibition, and their control by the brain via the nervous system.

S10 — Demographic responses to habitat fragmentation: contrasts across space and time (3 papers) uses cross-continent comparisons to identify the population, not species or individual, as the unit most affected by habitat fragmentation, as manifested in lowered survival and breeding success. For remedial action, it stresses the importance of identifying the parameters that initiate causal mechanisms for demographic change.

S11 — Forest management and conservation of Galliformes (3 papers) comprises studies of the general conservation requirements of landfowl in east Asia (pheasants, quail) and central America (Cracidae), focusing on habitat protection and use of particular taxa as indicators of habitat quality.

S12 — Migration and conservation of cranes and storks (5 papers) explores the use of new technologies, notably satellite-tracking, to trace the migratory routes and stopover refuges of large migratory birds with accuracy not possible with conventional ringing. The potential for such technologies to provide information vital for conservation management — routes, times, rest points and physiological condition — is particularly clear in the paper by Berthold et al.

S13 — Mating patterns and ecology (2 papers) addresses the importance of the link between food availability, breeding synchrony and patterns of extra-pair mating outside the social pair, and illustrates trade-offs in the frequency of mate guarding against resource availability and habitat density.

S14 — Integrating mechanism and function in bird behavior: how hormones can help (3 papers) integrates hormonal action with physiological function and behavioral expression from the molecular level to the organismal, at one of the cutting edges in biological science. It presents evidence that sex steroids can be produced in tissues outside the sex glands, enabling expression of sexual traits without activating the reproductive system; it shows how the organizing actions of sex hormones in early (embryonic) development affect mate preference in adulthood; and it correlates the production of sexually attractive male song

with features of the brain and their stimulation with testosterone.

S15 — Specialization in island land birds (5 papers) focuses on evolutionary specialization and flexibility in island land birds as strategies for survival, considered against backgrounds of diet-driven evolutionary radiation in Darwin’s finches and Hawaiian honeycreepers, the benefits of cooperative breeding in the Seychelles warbler, generalist foraging release in island Australasian silvereyes, and shifts in breeding times to synchronize with diverging food availability in different habitats in the blue tit, with implications for parapatric speciation on Corsica.

S16 — Chemical ecology and the study of bird reproduction (5 papers) considers the role of chemical compounds in proximate and ultimate aspects of reproduction, addressing such issues as differential composition of preen waxes between seasons, impacts of vitamin availability through the food chain, parasite suppression by volatile compounds in nest material, and the role of antioxidants such as carotenoids which strengthen immune response and express fitness through brighter coloring.

S17 — Evolutionary history of selected bird taxa from the Sino-Himalayan region (5 papers) produces, using grouse, the Sichuan jay, golden-spectacled warbler complex, snow and mountain steppe sparrows, and redstarts as examples, a series of studies illustrating the importance of the Sino-Himalayan horst as a refuge and center of evolutionary radiation for modern species-groups of Eurasian songbirds.

S18 — Sexual signalling and speciation (4 papers) connects sexual selection with morphological and genetic differentiation and speciation, drawn from comparative patterns of morphological and molecular differentiation, the interactive roles of male display, environment and female choice, the causes of pre- and post-mating reproductive isolation, and the consequences of learning sexual signals. The symposium summarizes the diverse forms of reproductive isolating mechanisms and their meaning for speciation.

S19 — The evolution of avian migration (5 papers) broadly covers not only the origin of migration in phyletic lineages but also mechanisms for adaptive change and supporting environmental conditions which underlie migration. It summarizes evidence for the development of long-distance migration by using tools of molecular-based historical biogeography and population genetics, by assessing ringing combined with stable isotope marking and satellite-tracking, by evaluating interactions between environmental variation and phenotypic plasticity, and by developing annual routine modeling.

S20 — Evolutionary genetics of the Phasianidae (4 papers) uses molecular technology, including a novel nuclear hemoglobin gene suitable for use at different taxonomic ranks, to present new advances in elucidating phylogenetic relationships among the Phasianidae at species, generic and supra-generic levels. Included is an overview

of the phylogeny of the landfowl, order Galliformes.

S21 — Visual behavior in birds: linking brain and behavior (4 papers) explores at both embryonic and adult levels the development of different functions in right and left eyes, and the role of the nervous system in transferring different classes of images by different pathways to different parts of the brain for processing. Highlighted here are some remarkable advances in unravelling “lateralization” in the sight of birds, showing that the left eye is used for wide search and orientation on distant objects and the right for control of manipulation and close-up responses.

S22 — Torpor in birds: regulation of energy metabolism and body temperature (5 papers) addresses the rationalization of terms used for describing the metabolic effects of torpor and reviews the occurrence, daily timing and stages of torpor in the Aves, with emphasis on Trochilidae and the Caprimulgiformes. One paper focuses on the development of models to predict torpor.

S23 — The biological species concept: application in pure and applied ornithology (5 papers) reviews the development of species concepts in general and the biological species concept (BSC) in particular, teasing out the philosophical differences between concept, rank in classification and the species in nature. Examples are given of difficulties in application, and of alternatives to the “biological species” as the basal biodiversity unit for conservation. One compromise solution, that of classifying species by a combination of concepts in a single classification, nevertheless begs the question: is it scientific?

S24 — New directions in avian molt ecology (4 papers) evaluates new concepts and statistical methods in elucidating molt patterns and their adaptations to environmental circumstances and seasonal availability of food. It covers seasonal effects on the rate of wing molt in migrating shorebirds, adaptations of molt to seasonal cycles, including double molt, and seasonal molt in penguins in relation to breeding and food availability.

S25 — Population regulation in heterogeneous landscapes: a means for predicting the consequences of environmental change (2 papers) reviews diverse issues of population regulation, one paper dealing with regulation in cooperatively breeding birds, and the other with the mechanisms and prediction of regulation more generally, demonstrating the important role of “site-dependence” in birds, outlining procedures for its identification and explaining why it needs to be distinguished from “crowding” in conservation management.

S26 — How birds sing (4 papers) examines the functioning of the syrinx and vocal sacs in birds, the airflow systems that drive them, the physical mechanism of song production and the phonic structure of sound produced. Included are papers demonstrating the newly-found importance of lateral, not medial, tympaniform membranes in producing complex, bi-lateral sounds, and of the nerve systems directing them. Such advances have been made pos-

sible by microlesion technology and endoscopic examination of the vocalizing syrinx with laser light.

S27 — Morphological integration and modularity (5 papers) deals with the emerging appreciation that evolution in birds has developed complexes or “modules” of co-varying morphological traits in response to such adaptive pressures as feeding and flight. The interplay of module heritability and selection is examined, along with correlations of form and life-style, and their phylogenetic basis, towards improving understanding of avian evolution and biological systems.

S29 — New developments in the study of seabird foraging (4 papers) reviews progress and technological advances in research into seabird foraging, illustrated by case studies of the way procellariiform seabirds track food by smell, how penguins manage buoyancy and search underwater, and how cormorants cope with different temperature regimes by budgeting foraging time.

S30 — Interactions between coastal aquaculture, fisheries and birds (2 papers) approaches this emerging conservation issue from two different perspectives, one involving development of behavior-based models to predict effects on coastal birds by changing environmental conditions, the other relying on actual demographic records to report serious declines in bird populations and species in shrimp-farmed mangrove environments in India.

S31 — Bird population explosions in agroecosystems: common factors in case histories (5 papers) draws together common threads, based on the starling in Britain, the quelea in Africa, cranes in India and the eared dove in South America, for causes of population explosions in birds, all of them linked to changes in local environment, habitat and an expanding agriculture.

S33 — Competition and hybridization from introduced waterbirds: a rising political issue (5 papers) addresses the effects of introduced waterfowl on indigenous waterfowl, and their control, by assessing the extent of introductions, illustrating the actual and potential impacts of the North American ruddy duck and mallard in Europe and New Zealand respectively, and reviewing available legislative capability and its needs.

S34 — Optimality in bird migration — the role of stopover ecology (4 papers) reviews advances in understanding the ecological and physiological mechanisms of migration, focusing on the importance of stop-over sites for refuelling. The symposium covers modeling that integrates fuel loading and flight mechanics to predict optimal flight times, and addresses factors affecting departure decisions and refuelling drawn from capture-recapture data, both theoretically and empirically.

S35 — Bird minds (5 papers) introduces the rather controversial field of avian cognition, and covers spatial recognition by birds, the learning of abstract skills, combinatorial skills, language and, in the case of the New Caledonian crow, tool manufacture. Comparisons with pri-

mates are drawn repeatedly, demonstrating that birds have higher cognitive capacity than is often thought.

S36 — Energetics, physiology and biochemistry of bird flight (2 papers) focuses on the use of wind tunnels to test predictions of the energetics of bird flight from theoretical modeling with empirical data that use heart rate as an indicator of metabolic rate and evaluate the effects of size on energy and water use during migratory flight.

S37 — Global seabird conservation (5 papers) has a central theme, namely, that approaches to seabird conservation must be global and international because seabirds are rarely tied to political boundaries. The theme is illustrated with case studies of fish-catch interactions between seabirds and fisheries, the conservation of particular rare and endangered species, management of mortality from long-line fishing, and assessments of sustainable harvesting of seabirds and global trends in survival.

S38 — Phenotypic plasticity and early developmental conditions in birds (5 papers) considers the adaptive functions of phenotypic plasticity, and how the quality of the egg (maternal effects), embryonic environment, and environmentally-induced responses in nestlings may all influence fitness in adulthood.

S39 — Ecological forestry and avian communities (5 papers) examines the effects of silviculturally managed forests and forest fragmentation on bird life in diverse global regions, using case studies from Taiwan, Japan, Central Canada, India and the longleaf pine ecosystem in eastern USA. All corroborate the importance of maintaining complexity in forest structure.

S40 — Periodic environmental changes: understanding the physiological basis of life history adaptations (1 paper) concerns the mechanisms underlying life history adaptations in breeding, migration and molt. The single paper addresses the constraining effects of environmental seasonality, breeding and migration on molt.

A further highlight of the Proceedings, as befits the host nation, is the focus on the new and remarkable discoveries of fossils of early, pre-Paleozoic birds in China over the last several decades. Not only do the discoveries throw

light on the ancestors and early evolution of birds but they also bring insights to the origin of feathers and development of flight, issues that are core subjects of three plenary addresses and one symposium paper (S06:2), and were implicated in one more plenary address and two further symposium papers.

It is to be regretted that the Proceedings of the 23rd International Ornithological Congress has appeared so long after the Congress itself. A product of unforeseen circumstances, delays began with impractical deadlines for submission of manuscripts, which were rarely kept and diverted me to much emailing to collate what I could. It was not until mid 2004 that sufficient material had arrived for putting the Proceedings together. Despite the facilities offered by computing and the internet, it is also clear that the publication of future Congress Proceedings can only be managed by professional editorial bodies with a number of full-time staff that can handle not only the actual editing, but also the coordination required to chase up late papers and the computing power to decode and reformat papers submitted in diverse programs with frustratingly perverse defaults.

Although delayed, the Proceedings nevertheless still fulfill their central goals, that of producing a formal record of the 23rd International Ornithological Congress and of recording the general state, progress and directions of ornithological knowledge and research at the time. For its final full publication in hard copy, I must thank, above all, the China Organizing Committee in general, and Professor Jia Zhi-Yun and Mr Liu Feng in particular. Professor Jia, editor, *Acta Zoologica Sinica*, and Mr Liu, Assistant Secretary-General for the Congress, handled the processing of papers in Beijing, and dealt with me promptly and patiently. Their innate professionalism was of immeasurable help in our collegiate interactions.

Richard Schodde,
General Editor,
Proceedings of the 23rd International Ornithological
Congress, Beijing

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The International Ornithological Congresses, 1884–2002

	City	Year	President	Secretary-general
I	Vienna	1884	Dr. Gustav F.R. Radde	Dr. Gustav von Hayek
II	Budapest	1891	Prof. Victor Fatio,	Dr. Geza von Horváth Otto Herman
III	Paris	1900	Dr. Émile Oustalet	G. Jean de Claybrooke
IV	London	1905	Richard Bowdler Sharpe	Dr. Ernst J.O. Hartert J. Lewis Bonhote
V	Berlin	1910	Prof. Dr. Anton Reichenow	Herman Schalow
VI	Copenhagen	1926	Dr. Ernst J.O. Hartert	E. Lehn Schioler
VII	Amsterdam	1930	Prof. Dr. A.J.E. Lönnberg	Prof. Dr. L.F. de Beaufort
VIII	Oxford	1934	Prof. Dr. Erwin Stresemann	Rev. Francis C.R. Jourdain
IX	Rouen	1938	Prof. Alessandro Ghigi	Jean Delacour
X	Uppsala	1950	Dr. Alexander Wetmore	Prof. Dr. Sven Hörstadius
XI	Basel	1954	Sir Landsborough Thomson	Prof. Dr. Adolf Portmann
XII	Helsinki	1958	Prof. Jacques Berlioz	Dr. Lars von Haartman
XIII	Ithaca	1962	Prof. Ernst Mayr	Prof. Charles G. Sibley
XIV	Oxford	1966	Dr. David Lack	Prof. Dr. Niko Tinbergen
XV	Den Haag	1970	Prof. Dr. N. Tinbergen 1966-1969, Prof. Dr. Finn Salomonsen 1970	Prof. Dr. Karel H. Voous
XVI	Canberra	1974	Prof. Jean Dorst	Dr. Harry J. Frith
XVII	Berlin	1978	Prof. Donald S. Farner	Dr. Rolf Nöhring
XVIII	Moscow	1982	Prof. Dr. Lars von Haartman	Prof. Valery D. Ilyichev
XIX	Ottawa	1986	Prof. Dr. Klaus Immelmann	Dr. Henri Ouellet
XX	Christchurch	1990	Prof. Charles G. Sibley	Dr. Ben D. Bell
XXI	Vienna	1994	Prof. Christopher M. Perrins	Prof. John Dittami
XXII	Durban	1998	Prof. Dr. Peter Berthold	Dr. Aldo Berruti
XXIII	Beijing	2002	Prof. Walter J. Bock	Prof. Xu Wei-Shu

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Official Report of the International Ornithological Committee, 23rd International Ornithological Congress, at the Beijing International Convention Center, Beijing, 11–17 August 2002

Dominique G. HOMBERGER, Permanent Secretary

Prologue by the President of the 23rd International Ornithological Congress, Walter J. Bock

The International Ornithological Congresses have many results, not the least of which is the publication of their Proceedings. These have appeared in many forms and represent the major record of what has taken place in each congress. The current Statutes and By-laws specify that a formal report for each Congress must be published, although not necessarily within the Congress Proceedings, all, nevertheless, have been so published. These reports have been the responsibility of the Secretary-General until the end of the 20th congress in Christchurch, after which they became the purview of the Permanent Secretary. Some official reports have been excessively brief, making the task of detailing the history of ornithological congresses difficult. I am especially pleased that the report prepared by Professor Dominique Homberger is so complete and detailed.

Another value of Congress Proceedings is overviews of ornithological science presented at congress, a task that has become increasingly difficult with each successive congress. The difficulties are three-fold. First is the increasing of plenary lectures, symposia, and contributed papers presented at congresses; second is the increasing cost of publication; and third is the getting of manuscripts from congress members. There does not appear to be any solution to the first of these difficulties which is a reflection of the increasing interest in and diversity of avian biology. The second may be solved, at least in part by the publication of a large part of congress proceedings electronically as a DVD disk, as was first done for the 22nd Congress in Durban. This was a remarkable achievement and I hope that it will be continued in the future. There may not be any complete solution to the last problem as there will always be members who will not submit their manuscripts on time or at all no matter how much pressure is applied. Another difficulty arises from the increased use of English as the international language since the 10th congress in Uppsala; for the last several congresses, the proceedings have been entirely in English. Having a single international language maximizes information exchange, yet many congress mem-

bers have difficulties in preparing their contributions. Hence the need exists for a dedicated editor for Proceedings. For many of the past congresses, this task could be assumed within the office of the Secretary-General, but not always. For the 23rd congress, we have been fortunate that Dr. Richard Schodde (Australia) has accepted this role. He has spent many months contacting congress members for their manuscripts and then editing them. In a number of cases, this required major rewrites. In addition to this editing, Dr. Schodde has his own major research program on the birds of Australia and could not devote full time to the congress proceedings.

Some ornithologists have been unhappy about the delay in the publication of the proceedings for the 23rd congress, but we should all appreciate the hard work done by the Permanent Secretary, Professor Dominique Homberger, the Proceedings Editor, Dr. Richard Schodde, the editor of the *Acta Zoologica Sinica*, Professor Jia Zhi-Yun, and his entire staff for the publication of this important document of the 23rd congress. Our sincere thanks go to all.

1 Minutes of the Executive Committee Meeting, Sunday, 11 August 2002, 9:00 am– 5:00 pm

1.1 Executive Committee 1998–2002 (* present)

- Alexander V. Andreev (Russia)
- Aldo Berruti (South Africa, ex officio)
- *Peter Berthold (Germany, ex officio)
- *Jacques Blondel (France, ex officio)
- *Walter J. Bock (U.S.A., ex officio)
- *Carlos Bosque (Venezuela)
- *Michael Clarke (Australia)
- *Fred Cooke (Canada)
- *John P. Croxall (United Kingdom)
- *Nathan N. Gichuki (Kenya)
- *Hiroyoshi Higuchi (Japan)
- *Dominique G. Homberger (U.S.A., ex officio)
- *Lukas Jenni (Switzerland)
- *Pilai Poonswad (Thailand)
- *John C. Wingfield (U.S.A.)

*Xu Wei-Shu (China, ex officio)

1.2 Welcome and report by IOCommittee President, Walter J. Bock

See presidential report below — item 4.

1.3 Welcome and report by Secretary-General, Xu Wei-Shu

See report of the Secretary-General below — item 5.

1.4 Report by IOCommittee Secretary, Dominique G. Homberger

See report of the Permanent Secretary below — item 6.

1.5 Report by the Chair of the Scientific Program Committee, Fernando Spina

See Scientific Program Committee report below — item 7. Some concern was expressed that outstanding scientific results might not be published in the IOCongress Proceedings, so reducing the quality and reputation of the IOCongress and its Proceedings. If the IOC Proceedings published contributions besides the plenary lectures and symposia, it could raise the profile of the congresses. Several last minute cancellations of symposia contributions resulted, moreover, because of lack of travel funds.

During the ensuing discussion, various issues were raised to improve future congress programs and proceedings, such as sanctions against congress contributors that choose not to show up at the last minute, and the publication of the complete proceedings on the official web page of the IOCongress.

Walter Bock thanked Fernando Spina for his tremendous job as chair of the Scientific Program Committee.

1.6 Report by the Chair of the Finance Committee, Tim Wood

See item 8 below. Tim Wood was not present, but the main points of the report were summarized by Dominique Homberger.

1.7 Report by the Chair of the Executive Committee Nominations Committee, Peter Berthold, on the nominations of IOCommittee officers (President, Vice-President, and Permanent Secretary) and of members of the Executive Committee for the 24th IOCongress, 2002–2006

Members of the Executive Committee Nominations Committee were Peter Berthold, chair; Carlos Bosque, Patricia Gowaty, Les Underhill, and Richard Schodde. Their nominations were:

President, 2002–2006: Jacques Blondel

Permanent Secretary, 2002–2006: Dominique G. Homberger

Honorary President, 2002–2006: Jiro Kikkawa

Vice-President, 2002–2006: Richard Schodde, John Wingfield

New members of the Executive Committee: Susan

Hannon (Canada), Elizabeth Höfling (Brazil), François Vuilleumier (USA)

During the ensuing discussion various issues were raised. The IOCommittee President should be one of the most prestigious ornithologists, but needs also to possess other extraordinary leadership qualities. The IOCommittee Vice-President is a one-term appointment and need automatically become president. He should not only serve as a replacement for an incapacitated President, but should have a defined task, such as the managing of the IOCommittee Standing Committees. Candidates should prepare a brief biographical sketch for distribution at the IOCommittee meeting, at which the candidates are elected.

As the IOCommittee Statutes allow only one EC-member per country, it therefore depended on the election results at the IOCommittee meeting whether one or two new Executive Committee members had to be elected, and whether the IOCommittee Statutes can be followed or require suspension in the circumstances.

A unanimous vote was taken to present the revised slate of names to the IOCommittee for voting.

1.8 Discussion of sites for the 25th IOCongress, 2010

While some opposed seeking concurrent invitations because of the substantial work required in preparing invitations, others supported it, partly because of the offering of choice and partly for insurance against unforeseeable natural or economic problems.

Some emphasized the need for the next two or three IOCongresses to be held in North America or Europe. Initial explorations for a Beringian IOCongress in 2006 had to be cancelled, leaving the invitation for an IOCongress in Hamburg, Germany, as the only one for 2006. Others spoke up for continuing the trend to hold IOCongresses in continents other than North America and Europe, so that congress venues remain truly international. Some emphasized the need for a South American congress, as that is the only continent yet to host an IOCongress. Invitations from Israel and Australia should also be considered. Hiroyoshi Higuchi has been considering Japan as a future host, an initiative supported by Pillai Poonswad. Thailand is another option: it has a good convention center but unfortunately lacks an organized ornithological society.

1.9 Presentation by Franz Bairlein of the invitation by Germany for the 24th IOCongress in Hamburg in 2006

See full report below — item 11. The invitation to Hamburg was submitted by the DO-G (German Ornithologists' Society) and the Vogelwarte Helgoland, Germany. Projected attendance is 1500 people. The meetings of the EOU (European Ornithological Union) will take place in 2003 and 2005, so that there are no conflicts.

The German Research Council will provide financial support for participants from Russia and the former Soviet Union. The Deutsche Forschungsgemeinschaft (the German equivalent of NSF in USA) would also provide funds

for invited speakers from low-income countries. It was recommended that delegates from high-income countries pay a higher registration fee. BioMedCentral was interested in launching an online journal called, for example, *Proceedings of the International Ornithological Congresses*, but only if it were not published only every four years.

During the ensuing discussion, it was suggested that the IOCongress in Hamburg should have a two-tiered registration fee structure. Some voices expressed doubts that Proceedings were necessary, especially because their abolition could lower the registration fee. But Peter Berthold was confident that the DO-G would find the funds to publish full proceedings.

The Executive committee agreed to recommend the German invitation to the IOCommittee with enthusiasm.

1.10 Presentation by the Chair of the IOCommittee Nominations Committee Fred Cooke

See Appendix 3 below. Members of the committee were Franz Bairlein, Walter Bock, Elizabeth Hoefling, Susumu Ishii, and Derek Pomeroy.

The IOCommittee members and some national ornithological societies were asked to submit names. Many nominees hailed from countries already well represented on the IOCommittee, creating potential over-representation. Three of the new nominees were from Brazil, but several countries still remained under-represented, and many countries were not represented at all. Remediating this situation will be pursued vigorously at the 24th IOCongress in Hamburg.

The ensuing discussion raised several issues concerning eligibility of candidates. One concerned national representation by ornithologists working in countries other than those of their birth. It was decided that national representation should be decided by country of residence, not origin. Another issue involved the need and desire to elect representatives from under-represented countries. Because most such countries are also low-income nations, few, if any, ornithologists from them have had the opportunity to attend an IOCongress. The IOCommittee Statutes, however, stipulate that IOCommittee members must have attended at least one IOCongress prior to election. As a compromise solution pending revision of the IOCommittee Statutes, it was agreed that candidates from under-represented countries who had never attended an IOCongress could be elected on the condition that they attend the first IOCongress after their election.

The vote on the list of names to be sent forward to the IOCommittee for potential election was unanimous.

1.11 Report by the Co-Chairs of the Resolutions Committee Eberhard Curio and Michael Rands

See item 12 below. The resolution was presented by Walter Bock.

1.12 Reports by the Chairs of the IOCommittee Standing Committees and their reappointment for the

IOCongress period of 2002–2006

The following IOCommittee Standing Committees are active:

- Clive Elliott: Working Group on Bird Damage to Agriculture of the IOCommittee Standing Committee on Applied Ornithology

- Richard Schodde: IOCommittee Standing Committee on Ornithological Nomenclature (see report below — item 9).

- David M. Bird and Bernd Ulrich-Meyburg: IOCommittee Standing Committee on Raptors (see report below — item 10)

- Jim Vanden Berge: IOCommittee Standing Committee on Avian Anatomy

During the ensuing discussion, the lack of activity of several standing committees was noted. It was recommended that the Vice-President be asked to serve as the liaison to the Standing Committees. It was further recommended that the Vice-President review the policies regulating the IOCommittee Standing Committees and provide the Executive Committee with recommendations. The need for committees that deal with over-arching international issues was recognized and stressed. Fred Cooke suggested that, in future, there should be no new standing committees, only ad hoc committees, because nonfunctional standing committees needed to be dissolved, whereas ad hoc committees were much easier to disband.

1.13 Discussion about possible changes in the organization of the IOCommittee

Discussion here addressed various issues that have been pending as well as recommendations made by the ad hoc Finance Committee (see item 8 below). There was a general feeling that various changes will need to be implemented to maintain the IOCommittee as a vital and dynamic organization.

For this, comments from all congress delegates would be sought, and boxes for suggestions for the future of the IOCommittee and IOCongresses were placed throughout the Congress venue in Beijing.

One pressing issue was the possible reorganization of the IOCommittee into an International Ornithological Society (IOS). The creation of a tax-exempt (not-for-profit) society would remedy the current unfortunate name IOCommittee, which shares the same acronym with the IOCongress and the International Olympic Committee. It would also enable the society to raise revenue through membership dues, grants, and donations.

Alternatively, an international federation or union of ornithological societies could grow out of the present IOCommittee and IOCongress. The question was raised whether the AOU, BOU, and DO-G would be interested in serving as the founders of the federation and in providing seed money to support the intersessional activities of the IOCommittee Secretariat and the IOCongress officers, as well as seed money for the preparation of congresses in

low-income, but bird-rich countries. Xu Wei-Shu suggested that institutional membership dues for such a federation may not be a problem even for low-income countries, because their governments are often willing to pay for such programs.

It was generally agreed that a reorganized IOCommittee will need to have funds to support a permanent secretariat, to provide financial support to delegates from low-income countries, to support the publication of proceedings and maintenance of a permanent web page, and to provide seed loans to ornithological societies that want to host an IOCongress. John Wingfield mentioned that the Society of Integrative and Comparative Biology (SICB) provides a very successful model for a biological organization. It has built up an endowment of 1.5 million dollars in about ten years. A federation also attracts the interest of foundations.

Fernando Spina stressed the importance of a defined message and mission for an organization to be able to raise funds. For the IOCommittee, an appropriate message would be the importance of basic science for conservation. And in this, the IOCommittee would be distinct from BirdLife International. In the words of John Wingfield: "The IOC brings together people who create science that can be used for conservation." Walter Bock also pointed out that basic research in ornithology has direct implications for human beings, and Hiroyoshi Higuchi emphasized that membership in ornithological societies is rapidly increasing in Japan, China, and probably the world over.

1.14 Close of meeting

Walter Bock thanked the Executive Committee for the most efficient meeting in a long time, and John Croxall thanked Walter Bock for chairing the meeting so effectively. It was decided that the Executive Committee would meet again at lunch on 17th August (12:00 noon–2:00 pm), to acquaint the new and old EC members with one another, and for any further discussion and action. At that meeting, no further business was in fact enacted.

2 Minutes of the first meeting of the International Ornithological Committee at the 23rd International Ornithological Congress, Tuesday, 13 August 2002, 8:00 pm

For attendance, see Appendix 1.

2.1 Opening and welcome by IOCommittee President, Walter J. Bock

2.2 In memoriam

See Appendix 2. The names of IOCommittee members who had passed away since the 22nd IOCongress in Durban, August 1998, was read by IOCommittee Secretary, Dominique Homberger. She also requested any additional names and biographical information. A list of deceased IOCommittee members with biographical information will

be posted on the IOCongress web page. A moment of silence was observed in honor of the deceased colleagues.

2.3 Report by the IOCommittee President, Walter J. Bock

At the IOCongress in Durban, two invitations for the 2002 IOCongress were presented, one from China and the other from Israel. The IOCommittee voted to accept the invitation from China. About ten days before the IOCongress in Beijing, Walter Bock received a letter from Yossi Leshem, who had prepared the Israeli invitation, saying that he was glad that the 23rd IOCongress was to be held in Beijing and sending his best wishes for a successful meeting.

Liu Feng did most of the organizational work for the IOCongress and has been extremely efficient. The meeting of the Scientific Program Committee (SPC) was held in Beijing on June 6–11, 2000. Walter Bock traveled again to Beijing in January 2002 for some last minute preparations. He was very satisfied with the smooth running of arrangements.

The IOCommittee Executive Committee had discussed the future and betterment of the congresses; and IOCommittee members were invited to provide suggestions relevant to this in a box near the registration desk during the Congress or to send them to Walter Bock, who would forward them to the incoming IOCommittee President, Jacques Blondel.

A more extended report is given below — item 4.

2.4 Report of Secretary-General, Xu Wei-Shu, and Assistant Secretary-General, Liu Feng

See report of the Secretary-General below — item 5.

2.5 Report by IOCommittee Permanent Secretary, Dominique G. Homberger

See report of the Permanent Secretary below — item 6.

2.6 Report by the Chair of the Scientific Program Committee, Fernando Spina

See report of the Scientific Program Committee below — item 7.

2.7 Presentation of the invitation for the 24th Congress 2006 in Hamburg, Germany, by Franz Bairlein

See report below — item 11. After his presentation, Franz Bairlein left the room and the invitation was discussed, and accepted unanimously.

2.8 Discussion of possible sites for the 25th IOCongress to be held in 2010

See report of the Permanent Secretary below — item 6. Any suggestions and proposals should be forwarded to the IOCommittee Secretary, Dominique Homberger.

2.9 Reports by the Chairs of IOCommittee Standing Committees

a. Standing Committee on Applied Ornithology, Working Group on Bird Damage to Agriculture: Clive Elliott, chair.

b. Standing Committee on Ornithological Nomenclature: Richard Schodde, chair (see report below — item 9).

c. Standing Committee on Raptors: David M. Bird and Bernd Ulrich-Meyburg, co-chairs (see report below — item 10).

d. Standing Committee on Avian Anatomy: Jim Vanden Berge, chair.

Some Standing Committees have not been very active, and the Standing Committee on Seabirds is defunct. If any member sees the need for one and is prepared to organize it, could they contact the President, or send him a proposal.

Walter Bock stressed that the work of the Standing Committees is essential as they deal with issues that are genuinely international. The committees, nevertheless, need to be more active. He proposed that the IOCommittee Vice-President should act as liaison for the Standing Committees, and John Croxall proposed that the Vice-President should review the functions and needs of the Standing Committees and bring back an evaluation to the IOCommittee. This was agreed. It was hoped that inactive Standing Committees can be re-activated.

2.10 Presentation by the Executive Committee of its nominations of officers (President, Vice-President, and Permanent Secretary) for the 24th IOCongress in 2006, by the Chair of the Executive Committee Nominations Committee, Peter Berthold

The nominees were:

President: Jacques Blondel

Permanent Secretary: Dominique G. Homberger

Honorary President: Jiro Kikkawa

All three candidates were elected.

Nominees for Vice-President:

John Wingfield (USA, chair of the Scientific Program Committee for the 1994 IOCongress in Vienna; organizer of IOCongress symposia; plenary speaker at the 2002 IOCongress in Beijing; current member of the Executive Committee);

Richard Schodde (Australia, chair of the Standing Committee on Ornithological Nomenclature; member of the Scientific Program Committee for 2002 IOCongress in Beijing; organizer of IOCongress symposia; editor of the Proceedings of the 2002 IOCongress).

Both nominees for the vice-presidency left the room during the ensuing discussion. The Vice-President does not automatically become president for the next congress. His main function is to be able to take over IOCommittee business if the president is incapacitated for some reason.

John Wingfield was elected.

2.11 Presentation by the Executive Committee of its nominations of members for the Executive Committee, 2002–2006, by the Chair of the Executive Committee

Nominations Committee, Peter Berthold

Three new IOCommittee members were needed to fill the Executive Committee for the term 2002–2006 because Fred Cooke had resigned, Alexander Andreev had completed his second term, and John Wingfield had just been elected Vice-President. Nominees were François Vuilleumier (American Museum of Natural History, New York, USA), Elizabeth Hoefling (University of Sao Paulo, Brazil), and Susan Hannon (University of Alberta, Canada). All three candidates were elected unanimously by show of hand.

3 Minutes of the second meeting of the International Ornithological Committee at the 23rd International Ornithological Congress, Friday, 16 August 2002, 8:00 pm

The minutes for this meeting were taken by IOCommittee member Lucia Severinghaus as a substitute and proxy for IOCommittee Permanent Secretary, Dominique Homberger.

3.1 Presentation by the IOCommittee Executive Committee of its nominations of continuing members of the Executive Committee, 2002–2006

Seven current members of the Executive Committee for the period 1998–2002 were eligible for re-election for a second term, and their nominations were presented by the Executive Committee. They were Carlos Bosque (Venezuela), Michael Clarke (Australia), John P. Croxall (United Kingdom), Nathan N. Gichuki (Kenya), Hiroyoshi Higuchi (Japan), Lukas Jenni (Switzerland), and Pilai Poonswad (Thailand). There being no additional nominations from the floor, the nominees were elected unanimously for 2002–2006 by show of hands.

3.2 Presentation by the Executive Committee of its nominations for new members of the IOCommittee, by the Chair of the IOCommittee Nominations Committee, Fred Cooke

See Appendix 3. Nominees were selected by approaching some of the larger ornithological organizations, and the Nominations Committee filled any gaps. The Nominations Committee has a mandate to ensure that the IOCommittee membership reflects the distribution of ornithologists worldwide and that there is a balance among the various regions. Seven of the 40 nominees were women (ca. 15%). The Nominations Committee sought out younger people and representatives of under-represented countries. In case of dual citizenship or emigrant status, the country of current residence and employment was considered the nation represented. The nomination process was closed one week before the 23rd IOCongress in Beijing.

Fred Cooke read the list; all nominees were elected unanimously. For two nominees that had never attended an IOCongress, it was proposed to suspend the Statutes for their election to ensure the representation of their countries (Algeria and Morocco), under the condition that they at-

tend the 24th IOCongress in Hamburg in 2002. Suspension of the Statutes was passed for this matter, and both nominees were elected.

Walter Bock explained that, according to the Statutes, members which miss two consecutive congresses are removed from membership of the IOCommittee. He suggested, however, that if they are the sole representative of a country, they should be notified of the circumstances in order to retain, if possible, their IOCommittee membership. He felt it particularly important for all nations to be represented on the IOCommittee.

Oscar Merne sought clarification of relationships among the IOCommittee, the British Ornithologists' Union (BOU), and the American Ornithologists' Union (AOU), because of the perceived role of the BOU and AOU in the nomination process. Fred Cooke replied that he had involved the AOU and BOU in the nomination process just to broaden the scope. Oscar Merne asked that the European Ornithologists's Union (EOU) also be asked for nominations next time. Walter Bock mentioned that there are still open spaces on the IOCommittee, so that eligible persons can be added at the next Congress. An updated IOCommittee membership list will be published in the Proceedings of the 23rd Congress and will be posted on the IOCongress home page.

3.3 Report by the Co-Chairs of the Resolutions Committee, Eberhard Curio and Michael Rands

Walter Bock read the resolution to thank the China Ornithological Society and all the persons who helped to make the 23rd IOCongress a success. The resolution is reported in full below — item 12.

3.4 Old business

There was no old business.

3.5 New business

3.5.1 Words of thanks to Walter J. Bock for his contributions to the IOCommittee

Christopher Perrins recorded that, although nothing is permanent, Walter Bock's relationship to the IOCommittee and its congresses comes close to it. His contributions for over a quarter of a century should be formally acknowledged in the minutes. There was a round of applause in unanimous support.

3.5.2 Proceedings of the 23rd Congress

Richard Schodde agreed to serve as the General Editor for the Proceedings and provide the following information. (1) The Proceedings will be published as a special issue of the *Acta Zoologica Sinica*. The issue will be published in hard copy and on CD, and will include the plenary lectures, symposia, reports of the round table discussions and special interest groups, and the minutes of the meetings and the reports on the general business of the IOCommittee. (2) Deadline for submission of manuscripts: All manuscripts should reach the person responsible by 31

October, who will then forward them to the General Editor. Manuscripts of symposium contributions should be sent first to the symposium conveners, who will edit the length of the manuscripts, etc. The format of the manuscripts is the same as that of the 1998 Proceedings in *The Ostrich*. All editing is planned for completion by 31 May 2003. The Proceedings should be published by the end of 2003.

Lester Short suggested that the 2002 Proceedings should be sent to the two newly elected IOCommittee members from North Africa.

3.5.3 Proposal for reports and agenda of IOCommittee meetings

The following points were proposed by David Parkin and agreed for action by the IOCommittee President:

- Preparation of an agenda before the next meeting of the IOCommittee in Hamburg.
- Preparation of written reports by the IOCommittee President and the Permanent Secretary to relay the activities of the administration over the preceding intersessional years.
- Preparation of written reports by the Standing Committees to describe their activities over the preceding intersessional years.
- Preparation of a full report by the Nominations Committee, relaying the names of the individuals proposed as (a) officers and (b) as elected members of the IOCommittee. Reasons why any nominees were ineligible should be presented.

• These reports and the agenda would be circulated to all members of the IOCommittee at least four weeks before the Hamburg meeting to allow sufficient time for discussion among the IOCommittee members prior to approval and ratification at the meeting.

Walter Bock agreed with David Parkin's comments. An agenda is easy to prepare and circulate. Appropriate instructions will be passed along to the incoming IOCommittee President and IOCommittee Secretary. According to the Statutes and By-laws, proposals for the amendment of the Statutes and By-laws need to be signed by five members from at least three countries and sent to the President and Permanent Secretary to be circulated well before the ensuing Congress (Article V of Statutes).

3.5.4 Future of the IOCongresses and IOCommittee

Walter Bock mentioned that the Finance Committee had produced a report with recommendations (see report below — item 8), which needed to be discussed and considered. Any changes in the organization of the IOCommittee would also require a revision of the Statutes. For example, a treasurer would be needed if the Committee were to raise funds. Mario Ramos explained that the IOCommittee could be registered as a nonprofit organization in the United States if it wanted to raise funds, for example for conservation and related aspects. Walter Bock added, nevertheless, that the core work covered by the

IOCommittee was scientific reach in ornithology and its application to practical aspects.

John Dittami suggested that there should be institutionalized Proceedings, which should be ready by the next Congress in Hamburg. In addition, the IOCommittee needs a judicial basis and financial continuity between congresses.

Nathan Gichuki remarked that African participation in IOCongresses is low. Interest in ornithology is growing in Africa, but the cost of participating in congresses is too high for most African ornithologists. At the 1986 IOCongress in Ottawa, there were nine delegates from Africa, but only six at the 1990 IOCongress in Christchurch. It is necessary to raise awareness among African ornithologists that participating in the IOCongresses is useful and good for conservation. Walter Bock mentioned that at the 1986 IOCongress in Ottawa, the Canadians had raised funds to support people from low-income countries to attend, but added that this type of fund-raising ought not be the task of the Local Organizing Committee, but that of the IOCommittee. For that reason, the IOCommittee should be in a position to raise funds.

Pierre Devillers proposed that funding for biodiversity should be tapped. The IOCommittee does not compete directly with conservation organizations, because the IOCommittee's work is basic research and complementary to conservation. The IOCommittee should be explicit in its scientific focus and then tap conservation funds. Walter Bock added that at the 1994 IOCongress in Vienna, there was good cooperation with the ICBP, but now that the ICBP has disbanded, the void needed to be filled, perhaps by BirdLife International.

Mario Ramos encouraged the new IOCommittee President and the Executive Committee to do some strategic thinking and planning. The IOCommittee should consider new needs and to think about the IOCommittee's standing and the committees it should have. John Dittami felt that IOCongresses are better than many other conferences, but that they need to be topical and up-to-date, not narrowly defined. Fernando Spina felt that conservation is an important topic at IOCongresses and that top ornithologists from around the world attend them. He stressed that while the IOCommittee may not compete with conservation bodies or organizations, the type of science presented at IOCongresses can help conservation.

John Croxall reminded the assembly that the Executive Committee will meet tomorrow, Friday, and decide on a Finance Committee to address the following issues: (1) capital needs for initiation of committees; (2) funds for the functioning of a secretariat; and (3) funds to support the attendance of members from low-income countries at IOCongresses. The Finance Committee will also need to examine the governance of the IOCommittee to ensure that its business is conducted efficiently, both at congresses and between them. Jacques Blondel asked "How can we improve the beautiful work that was done under Walter Bock?" He agreed with all the previous comments: science and

conservation are not in competition, but can be brought together in a synthesis. Fred Cooke concluded that such a synthesis goes beyond the individual IOCongresses. In the next four years, the Executive Committee will work on the structure of the IOCommittee and on other aspects that were raised at this Congress.

3.5.5 Resolution on Nominations for Membership of the Permanent Executive Committee of the IOCommittee

This resolution was introduced by Christopher J. Robertson, seconded by Pierre Devillers, with a friendly amendment by Walter J. Bock. It read:

Welcoming the continuing progress by the Permanent Executive Committee (PEC) towards executing recommendations of the International Ornithological Committee, it is moved that:

1. The Nominations Committee of the PEC formally invites nominations from all members of the International Ornithological Committee for future office-bearers of the Congress and members of the PEC no later than twelve (12) months before any Congress; and
2. The PEC select a short-list from the nominations received to ensure, where possible, that the International Ornithological Committee has a choice of candidates when considering the election of Office-bearers and members of the PEC.

Responding to the resolution, Walter Bock suggested that the deadline date be amended to a year before each congress. Chris Robertson accepted this friendly amendment. John Croxall mentioned that the Statutes do not state any time limits for nominations. Walter Bock added that the process of nomination takes time. IOCommittee members are encouraged to get in touch with the Permanent Secretary or the President of the IOCongress and submit names and recommendations.

Jacques Blondel was not concerned so much about the nomination process of the IOCommittee members as with that for the officers and the members of the Executive Committee. The IOCongress web page should be used to send in feedback and suggestions on nominations and the nominating process. All accepted this suggestion with acclamation.

3.5.6 Satellite meetings of the IOCongresses

Walter Bock mentioned that the Scientific Program Committee had decided to make satellite meetings possible because it seemed like a good idea. Those people who attended any of the satellite meetings at the 23rd IOCongress in Beijing were asked to submit comments to the Scientific Program and to the Local Organizing Committee for the 2006 IOCongress in Hamburg.

3.5.7 Circulation of the minutes

Ben Bell asked whether the minutes of the two IOCommittee meetings would be circulated. John Croxall replied that the Statutes stipulate that the minutes be circulated within two months of the Congress.

3.5.8 Changes of the Statutes

David Parkin asked whether the Statutes can be changed. Walter Bock responded that any changes made now to the Statutes will come into effect at the end of the next Congress in Hamburg in 2006.

4 Report of the IOCommittee President, Walter J. Bock

In the late fall of 1997, I, as the then Permanent Secretary of the International Ornithological Committee, received an enquiry about a possible congress invitation from the People's Republic of China, together with an invitation to visit Beijing in December 1997 to discuss this invitation with a large group of ornithologists in the Beijing area, who would be responsible for the organization and running of the congress. The trip was successful, but not without problems, with an aborted takeoff on my first attempt to fly to Beijing because one engine exploded just before the plane became airborne. The second attempt was successful, and I had extensive and detailed talks with those ornithologists who would be responsible for diverse aspects of the Congress, as well as with Mr. Liu Feng who would serve as the Assistant Secretary-General. I also had the opportunity to visit Professor Cheng Tso-Hsin, the teacher of modern Chinese ornithologists, in his hospital room. Professor Cheng gave me a greeting for the members of the 22nd Congress in Durban 1998, which was read at the opening of that Congress and published in its Proceedings. Sadly, Professor Cheng did not live to hear about the decision of the IOCommittee to hold the 2002 Congress in China, one of his lifelong dreams.

The Beijing invitation was sent to me, and a copy of it forwarded to IOCommittee President Peter Berthold. It was discussed, together with an invitation from Israel, at the meetings of the Permanent Executive Committee (PEC) and of the IOCommittee at the 22nd Congress in Durban. The choice was difficult, but the final vote was in favor of Beijing and of the first International Ornithological Congress in Asia.

Immediately following the close of the 22nd Congress, I appointed Professor Xu Wei-Shu as Secretary-General, and Mr. Liu Feng of the Conference Section of the Chinese Academy of Sciences, as Assistant Secretary-General of the 23rd Congress. A National Committee was established to deal with all aspects of the congress under the chair of Professor Zheng Guang-Mei, with the necessary subcommittees.

The Scientific Program Committee (SPC), under the chair of Dr. Fernando Spina, was then appointed; and it set to work immediately. The SPC met in Beijing in June 2000, and planned an intensive program of 10 plenary lectures, 40 symposia, oral (limited to 200) and poster contributions, and Round Table Discussions. In view of the problem with no-show poster papers that had plagued the 22nd Congress in Durban, the decision was made that abstracts of

contributions would be published and included in the Congress program only if the full congress registration fee was paid by 31 May 2002. A request was made to exhibit some of the famous Chinese Mesozoic birds at the Congress, which was carried out to the great benefit of Congress members. In addition, a special symposium in the form of a plenary Presidential Debate was to be held on one evening on the topic of the origin of birds, whether from early archosaurians or later dinosaurs.

I visited Beijing for a third time early in January 2002, for a week as a guest of the Beijing Normal University to work with the members of the Local Committee and, especially, with the very efficient Mr. Liu Feng, on many of the details of the Congress organization, including the arrangement of the sessions of the scientific program.

In early February 2002, Vice-President Jacques Blondel was informed that he should be ready to assume the duties of the IOCommittee President, because I had to undergo surgery to repair a major aneurysm of the dorsal aorta at the end of April 2002. Fortunately for me, as well as for Jacques Blondel, the operation was not only successful, but I received permission from my doctors to travel to Beijing in August for the Congress as well. The Beijing Ornithological Congress was of special significance because it permitted face-to-face interactions between a large number of Chinese workers and those from other parts of the world, which is, after all, the primary function of our congresses.

I would like at this time to express my sincere thanks to all of the Chinese organizers and their numerous students for the successful 23rd Congress in Beijing in 2002. Special thanks are to be given to Professors Xu Wei-Shu, Zheng Guang-Mei and Zhang Zheng-Wang for their activity in organizing the Congress. I also acknowledge and thank the three people who were most central to its planning: Mr. Liu Feng for his careful attention to all details of operation, Dr. Fernando Spina for his years of hard work as chair of the Scientific Program Committee, and Professor Dominique Homberger for her activities as Permanent Secretary since the 22nd Congress in Durban 1998. Special thanks must also go to Dr. Richard Schodde for his careful editing of the entire Proceedings of this Congress. Finally I want to thank all the ornithologists who presented the results of their work and those attending the Congress, because their collected effort made the first Asian Congress a most memorable occasion.

5 Report of the Secretary-General of the 23rd International Ornithological Congress, Xu Wei-Shu

Attendance at the 23rd IOCongress: 642 registered delegates from abroad, and 172 delegates from China. Approximately 300 people also registered for the birding tours, as follows. Pre-congress tours to Mai Po (Hongkong): 30 people; Chongming Island (near Shanghai): 20 people; Xiao Long Men (Beijing): 20 people. Post-congress tours to Happy

Island (Beidaihe): 45 people; Xishuangbanna (Yunnan): 54 people; Zhalong Reserve (Heilongjiang for cranes): 13 people; Tibet: 42 people; Sichuan Woo Long: 54 people; Xian and Changqing Reserve for crested ibis: 32 people.

Finances: The 23rd IOCongress was able to attract two major sponsors, namely Swarovski and IFAW. China currently enjoys a good economy and a stable political situation. 250 delegates were funded through reduced registration fees, and some delegates were given funding for accommodations. There is a rule in China not to provide support for international air fares, but an exception was made to support the attendance of Nathan Gichuki as a member of the Executive Committee of the IOCommittee. Delegates and some retired people from within China also received financial support in the form of reduced registration fees of only 1000 RMB (ca. US\$125, equal to about one month's local salary). Chinese delegates came from all over China. There will be left-over funds, which will be used for ornithology in China or to fund Chinese participants to future IOCongresses. President Walter Bock came to China three times for supervision and on-site information on the progress of preparations.

Press Conference (Saturday, August 10): Journalists of several Chinese newspapers and one English language newspaper (China Daily) attended. Environmental and conservation issues were hot topics, and were discussed at length. Copies of published articles are to be given to the IOCommittee Permanent Secretary for archiving.

IOCongress Proceedings: The plenary addresses will be published in *Acta Zoologica Sinica*, and the symposia, round table discussion reports will be published in a supplementary issue of that journal.

Thoughts for future IOCongresses: The majority of bird species are found in Asia, Africa, and South America; but, somewhat paradoxically, most ornithologists are trained and professionally employed in Europe and North America. We hope that future IOCongresses can be held in bird-rich continents, such as South America, for their instruction.

6 Report of the IOCommittee Permanent Secretary, Dominique G. Homberger

Of a variety of tasks handled by the Secretariat, the major ones are summarized below.

IOCommittee membership: A data base to store and manage information on IOCommittee membership was created to facilitate communication.

Scientific Program Committee: Ex officio member; preparation of the minutes of the Scientific Program Committee meeting in Beijing, 6–11 June 2000 (see report below — item 7).

Finance Committee: Ex officio member (see report below — item 8).

Invitation for the 24th IOCongress 2006: Various potential organizers were approached, and information and

assistance was provided for the preparation of an invitation, including the preparation of the present invitation to Hamburg (see report below — item 11).

Invitations for the 25th IOCongress 2010: Various potential organizers have been approached. Currently, possible invitations have been discussed with representatives from Brazil, Spain and Australia.

Invitations for the 26th IOCongress 2014: Various potential organizers have been approached, but nothing concrete has developed yet.

7 Report of the Chair of the Scientific Program Committee, Fernando Spina

The Scientific Program Committee (SPC) for the 23rd IOCongress in Beijing was appointed in 1998 by the President Walter Bock. Members of the Committee were: Alexander Andreev (Russia), Walter Bock (President, USA), Ding Chang-Qing (delegate of the Local Committee, China), Liu Feng (Assistant Secretary-General, China), Patricia Gowaty (USA), Zheng Guang-Mei (Chair of the Local Committee, China), Dominique Homberger (Secretary of IOCommittee, ex-officio, USA), Hiroyoshi Higuchi (Japan), Marek Konarzewski (Poland), Lukas Jenni (Switzerland), Theunis Piersma (The Netherlands), Pilai Poonswad (Thailand), Richard Schodde (Australia), Lucia Severinghaus (China), Fernando Spina (Chair, Italy), Xu Wei-Shu (Secretary-General, China), Hans Winkler (Austria), Zhang Zheng-Wang (delegate of the Local Committee, China). The SPC was very active and fully involved in the organization of the Congress, giving consistent support to the SPC Chair.

7.1 Announcements

A first announcement for the 23rd IOCongress and program contributions was distributed to all main ornithological journals in the summer of 1998, and published in their first issues of 1999. A more detailed announcement to journals was also sent by e-mail in October 1999; this announcement included the date and place of the venue, the names of the officials and of all members of the SPC, and the deadline for submitting proposals for symposia and plenary speakers, which was set at the end of April 2000.

In February 2000, calls for contributions were distributed by post and e-mail to IOCommittee members and, by e-mail, to all delegates at the Durban Congress; a further announcement from the President was sent in March 2000. The deadline for contributed papers and RTD proposals was set at end of June 2001.

In July 2001, a reminder call for contributions was sent to the above-mentioned address lists (over 1 600 addresses).

7.2 Questionnaire to the members of the IOCommittee

Following the positive example of the questionnaire circulated by Lukas Jenni before the Durban Congress, I

sent a new one to the members of the IOCommittee in July 1999. This questionnaire with 16 questions was sent both by post and e-mail wherever possible. The response to the questionnaire was quite poor, with only 55 colleagues responding, despite two different e-mail reminders. Although not completely representative, the respondents were very thoughtful in their replies. The results of the analysis were summarized in a report which was distributed to the members of the SPC and used by them when deciding on the structure of this Congress.

7.3 Meeting of the SPC in June 2000

The SPC held its conventional meeting over 6–11 June 2000 in Beijing, where we were commodiously lodged by our Chinese hosts in the gardens and forests of the Fragrant Hills. Unlike the previous Congress, the SPC met only 2, not 3 years before the Congress.

The SPC was introduced first in its program to the facilities of the Beijing International Convention Center (BICC), and the range of accommodation nearby, and it met the local organizing committee, officials of the China Association for Science and Technology (CAST) and colleagues of the Beijing Normal University.

The first four days of the meeting were devoted to a detailed discussion on the structure of the Congress. Decisions were taken on the format and time table of the scientific program, as well as on the different types of presentations. We decided on the same structure and timetable for each of the five days of the Congress, apart from the opening ceremony on the first day and a shorter program with a brief closing ceremony on the last, in order to allow delegates to get ready for the evening banquet. Plenary speakers and symposia were selected, and decisions taken on the strategy to adopt when selecting contributed papers for oral sessions. We also discussed the format and perceived value of the Congress Proceedings, basically to contribute to decisions to be taken by the Local Committee. The timing and deadlines for the further planning of the Congress were also agreed upon, together with the tasks of the members of the SPC. Detailed minutes of the meeting were kindly produced by Dominique Homberger, while I produced a brief summary with the final list of decisions.

7.4 Plenary lectures

From the questionnaire, no clear preference emerged between having 5 or 10 plenaries. Those in favor of 10 had on average attended more plenaries (8) at the Durban Congress than those favoring 5 (6).

We decided on 10 plenaries, each opening the morning and afternoon sessions, respectively. Plenaries at the start of the sessions help in attracting delegates to meeting rooms to enjoy top-level review contributions on different subjects of ornithology. I provided SPC members with a list of plenaries from Berlin to Durban by congress and subject, together with a list of suggested plenary speakers for this congress. Through proposals stimulated by the question-

naire as well, we selected the 10 plenary speakers out of a total of 67 candidates. We also decided on a total of 5 backup speakers. When selecting candidates, special attention was paid to achieving a balance in gender and national representation.

Selected plenary speakers were first formally invited by the President, and subsequently kept informed on different aspects by me through a series of circulars. Abstracts of plenaries were reviewed by the President. Plenary speakers were to be introduced by SPC members, apart from the introduction of the Presidential address by the past President.

7.5 Symposia

The questionnaire indicated that delegates preferred symposium papers of a review nature. This was also the decision of the SPC, in order to offer the general ornithologist updated overviews of the state of the art in the different fields of ornithology. Although the majority of respondents to the questionnaire favored selection of at least some of the contributed papers for the symposia, we considered this process would have been too difficult to organize, and might have led to risky delays against the deadlines set for the proper organization of the congress.

As in previous congresses, we decided on the following rules: a person was allowed to give one symposium paper as first author, and could act as convener or co-convener in only one symposium. Any one person, however, could be a convener in one symposium (without presenting a talk), and a speaker in another symposium. Both symposium speakers and conveners were additionally allowed to submit contributed communications and/or Round Table Discussions. A relaxation of these rules was unfortunately needed in several cases, due to last-minute cancellations.

In previous congresses, symposia had always overlapped at least partly with other events. Here, however, we decided to select fewer symposia, so that all could be presented during morning sessions and avoid overlap with other events during the afternoon; this gave higher profile to other forms of presentation, particularly orals (see below). The final total of 39 symposia presented was unfortunately due to the late cancellation of symposium 28 at the end of June, 2002.

Initially, I provided SPC members with a compilation of all IOCongress symposia from Ottawa (1986) to Durban (1998) — the list from Ottawa to Vienna was compiled by Lukas Jenni as SPC Chair for the 22nd IOCongress. I also provided dossiers on all symposium proposals for Beijing, together with a list of people proposed as speakers and conveners. A total of 68 symposium proposals were submitted, out of which 40 were selected after considerable deliberation. In 11 cases, the SPC decided to ask conveners to merge symposium proposals on similar subjects. When selecting symposia, we also took into account international representation of speakers, gender and topic. Conveners for each symposium, too, were sought from different

countries.

Addresses were structured in order to allow delegates to commute between symposia. Together with opening and closing remarks from conveners, each symposium was to comprise five talks each of 17 minutes plus 3 minutes for discussion. Abstracts of symposium papers were reviewed by the conveners.

Symposium conveners were informed of the decisions taken by the SPC, and those of the symposia selected were invited twice to confirm commitment to convene and to attend the Congress. Delegates who had submitted unsuccessful symposium proposals were invited to offer contributed papers. In 14 cases we suggested that symposium proposals be redrafted as round table discussions (RTDs).

Eight circulars were sent to symposium conveners in order to provide them with all necessary information on the format of the symposia, the local facilities and visual aids, and schedules. Conveners were also requested to update and confirm the sequence of speakers, and title and authorship of papers. Circulars confirming the timing of each symposium were also sent directly to all invited symposium speakers.

A total of 20 symposium papers were cancelled before the Congress; and in some cases it was impossible for conveners to replace missing speakers. There were also two replacements in conveners.

7.6 Contributed papers

7.6.1 Oral papers

At the Durban Congress, oral papers were very well received and attended, as clearly shown also by the results of the questionnaire and generally very positive comments by delegates. While symposia feature invited review talks, oral papers selected out of the contributed papers offer an opportunity to present recent results produced by authors who, for various reasons, were not invited to contribute to symposia. The SPC therefore decided to feature both posters and 15 minutes oral papers, allocating, in particular, more time for orals than in previous congresses while avoiding overlap between oral sessions and symposia. Authors were offered the opportunity of nominating their preference for giving their paper as an oral or poster.

Contributed papers were grouped in 12 subject areas and reviewed by a panel of 14 members of the SPC who grouped them into categories of high, medium and low value. In order to apply uniform judgement across all subject areas, I also reviewed and scored all abstracts.

Out of a total of 678 contributed papers, 397 submissions were received for oral papers. Of these, 200 were selected, which I then grouped by subject into a total of 25 oral sessions, each lasting 2 hours, with a total of 8 papers of 12 minutes each, plus 3 minutes for discussion. The selection process also looked for a wide geographical representation among authors. Replacement papers were selected as well, and in 39 cases, replacement speakers were

invited to present an oral communication because of cancellations. Contributions not selected for orals were all accepted as posters.

Richard Schodde provided a most important contribution by reviewing and editing the abstracts of all contributed papers (posters and orals).

In June 2002, I selected and invited a chairperson out of the speakers for each of the oral sessions. The talks of the selected chairs were scheduled as the last ones of their sessions, in order to enforce the control of timing. To support the work of the chairs in introducing the talks, I also asked all speakers to provide the chairs with details on their affiliation and research, together with an extract from their abstracts.

7.6.2 Posters

The SPC felt poster papers to be a very important form of presentation, which can often reach a wider audience than symposia and orals. We therefore decided to have no overlap between poster sessions and other events. This decision had to be revised later for logistic reasons, and poster sessions were overlapped with oral sessions in the final structure of the Congress. Poster sessions were scheduled for 4 out of the 5 working days of the Congress.

All poster presentations were accepted, provided the abstracts met the required format. One person was allowed to submit only one poster paper as first author. Abstracts of posters were sent directly to the Assistant Secretary-General, were not reviewed by the SPC but were edited by Richard Schodde.

7.7 Round Table Discussions

RTDs are used for a variety of tasks, such as presenting and discussing new methods and techniques, updating ongoing projects, and proposing new lines of research, etc. At the SPC we decided that RTDs must not develop into symposia, that they should be based on few and well-presented aspects to be illustrated and discussed. In order to further increase the profile of RTDs, we decided to publish brief summary reports in the Congress Proceedings.

We also decided that the conveners should guide discussion through contributions from a core of participants on well-prepared issues. All RTD submissions were accepted. Chairs of Standing Committees were asked to organize their meetings within the frame of a RTD as well. A total of 20 RTDs was scheduled, later reduced to 19 by a late cancellation.

7.8 Meetings of special interest groups and Standing Committees

We decided to encourage special interest groups to meet during the Congress. Their meetings could be held at any time, providing that they did not overlap with plenary lectures, or with the opening and closing ceremonies of the congress. The participants of special interest groups meetings were requested to pay full registration fees. Standing Committees of the IOCommittee would meet as RTDs.

One Special Interest Group Meeting was planned and included in the program.

7.9 Congress web site

The congress web site proved to be a very important tool for communication, as I heard from many delegates who checked it regularly for updates and details. I suggested its use to make the Congress program available before the Congress, *inter alia* to enable delegates to better plan their priority sessions. The scientific program of the Congress was published on the web site on June 24, 2002, making it available for advance checking. This proved finding errors and updating lists of authors, as well as for providing delegates with advanced knowledge of the scientific program.

7.10 Conservation and applied aspects

Throughout the program of this Congress, the “fil-rouge” has been the decline of birdlife worldwide and the conservation problems originating from human activities. The Congress focused expansively on these aspects, simply because so many delegates, working in completely different fields of ornithology, have shown that these are prominent factors affecting all birds throughout the world. It is clear that IOCongresses have become unique venues where cutting-edge scientific results can be displayed to provide solutions and counterbalancing strategies to conservation problems.

I hope the Beijing IOCongress has left a message for the need to further increase our knowledge of the birds of Asia, for the better planning of wise-use policies in the managing of natural resources in a highly populated continent that hosts immense avian biodiversity, the preservation of which we owe to future generations.

7.11 Collaboration within the SPC and with the Organizing Committee

There was very positive, responsive and friendly cooperation within the SPC and between the SPC and the Secretary-General, the Assistant Secretary-General and the Local Committee. Having an SPC meeting in Beijing in June 2000 was crucial in reaching the necessary decisions on which to base the organization of the scientific program of the Congress. We had a most positive and cooperative atmosphere at the meeting, which was perfectly arranged by our Chinese hosts. Ample time was allowed also for informal discussion and brainstorming, which greatly contributed to the initiatives and outcomes of the meeting. At the meeting, we decided the structure of the Congress, the time to allocate to different types of presentations, the selection criteria and process, and all deadlines. We selected the plenary speakers and symposia as well.

After the meeting, the SPC became actively involved in reviewing the submissions for oral communications. As chairman of the SPC, I reviewed all submitted abstracts, finalized the list of oral papers, took care of all correspondence with plenary speakers, symposia conveners and in-

vited speakers, conveners of RTDs and authors of oral papers. I scheduled the scientific program and tried to solve all problems related to cancellations, apart from a few cases of dropouts that were so late that replacements could not be found.

The Secretary-General, Assistant Secretary-General and Local Committee received the abstracts of posters and RTDs, interacted with Richard Schodde for editing all abstracts, and took care of the instructions to authors for the Proceedings and of all other logistic aspects.

7.12 Closing remarks — and a look to the future

IOCongresses are aimed uniquely at offering updated overviews of progress in the many and different fields of ornithological research. It is therefore important to attract top scientists from all over the world, together with their most recent results. Despite our hopes for a better future, the present situation is characterized by shortage of funds for biological research worldwide. Financial constraints are therefore likely to affect attendances at IOCongresses in the future; ours are large meetings, requiring considerable facilities, organization and correlated activities, which result in generally high registration costs. Despite the fact that poster papers are arguably the best type of presentation for such large congresses, I have found that delegates often have better chances of getting travel funds if giving a spoken address. This is particularly true for young Ph.D. students, who can often offer most stimulating and fresh, new results. It is therefore important to take these aspects into account when deciding on the format and structure of the scientific program.

Another crucial aspect likely to affect the scientific program is the type of Proceedings that the Secretary-General and Local Committee will want to produce. There is, in fact, a clear tendency for authors to refrain from offering top and unpublished results to appear as full papers in volumes of Proceedings. The “impact factor game” forces scientists to publish in high impact, peer-reviewed journals; this is often also the best strategy to get research funds, and I think this aspect might become a major factor affecting the scientific quality of future congresses. The trade-off between a volume of Proceedings published with full papers after the congress, and most recent and unpublished results offered during the congress is an important aspect to be taken into account. A compromise might be represented by Proceedings that comprise peer-reviewed, full plenaries and (symposia of review papers?) review papers; and abstracts of the other contributed papers.

Another potential improvement on the present format could come from selecting a percentage of symposium addresses out of the contributed papers (e.g., 2 out of 5). From this respect, widespread and efficient electronic connections could help organize the process, with symposium proposals confined to a subject and 3 papers and the remaining papers selected by the conveners through help of the SPC chair. This was a strategy recommended also by

the majority of people replying to the questionnaire; but there are doubts about how such a system would work for a large congress: hence we refrained from attempting it here.

7.12.1 Electronic mail

E-mail has been crucial in the organization of this congress; apart from printed copies of the questionnaire circulated well before the SPC meeting, and announcements posted to journals and IOCommittee members, virtually all correspondence has been by e-mail. Out of a total of 6 900 messages that I have exchanged during these years (about 11 000 when circulars are added), I only received a total of 3 printed letters. Of the different types of invitation letters that I was requested to write, I sent only two as printed copies; the rest were in *.pdf format.

Electronic connections have, of course, eased my task enormously, and I surely admire former SPC chairs working with printed mail only. However, e-mail allows real last-minute replies, which can become “too-late” replies; furthermore, many people use e-mail in a strange way, and messages seem to be either answered immediately, or never. This exposes a need for frequent reminders.

7.12.2 Deadlines

Unlike previous practice, the SPC met 2 rather than 3 years before the congress. The deadline for submission of abstracts was also set at 2 years before the Congress (1 April 2001, and 1 July 2001, for symposia and contributed papers - RTDs, respectively). I think it is good to have as late as possible deadlines, in order to include more recent and updated contributions.

We have suffered much from delegates not meeting deadlines. Symposium proposals kept on arriving until my departure for the SPC meeting, over 2 months post the deadline; and contributed papers were still being received up to a few weeks before the Congress. The problem of deadlines has been very serious, due to the high percentage of late proposals. Again, circulating reminders is easy with e-mail, and possibly the only way to reduce the problem.

7.12.3 Cancellations

Problems here arise from delegates that confirm commitment to attend the Congress and to organize sessions, and then cancel at the very last moment. Uncertainty of funds is the main problem; but last-minute dropouts are difficult to replace and cause serious disruptions to the program. Fees paid immediately upon having an abstract accepted, with restrictions in refunding, could be a strategy, but surely not the solution. Selecting backup papers and speakers is an important task for the SPC chair.

7.12.4 Post-Congress questionnaire

As decided at the SPC meeting, a questionnaire will be circulated to all participants shortly after the Congress. The questionnaire is aimed at collecting comments and suggestions for the better planning of the next Congress. The one that I sent around before the 2002 congress reached delegates over 1 year after the Durban congress, which

might be one reason for the poor response. I hope the new questionnaire will be more successful, as this will allow me to provide the next SPC Chair with more detailed information and suggestions for planning the 2006 Congress. I take this opportunity to wish my successor all the best for her/his work, which I am happy and ready to support if needed.

7.13 Acknowledgements

Being chair of the Scientific Program Committee for an IOCongress is a once-in-a-lifetime opportunity. I wish to warmly thank the President Walter Bock for offering me this chance. I have always had a deeply positive relationship with him, and I could only learn from his unique knowledge and experience of the IOCongresses and their workings. I greatly benefited from the many and important suggestions and comments that the IOCommittee Secretary, Dominique Homberger, has always offered me in such friendly fashion. Chairing the SPC meeting was also a very interesting and positive experience. Not just for their constructive and enthusiastic advice but also for the crucial help arising out of their vast and varied knowledge of ornithology, I wish to thank all SPC members. For providing me with much material and many suggestions from the Durban Congress, I extend special thanks to Lukas Jenni. I am also grateful to Richard Schodde for having edited the abstracts of all contributed papers. Working with our Chinese colleagues has been another very constructive aspect of this experience. My warmest thanks go to all the Local Committee, and in particular to the Secretary-General, Xu Wei-Shu and to the Assistant Secretary-General, Liu Feng. With Liu Feng I exchanged uncountable messages, which invariably got immediate, efficient and clear replies. For helping me to produce the booklet of symposium proposals, I thank my colleague Maria Luisa Romagnoli.

8 Report of the Chair of the ad hoc Finance Committee, Tim Wood

After the 22nd Congress in Durban, the incoming President of the International Ornithological Committee, Professor Walter Bock, set up an investigative financial committee to look into the financial affairs of the IOCommittee. The reason: there had been discussion for years by its officers and Executive Committee about the need for information about its financial needs for operating and supporting congresses, but nothing had been done and no solutions found.

8.1 Professor Bock's brief to the committee

8.1.1 Background

The IOCommittee is a nonprofit organization. It has no funds. The finances of each Congress are separate from the Committee and from other congresses. Congress finances are strictly under the control of the Secretary-General of each congress, who appoints a member of the Local Committee to deal with money matters. These include all expenses leading up to the Congress, those of the Scientific Program Committee, and sponsorship of chosen third-

world delegates and students. The expenses of the individual officers of the Executive Committee, such as President and Permanent Secretary, are covered personally, independently of the Congress and presumably through the institutions for whom they work. These arrangements are very advantageous to the IOCommittee.

There have been discussions on whether such arrangements might be modified so that funds for the operation of the IOCommittee can be raised independently of congress finances. Funds are needed for several purposes, such as the expenses of officers of the Executive Committee (EC), for providing seed money for congresses and the meetings of the Scientific Program Committee, and for maintaining a home page on the Internet, etc.

Before embarking on any fund raising, however, several issues need resolution.

8.1.2 Issues for the Finance Committee to consider

1. costs facing the IOCommittee in the future — these should be itemized in order of priority;

2. mechanisms for raising an Endowment for the IOCommittee;

3. whether or not a membership should be established for an international body of ornithologists — an International Ornithological Society (to replace the Committee); and whether dues should be charged;

4. methods of conveying funds internationally to avoid high banking fees on individual checks, including use of credit cards for paying dues;

5. choice of country in which to keep and invest funds, and where the IOCommittee can be registered as a non-profit organization;

7. officer(s) in the IOCommittee responsible for handling funds;

8. interaction between the funds of the IOCommittee and the finances of congresses;

9. necessary changes in the Statutes and By-laws of the IOCommittee to effect new financial arrangements; and whether such changes should be introduced at the 23rd Congress in 2002.

8.2 Finance Committee

The members invited by Professor Bock to serve on the Finance Committee, and who eventually took an active part in formulating the proposals detailed here, were: Dr. A. Berruti (South Africa), Dr. J. Croxall (United Kingdom), Dr. D.G. Homberger (USA), Dr. C.J.R. Robertson (New Zealand) and Mr. T. G. Wood (South Africa).

The committee did not formally meet, handling its deliberations by e-mail. There were, however, individual meetings between Dr. Robertson and Mr. Wood in New Zealand in April 2000, and between Dr. Croxall and Mr. Wood in England in April 2001, as well as frequent meetings between Dr. Berruti and Mr. Wood in Johannesburg, where Dr. Berruti is Director of BirdLife South Africa, and Mr.

Wood a Council Member. Unfortunately, a scheduled meeting between Dr. Homberger and Mr. Wood in England in April 2001 did not eventuate.

A questionnaire was developed arising mainly out of the New Zealand meeting in April 2000, but with major contributions from the other members of the Committee and a comprehensive reply from Dr. Homberger. Subsequent comments also came from Professor Bock and Dr. Croxall.

The Finance Committee felt that the questionnaire was so wide-ranging and covered so much ground that it went beyond Professor Bock's brief and needed answers to many other questions affecting the future of the IOCommittee and its structure. The financial structure of the IOCommittee itself could not be adequately addressed. We have, however, been able to examine some of the problems and to make recommendations that may be implemented when other issues have been debated and resolved by the Executive Committee.

8.3 Local Organizing Committee finances

It is possible that local organizations that run future congresses could be bankrupted. The money to run a congress is generated from registration fees, sponsorships, grants and trading activities, such as tours and merchandizing. Commissions need to be negotiated with officially appointed suppliers to supplement income. The 22nd Congress in Durban was lucky because interest rates on call monies rose to over 20% in 1998.

It should be noted that the grant-in-aid from the Durban Corporation, together with sponsorships, funded the initial expenses of the congress, as follows:

Scientific Program Committee Expenses	R82 758
First and Second Program	R28 534
Insurance	R10 000
Local Organizing Committee	R15 000
ICC Deposit	R40 000
PCO Deposit	R10 000
Vienna Bid	R18 787
	R 205 079

It was expected that the Congress would repay the grant-in-aid, but, in fact, it was utilized to subsidize overseas delegates (R136 130); only R57 000 was repaid. It was felt by various members of the Local Organizing Committee, before the Congress was held, that the costs of Scientific Program Committee meetings and the funding for third world delegates should be paid for by the IOCommittee.

The Chair of the IOCommittee's Finance Committee is currently acting as treasurer for another congress to be held in Durban in September 2002. Each congress has its differences. A profile of income and expenditure of the second congress is attached. The trade connected with the business of the congress (an important financial component) has largely paid for the costs of invited speakers (R900 000) and subsidization of delegates (R800 000) by keeping fees down. There is no subsidization of Third World delegates.

The International Secretariat has funded the Scientific Program meetings at a convenient venue overseas, as well as a certain number of postgraduate students and an interest free loan to provide seed money for initial expenses which must be repaid. Budgets were agreed with the International Secretariat at R7: \$1. The exchange rate was R11: \$1 when this report was written. That congress is assured of a surplus, of which 50% is paid to the International Secretariat. The size of the congress is the same as IOCongresses. Trade, of course, has not so far been relevant to the IOCommittee and its congresses.

8.4 IOCommittee Secretariat

The secretariat has traditionally consisted of one or two officers whose expenses have been paid by the institutions for whom they work. This has worked well; but what happens if an elected Permanent Secretary works for an institution that cannot pay his or her expenses?

8.5 IOCommittee

The Finance Committee considered the structure of the IOCommittee, the future relevance of its congresses, and the interaction between the IOCommittee and other organizations dealing with ornithology and birds. It was felt that the questions raised, which are detailed in the questionnaire, are relevant to the future of the IOCommittee, and, therefore, to any financial structure that is put in place. The Finance Committee, however, was not asked to provide the answers; such issues need to be resolved by the Executive Committee, affecting as they do the future of the IOCommittee and its congresses.

8.6 The IOCommittee and the Local Organizing Committee

The Finance Committee perceived a functional division between the IOCommittee and the Local Organizing Committee (LOC). The actual finances of both have been dealt with above. It is all a question of where the responsibility rests, and how it should be partitioned. The Executive Committee of the IOCommittee delegates responsibility for the running of a congress to LOCs. It is an honor for a country to hold a congress; but it could bankrupt the LOC in the process.

It was felt that the responsibility for IOCongresses lies ultimately with the Executive Committee and its appointed officers. It is, presumably, an honor for those officers to be so appointed, namely:

- President
- Permanent Secretary
- Chairman of the Scientific Program Committee (SPC)
- Other members of the Executive Committee (EC)

Such committees need not meet in the host country, but where it is most cost-effective. All costs relating to the Executive Committee and Scientific Planning Committee should be met by the IOCommittee. The Executive Committee should also agree to the Registration Fee and the budgets for congresses, and provide seed money, if required,

to meet start-up expenses and finance Third World delegates within parameters determined by it.

The LOC is essentially responsible for the successful running of congresses. All peripheral activities, i.e., tours, that the LOC decides to undertake to make its Congress a pleasurable event, must be kept financially separate from the Congress and accounted for separately. Any Interest Free Loans (as seed money) must be repaid, and surpluses should be shared on a 50:50 basis.

8.6.1 IOCommittee expenses

The expense categories for the IOCommittee and LOC are detailed below. It is realized that the IOCommittee does not hold any funds; but targets should be set to obtain funds for:

- Permanent Secretary office expenses
- Permanent Secretary travel
- Scientific Program Committee meeting expenses, including travel
- Delegates from Third World countries
- Student attendance
- Congress seed money (Interest Free Loan)
- Congress Plenary Lecturers expenses
- Publication of Congress Proceedings (if LOC fails to do it)
- Preparation of Invitation for a congress

These expenses are listed in approximate order of importance.

8.6.2 LOC expenses

- Venue hire
- Professional Congress Organizer
- Congress Brochures
 - Invitation
 - Reminders and Publicity
 - Program
- Congress Proceedings
- LOC incidental expenses and meeting expenses
- Entertainment
 - Welcome Ceremony
 - Daily tea and coffee
- Transport of delegates
- Insurance
- Poster stands
- Exhibition costs
- Accompanying persons costs
- Loan (seed money) repayment

8.7 International federation of societies of ornithology and ornithologists (IFSOO)

The Finance Committee agreed that such an international society should be formed, although, on reflection, a federation would be better. A federation is more inclusive of scientific ornithology and “hobby” ornithology, professionals and amateurs, and any “splinter” groups within ornithology.

Membership of the federation should be open not

only to individual scientists, but also to amateurs. It is anticipated, though, that the bulk of the members would be professional bodies, unions, societies, universities, and institutes from all over the world.

It would be the responsibility of the federation to organize the congress (IOCongress) every four years. Professor Bock has stressed that the core purpose of the congresses are to permit scientific ornithologists to come together to exchange information and ideas and to establish working cooperation. The scientific program for each Congress must be inclusive of all scientific bodies making up the federation, as the Congress must appeal to all scientists to induce them to attend such an international meeting. There could be further inducements to become members of a federation such as:

- discounts for members for attendance at congresses
- production of an international Journal of Ornithology besides the Proceedings

The Finance Committee did not give any consideration to changes that might have to be made to the Statutes and By-laws. It believed that this should follow on general acceptance of its report, and that a “friendly” legal expert should be involved. Should it be agreed by the Executive Committee that a federation be formed, then members of the EC must decide on its structure. The Finance Committee suggests that it should be run by a board consisting of

- President
- Vice President
- Permanent Secretary
- Treasurer
- Scientific Committee Chair
- Editor
- Other Members (4)

The board would report to a council. Members of the board would be appointed by the council.

8.8 Finance

The Finance Committee recommends that a member-based federation or international society should be formed, registered as a nonprofit organization, and charge membership dues. The size of the membership fee could be determined by the size of the institution that joins, and whether it is First or Third World. Initially, a discount might have to be offered on registration fees to congresses in order to build up membership.

There are also other methods of raising funds such as

- Sponsorship from corporate, government and non-government organizations, UN etc.
- Donations
- Bequests
- 50% of proceeds of each Congress
- International ornithological scientific web portal

Attendance at congresses will always be higher in North America and Europe. Therefore, the next two congresses should be held there in order to raise funds. It was

felt that if a federation/society is created, it would be easier to raise funds from the European Union, USA, NSF, GEF, etc. to fund congresses, students, Third World delegates and other costs.

It was agreed that a trust/endowment should be created and placed with an institution in the USA or Europe for the purpose of growing a capital base to fund the expenses of any federation/society that is formed. The Durban branch of HSBC, an international bank, was approached by Mr. Wood to advise on the mechanisms for setting up such a fund. HSBC advised that the country where the endowment fund will be domiciled must first be chosen by the IOCommittee, after which its staff in that country will be able to set up the fund and give any other advice required. They advised that their Jersey Branch is well equipped to do all that is necessary.

The bank or committee of the federation/society would appoint the trustees of the endowment fund/trust. The IOCommittee would lay down the terms and conditions for the use of the funds. The costs of transferring funds around the world should not be a consideration, as they would be minimal and could be a cost levied against each Congress. Repatriation of funds from any country must be part of the conditions of holding the Congress.

It would be necessary to appoint a treasurer of the IOCommittee to raise funds, control funds, and distribute funds. Such a function is not a full time job.

8.9 Summary

This report is a synopsis of the discussions, thoughts, and ideas of all members of the Finance Committee, as well as input from Professor Bock. The members of the ad hoc Finance Committee are agreed on the way forward, which is summarized below, bearing in mind that it would be presumptuous of the Committee to propose constitutional reform.

1. Constitutional reform needs to be agreed and be effected through the Executive Committee of the IOCommittee, acting on the basis of the Interim Report by the ad hoc Finance Committee appointed by Professor Bock.

2. The Executive Committee needs to agree that an international Federation or Society should be created, and on how it should be run, that is through a Board and Council.

3. Once such agreement has been reached, an appointed person or group of persons must review the Statutes and By-laws of the IOCommittee, and put forward recommendations for required changes to the Executive Committee to give effect to the creation of a federation, its structure, and reporting mechanisms.

4. The Executive Committee can then approve the creation of an endowment/trust fund, the trustees thereof, the country of jurisdiction where the fund will be placed as a tax-exempt trust, and the parameters whereby the funds will be used. The federation must also have tax-free status.

The issues raised in this report of the ad hoc Finance

Committee will affect the IOCommittee and its future vitally. The report should now be circulated to a wider audience for consideration and comment. Hopefully, discussion will be robust and positive decisions made.

9 Report of the Chair of the IOCommittee Standing Committee on Ornithological Nomenclature, Richard Schodde

The 14th congressional meeting of the Standing Committee on Ornithological Nomenclature (SCON) was held as a meeting open to all delegates of the 23rd IOC; only members of the committee voted. In all, 25 delegates attended, including seven of the SCON committee of ten: Dr. Per Alström, Sweden, Professor Walter Bock, USA, Murray Bruce, Australia, Dr. Siegfried Eck, Germany, Dr. Hiroyuki Morioka, Japan, Dr. Carlo Violani, Italy, and Dr. Richard Schodde, Australia and Chair; apologies were received from Professor Ernst Mayr and Alan Peterson, both USA. Members of the SCON are appointed by the President of the Congress to serve for the four-year term of that Congress, and may be re-appointed. The designated functions of the SCON are two-fold: to advise the ornithological community on questions of nomenclature, and to initiate action with the International Commission on Zoological Nomenclature to resolve them. The SCON's objectives in exercising these functions have been, by tradition, to maintain nomenclatural stability without interfering with taxonomic process.

9.1 Issues

Issues addressed fell into four categories: (1) alternative codes of zoological nomenclature; (2) implications of the new 4th edition of the International Code of Zoological Nomenclature (the Code); (3) specific nomenclatural questions requiring resolution; and (4) formal association between the SCON and the International Commission on Zoological Nomenclature (the Commission).

9.1.1 Alternative codes of zoological nomenclature

Two alternatives to the present system for naming birds have appeared over the last decade: (i) Project Biocode (International Code of Biological Nomenclature), which has as its objective the integration of zoological and botanical codes (Greuter et al., *Taxon* 131(1994) 1–389); and (ii) the PhyloCode, a system of nomenclature designed for phylogenetic ordering in biology (de Queiroz and Gauthier, *Ann. Rev. Ecol. Syst.* 23 (1992) 449–480). The SCON was briefed on both alternatives, and took no position other than to agree that their acceptance was premature and that neither should affect the *status quo* for the foreseeable future.

9.1.2 New edition of International Code of Zoological Nomenclature

Novel provisions in the new edition of the Code were summarized by Professor Bock, namely (i) improved precision for the typification, (ii) prescribed publication in electronic format, (iii) empowerment for authors to preserve established usage affected by priority, and (iv) acceptance of official lists of available names by the Commission.

9.2 Outcomes

Apart from two matters concerning conflicting generic names in Dendrocolaptidae and subspecific names in *Lanius* and *Larus* being handled by correspondence, seven issues were addressed:

9.2.1 Gender-endings to species group names

David and Gosselin's corrections to the gender endings of 230 plus species-group names in the Bull. BOC 122 (2002) 14–49 would, if accepted, result in multitudinous changes to current spellings. Those affecting simple adjectives were usually straightforward. Most, however, involve compound specific names formed from a qualified noun, e. g. *melanoptera* (from the adjective “black” and the noun “wing”) which have been interpreted as either adjective or noun in apposition. David and Gosselin reached their conclusions by doctrinaire lexical interpretation that would, the meeting felt, take zoological nomenclature out of the realm of the practising systematist. Because of this, and the fact that the Code, through Article 31.2.2, is open on the issue, the meeting unanimously deprecated the David and Gosselin approach. The SCON, however, was divided on the solution, the majority (five) carrying the case for rewording Article 31.2.2 of the Code to give it teeth to maintain prevailing usage. The proposed rewording is as follows, the changes in italics:

“Where an author of a species-group name did not indicate whether he or she regarded it as a noun or as an adjective, and where it may be *or has been* regarded as either, the evidence of prevailing usage *shall be decisive*. *Where this condition is not met, the name* is to be treated as a noun in apposition to the name of its genus (the original spelling is to be retained, with gender ending unchanged; see Article 34.2.1).” Pending decision by the Commission, prevailing usage is to be maintained.

9.2.2 Typification of *Archeopteryx lithographica* von Meyer

Specification of the type of this historic bird has been made necessary by the recent recognition of several associated taxa. After reviewing the protologue (Drs. Eck, Bock), the SCON concluded that the present type (= holotype) is an unidentifiable feather impression. Accordingly, the SCON resolved to support Drs Paul Bühler and Walter Bock in asking the Commission to set aside the holotype and designate as neotype an identifiable skeleton in the Natural History Museum, London.

9.2.3 Publication date of Latham's *Supplementum Indicis ornithologicis*

Publication of Latham's *Supplementum* in 1802, not 1801 (Browning and Monroe, *Arch. Nat. Hist.* 18 (1991) 381–405) changes the traditional date of publication of 224 species names, most of them Australian. The only nomenclatural consequence is potential replacement of these names by others previously thought junior; yet only one has come to light: *Menura superba* Davies, 1801 over *Menura novaehollandiae* Latham, 1802 for the iconic Australian superb lyrebird. After considering options, the SCON voted

4 to 2 (1 abstention) to accept the revised date of Latham's *Supplementum* (1802), and then by 6 to 1 to ask the Commission to suppress *M. superba* Davies.

9.2.4 *Creadion* Vieillot, a source of confusion

Vieillot based the genus *Creadion* on wattlebirds from both Australia (Meliphagidae) and New Zealand (Callaeatidae). As a result, the name has been used in both families according to differing interpretations of the type species. The SCON reaffirmed its decision at the 20th IOCongress in 1990 to ask the Commission to suppress *Creadion* Vieillot.

9.2.5 The identity of *Columba recurvirostra* Gmelin

The identity and status of *Columba recurvirostra* Gmelin, type species of *Treron* Vieillot, have been confounded over the years such that action is needed to specify identity to affirm current usage. The SCON unanimously resolved to do this by applying to the Commission to designate a neotype from a locality ensuring nomenclatural stability.

9.2.6 Unresolved generic names from the 12th IOCongress, Helsinki, 1958

At the 12th IOCongress, the SCON opted to "correct" original spellings of three generic names by Swainson in Meliphagidae: *Gliciphila* to *Glyciphila*, *Anthomiza* to *Anthomyza* and *Zanthomiza* to *Xanthomyza*. No further action was taken. Since then, the original spelling *Gliciphila* has been re-established and *Anthomiza* has become a *nomen oblitum* under Art. 23.9 of the Code, leaving only validation of *Xanthomyza* to be actioned.

9.2.7 Competition between the family-group names Sylviidae/inae Leach, 1820 and Timaliidae/inae Vigors and Horsfield, 1827

Current molecular evidence indicates that *Sylvia* Scopoli, type genus of the Sylviidae/inae, is nested phylogenetically within the Old World babblers, potentially shifting the conventional family name for the Old World warblers to the babblers. Action was considered premature at this stage; if required, the preferred solution was one of conditional suppression of Sylviidae Leach, whereby that name would be used for familial taxa combining warblers and babblers but subordinate to Timaliidae when they are separate.

9.2.8 Association of the SCON with the International Commission on Zoological Nomenclature

The initiative of the Commission to liaise with international bodies in producing official lists of available names offers scope for the SCON to serve as the Commission's arm in matters of ornithological nomenclature *through* such lists. Submission of Professor Bock's 1994 list of bird family names was agreed as a first step in developing this association. In this role, the meeting felt that the SCON should be more representative of national taxonomic committees, noting that those committees too needed to improve their participation in the SCON and its meetings.

10 Report of the Chairs of the IOCommittee Standing Committee on Raptors, David M. Bird and Bernd Ulrich-Meyburg

10.1 Background

Raptors are at the top of the food chain and enjoy a large following of concern and interest among scientific and conservation communities throughout the world. To monitor and act on the issues and problems associated with such high-profile birds, the IOCommittee allows for the establishment of specialist standing committees. At a Round Table Discussion 17 at the 22nd IOCongress in Durban, South Africa, organized and chaired by David Bird, past-president of the Raptor Research Foundation, and Bernd Ulrich-Meyburg, president of the World Working on Birds of Prey and Owls, about 25 interested people discussed the establishment of a Standing Committee on Raptors after a brief address by the then IOCommittee Permanent Secretary, Walter Bock, on how standing committees function and what roles they serve. That meeting decided unanimously to request the IOCommittee to establish such a standing committee.

10.2 Functions of the Standing Committee on Raptors

The committee was established to:

1. encourage and implement the airing of hypotheses concerning birds of prey at IOCongresses by means of symposia, e.g. on phylogeny, reversed size dimorphism;
2. encourage discussion on the conservation of raptors through Round Table Discussions;
3. bring conservation issues concerning raptors to the attention of the IOCommittee and determine what ornithological research needs to be done in seeking solutions, e.g. effects of chemical pollutants, raptors as indicators of habitat fragmentation, impact of agriculture on raptors; and
4. stimulate networking among international raptor groups, e.g. Raptor Research Foundation (RRF), World Working Group on Birds of Prey (WWGBP).

During the discussion, however, some reservations were expressed by several participants that the fourth objective might not be easy to achieve politically. The RRF and the WWGBP have on occasion shared their meeting venues and certainly many raptor researchers and conservationists around the world belong to both organizations. Moreover, both organizations have independently assessed and acted upon various international and local conservation issues involving raptors. Thus, some questioned the need to create yet another raptor group, i.e. the IOCommittee Standing Committee on Raptors. A long list of potential names to serve on the Committee was generated to represent the main geographic areas around the world.

10.3 Progress

The Standing Committee on Raptors submitted a proposal for a symposium to the organizers of the 23rd IOCongress to be held in Beijing, China in August 2002, but

due to a series of misunderstandings its proposal was not accepted by the Scientific Planning Committee for that Congress. In the circumstances, it was agreed that David Bird and Bernd Ulrich-Meyburg would continue to chair the IOCommittee Standing Committee on Raptors until successors could be found. It was further agreed that, in addition to the two co-chairmen, the Committee would consist of ten international representatives with a demonstrated record of scientific publishing on raptor biology and who would be likely to attend IOCongresses. David Bird has now contacted the following people who have agreed to serve: Ian Newton (UK), Anita Gamauf (Austria), Beatrice Arroyo (currently Scotland), Erkki Korpimäki (Finland), Pertti Saurola (Finland), Marc Bechard (USA), and Jean-Marc Thiollay (France). The remaining three have yet to be coopted.

Ian Newton counseled the raptor group to contact other Standing Committees of the IOCommittee to see how they function, whether they held their congress meetings in the form of a Round Table Discussion (RTD), and whether the IOCommittee does indeed guarantee a place for RTDs for Standing Committees.

11 Invitation to hold the 24th International Ornithological Congress in Hamburg, Germany, 13–19 August 2006, presented by Franz Bairlein

11.1 Hosts

Deutsche Ornithologen-Gesellschaft e. V. (German Ornithologists' Society; DO-G), and Institute of Avian Research "Vogelwarte Helgoland", Wilhelmshaven (IfV), supported by Naturschutzbund Deutschland, European Ornithologists' Union, and First Mayor of the Free and Hanseatic City of Hamburg.

11.2 Patronage

Federal Ministry for Education and Science of the Federal Republic of Germany.

11.3 Location

CCH-Congress Centrum, Hamburg

11.4 Proposed Committees (* IOC member; ! deceased)

11.4.1 Secretary-General

Bairlein, Franz (Wilhelmshaven)*

11.4.2 National Committee

Helbig, Andreas, Chair (Kloster)*!

Becker, Peter H. (Wilhelmshaven)

Berthold, Peter (Radolfzell)*

Böhning-Gaese, Katrin (Mainz)*

Dien, Jürgen, Chair, Local Committee (Hamburg)

Eck, Siegfried (Dresden)*!

Exo, Klaus-Michael (Wilhelmshaven)

Nipkow, Markus (Bonn)

Gwinner, Eberhard (Andechs)*!

Martens, Jochen (Mainz)*

Prinzinger, Roland (Frankfurt)*

Starck, J. Matthias (Jena)*

Wiltschko, Roswitha (Frankfurt)*

Wiltschko, Wolfgang (Frankfurt)*

11.5 CCH-Congress Centrum Hamburg

- A world-renowned congress venue in the heart of the city of Hamburg
- 19 conference halls, seating 30–3 000, including 4 600 sqm of floor exhibition space
- Registration desk
- Service Center (cash dispenser, credit card, phones, faxes and phone services, Internet, photocopy machines)
- Wheelchair access to all areas, sanitary facilities for handicaps
- Medical service
- In-house catering, seating 750, additional restaurants and bistros around the CCH
- Underground parking
- 7 miles from Hamburg's international airport
- International railway links, intercity trains, subway and bus stations in the vicinity of CCH

11.6 Routes to Hamburg

Hamburg Airport serves flights to and from more than 50 countries worldwide. Hamburg offers direct destinations to all European capitals, and can be reached from most world capitals with only one stop over via Amsterdam, Brussels, Copenhagen, Frankfurt, Helsinki, London Heathrow, Munich, Paris, Vienna and Zurich.

The intercity rail station Dammtor is right next to CCH.

11.7 Public transport

Rapid-transit underground and suburban rail links, numerous bus routes and even port ferries are all included in the same transport system. CCH is right next to several stations and bus stops. A special congress ticket will allow participants to use Hamburg's public-transport system free of charge.

11.8 Hotels

Hamburg has some 20 000 beds in every category of hotel. Apart from numerous 5 and 4 star hotels, Hamburg also offers a wide range of budget hotels, pensions and hostel-accommodation. 870 rooms have already been pre-reserved in all five categories, ranging from US\$ 20–150 per person and bed and night. The Radisson-SAS Hotel with 560 rooms is adjacent to the CCH. The pre-reserved hotels are close by or can be reached by public transport within 15–20 minutes.

11.9 Congress Tours

Pre- and post-congress tours will be organized to various natural and cultural sites in northern, eastern and central Europe, ranging from 3 to 7 days.

Mid-congress tours will include the Wadden Sea, the island of Helgoland, the Lueneburg Heath, the Harz Mountains, the German Baltic Sea Coast, the Mueritz Lake District, the River Elbe Biosphere Reserve, and the City of Berlin.

Early morning birding trips will be organized during the congress.

11.10 Accompanying Persons Program

Hamburg and its surroundings offer a wide range of events and trips. The accompanying persons program will include guided tours to the city of Hamburg, the city of Berlin, the island of Helgoland, the German Wadden Sea, and the Lueneburg Heath.

11.11 Contact institute of avian research

“Vogelwarte Helgoland”
An der Vogelwarte 21
D-26386 Wilhelmshaven
Germany
Phone: int-(0)4421-96890
Fax: int-(0)4421-968955
e-mail: ifv@ifv.terramare.de
<http://www.vogelwarte-helgoland.de>

12 Report of the Co-Chairs of the IOCommittee Resolutions Committee, Eberhard Curio and Michael Rands

12.1 Resolution 1: vote of thanks to our Chinese hosts

AWARE that the demanding objectives of the International Ornithological Congress can only be met when the meeting takes place in a well equipped and efficiently managed setting;

EMPHASIZING that a congenial and friendly atmosphere contributes immensely to the successful outcome of such meetings; and

NOTING with appreciation that these conditions were met in full measure at the 23rd International Ornithological Congress, Beijing,

The International Ornithological Committee at its 23rd Congress in Beijing, China, August 11–17 2002:

1. WARMLY thanks the China Ornithological Society for so generously hosting the 23rd International Ornithological Congress in Beijing, China, 11–17 August 2002.

2. ACKNOWLEDGES with gratitude the dedicated support provided by the State Forestry Administration, Beijing Normal University, National Natural Science Foundation of China, China Wildlife Conservation Association, China Association for Science and Technology; and China Committee for the International Union for Biological Sciences.

3. EXPRESSES particular thanks to Mrs. Cheng Tso-Hsin, Mr. Ma Fu, Professor Zhong Bin-Ling, Professor Song Yen-Ling, and Mr. Chen Run-Sheng for honoring the IOCommittee with their presence and welcome at the open-

ing ceremony.

4. FURTHER EXPRESSES very special appreciation and thanks for their hard work planning the Congress over the past four years and for their excellent running of the Congress for the past week, the following key persons working for the 23rd International Ornithological Congress:

Professor Zheng Guang-Mei (Beijing Normal University, President of the China Ornithological Society, and Chair of the Local Committee);

Professor Xu Wei-Shu (Vice President of the China Ornithological Society and Secretary-General of the 23rd Congress);

Mr. Liu Feng (China International Conference for Science and Technology and Assistant Secretary-General of the 23rd Congress), who was central to all the planning of the Congress during the past four years and for its smooth running during the Congress;

Professor Zhang Zheng-Wang (Beijing Normal University and in charge of Congress tours);

Professor Song Jie (Beijing Normal University and Secretary-General of the China Ornithological Society); and

Professor Zhang Ten-Yun (Beijing Normal University and in charge of grants and director of volunteers);

and, in addition, expresses appreciation and thanks to the following persons who have worked hard for the success of the 23rd International Ornithological Congress in Beijing:

Professor Xu (Institute of Zoology of the Chinese Academy of Science and Vice President of the China Ornithological Society);

Professor Lei Fu-Min (Institute of Zoology of the Chinese Academy of Sciences and Treasurer of the China Ornithological Society);

Professor Ding Chang-Qing (Institute of Zoology of the Chinese Academy of Sciences);

Professor Sun Yue-Hua (Institute of Zoology of the Chinese Academy of Sciences);

Professor Chu Guo-Zhong (National Bird Banding Center);

Professor Li Xiang-Tao (Beijing Natural History Museum);

Professor Hou Lian-Hai (Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences);

Professor Chen Hong (Peking University);

Professor Gao Wu (Capital Normal University);

Professor Jia Zhi-Yun (Acta Zoologica Sinica Editorial Board and in charge of publishing the Proceedings);

Professor Zhang Yong-Wen (Chinese Zoological Society);

Professor Huang Hua-Qiang (Chinese Forestry Publishing House and in charge of new bird stamps);

Dr. Zhong Jia (People's Daily, Overseas Edition);

Dr. Wang Wei (State Forestry Administration);

Dr. Hou Pao-Kun (Beijing Forestry Administration);

Dr. Chen Ke-Ling (Wetland International — China Programs);

and lastly to the large number of students at the Beijing Normal University who worked hard and cheerfully as volunteers during the Congress.

5. ACKNOWLEDGES with gratitude the dedicated support provided by:

The International Fund for Animal Welfare;
The World Wildlife Foundation, China Program;
The International Crane Foundation;

The Institute of Vertebrate Paleontology and Paleoanthropology — for the excellent display of Chinese avian fossils; and

Swarovski Optiks.

6. CONVEYS its great and lasting appreciation to the Government and people of China for their gracious hospitality and warm welcome.

12.2 Resolution 2: a special vote of thanks to the Scientific Program Committee

The 23rd International Ornithological Congress ex-

tends grateful thanks to the Scientific Program Committee and, especially, to Dr. Fernando Spina, Chair, for their dedicated work in planning the scientific program of the Congress which was central to the exchange of scientific ideas among delegates. Dr. Spina presided over the meeting of the SPC in 2002 and corresponded tirelessly with members of the Congress on the scientific program, all of which guaranteed a successful scientific program.

12.3 Resolution 3: a special vote of thanks to the Editorial Committee

The 23rd International Ornithological Congress also thanks the Editorial Committee, and especially Dr. Richard Schodde, Chair, for their exacting work editing all contributions of the Congress. Dr. Schodde edited the abstracts of the Congress contributions and is in charge of editing the Congress Proceedings which will be the lasting contribution of the Congress for all ornithologists.

Appendices

Appendix 1

Attendance list of members at IOCommittee meetings at the 23rd International Ornithological Congress, Beijing, 13 and 16 August 2002

Name	13 Aug.	16 Aug.	Name	13 Aug.	16 Aug.
Bairlein, Franz	X	X	Louette, Michel	X	
Baker, Allan John	X		Martens, Jochen	X	X
Bankovics, Attila		X	Matthysen, Erik	X	X
Bech, Claus	X		McNeil, Raymond	X	X
Bell, Benjamin D.	X	X	Merne, Oscar J.	X	X
Berthold, Peter	X	X	Moreno, Juan	X	X
Blondel, Jacques	X	X	Morioka, Hiroyuki	X	
Böhning-Gaese, Katrin	X	X	Nakamura, Tsukasa	X	X
Bock, Walter J.	X	X	Parkin, David T.	X	X
Boles, Walter	X	X	Perrins, Christopher M.	X	X
Bosque, Carlos	X	X	Piersma, Theunis	X	
Bruderer, Bruno	X	X	Poonswad, Pilai	X	X
Busse, Przemyslaw	X	X	Potapov, Roald L.		X
Clarke, Michael F	X	X	Ramos-Olmos, Mario A.	X	X
Cooke, Fred	X	X	Robertson, Christopher		X
Crowe, Timothy M.	X	X	Saurola, Pertii Lauri	X	X
Croxall, John P.	X	X	Schodde, Richard	X	X
Curio, Eberhard	X	X	Severinghaus, Lucia LiuX		X
Devillers, Pierre	X		Short, Lester L.	X	X
Dittami, John	X	X	Silverin, Bengt	X	X
Dyck, Jan	X	X	Smith, Henrik	X	
Eck, Siegfried	X	X	Somadikarta, Soekarja	X	X
Falls, J. Bruce	X	X	Spaans, Arie L.	X	X
Gichuki, Nathan N.	X	X	Spina, Fernando	X	X
Gwinner, Eberhard	X	X	Underhill, Les G.	X	X
Hegelbach, Johann	X	X	van Noordwijk, Arie J.	X	X
Higuchi, Hiroyoshi	X	X	Violani, Carlo	X	X
Höfling, Elizabeth	X	X	Wada, Masaru	X	X
Holmes, Richard T.	X		Williams, Murray	X	X
Homberger, DominiqueX		*	Wingfield, John C.	X	X
Ishida, Ken	X	X	Winkler, Hans	X	X
Jenni, Lukas	X	X	Xu, Wei-Shu	X	X
Kikkawa, Jiro	X	X	Zhang, Zheng-Wang	X	X
Kristin, Anton	X	X	Zheng, Guang-Mei	X	X
Lei, Fu-Min	X	X			

* Lucia L. Severinghaus proxy

Appendix 2

IOCommittee In memoriam (for updates, see <www.I-O-C.org>)

IOCommittee members whose passing away has been learned between the 22nd IOCongress in Durban, August 1998, and the 23rd IOCongress in Beijing, August 2002 are:

Jürgen Aschoff: 1913–12 October 1998. Senior Member (Germany). *Obituaries*: (1) Gwinner E, 1999. Jürgen Aschoff. *Journal für Ornithologie* 140 (4): 384–387; (2) Chandrashekar MK, 2002. Jürgen Aschoff. *Current Science* 83 (6): 1 420–1 421.

Luis F. Baptista: 1941–12 June 2000. National Representative (U.S.A.). *Obituaries*: (1) Perlman D, 2000. Dr. Luis Baptista, renowned expert on songbirds. *San Francisco Chronicle* (June 14): B2; (2) OSNA Ornithological Newsletter No. 137, August 2000; (3) Gaunt SLL and DeWolfe BB, 2001. *In memoriam*: Luis Felipe Baptista, 1941–2000. *Auk* 118(2): 496–499.

Biswamoy Biswas: 1923–10 August 1994. Senior Member (India). *Obituaries*: (1) Ray S, 1995. Biswamoy Biswas: Tribute to a bird man. *Environment* 3 (1): 71; (2) Das PK, 1995. Obituary of Biswamoy Biswas (1923–1994). *Journal of the Bombay Natural History Society* 92: 398–402 and 1 plate; (3) Mayr E, 2000. *In memoriam*: Biswamoy Biswas, 1923–1994. *Auk* 117(4): 1 030.

Cheng Tso-Hsin: Senior Member (China), Honorary President, 22nd Congress.

Jean Dorst: 7 August 1924–8 August 2001. Senior and Permanent Member (France). President 16th Congress. *Obituaries*: (1) Erard C, 2002. Jean Dorst (1924–2001). *Ibis* 144 (2): 370–371; (2) Erard C, 2002. Le Professeur Jean Dorst (1924–2001) – *In memoriam*. *Bulletin de la Société Zoologique de France* 127 (3): 207–209; (3) Vuilleumier F, 2004. *In memoriam*: Jean Dorst, 1924–2001. *Auk* 121 (4): 1 289–1 290.

Peter R. Evans: 20 July 1937–28 September 2001. National Representative (U.K.). Obituary: Perrins C, 2002. Peter Richard Evans 1937–2001. *Ibis* 144 (4): 713–714; (2) A full list of his scientific publications is filed in the Alexander Library at the Edward Grey Institute at Oxford University, Oxford, United Kingdom.

Hans Löhrl: 1911–26 June 2001. Senior Member (Germany). *Obituaries*: (1) Nicolai J, 2002. Abschied von Hans Löhrl. *Gefiederte Welt* 126 (2): 56–57; (2) Gwinner E, 2002. Hans Löhrl (1911–2001). *Journal für Ornithologie* 143 (2): 262–264; (3) Gwinner E, 2003. *In memoriam*: Hans Löhrl, 1911–2001. *Auk* 120 (2): 539.

Bernt H. O. F. Løppenthin: 13 May 1904–19 November 1994. Senior Member (Denmark). *Obituaries*: (1) Preuss NO, 1996. Bernt H. O. F. Løppenthin — 13 May 1904–19 November 1994. *Dansk Ornithologisk Forenings Tidsskrift* 90: 34; (2) Preuss NO, 2001. *In memoriam*: Bernt H. O. F. Løppenthin, 1904–1994. *Auk* 118 (4): 1 029.

Wilhelm Meise: 1901–24 August 2002. Senior Member (Germany). *Obituaries*: (1) OSNA Ornithological Newsletter. No. 150, October 2002; (2) Hoerschelmann H and Neumann J, 2003. Prof. Dr. Wilhelm Meise 12.9.1901–24.8.2002. *Journal für Ornithologie* 144 (1): 110–111; (3) Haffer J, 2003. *In memoriam*: Wilhelm Meise, 1901–2002. *Auk* 120 (2): 540; (4) Steinheimer FD, 2002: Obituary — Prof. Dr. Wilhelm Meise. *Bulletin of the British Ornithologists' Club* 122 (4): 241–242; (5) A more detailed and illustrated appreciation of his life and scientific contributions is found in *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* (2003).

Henri Ouellet: 29 January 1938–10 January 1999. Senior and Permanent Member (Canada). Secretary-General, 19th Congress. *Obituaries*: (1) McNeil R and Godfrey WE, 1999. *In memoriam*: Henri Roger Ouellet, 1938–1999. *Auk* 116 (4): 1 118–1 121; (2) OSNA Ornithological Newsletter No. 129, April 1999.

S. Dillon Ripley, II: 20 September 1913–21 March 2001. Senior Member (U.S.A.). *Obituaries*: (1) Hussain SA, 2002. Sidney Dillon Ripley II — 1913–2001. *Ibis* 144 (3): 550; (2) Beehler BM, Pasquier RE and King WB, 2002. *In memoriam*: S. Dillon Ripley, 1913–2001. *Auk* 119 (4): 1 110–1 113.

Erich Rutschke: 26 May 1926–2 February 1999. Senior Member (Germany). Obituary: Kalbe L, 1999. Erich Rutschke (1926–1999). *Journal für Ornithologie* 140 (3): 388–389.

Ernst Sutter: 1914–10 November 1999. Senior Member (Switzerland). Honorary President, 23rd Congress. Obituary: (1) Winkler R and Schifferli L, 2000. *Auk* 117 (4): 1 031–1 032; (2) Winkler R, 2000. Ernst Sutter (1914–1999). *Journal für Ornithologie* 141 (2): 255–256.

Lars von Haartman: 24 March 1919–28 October 1998. Senior and Permanent Member (Finland). Secretary-General, 12th Congress, President, 18th Congress. On 60th birthday: Hildén O, 1979. Lars von Haartman 60 years. *Ornis Fennica* 56 (2–3): 41–44. *Obituaries*: (1) Soikkeli M, 2000. *In memoriam*: Lars von Haartman, 1919–1998. *Auk* 117 (4): 1 029–1 030; (2) OSNA Ornithological Newsletter No. 135, April 2000.

Karel H. Voous: 1920–31 January 2002. Senior and Permanent Member (The Netherlands). Secretary-General, 15th Congress, Honorary President, 21st Congress. *Obituaries*: (1) Drent R, Roselaar C and Wattel J, 2002. Karel Hendrik Voous 1920–2002. *Ibis* 144 (3): 551v552; (2) Wattel J, 2002. Karel Hendrik Voous (1920–2002). *Ardea* 90 (1): 189–200; (3) Vuilleumier F, 2005. *In memoriam*: Karel Hendrik Voous, 1920–2002. *Auk* 122 (1): 355–356.

Appendix 3

List of nominees for IOCommittee membership

#	Name	Country	Nominated by	IOCongress attendance
1	Slim Benyacoub	Algeria	Blondel	None
2	Herbert Hoi	Austria	Bairlein	1994, 1998
3	Paulo Antas	Brazil	Croxall	1994, 1998, 2002
4	Reginaldo Donatelli	Brazil	Hoefling	1994, 1998, 2002
5	Cristina Miyaki	Brazil	Hoefling	1994, 1998,
2002				
6	Tony Diamond	Canada	Sco	1994
7	Gilles Gauthier	Canada	Sco	1994
8	Susan Hannon	Canada	Sco	1998, 2002
9	Ross Lein	Canada	Barlow	1994, 1998, 2002
10	Kathy Martin	Canada	Sco	1994
11	Chang-Qing Ding	China	Xu Wei-Shu	1998, 2002
12	Ping Ding	China	Ishii, Xu Wei-Shu	2002
13	Carsten Rahbek	Denmark	Fjeldsa	1994, 1998
14	Etienne Danchin	France	Blondel	1994, 1998
15	Henri Weimerskirch	France	Blondel	1994, 1998
16	Ranjit Daniels	India	Homberger	2002
17	Berry Pinshow	Israel	Bock	1994, 1998
18	Nicola Saino	Italy	Spina	1994
19	Anatoli Levin	Kazakhstan	Kurochkin	1982
20	Adolfo Navarro	Mexico	AOU	1994
21	Mohamed Dakki	Morocco	Bairlein	None
22	Mick Clout	New Zealand	Croxall	1990, 2002
23	Lloyd Davis	New Zealand	Croxall	1990
24	Bernt-erik Saether	Norway	Croxall	1994, 1998
25	Marek Konarzewski	Poland	Tomialowojc, Bock	1994, 1998, 2002
26	Casimir Bolshakov	Russia	Andreev, Bairlein	1994
27	Natalia Lebedeva	Russia	Kurochkin	1994
28	Pavel Tomkovich	Russia	Kurochkin	1994, 1998
29	Victor Zubakin	Russia	Kurochkin	1994
30	Santiago Merino-rodriguez	Spain	Moreno	1994, 1998
31	Daniel Oro	Spain	Croxall	1994
32	Charles Mlingwa	Tanzania	Bairlein	1998
33	Colin Bibby	UK	BOU	1994, 1998
34	Andy Gosler	UK	BOU	1994, 1998
35	Pat Monaghan	UK	BOU	1994, 1998, 2002
36	Bill Sutherland	UK	BOU	1990, 1994, 1998
37	Pam Pietz	USA	AOU	1994, 1998
38	Joanna Burger	USA	Homberger	1994, 1998, 2002
39	A. Townsend Peterson	USA	AOU	1986
40	François Vuilleumier	USA	Bosque, Bock	1994, 1998, 2002

Appendix 4

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Round Table Discussions

RTD01 Birds as monitors of environmental contamination in Asia

convenors: Mauro FASOLA¹, Claudio LEONZIO²

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1 Issues

The meeting discussed methods, ongoing projects, and opportunities for investigating environmental contamination in Asia, using birds as biomonitors. It was opened by M. Fasola who, noting that Asian environments were subject to increasing pollution from industrial, urban and agricultural sources, stressed the need to monitor contaminant levels and assess their effects as a matter of urgency. Such studies, however, had been very scanty (Table 1). Convener Leonzio then discussed methods for assessing contaminants in wildlife, with special emphasis on biomarkers that can be used to assess both persistent and nonpersistent contaminants. The use of noninvasive methods for monitoring the health of species and populations at risk was also reviewed.

2 Outcomes

Case histories from recently completed research by X. Ruiz and Y. Dong (“Coastal and inland wetlands in China and Pakistan: colonial waterbirds as bioindicators of pollutant levels and effects”, funded by the European Union, IC18-CT98-0294) were presented to illustrate the current state of information. Three study areas (one with presumed low contamination, one contaminated from industrial sources, and one contaminated from agricultural sources) were sampled in China, and these were compared with three analogous sites in Pakistan. Bioindicator samples comprised eggs, feathers and prey of little egrets (*Egretta garzetta*), and sediments from their foraging habitats. Analyses of chlorinated hydrocarbons, PCBs, and trace elements from the study sites in both countries revealed that concentration levels in these pollutants were generally lower than thresholds harmful to wildlife, except for high, localized contamination in several trace elements reported below.

The results from Pakistan, in press in *Archives Environmental Contamination and Toxicology*, were summarized as follows. Environmental pollution was assessed in three Pakistani wetlands — Taunsa Barrage, Haleji Lake and Karachi Harbor — presumed to be affected by different pollution regimes: Taunsa Barrage mainly by agricultural pollutants, Karachi Harbor by supposed exposure to industry-related POPs, and Haleji Lake the unaffected control, because, isolated in a stony desert, it is relatively pristine.

Taunsa Barrage and Haleji Lake are wetlands of international importance under the Ramsar Convention, while the Karachi Harbor is of concern because of its large human population.

For organic contaminants, there were significant differences in egg pollutants (HCB, HCHs, cyclodienes, DDTs and PCBs) between sites. Overall, organochlorine pollutant in eggs from the Haleji Lake and Karachi were at respective lowest and highest levels of detection and concentration. Biomagnification of pollutants from sediments in prey and eggs of little egrets was carried out in the three sites, together with the proportions of different compounds. Between-site differences in biomagnification were small, even when differences in pollutant concentration were high. This indicates that eggs are reliable environmental indicators of POPs. The values found were generally lower than reported in eggs of large herons from North America or the Mediterranean basin, yet are of the same order of magnitude as those for medium-sized egrets from other parts of the world.

For trace elements, concentrations of As, Cd, Cr, Pb, Hg, Mn, Se, and Zn were found generally to be within the “normal background” level, and mostly below thresholds that might affect bird survival or reproduction. However, high concentrations of Pb and Hg were found in fish from Karachi, the first at concentrations harmful to fish reproduction, and the second at the limit of concentration for human consumption. Alarming concentrations of Cr and Se, above the critical level for soil contamination, were also found in sediments from Karachi, perhaps enough to affect reproduction in egrets. Even so, overall differences among the three wetlands were less marked than hypothesized. The species of egrets within a given area differed in the concentration of certain elements in their eggs, possibly because the females of each species had foraged in different habitats before breeding. In contrast, no between-species differences were found in chick feathers, presumably because young had been fed prey collected in similar habitats around the colony. High bioaccumulation was recorded for Hg, and lower but still significant for Cd, Se and Zn; for all these elements, feathers of predatory birds such as the egrets were considered the best indicators of environmental contamination. On the other hand, As and Cr did not accumulate in the birds screened, and sediments or organ-

isms low in the food chain were found to be better indicators of their presence.

Participants also reported on other ongoing projects, particularly in relation to the collapse of vulture populations (RTD 09), and to persistent organic contaminants in egrets in Hong Kong.

3 Conclusion

Using eggs, feathers, excreta and other such material, effective biomonitoring and chemical analyses for pollutants can be conducted on biological materials with little or no disturbance to the animals themselves. Through analy-

ses of such material, useful information can be obtained about the presence and concentrations of organochlorines, trace metals and porphyrins (copro-, uro- and protoporphyrins). Further information may also be obtained by nondestructive bleeding. J. Burger and M. Gochfeld pointed out that, despite the work already completed, the studies on contamination in Asian wildlife remain insufficient for adequate environmental assessment. Such research, the meeting agreed, should focus as a matter of priority on (i) aquatic birds and raptors as biomonitors, and (ii) areas of intensive industrial and agricultural development as sources of contamination.

Table 1 Numbers of publications combining the keywords “Asia and contamination in wildlife”, from 1990 to 2001

From citations in *Current Contents* and the *Science Citation Index*

Country	Main study material					
	Water	Air	Sediments	Birds	Aquatic biota	Humans
China	2	2	5	3		4
Korea	1			1		
India	1			1		1
Japan			1	2		2
Pakistan	5				3	
Russia	1			1		
Rest of S Asia					1	
Rest of W Asia	1		1		1	3

RTD03 Threatened birds in East Asia

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1 Issues

A large number of east Asian bird species were recently identified as at risk of extinction in BirdLife International's *Threatened Birds of Asia*. Many are large migrants which require conservation through a network of reserves and a suite of management actions. Others are resident passerines whose ranges and numbers remain poorly known. This IOC round table discussion provided a unique forum for ornithologists from around the world, and particularly from within east Asia, to examine the most appropriate responses to the diverse needs of the region's threatened birds. Crucial to this, it offered the opportunity to develop links between biologists working on the same species or habitats, and between researchers in east Asia and conservation biologists elsewhere in the world. The round table explored the development of partnerships at the international level in pursuit of threatened bird conservation in the region.

The session began with a short presentation by Mike Crosby about the BirdLife International Threatened Species Program, with emphasis on east Asia and an overview of the main conclusions from the *Threatened Birds of Asia*. The following questions were then addressed: (1) how can collaborative networks of ornithologists and conservationists be developed further to progress the conservation of the region's threatened birds, and (2) what can be done to promote new research projects that address the many gaps in knowledge of the region's threatened birds, particularly those that involve institutional exchange and partnership at the international level?

2 Outcomes

2.1 The BirdLife International Threatened Species Program

BirdLife International has been documenting the status of the world's threatened bird species since the 1970s. The results have been published in a series of global lists and regional Red Data Books, most recently *Threatened Birds of the World* (BirdLife International, 2000) and *Threatened Birds of Asia: the BirdLife International Red Data Book* (BirdLife International, 2001). The latter includes indi-

vidual assessments of 323 globally threatened bird species (c. 12% of the entire Asian avifauna, including 41 which are "critically endangered" and 65 which are "endangered"). These assessments detail distribution, population sizes and trends, and ecological parameters (habitat, food, breeding, migration) of the species concerned, as well as threats affecting the species and current management activities. Most crucially, they identify projects, programs and policies for the conservation recommended on the basis of the assembled evidence. A unique feature of the manual is its distribution maps: for the first time in the history of either zoology or conservation, a major segment of an entire fauna is mapped using fully referenced point localities.

Another product that will use material from *Threatened birds of Asia* is BirdLife International's forthcoming *Strategy for the threatened birds of Asia*. It is designed for nontechnical audiences, so that the conclusions of *Threatened birds of Asia* become available to decision-makers in more accessible format. Focus is placed on critically endangered and endangered species, highlighting issues that could cause extinctions in the short to medium term, and identifying conservation actions needed to prevent this. It also identifies the most important sites for threatened birds in the region, and priorities for survey and research. Outputs will include a short publication, and more detailed material in a map-based interface on CD-ROM and the Internet.

2.2 Networks in east Asia and their interaction

Many networks needed to progress the conservation of birds and their habitats in east Asia were identified during the round table discussion. Several IUCN/SSC/BirdLife specialist groups are active in the region, notably the galliformes and crane groups. These groups have prepared action plans for a number of taxa (e.g. three galliform groups) which have had considerable success in promoting conservation in East Asia. The action plans identify priorities for conservation research; and the resulting projects and publications (supported by capacity building for local scientists from within the specialist groups) help to identify appropriate management actions. Similar action plans have been developed by groups of individual scientists and conservationists in east Asia, e.g. for the black-faced spoonbill *Platalea minor* and great bustard *Otis tarda*.

This has fostered regional networks that coordinate conservation efforts for these species. The concept of habitat-specialist groups, rather than taxonomically-focused groups, has been proposed as a new approach that could lead to action plans which address the conservation of whole ecosystems and their biodiversity as well.

Other types of networks identified by the round table discussion included those focused on site conservation (North East Asian Crane Site Network, East Asian-Australian Shorebird Reserve Network), bird counting (the Asian Waterfowl Census organized by Wetlands International) and regional coordination of conservation efforts (e.g. a network covering three provinces of southeast China). Several computer list-servers are active in the region, notably the Oriental birding mailing list which covers wild birds, birding and conservation in the Oriental region. BirdLife International is currently developing two websites. One will contain discussion forums to provide opportunities for users to contribute information on threatened birds relevant to their conservation and the assessment of threat status.

The other will allow users to contribute new information on threatened birds and their conservation in Asia, in order to keep the *Threatened Birds of Asia* database up-to-date. Most participants in the round table discussion were aware of some of these networks, but not all of them. It also became apparent that, although the networks often function very efficiently within themselves, there is often little or no communication between them. Other issues raised included the role of bird tour companies in conservation in east Asia, the importance of conservation education and capacity building, and the problems posed by pollution and coastal reclamation.

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RTD04 Bird collection management: an information network initiative

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1 Issues

Information contained within biological collections is a key resource for countries fulfilling their obligations under the Convention on Biological Diversity (CBD) and other significant environment conventions. With the DARWIN DECLARATION (Environment Australia, 1998), scientists worldwide agreed upon the value, importance and significance of biological collections as... "*records of genetic and morphological variation, past and recent geographical distribution and other biological information.*" Therein, too, the tasks, aims and obligations of institutions housing biological collections, such as museums and universities, are clearly defined: collections (and their contingent information) have to be documented, stored safely and given free access. Especially for issues of nature conservation in third world countries, repatriation of biodiversity data is essential, as species-locality data for birds are often available only from museum specimens.

Despite unconditional acceptance of these needs by politicians and nature conservation and scientific communities, there has been only limited progress in specimen data-basing, fundamental to any data repatriation; and the "virtual world bird collection on the internet" is still a distant vision. Lack of financial support and manpower in biological collections are the reasons. Apart from a few key collections (e.g. Australian bird collections generally and the Africa-collection in Tervuren, Belgium) or key areas (Mexico within CONABIO, Colombia within BioMAP, or the Inter-American Biodiversity Information Network, IABIN), little progress has been made in data-sharing either.

2 Outcomes

Many curators and scientists at the RTD made strong statements that virtual data repatriation should have priority over curatorial initiatives. Obstacles nominated were lack of funding (outside of the U.S.A. only?), security risks and copyright, as well as compatibility of databases. The latter could be overcome by an agreement on international standards now in progress. The University of Kansas offered its software (The Species Analyst) for use free of charge, though many institutions are bound to specific database

programs by prior agreements. Moreover, meta database software, as operated by GEF in Bogor, Indonesia, is better than specimen-based models for such exchange.

For African museums, the situation is probably the least advanced and most difficult. Although the PAOC is said to be preparing an inventory of its continent's bird collections, African museums are now facing hard times: some are submerged in consortia and others have been without curators for years. Programs for training taxidermists and curators are urgently needed, as well as information on bird distribution vital for conservation prioritization.

In Europe, an inventory of major bird collections is seen as a first step towards documenting holdings in research institutes and museums (Roselaar, in press). The inventory gives summary data on European collections, covering their holdings of species, their history, whereabouts and curation. A preliminary estimate puts European and North American collections at about 4 million avian study skins each; another c. 1 million are held in institutions elsewhere in the world, a quarter of which are in Australia. The largest avian collections within Europe are held at the British Natural History Museum, Tring, its holdings four- or five-fold greater than those of the largest collections on the continent, at Leiden, St. Petersburg, Paris, Tervuren and Berlin. None are yet fully data-based. Most study skins, including type specimens and ancient historical material, are nevertheless spread over a large number of smaller collections in diverse European countries, and are partly data-based.

European bird curators now meet every two years to progress matters. A general inventory of biological research collections (ZEFOD) has now begun in Germany, covering holdings of botanical and zoological gardens as well. Similar programs are underway in other countries, such as Australia. Within the German contribution to GBIF (Global Biodiversity Information Facility), a virtual catalogue of vertebrate type specimens is being funded by the German Federal Research Ministry. RTD attendants agreed to further communicate and spread information on activities concerning specimen data-basing and fund-raising via a newsletter, for which the contribution address is majordomo@nhm.ac.uk, with the subject title "ebeac".

RTD06 Agricultural intensification as a major threat to bird biodiversity

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1 Issues

Current predictions (Tilman et al., 2001) suggest that around a billion hectares of new land will be placed under cultivation in the developing world in the next 50 years. That area roughly equals the earth's total area of rainforest. In contrast, 100 million hectares of currently farmed land in the developed world is likely to fall out of production. Both the spread and the loss of farmland can impact severely on bird populations. Moreover, new agricultural technologies, such as genetic modification, may also affect wildlife in various ways. So this RTD aimed to discuss research relating to such effects and to identify priority areas for attention.

The RTD began with several presentations. The first outlined the scale of the threat posed by crop production systems to bird populations around the world, using as examples the intensification of European arable agriculture and tropical coffee and cocoa systems. In the former, declines of farmland birds have been greatest in countries with the most intensive agriculture (Donald et al., 2001), a trend currently regarded as the greatest single threat to Europe's bird populations. Tropical crop systems, moreover, can have a disproportional effect on biodiversity because their centers overlap closely those of earth's biodiversity hotspots. For example, oil palm *Elaeis guineensis* production, which expanded from 250 000 ha. in 1970 to 5 million ha. in 2001, represents one of the main causes of tropical forest loss in southeast East Asia. Increasing demand for agricultural products will be met through two different strategies: intensifying production on land already given over to cultivation, or expanding production into new areas. The choice of which system to use will have different environmental impacts in different parts of the world. In Europe and North America, where a high proportion of wildlife resources remain on farmland, it might be better to maintain or expand existing farmland while keeping intensity of production low. In tropical countries, on the other hand, it is often preferable to intensify existing production systems without expanding into pristine habitats of high nature conservation value.

Three further presentations detailed the effects of intensification in particular production systems. The relationship between skylark *Alauda arvensis* populations in the UK and the intensification of cereal production systems illustrates the subtlety of the impacts. One of the causes for the decline of skylarks in Europe is the greater height and density of cereal crops today, forcing later-breeding birds to nest in areas more vulnerable to predation. The effects on bird populations of intensifying coffee *Coffea arabica* systems in Mexico and central America were also examined. These studies concluded that, although lower intensity systems kept a façade of natural forest and held high bird diversity, particularly of neotropical migrants, even the lowest of them remained unattractive to, or unusable by, species adapted to pristine forest.

2 Outcomes

Group discussion centered on a number of questions relating to future research needs for assessing the impacts of agriculture. The following priorities were suggested:

- rice production systems in Asia
- water abstraction for agriculture in Australia
- genetically modified (GM) crops globally
- agrochemicals, particularly in the developing world
- interactions between agriculture and climate change
- relative impacts of clearing versus intensification
- sociological factors — the attitudes of farmers towards wildlife
- identification of key agricultural systems and areas in conservation
- improved interdisciplinary collaboration
- environmental services for low intensity agriculture
- identification of mechanisms that drive population changes in farmland birds

The need to understand more about the environmental effects of transgenic crops was stressed repeatedly. Further research might identify such crops as environmentally beneficial, in that they might reduce the need for pesticides and could increase yields, so averting habitat loss

elsewhere. Or they could prove environmentally damaging, reducing non-crop food supplies for wildlife and tying farmers into particular production systems. The introduction of transgenic crops in the USA has led to a decrease in the total area farmed, presenting conservationists with opportunities, so far little explored, to consider what should replace farmland.

The RTD recognized that, in order to advise and influence global agriculture and biodiversity issues, conservation scientists and advocates must:

- adopt a perspective that is as global as agriculture
- appreciate and address the needs of people, particularly in developing countries.
- develop a better understanding of the economic issues in national and international agricultural trade
- adopt a more multidisciplinary approach to research, because agriculture is a multidisciplinary industry
- identify areas where agriculture is likely to be or become a serious threat to wildlife populations, and to develop conservation priorities
- develop a strategy that blends pragmatism with a vision of sustainable development

Participants recommended that the International Ornithological Committee should adopt the following resolution recognizing the importance of agriculture as a driving force in bird conservation. The draft resolution reads:

Agricultural production as a major threat to bird populations globally

The International Ornithological Committee recognizes that major changes are taking place in global agriculture, with consequent threats to, and opportunities for, the con-

servation of biodiversity. These changes may affect agricultural systems directly, and all related ecosystems indirectly, e.g. the abstraction or eutrophication of water and the environmental impacts of burning. Birds are an important, valued and conspicuous element of biodiversity in all habitats, with regard to which recent research has identified causal links between shifts in global agriculture and severe declines in bird populations.

The International Ornithological Committee therefore urges all responsible authorities to support research into the effects of agricultural change on biodiversity in general, and birds in particular, especially in developing countries with high biodiversity. It also urges conservation scientists to participate in multidisciplinary research to devise innovative approaches that capitalize on the opportunities and minimize the threats to biodiversity conservation. Management efforts should be focussed at the broad landscape scale of catchments or regions. They should involve all stakeholders and consider both socio-economic and biological issues. High priority should be given to understanding and managing new agricultural processes that may influence biodiversity values of global significance, regardless of whether they reside in farmland itself or associated ecosystems.

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RTD07 Progress in avian vision

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1 Issues

Vision is the key sense that guides many important aspects of bird behavior. Recent progress ranges from understanding the retinal mechanisms of color vision, including the tetra-chromatic visual system and wide distribution of UV sensitivity into UV (ultraviolet) light, to details of eye structure, visual fields and their relation to foraging. This RTD sought to summarize important recent findings and to identify, for interdisciplinary and collaborative investigation, areas of research that link eye, vision, and behavior. Two main areas were discussed: (1) vision and plumage coloration and their interactive roles in conspecific signalling, and (2) how knowledge of visual fields and color vision might be applied to reduce the hazard of bird collisions, especially with power wires.

Two speakers presented brief papers to stimulate discussion. First, Geoffrey E. Hill, Dept. Biological Sciences, Auburn University, USA, spoke on the effects of carotenoid acquisition and utilization on expression of colorful plumage in the house finch, *Carpodacus mexicanus*. Carotenoid pigments produce most of the red, orange, and yellow colors of feathers. Because birds cannot synthesize their own carotenoids, they must ingest such pigments to color their plumage. Given such diet-dependence, it is not surprising that access to carotenoid pigments during moult in house finches affects carotenoid-based plumage coloration, as demonstrated in both field observations and laboratory experiments.

Secondly, the senior convener addressed the question: what can vision research tell us about how to reduce bird-collisions with power wires? A review of eye structure and visual field capacity across 23 species of birds differing in ecology, phylogeny, size and flight capability suggested across-the-board convergence in three main topographies of visual field. Common to the majority of species is extensive visual coverage about the head, complemented by a narrow binocular field in front, of 20°–30° maximum width in the approximate horizontal plane. Some species even achieve complete visual coverage of the ce-

lestial hemisphere. In flight, objects ahead of such birds constitute a small fraction of the total space to which they might be attending at any one time (*cf.* human experience of visual space which stems from frontally-placed eyes). Moreover, many birds have foveae that project laterally rather than frontally, suggesting that attention may often be directed sideways and downward. Species that commonly experience aerial collisions (e.g. wildfowl, bustards, cranes, raptors) usually fly about in open space devoid of obstruction. It allows them to search around and down for conspecifics or suitable foraging sites, yet can distract them from “attending” to what is ahead.

2 Outcomes

1. Dr. Hill concluded that variation in the expression of carotenoid-based ornamental coloration is not explained entirely by differential access to carotenoid pigments. Male house finches must also utilize efficiently those pigments that they acquire in their diet. Even with abundant access to carotenoid pigments, parasitic infection and nutritional stress during moult can significantly reduce expression of plumage coloration. His data indicated that carotenoid access, parasite load, and nutritional condition combine to determine the brightness of plumage in male House Finches. What remains to be resolved in any wild population of birds is the relative importance of these factors.

2. Dr. Martin concluded that the avoidance of obstacles by birds flying under the conditions he described could be a perceptual rather than visual problem. To enable it, devices were needed to attract attention from below, to encourage the birds to fly lower or higher, or even land, rather than those which simply raised the visibility of hazardous objects in the flight path ahead. The aerial maneuverability of many of the species most at risk, moreover, was low, due to high wing loading and flight speed. Thus hazards needed to be signalled at considerable distances in advance. It was argued that color marking, including use of UV reflectivity, are not likely to increase significantly the detectability of hazards.

RTD08 Impacts of long-line fishing on seabirds: towards identifying geographical “hotspots” of seabird mortality

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1 Introduction

The purpose of RTD 08 was to canvass the collating, into a centralized database, of all tracking data on seabirds (principally albatrosses and petrels) affected by long-line fisheries. The objective: to identify the areas of ocean utilized most intensively by each species. The resulting map of records would be used to pinpoint areas where interaction with long-line fisheries is highest, thus warranting priority conservation attention. Beyond that, the initiative was seen as the first fundamental step towards the identifying Important Bird Areas (IBAs) on the high seas.

BirdLife International's Seabird Conservation Programme offered its services as an independent NGO (with no academic interest in the data) to take the program forward, and proposed to seek funding for a technical workshop in South Africa in the latter part of 2003. Prior to the present RTD, a circular outlining the initiative was distributed to all interested and affected parties; and responses from data-holders were overwhelmingly positive.

2 Issues

2.1 Progressing the initiative to conservation action

To the question of how the mapping program would be taken through to conservation action of benefit to seabirds, it was felt that various international and regional forums were the appropriate venues. The Agreement for the Conservation of Albatrosses and Petrels (ACAP) would require the proposed distributional inventory to identify priority areas at sea. Where such areas fell within the national waters or Economic Exclusive Zones of signatory states, the states would be expected to provide appropriate conservation measures. The exercise would also assist Regional Fisheries Management Organisations (RFMOs) to take due account of the most important areas. A range of conservation procedures could be implemented under the auspices of the RFMOs, ranging from more thorough investigation of seabird/fishing interactions by signatory fishery states, to the use of more comprehensive mitigation measures, including regulation of the timing (seasonality)

and scale of fishing effort.

2.2 Inclusion of ship-based transect data

Such data, it was agreed, would make an invaluable complement to satellite-tracking information; and every effort should be made to facilitate their combining when appropriate. Initially, however, emphasis would be placed on collating the tracking data and setting up a framework to receive and process them. Once this basal data-layer had been incorporated and analyzed, ship-based data-layers (for geographically confined areas) could easily be added, to improve and refine outputs.

2.3 Fisheries distributional data

Following enquiries, it was determined that spatiotemporal analyses of the long-line fishing effort in the Southern and north Pacific Oceans were already available, and that scientists involved had indicated an interest in participating in the present project. Much data was also available directly from Regional Fisheries Management Organizations.

2.4 Identifying gaps in data sets and refinement of analyses

It was recognized that the coverage of species and populations at different stages of their breeding and life cycles would not be complete. The project could help to identify such gaps; moreover, the database would become more complete as more data were collected, enabling improved analyses. Initial emphasis, nevertheless, needed to be placed on getting a working framework in place, to which further data could be added.

2.5 Home for the database

A brief description of Birdlife International's World Bird Database (BIWBDb) was given to the meeting. It was pointed out that the BIWBDb currently held point location data and could be a logical home for the new database. The Avian Demography Unit, based in Cape Town (and thus geographically close to the Global Seabird Programme) also had the capacity to manage such a database. It was decided, however, that resolution of this issue should be postponed

to the proposed technical workshop in South Africa, at which the picture of the product and its management structure would become clearer.

2.6 Compatibility of data

Issues relating to compatibility of data (e.g. for different geographical areas with different uplink rates, different devices, different duty cycling, etc.) and to the most appropriate ways of converting the uplinks into density-distribution maps, were felt to be key elements that the proposed technical workshop should address.

2.7 Ephemeral habitats

Although some areas utilized by seabirds were ephemeral, current data suggest that many sites are linked to bathymetric features and so predictable in space and

time. Such sites could serve as foci for management strategies.

3 Outcomes

The meeting concurred that the project would be valuable for the conservation of pelagic seabirds; and data holders present agreed to participate in the process. Based on such a positive response, the BirdLife International Seabird Conservation Programme would proceed to seek funding for a technical workshop to be held in Cape Town during latter 2003. All holders of relevant tracking data and fisheries scientists would be invited to the workshop. Just as importantly, specialists in the field of spatial analysis and statistics would be included to ensure that data are incorporated and analyzed in a statistically appropriate manner.

RTD09 Collapse of vulture populations in southern Asia

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1 Issues

1.1 Introduction

Once-numerous populations of three species of vultures, the white-backed vulture (*Gyps bengalensis*), the long-billed vulture (*G. indicus*), and the slender-billed vulture (*G. tenuirostris*), have collapsed on the Indian subcontinent within the last five years. Earlier declines in the white-backed, slender-billed, and red-headed vulture (*Sarcogyps calvus*), moreover, have been recorded in the countries of southeast Asia. This report summarizes scientific assessments of the contributing causes while focusing on current priorities in scientific investigation and conservation programs. As previously proposed, contributions by persons who could not attend the Congress are incorporated. Space limitations preclude a bibliography; contributions by the individuals named come from their oral or written communications, unpublished manuscripts, manuscripts in press and published papers.

1.2 Southeast Asia

Surviving populations appear to be restricted to northern Cambodia and adjacent regions, and to have a low rate of reproduction. Loss of habitat cannot explain such population collapses, although human persecution has had a significant impact on other species of larger, conspicuous wildlife. There is no unequivocal evidence that a disease factor has contributed. A greatly diminished food supply, both of domestic animals and of the formerly abundant wild ungulates, could be the cause instead. Thus the best strategy for long-term conservation could be a still broader strategy to restore a diversity of large wildlife species, including ungulates. Feeding stations in northern Cambodia would also benefit surviving birds and facilitate studies of their abundance, distribution and rate of reproduction (J.W. Duckworth and C.M. Poole).

1.3 Vulture mortalities on the Indian subcontinent

During the 1996–1997 nesting season at Keoladeo National Park in India, V. Prakash recorded both a 50 % decrease in the numbers of nests since the late 1980s, and a high rate of mortality in nesting and fledging white-backed

vultures. By 1999–2000, no *Gyps* vultures were nesting in Keoladeo. In April 2000, dead and dying white-backed vultures were found in or under nests in Ranthambhore National Park to the west (H. Vardhan, Virani and Risebrough). Reports of additional vulture mortalities in west Bengal, in Nepal and in Pakistan were compiled by Virani. In 2000, white-backed vultures were still numerous in the Indus Valley in Pakistan, yet the high rate of mortality documented over the past two seasons since (M. Gilbert, Virani and A.A. Khan) could result in the extinction of this population. Deaths continued in a remnant colony in lowland eastern Nepal in 2002 (H. Sagar Baral and J.B. Giri). Sightings of *Gyps* vultures in India are now rare events, in contrast to their abundance only five years ago.

2 Outcomes

2.1 Causes of mortalities

S. Satheesan has proposed that food shortage and poisoning were the principal causes of population declines, and that feeding stations are now necessary. Yet there is an abundance of apparently uncontaminated food and many of the dead birds autopsied have had adequate, even abundant supplies of body fat. Both D. Pain and L. Oaks have pointed out that a noninfectious “disease factor”, defined here as the agent causing the mortalities, in the form of a pesticide or other poison cannot be ruled out. Yet it would be an unusual toxin that would affect only *Gyps* vultures and not other species that feed on carcasses, and which has appeared at different times over several or more years over a very broad area in three different countries. Unlike most pesticides, it does not act as a nerve poison producing body tremors. Moreover, once active, it appears to exert its effects relatively quickly, without affecting the birds’ ability to feed. An infectious disease that appeared by mutation or that was acquired from another species remains one plausible explanation. A striking parallel has been noted between the pattern of mortality in *Gyps* vultures, which have close body contact during feeding, and in house finches (*Carpodacus mexicanus*) in the eastern USA which die of infections by a bacterium (*Mycoplasma* sp.) passed by body contact at bird feeders.

2.2 Research facilities

At present, there is no country that can undertake experiments on captive birds with facilities that are adequately quarantined, have effective and efficient permit requirements in place, possess access to veterinary facilities and an international airport, and which can send or receive birds, tissues, or isolates to or from any other country. Construction of such a facility, one that would work closely with and complement the facilities already developed in both India and Pakistan, is considered to be of the highest priority in identifying and confirming the “disease factor” and is a prerequisite for developing a crude vaccine or mitigant.

2.3 Status of vultures still surviving in India

“In the Indo-Gangetic plains ... (the) population is very slowly recovering...(according to)... reports coming in from various quarters” (R.B. Grubh). Yet such occasional reports of small groups of white-backed or long-billed vultures have included no information on reproduction or whether excessive mortalities are still occurring. Observations at one site in lowland eastern Nepal by Bird Conservation Nepal and Himalayan Nature showed a 5-fold reduction in the number of nests between 2000–2001 and 2001–2002. Twelve nests monitored from December 2001 through June 2002 produced only one young, with the death of adults being documented at one site (Sagar Baral and Giri). Casual observations at this site might have suggested that the local population had “stabilized”. Conclusions that populations in India are recovering therefore are premature. Detailed, intensive studies of each of the three species there over the entire nesting cycle have become a priority for the nearer future, to determine whether some birds have escaped exposure to the “disease factor” or have become resistant. Assam is a critical area for this, being a center of abundance of the slender-billed vulture, about which less is known than the other two species; the impact of the “dis-

ease” was noted there only in 2000–2001, later than in western India (A. Choudhury).

2.4 Captive breeding and development of disease-free flocks

If groups of each species are confirmed as breeding successfully in the wild today, the creation of “disease-free” captive groups assumes a lower priority. If, however, successful breeding with near-normal reproductive success is not found during the current 2002–2003 season and mortalities continue, eggs from the wild should be obtained the following season for artificial incubation. Despite uncertainty, we believe that eggs are more likely to be free of the “disease factor” than adults or juveniles in the wild.

2.5 Detection of westward and northward spread of the “Disease Factor”

No abnormalities have yet been observed in the population of Himalayan Vultures (*Gyps himalayensis*) in Tibet (S. Chan). Studies in Mongolia of cinereous vultures (*Aegypius monachus*) provide a baseline for detecting any future infection of that population (N. Batbayar). The monitoring of mortalities and reproductive success of Eurasian griffons (*Gyps fulvus*), many of which winter in India, is now an urgent priority in countries to the west and north of India.

2.6 Summary: priorities in research and conservation programs

In addition to programs underway, we recommend: (1) an expansion of surveys in India to determine reproductive success and mortality rates during the coming nesting seasons of the surviving birds; (2) experimental investigation of the “disease factor” using captive birds; (3) monitoring of colonies of Eurasian griffons in countries between India and the Middle East for deaths during the breeding season; and (4) active field management of the remnant populations of northeast Cambodia.

RTD10 Life history strategies of tropical and temperate birds

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1 Issues

Traditionally, temperate breeding birds, especially passerines, were thought to have life history strategies characterized by low annual survival rates, high reproductive rates and early maturity, while tropical birds had high survival rates, low reproductive rates, protracted parental care, and delayed breeding. These differences have been attributed to differences in seasonality of food supply, migratory behavior and rates of nest predation. Recent studies suggest, however, that the pattern is more complex. Karr et al. (1990; *American Naturalist* 136:277–291) found that survival rates of tropical birds in Panama, based on capture-recapture estimates, were no higher than those in a suite of species breeding in North America. Several subsequent capture-recapture analyses from other tropical areas found higher survival rates than those in Panama, but nevertheless provided estimates lower than expected from life history models. At the same time, many north temperate breeding species have been found to have higher adult survival rates than previously assumed. Recent work also suggests that latitudinal variation in nest predation cannot explain clutch size patterns, counter to long-standing beliefs (Martin et al., 2000; *Science* 287: 1482–1485). Furthermore, south temperate breeding species in Africa, Australia and southern South America appear to have life history traits that more closely resemble those of tropical birds. Thus, despite clear latitudinal gradients in clutch size from north temperate to tropical regions, supposedly associated traits, such as survival and predation, do not co-vary in such a simple way, obscuring the definition of differences in life history patterns and their causes.

Accordingly, we convened an RTD to review current knowledge on geographic variation in life history traits and to identify research priorities in the field. The session, which was attended by researchers from around the world, led to a focus on several key questions:

- (1) Are tropical-temperate life history strategies a result of a trade-off between survival and reproduction, or are these parameters largely constrained independently by external factors such as food supply and predation?
- (2) How important is dispersal, both of young and

adults, in the demography of tropical species?

- (3) What factors influence the evolution of clutch size in tropical birds?
- (4) How does the unpredictability of environments, especially for xeric species, affect avian life history strategies?
- (5) How much can be understood about demographic patterns from periodic mist-netting and banding, as opposed to long-term observational studies of marked birds?

2 Outcomes

The discussion highlighted the need for further field research to address some of these questions. It was felt particularly important to gather more information on the following:

- (1) geographical variation in the availability and seasonality of food, particularly invertebrates, and the impact of food supply on clutch size
- (2) heritability of clutch size in tropical species
- (3) changes in demographic parameters of species that have been introduced into new environments
- (4) metabolic rates of tropical birds in relation to energetic requirements
- (6) natal and breeding dispersal of tropical birds, including how this differs between sexes and after mate loss
- (7) estimates of age-specific survival rates (both breeding and out-of-breeding), based on multiple methods from the same population (e.g., capture-mark-recapture, and resightings of color-marked birds)
- (8) annual variation in survival rates and dispersal of tropical birds in relation to environmental factors, such as El Niño events

Long-term studies that consider many factors simultaneously (e.g. food availability, clutch size, survival) are clearly needed to address many of these questions, particularly to understand the impact of supra-annual variation on demographic parameters.

RTD11 Re-introduction of the endangered ibises of the world

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1 Issues

After the rediscovery of crested ibis (*Nipponia nippon*) in China in 1981, the wild population has been increased, at enormous effort and cost, from 7 to over 120. In addition, another 180 birds have been raised in captivity. At present, wild crested ibis are confined to a small region in central China, where increasing human population has reduced habitat availability and depleted food resources. To ensure the survival of the species, Chinese and Japanese ornithologists are planning a re-introduction program for captive-bred birds, bearing in mind that the transition from captivity to the wild is seldom easy.

A similar situation pertains to the northern bald ibis (*Geronticus eremita*), which is confined to west Morocco and Algeria and numbers about 220 birds in the wild. This species has been helped by a re-introduction program over several years, from which much experience about re-intro-

ducing ibis to the wild has been gained.

2 Outcomes

This RTD offered a unique opportunity for ornithologists worldwide who were involved or interested in re-introduction as a conservation tool to meet and exchange ideas towards developing a re-introduction program for the crested ibis. Using case histories of reintroduction programs for northern bald ibis, whooping cranes and other endangered species, the RTD focused on (1) application of research results and experience to devising re-introduction programs for northern bald and crested ibises and other endangered species, (2) criteria for site selection, including public awareness, (3) methods for release, and post-release monitoring, and (4) strategies for maintaining viable populations of re-introduced crested ibis in the wild.

RTD12 Bird trade: conservation strategy or extinction catalyst?

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After Ernesto C. Enkerlin Hoeflich distributed written materials, and Steven R. Beissinger, Ranjit Daniels and Peter Mawson presented introductory talks, this RTD examined issues of sustainability and impacts of the bird trade on birdlife.

1 Issues

The sustainable use of wild populations of plants and animals has emerged as a strategy for conserving biological diversity. Even so, assigning economic value to wildlife through sustainable use is controversial and may accelerate the rate of decline of many populations (Beissinger, 2001). Shipping birds around the world risks establishing exotic species and spreading otherwise geographically restricted pathogens, both of which may affect native birds deleteriously.

1.1 International bird trade

The international bird trade is a multimillion dollar business. The U.S. was the largest importer of live wild-caught birds prior to the 1992 Wild Bird Conservation Act (WBCA), which prohibits the importation of birds listed on CITES I and II, including all parrots, unless they originate from licensed breeding or sustainable harvesting programs. As a result, the number of imported birds dropped from 150 000–200 000 birds a year in the 1980s–early 1990s to 3 500 birds a year in 1994–1997, and poaching may have decreased (Wright et al., 2001). It is still unknown whether wild populations have started to recover. Currently, the EU and Japan are the biggest importers of live wild-caught birds; and the smuggling of eggs is perhaps an increasing problem.

1.2 Internal bird trade: three examples

Australia enacted a total embargo on the import and export of live wild-caught birds in 1961, which invigorated the breeding of species already in captivity at that time. The internal trade in wild-caught native birds, at least in Western Australia, has declined through a change of culture among plant crop growers, licensed trappers, and aviculturists (Mawson and Johnstone, 1997).

India exported 3.5 million birds per year prior to a total ban on international trade in 1980. However, over 300 out of

1200 native species are still traded internally, despite the Wildlife Protection Acts of 1972 and 1991. This trade is driven by economic as well as socio-cultural and political forces. Most birds are used for ritualistic release; and the declaration of different species as pest or protected has become increasingly politicized.

Mexico, which has a long tradition of keeping and trading live wild-caught birds, became a significant but unregulated source, and a transit center for Neotropical, Australian and Asian species, for the U.S. market in the 1970s. The 1992 legislation banning trade in live native birds pushed the bird trade underground. In 1995–1996, the UMA (Units for Management and Sustainable Use of Wildlife) allowed sustainable harvesting of native birds.

1.3 Sustainable harvesting of wild birds

Trade can be as threatening to parrots as habitat destruction, as many parrots can adapt to changing habitats. Parrots are nest-limited, resulting in low population growth rates. Any sustainable harvest rate has to be set at well below the rate of productivity in wild populations of given size because of the effects of environmental stochasticity (Beissinger, 2001). Practices of sustainable harvest require local control and permanent identification of legally harvested individuals (e.g., Kummerfeld et al., 2002). Because parrots are difficult to assess in the wild, the data needed for setting sustainable harvest or export levels, such as population size and range, habitat requirements and movements, etc., are generally incomplete.

1.4 Economics and ethics in the bird trade

Because the demand for parrots far exceeds production from captive breeding, it induces local people to harvest or poach for the bird trade. Yet the economics of the bird trade are poorly understood, and many assumptions may not hold true. For example, supplying markets with legal birds not only seems unlikely to reduce illegal trade, but instead may stimulate it by generating increased demand. Statistics for the current volume of illegal trading do not exist, but it may be sizable as it is thought to follow the same routes as the illegal drug trade.

Many assumptions supporting the sustainable use

of wild birds have not been scrutinized and may not be tenable. For example, sustainable harvesting may not benefit local communities, because of the volatility of the market, with its boom-and-bust cycling of popular species (Robinson, 2001). The benefits of avitourism as an alternative to bird trade are questionable because the species and places of interest to tourists are usually very different from those used to source the bird trade.

A dilemma is also posed by the large numbers of wild-caught birds that are confiscated at national borders or are of degraded condition due to captivity. Returning such birds to the market may be counterproductive; and returning them to the wild is questionable if not impractical, because the origin of traded birds is often unclear and because of the potential for introducing diseases into wild populations.

2 Outcomes and recommendations

Stimulated discussion led to the following conclusions:

1. The principles of the American Ornithologists Union for guiding the international trade in live birds (Beissinger et al., 1991, 2001) could serve as a model for worldwide application.

2. Equitable human development in areas where birds are endangered by trade is a better solution for conservation than encouraging bird trade.

3. Self-sustaining, profitable breeding of captive birds, especially of highly desirable color mutants, should be encouraged for internal markets.

4. The public needs to be made more aware that captive-bred birds make better pets and breeders than wild-caught birds.

5. It is not true that captive breeding of wild-caught birds helps conservation through its potential for reintroducing species that have lost their habitat. Reintroductions, even if successful (Brightsmith et al., 2003), cannot replace

the local “culture” of birds with higher cognitive abilities or the genetic markers of natural populations that could be used for evolutionary studies.

6. Efforts by organizations that are dedicated to rescuing confiscated and undesirable birds need to be coordinated and guided.

7. Import and transport bans are more realistic and effective than export bans in curbing bird trade.

8. The establishment of an IOC Standing Committee on bird trade was considered, but it was agreed that further discussions were needed to clarify the mission and goals of such a committee. One of the most pressing needs may be the collection and dissemination of scientific and socio-economic data that relate to the bird trade.

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RTD13 Ecology: birds and forestry

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1 Introduction

This RTD canvassed ways in which ornithologists can contribute to knowledge about how various forms of forest management affect the quality of forests as habitat for birds. The same topic was addressed in symposium S39 and in an oral session (O05); it has become part of a new field of ecology called “sustainability science” (Kates et al., 2001).

2 Issues

The U.N. Food and Agricultural Organization (FAO, 2001) estimates that the global net loss of forest cover in the last decade of the 20th century was 94 million ha. That estimate comprises a loss of 130 million ha. in developing countries and a gain of 36 million ha. in the industrialized world, where abandoned agricultural fields are returning to forest. The estimate for the loss of natural forest itself, at 160 million ha., is larger than the loss of forest cover, being the sum of the loss to deforestation and the loss of converting natural forest to tree plantations. In addition to this alarming decline, most of the remaining natural forests have been changed in their composition by the activities of man and especially by forestry (Noble and Dirzo, 1997; Brown, 2001, pp. 169–186; Larson, 2002). Surely, then, it is a responsibility for ornithologists to study the effects of forestry practices on bird populations, and to estimate the consequences of the various options available to land managers.

Despite the conventional reasons of local population growth and shifting cultivation, the underlying forces driving deforestation and unsustainable use of forests are actually the policies of national governments and multinational institutions such as the World Bank and International Monetary Fund, as well as economic factors remote from local scenes (Geist and Lambin, 2002). National forest policies in various countries were described, many of which have conservational and sustainable resource use goals. In China, for example, where one fourth of the forests are plantations, the National Forest Conservation Program, initiated in 1998, lists as one of its objectives the increasing of areas of natural forest. In India, a program called Joint Forest Management emphasizes collaboration between government and local communities and focuses on sustainable

harvesting of non-timber forest products. In some regions of North America, a triad approach is used, which assigns explicit goals for landscape management to encompass extensive forestry, plantations, and protected areas. Forest landscapes in different countries are, according to circumstance, subjected to different patterns and intensities of use. Patterns, commonly mixed in varying proportions, range from fully protected areas to unlogged areas with grazing or harvesting of firewood to areas with extensive large-scale forestry operations that may themselves range from clear-cutting with natural regeneration to intensive agro-forestry and plantation development.

3 Outcomes

Although most ornithologists are not trained to participate in policy matters, attendees at the RTD agreed that ornithologists should try to become more engaged in dialogue with policy makers, to inform them at governmental and even multinational institution levels of the environmental effects of their policies. Participants were also concerned about the possibly unintended consequences of “balanced” forestry operations that are skewed toward intensive forestry at the expense of other uses and values. Some thought that the ecological utility of birds (dispersing seeds, pollinating flowers) should be enough to justify emphasis on fully protected areas. Others argued that, if forest policy were guided by a combination of biological, social, cultural, and ethical values, adequate protection of birds should follow. Even so, specific goals (e.g. that no forest bird species should be lost or allowed to decline in population size by more than a certain percentage) could provide measurable indicators against which policy objectives could be set clearly and objectively.

Two particular types of required research were identified: retrospective research that provides estimates of the impact of past forest policies on bird populations, and prospective research that assesses and predicts the responses of birds to the various silvicultural options that managers are facing now. Experimentation is the most powerful way to conduct the second type of research. Ongoing examples that combine ecological forestry with such ornithological research are the Calling Lake Project in Alberta, Canada (Schmiegelow and Hannon, 1999), and a project in

the Apalachicola National Forest in Florida, USA (Stephenson and Ritchie, 2003).

The RTD concluded that ornithologists and the IOC should raise the effort in addressing the issue of the unintended consequences of forest policies on the conservation of birds. In many if not most cases, timber companies and land managers would welcome clear advice based on sound research on the effects of their practices.

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RTD14 The role of infectious and parasitic diseases in threatened and endangered avian populations

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1 Issues

This RTD addressed the importance of infectious and parasitic diseases as an additional threat to endangered bird populations. Although disease pressures have not traditionally been considered as threats to endangered avian populations, there is growing evidence of their significance. Certain specific conditions have come to be recognized in which diseases are the major factors determining the survival of a population; indeed, as populations shrink, and their genetic diversity reduces, they can become increasingly susceptible. In general, threats of disease tend to be of greater significance in avian K strategists residing within closed systems rather than r strategists or migrants. Thus diseases can have a marked impact on small isolated populations such as those restricted to islands or confined ecosystems. For example, it has been well recognized that disease caused by avian malaria has been a major factor in the decline of native Hawaiian birds. This highlights the potential risk to populations such as those of the kakapo (*Strigops habroptilus*), a priceless biological resource on Codfish Island off New Zealand.

The role of disease was also examined in species that had suffered contractions of range to relatively small areas. An example is the rapid terminal decline of the regional subspecies of Attwater's prairie chicken on the gulf coast of Texas. Loss of habitat through urban sprawl and changed agricultural practices led to a decline of that regional form to low but sustainable numbers. However, the spread of reticuloendotheliosis virus from poultry into the survivors resulted in a further rapid drop, and the subspecies is now surviving only through captive breeding programs. Susceptibility conferred by life in confined space is manifest too in colonies of breeding sea- and water-birds, and indeed, all colonially breeding birds. Recent major declines in the population of the Amsterdam Island albatross (*Diomedea* sp.) may well be due to introduced disease, although this remains speculative.

2 Outcomes

Discussion made it clear that, while the number of good examples of extinction or severe population reductions mediated by disease were relatively few, the issue may well be growing in significance. This was especially true for small, residual populations of critically endangered species in captive breeding programs or other conditions of isolation. The continued spread of avian malaria in the Hawaiian Islands exemplified the situation, posing a threat not only to surviving wild native birds but also to those in captive breeding programs and presenting a dilemma over release. While it is possible to carry out captive breeding in insect-free facilities, released birds become totally susceptible to infection. To this there seems to be no easy answer.

Much of the discussion centered on the "quarantining" of endangered species on islands or in captive breeding colonies. It was agreed that functional barriers needed to be established between poultry or avicultural operations and the isolated populations of endangered taxa. Indeed, even humans exposed to poultry or avicultural operations should not be permitted to come into contact with the Codfish Island population of kakapos. Circumstances are a little different in the Galapagos where commercial poultry operations are already established, presenting a significant disease threat to the wild birds. However desirable, the removal of commercial poultry from the Galapagos is not practical. An alternative solution aired would replace all present commercial poultry on the Galapagos with guaranteed disease-free stock.

The meeting clearly felt that ornithologists needed to become increasingly aware of avian diseases and their potential to spread. The recent introduction of West Nile Virus into North America and its rapid expansion across that continent will probably prove an unwelcome opportunity to investigate disease spread in natural populations and to remind us all that wild birds get sick too.

RTD15 Avian brood parasites and their hosts

conveners: Hiroshi NAKAMURA¹, Fugo TAKASU²

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1 Issues

Avian brood parasitism continues to attract great interest not only in ornithology but also general evolutionary ecology because it provides an excellent system for examining co-evolutionary interactions between parasites and their hosts. The aims of this RTD were to (1) provide an opportunity to present and exchange up-to-date research findings in avian brood parasitism, and (2) construct and launch an international network to promote research in avian brood parasitism, especially in Asia where many brood parasite species breed but where their ecology and behavioral features are rarely studied.

Four discussion papers were presented to illustrate current issues:

(1) “Models in avian brood parasitism” (Fugo Takasu) focused on two mathematical models, one for defense establishment in hosts in a host meta-population in structured habitat, the other for co-evolutionary change of egg pattern in host and parasite. In the first model, he analyzed how host defense spreads in situations where some but not all local populations suffer parasitism. In the second, he investigated the theoretical consequences of a co-evolutionary arms race between parasites and hosts (in press). The results of these analyses stressed the value of combining theoretical modeling with empirical field research.

(2) “Battle and co-evolution between cuckoo and host” (Hiroshi Nakamura) concerned a recent shift in the relationship between a host, the azure-winged magpie (*Cyanopica cyana*), and its parasite, the common cuckoo (*Cuculus canorus*), in Nagano, Japan (Nakamura, 1990; Nakamura, Kubota and Suzuki, 1998). He showed that the magpie had been developing defense against cuckoo parasitism (rejection rate of cuckoo eggs) rapidly in recent decades and discussed the co-evolutionary change in the field.

(3) “Mafia or Paisano? — theoretical consequences and empirical evidence for host-brood destruction by female cowbirds” (Mark E. Hauber) developed a game model to analyze which tactic, mafia or paisano, becomes adaptive for brood parasites (Hauber, submitted). Paisano parasites destroy host broods that do not contain parasitic offspring,

while Mafia parasites destroy only those host broods from which their offspring are rejected. With experimental evidence, he discussed the relevance of both of these tactics in the brown-headed cowbird (*Molothrus ater*) and other brood parasites.

(4) “Geographic variation in egg appearance and egg rejection behavior by hosts” (Eivin Røskft and Arne Moksnes) centered on the hypothesis that the spatial structure of breeding habitat reflects various degrees of host defense level, judged by rejection rate etc. (Røskft et al., 2002a, b). The “spatial structure of habitat hypothesis” applies to host populations segregated into several subpopulations by different habitat type. In test cases, the breeding habitats of the host were separated into three — woodland, open areas and the edges between them — in situations where each subpopulation in each habitat was connected with the others by gene flow. Based on field data, tests of the hypothesis showed that spatial structure is a crucial explanant of the imperfections in host defense commonly observed in many host species.

2 Outcomes

Egg patterning and methods for their quantitative measurement were the focus of much discussion. Studies using models have shown that some hosts reject eggs unlike their own, and that they can recognize subtle differences in egg patterns. Because birds are sensitive to additional spectral colors (e.g. UV), field experiments using artificial eggs painted under the control of the human eye, whether to mimic the eggs of hosts or not, could be biased. The meeting agreed that a standard formula for modeling implanted eggs was a priority need for future field studies.

Another point of debate was the lack of comparative information at larger scales. Field programs are commonly carried out by one researcher on single parasite-host interactions in the one local breeding population or area. To assess the broader operation and functions of parasite-host co-evolution, data needs to be compared from diverse parasite-host interactions over wide regions. For this, it is desirable too that researchers develop standardized methods for measuring basic features of brood parasitism (rejection rate, degree of mimicry etc.). Building an international net-

work of researchers would facilitate such studies. So far, research on avian brood parasitism has been centered in Europe and North America, leaving enormous gaps waiting to be filled in Asia, Australasia and South America.

The combining of empirical and theoretical research was also needed, particularly in view of increasingly theoretical approaches to avian brood parasitism. Better collaboration between field ornithologists and mathematical biologists can only improve our understanding of the details of behavioral and population-level interactions between brood parasites and their hosts.

In summary, the group looked forward to launching a worldwide network of researchers in brood parasitism, with two immediate objectives: to facilitate the development of standardized methods of experimentation in the field, and to expand research outside Europe and North America into and beyond Asia.

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RTD16 Shorebird conservation in the East Asian-Australasian flyway: time is running out

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1 Issues

Wetlands International-Oceania presented an overview of threats in the East Asian-Australasian flyway (EAAF). Each year millions of shorebirds (waders) migrate along the flyway between breeding grounds in arctic east Russia, Alaska and northern China to overwintering grounds in southern Asia and Australasia. The birds need to stop at various staging areas en route to feed in order to replace body reserves before continuing their migration. At August 2002 the East Asian-Australasian Shorebird Site Network had 31 monitoring sites along the EAAF, with the aim of establishing 100 by 2005. The Network, an international cooperative program rather than a politico-legal project, provides the key data-gathering framework for shorebird conservation on the flyway. The ensuing discussion addressed some of the survival problems facing shorebirds within the EAAF, as well as management and conservation issues.

2 Outcomes

2.1 Threats

It was felt that the biggest threat to shorebird conservation in the EAAF was the continuing loss of foraging habitat in staging areas, especially the intertidal mud-flats along the shores of the Yellow Sea. These mud-flats are the largest staging area in the flyway and the furthest north that the birds can feed before reaching icebound breeding grounds; large proportions of shorebirds rely on them, including most of the world's population of great knots (*Calidris tenuirostris*). In China, 37% of intertidal habitat has been lost since 1950 and there are plans for reclaiming a further 45%. In South Korea, 43% of the intertidal feeding area has been lost since the early 1900s and there are plans to reclaim a further 37%. Jeong-yeon Yi from South Korea highlighted the situation at Saemangum where 400 km² is being reclaimed, largely for agriculture. This area alone has been identified as internationally important for 17 species of shorebirds and up to 50% of the world's great knots.

Other threats from human interference were considered secondary. Nevertheless, their collective impact, from product harvesting (e.g. shellfish and crustacea) to water

extraction and hunting, was still considerable.

2.2 Management and conservation

To be effective, conservation must be initiated at national levels and then followed up by contact at local levels, particularly in China. Governments and the public need to be made aware of the issues relating to the loss of important habitat and the threat to many species of birds, some facing extinction. Management needs to include national biodiversity plans and coastal protection policies. Although there are some bilateral agreements between countries in the Flyway, the need for comprehensive multilateral international agreements between countries has become pressing.

Bringing international attention to bear is useful. In China, international opinion counts as long as it is handled with tact and sensitivity. In Taiwan, where international attention has focused on the endangered black-faced spoonbill, political leaders have received international communications almost every day. In Japan, international attention has been sought in a number of instances when important shorebird sites were threatened. There have been some notable successes, although Japan is still forging ahead with reclamation of intertidal mud-flats at some localities.

2.3 Establishment of compensatory wetlands

Re-establishing lost or replacement wetlands may take many years to achieve. In the UK, intertidal mud-flats have been created within 5 years but they may take 20 years or more to develop a foraging structure comparable with "natural" sites. The principle of "no net loss mitigation" needs to be practised by creating new habitat *before* original habitat is lost.

2.4 Information needs

Improved networking between researchers is vital to facilitate sharing of data; such information can be disseminated via media such as "The Tattler" (newsletter for the Flyway). Research along the flyway as a whole appears to be low. While there has been good work in Russia over many years, this is now becoming more difficult because only 20% of the former environmental agency still exists. At

Topai University in Taiwan, one or two out of every three masters students in the biological sciences usually work on shorebirds.

2.5 Endangered species

In 2002, Evgeni Syroechkovski identified a dramatic decline (60%) in the population of spoon-billed sandpipers (*Eurynorhynchus pygmaeus*) at study sites that had been monitored over 17 years. The sandpiper has a very limited breeding range associated with lagoons in far eastern Siberia. The recent publication of the Asian Red Data Book placed the world population at about 5 000 pairs, but this appears to be overly optimistic, Syroechkovski suggesting that the population is closer to a maximum of 1 000 pairs, and probably between 500 and 800. Urgent action is needed to prevent further loss and possible extinction. For this, better

knowledge of feeding ecology outside breeding grounds is essential, together with clarification of migration routes, staging areas and overwintering grounds.

2.6 Next steps

There is a need for international networking between shorebird researchers, conservationists and government agencies. Critical issues such as the plight of the spoon-billed sandpiper and Nordmann's greenshank would benefit from attention from an international taskforce.

Obtaining international recognition of sites of international importance is crucial. Increased work at such sites, especially scientific effort, is needed. There are many gaps in knowledge on even common species. Population monitoring is important, especially in Australia and New Zealand, for assessing trends in flyway populations.

RTD17 The present and future of bird ringing

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1 Issues

Bird ringing (or banding) is a widespread research technique for marking birds individually. Originally introduced just over a century ago to determine the routes of migrating birds, it is still the most widely used method to monitor bird migration. More recently, improvements in techniques for analyzing mark-recapture data have led to increasing use of ringing for other purposes, such as monitoring demographic parameters of bird populations (Seber and Schwarz, 2002). Ringing is also used in behavioral studies and, indeed, any research in which the identity of individual birds needs to be known.

Given its historical aim to track migratory routes across continents, ringing has traditionally required cooperation and efficient exchange of data among different research centers across countries. This has positive benefits in ornithology. The coordination of ringing has led ringing centers in different countries to adopt common procedures both for exchanging data concerned with recoveries of marked birds, and for collecting information from birds being newly marked. This is particularly true in Europe, where there are many national ringing schemes in many countries, all with different languages. Since 1963, EURING (The European Union for Bird Ringing) has coordinated research activities based on ringing, and has introduced the use of common alphanumeric codes for exchanging data.

Experience in Europe highlights the many advantages provided by international coordination of field protocols and data management, as well as in planning large-scale research projects. Out of this experience, considerable interest was expressed at the 1998 IOC in Durban to establish a standing committee of the IOC through which international cooperation on bird ringing could be expanded. A conference celebrating 100 years of bird-ringing at Helgoland in 1999 further reinforced the benefits of such an initiative (Jenni and Camphuysen, 2001).

So the main aim of the present RTD was to bring together scientists concerned with coordinating ringing activities to air common problems and ways of improving the standardization of ringing worldwide, and to consider further the value of establishing an IOC standing committee on bird ringing.

2 Outcomes

This RTD was attended by over 70 delegates from 28 countries representing five continents. The program featured a series of contributions on the current status of bird ringing in different continents and countries. Different potential uses of ringing recoveries in migration atlassing were illustrated, together with some of the opportunities offered by analyses of first-capture data. There was also discussion of recent advances in the statistical tools available to estimate survival and dispersal in bird populations, based on mark-recapture models.

Participants agreed in general on the need to further enhance international exchange of information and its organization. Activities along these lines will be carried out over the next few years, with the aim of reactivating the former IOC standing committee on bird ringing in time for the 2006 IOC in Hamburg, Germany. There was also considerable interest expressed in having a full-day workshop on bird ringing then, organized by this committee. The workshop could consider many aspects of ringing, including new developments in field methods covering marking techniques, data standards and data exchange, advances in statistical analysis and modelling techniques, and international cooperative research projects.

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RTD19 Climate change impacts: key issues and future research

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1 Issues

Climate change is developing rapidly into one of the most important pressures that will affect bird populations and their conservation over the next 50–100 years. Impacts will be both direct (e.g. through changes in average weather patterns, occurrence of extreme events and sea-level rise) and indirect (e.g. through changes in habitats, land-use and employment of sea-defences). The overall aim of this RTD was to identify the important gaps in knowledge that need to be filled to allow the ornithological community to advise policy makers on how to mitigate the impacts of climate change on birds. The key issues discussed were:

(1) What are the key habitats for which climate change will be most important?

(2) What are the key factors that will make it difficult for birds to cope with change?

(3) What aspects of the impact of change need study urgently?

(4) What methodological issues need to be highlighted?

(5) Is there scope and need for international collaboration?

2 Outcomes

2.1 Key habitats

Although all habitats can be considered important, some are more vulnerable to change in the near future than others; these are where research effort should be increased. The key habitats identified were: (1) polar regions, (2) areas strongly affected by the El Niño Southern Oscillation, (3) low-elevation islands and mangrove habitats, and (4) cloud forest and other montane habitats. Habitats supporting locally endemic species were also identified as special.

2.2 Key factors of climate change affecting birds

Diverse intrinsic and extrinsic factors were suggested as inhibitors of adaptation to climate change. Any of those listed below could be important to individual species; all need further investigation:

- small population size
- lack of phenotypic adaptability

- reduced adaptability in the timing of migration by long-distance migrants, but greater plasticity in short-distance migrants, potentially improving their competitive status

- clash between photoperiodic control and shifts in phenology

- differential rates of effect/response between birds (at 1–2 days per °C, on average) and plants and invertebrates (5–8 days per °C)

- genetic constraints on adaptability

- mobile and generalist r-selected species coping better than sedentary, habitat-specific k-selected species in fragmented landscapes

- dispersal ability

- increase in frequency of extreme climatic events

- loss of habitat and decline in habitat quality

- changes in timing and abundance of food

- changes in agriculture, e.g. crop types and pesticides in response to pest changes

- non-analogue climate spaces

- range expansion by other species - increasing competition/predation, including impacts of invasive and alien species

2.3 Key impacts needing urgent examination

A number of such factors were identified by the study group:

- phenotypic and genetic adaptability

- climate sensitive areas for birds

- biodiversity hotspots and Important Bird Areas

- impacts of socio-economic change on habitats

- population monitoring (especially to detect range shrinkage)

- indirect effects, e.g. trophic level interactions, competitors, disease

- value of habitat corridors to aid dispersal

- impacts on species showing no phenological re-

sponse to climate change

2.4 Key methodological issues

A number of methodological qualifications in the study of climate change needed airing:

- unidirectional correlations in climate change, particularly in short-term data-sets, may be spurious, and could reflect other co-correlated factors; alternative hypotheses need consideration

- scientists must not exaggerate the significance of results and should make uncertainties clear; uncertainties in model predictions need to be articulated

- viewing publication bias towards “significant” results, as in any field of study, cautiously

- cautious use of meteorological data to ensure standardization, e.g. the same value of the North Atlantic Oscillation index may correspond to different European temperatures in the first and second halves of the 20th century, as average temperatures have warmed

2.5 International collaboration

The RTD concluded that the need for international collaboration was most important, particularly for migratory species that cross many national borders and use a network of stopover sites for replenishing nutrient reserves (e.g. shorebirds). Global climate change is a global phenomenon, and so a network of regional and continental monitoring stations is essential for assessing impacts on bird populations. Many such networks already exist (e.g. bird ringing observatories), and should now begin to incorporate climate change information as a key goal.

The ornithological community also needed to ensure that its results are fed into the deliberations of the Intergovernmental Panel for Climate Change. This was thought to be a proper role for the International Ornithological Committee and its congresses to facilitate. Thus the RTD proposed that the IOC should set up an active working group on climate change that would act as a conduit of information to the IPCC from world’s scientific ornithological community.

RTD22 Working Group on Bird Damage to Agriculture: a review of progress and practices

convener: Clive C. H. ELLIOTT

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1 Issues

Twenty-six people from 14 countries participated in the RTD 22. The convener recorded that he had taken over chairmanship of the Working Group upon request and with the agreement of IOCommittee Permanent Secretary, Dominique Homberger. He noted that the Group was a subsection of the Standing Committee on Applied Ornithology (SCAO), which itself appeared to be inactive. There appeared to be no established structure for the modus operandi of the Group, whose essential purpose was to bring together scientists concerned with the problems posed by birds to agriculture and how they might be variously solved. In discharging its functions, the Group could arrange symposia, RTDs or other activities for future IOCongresses.

Participants gave a brief summaries of their interest in bird pest problems in agriculture. The range of species recorded was remarkable, several unexpected: eared doves (*Zenaida auriculata*) on sorghum and soybeans in Argentina and Brazil; parrots (Psittacidae spp.) on maize in Argentina; great cormorants (*Phalacrocorax carbo*) on aquaculture in Germany; greater flamingos (*Phoenicopterus ruber*) on rice in southern France; various species of geese (Anserinae spp.) on crops and pastures in China, Germany, Japan, Sweden and the UK; sandhill cranes (*Grus canadensis*) on crop seedlings and potatoes in the USA; vultures (Gypinae spp.) possibly transmitting disease to livestock in South Africa; cockatoos (Cacatuinae spp.) and other parrots on cereals in Australia; wood pigeons (*Columba palumbus*) on cereals and braccid crops; mute swans (*Cygnus olor*) on cereals; peregrine falcons (*Falco peregrinus*) predating on domesticated/racing pigeons (*Columba livia*) in the UK; red-billed quelea (*Quelea quelea*) on small-grain cereals in sub-Saharan Africa; and a range of species on cereals in India.

Several speakers raised the issue of repellents. Others described how they had tried, in some cases successfully, to manipulate agricultural habitat to make it less attractive to birds or to create alternative attractions. In several areas, successful conservation had turned previously rare or uncommon species into agricultural nuisances, e.g. sandhill cranes, flamingos, and even, possibly, the peregrine falcon. It was becoming increasingly important to find solutions to such

problems so that the support of farmers for conservation was not undermined. Bird damage to agriculture was often very patchy, making it difficult to assess of damage levels realistically and hard to achieve cost-effective controls.

Another issue concerned the conversion of bird pests from villain to useful resource. Examples given included trapping quelea for food, even as a luxury export item, exploitation of eared doves by touring hunting parties from Texas, and the early season hunting of geese in Canada. It was noted that such exploitation had to be handled sensitively because of potential conflict of interest among farmers and hunting promoters through unequal distribution of benefits. Such activities also required careful regulation to avoid accidental destruction of non-target birds. Where poisons had been used to kill pest birds, as in Australia for cockatoos and Africa for quelea, the side effects were potentially serious; better alternative solutions were needed.

2 Outcomes

There was sufficient overlap among the activities and lines of research being pursued by participants to suggest that some form of permanent communication, in between IOCongresses, would be useful. The Group agreed that the e-mail network list-server initiated at the 1998 IOCongress and subsequently administered by the Avian Demography Unit, University of Cape Town, South Africa, should be expanded to cover all bird pest problems in agriculture. Pending agreement from existing list-server members, all participants who had provided their email addresses to the 2002 RTD would be automatically enrolled in the network. Each person so enrolled would be asked to provide a brief summary of their background and interest in bird problems in agriculture. In about two years' time, the Chair would circularize participants, asking for suggestions for symposia and/or RTDs to examine specific issues at the next IOCongress in Hamburg in 2006.

Several participants mentioned difficulties in finding suitable journals in which to publish papers or reports on bird pest problems in agriculture. Much information had appeared in "grey" literature which was often difficult to access. It was agreed that such reports could be placed on the list server or that references or addresses for the report could be given there.

RTD23 Integrating the avian annual cycle

conveners: Barbara HELM¹, Marcel E. VISSER²

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1 Issues

In recent years, there have been exciting developments in understanding the interaction of seasonal activities (e.g. Nilsson and Svensson, 1996; Hemborg and Lundberg, 1998; Dawson et al., 2000; Both and Visser, 2001; Webster et al., 2002). So it is timely to integrate research carried out on various stages of the life-cycle. The aim of this round table was to bring together ornithologists working on various stages of the life-cycle to encourage discussion and exchange ideas. The workshop attracted c. 50 researchers from very different backgrounds. To stimulate discussion, six ornithologists commented, from their research background and perspective, on core issues confronting integration of the annual cycle.

Christiaan Both, Heteren, The Netherlands, illustrated the integration of different stages in the life-cycle with his work on the pied flycatcher (*Ficedula hypoleuca*). This long-distance migrant has advanced its laying date over the past 20 years in response to climate change (Both and Visser, 2001). However, further advancement of laying has been hampered because the date of arrival has not changed. Here the timing of reproduction is directly affected by the preceding stage of the life-cycle, migration to breeding grounds.

Francisco Pulido, Radolfzell, Germany, addressed the tight correlation between timing of moult and onset of migration in the blackcap (*Sylvia atricapilla*). The interval between moult and migration was highly heritable, being unaffected by experimental delays in the moult process. This clearly illustrates that the timing of one stage in the life-cycle is tightly linked to the timing of the next. Due to genetic correlation, evolutionary change in one stage is not independent of changes in others (Pulido and Berthold, 2002).

Lukas Jenni, Sempach, Switzerland, summarized the function and costs of moult, stressing the central role of moult in the annual cycle (Jenni and Winkler, 1994). He suggested that although the direct costs of moult may be less dramatic than generally assumed, indirect costs may have extremely high consequences for subsequent stages of the life-cycle. Thus delayed initiation of moult can lead to a more rapid moult, and as a consequence reduced feather

quality (Dawson et al., 2000; Serra, 2001). This, in turn, can affect survival and the timing and success of all subsequent events in the annual cycle.

Thomas Weber, Lund, Sweden, introduced a conceptual approach to modelling annual routines (Houston and McNamara, 1999; Clark and Mangel, 2000). State-dependent models can be based on a state variable that is resilient against short-term fluctuations and takes a relatively long time to be depleted and restored. For example, body condition decreases over the breeding season and cannot be restored within that stage of the life-cycle. Thus it facilitates the interdependence of stages in the life-cycle. Questions relating to which state variables are the most important, and how their dynamics may best be described, are still open.

Michaela Hau, Princeton, USA, emphasized the advantages of using a comparative approach to understanding interactions between stages of the life-cycle. Comparative analyses could elucidate the “scope” of physiological systems controlling the stages, revealing the extent to which annual cycles can be modified. As one example, comparison of seasonal regulation of the reproductive stage between temperate-zone and tropical birds reveals different breeding strategies. She compared cycles in an opportunistic tropical breeder, a Darwin’s finch (*Geospiza fuliginosa*), and a seasonal tropical breeder, the spotted antbird (*Hylophylax naevioides*), to breeding in temperate zone birds. Her results indicate that annual cycles may be regulated more flexibly in tropical birds, which live in seasonally more variable environments than temperate zone birds (Hau, 2001).

Richard Holmes, Hanover, USA, introduced the concept of migratory connectivity (Webster et al., 2002). He emphasized that population dynamics have to be studied year-round over the entire annual cycle (Marra et al., 1998; Sillert et al., 2000) and presented a number of techniques that could be used to link cyclic behavior between breeding grounds and winter quarters. Stable isotopes are one of the most promising tools, as he showed for the black-throated blue warbler (*Dendroica caerulescens*; Rubenstein et al., 2002). Identifying the degree of connectivity as well as the amount of mixing in populations in both breeding and wintering areas is essential for modeling year-round popula-

tion dynamics and for conservation planning. Real information from wintering quarters, rather than the “black-box approach” that is often applied in migrant species, might improve our knowledge about interrelations among life-cycle stages greatly.

2 Outcomes

Lively discussion followed the presentations, raising a number of topics. One emerging theme was the perhaps central role of moult in the annual cycle. Feather quality might serve as a good state variable because its long-lasting effects contribute to the interdependence of life-history stages. The RTD revealed the considerable extent to which different stages in the life-cycle affect one another. One outstanding problem is how to break into the annual cycle experimentally to assess the fitness consequences of its stages. Furthermore, constraints imposed by physiological mechanisms, as well as the genetic bases underpinning the interdependence of life-cycle stages, remain little known. Progress in answering these questions promises to lead to a deeper understanding of the evolution of avian life histories and of the factors and processes affecting population dynamics.

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RTD24 Heron Specialist Group: heron conservation

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1 Issues

1.1 Background

Hérons are a worldwide family, the 62 species of which have undergone remarkable changes in distribution and numbers during the past century, both retractions and expansions. Both processes are of conservation concern. Many heron populations occur in human-dominated landscapes and have come to depend on human action for their continued well-being and conservation.

This was the third meeting of the Heron Specialist Group (HSG). At the previous two IOC's, the Group focused on a world wide review of heron conservation, resulting in the published volume, Heron Conservation (Kushlan and Hafner, 2000). More recently, the Group has participated in surveying highly endangered herons in Asia, a major topic for present meeting.

1.2 Improving coordination in Asia and global conservation planning

The HSG is charged by its three parent bodies (IUCN Species Survival Commission, Wetlands International and BirdLife International) with overseeing and facilitating activities concerned with the conservation of herons worldwide. This requires that it be structured with an efficient communication network to assist effectively in developing conservation and research projects. Since the creation of the HSG in 1982 (Hafner et al., 1986), responsibilities for its operation have been shared between two chairs, Old World (Heinz Hafner) and New World (James Kushlan), who have carried out business by correspondence.

1.3 Species, subspecies and populations of conservation concern in Asia

Asia has some of the most threatened herons in the world, e.g. white-bellied heron *Ardea insignis*, Chinese egret *Egretta eulophotes*, white-eared night heron *Gorsachius magnificus*, and Japanese night heron *Gorsachius goisagi*. For these species and a number of subspecies and populations, data is insufficient to address conservation requirements adequately. Surveys need to be continued for these taxa, and methods developed for determining habitat used and its availability.

1.4 Status update on the white-eared night heron, *Gorsachius magnificus*, in south China

Considered to be the most endangered heron of the world by the HSG, this species has been surveyed intensively from 1998 to 2001 by the HSG and the Kadoorie Farm and Botanic Garden Corporation (KFBG), a conservation charity based in Hong Kong.

1.5 Preparation of a worldwide Action Plan for the Conservation of Herons

Despite many gaps in knowledge, the results of a plethora of studies by such a multinational group as the HSG over the past twenty years on all continents and producing synthetic treatises on heron biology (Kushlan and Hancock, 2003) and conservation (Kushlan and Hafner, 2000) provide the foundation for preparing a worldwide Action Plan for herons.

2 Outcomes

2.1 Attendance of meeting

63 delegates attended the meeting, including 26 from Asian countries/regions (China, Japan, Korea, Malaysia, Taiwan and Hong Kong), many of them potential members of the HSG. Because of them, ensuing discussions were particularly enlightening and valuable.

2.2 Improving coordination in Asia and global conservation planning

H. Hafner continues as Chair of the HSG, with J. Kushlan as Deputy Chair and 7 Vice Chairs be recruited and appointed for West Asia, East Asia, Australia-Oceania, Europe, Africa-Malagasy, South America and North America. Major initiatives taken were: (1) development of a website that includes resources, a newsletter and topical chat rooms, and (2) development of a global population data base accessible via the internet. As in the past, the HSG will continue to meet at International Ornithological Congresses, and regionally where appropriate, and hold symposia on topics of interest and concern to heron biology and conservation.

2.3 Species, subspecies and populations of conservation concern in Asia

An overview presented by H. Hafner generated much interest and discussion. Concrete decisions were made for future surveys and research on the Malayan night heron *Gorsachius melanolophus* in central Taiwan and the white-eared night heron *Gorsachius magnificus* in south China. The research team working on the Malayan night heron in Taiwan, Cheng-Te Yao, Liang-Kong Lin and Shao-Pin, have already put together a fine data set on nesting success in this little known species. In south China, the KFBG and HSG will continue surveys of the white-eared night heron and prepare a species action plan together.

2.4 Status update on the white-eared night heron, *Gorsachius magnificus*, in south China

Lee Kwok Shing from the KFBG presented a comprehensive update of the status of the white-eared night heron, based on the surveys carried out between 1998 and 2000 (Fellowes et al., 2001) and in 2001. This species has the most restricted breeding range of any heron, with just two known breeding sites: one in southern Guangxi and another suspected in neighboring Guangdong Province (Chebaling Nature Reserve). In the 1990s, one nest (Zhou F, 2002) was also found in Shennongjia Nature Reserve and environs, Hubei Province. Prime habitat there, however, has since been converted into a reservoir, and subsequent surveys in 1999–2001 failed to find the species. Outside China, the white-eared night heron has also been reported from North Vietnam, including one recent record. Several remote

areas in south China, where isolated breeding sites may have gone unnoticed in forested mountain habitats, have yet to be surveyed to clarify population size and distribution.

2.5 Preparation of a worldwide Action Plan for the Conservation of Herons

A draft Action Plan prepared by James Kushlan and Heinz Hafner was distributed to all attendees, who were asked to comment as they felt obliged. Its aim: to identify priorities, set goals and detail specific actions needed for conservation of the herons of the world. It will be the first global plan for conservation action for herons to be published by the IUCN.

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Supplementary Plenary Resumés

P04 The life history of the wandering albatross: how does the marine environment influence the demography of seabirds?

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Compared with other birds, seabirds have a lower fecundity, breed at older age and have higher adult survival. The reasons for such characteristics are usually looked for in the marine habitat itself. The low fecundity of seabirds is often attributed to the poor, patchy and unpredictable environment on which they rely. The distances between breeding colony and food resources also places constraints on the amount of energy seabirds are able to invest in reproduction. The development of life history theory, and especially of the concept of reproductive cost and residual reproductive value, bring an additional dimension to these correlates.

To examine the different hypotheses, I use the single best-known life history of perhaps any seabird, instead of comparing species, families or orders of seabirds for which information on life history is always limited and often too general. The life history concerned is that of the wandering albatross, based on a study carried out in the Crozet Islands, Indian Ocean, over the past 40 years. The wandering albatross is one of the largest flying seabirds, with a wing span of more than 3 meters. It is sexually dimorphic, males being 20% larger than females. My main objective will be to relate the foraging constraints imposed by the marine environment to the processes of resource allocation and their consequence for the demography of the species. The foraging ecology of juveniles, immatures and adults, both during breeding and sabbatical years, is reviewed, based on information from various telemetry systems (GPS, Argos

transmitters, geo-location systems) for locating birds and on activity recorders, stomach temperature sensors and heart rate recorders, *inter alia*, for recording behavioral and physiological parameters.

These studies have allowed us to understand how the albatrosses forage in relation to environmental conditions and to the distribution of resources, and how they acquire energy for breeding in relation to the energetic costs of foraging over very long distances. Combined with foraging studies, land-based studies have been carried out as well to relate foraging and allocation processes through the study of mass regulation during incubation and offspring provisioning strategies, and to understand how birds deal with the constraint of distant foraging. The consequences of allocation processes for the demography of the species are reviewed, paying particular attention to the influence of parental provisioning on the survival and future reproduction of offspring, to the acquisition of sexual maturity, and to biased sex ratios and senescence. The influence of environmental variability and density dependence on demographic parameters such as survival, breeding success and dispersal will also be reviewed.

Like many species of Procellariiformes, albatrosses are declining in most regions today, not only because of fisheries, but also due to disease and possibly global changes in their environment. I will examine how these long-lived seabirds can survive in a changing and variable world.

P10 Bird conservation in South America

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Conservation priorities for birds in South America require an extraordinarily large diversity of actions, commensurate with the continent's biological richness and heterogeneity. Large portions of the region are unsurveyed, particularly in Amazonia, the Cerrado and the eastern Andes. New taxa are regularly described throughout the continent, even in well-studied areas such as the Atlantic Forest. The largest tracts of intact tropical forest ecosystems are here, as well as globally important savannas, wetlands and montane environments. So the combination of a large endemic fauna with species richness as high or higher than anywhere else poses unique conservation challenges.

Yet of the world's twenty five biodiversity "hotspots" — areas of exceptional concentration of endemic species — five found in South America are experiencing dramatic habitat loss. While the region offers opportunities for conserving intact species assemblages on a very large scale in Amazonia, it also needs emergency habitat conservation and restoration to prevent catastrophic species losses in biomes such as the Atlantic Forest and the tropical Andes.

Comparatively low human population densities, and the absence of widespread chemical and industrial

pollution, allow for landscape-level conservation measures, such as the connecting of protected areas with substantial corridors, restoration of natural forests, and the designing of buffer zones for protected areas. Relatively few avian species are pests or disease-bearers; and people generally are predisposed towards bird protection. Although hunting for food and trading in wildlife are widespread, education and enforcement can curtail these practices substantially.

For many species, the major threat is not impending extinction but substantial population loss and range contraction as vast portions of South America are converted to agriculture, pasture-lands and plantation forestry. Recent advances in infrastructure development, planning and capital investment have unlocked access to much of Amazonia and are pushing into the eastern Andes and lowland Bolivia. Unfortunately, conservation plans for these regions are still moving at a slower pace than the agricultural frontier. Conservation of essentially all of the South American avifauna is an attainable goal today, and we must gather allies and support to do this while we can.

Symposia

Symposium 01 Perspectives in avian acoustic communication: in memory of Luis Baptista

Introduction

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Luis Baptista, an outstanding ornithologist, was well known for the eclectic range of his knowledge; his interests embraced areas such as phenotypic variation in pigeons, conservation issues in many species, music broadly defined to encompass that in nature as well as the symphony hall, and all aspects of vocal behavior, including that of humans. This symposium in his honor, which focuses on the field of vocal learning, was organized to reflect just a few of his many interests and enthusiasms.

The papers presented cover a substantial range of topics, examining numerous aspects of sound production. The first paper (Bostwick) reviews nonvocal communication signals produced by feathers and examines how male manakins create such sounds for the primary purpose of mate attraction. The second paper (Severinghaus, Tu and Hau) addresses interactive effects among sympatry, hybridization, and song modification in closely related species of bulbuls. The next paper (Okanoya) hypothesizes that female choice is a factor in the evolution of song complexity in the Bengalese finch (Fig. 1), and discusses the evolution of such complexity with respect to associated changes in the brain. The fourth paper (Todt and Hultsch) also discusses song complexity, but from the standpoint of the social variables that influence the learning and organization of large repertoires in the nightingale. The final paper (Jarvis) examines the evolution of vocal learning in three

orders of birds, using behavioral molecular mapping to identify specific brain structures involved in such learning, and then presents hypotheses for the origin of vocal avian learning. Although the papers touch on only a part of Luis Baptista's areas of expertise and interest, they stand as a testament to his enthusiasm for examining all aspects of avian behavior. Fig. 1, contributed by the third paper in this symposium, has been reproduced here as a testament to Luis' love of aviculture, especially of finches.

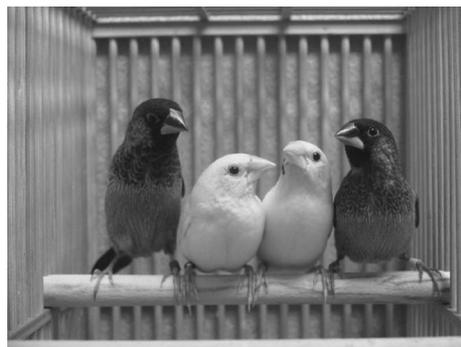


Fig. 1 White-rumped munias (both ends) and Bengalese finches

Photograph by Miki Takahashi.

S01-1 Mechanisms of feather sonation in Aves: unanticipated levels of diversity

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Abstract Sonations, intentionally modulated acoustic signals produced by nonvocal structures, are poorly studied in birds and little is known about the diversity of mechanisms used. Here I review feather-produced sonations and proposed sound-production mechanisms, with particular emphasis on sounds produced by wings. I then summarize the results of my own research on mechanisms of sonation in the Neotropical manakins (Pipridae). This research demonstrates for the first time how various *snap* sonations are produced, and shows that many mechanisms can be used to generate acoustically similar sounds.

Key words Acoustic communication, Mechanical sounds, Pipridae, Sonations, Wing sounds, High-speed video

1 Introduction

Although birds are renowned for their voices, many species also communicate acoustically by nonvocal means. Such signals have been termed instrumental music (Darwin, 1871), mechanical sounds (Prum, 1998), and *sonations* (Bostwick and Prum, 2003). The latter term was proposed to emphasize the distinction between nonvocal and vocal signals, and to create a companion verb, to *sonate*, to refer to the act of producing nonvocal acoustic signals. Avian sonations are thus intentionally modulated, communicative sounds produced by non-syringeal structures such as bills, feet, and feathers.

Feather sonations can be difficult to observe under field conditions as they are often produced by extremely rapid movement of small structures during complicated courtship displays, and often at some distance from the observer. Indeed, many of the best-known sonations have been subject to lengthy debate about their nonvocal nature (Bent, 1927; Baptista and Matsui, 1979; Sutton, 1981; Pytte and Ficken, 1994). Consequently, most hypotheses of the mechanics of sound production by feathers are speculative, and the range of physical and kinematic mechanisms used to produce such sounds is largely unknown.

I here provide a brief overview of the diversity of feather-produced sonations, summarize the means by which birds are thought to produce wing-sonations, and then summarize the results of recent research which demonstrates that the mechanisms of sonation are far more diverse than previously thought.

2 Sonating feathers

Birds use nearly every conceivable part of the body

to sonate, from bills and feet to feathers and combinations thereof. Mechanisms of bill and foot sonations are relatively easy to infer and commonly involve percussive contact between body parts and/or substrate. Feather sonations are more diverse and widespread, yet most are poorly understood mechanistically. I discuss feather sonations and mechanistic hypotheses by feather types below.

2.1 Conture feathers

High-speed videos of courting in sage grouse (*Centrocercus urophasianus*) have shown that displaying birds rub the manus or wrist feathers against specially stiffened breast feathers to create a *whoosh*-like sound (Dantzker, pers comm.). In this case, the mechanism of sound production is clearly feather-to-feather friction.

2.2 Tail feathers

Two types of tail-generated sounds are produced in different behavioral contexts: *whistles* produced in flight and *rustles* produced while perched. Whistles emanating from birds diving aerially have often been attributed to specialized tail feathers which are thought to vibrate regularly when air flows over them at high speeds (Carr-Lewty, 1943; Thonen, 1969; Reddig, 1981; Sutton, 1981). This interpretation has been supported by artificial manipulation of feathers. Even so, it needs to be treated with caution for, although manipulation of isolated tail feathers of Anna's hummingbird (*Colypte anna*) produced sounds similar to the flight sound given at the bottom of its dynamic display (Rogers, 1940), Baptista and Matsui (1979) demonstrated that a vocalization given by the bird when perched was spectrographically identical and argued that such sounds produced in the dynamic display could be syringeal in origin. Several species of snipe (*Gallinago*, and *Coenocorypha*),

nevertheless, do produce whistling sonations with specialized tail feathers (Sutton, 1981; Miskelly, 1990), as do hummingbirds (Wells and Baptista, 1979), honeyguides (Mackworth-Praed and Grant, 1957) and manakins (Prum et al., 1996).

Tail rustles, in contrast, have been described primarily from the ground-based courtship displays of male grouse (Johnsgard, 1983). The physical mechanisms of sound production behind tail rustles and rattles in such circumstances are unknown, but probably involve friction and/or percussion.

2.3 Wing feathers

In birds, the wing is by far the most frequently used vehicle for sonation. Passeriformes (Payne, 1973; Craig, 1984; Manson-Barr and Pye, 1985; Zimmerman et al., 1996; Prum, 1998), Piciformes (Raffaele et al., 1998), Caprimulgiformes (Miller, 1925), Apodiformes (Miller and Inouye, 1983; Calder and Calder, 1992), Charadriiformes (Pettingill, 1936), and Galliformes (Johnsgard, 1983) all contain members known to produce prominent and intentionally modulated wing-sounds. Scores of other birds produce wing-sounds of lesser strength and prominence, and less clear modulation. Morphological modifications such as attenuated primary feathers are associated with sonations produced in flight, and are described frequently in the literature. As in tail sonations, *whistles* produced during flight are common; and *rustles*, produced both in flight and when perched, are known too. There is, as well, an additional category of sounds that is acoustically and, presumably, mechanistically different. These are often called *claps* or *snaps*.

3 Categories of wing sounds

There are three basic wing-produced sonations, classified by the quality or acoustic structure of the sound produced. Acoustic structure has as yet undetermined connections with sonation mechanisms. For the sake of simplicity, I refer here to these three general classes of wing sonations as *whistles*, *rustles* and *snaps*.

3.1 Whistles

Whistles, comprising a variety of pulsed and tonal sounds produced in flight, are often described as chirps, whirrs, whistles, winnows, and roars. Analogous to tail whistles, such sounds are universally attributed to vibrations caused when air is forced through flight feathers (Miller, 1925; Pettingill, 1936; Tuck, 1972; Craig, 1984; Miskelly, 1990). It is further hypothesized that the pulsing nature of some of these sounds corresponds to wing-beat cycles. Miller and Inouye (1983) glued together modified primaries implicated in the flight whistle of the broad-tailed hummingbird (*Selasphorus platycercus*) and succeeded in silencing the sound, which was subsequently restored when the glue was removed. Several researchers have found that modified feathers can be induced to vibrate experimentally at frequencies overlapping those of sounds given in nature

(Carr-Lewty, 1943; Reddig, 1978). Thus, air-induced vibration of feathers seems the most conceivable means of sound production in the wing, with the caveat that syringeal sources must be eliminated before such a cause is accepted in each case.

3.2 Rustles

I suspect that rustles will ultimately be shown to be caused by feather-to-feather friction during flight. For example, Stephanie's bird of paradise (*Astrapia stephaniae*) produces a loud rustling *buzz* during flight (Frith and Beehler, 1998), which can be produced by just one flap of the wing (E. Scholes, pers. comm.). In this species, unusually pointed, curved, and thickened barbs are developed along the leading edges of otherwise normal primary feathers (Bostwick and Scholes, pers. obs.).

3.3 Snaps

Such sounds comprise brief, usually loud or sharp, broad-frequency (toneless) notes, often referred to as *clicks*, *snaps*, *pops*, or *claps*. When describing such sonations, authors rarely speculate on how they are produced beyond implicating the wings (Payne, 1973; Bomford, 1986; Sankaran, 1996). Bertram (1977) nevertheless suggested that the flight "claps" of *Mirafra* larks are made either by striking adjacent wing feathers together or by an abrupt interruption of the airflow between wing flaps; but evidence that would shed further light has not been forthcoming.

4 Mechanisms of *SNAP* sonations in Pipridae

4.1 Results of prior studies

Sonations reach the zenith of their use in the Neotropical manakins, family Pipridae. Males of over half of the species of manakins incorporate such sounds into their elaborate courtship displays; and many have repertoires that include more than one behaviorally and acoustically distinct sonation. Phylogenetic relationships in the Pipridae indicate that many of the sonations have arisen independently of one another (Prum, 1998; Bostwick, 2000). The genus *Manacus* is perhaps best known for its gratingly loud sonations. At least six behaviorally or acoustically distinct sounds have been described from its members (Chapman, 1935; Skutch, 1969; Snow, 1962a). Two of the most striking, the *snap* and *roll-snap*, are also the most frequently used, and fall into the category of wing-snap sonations.

Many authors have proposed mechanisms for sonations in *Manacus*; and most agree that modified secondary feathers are involved in producing the *snap* and *roll-snap* (Chapman, 1935; Sick, 1959; Snow, 1962a; Skutch, 1969; Prum, 1998). Chapman (1935) and Stolzmann (1884) attributed *snaps* and *roll-snaps* to the striking together of adjacent secondary rachii within a wing, such that opposite wings do not contact one another. Snow (1962b) suspected that the wings are rapidly "vibrated," so that the secondar-

ies brush “against one another rapidly as the wing is opened and closed.” Skutch (1969) described the wings as being lifted above the bird’s back and “beat(en)”. Prum (1998) thought that the wing feathers were clapped against the body. Both Prum (1998) and Skutch (1969) concluded that *roll-snaps* arose from repetition of the motions used to produce single *snaps*.

Like the species of *Manacus*, *Pipra mentalis* (red-capped manakin) also sonates. Skutch (1949, 1969) described two sonations in this species: *snaps* made while perched, and *rustles/whirrs* produced in flight. He found that *snaps* were used in three different behavioral contexts, and that the rate of snap production varied according to the context. Thus there was a single, simple snap given before flight, a rapid *whirring snap* made periodically after alighting on a perch, and more slowly-delivered snaps produced by the male “while resting”. All of these behaviorally distinct snaps have since been considered variations of a single basic sonation, called the “*klok*”, in this and other species of *Pipra* (Snow, 1963, 1977; Schwartz and Snow, 1978; Robbins, 1983; Tello, 2001).

In descriptions similar to those of Chapman (1935) for *Manacus*, Skutch (1969) attributed the snaps of *Pipra* to “rapid movements of the wings causing the thick shafts of the plumes to strike noisily together.” Prum (1998) also suggested that *Pipra* uses the same mechanism as *Manacus* to snap, clapping wings feathers against the body. Prum’s (1998) acoustic analysis revealed the occasional presence of two sound pulses in extremely rapid sequence as well; these he attributed to the staggered percussion of right and left wings against the body.

4.2 Results of new research

Recent advances in high-speed video technology now make it possible to record birds sonating in field conditions. I used a high-speed video camera at recording rates of 500 and 1 000 frames/second to document sonation in *Manacus manacus* (white-bearded manakin), *M. candei* (white-collared manakin), *M. aurantiacus* (orange-collared manakin), and *Pipra mentalis* (red-capped manakin) at either San Diego Zoo and Wild Animal Park or La Selva Reserve and Carara National Park in Costa Rica. The recordings show that eleven distinct sonations are produced among the species of *Manacus* and *Pipra mentalis*. Five of these, the *snap* and *roll-snap* of *Manacus*, and the three behaviorally distinct snaps of *Pipra mentalis*, now named the *click*, *rub-snap* and *clap*, fall into the *snap* category of wing sonations (Bostwick and Prum, 2003).

The results of this research provide the first mechanistic data to explain how manakins wing-snap, and show that *Manacus* and *Pipra* use diverse kinematic methods to produce such sonations. Members of *Manacus* produce the *snap* and *roll-snap* by clapping the dorsal surfaces of the wings together in the region of the bird’s wrists. Single *snaps* are produced while the bird is flying between saplings on its display court, and the *roll-snaps* are produced

by cyclic repetitions of the snap-clapping motion while the bird is perched (Bostwick and Prum, 2003). Surprisingly, *Pipra mentalis* does not employ this wing-clapping method to sonate, but instead uses three distinct mechanisms to produce each of its behaviorally distinct snaps. The *clicks* are produced when the wings are flicked out laterally from the bird’s sides; the triple-pulsed *rub-snap* is produced when the bird rubs its primaries down the sides of its tail in three cycles of motion; and the double-pulsed *claps* are produced when the bird first flicks its wings up, producing one pulse, and then claps them down against its thighs, producing the second pulse (Bostwick and Prum, 2003). Thus, not one but nearly every mechanism that previous authors had put forward to account for the wing-snap displays in manakins is in fact used by *Manacus* and *Pipra* in diverse yet stereotyped ways.

5 Conclusions

Luis Baptista expressed a fascination with vocal and nonvocal communication alike. Until recently, however, sonation itself was too diffuse and cryptic a phenomenon in birds to generate much attention. Increased awareness of the phenomenon and new field video technology now allow us to clarify and synthesize the little we know about such sounds and their underlying mechanisms and purpose. This brief summary hints at considerable diversity in feather-generated sonations in birds. They are found in disparate families and orders, and have evidently evolved independently numerous times. Surprisingly, mechanistic diversity has been hiding in even the simplest sounds produced, such as the wing-snaps in manakins. Such diversity highlights the importance of such nonvocal modes of communication in birds, and begs detailed comparative research aimed at exploring the similarities and differences between vocal and nonvocal communication, and their functions.

Acknowledgements Everyone, including myself, who works on acoustic communication in birds will find themselves indebted to Luis Baptista in one way or another for generations to come; I am grateful to have known such a modest, inspiring, and curiosity-driven man. Thanks are due also to Rick Prum who initiated research on sonation in manakins and recognized its evolutionary relevance. Thanks also go to Marc Dantzker, Ed Scholes, Peter Stettenheim, and Kristof Zyskowski, all of whom have brought my attention to new species of sonating birds. Finally, I thank Irene Pepperberg and Sandra Gaunt for organizing this fascinating symposium and inviting me to participate in it.

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S01-2 Breaking down reproductive isolation between closely related species

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Abstract One of the functions of bird song is its use in species identification, which contributes to the maintenance of reproductive isolation between closely related species (Welty, 1975). For species that can modify their vocalizations, the isolating function of song difference sometimes breaks down. Formerly allopatric Chinese bulbuls (*Pycnonotus sinensis*) and Styan's bulbuls (*P. taivanus*) live under similar ecological conditions on Taiwan and have songs that resemble one another. In the 1950s they came into secondary contact and the two species hybridized. This study analyzes the vocalizations of these taxa recorded from both allopatric and sympatric populations, and demonstrates vocal modification in sympatric populations.

Key words Reproductive isolation, Hybrid zone, Vocal types, Bulbuls, *Pycnonotus sinensis*, *Pycnonotus taivanus*

1 Introduction

Bird songs are signals commonly used in intra- and inter-sexual communication. Because songs can be heard at a distance, they are effective and efficient cues for species identification. Many studies have demonstrated that birds rely on vocal signals in territorial defense and in mate selection. For example, *Streptopelia* doves react more strongly to playback of congeneric than heterogeneric doves, and more to allopatric than sympatric members of species pairs (de Kort and ten Cate, 2001). Even among subspecies, song barriers have been found, as in the chiffchaff (*Phylloscopus collybita*) (Salomon, 1989). Differences in vocalization between species are powerful isolating mechanisms (Martens, 1996), and many studies have focused on the role of bird song in promoting speciation (citations in Slabbekoorn and Smith, 2002). In contrast, this paper discusses the role of bird song in facilitating the breakdown of species isolation.

If differences in vocalization between species function as isolating mechanisms, such differences should be especially effective between closely related sympatric species where potential for hybridization is greater. Songs are often found to be more similar in distantly than closely related species; closely related species with similar songs, moreover, may differ in how they use them (Smith, 1996; Jones, 1997). Thus differences in songs evidently contribute significantly to premating separation of closely related species.

Many bird species learn their songs (Marler and Peters, 1977; Kroodsma, 1982; Slater, 1983, 1986; Jarvis et al., 2000). Although many species preferentially learn the songs of their own species (Marler and Peters, 1977; Baker, 1983; Clayton, 1988; Beecher, 1996), or of their own popula-

tion or their male parents (Clayton, 1988; Baptista and Schuchmann, 1990; Grant and Grant, 1997), mistakes happen and songs of another species are sometimes learned (Baptista, 1972; Baptista and Morton, 1981). This may facilitate hybridization.

Nearly 10% of bird species hybridize in nature (Grant and Grant, 1992). The vocalizations of some hybridizing pairs have been studied, including the turtle doves *Streptopelia vinacea* and *S. capicola* (de Kort et al., 2002), buntings *Passerina amoena* and *P. cyanea* (Payne, 1996; Baker and Boylan, 1999), flycatchers *Ficedula hypoleuca* and *F. albicollis* (Gelter, 1987), and Darwin's finches *Geospiza fortis*, *G. fuliginosa* and *G. scandens* (Grant and Grant, 1992). The songs of some well differentiated but hybridizing subspecies have also been documented, as in the common chiffchaff, *Phylloscopus collybita* (Salomon, 1989; Martens, 1996) and great tit, *Parus major* (Martens, 1996). In such cases, failure to discriminate between conspecific and heterospecific signals has led to hybridization (e.g. Baker and Boylan, 1999; de Kort et al., 2002).

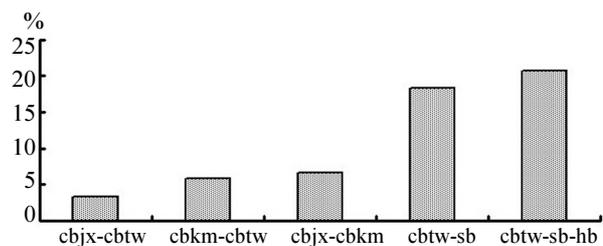


Fig. 1 Proportion (%) of syllable types shared

The closer the populations, the greater the syllable sharing. key to acronyms: cb = Chinese bulbul; sb = Styan's bulbul; hb = hybrid Chinese × Styan's bulbuls; tw = Taiwan; jx = Jiangxi, China; km = Kinmen Island.

In this paper we examine the songs of allopatric, parapatric and sympatric populations of Chinese (*Pycnonotus sinensis*) and Styan's (*P. taivanus*) bulbuls that hybridize in a zone of sympatry on Taiwan. We do so to test the hypotheses that (1) when two closely related taxa come into secondary contact, learnt songs will increase the chance that songs will contain characteristics of both parental forms; and that (2) this will, in turn, weaken the isolating function of species-specific song, so creating the initial circumstances for facilitating hybridization.

2 Methods

2.1 The taxa

Styan's bulbul is endemic to lower altitudes in eastern and southern Taiwan (Cheng, 2002). The Chinese bulbul is found in southeastern China, Hainan, northern Indochina, and on northern and western Taiwan at low to mid altitudes. Mountains in central Taiwan confine both species to the periphery of the island. There both species are common in city parks, farms, orchards, and most types of secondary vegetation. Over the last 50 years, the range of Chinese bulbul has been expanding on Taiwan into the range of Styan's bulbul, and the two taxa hybridize where they overlap.

2.2 Sound recording

A Nagra IS tape recorder coupled with a Sennheiser MKH 816 shotgun microphone were used to record the songs of Chinese and Styan's bulbuls in northern, central, southern and eastern Taiwan where the bulbuls are parapatric and sympatric. We also recorded the songs of Chinese bulbuls on Kinmen Island (24°27'N, 118°24'E) and in Jiangxi, China (28°41'N, 115°53'E) where they are allopatric with respect to Styan's bulbuls. In areas where the two bulbuls are sympatric on Taiwan, we sound recorded the songs of hybrids as well. Each song exemplar was obtained from a different individual.

2.3 Sound analyses

We produced sound spectrograms with Canary Version 1.2 software. Spectrograms of almost all bulbul songs reveal syllables that have two parts, allowing the syllables

to be described by five traits: the duration of each part (2 traits), the initial frequency, the frequency of the transition point, and the terminating frequency. Frequency values were taken at the point where energy was highest, as determined by the power spectrum. We grouped all syllables into syllable types by first performing a Principle Component Analysis, and then using the values of the five trait axes in a cluster analysis to group and separate the syllable types. The following analysis of song variation is based on these types.

3 Results

We analyzed 1 731 syllables extracted from 244 bulbul songs and grouped these into 167 syllable types (Table 1). Most syllable types were rare and often unique to one population or taxon. The proportion of unique types in the three populations of Chinese bulbuls and Styan's bulbul did not differ statistically (chi-square, $P > 0.05$). Twenty-eight syllable types were recorded in more than one population or taxon (Table 1). Sharing occurred generally between neighboring regions; and the proportion of syllable types shared between two populations increased with the proximity of the populations (Fig. 1). Parapatric and sympatric Chinese and Styan's bulbuls shared significantly more syllable types than allopatric populations of Chinese bulbuls (chi-square, $P < 0.013$).

The majority of shared and unique syllables were rare. Chinese bulbuls had 42 unique phrases, Styan's 22, and hybrids 46. Only five shared types were very common, and these formed more than 80% of the songs of both taxa on Taiwan (types A–E; Table 2). Four of them were also found on Kinmen, and two on Jiangxi, but all were relatively rare there. On Taiwan, the frequency of the five common types differed significantly between the two taxa (chi-square, $P < 0.0001$). Thus type C was more common in Chinese bulbuls and type E in Styan's (Fig. 2); hybrid (sympatric) populations had syllable frequencies similar to Styan's.

The five common syllable types also occurred at significantly different frequencies in the four regions of Taiwan (chi-square, $P < 0.001$). Type A and B syllables were relatively rare everywhere, while type C was very common in northern and central Taiwan, and type E very common in

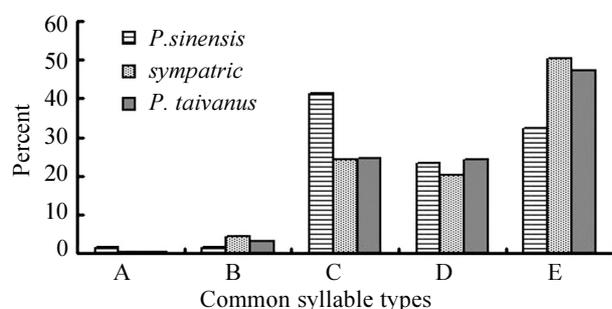


Fig. 2 Distribution of syllable types among the songs of two taxa of bulbuls and their hybrids
Sympatric populations include hybrids and parental types.

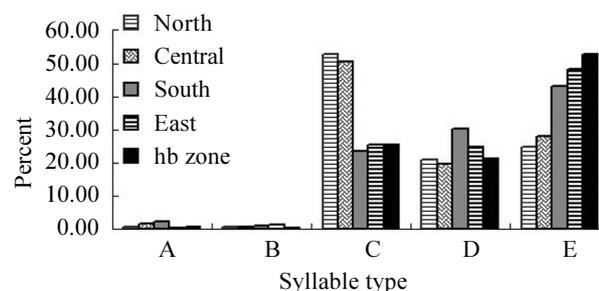


Fig. 3 Distribution of the five commonly shared syllable types (A–E) in different sectors of Taiwan
Syllable distribution in hybrid bulbuls shows a high degree of similarity to that in eastern Taiwan, which was sung only by Styan's bulbuls.

Table 1 Syllable types and sample sizes for different populations

Population*	Song no	Note no	Total syllable types	Unique types	Shared types	%
cbkm	18	92	31	23	8	25.81
cbjx	12	53	34	29	5	14.71
cbtw	82	604	60	41	19	31.67
sb	53	382	37	19	18	48.65
hb	79	600	46	27	19	41.30
sum	244	1731	169	139	28	16.57

*cbkm=Chinese bulbul from Kinmen Island, cbjx=Chinese bulbul from Jiangxi, cbtw=Chinese bulbul from Taiwan, sb=Styan's bulbul, hb=hybrids.

the south and east. Bulbul songs in Taiwan can be divided into two regional groups according to syllable frequency: the northern and central group, and the south and east group. Because only Styan's bulbul occurs on eastern Taiwan, Chinese bulbul syllables in the south are thus more similar to those of Styan's than to conspecifics elsewhere. The distribution of syllable types in hybrids was similar to that of Styan's bulbul (Fig. 3).

Some syllables often occurred in sequence to form phrases, either repeated or in combination with others. For two-syllable phrases, those containing type C syllables occurred more often in Chinese bulbul songs (52.57%). Type E syllables were most common in Styan's bulbul and hybrid phrases (47.67% and 54.79% respectively). All three populations used phrases containing type D syllables around 30% of the time. Syntax in two-syllable phrases was very similar between hybrids and Chinese bulbuls (Mantel test, CB:HB, $g=7.304$, $P<0.0001$), and between Chinese and Styan's bulbuls (Mantel test, CB:SB, $g=2.283$, $P=0.0025$); but syntax similarity between hybrid and Styan's bulbuls was not significant. For allopatric populations, the great differences in syllable types and their frequency made comparisons of syntax impossible. For three-syllable phrases, Chinese and Styan's bulbuls and their hybrids had 18 phrases in common. Chinese bulbuls and hybrids shared another 21 phrases, whereas Chinese and Styan's bulbuls shared only three more, and Styan's bulbul and hybrids only two more.

These comparisons reveal that the hybrids produce common syllables in much the same frequencies as Styan's bulbuls, but in a syntax much more like that in Chinese bulbuls.

4 Discussion

This study found that the songs of Chinese and Styan's bulbuls differ markedly between allopatric populations, but share many characteristics in parapatric populations and merge in sympatric populations. If convergence of syllable and song structure is accepted as evidence for song learning (Kroodsmma, 1982; Gaunt et al., 1994), then Styan's and Chinese bulbuls on Taiwan demonstrate mutual learning and song modification. Evidence for learning comes from an avicultural report of a caged Chinese bulbul, reared among hwameis (*Garrulax canorus*), singing hwamei-type songs, as well as our captive-bred hybrid bulbuls singing unusual songs due, apparently, to their keeper talking habitually to them during their rearing.

Between related sympatric species, signals and their recognition are assumed to diverge and enhance species isolation (Miller, 1982; Saetre et al., 1997; de Kort and ten Cate, 2001). For allopatric species, however, there is no selective pressure to maintain that isolation through interspecific signal divergence. The two taxa of bulbuls were allopatric on Taiwan before secondary contact occurred. No signal isolating mechanism had evolved due either to allopatry or recency of speciation or both. Birds may learn songs from neighbors because of the need to match in countersong (McGregor and Krebs, 1984). The function of countersinging is primarily territorial. Because the two species of bulbuls are ecological equivalents, interspecific territoriality and countersinging became necessities with their sympatry. The fact that bulbuls learn their songs facilitates their acquiring the community language; and this has accelerated the merging of songs in the hybrid zone. Since vocalized differentiation between closely related species is the "first line of defense" in maintaining species boundaries in zones of secondary contact, species that modify their songs through learning should be more prone to

Table 2 Distribution of syllables among types

Population	Unique types	Major type	Other shared types	% in major type
Kinmen	52	35	5	38.04
Jiangxi	42	3	8	5.66
Taiwan CB	45	512	47	84.77
SB	23	311	48	81.41
hybrid zone	41	536	23	89.33

hybridization. This is reflected in the interaction between Chinese and Styan's bulbuls on Taiwan.

Hybridization is known between the thrush nightingale (*Erithacus megarhynchos*) and nightingale (*E. luscinia*) in a narrow zone from Denmark to the Balkans (Hagemeijer and Blair, 1997). Becker (1995) suspected that hybridization was triggered by the high percentage of non-breeding males in the overlap zone. Because members of these two species are mixed singers that regularly add the songs of the other species to its own, we propose that hybridization is initially facilitated by the breaking down of their vocal isolation.

The songs of Taiwan hybrid bulbuls are similar to those of Styan's bulbul in frequency but the Chinese bulbul in syntax. The population sizes of the two parental taxa are comparable in the area where songs were recorded. However, mixed pairs tend to comprise Chinese bulbul males and Styan's bulbul females rather than the converse. How this affects vocal asymmetry in the offspring has yet to be determined.

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S01-3 Neuro-ecology of song complexity in Bengalese finches

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Abstract The Bengalese finch, *Lonchura striata* var. *domestica*, a strain derived from the wild white-rumped munia, *Lonchura striata*, has been under domestication in Japan for 240 years. We compared song syntax of these two strains and found that the domesticated strain developed highly complex, conspicuous songs, whereas the wild strain sang very stereotyped songs. To identify a possible neural substrate responsible for this difference in song behavior, we performed a lesion study. In Bengalese finches, lesions of the NIf, a higher order song control nucleus, resulted in simplification of complex song syntax. We then compared the levels of serum estradiol in female birds that were stimulated with complex or simple song. Estradiol levels were significantly higher in the females stimulated by complex songs. Based on these data, we hypothesize that a mutation in the song control nucleus occurred in the domestic strain that enabled the development of complex song syntax, and that this mutation became fixed in the domestic population through sexual selection.

Key words Estrildid finches, Domestication, Song complexity, Neuro-ecology

1 Introduction

Tinbergen's four questions (1963), the pillars of classical ethology, have been divided into two major areas of ethological inquiry, namely neuroethology and behavioral ecology (Wilson, 1975). Adherence to this approach has led to the neglect of the relationship between ecological adaptation and associated changes in central nervous system. The comparative study of birdsong presents an opportunity to integrate ethological science in such a way as to simultaneously address proximate and ultimate causes of behavior (Baptista and Gaunt, 1994).

Luis Baptista was interested in our behavioral studies of the domesticated Bengalese finch (Okanoya, 1997; Okanoya and Yamaguchi, 1997), partly because they addressed the importance of auditory feedback in adulthood (Brainard and Doupe, 2000), and partly because of his enthusiasm for aviculture (e.g. Baptista, 1995). He encouraged us to compare Bengalese finches, which are all white, and white-rumped munias, which are pigmented, because the latter are considered to be the source stock of Bengalese finches (Buchan, 1976). Molecular techniques have established that these finches, indeed, are the same species (Yodogawa et al., unpublished).

We began by making field observations of wild white-rumped munias (Okanoya et al., 1995) and found that their distance calls were the same as those of Bengalese finches. We then imported white-rumped munias and compared their songs with those of Bengalese finches (Honda and Okanoya, 1999). This comparison suggested a process of behavioral evolution, the study of which would be tractable from a

neuro-ethological perspective and provide us with a unique opportunity for truly fruitful "neuro-ecology" (Bolhuis and Macphail, 2001).

To that end we performed three studies in our laboratory. First, we compared syntactical complexity in domesticated and wild strains of white-rumped munias (Honda and Okanoya, 1999). Next, we undertook a lesion study, to find that a higher-order song control nucleus is responsible for song complexity in Bengalese finches (Hosino and Okanoya, 2000). Finally, we assessed the levels of estradiol in females exposed to simple and complex finch songs, finding that song complexity is an important parameter for females when selecting potential mates (Takashima et al., unpublished). These three studies are reviewed here.

2 Comparisons of song parameters

2.1 Rationale

When white-rumped munias were imported into Japan, aviculturists selected birds for parental ability and white mutations. There are no records in the avicultural literature indicating that the resulting Bengalese finches were selected for song. To begin asking evolutionary questions on the complexity of songs, we first compared song morphology in white-rumped munias and Bengalese finches (Honda and Okanoya, 1999).

2.2 Methods

Eight Bengalese finch songs and five white-rumped munia songs were randomly sampled from a library of recordings in our laboratory, and spectrograms made. Fig. 1

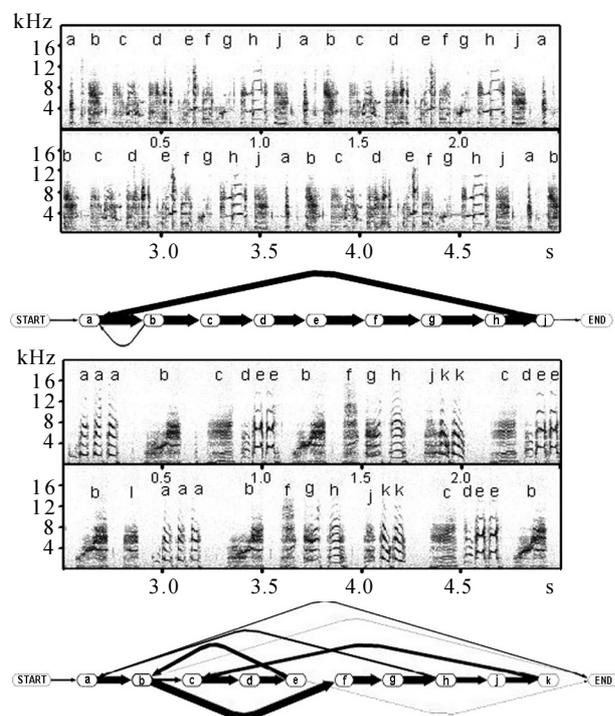


Fig. 1 Sonograms and song note transition diagrams of a white-rumped munia song (upper) and a Bengalese finch song (lower)

Re-plotted from Honda and Okanoya (1999).

shows phrase transition diagrams from each finch strain.

2.3 Results

The average number of song notes used by white-rumped munias (average 8.40, range 7–10) and Bengalese finches (average = 9.25, range = 6–15) was similar ($P=0.64$). However, the average song linearity, an index of song simplicity (Scharff and Nottebohm, 1991), was significantly lower ($P<0.001$) in Bengalese finches (average 0.33, range 0.24–0.43) than in white-rumped munias (average 0.61, range 0.41–0.69). In other words, Bengalese finches sang songs with more note-to-note transitions.

Song complexity in Bengalese finches must have evolved in the past 240 years of domestication, which seems a short time, but translates to 500–1 000 generations and corresponds roughly to 20 000 human years. Though it might be attributed to cultural drift, genetic constraints could also be involved (Okanoya, 2002).

3 Mechanism of song complexity

3.1 Rationale

What mechanisms make the more complex song of Bengalese finches possible? Central and peripheral mechanisms for birdsong production have been well studied (Margoliash, 1997; Suthers, 1997). To describe the brain areas used in them, we use acronyms as proper names because the acronyms were originally based on many neuroanatomical terms that have since proved incorrect or inappropriate. Song is produced physically by the com-

bined activity of respiratory, syringeal, and resonating apparatus (trachea, tongue, and beak). Control of song production is governed by a set of discrete brain nuclei.

Syringeal activity is controlled by what is sometimes called the posterior pathway (Margoliash, 1997). The syringeal muscles are directly controlled by the tracheo-syringeal branch of the hypoglossal nerve NXIIIts. This nucleus is innervated both by the telencephalic motor nucleus, the RA, and by the mesencephalic motor nucleus, the DM. The RA is in turn innervated by the telencephalic sensory/motor integration nucleus, the HVC. This nucleus receives auditory input from the primary auditory center, the Field L, and from surrounding higher auditory structures, including the Nif nucleus which sends auditory/motor input to the HVC.

Because the Nif is at a higher order than the HVC, the former nucleus was thought to govern a higher organization of song syntax (Margoliash, 1997). Bilateral lesion of the Nif was attempted in zebra finches (*Taeniopygia guttata*), but lesion effects were not detectable on song, except for some transient deterioration that lasted about two weeks post-surgery (Vu et al., 1995). We suspected that the zebra finch songs might be too simple for detecting the effects of nucleus Nif lesion, because their songs are composed usually of repeated sequences of the same syllable order (Zann, 1997). If the Nif does in fact govern higher order song organization, the song should have higher order syntactical organization than the level of one song phrase. In Bengalese finches, song is organized into several different phrases by following different paths, so we predicted that lesion effects might be detectable in these song paths (Fig. 1).

3.2 Methods

Accordingly, we attempted to make lesions to the Nif nuclei of 12 Bengalese finches. Of these, only three were successful bilateral Nif lesions. Of the remainder, two were unilateral and the rest misplaced. All successful lesions completely eliminated the Nif nucleus.

3.3 Results

Unilateral and misplaced lesions produced no change in song syntax. For bilateral lesions, moreover, the result depended upon the degree of song complexity demonstrated by the bird prior to surgery. In two birds that sang complex, multi-phrased songs, bilateral Nif lesion eliminated phrase level complexity; the multi-phrased organization of the song was reduced into single phrase song (Fig. 2). The third bird had initially sung a simple, single-phrase song, and it showed no effect from bilateral Nif lesion. Thus we conclude that the Nif is responsible for phrase-to-phrase transitions in song (Hosino and Okanoya, 2000).

4 Function of song complexity

4.1 Rationale

Given that song syntax differs between Bengalese

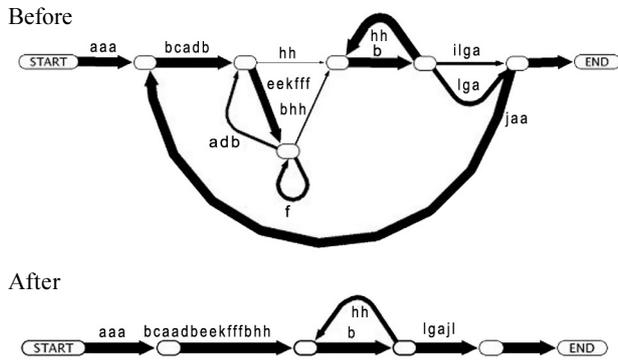


Fig. 2 Changes in song syntax of a NIf lesioned Bengalese finch

Pre-operative song (upper) has a complex transition pattern as in most Bengalese finches, while post-operative song (lower) lost complex transitions. Post-operative song syntax is similar to that of white-rumped munias (Fig. 1). Re-plotted from Hosino and Okanoya (2000).

finches and white-rumped munias, and that its complexity is controlled by the auditory-motor interface nucleus, the NIf, our next step was to examine its functional implications. For this, we chose to examine the hormonal state of females stimulated by either complex or simple syntax songs (Takashima, Otsuka, Wada and Okanoya, pers. obs.).

4.2 Methods

Song recordings obtained from a male Bengalese finch were analyzed, and four distinctive song phrases identified. In the song, the four phrases were organized in such a way that phrases A or B were repeated several times, then phrases C or D followed but without repeat; and after phrase C or D was sung once, phrases A or B were again repeated. We wrote computer software that produced (1) this sequence of song phrases (complex syntax song) and (2) a sequence that repeated only phrase B (simple syntax song). It should be noted that phrase B includes most of the song notes used in phrases A, C, and D.

Three groups of female Bengalese finches were used. Each group consisted of four finches, separately caged, and kept together in a sound isolation box. The first group was stimulated with the complex syntax song, the second group with the simple syntax song, and the third group, as the control, received no playback songs. The levels of serum estradiol were compared among groups both prior to and after the experiment so that baseline level differences could be taken into account.

4.3 Results

Estradiol levels were on average 2.23 times (range 1.58–3.65) higher than baseline in the females stimulated with complex song, 1.08 times (range 0.91–1.45) higher in the females stimulated with the simple song, and 1.12 times (range 0.81–1.43) in control females. Thus complex song was more effective in stimulating female Bengalese finches into reproductive condition ($P < 0.05$, by post-hoc tests).

5 Discussion

In our comparison of the syntactical characteristics of songs in the white-rumped munia, and its domesticated strain, the Bengalese finch, we expected to find simplified traits that would be favored in a domesticated environment. Yet the most remarkable difference that appeared was the more complex song of the domesticated strain, with more note-to-note transitions than in the wild form.

In previous studies, female Bengalese finches performed more copulation displays to the playback of a 6-element song than a 4-element song (Clayton and Prove, 1989). Female Bengalese finches also perch-hopped more often when stimulated by songs with more rather than few elements (Nakamura et al., 1985). These results suggest that female choice might favor more variety in song element types. However, we did not find significant differences in the number of song element types between the strains. In the studies by Clayton and Prove (1989) and Nakamura et al. (1985), the degree of complexity in the temporal domain of the stimulus songs was not reported, and these authors did not introduce temporal-domain dynamics into their playback regimes. Thus, how song complexity in that domain might cause different effects on female Bengalese finches is unknown. Although several studies address “song complexity” and female choice (Kroodsma, 1976; Clayton and Prove, 1989; Eens et al., 1991; Catchpole and Leisler, 1996), most of them treat variations in note type as “complexity.”

In our study, song complexity in Bengalese finches involves dynamics in time series, i.e. temporal domain, rather than variations in note types. In this context, our results on estradiol measurements are of interest. Females stimulated with complex song had estradiol levels elevated to twice the height of base levels. Song complexity, as opposed to note complexity, thus, stimulated female reproductive condition.

Lesions of the NIf also disrupted phrase-level variability in Bengalese finches that sang multi-phrase songs. When the same operation was performed on birds with simpler song, it had no discernible effect on song syntax. Based on our limited data, we postulate that the NIf nucleus may control higher-order song transition or phrase-to-phrase transition. In addition, the finding that NIf-lesioned birds did not change the pattern of note-to-note transition within a phrase suggests that NIf is responsible only for phrase level transition and not for note level transition.

These findings taken together lead us to propose the following scenario to explain song complexity in the Bengalese finch. A mutation involving the NIf nucleus enabled the development of syntactically complex song during the process of domestication. Female bias for syntactical complexity then selected this mutation in domesticated populations. Further work is necessary to test this prediction, as well as to address the more fundamental question: what is the genetic component determining observed song complexity?

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S01-4 Social aspects of song learning and repertoire use in birds

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Abstract Two results from song tutoring experiments with nightingales (*Luscinia megarhynchos*) are presented: song learning by males, and the behavior of females tutored with conspecific master songs as young birds and again as adults. In these learning experiments, human individuals who cared for the birds served as social tutors, controlling for differences in social or experimental variables. The study supplemented results from our earlier work with four findings: 1) when exposed to tutoring regimes that simulated vocal interactions between two different tutors, one familiar and one unfamiliar, male subjects learned well from either tutor; 2) males, however, performed songs imitated from the unfamiliar tutor more frequently than songs imitated from a familiar tutor; 3) either type of imitation was always delivered with those derived from the same social origin, familiar or unfamiliar tutor; and 4) females did not develop any song-like vocalization. In order to determine if they learned and remembered cues from the earlier tutoring programs, we exposed these females to an additional playback of nightingale song. Results were equivocal as their behavioral responses did not allow us to determine if females discriminated between tutored and novel songs. Rather, adult females approached loudspeakers presenting “whistle-songs” (details in Metz and Todt, in prep.). In conclusion, our results point to strategies of song learning and use that appear flexible in either sex and which in males reflect an adaptation for using large repertoires of different songs as well.

Key words Social factors, Song learning, Repertoire use, Gender-related differences, Nightingale

1 Introduction

In most oscines, song learning is gender-related and mainly limited to young males (Baptista, 1996). Usually, such males are affected strongly by the social properties of their environment, i.e. they acquire their songs from a live tutor. Such selective choices can be based on interaction or experience with individual conspecifics or individuals of other species that are accepted as tutors. Some species, for example bullfinches (*Phyrrhula phyrrhula*), nightingales (*Luscinia megarhynchos*) and European starlings (*Sturnus vulgaris*), learn songs even from a human tutor provided he/she has hand-reared them (review in Hultsch and Todt, 1998). The age of birds when interaction begins plays a prominent role in tutor acceptance (Baptista and Petrinovich, 1984).

In classical approaches, social factors were studied by testing individuals with only one particular experimental variable, e.g. a live tutor either present or absent (Baptista and Petrinovich, 1984, 1986, 1987; Marler, 1987; Marler and Peters, 1988). However, another experimental design deserves attention wherein birds are exposed to more than one learning experiment. Here individual birds experiencing different settings then express their preference for a setting by imitating songs heard in that particular situation (Hultsch and Todt, 1989; Todt and Hultsch, 1998). Application of this “choice design” has special advantages for species that, like nightingales, develop large repertoires of different songs

(Fig. 1).

Here we review studies of nightingales exposed to such a “choice design” (Hultsch et al., 1999). Such studies, in particular, have addressed the role that social variables play when young individuals of both sexes were tutored with conspecific master songs. In addition, we report gender-related differences that become apparent among tutored subjects when they, as adults, are again exposed to the master songs. Our reports pay tribute to Luis Baptista and his valuable work on the learning and use of birdsong, on the diversity of song-related behaviors in males or females, and on their colorful distribution across oscine species (Baptista, 1996).

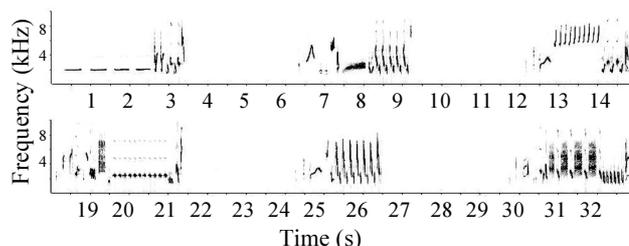


Fig.1 Frequency spectrograms of six songs in succession (section of a longer bout of singing) by a male nightingale. The vocal repertoire of an adult male comprises about 200 different types of songs, some of which may show similar patterns in the beginning (here: songs 3 and 5). Note: The first song is a “whistle-song” that serves to attract females (Hultsch 1980; see text).

2 Methods

2.1 Subjects

Our subjects were eight hand-reared nightingales. Shortly before fledging they were transferred to individual cages in a housing room where subsequent tutoring was conducted. At an age of three months, i.e., the time when occasional subsong begins, the birds were housed individually in sound proofed chambers.

2.2 Tutoring

Tutoring followed our standard experimental protocol. Subjects were exposed to different strings of master songs that served to label an experimental regime. Each string, or learning list, contained a different set of master songs drawn at random from our catalogue of song models that, in former experiments, had proven themselves as learning stimuli (Fig. 1). Selected songs were recorded on digital tapes with 4 seconds of silence between each (the typical duration of intersong intervals in nightingales). Each tape was presented twice at about one hour after light onset, on five successive days. Thus, the birds were exposed to every master song a total of 20 times. Two learning programs (PRESENT and INTERACT) were presented on the same day, with a silent interval of 10 minutes between them. Their presentations were reordered each day, and their procedures were as follows:

(1) PRESENT (control regime, familiar human tutor present). Five minutes before the start of training, the tutor entered the room to a position 2 meters from the birds and with a loudspeaker (Bose, Room Mate II) positioned in front of the him/her. From that position the tutor operated the playback of master songs (string: control). At the end of the playback the tutor remained seated for another 5 minutes. Behaviors of the tutor and bird were monitored and recorded audiovisually from outside the room.

(2) INTERACT (experimental regime, two human tutors present). The procedure here differed from (1) in the following details. Both a tutor familiar to the subject and one unfamiliar to it were present simultaneously during a training session, and positioned with their speakers in opposite corners of the room. During stimulus presentation, the birds were exposed to one long string of master songs. However, while this playback was running, either the right or the left speaker was activated, i.e., the birds heard selected songs (e.g., 1, 2, 3) only from the familiar tutor (on the right), and other songs (e.g., 4, 5, 6) only from the unfamiliar tutor (on the left side). To exclude serial effects, the successions of master song subsets were changed from day to day, i.e., the birds heard songs 4, 5, 6 ahead of songs 1, 2, 3.

2.3 Recording and analysis

Throughout song development (November to April) and later during adult male singing, vocal behaviors were automatically recorded by a computer-controlled registration using Panasonic Hi-fi F55 stereo video recorders and

Sennheiser ME80 microphones. Recordings were analyzed by sound spectrography using the program "Avisoft" (R. Specht, Berlin). For the analyses we selected longer records of coherent singing (20 minutes or longer) and sampled at least a total of 2 hours of singing from each male. Due to the versatile singing style of nightingales, such sampling is sufficient to assess the complete repertoires of the birds. Spectrographic displays of song patterns were compared to spectrograms of the presented master songs by two independent persons who were not informed about the regimes in which master songs were played: see Hultsch and Todt (1989) for criteria used to identify a given song pattern as an imitation of a master song.

2.4 Testing of adult females

As they did not develop any song-like vocalization, females were tested further to determine how they were affected by the experimental variables. Females that had reached an age of about one year were exposed to a second playback of conspecific songs. Stimuli included (1) songs that had been tutored versus songs that were new for the birds, and (2) whistle-songs versus non-whistle-songs (Fig. 1, based on Metz (1998) for the whistle-songs). Experiments with other songs were conducted and evaluated accordingly.

The testing situation was a central home cage, which housed the subject and to which single cages were attached at either end. Thus, a test bird could move voluntarily between the middle cage and the two end cages which each held loudspeakers (Bose Roommate II) to present song playbacks simulating the singing of a male. To control for the influence of specific songs on the subject's responses, we prepared playback-tapes that each contained a different set of 10 song stimuli for presentation over a total of 10 minutes. All experiments were recorded by audiovisual equipment. Since females did not show copulation solicitation displays consistently, we analyzed spatial behaviors, i.e., movement rates, movement direction, and time-related features of spatial behavior. A movement was defined as a perch change or a jump on the ground (details in Metz, 1998).

2.5 Statistical analysis

Because movement patterns measured were not distributed normally ($P < 0.08$, with $P > 0.2$ safe), we used only ranked data. We did not run a Principal Component Analysis, because most measurements did not correlate with each other. Each movement pattern was tested separately. To detect any significant differences between responses to playbacks, a nonparametric ANOVA for related samples was used. The Wilcoxon-Single Comparison was applied to determine playback-trials that elicited responses detected by the ANOVA. P -values between 0.10 and 0.05 were regarded as trends, and P -values equal to 0.05 or lower were regarded as significant.

3 Results

3.1 Song learning

All males ($n=4$) developed songs that could be identified unambiguously as imitations of the master songs presented by a social tutor. Although there was inter-individual variation in the overall learning success, acquisition from the PRESENT-regime was in no case higher than from the INTERACT-regime, and two of the four males had acquired more imitations from the latter tutoring than the first (Wilcoxon matched pairs sign test, $n=4$, $P < 0.01$). A closer inspection of imitations derived from the INTERACT-regime showed that these birds had indeed preferentially copied master songs presented by the unfamiliar tutor. In contrast to males, none of the females developed any song-like vocalization, consistent with findings from other learning experiments with female nightingales.

3.2 Song performance

Analyses revealed two remarkable results. First, males sang imitations of songs presented by the unfamiliar tutor more frequently than those from the familiar tutor (Wilcoxon matched pairs sign test, $n=4$, $P < 0.05$). Secondly, song imitations were not given randomly but delivered instead in clusters derived separately from each tutor (Fig. 2), i.e., the birds performed imitations learned from one tutor in a single sequential block separated from sequences of imitations of the other tutor.

3.3 Female responses

Analysis yielded two results. First, we could not find evidence that the females discriminated between tutored and novel songs. Thus, it remained open whether the females remembered any cues from the tutoring programs experienced early in life. Secondly, however, females did discriminate clearly between two specific classes of nightingale song: whistle-songs and non-whistle-songs (Fig. 1).

In addition, females displayed a number of remarkable behaviors in preferential response to whistle-songs. When exposed to playbacks of conspecific song, adult fe-

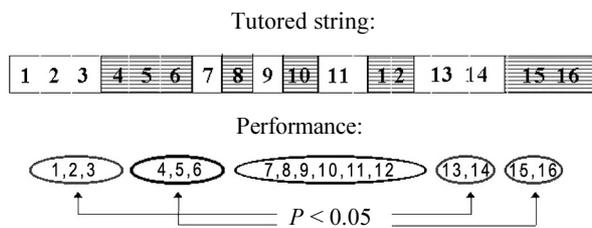


Fig. 2 Relationships between a string of master songs (top) and imitations developed by the birds (bottom)

Master songs were presented in an interactional learning regime: songs 1,2,3,7,9,11,13,14 were presented by the familiar tutor, and songs 4,5,6,8,10,12,15,16 by the unfamiliar tutor. During their performance, the imitations occurred sequentially clustered according to social origin; i.e. birds developed a sequential association among imitations 1,2,3,13,14 from one social source and another one among imitations 4,5,6,15,16 from the other source. This effect was not significant in imitations of songs that the birds had experienced from an immediate alternation of tutor roles (songs 7,8,9,10,11).

males neither vocalized nor gave soliciting displays, but instead performed particular movement patterns. There were more movements per minute during playbacks of whistle-songs than during other nightingale songs ($P = 0.026$). Females approached the compartment contiguous to the active speaker most quickly during playbacks of whistle-songs. Latencies tended to be shorter than latencies during playback of control songs ($P = 0.005$). The greatest number of movements towards the speakers happened during playbacks of whistle-songs. Difference from movements towards speakers during playbacks of control nightingale songs ($P = 0.015$) was significant. Females spent the longest time in the compartment connected with the active speaker during playback of whistle-songs ($P = 0.005$). Latencies to the perch next to the active speaker were also shortest during playbacks of whistle-songs ($P = 0.045$; further details in Metz and Todt, in prep.).

4 Discussion

4.1 Song learning

Social factors can influence the vocal learning of various bird species (Todt, 1975; Pepperberg, 1993; Baptista and Gaunt, 1997), including oscines (reviews in Kroodsmma, 1982; Todt and Hultsch, 1998). In zebra finches (*Taeniopygia guttata*), for instance, social interaction with a live tutor is crucial (review in Tchernikowski et al., 2001). White-crowned sparrows (*Zonotrichia leucophrys*) are likewise sensitive to social stimuli (Baptista and Petrinovich, 1984), and they may even learn alien songs from live tutors while rejecting the same songs presented by tape playback alone (Baptista and Petrinovich, 1987). Moreover, species that develop large vocal repertoires, such as nightingales and European starlings, behave similarly; both accept a human caretaker as a social tutor (Todt et al., 1979; Boehner and Todt, 1996).

The results presented here supplement such findings by showing that nightingales can also learn from an unfamiliar tutor. This outcome suggests that “being reared by a human” may open a window of acceptance for “being tutored by another human”. Enhanced song memorization and/or sensorimotor song learning in these trials may have been facilitated by variables that aroused the birds or their attention. This explanation agrees with results of other studies suggesting that an essential property of song factors may be their operation as attention or arousal mechanisms (review in Hultsch et al., 1999).

4.2 Song performance

Our study uncovered a relationship between specific properties of learning stimuli and the performance mode of learned songs. In the literature on song acquisition by oscines, this issue has been widely neglected. Nevertheless, it merits consideration because it points to both potential influences of intrinsic state variables, such as attention or arousal, and cognitive processes involved in song performance, such as a cue-related categorization of songs. Our birds uttered songs imitated from an unfamiliar tutor

more frequently than songs acquired from a familiar tutor, and at the same time sang imitated songs in clusters according to social origin. These results correspond to findings on the song performance of other nightingales that had been exposed to two different learning regimes, one in which the birds were tutored normally and the other in which they experienced auditory stimuli paired with specific visual stimuli, e.g., stroboscopic light (Hultsch et al., 1999).

Therefore, we conclude that stimuli which raise the attention or arousal levels of a given bird can facilitate the development and also the performance of specific vocal imitations. In functional terms, this implies that the mechanisms underlying such processing could indeed improve a given bird's outcome in song contests with rivals, as also would clustering song according to origin. The results suggest that the birds were indeed able to extract and memorize social information encoded in a given tutoring regime, and that they also used such information when organizing their song performance as adults. We assume that such a cue-related categorization of songs points to a cognitive processing of acquired song stimuli. This assumption is in line with predictions derived from an earlier study that provided evidence for the formation of so-called "context groups" (Todt and Hultsch, 1998). The results of that study indicated, as well, that such group formation reflected a process of categorization, such as sorting learned songs according to specific contextual cues. In the field, a repertoire performance following such cues could enhance a rapid addressee-related memory retrieval of specific types of songs. However these conjectures require further investigation.

4.3 Gender-related issues

Oscines vary remarkably in whether and how females develop a species typical song (Baptista and Gaunt, 1994). In some taxa, even closely related species may differ in a gender-related distribution of singing behavior. For instance, although sex differences seem clear in white-crowned sparrows where singing is specific to males, females of the sedentary race *Z. l. nuttalli* and the migratory race *Z. l. oriantha* can sing at certain times. In white-throated sparrows (*Zonotrichia albicollis*) that occur as white-striped and tan-striped morphs, moreover, females of white-striped morphs sing in the wild, but tan-striped females do not (reviews in Baptista et al., 1993; Baptista, 1996).

Given such gender-related differences of song learning and singing, we addressed this issue in nightingales and found that nightingale females neither learn nor vocalize conspecific songs. In addition, their behavior did even not reveal whether, as adults, they remembered songs heard during a tutoring experiment early in life, let alone discriminate such songs from completely novel ones. Although we cannot exclude the possibility that these results were affected by methodological factors, we nevertheless assume that they reflect some biologically meaningful differences. In a species like the nightingale, in which males sing large repertoires of songs and song learning is not constraint on a bird's natal summer, it seems prudent not to discriminate

individuals by single types of songs. Rather, it would be wiser to identify a given male by his particular song sequencing, which provides a more reliable individual cue than a single song pattern (Todt and Hultsch, 1998).

Female nightingales were attracted to a special class of songs, namely whistle-songs, a response that may be species typical. Such a functional role of whistle-songs was postulated earlier by Hultsch (1980) who found this song to be given particularly frequently by unpaired males and predominantly when migrating females were returning to their breeding areas. This finding is a prime example of congruence in laboratory investigation and field study — something that the late Luis Baptista stressed as an essential aim in biological research (Baptista, 1996).

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S01-5 Evolution of brain structures for vocal learning in birds: a synopsis

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Abstract Vocal learning, the ability of animals to reproduce vocalizations, is found in only three mammalian groups (humans, cetaceans and bats) and three avian groups (parrots, hummingbirds and songbirds). Surprisingly, learners in each of the mammalian or avian groups are not closely related, and have close non-learning vocal relatives, suggesting that vocal learning evolved independently in each. Yet, behaviorally driven gene expression and other studies have identified in all vocal-learning birds seven remarkably similar telencephalic brain structures that are not found in vocal non-learners. These findings suggest that within the past 65 million years, three out of *c.* 30 avian orders evolved seven similar brain structures for a complex behavior, and that the evolution of such brain structures is under strong epigenetic constraints. Alternatively, vocal learning and the associated brain structures might have been present in a common ancestor, followed by major independent losses, again suggesting strong epigenetic constraints affecting this complex function. Here I review findings on the evolution of vocal learning and associated brain structures in birds, and consider their potential relevance to understanding vocal learning in general.

Key words Songbird, Parrot, Hummingbird, Neurobiology, Language, Constraints

1 Introduction

Vocal learning, the ability to imitate or improvise upon sounds, is rare, found in only six animal groups: three of the some 30 avian orders (parrots, hummingbirds, and songbirds) and three of the 28 or so mammalian orders (humans, bats, and cetaceans) (Nottebohm, 1972; Jarvis et al., 2000). Auditory learning, upon which vocal learning depends (Konishi, 1965), is merely the ability to form memories of the sounds heard and is present in all vertebrates that have been tested. For example, pet animals can acquire the meaning of sounds “sit” (in English) or “sientese” (in Spanish) through auditory learning even though knowledge of human words is not in their innate auditory repertoire. However, a pet cannot imitate and produce these sounds, which humans, parrots, and some songbirds can. Most vocal learners, nevertheless, imitate sounds of only their own species.

Nottebohm (1972) proposed that songbirds, hummingbirds, and parrots evolved their vocal learning abilities independently, because the closest relatives of each were vocal non-learners like more distantly related orders, such as chickens (Fig. 1A). Species of non-learning orders produce only innate vocalizations, presumably the ancestral condition. A similar case can be made for independent evolution of vocal learning in mammals. Nottebohm and colleagues also discovered that songbirds and parrots have cerebral brain nuclei that control vocal learning, and that some of these cerebral nuclei are similar to one another (Nottebohm et al., 1976; Paton et al., 1981). Vocal non-learners possess only midbrain vocal nuclei, which are involved in the production of innate vocalizations (Kroodsma and

Konishi, 1991).

Accordingly, Brenowitz (1991) proposed that, similar to the behavior they control, the cerebral vocal nuclei of songbirds and parrots evolved independently though with some shared properties. Jarvis and colleagues used behavioral-molecular approaches to reveal an entire set of cerebral vocal structures in hummingbirds (Jarvis and Mello, 2000), as well as additional structures in songbirds and parrots (Jarvis and Nottebohm, 1997; Jarvis et al., 1998; Jarvis et al., 2000). These findings led to the novel conclusion that all three vocal-learning bird groups have a similar set of seven cerebral vocal brain nuclei (Fig. 1B), and produced hypotheses for how such similarities could have evolved (Jarvis and Mello, 2000). Herein I present (1) a comparative synopsis of cerebral vocal nuclei in the three vocal-learning bird groups, and (2) three alternative hypotheses to explain the evolution of vocal learning and associated cerebral vocal nuclei.

2 Cerebral vocal nuclei of vocal-learning birds

Most information on vocal cerebral nuclei comes from songbirds and the least from hummingbirds. The main techniques used to identify and study these nuclei are lesions, electrophysiological activity, and behaviorally-driven gene expression. Only behaviorally-driven gene expression has been used effectively in all three vocal-learning bird groups; and accordingly I focus on results from this approach.

2.1 Behaviorally-driven gene expression

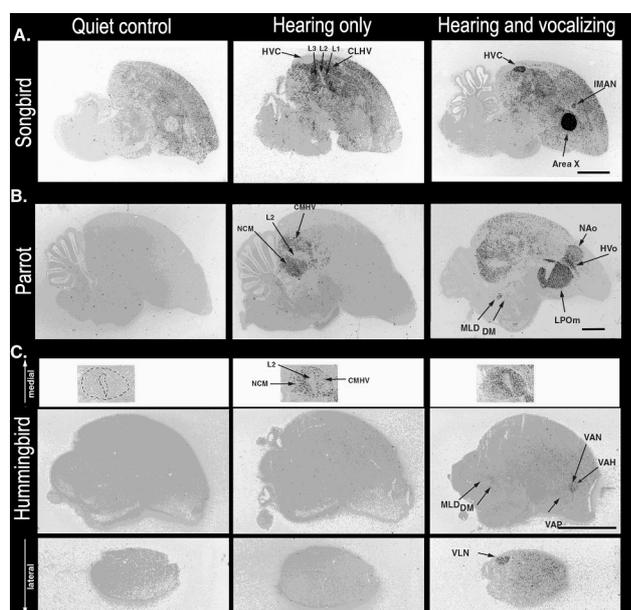


Fig. 2 Hearing and vocalizing-driven ZENK expression in songbirds (canary), parrots (budgerigar) and hummingbirds (*Aphantochroa*)

Shown are dark-field views of parasagittal brain sections hybridized to a radioactively-labeled canary ZENK riboprobe (black silver grains) and counterstained with cresyl violet (gray). Images are from one representative bird of each group. In the songbird brain, NCM, CMHV and the major part of HVo are not shown, as they are more medial. In the parrot brain, NLc, AAc, IAN, and IAHV are not shown, as they are located much more laterally. In the hummingbird brain, different medial-to-lateral planes are shown. For explanation of acronyms, see Jarvis et al. (2000). Scale bars 1 mm.

and non-cerebral brain areas (Figs. 1B, 2). The hearing-activated areas occurred in the posterior part of the cerebrum, and in almost the same position in all three vocal-learning groups. These brain areas form an auditory pathway found in both vocal-learning and vocal non-learning birds that begins in hair cells in the ear. They send their axons to cochlear nuclei in the brainstem, and from there to MLd of the midbrain, to Ov of the thalamus, to the primary auditory cells of the cerebrum (L2), and to secondary and tertiary auditory cells (L1, L3, NCM, CMHV, HVC shelf and RA cup) (Vates et al., 1996) (Fig. 1B, white structures; ZENK expression shown in Fig. 2).

The seven vocal-activated areas in the three orders of vocal-learning birds fall into two positional groups: (1) three in nearly identical locations in the anterior cerebrum (Fig. 1B, light gray regions; Fig. 2), though each with different shapes; and (2) four in different locations of the posterior cerebrum, but still within the same brain subdivisions relative to one another and with similar shapes to some of them (Fig. 1B, dark gray regions). The position of the four posterior nuclei relative to the auditory areas differs in accord with the presumed age of each avian order. In parrots, presumably the oldest vocal-learning order, the posterior vocal nuclei are located away from the auditory areas; in

the next oldest, hummingbirds, they are adjacent to auditory regions; and in songbirds, the most recent, they are embedded within the auditory areas.

2.2 Posterior vocal nuclei

In songbirds, the posterior vocal nuclei are part of a posterior vocal pathway that connects nucleus Nif→HVC→RA to the vocal nucleus of the midbrain (DM), as well as to sets of brainstem nuclei (nXIIIts) that control syringeal muscles and respiratory muscles during vocalization. When the HVC and RA are bilaterally lesioned in a songbird, it is unable to produce learned song (Nottebohm et al., 1976, Simpson and Vicario, 1990). Innate vocalizations, however, are retained. After the Nif is lesioned, the bird can produce most learned syllables; but syntax, the ordering of learned vocalizations, is affected and becomes more variable (Hosino and Okanoya, 2000). The nuclei fire action potentials immediately before song output and during singing, and stop milliseconds before sound output ceases. Combined, these findings show that the posterior vocal pathway produces the learned vocalizations of songbirds.

Connectivity in the posterior nuclei of parrots is partly similar insofar as HVC-like (NLc) and RA-like (AAc) nuclei project to brainstem motor neurons involved in the production of sound (Durand et al., 1997). Lesion studies also implicate the posterior vocal nuclei in the production of learned vocalizations in parrots. For example, lesion of their HVC-like nucleus (NLc) revealed that it is required for the ability to speak English words (Lavenex, 2000).

Preliminary connectivity studies performed on hummingbirds (Gahr, 2000) indicate that their HVC-like nuclei (VAN), via their RA-like (VA) vocal nuclei, also project to vocal brainstem motor neurons. Neither lesioning nor electrophysiological studies have been conducted on the vocal nuclei of this order.

2.3 Anterior vocal nuclei

In songbirds, these nuclei are part of an anterior vocal pathway that forms a loop with projections from MAN→Area X→DLM→MAN (Luo et al., 2001). All connections of this pathway lie within the forebrain, consisting of the cerebrum and thalamus combined. When the main lateral portions of the anterior vocal nuclei are lesioned, as in lateral MAN (IMAN) or lateral Area X (lArea X), songbirds are still able to sing previously learned vocalizations but cannot learn new vocalizations (Scharff and Nottebohm, 1991). During non-imitative stages, which some adult songbirds undergo, anterior vocal pathway lesions have no obvious affect. However, as shown in gene expression results (Jarvis and Nottebohm, 1997), song-driven electrophysiological firing still takes place in anterior vocal nuclei in adults (Hessler and Doupe, 1999a). In adults though, lesions to Area X temporarily affect song syntax and song-driven gene expression; and song activity differs according to the social context in which the birds sing (Jarvis et al., 1998; Hessler and Doupe, 1999b; Kobayashi et al., 2001).

Hence in songbirds, the anterior vocal pathway may be responsible for vocal learning and some as yet undefined role in the social context of singing, as well as song syntax.

Connectivity studies in parrots have also shown that their anterior vocal nuclei are part of a forebrain loop (Durand et al., 1997). Lesions to the HVo-like (HVo) and MAN-like (NAo) vocal nuclei in parrots have shown that these, too, are required for vocal learning. No such studies have been conducted in hummingbirds.

Key differences between parrots and songbirds in known connectivity lie in the interactions between posterior and anterior vocal pathways (Durand et al., 1997; Jarvis and Mello, 2000). In songbirds, the posterior pathway sends input into the anterior pathway via a projection from HVC→Area X. The anterior pathway in turn sends output to the posterior pathway via a projection from lateral MAN→RA and medial MAN→HVC. In parrots, the posterior pathway sends input into the anterior pathway via a projection from RA-like (AAc) into all three anterior vocal nuclei: HVo-like (HVo), MAN-like (NAo), and Area X-like (LPO) sections. The anterior pathway uses the same region of the MAN-like nucleus (NAo) and projects to both its RA-like (AAc) and HVC-like (NLc) vocal nuclei. As connectivity for the HVo-like nucleus in songbirds has not been yet determined, it is not possible to make comparisons with parrots.

3 Hypotheses for the origin of vocal learning

It is established that the basic cellular arrangement for learned vocal communication in birds comprises an auditory pathway to acquire sounds, vocal nuclei in the cerebrum, and seven nuclei with one or more of each in each major cerebral subdivision except the *pallidum* (an area homologous to the mammalian *globus pallidus*). Because the auditory pathway also has one or more nuclei in each major cerebral subdivision, I suggest that this is a basic system of organization in the avian brain, comparable to the different systems in the mammalian brain which involve all six layers of the cortex and the basal ganglia below it.

For vocal learning, and perhaps motor learning in general, cerebral nuclei need to be divided into two pathways: a posterior vocal pathway that must project to lower vocal motor neurons for the production of learned vocalizations, and an anterior vocal pathway that must form a loop and control vocal learning and other aspects of learned vocalizing. The projections of the posterior pathway to motor neurons are akin to the motor cortex projections in the mammalian brain; the anterior loop, in contrast, is akin to cortical-basal ganglia-thalamic-cortical loops in mammals. Variation is permissible. The shapes of the vocal nuclei and their relative sizes, the location of the posterior vocal pathway relative to auditory and anterior vocal pathways, and their connectivity, may vary without impairing vocal learning. For example, the HVo and MAN-like vocal nuclei in parrots

are, relatively, much larger than in songbirds and hummingbirds. Parrots display more vocal plasticity than songbirds or hummingbirds, and the enlargement of these nuclei could be implicated in its facilitation.

Although clear differences exist, the striking similarities beg the question as to how such similarities evolved. Modern birds supposedly evolved from a common ancestor around the cretaceous-tertiary boundary at the time of the extinction of dinosaurs, ~65 million years ago (Feduccia, 1995). How did seven similar brain structures appear in three distantly related vocal-learning birds in the ensuing time? To put these questions in perspective, the phylogenetic relationship between parrots and songbirds (Fig. 1A) is as far distant as that between humans and dolphins (Novacek, 1992). To explain these similarities, colleagues and I have put forward three hypotheses (Jarvis et al., 2000).

Hypothesis 1: Three out of the 30 or so avian orders evolved vocal learning independently in the past 65 million years (Fig. 1A, dots). For each event, seven similar brain structures for learned vocal communication evolved convergently. This would suggest that the evolution of brain structures for complex behavior is under strong epigenetic constraint. Such constraints may be in part outside the genes, i.e. imposed by environment and/or the morphology of the syringial/respiratory system. Such selection in the brain may have to adhere to some genetic constraints, with a requirement that an anterior part of the cerebrum, which normally controls motor learning, hooks up with a more posterior part that normally controls movement, so that all then hook up to muscles that control vocalizations. According to this hypothesis, if pigeons or some other group were to evolve vocal learning, one would predict that in another 50 million years or so, another seven similar brain regions in well-defined posterior and anterior locations would be present.

Hypothesis 2: An alternative hypothesis invokes a common ancestor for all modern birds that possessed vocal learning and the seven cerebral vocal nuclei. These traits were retained in only the three orders today, and lost independently at least four times in the interrelated vocal non-learning orders (Fig. 1A, squares). Such independent losses would suggest that maintenance of vocal learning and cerebral vocal structures is under strong epigenetic constraint too, and that considerable survival costs accrue to vocal learning or that many bird groups evolved in adaptive zones that did not require vocal learning. One constraint could be predation, in which context-learned vocalizations are more variable and thus less habituated to by predators (Jarvis and A Ferreira, in preparation). If such losses in vocal learning occurred independently, a similar scenario applies in theory to mammals. However, chimpanzees and other primates would have had to lose the trait recently and independently many times.

Hypothesis 3: The third hypothesis proposes that avian vocal non-learners have rudimentary cerebral vocal nuclei, previously overlooked, which have become enlarged

independently in the vocal learners. If true, this challenges the idea that cerebral vocal nuclei are unique to vocal learners. It would suggest that these brain structures are universal, even for mammals, with potential for vocal learning not yet widely expressed.

Because the auditory pathway is remarkably similar among all vocal learning and non-learning birds, I argue that the pathway in the vocal learners was inherited from a common avian ancestor with non-learners, or even from a common reptilian ancestor with mammals. Because the auditory pathway consists of cerebral nuclei in most vertebrate groups, I argue that this is why pets succeed at auditory learning. Whichever of the above hypotheses is true, singly or in combination, the answer for the evolution of cerebral vocal pathways in birds will be fascinating. Each hypothesis suggests that the evolution of brain pathways for complex behaviors is constrained by as yet unknown factors.

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Symposium 02 The role of high quality individuals in populations of long-lived birds

Introduction

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Long-term studies have shown the importance of individual quality for fitness and bird population dynamics. This symposium seeks insights into the nature and consequences of individual quality, reviews the phenomenon, and focuses on recent findings of extended studies of long-lived birds using new field, laboratory and statistical techniques.

The papers address individual quality from various points of view and by a variety of field and statistical methods in long-lived sea- and water-birds during different life stages. S. Bradley and C. Meathrel focus on the prediction of individual reproductive success as a quality trait in short-tailed shearwaters, *Puffinus tenuirostris*, J.-D. Ludwigs and P. H. Becker address the influence of chick quality and conditions during early development on return and recruitment rates of common terns, *Sterna hirundo*, at the natal colony. C. Barbraud and H. Weimerskirch investigate the trade-off between survival and reproduction in the blue petrel, *Halobaena caerulea*, and its dependence on individual quality and environmental conditions. In two oral contributions, B. Ebbinge, G. Müskens and B. Spaans considered the importance of high quality individuals in a stabilizing population of dark-bellied brent geese *Branta bernicla bernicla*, and C. Perrins, R. McCleery, D. Wheeler and S. Groves focused on survival and senescence in mute swans *Cygnus olor* and the effects of age and quality on probability of their attempting to breed. Abstracts of the two oral papers are published in the Abstract Volume for the Congress.

The papers make clear that only a small percentage of individuals contributes recruits to the next generation, and show that selection favors one particular individual trait for breeding success and the survival of adults and subadults: body mass and condition. Assortative mating by age and/or condition, and mate fidelity, enhance fitness of the individuals further (short-tailed shearwater). Body mass in the blue petrel, furthermore, affects the probability of becoming a breeder, as well as the probability of survival, particu-

larly among first time breeders; this may indicate that first reproduction imposes costs on survival. Age is of specific importance: in short-tailed shearwaters and brent geese, reproductive output increases with age, and in mute swans, age is the most important factor in reproductive success over lifetime.

All presentations reflect the value of long-term studies of individual birds for gaining insights into the nature and consequences of individual quality. Even if the evidence presented stresses the importance of high quality individuals in the dynamics, ecology and genetics of bird populations, and for evolution, many questions remain unanswered. Future research should move towards refining parameters of individual quality, using hormones, metabolism and cognitive abilities. The causes of strong inter-individual differences in quality and fitness should provide cues. Unequal information-gathering and learning, as well as cultural traits, may well be involved with quality too (see Annett and Pierotti, 1999) and might promote rapid evolutionary change through selection of the more adept individuals. These issues need investigation.

So do others. Do high quality individuals produce high quality offspring, and are quality related traits inherited? How important is the influence of parental effort in interactions with environmental effects and in controlling early development (Lindström, 1999)? Yet another is whether differences between gender involve fitness and individual quality. Furthermore, the role of high quality individuals as a possible buffer against environmental fluctuations, especially in declining populations (Newton, 1989), needs to be clarified by detailed population studies.

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S02-1 Prediction of individual reproductive success in short-tailed shearwaters, *Puffinus tenuirostris*

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Abstract Previous studies of the short-tailed shearwater, *Puffinus tenuirostris*, have identified assortative mating based on age from first breeding as a strong predictor of reproductive success. The physical traits of a large number of breeding pairs were measured on Great Dog Island, Tasmania, and their breeding success recorded. Modest sexual dimorphism was found, primarily in bill depth. Significant correlations between pair members were recorded in bill depth and tarsus length. In addition, those females having a lower absolute deviation from the mean in bill depth had a significantly greater likelihood of producing an egg, as did those males that had a higher absolute deviation from the mean in head length. Female body condition indices at hatching and at laying were also predictors of breeding success.

Key words Assortative mating, Breeding success, Morphometrics, Condition index, Natural selection, Darwinian fitness

1 Introduction

Short-tailed shearwaters *Puffinus tenuirostris* are medium-sized (500 g), burrow-nesting procellariiform seabirds which breed in southeastern Australia, mainly on islands around Tasmania. They are transequatorial migrants that return to colonies in late September and lay in late November. The single young leaves late April (Warham, 1990, 1996).

A small colony of 100–200 shearwaters on Fisher Island in Bass Strait has been studied annually since 1947. All individuals have been identified reliably since 1950 and their mates and reproductive performance recorded each year. Of the birds that have completed their life histories, 8% have produced over 50% of the birds that have returned to Fisher to breed (Wooller et al., 1988). Thus, a core of very successful breeders produces the majority of the subsequent generation.

Breeding age (measured from the year of first breeding) has a substantial effect on reproductive success (Bradley et al., 1995, 2000; Wooller et al., 1990). Bradley et al. (2000) found curvilinear relationships with age in the proportion of breeders attending the colony and, given the existence of an egg, the probability of producing a fledgling. In both cases, success increases with breeding age to an optimum, after which success declines as the birds grow old. However, the probability of an attending bird being associated with an egg continues to increase through life.

The number of years spent breeding with a particular mate is also a highly significant predictor of breeding success (Bradley et al., 1990; Wooller et al., 1990; Wooller and Bradley, 1995). Given age dependent effects, it is logical to

find evidence of assortative mating in breeding age. Bradley et al. (1995) used a random model of re-pairing birds (birds requiring a mate because of mate death, divorce or recruitment) to show that older birds had a greater probability of pairing with older birds than chance alone could predict.

The Fisher Island study has required minimal interference to breeding adults. Consequently, although they were handled to establish identity and burrow occupancy, they have never been weighed or measured. Although the Fisher data provide very high power in measuring variation in lifetime reproductive success, or in testing for age or historical effects, they do not, to date, provide information on physical predictors of success. Hence, since 1991, a second site on neighboring and much larger Great Dog Island, 5 km south of Fisher, has been used as a monitoring and experimental site to add to the information from Fisher and to provide some replication of our findings. In 1991, an extensive program was initiated on Great Dog to measure and weigh breeding birds at various stages of reproduction. Over a single season, this study provided an opportunity to use large sample sizes to search for evidence of physical predictors of breeding success.

Successful breeding is a joint and interactive process between two individuals (Black, 1995). Individual and joint measures can be used to predict breeding success on the basis that the pairings represent random subsets, at least from the aspect of physical variables. If, however, there is a degree of assortative mating associated with physical parameters, or the behavior of one individual through the breeding process affects the weight or body condition of the other, then there is the opportunity for a pair member to

influence, directly or indirectly, the physical attributes of the mate.

2 Breeding success and physical measures

Physical measures fall into two categories which behave in different ways. First, skeletal or body shape variables (e.g., tarsus length, wing length) have, in general, high heritabilities (e.g., Gustaffson, 1986) and are highly repeatable in adults. Where these variables provide a prediction of breeding success, which is itself a component of Darwinian fitness, they flag the action of natural selection and may change or stabilize gene frequencies at the polygenic loci modifying these traits (Gustaffson, 1986; Kruuk et al., 2001; Gibbs and Grant, 1987). The second category includes measurements of mass and condition indices. These variables have lower repeatabilities, and evidence from other procariiform studies (e.g., Weimerskirch and Lys, 2000) indicate that they change in value systematically through the breeding process.

Differences in the mean values of skeletal variables between successful and unsuccessful birds indicate at least the possibility of directional selection. Heritable changes in beak shape and other morphological traits have been demonstrated in one of Darwin's finches (*Geospiza fortis*) in drought and heavy rainfall years (Gibbs and Grant, 1987). This example reinforces the point that selective change need not be constant from year to year. However, a more common situation, according to quantitative genetics theory (Robertson, 1955; Stearns, 1992; Falconer and MacKay, 1996), is that of stabilizing selection where individuals close to the mean are fitter than those at one or other of the extremes of the distribution of the trait. In this situation the convergence of the mean and optimum fitness is the outcome of past selection, and the mean tracks the optimum. Under this model, we would expect successful birds, on average, to exhibit a lower absolute deviation from the mean than unsuccessful birds. For example, in Bewick's swans (*Gygis columbianus bewickii*), large males tend to have the highest reproductive success (Rees et al., 1995), whereas medium-sized males have the highest success in whooper swans (*C. cygnus*) and mute swans (*C. olor*). A third form of natural selection, disruptive selection, acts in the opposite way to stabilizing selection. In this case, fitness should be lowest close to the mean; and thus, under this model, successful birds will exhibit a higher absolute deviation from the mean than unsuccessful birds.

3 Correlations in physical measurements between pair members

Skeletal traits are generally invariant and highly repeatable. If they have the potential to be indicators of reproductive success because, for example, they affect the individual's foraging efficiency, then we might expect them to be good indicators to a potential mate also. For example,

size in the pinyon jay (*Gymnorhinus cyanocephalus*) is a predictor of reproductive success, and is also a demonstrable factor in mate choice (Marzluff et al., 1995). The behavior of assortative correlations between trait values in pair members will depend upon which selection model applies to the skeletal traits.

Under stabilizing selection, individuals close to the mean should select each other, and more extreme individuals will be left with each other by default. However, this would not show up as a correlation in raw values since, presumably, an individual with an extreme low value would be just as likely to mate with an individual with an extreme high value. Under these circumstances, however, absolute deviations from the mean would be positively correlated. If the measure in question were subject to disruptive selection, the reverse would apply. Mates with extreme values would be preferred. In terms of correlation this would be indistinguishable from stabilizing selection. Under directional selection, if a trend was sufficiently long term, we would expect assortative mating to evolve on the raw value of the measure. However, as Merilä et al. (2001) point out, long term directional selection on heritable traits need not produce the expected shift in the trait mean.

4 Methods

In the 1991–1992 breeding season, 1 750 burrows on Great Dog Island were checked 1–3 times per week for their contents. Occupant adults were weighed, measured and banded; eggs were weighed and measured. The adult pre-laying mass was taken before the birds departed on the pre-laying exodus, from 15 October to 3 November. The adult laying mass was taken upon return from exodus, from 21 November to 4 December. Because of the extreme synchrony of laying in this species, all females at this point were still on the first incubation shift and had not fed. The adult hatching mass was taken from 16–30 January. Final checks to ascertain fledging of the chicks took place from 6–11 April.

The measurements taken of adults were: head length, bill length, bill depth, tarsus length and wing length. Condition indices were calculated for each bird at each weighing by transforming each morphological measurement into standard deviations from the mean (zscores), summing the zscores across variables and dividing the mass by this result. Joint or mid-parent values for each pair were calculated by averaging male and female measurements. Absolute deviations from the mean were also calculated for each variable by subtracting the mean of the appropriate sex and taking the absolute (unsigned) value of this difference.

Six binary indices of breeding success were used: from pair down a burrow to production of an egg (pair to egg); from pair down a burrow to hatching (pair to hatching); from pair down a burrow to fledging (pair to fledging); from egg to hatching; from egg to fledging; and from hatching to fledging. Some categories included others (e.g., pair to hatching includes egg to hatching), and therefore these

Table 1 Sexual dimorphism in breeding short-tailed shearwaters

Variable	Gender		Difference	F-test		
	Female	Male		df	F	P
Head length (mm)	80.83±0.09	82.75±0.08	2.34%	1 104	245.92	0.000
Bill length (mm)	31.84±0.06	32.72±0.04	2.71%	1 104	150.21	0.000
Bill depth (mm)	8.15±0.02	8.85±0.02	8.22%	1 104	872.05	0.000
Tarsus length (mm)	58.22±0.09	58.97±0.07	1.28%	1 104	44.50	0.000
Wing length (mm)	270.90±0.29	273.13±0.24	0.82%	1 104	34.58	0.000
Pre-laying mass (g)	533.80±2.74	555.83±2.75	4.04%	469	30.73	0.000
Laying mass (g)	617.63±4.37	630.87±2.74	2.12%	760	7.09	0.000
Hatching mass (g)	639.18±8.52	660.83±7.26	3.33%	119	3.79	0.054

Mean ± standard error is given. The column "Difference" gives the female mean subtracted from the male mean expressed as a percentage of the average of the two means.

variables were not independent of each other. However, because all members of each pair were not included at each weighing, sample sizes, and hence the power of each test, will differ within each of these measures.

Using the SPSS statistical package, unequal sample size *t*-tests were performed for each of the body measurements, masses, condition indices and absolute deviation variables, using the success indices as categorical variables. Because of the substantial repeat testing involved for each breeding success variable, nominal significance levels were set at one in 100 rather than one in twenty (Bonferroni correction).

5 Results and discussion

The measurements of breeders within pairs demonstrate that detectable but small sexual dimorphism exists in this species (Table 1). The most marked difference occurs in bill depth, where the difference between the sexes is 8%. Bill length and head length are approximately 2% different, and tarsus and wing length 1%. Mass measurements vary between 2% and 4% depending on the stage of the breeding cycle. The male is the bigger bird for all variables.

No linear (i.e., untransformed) skeletal variables are

significantly different between successful and unsuccessful birds for any of the measures of reproductive success (Table 2). The only linear (as opposed to absolute deviation) variables for which $P < 0.01$ are female condition index variables. There are two absolute deviation variables which are significant at this level: male head length and female bill depth. This would indicate that skeletal variables are not subject to detectable fluctuating or directional selection. However, female bill depth appears to be subject to stabilizing selection where the production of the egg is concerned. The effect is stronger, with a deviation 20% greater on average, in unsuccessful females than in successful ones. Also, male head length appears to be subject to disruptive selection because males successful in egg production have a deviation from the mean which is 25% greater than in unsuccessful ones.

It is obvious that male head length is unlikely to be a direct determinant of the ability of the female to lay an egg, and it is difficult to envisage how disruptive selection will act on this trait unless an assortative mating effect is involved. Male head length deviation also approaches significance for the pair-to-hatching reproductive success measure, but since this includes the pair-to-egg measure,

Table 2 Proportionate differences between individuals showing reproductive success or failure

	Pair to egg	Pair to hatching	Pair to fledging	Egg to fledging	Hatching to fledging
Female hatching index	0.176	0.145	0.401	0.392	0.377
<i>P</i>			0.002	0.003	0.014
Female laying index	-0.071	-0.072	0.008	0.039	0.136
<i>P</i>					0.010
Male head length deviation	0.253	0.297	0.273	0.178	0.013
<i>P</i>	0.006	0.020			
Female bill depth deviation	-0.205	-0.136	-0.210	-0.074	-0.157
<i>P</i>	0.01				

Difference of success-failure is standardized by dividing by the average. Only variables with a significant difference have been included. *P* = probability value.

and the magnitude is only slightly larger (30%), this is probably measuring the effect of egg production alone.

The strongest effects on fledgling production are produced by the female hatching condition index (Table 2). The reproductive success measures of pair to fledging and egg to fledging are all significant at $P < 0.01$; and hatching to fledging approaches this ($P = 0.014$). The magnitude of the effect is large in that the successful females have a condition index which is approximately 40% greater than the unsuccessful ones in each case. The fact that pair to egg, pair to hatching, and egg to hatching measures are not significant suggests that the effect is restricted to the fledgling from hatching stage. In addition, since both birds feed the chick, the question remains why the difference occurs in the condition index for the female and not for the male.

The female laying condition index has a significant effect (14%) on hatching to fledgling production. One possible mechanism explaining this effect is that female condition is correlated with egg quality and that the effect is transmitted through the egg. On the hand, Nager et al. (1999) point out that egg production has a major effect on female condition in the lesser black-backed gull (*Larus fuscus*). In the shearwater, it is possible that females are more prone to desert than males because of poor condition during chick feeding, brought on by egg production, so threatening their future reproduction.

Some evidence exists of assortative mating in linear variables (Table 3). There are modest correlations between tarsus lengths and bill depths among pairs. Male head length also correlates with female bill depth, as does male summed zscore. Male prelaying mass and prelaying condition index correlate negatively with female bill length. Male laying condition index negatively correlates with female bill depth, and vice versa. While we might expect the strongest correlations between sexes to exist between like variables, this need not be the case. Forero et al. (2001) have demonstrated the occurrence of assortative mating from bill depth and body mass in magellanic penguins (*Spheniscus magellanicus*).

Adult prelaying mass is substantially correlated across the sexes (Table 3). This may be evidence that pair members feed together before laying, or, at least, share common experiences. Alternatively, such a correlation could be generated by assortative mating for foraging skills. There is evidence of a modest degree of assortative mating for breeding age in this species (Bradley et al., 1995). It is possible that increasing the age of breeding tends to generate heavier prelaying birds because they are more efficient foragers. In addition, there is a strong correlation between the male prelaying condition index and female laying condition index. This suggests that good male condition early in the reproductive period is linked to good female condition later. A possible explanation for this effect is that prelaying males in better condition are replaced later in the first incubation shift, allowing females to build up better condition.

6 Conclusion

We have found evidence in the short-tailed shearwater that individual quality, which is a constant attribute from year to year, is related to, and indicated by, specific physical traits, notably condition and bill depth. Such traits are predictors of reproductive success and, since studies of other avian species (e.g. Gustaffson, 1986; Gibbs and Grant, 1987) indicate that they have substantial heritability, the evidence suggests the operation of some form of natural selection.

Previous studies of this species have established assortative mating based on age from first breeding, which is itself a strong predictor of reproductive success (Bradley et al., 1995). Thus, it is likely that mate selection involves cues that give some indication of an individual's reproductive abilities. In this study, bill depth, which shows strong sexual dimorphism, also exhibits correlation between pair members, and, in the female, predicts reproductive success. It is possible that a mixture of significant sexual and stabilizing selection acts upon this trait, and that its strong dimorphism is the outcome of the balance between these effects.

Table 3 Correlations between physical traits of pair members

Female variables	Male variables					
	Head length	Bill depth	Tarsus length	Prelaying mass	Summed zscores	Prelaying condition index
Bill depth	0.164	0.135	0.056	-0.009	0.151	-0.118
<i>P</i>	0.003				0.007	
Tarsus length	0.062	0.053	0.163	-0.045	0.065	0.001
<i>P</i>			0.004			
Prelaying mass	-0.048	0.027	0.019	0.277	0.032	0.095
<i>P</i>				0.000		
Laying condition index	-0.103	-0.253	-0.200	-0.016	-0.194	0.378
<i>P</i>		0.002				0.007

The top figure is the Pearson correlation coefficient. Only variables with a significant correlation between pair members have been included. *P* = probability value.

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S02-2 Individual quality and recruitment in the common tern, *Sterna hirundo*

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Abstract We investigated the individual histories of more than 1 300 fledglings from an intensively studied colony of common terns, *Sterna hirundo*. Based on six cohorts (1992–1998), which had recruited almost completely by 2002, we found that the body mass of a fledgling was positively related to return and recruitment probability. Even in subadult stages, pre-fledging characteristics affect the probability of recruitment in this medium-sized seabird. Our results tend to be consistent for both sexes. In addition, older age at fledging reduced recruitment probability, particularly for late fledged young, reflecting indirectly on parental quality. However, other parameters of the egg and nestling period, such as clutch size, hatching order, and number of fledglings per brood, had no influence on recruitment of fledged young. The results suggest that body mass of young can be used as a predictor of recruitment probability and as an indicator of individual quality. These conclusions are discussed in the light of the meager information on pre-fledging characteristics and post-fledging survival in birds.

Key words Fledging mass, Pre-fledging characteristics, Post-fledging survival, Natural selection, Philopatry

1 Introduction

Only a small percentage of fledged young are recruited into the breeding populations of birds (review in Newton, 1989). In the common tern (*Sterna hirundo*), for example, barely a quarter return (Becker et al., 2001). Obviously, strong selection pressures operate during the pre-breeding stage. Effects of pre-fledging characteristics for survival in the natal period are well known and described for different seabirds (e.g., Parsons et al., 1976; Viksne and Janaus, 1990; Spear and Nur, 1994; Nisbet et al., 1995; Royal and Hamer 1998). Although some investigations have been able to show an influence of these parameters on survival after fledging, other studies have found none (Table 3). Accordingly, we ask here: do parameters of individual "quality" such as body mass, which is constant across years in individual terns (Becker and Wendeln, 1999), and other pre-fledging characteristics, influence return and recruitment of individual common terns in natal colonies?

2 Materials and methods

Our studies were carried out over 1992–2002 at the common tern colony "Banter See" in the harbor of Wilhelmshaven on the German North Sea coast (Becker et al., 2001). Over that period the colony increased from 90 to 280 pairs. All nests were marked and checked every 2–3 days to record the fate of eggs and banded chicks. Most chicks were also weighed to obtain continuous data on growth until fledging. All fledglings were marked with transponders enabling annual and lifetime identification (Becker and Wendeln, 1997).

Year after year, marked breeders as well as non-breeders were recorded remotely and automatically by an antenna system (Becker and Wendeln, 1997; Ludwigs and Becker, 2002), in order, according to the total population approach, to detect all returning and prospecting individuals as well as natal recruits. Any bird not re-recorded in the natal colony was

Table 1 Survival of common tern fledglings until recruitment in relation to different pre-fledging characteristics

Characteristic	B ± SE	Wald	df	P
Hatching order	-0.029 ± 0.151	0.036	1	0.849
Fledglings per brood	0.130 ± 0.150	0.752	1	0.386
Fledging date	-0.002 ± 0.009	0.029	1	0.866
Fledging age	-0.010 ± 0.036	0.081	1	0.776
Fledging mass	0.027 ± 0.012	5.537	1	0.019

Cohorts 1992–1998, multiple logistic regression, dependent variable = recruited or not until 2002: -2 log likelihood = 597.97, $\chi^2 = 7.64$, $df = 5$, $P = 0.177$, $n = 469$.

Table 2 Influence of fledglings per brood on recruitment rate in common terns

Fledglings per brood	Fate of the fledged tern					
	Not returned		Returned only		Returned and recruited	
One	130	54.9%	37	15.6 %	70	29.5%
Two	219	59.3%	41	11.1 %	109	29.5%
Three	101	56.1%	21	11.7 %	58	32.2%

Cohorts 1992–1998 ($\chi^2 = 3.375$; $df = 4$; $P = 0.497$)

considered as dead. We sexed terns by their mating behavior at the colony site. Beginning comprehensively in 1998, we sexed all fledglings by PCR, maintaining that information for all fledglings including non-returners.

From these data we analyzed the influences of pre-fledging characteristics on return and recruitment in the natal colony. The analyses cover all fledglings of cohorts 1992–1998 and their fate (= recruited or not) until 2002. Because the majority (~90%) of all fledglings were recruited to the natal colony within four years (Ludwigs and Becker, 2002), we include here nearly all recruits out of the total 983 fledglings from the seven cohorts, except for a few birds still to be recruited in ensuing seasons. In some cases, information on some variables was missing; and sample sizes therefore vary between analyses: χ^2 -test, T -test, ANOVA. In the logistic regression (Table 1), we did not use all pre-fledging characteristics measured, in order to prevent proliferation of subgroups with small sample sizes. The level of significance used in the analyses is $P < 0.05$.

3 Results

41% of fledged cohorts 1992 through 1998 returned as prospectors from 1994 through 2002, and 28% were recruited into their natal colony at Banter See. During the subadult period, most pre-fledging characteristics had no influence on recruitment of the fledglings, which had left the colony (Table 1).

3.1 Clutch and nestling characteristics

Clutch size had no influence on recruitment (two and three eggs only: $\chi^2=0.558$; $df=2$; $P=0.756$; $n=834$). Neither did hatching order ($\chi^2=1.646$; $df=4$; $P=0.800$; $n=677$) nor the number of fledglings per brood (Table 2), or even on return to the colony (Table 1).

3.2 Fledgling characteristics

Body mass of fledglings was very significantly different between recruits and terns not recruited. On average, the body mass of fledglings recruited was 2% higher than those not (maximum chick mass: 127.8 \pm 9.2 g versus 125.5 \pm 9.4 g, $T_{582} = 2.766$, $P < 0.01$; fledging mass: 119.3 \pm 8.6 g versus 117.2 \pm 9.5 g, $T_{582} = 2.488$, $P < 0.02$). Both mass parameters were related to return and recruitment probability, but in this paper we concentrate on fledging mass (Fig. 1, Table 1). Even in the broader group of returned fledglings, this parameter affected the chance of recruitment into the colony according to the analysis: returned terns of the cohorts

1992–1998; dependent variable: recruited or not until 2002; log.reg.: $B = 0.032 \pm 0.016$; Wald = 4.126, $df = 1$, $P < 0.05$, $n = 256$. Of the fledglings recruited into the colony, 10%–35% reflected the effect of fledging mass (Fig. 1).

Both fledging age and fledging date were correlated negatively with fledging mass, but fledging age was correlated positively with fledging date. What this means is that old fledglings left the colony late in the season. However, a partial correlation of mass with fledging age corrected for fledging date revealed the importance of fledging age rather than date for recruitment (fledging age by fledging mass controlled for fledging date: $r = -0.280$; $P < 0.001$). Terns fledged older were lower in mass. The fledging mass of birds with median fledging age (25–27 d; 118.6 \pm 7.9 g) was similar to the mass of those fledged younger (119.8 \pm 8.6 g), but both groups differed significantly from terns fledged older than 27 d (114.1 \pm 11.5 g; ANOVA: $F_{2,580} = 16.528$, $P < 0.001$; post hoc Scheffé-test result: fledglings <25 d and 25–27 d versus >27 d; $P < 0.001$).

The difference of fledging mass between recruits and non-recruits was particularly distinct in the old fledged young (>27 d; 116.6 \pm 9.5 g versus 113.2 \pm 12.0 g; T -test: $T_{134} = 1.487$, $P = 0.139$). When cohort 1999 (not yet completely recruited by 2002) was included, this difference became significant: 116.5 \pm 9.8 g versus 111.5 \pm 11.6 g; T -test: $T_{190} = 2.464$, $P < 0.02$. From another view, recruited late fledged young (>2 d later than the median date) were significantly younger at fledging than those not recruited (26.5 \pm 2.9 d versus 27.8 \pm 3.6 d; T -test: $T_{335} = -2.867$, $P < 0.005$); but this was not found in terns that fledged early or at median dates (T -test, n.s.).

3.3 Sex differences in fledging mass and recruiting rates

There were some differences between females and males in recruiting rates and fledging mass (Fig. 2), with fledging mass showing a tendency to influence recruitment in both (Fig. 2; combined data: $B = 0.029 \pm 0.012$; Wald = 5.893, $df = 1$, $P < 0.02$).

3.4 Fledging mass and recruitment age

We found no effect of fledging mass on age of recruitment. The mean fledging mass of 3-year-old recruits (118.1 \pm 8.0 g) was similar to younger (118.1 \pm 8.4 g) or older recruits (119.7 \pm 9.6 g; ANOVA: $F_{2,220} = 0.769$, $P = 0.465$). A separate analysis for each sex indicated no significant effect either. According to the data for males: cohorts recruited completely 1992–1997; $n = 77$; 2 year old = 120.0 (3.6 g, 3 y = 120.2 \pm 6.9 g, >3 y = 121.5 \pm 9.6 g. However, in females, a nega-

Table 3 Studies reporting effects of pre-fledging characteristics on post-fledging survival in long-lived birds

Characteristic	Influence	No influence
Clutch size	15, 18	22
Hatching order	18	8, 15, 22
Hatching date*	5–7, 9, 10, 13–17	2, 4, 12, 21
Fledgl. per brood	15	22
Growth rate	18	
Body size	1	
Chick peak mass	6, 22	21
Fledging mass	2–6, 22	(12), 19, 21
Body condition	1, 11, 13	19
Fledging age	22	12, 21

*or fledging date

1. *Diomedea exulans* (Weimerskirch et al., 2000).
2. *Calonectris diomedea* (Mougin et al., 2000).
3. *Puffinus gravis* (Elliot et al., 1973).
4. *Puffinus griseus* (Richdale, 1954; Sagar and Horning, 1998).
5. *Puffinus puffinus* (Perrins 1966; Perrins et al., 1973).
6. *Sula capensis* (Jarvis, 1974).
7. *Phalacrocorax aristotelis* (Harris et al., 1994).
8. *Egretta garzetta* (Hafner et al., 1998).
9. *Anser caerulescens* (Cooke et al., 1984).
10. *Aythya affinis* (Dawson and Clark, 2000).
11. *Somateria mollissima* (Christensen, 1999).
12. *Haematopus ostralegus* (Kersten and Brenninkmeijer, 1995).
13. *Stercorarius parasiticus* (Phillips and Furness, 1998).
14. *Catharacta skua* (Cetry et al., 1998).
15. *Larus ridibundus* (Viksne and Janaus, 1993).
16. *Larus argentatus* (Nisbet and Drury, 1972; Parsons et al., 1976).
17. *Larus occidentalis* (Spear and Nur, 1994).
18. *Rissa tridactyla* (Coulson and Porter, 1985).
19. *Uria aalge* (Hedgren, 1981, Harris et al., 1992).
20. *Alca torda* (Lloyd, 1979).
21. *Fratercula arctica* (Harris and Rothery, 1985).
22. *Sterna hirundo* (this study).

tive trend in fledging mass with recruitment age was suggested: $n = 61$; $2y = 122.0 \pm 6.1$ g, $3y = 118.6 \pm 8.2$ g, $>3y = 117.3 \pm 11.6$ g, ANOVA n.s.).

4 Discussion

There are very few studies addressing influences of pre-fledging characteristics on post-fledging survival in long-lived birds, particularly with respect to body mass. Moreover, all such investigations listed in Table 3 are based on ring recoveries, resightings and/or live recaptures, where the effort spent on recatching or resighting particular banded birds carries limitations. Consequently, the proportion of recovered to unrecovered birds can be very low, often $<3\%$ versus $>97\%$ and almost never as high as 10% versus 90% (e.g., Hedgren, 1981; Viksne and Janaus, 1993; Phillips and Furness, 1998). Therefore it seems likely that such studies include moderate proportions of surviving birds in their groups of non-returners, as some workers have admitted: about 10% estimated by Harris and Rothery (1985). Recorded differences in proportions of surviving versus lost individuals are thus biased against survivors, particularly

where the differences are small or, as Nisbet (1996) points out, the data are “relatively insensitive to detect influences”. The use of transponders in our common tern study enabled us to use a total population approach by recording each individual returning to the natal colony ($>40\%$ of fledglings). However, dispersal rate could not be calculated.

Nearly all pre-fledging characteristics investigated here were unimportant for post-fledging survival in common terns (also Dittmann et al., 2001). Body mass, however, is a decisive pre-fledging factor for recruitment. Even if the difference in pre-fledging mass was only a few grams (2% of body mass), it had a significant influence on recruitment probability. In some shearwaters and the South African gannet (*Sula capensis*), several studies have also shown the importance of high fledging mass for post-fledging survival (Elliot, 1970; Jarvis, 1974) or for return to the natal colony (Perrins et al., 1973; Sagar and Horning, 1998), or survival until breeding age (Mougin et al., 2000). Shearwaters have to manage the time after fledging without adult guidance. In consequence, mortality is high immediately after fledging and fledglings need to leave their colony as fat as possible (Mougin et al., 2000), as reflected in distinct mass-differences between returners and non-returners, small sample sizes notwithstanding.

Terns benefit from prolonged parental guidance after fledging (Burger, 1980; pers. obs.). In this respect, they could be described as intermediate between auks, which leave the colony under parental care at a pre-fledging stage (Lloyd, 1979; Hedgren, 1981; Harris et al., 1992), and shearwaters, which are all but independent at fledging (Perrins et al., 1973; Sagar and Horning, 1998; Mougin et al., 2000). Chicks of common murre (*Uria aalge*) (Hedgren, 1981; Harris et al., 1992) and razorbills (*Alca torda*) (Lloyd, 1979) leave the colony long before independence, and are fed by their parents for a long period at sea before reaching their “independence” mass. That may well be one reason why, in the Alcidae, no evidence has been found for any influence by pre-fledging body mass on survival after fledging.

Our results for the effect of fledging body mass on survival support those from other species in which parental care is reduced or lacking at the post-fledging stage. Similar pre-fledging characteristics, such as body size in male wandering albatrosses (*Diomedea exulans*) (Weimerskirch et al., 2000), body condition in arctic skuas (*Stercorarius parasiticus*), common eider females (*Somateria mollissima*) and wandering albatross females (Phillips and Furness, 1998; Christensen, 1999; Weimerskirch et al., 2000), and growth rates in kittiwakes (*Rissa tridactyla*) (Coulson and Porter, 1985), and their positive correlation with survival after fledging, support the generality that individual body mass at early stages of life is significant for later recruitment probability in long-lived birds, just as it is in songbirds (e.g., Garnett, 1981; Magrath, 1991; Ringsby et al., 1998; Both et al., 1999; Naef-Daenzer et al., 2001).

As Sagar and Horning (1998) suggested for shearwaters, sex-related philopatry which is higher in males,

and the tendency of males to be larger than females, might influence mass-related survival in fledglings. In the common tern, the sexes showed differences in philopatry and mass dimorphism (Fig. 2). Both sexes, nevertheless, trended in the same way, so we consider that our results were not mediated by sex-related differences.

Hatching date has an influence on post-fledging survival in a number of species (Table 3). Most workers have not clearly separated the periods before and after fledging in their studies, because chicks were often banded and measured at some time during development, without knowledge of whether they actually fledged. As a parameter for survival, hatching date is much easier to use than age at fledging age or body mass during development which need more effort in fieldwork.

In the common tern, fledging age and not hatching or fledging date was a principal factor affecting recruitment probability. The advantages of hatching or fledging early are described in the literature as direct effects influencing survival, as in providing more time to prepare for migration (Cooke et al., 1984; Dawson and Clark, 2000), establishing dominance over late-fledged young (Nisbet and Drury, 1972; Spear and Nur, 1994), and allowing more time to gain experience in hunting (Newton, 1986), or indirect effects, such as parental quality (Spear and Nur, 1994; Catry et al., 1998). In late fledged common terns, we found lower masses, particularly in terns fledged >2 d later than the median fledging date. These older and lighter fledglings were handicapped.

Fledging age rather than date suggests here an indirect effect: reduced parental quality in parents that breed late and need more time to rear their young. In comparison, high quality breeders are those that can rear their young and bring them to high mass levels in a shorter time, even late in the season. In the snow petrel (*Pagodroma nivea*), Tveraa and Christensen (2002) found evidence that fledging mass of young is affected by parental quality, because

adults with higher body condition guarded their chicks for a longer periods and left them with higher body mass at independence. In the thick-billed murre (*Uria lomvia*), Hipfner (2001) found no differences in survival to recruitment age between early- and late-hatched chicks if late-hatched young came from replacement clutches. Thus, the influence of hatching date advocated in such studies might reflect other pre-fledging characteristics instead, notably body mass and the indirect effect of parental quality.

The positive link between fledging mass and recruitment probability in the common tern was evident at different stages of subadult life, at first return to the natal colony when two or three years old (Fig. 1), and during the prospecting period until recruitment at least one year later (Ludwigs and Becker, 2002). In Kittiwakes, recruits showed higher body masses in their year of first breeding compared to prospectors of the same year (Porter and Coulson, 1987), indicating the immediate importance of body mass in the decision to breed. However, we found no mass differences between recruits of different age in the common tern. Owing to sexual differences in the mass of fledglings, and the younger recruitment age of female common terns (Ludwigs and Becker, 2002), it was necessary to separate sexes; females recruited younger tended to be heavier. For males, other factors seem to influence delayed first attempts to breed.

Body mass has been found to be an important parameter for survival not only for the subadult period but also in other aspects of life history in the common tern. It is positively linked with reproductive success (Wendeln and Becker, 1999), related to fitness (Becker, 1999) and seems to be highly heritable (unpubl. data), as Phillips and Furness (1998) suggested for body condition in the arctic skua. The evidence presented here for the decisive influence of pre-fledging and fledging body mass on survival and recruitment in the common tern leads to the assumption that this phenomenon may be more widespread in birds than supposed so far.

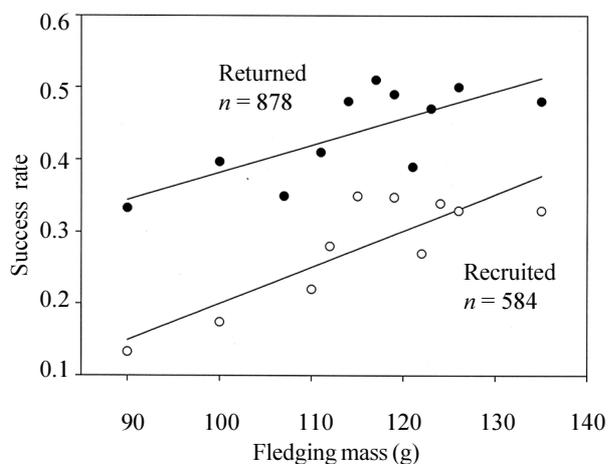


Fig. 1 Return and recruiting rate of common terns in relation to fledging mass

Fledging mass showed a significant influence on return rate (cohorts 1992–1999 log. reg. = $B = 0.019 \pm 0.007$; Wald = 6.617, $df = 1$, $P < 0.02$) and recruiting rate (cohorts 1992–1998 log. reg. = $B = 0.025 \pm 0.010$; Wald = 6.069, $df = 1$, $P < 0.02$).

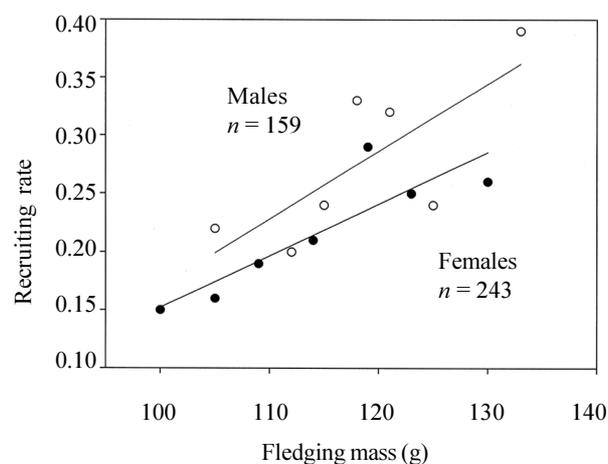


Fig. 2 Recruiting rate of common tern in relation to sex and fledging mass

Cohorts 1997–1999, dependent variable — recruited or not until 2002: females log. reg., $B = 0.020 \pm 0.017$; Wald = 1.319, $df = 1$, $P = 0.251$; males log. reg., $B = 0.030 \pm 0.020$; Wald = 2.235, $df = 1$, $P = 0.135$.

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S02-3 The trade-off between survival and reproduction in long-lived birds, and the role of individual quality

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Abstract We tested the influence of individual body mass on survival and reproductive performance in the blue petrel, *Halobaena caerulea*. Body mass varied between and within individuals, as well as between reproductive states: non-breeders were lighter than failed and successful breeders, and failed breeders were lighter than successful breeders. The probability of survival was affected by individual body mass, particularly for first time failed breeders which had a lower probability of survival than experienced breeders. This suggests the existence of a costs-of-first reproduction on survival, and that first reproduction may act as a filter selecting for individuals of intrinsically high quality. Non- and failed breeders had a higher probability of breeding failure in the next years than successful breeders, suggesting that these birds were poor quality individuals. This was reinforced by the fact that non-breeders had a high probability of remaining so, and by the fact that non-breeders and failed breeders had a low probability of becoming successful breeders. The results indicate that body mass is a good indicator of individual quality in blue petrels.

Key words Blue petrel, Body mass, Reproduction costs, Individual quality, Multistate capture-recapture models, Survival probability, Trade-offs

1 Introduction

Life-history theory predicts that animals balance their investment in young raised against their own chance to survive and reproduce in the future (Williams, 1966; Roff, 1992; Stearns, 1992). This trade-off, referred to as the cost of reproduction, holds a central place in life-history theory. Long-lived seabirds are good candidates for models to detect these costs. They can be expected to be more restrictive than short-lived birds in the degree to which they exhibit increased effort, because even a small reduction in adult survival will reduce the number of subsequent breeding attempts, thereby lowering lifetime reproductive success considerably (Reznick, 1985; Roff, 1992; Stearns, 1992). However, at least two factors are likely to confound measurements of this trade-off in the wild. First, differences can arise in the amount of energy individuals acquire and allocate to various functions. In that case, we might expect some (high quality) individuals to perform well in both reproduction and survival, and other (low quality) individuals to die sooner (Curio, 1983; Reznick, 1992; Viallefont et al., 1995; Cam et al., 1998). Secondly, there can be variation in resource availability affecting energy acquisition and allocation (Erikstad et al., 1998; Orzack and Tuljapurkar, 2001).

Theoretical models examining the optimal phenotypic balance between reproduction and adult survival under variable breeding conditions have recently investigated the second issue (Erikstad et al., 1998). However, very little is known of the influence of individual quality on the costs of reproduction. Here, we use a capture-recapture dataset of

blue petrels (*Halobaena caerulea*) to test the influence of body condition, as an indicator of individual quality, on survival and reproductive performance.

2 Materials and methods

This study was conducted on Mayes Island in the Kerguelen group, South Indian Ocean (48°38'S, 68°38'E). Each year between 1987 and 2001, 72 to 233 burrows of blue petrels were monitored (see Chastel et al., 1995a). All birds found in burrows were given individual leg bands and their identity recorded. Burrows were checked a few days after laying to identify the two breeding partners, and after hatching and fledging to record hatching and breeding success respectively. Each bird captured at the colony was classified either as a non-breeder (no egg laid), as a failed breeder (when the bird did not successfully hatch its egg or fledge its chick), or as a successful breeder (when the bird fledged a chick).

Body mass at the onset of the breeding period (measured to the nearest 2 g with a 300 g Pesola balance) was recorded each year from birds caught in their burrows. In this data set we used birds weighed after the pre-laying exodus (Warham, 1990), when birds arrive from the sea to start their first incubation shift. Although body mass is partly the result of structural body size and body fat reserves (Piersma and Davidson, 1991), earlier studies have demonstrated that in the blue petrel, body mass alone is a good indicator of body reserves (Chastel et al., 1995a). Consequently, we used body mass as a surrogate for body condition.

From this long-term study we extracted individual capture histories, including information on whether an individual was re-sighted each breeding season, and if so, on its breeding state: 1 = non-breeder, 2 = failed breeder, 3 = successful breeder. Data were analyzed using multistate capture-recapture models (Brownie et al., 1993) and program MARK (White and Burnham, 1999). These models included three kinds of parameters: recapture probability p_{r^*p} , survival rate S_{r^*p} , and conditional transition probability Ψ_{r^*t} (Nichols et al., 1994). In order to draw inferences about the evolutionary consequences of breeding successfully, unsuccessfully or not at all, we first investigated two complementary fitness components, estimating and comparing (1) survival of successful, failed and non-breeders, and (2) the respective probabilities that these three categories of birds would breed again, given their survival. Then, because we wanted to draw inferences on the cost of first reproduction to test the hypothesis that poor quality individuals die sooner, we started our model selection by using a model with two age classes for survival and state transition probabilities: first time breeders *versus* experienced breeders.

For non-breeders, we only considered one age class since there was no cost associated with reproduction. Because we wanted to test for the effect of the mean body mass of individuals on transition and survival probabilities across years, we started with a model where survival and transition probabilities were constant across years but state specific. Capture probabilities were not constrained and were state and time dependent. Thus, we derived our initial model ($S_{r,s^*a_2} p_{u^*t} \Psi_{u^*a_2}$), where $r = 0$ (not seen) or 1 (non-breeder); $s = 0$ (not seen), 2 (failed breeder), or 3 (successful breeder); $u = 0$ (not seen), 1 (non-breeder), 2 (failed breeder), or 3 (successful breeder); a_2 is the age with two age classes; and t is time. As goodness-of-fit tests suitable for multistate capture-recapture models do not exist, we performed a goodness-of-fit test of the Cormack-Jolly-Seber model with all states pooled using the program U_CARE (Choquet et al., 2001).

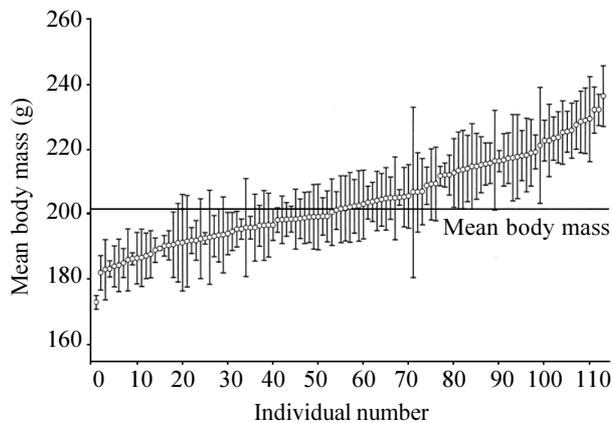


Fig. 1 Mean (\pm SD) body mass for 113 individual blue petrels ranked according to body mass

The plain horizontal line indicates the grand mean body mass for all individuals across years.

Because we detected dependence in sighting probabilities (see Results: goodness-of-fit tests), we used the modification proposed by Pradel (1993) for trap dependence. However, even when accounting for trap dependence in sighting probabilities, the goodness-of-fit test still indicated significant lack of fit. To account for that extra-binomial variation, we computed a conservative variance inflation factor, \hat{c} (see Lebreton et al., 1992). Consequently, we started our model selection from the general model ($S_{r,s^*a_2} p_{u^*t^*m} \Psi_{u^*a_2}$), where m is trap dependence. We used the quasi-likelihood Akaike's Information Criterion adjusted for sample size, QAICc (Akaike, 1973; Lebreton et al., 1992) to select parsimonious models for the data; the model with the lowest QAICc was selected.

A particular kind of model resulted, where state-specific parameters are modeled as a function of mean individual body mass on a logit scale (Lebreton et al., 1992). For each individual we calculated the average body mass across years during the incubation. This mean individual mass was then used as an individual covariate in our modeling. For example, survival was modeled as a function of mean individual body mass using the equation: $\text{logit}(S_r) = a + b \times \text{mass}$, where a is an intercept parameter, b is a slope parameter and mass is the mean individual body mass.

3 Results

3.1 Body mass and reproductive success

Body mass was variable both within and between individuals (Fig. 1). Body mass varied between years and reproductive status *GLM* using SAS (2001), with individual number nested within status to account for related samples of birds which have been treated for several years; year:

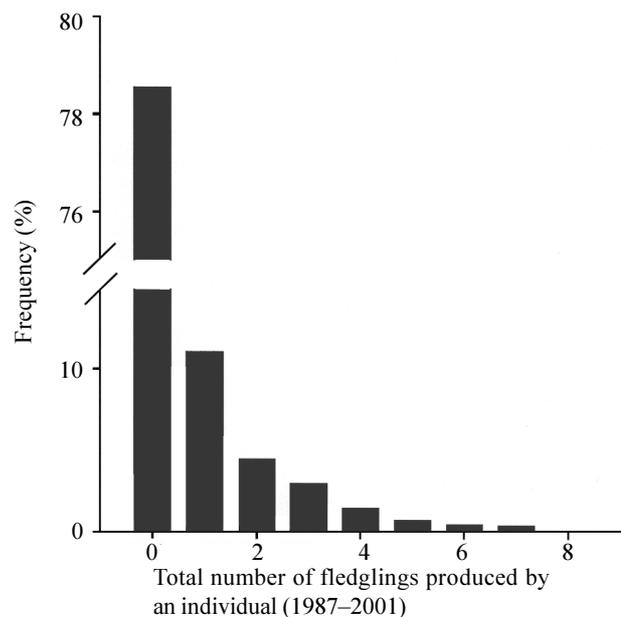


Fig. 2 Percentage of individual blue petrels in the studied population that produced from 0 to 8 chicks between 1987 and 2001

$F_{14,957} = 17.73, P < 0.0001$; status (individual): $F_{1552,957} = 1.76, P < 0.0001$; year*status: $F_{27,957} = 2.12, P = 0.0008$. Successful breeders were heavier than failed breeders (post-hoc Tukey test = 2.479, $P = 0.038$) and non-breeders (post-hoc Tukey test = 11.104, $P < 0.001$), and failed breeders were heavier than non-breeders (post-hoc Tukey test = 8.625, $P < 0.001$). During the study period, a high proportion of the population did not produce any chicks (Fig. 2), and the number of chicks produced by individuals was positively correlated with the mean individual body mass (ANOVA: $F_{7,556} = 2.999, P = 0.004$).

3.2 Goodness-of-fit tests

The goodness-of-fit test of the initial model ($S_{r,s^*a2}P_{u^*t} \Psi_{u^*a2}$) indicated that this model fitted the data poorly ($\chi^2 = 368.117, df = 74, P < 0.001$), and that there was trap dependence (see Pradel 1993). After taking into account trap dependence, the goodness-of-fit test of the general model ($S_{r,s^*a2}P_{u^*t^*m} \Psi_{u^*a2}$) was still unsatisfactory ($\chi^2 = 104.435, df = 62, P = 0.0004$). In order to correct for overdispersion, we used an inflation factor in the remaining analysis, $\hat{c} = 1.684$. This inflation factor remained well below 3 as recommended by Lebreton et al. (1992).

3.3 Modeling recapture, survival and transition probabilities

Examination of temporal variation in recapture probabilities suggested that recapture rates varied with year (Table 1, model 4 vs. model 8) and state (model 4 vs. model 5). A model where trap dependent temporal variations of state-specific parameters are parallel on a logit scale (model 6) was not preferred to model 4. We could reduce the number of parameters by setting capture probabilities constant for non-breeders and successful breeders but time dependent for failed breeders (model 3). As we could not reduce further the number of parameters corresponding to recapture probabilities, we continued our modeling with model 3. In this model, recapture probabilities varied between years for failed breeders, but were constant for successful breeders (≈ 1.0) and non-breeders (0.557 ± 0.047).

A model without an age effect on transition probabilities was preferred to a model where transition probabilities

were only state dependent (model 2 vs. model 3). However, transition probabilities were clearly state dependent (model 2 vs. model 7). Consequently, our best model before integrating the effect of body mass was the model ($S_{r,s^*a2}P_{NB^*m, FB^*t^*m, SB^*m} \Psi_u$), which indicated that blue petrel survival differed between breeding states and the age classes of breeders. Parameter estimates from this model indicate that the survival probabilities of non-breeders (0.863 ± 0.011) are significantly lower than those of failed (0.915 ± 0.021) and successful (0.957 ± 0.020) breeders. Survival probabilities are also lower for first time breeders than for experienced breeders, especially among those that failed (Fig. 3); and survival probabilities for first time failed breeders were lower than for non-breeders (Fig. 3A). The probability of both non-breeders and failed breeders becoming successful breeders was low (Fig. 3B). By contrast, non-breeders and failed breeders had a much higher probability of respectively becoming and remaining failed breeders (Fig. 3B). Successful breeders had a roughly similar chance of remaining successful or failing (and not breeding) (Fig. 3B).

We then examined the effect of individual body mass on survival and transition probabilities. Incorporating body mass as a covariate in our best QAICc model greatly improved the fit of the model (model 1 vs model 2; Table 1). This indicated a strong effect from individual mass on both survival probabilities and breeding state transition probabilities. In our attempts to reduce the number of parameters, we tried to eliminate the interactions between breeding status and body mass. The best model retained was $S_{r^*mass, s+a2+mass}P_{NB^*m, FB^*t^*m, SB^*m} \Psi_{u^*mass}$. Slope estimates from this model indicated that the survival probability of first time failed breeders was related to body mass almost significantly (slope = 9.525 ± 8.525), but that the survival probability of non-breeders and experienced breeders was not related to body mass (slope = 0.795 ± 0.609 and -0.823 ± 1.425 , respectively). Slope estimates between state transition probabilities and body mass indicated that the probability of a non-breeder or a failed breeder breeding successfully increased with body mass (Fig. 3C; slope = 2.604 ± 0.932 and 1.598 ± 1.260 , respectively). By contrast, the probability of being a non- or a failed breeder tended to decrease with body mass for failed breeders (slope =

Table 1 Modeling recapture, survival and transition probabilities between states for blue petrels at Mayes Island, Kerguelen Archipelago, between 1987 and 2001

Model	QAICc	Δ QAICc	#	DEV
1) ($S_{r^*mass, s+a2+mass}P_{NB^*m, FB^*t^*m, SB^*m} \Psi_{u^*mass}$)	5 313.18	0.00	45	5 221.43
2) ($S_{r, s^*a2}P_{NB^*m, FB^*t^*m, SB^*m} \Psi_u$)	5 348.28	35.09	54	5 237.75
3) ($S_{r, s^*a2}P_{NB^*m, FB^*t^*m, SB^*m} \Psi_{u^*a2}$)	5 358.74	45.55	60	5 235.61
4) ($S_{r,s^*a2}P_{u^*t^*m} \Psi_{u^*a2}$)	5 386.64	73.46	98	5 182.23
5) ($S_{r,s^*a2}P_{t^*m} \Psi_{u^*a2}$)	5 414.45	101.26	44	5 324.77
6) ($S_{r,s^*a2}P_{u+t+m} \Psi_{u^*a2}$)	5 425.70	112.52	37	5 350.51
7) ($S_{r, s^*a2}P_{NB^*m, FB^*t^*m, SB^*m} \Psi$)	5 431.52	118.34	49	5 331.44
8) ($S_{r,s^*a2}P_{u^*m} \Psi_{u^*a2}$)	5 452.49	139.30	23	5 406.03

The sign # indicates the number of parameters of the model, and DEV is the model deviance. For model notations, see Methods. The selected model is indicated in bold characters.

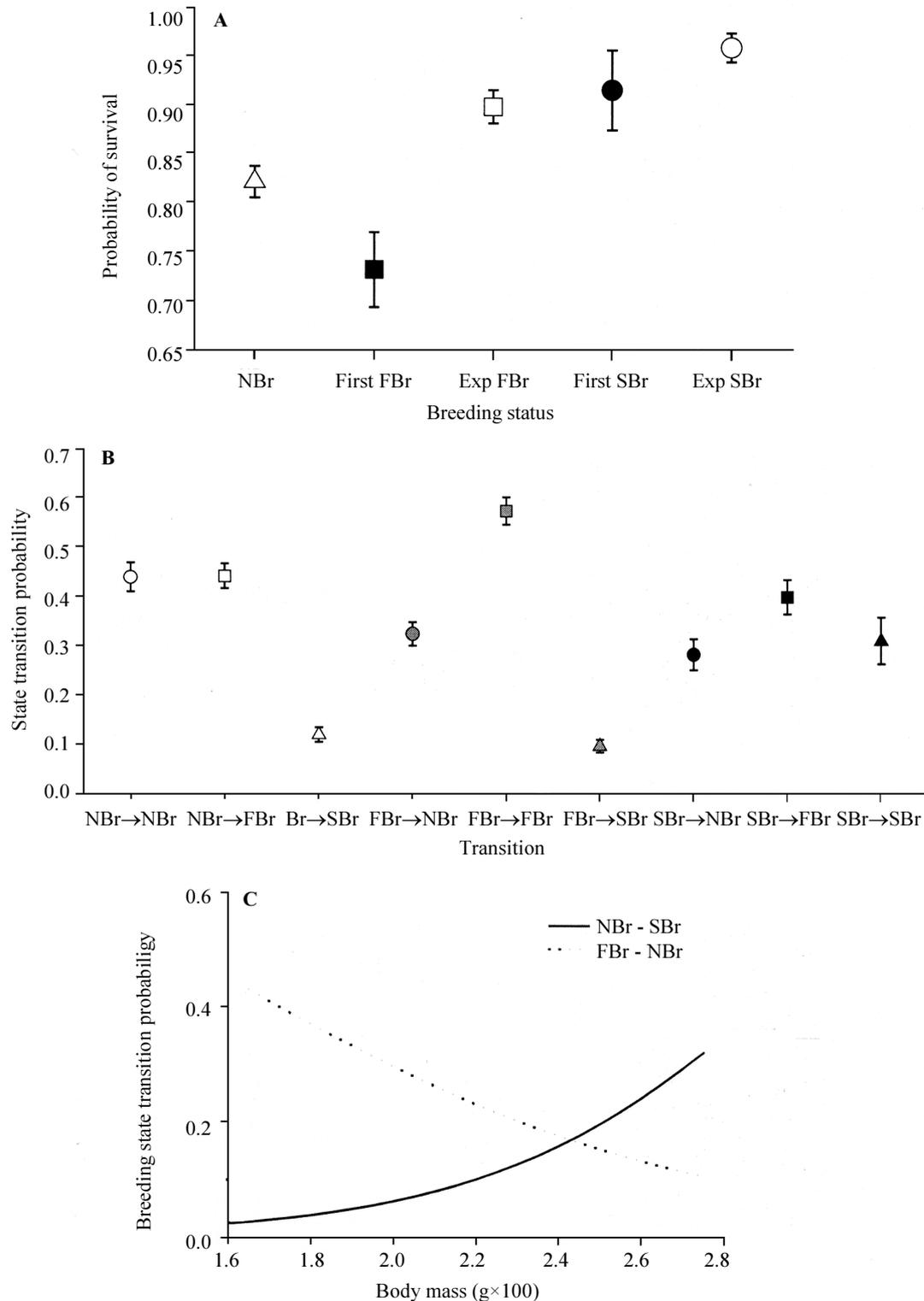


Fig. 3 A: Adult survival probability estimates as a function of the breeding status of blue petrels at Kerguelen Islands; B: Annual state transition probability estimates for blue petrels at Kerguelen Islands; C: Breeding state transition probabilities modeled as a function of body mass

In subfig. A: NBr = non-breeders (open triangle), First FBr = first time failed breeders (filled square), Exp FBr = experienced failed breeders (open square), First SBr = first time successful breeders (open circle), Exp SBr = experienced successful breeders (filled circle). Estimates are from model $S_{r,s^*a2}P_{NB^*m,FB^*t^*m,SB^*m}\Psi_u$; bars indicate $\pm SE$. In subfig. B: NBr = non-breeder, FBr = failed breeder, SBr = successful breeder. Estimates are from model $(S_{r,s^*a2}P_{NB^*m,FB^*t^*m,SB^*m}\Psi_u)$; bars indicate $\pm SE$. In subfig. C: estimates are from model $(S_{r^*mass,s^*a2+mass}P_{NB^*m,FB^*t^*m,SB^*m}\Psi_{u^*mass})$.

-1.669±1.352). No other relationship between state transition probabilities and body mass was significant.

4 Discussion

In blue petrels, individual body mass varies significantly between individuals. Interestingly, we recorded heavier individuals producing more fledglings during their breeding life than lighter birds. Previous work on blue petrels has revealed that body mass is a major factor affecting the decision to breed and the breeding output of individuals, heavier individuals having a higher probability of breeding successfully than lighter ones (Chaurand and Weimerskirch, 1994; Chastel et al., 1995a, 1995b). Here we have shown that mean individual body mass measured over several years, although variable from year to year, may be used as a surrogate of individual quality since it partly reflects the probability of breeding and the breeding output of an individual during its breeding life. This is an important finding because it is often difficult to identify a state variable reflecting individual quality. Although body mass is a dynamic variable (McNamara and Houston, 1996), in blue petrels it can be viewed as good an indicator of individual quality as in common terns, *Sterna hirundo* (Wendeln and Becker, 1999). Furthermore, there is evidence that some individuals are consistently heavier than others, notwithstanding variation between years (Barbraud and Weimerskirch, unpublished data).

Survival in non-breeders averaged lower than in failed breeders, which in turn was lower than in successful breeders. Because of the influence of body mass (i.e., individual quality) on reproductive status, we suspect that these differences are linked to differences in individual quality, as suggested by Mills (1989), Harris and Wanless (1995), Cam et al. (1998) and Sandercock et al. (2000) for red-billed gulls (*Larus novaehollandiae*), common guillemots (*Uria aalge*), kittiwakes (*Rissa tridactyla*) and green-rumped parrotlets (*Forpus passerinus*), respectively. These studies and ours are not in line with the hypothesis that non-breeding leads to an increase in survival, and provide no reason to interpret non-breeding as a means for preserving residual reproductive value (Coulson, 1984; Wooller et al., 1989; Aebischer and Wanless, 1992; Pugesek and Wood, 1992). Rather they suggest that a significant proportion of the non-breeders in any year might be low quality individuals, the remainder being individuals that skip reproduction for a year.

First time breeders had low survival, particularly among failed breeders, suggesting a cost of first reproduction on survival. The fact that this cost was less pronounced among successful breeders reinforces the individual quality hypothesis: successful breeders, being higher quality individuals, pay less in first reproduction. First reproduction costs may be particularly high for failed breeders because they engage those breeders in the novel investment of energy that would otherwise allocated to maintenance. Because blue petrels spontaneously desert their nests if they fall below a threshold body mass (Chaurand and

Weimerskirch, 1994), failed breeders are probably in poor condition at desertion, and thus may experience survival costs, particularly when environmental conditions are bad. Such first reproduction costs have recently been found in other long-lived species: the greater flamingo, *Phoenicopterus ruber roseus* (Tavecchia et al., 2001) and western gull, *Larus occidentalis* (Pyle et al., 1997).

Further insights into individual quality are revealed in breeding state transition probabilities. The fact that non-breeders and failed breeders had a higher probability of breeding failure than successful breeders strongly suggests that these birds were poor quality individuals. This is also reinforced by the fact that non-breeders had a high probability of remaining non-breeders, and by the fact that non-breeders and failed breeders had a low probability of becoming successful breeders, thereby suggesting that both had difficulties in attaining sufficient body mass to begin nesting. One may argue that there is a paradox in that successful breeders had nearly the same probability of becoming non-, failed or successful breeders. Indeed, according to the individual quality hypothesis and our previous results, one may expect that successful breeders should have a much higher probability of staying successful than our estimates indicate.

This, however, does not refute the individual quality hypothesis because it is the relative estimates of the breeding state transition probabilities, not their absolute values, that are important. Moreover, we suspect that successful breeders may skip breeding in some years (which may also reflect some costs of reproduction), thereby decreasing the average probability of remaining a successful breeder. In that perspective, this reinforces the individual quality hypothesis, because successful breeders that skip a year may be prudent parents (Drent and Daan, 1980). This idea could be tested further by investigating the influence of environmental conditions on breeding decisions and costs of reproduction with multistate time dependent models.

Overall, the results of this study indicate that body mass is a good surrogate of individual quality in blue petrels. The breeding states that were used appear to reflect individual quality, but these states probably partly reflect inter-individual body mass variations, which is the major determinant of breeding state in small procellariiform species (Chastel et al., 1995a). In other words, our results suggest that the relative quality of an individual, although measured with a dynamic state variable such as body mass (McNamara and Houston, 1996), is fairly constant over time.

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Symposium 04 Influence of birds on ecosystem structure and function

Introduction

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Birds are one of the best studied groups of organisms, receiving much attention because of their interesting morphological and physiological characteristics and their fascinating behavior. Many studies have shown that these traits are adaptations to both the biotic and abiotic environments in which birds live. However, birds are not just influenced by their environment; they themselves influence it, impacting on cohabiting species in ecological communities and on processes operating in ecosystems.

One of the major questions now being addressed in ecology is the influence of biodiversity, i.e. species richness, on ecosystem structure and function (Loreau et al., 2001). Surprisingly, little is known about the effects that birds have on other species in ecological communities and on ecosystem processes. Nor, in this context, has much attention been paid to keystone species, which are those species that have disproportionate impacts on ecosystems (Power and Mills, 1995). Changes in the abundance of keystone species can lead to especially large changes in ecosystem structure and function.

Situations in which birds can have especially marked impacts in ecosystems include: 1, bottom-up control of food webs; 2, top-down control of food webs; 3, flower pollination; and 4, seed dispersal. The role of birds in the bottom-up control of food webs has been shown in a series of excellent studies by Gary Polis and co-workers. They demonstrated that breeding seabirds transport sufficient energy and nutrients from the sea on to land to shape the food webs of whole islands (e.g., Stapp et al., 1999). Top-down control of food webs can act through grazing or predation, birds being particularly important as predators in marine systems (e.g., Wotton, 1992) and on invertebrates in terrestrial ecosystems (e.g., Murakami and Nakano, 2000). Reviews in this symposium highlight other examples. Gilles Gauthier et al. examine the impact of geese as grazers on arctic and temperate wetlands. Sandra Anderson et al. dem-

onstrate that birds play a crucial role as pollinators in New Zealand's terrestrial ecosystems. And Bärbel Bleher and Katrin Böhning-Gaese show that birds can have profound effects on forest regeneration as seed dispersers.

Two further papers, one by Klaus-Michael Exo on balances in predation by shore birds on the benthic community in the Wadden Sea, the other by Charles Brown and Scott Robinson on decision-making in habitat selection and dispersal, were presented as orals only. Abstracts of their papers are published in the Abstract Volume of the Congress.

Several of these studies make the point that a certain species richness of birds is necessary for the successful servicing of ecosystems (Anderson et al.; Bleher and Böhning-Gaese). In some circumstances, moreover, bird species operate alone as keystone taxa (e.g., snow geese *Anser caerulescens*, tui *Prosthemadera novaeseelandiae*, New Zealand bellbird *Anthornis melanura*, and the New Zealand pigeon *Hemiphaga novaeseelandiae*). Conservation and management of such species is necessary not only because of their intrinsic and aesthetic value but also because of the ecosystem services that they provide.

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S04-1 The impact of goose grazing on arctic and temperate wetlands

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Abstract Geese are large, herbivorous birds that graze in huge flocks in ways that may have a considerable impact on vegetation. This is exemplified best in two subspecies of snow geese, the lesser and the greater, both of which have increased dramatically in numbers in recent decades. In arctic coastal salt marshes, moderate goose grazing on *Puccinellia phryganodes* enhances plant production, but if it intensifies beyond a certain threshold it destroys the plant cover, leading to hypersalinity, soil erosion and little revegetation for long periods. In freshwater tundra wetlands dominated by *Dupontia fisheri*, *Eriophorum scheuchzeri* and brown mosses, grazing changes plant composition and reduces production of *Eriophorum*. Grazing may also favor mosses at the expense of grasses and sedges because mosses short-stop most of the nitrogen released from goose faeces. In temperate salt marshes, damage to the binding plant *Spartina alterniflora* from goose grubbing has been locally severe and has led to the devegetation of large areas. In temperate brackish marshes, geese heavily grub the rhizomes of *Scirpus pungens*. Their grubbing depresses *Scirpus* production, alters plant species composition, and influences marsh dynamics by enlarging ice-made depressions which are then colonized by other species. Grazing and grubbing in arctic and temperate freshwater wetlands apparently leads to a low-level production equilibrium between geese and the plants, but not in salt marshes.

Key words Snow geese, Grazing, Grubbing, Herbivory

1 Introduction

Herbivores can have a profound effect on ecosystems. Large mammalian herbivores, such as the ungulates on the African savannas and Caribou on the arctic tundra, commonly affect production, structure and species composition in plant communities. Geese are among the few herbivorous groups of birds; and, in some circumstances, they too can impact significantly on natural plant communities. In this paper, we examine the impact of goose grazing on four different communities: arctic salt marsh, arctic freshwater meadow, temperate salt marsh, and temperate freshwater/brackish marsh. Due to their migratory habits, geese use arctic marshes in summer and temperate habitats during winter and on spring and fall migration. Our focal goose is the snow goose (*Anser caerulescens*), an abundant and widespread species in North America.

Several factors predispose geese to have a large impact on ecosystems. First, they are strictly herbivorous. Secondly, they have a low digestive efficiency (~35%) and thus eat large quantities of forage daily, of up to 1/3 of body mass, to meet energy requirements. Thirdly, geese are gregarious and feed in flocks, often numbering in the thousands. Fourthly, geese forage by two methods in natural habitats: grazing on above-ground leaves and shoots, and grubbing below the ground for rhizomes and bulbs. Fifthly, many goose populations have increased recently in North America, due in part to a fortuitous supply of food on

agricultural lands in winter and spring. This is especially true for the two subspecies of snow goose, both lesser (*A. c. caerulescens*) and greater (*A. c. atlanticus*), which have exploded exponentially in recent decades to reach about 6 and 0.8 million birds, respectively (Abraham and Jefferies, 1997; Menu et al., 2002).

2 Arctic salt marshes

The west coast of Hudson Bay in subarctic Canada is a breeding site for lesser snow geese. Broad intertidal coastal flats dominated by a grass (*Puccinellia phryganodes*) and a sedge (*Carex subspathacea*) are the most important foraging habitat there. Grazed at a moderate level, the graminoids overcompensate in growth, so that by the end of a season under such a grazing regime, total above-ground production is higher there than in un-grazed sites (Cargill and Jefferies, 1984; Hik and Jefferies, 1990). Such a response results from the fertilizing effect of goose faeces and the colonization of bare sediments in grazed swards by nitrogen-fixing cyanobacteria (Bazely and Jefferies, 1985, 1989). Thus, moderate goose grazing increases productivity in this nutrient-poor community by speeding up the cycling of nutrients, especially nitrogen.

The state of the system can change dramatically, nevertheless, if this threshold in grazing intensity is exceeded. When this has happens, due, for example, to exploding population goose populations, the pseudostems

of the grasses are damaged and the regrowth of swards severely impaired. Even more serious is the intense spring grubbing by staging geese en route to more northern breeding colonies. At snowmelt, geese excavate rhizomes around ponds and can strip vegetation from large areas (Jefferies, 1988).

When bare soil is exposed by such foraging, evaporation rate increases from surface sediments; and inorganic salts, which are abundant in the underlying marine clay sediments, rise to the surface. Salt accumulation at the surface leads to hypersalinity (>32‰), which is deleterious to graminoid growth and other vascular plants. Hypersaline conditions can lead further to death of surrounding vegetation (Iacobelli and Jefferies, 1991), which in turn exposes more sediments and promotes further evaporation and increase in salinity. Thus, goose damage to vegetation can lead to a runaway process of increasing destruction of salt marsh swards that is analogous to desertification (Srivastava and Jefferies, 1996). These processes have led to vegetation loss over large expanses of the Hudson Bay lowlands (Jano et al., 1998).

Goose-driven degeneration of the arctic salt marsh ecosystem has had an impact on the goose population itself, as goslings have undergone a dramatic drop in growth and survival (Williams et al., 1993). Destruction in this ecosystem also affects other bird species. Thus passerines and shorebirds such as the semipalmated sandpiper (*Calidris pusilla*) have declined in habitats damaged by geese (Gratto-Trevor, 1994; Abraham and Jefferies, 1997).

3 Arctic freshwater wet meadows

In many arctic landscapes, geese, such as the expanding breeding colony of snow geese on Bylot Island in the Canadian High Arctic, use freshwater wetlands for feeding. Their preferred feeding habitats are fens, often called wet sedge meadow (Gauthier et al., 1996). The fens are peat-accumulating systems because brown mosses cover them. They also have a lush graminoid cover dominated by the grass *Dupontia fisheri* and the sedges *Eriophorum scheuchzeri* and *Carex aquatilis*. The first two species are preferred by foraging geese (Manseau and Gauthier, 1993).

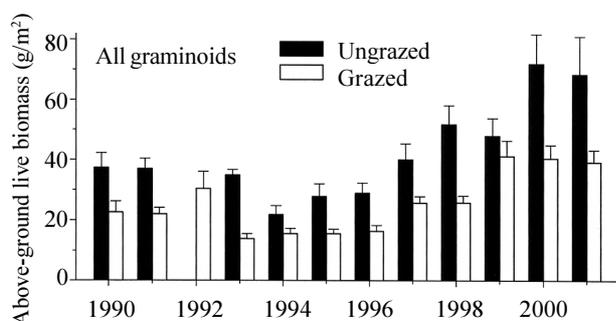


Fig. 1 Live above-ground biomass (mean \pm SE, dry mass) of graminoids at mid August in grazed and ungrazed wet meadows on Bylot Island, Canadian High Arctic ($n = 12$) Graminoids include *Eriophorum scheuchzeri*, *Dupontia fisheri* and *Carex aquatilis*.

We have been monitoring the impact of goose grazing on Bylot Island since 1990, comparing the biomass at peak production in August inside and outside 1×1 m exclosures set up for one year. We have also been monitoring long-term changes in vegetation in the absence of grazing in 4×4 m permanent exclosures since 1994. Annual exclosures show that goose grazing reduces the standing crop but does so variably between years (Fig. 1; Gauthier et al., 1995). For example, the reduction in standing crop in 1993 was >60% whereas in 1999 it was negligible. *Eriophorum* also tends to be more heavily grazed than *Dupontia*.

Against the trend in increasing goose population, there has been no corresponding decline in plant production over the past decade. On the contrary, the highest productions have followed immediately on from a very low production in 1994, a drought year. Such annual variations in grazing impact can be explained by variations in the size of the “local” goose population. In that population, there is a close association between the young to adult ratio at the end of the summer (an index of reproductive effort and hence goose density), and the proportion of biomass grazed. In the high Arctic, the reproductive effort of geese is strongly affected by climatic events.

Moderate goose grazing does not enhance plant production as occurs in salt marshes, i.e., there is no overcompensation (Gauthier et al., 1995; Beaulieu et al., 1996), because goose faeces do not seem to have the same fertilizing effect on graminoids. The results of Pineau (1999) indicate that this is due to the presence of a thick layer of mosses in fens. When nitrogen is added to the surface to simulate nutrient leaching from faeces, mosses readily absorb it, but not the roots of vascular plants which are buried in the moss. Thus, mosses appear to act as a sponge, soaking up most nutrients released from goose faeces and preventing vascular plants from benefiting.

Results from our long-term exclosures show that moderate to chronic goose grazing still has an impact on plant communities in this ecosystem. After five years of goose exclusion on the permanent plots, the *Eriophorum* biomass grew 5-fold compared to the increase in control plots (one year exclosures); but not the *Dupontia* (Fig. 2). The number

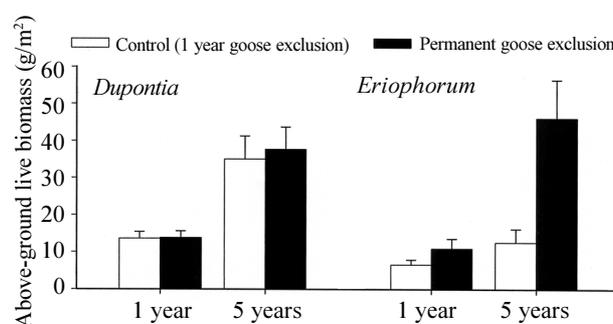


Fig. 2 Annual above-ground biomass of *Dupontia* and *Eriophorum* in permanent exclosures protected from goose grazing for 5 years ($n = 17$) and in annual control exclosures protected from grazing only for 1 year ($n = 12$) Mean \pm SE.

of *Eriophorum* tillers also more than doubled, and the number of flowering heads increased almost 10-fold. Hence, after 5 years of goose exclusion, *Eriophorum* had become the dominant plant in the long-term exclosures (>50% of biomass, compared to only 36% of biomass at the start of monitoring). Total above-ground graminoid biomass in exclosures averaged 87 g/m² per year over 5 years, compared to only 52 g/m² when grazing was stopped for a single year. In this ecosystem, therefore, it appears that grazing reduces plant production and changes specific composition due to selective grazing of *Eriophorum*.

4 Temperate salt marshes

Grubbing is the most common method of foraging used by snow geese in temperate marshes. On their wintering grounds along the Atlantic coast of North America, they can reduce significantly the primary production of *Spartina alterniflora*, which then requires several grubbing-free years to recover fully (Smith and Odum, 1981). These areas, commonly referred as “eat-outs”, occur mostly in wildlife refuges and occupy a small proportion of the total area of salt marshes along the Atlantic coast. Degraded areas have not increased in the last decade because of hunting controls in the refuges and increased use of adjacent agricultural lands by the geese.

5 Temperate freshwater/brackish marshes

During spring and fall, greater snow geese feed in tidal brackish marshes along the St. Lawrence River estuary in southern Quebec. These marshes are dominated by three-square bulrush (*Scirpus pungens*, formerly *S. americanus*), with a sparse growth of wild rice (*Zizania aquatica*) and arrowhead (*Sagittaria latifolia*) (Giroux and Bédard, 1988). The rhizomes of three-square bulrush comprise >75% of the diet of geese feeding in the marshes in those seasons.

We have been monitoring plant production and goose use in the Montmagny and Cap St-Ignace marshes on the south shore of the river for several years, using exclosures. Giroux and Bédard (1987) estimated that up to 62 g/m² of rhizomes were eaten annually, which represented 23% of the below-ground biomass available and 59% of the net below-ground primary production. At a wildlife refuge at Cap Tourmente on the north shore of the river, Reed (1989) estimated that geese removed 55 g/m² during their fall staging period, or 32% of the below-ground biomass available.

In the heavily-used marshes of Montmagny, Giroux and Bédard (1987) observed that after two years *Scirpus pungens* production was 62% higher in plots protected from geese. The higher biomass in the control plots was due to both a greater number and mass of shoots. Similar results were obtained in the Cap St-Ignace marshes: 28% higher plant biomass in control plots after one year of goose exclusion. However, the above-ground biomass in the grubbed plots remained stable at both sites (Fig. 3). In the

mid eighties, Giroux and Bédard (1987) concluded that geese maintained the system at a low-level steady state, and this seems still to be the case. Boyd (1995) reached similar conclusions in the Fraser River delta marshes along the west coast of Canada. Bélanger and Bédard (1994a) argued that this equilibrium resulted from the geese shifting their foraging sites within the marsh as soon as available food reached a minimum threshold. Despite an increase in goose numbers and foraging along the St. Lawrence River over the last two decades, grazing pressure on the marshes has remained stable because the geese have taken increasingly to feeding on adjacent agricultural fields.

Selective feeding on bulrush rhizomes by the geese also alters the species composition of the marsh plant communities. At Cap Tourmente, Reed (1989) found an inverse relationship between three-square bulrush and wild rice stem densities in grubbed marsh; and at Montmagny, Giroux and Bédard (1987) found a greater production of wild rice in grubbed plots than in the controls. The small depressions created by geese when grubbing may offer a good substrate of unconsolidated sediments for the germination of wild rice, an annual plant. This prediction is supported by the results of Bélanger and Bédard (1994b) who observed a greater production of wild rice in grubbed, disturbed patches (ice-made depressions) than in undisturbed patches. *Scirpus pungens* does not respond to goose grubbing by increasing sexual reproduction. This may be re-

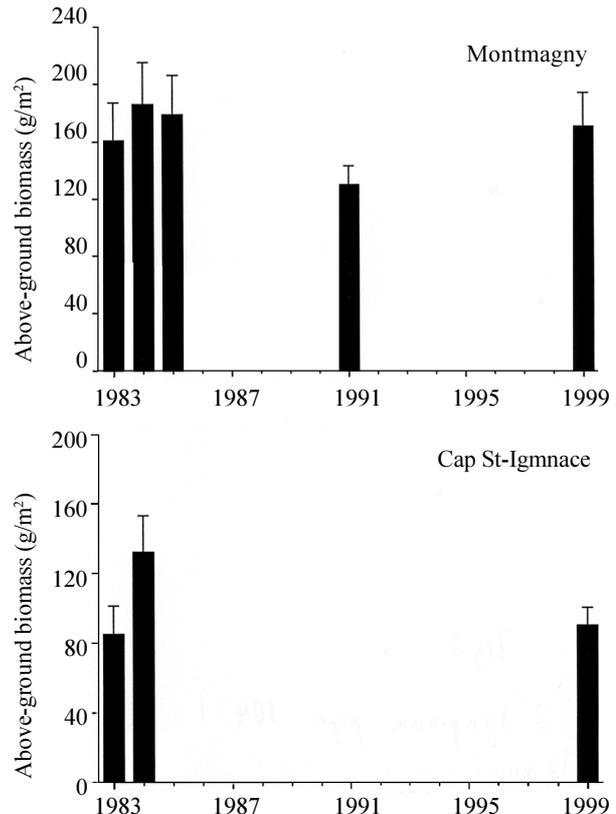


Fig. 3 Above-ground biomass of three-square bulrush (mean \pm 1 SE) in grazed plots at Montmagny and Cap St-Ignace, 1983–1999

Means are calculated on 27 plots, each with 9 nested quadrats.

lated to poor seedling establishment due to sediment accretion in the marshes in such circumstances (Giroux and Bédard 1987, 1995).

6 Conclusions

Snow goose grazing in arctic freshwater fens decreases overall production and leads to a low level equilibrium between the herbivore and the plants. At present, the system on Bylot Island appears stable despite the increase in goose density, as no long-term decline has been observed in plant production in the annual exclosures. Certainly there has been no damage on the scale observed in the salt marshes of west Hudson Bay. Whether this is because the arctic freshwater fen/goose interaction is inherently more stable than that for salt marshes (e.g., due to differences in soil type, absence of salt or low intensity of grubbing), or because the response threshold of fen plants has not yet been exceeded, is not yet known.

A similar situation seems to pertain in temperate freshwater/brackish marshes. Snow goose grubbing in bulrush marsh appears to be affected by a minimum threshold in food availability, beyond which feeding becomes unprofitable: this may be sufficient to maintain the marshes at a low-level steady state. Three-square bulrush has the capacity to withstand high, chronic grubbing, judged by its rapid recovery once geese are removed. In contrast, the limited information from temperate salt marshes suggests that damage to vegetation due to goose grubbing can be locally severe and lead to the disappearance of vegetation over large areas.

Based on these data, we suggest that goose grazing/grubbing of high intensity grubbing may be less harmful to plants in freshwater and brackish marshes than in salt marshes, both in arctic and temperate ecosystems. Adaptations to salt tolerance in plants may limit their capacity to withstand other perturbations, in this case herbivory.

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S04-3 Birds as pollinators and dispersers: a case study from New Zealand

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Abstract One special legacy of New Zealand's long biogeographic isolation is a distinctive flora and fauna. The flora is characterized by a high percentage of trees (33% of species), a high percentage of bird-dispersed species (72% of trees), and a low incidence of ornithophily (4% of genera). In the prehuman avifauna, twelve species dispersed seed, and five were pollinators. Native ecosystems have since suffered clearance of 71% of forests, extensive hunting, and the introduction of 14 now-widespread predatory or browsing mammals. As a result, pollinating and seed dispersing birds are either regionally or nationally rare (7 species), or extinct on the New Zealand mainland (6 species). Six of seven bird-pollinated plant species examined so far are pollen-limited, to some extent, at mainland sites. Three of eight fruiting species studied are suffering reduced dispersal on the mainland, where large (>1.4 cm) diameter fruits now depend on a single disperser, the New Zealand pigeon, *Hemiphaga novaeseelandiae*. Conservation of these plants requires management of native bird populations, especially the tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*), and the pigeon to avert long-term shifts in vegetation composition. Intensive predator control has been shown to increase the densities of mutualist bird species, suggesting that New Zealand conservation managers can assist bird-serviced plant populations by controlling predators, a third-order ecological manipulation.

Key words Bird pollination, Bird dispersal, Mutualisms, New Zealand

1 Introduction

New Zealand provides an interesting test for the importance of birds as pollinating and seed-dispersing mutualists. The woody flora is overwhelmingly fleshy-fruited, and ornithophilous flowers (large, red, copious, unscented, with dilute nectar) are a small but important botanical element. Aside from one nectarivorous bat (Arkins et al., 1999) and several lizards (Whitaker, 1987), birds are the only vertebrates filling the two roles. Human influence has greatly reduced the density and diversity of native birds throughout the two main islands, hereafter the "mainland" (Brockie, 1992). Thirty-nine exotic birds have established themselves but few are important dispersers or pollinators. Therefore, if native birds are important to ecosystem function, there should be evidence in New Zealand of floristic change resulting from the decline of native birds.

Clout and Hay (1989) reviewed the relative importance of avian dispersal and pollination mutualisms in New Zealand. They stressed the negative effect of avian extinctions and range reductions on dispersal mutualisms, particularly for large-seeded trees which now rely on a single, possibly keystone, disperser, the New Zealand pigeon (*Hemiphaga novaeseelandiae*). Here we show that reduc-

tion in bird densities is also causing widespread pollination failure on the mainland. We argue that pollination has been affected as much as dispersal, and that two honeyeater species, the tui (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*), are probably also keystone species as the predominant pollination and dispersal mutualists on the mainland.

2 Prehuman situation

Before the arrival of man, almost all of New Zealand was forested. This is reflected in the flora, with a high percentage of trees (33% of species) compared to a mean of 9% for the temperate zone worldwide (Atkinson and Cameron, 1993; Begon et al., 1996, p 34). Unusually for a temperate area, the woody flora is overwhelmingly fleshy-fruited: 72% of trees cf. 17%–47% at comparable northern latitudes (Burrows, 1994). Plants with typically ornithophilous flowers are relatively few (4% of genera) but nonetheless prominent (Castro and Robertson, 1997, Webb et al., 1999). However, birds also visit and pollinate many flowers with non-ornithophilous syndromes, especially those of canopy trees and winter-flowering plants (Castro and Robertson, 1997; Anderson, 2003).

Famously, New Zealand lacked terrestrial mammals apart from several ground-foraging bats; and the 67 species of native forest birds filled many of the roles that mammals do elsewhere (Atkinson and Millener, 1991). Although Clout and Hay (1989) list 31 species which ate fruit, many were opportunistic insectivores or acted primarily as seed predators (moa, parrots). Holdaway (1989) and Atkinson and Millener (1991) record twelve bird species as responsible for most seed dispersal: piopio (*Turnagra capensis*), two moas with small gizzard stones (*Euryapteryx* spp.), huia (*Heteralocha acutirostris*), saddleback (*Philesturnus carunculatus*), New Zealand pigeon, tui, bellbird, hihi (*Notiomystis cincta*), kokako (*Callaeas cinerea*), whitehead (*Mohoua albicilla*) and the flightless weka (*Gallirallus australis*). Of eight flower-visiting species, the three putative Meliphagidae (tui, bellbird and hihi) were the most important pollinators (Craig et al., 1981; Angehr, 1986). The kaka (*Nestor meridionalis*) and saddleback also pollinated some flowers, while whiteheads and two parakeets (*Cyanoramphus* spp.) did so incidentally. This is in contrast to Australia, which has about 100 species of flower-visiting birds including nearly 70 species of Meliphagidae (Ford et al., 1979; Pyke, 1980).

3 Human impacts

Since human arrival some 700 years ago, forest cover has fallen to 23% of land area (Taylor and Smith, 1997: 8.27), and the remaining forests have been affected by introduced mammalian herbivores (Veblen and Stewart, 1982). Over the same time, there have been massive extinctions and range reductions in the avifauna, with 45% of native bird species eliminated from the mainland and 29% going extinct globally, largely due to introduced mammalian predators (Holdaway, 1989; King, 1990; Holdaway et al., 2001).

Of the avian pollinators, the hihi and saddleback are now extinct on the mainland, while the kaka, tui and bellbird are in lower numbers in smaller ranges there (Bull et al., 1985). None of the exotic birds introduced since are significant pollinators, although the European starling (*Sturnus vulgaris*) and recently self-introduced silvereye (*Zosterops lateralis*) pollinate some flowers (Delph and Lively, 1985; O'Donnell and Dilks, 1994).

Four avian dispersers of seed are now extinct. Of those remaining, the hihi and saddleback are confined to predator-free offshore islands, the kokako and weka have restricted distributions, the New Zealand pigeon is widespread but reduced in numbers, and the tui, bellbird and whitehead are absent from parts of the mainland as well. Of the introduced species, all widespread, the silvereye, European starling, Eurasian blackbird (*Turdus merula*), song thrush (*Turdus philomelos*), and common myna (*Acridotheres tristis*) also disperse seed (O'Donnell and Dilks, 1994).

4 Current status of pollination mutualisms

Work on current pollinator service to flowering plants

shows that inadequate visitation by birds is resulting in a fall in seed set. This is apparent from data for the bird-pollinated forest shrub, *Rhabdothamnus solandri* (Gesneriaceae), which we studied at two mainland sites near Auckland, where only the tui is present, and at one offshore bird sanctuary (Little Barrier Island), where all extant native bird pollinators are abundant. We performed three pollination treatments: un-manipulated flowers accessible to birds, bagged flowers from which all pollinators were excluded, and hand-pollinated flowers. Fruit set in un-manipulated flowers (67%) on the bird sanctuary was almost as high as for hand-pollinated flowers (70%), showing that pollen servicing by birds was very thorough.

In contrast, un-manipulated fruit set (mean 16%) at both mainland sites was far lower than that for hand-pollinated flowers (83%). Birds visiting *Rhabdothamnus* flowers leave marks on the anther disk, and examination of flowers showed that 83% of flowers had been visited on the bird sanctuary, compared to 20% on the mainland. Evidently, inadequate visitation by avian pollinators is a primary contributor to low fruit set on the mainland. Moreover, ripening fruits contained more seed on the bird sanctuary (395 seeds per fruit) than on the mainland (168). The combined effect of lower fruit set and fewer seeds per fruit on the mainland produces a seed crop in *Rhabdothamnus* that is only 10% of production at sites where prehuman bird densities still exist.

Pollination failure is not restricted to *Rhabdothamnus*. Of seven bird-pollinated plants that were tested, only one, the self-compatible *Alepis flavida*, was found still pollinated adequately at all sampling sites (Table 1). We defined inadequate pollination as a "pollination index" of < 50%, i.e. un-manipulated fruit set was less than halfway between that for pollinator-excluded flowers (the worst-case scenario) and hand-pollinated flowers (the best case). Overall, pollination was inadequate at about half the sites; and in most cases there is evidence that low bird densities are the primary cause.

The reproduction of non-ornithophilous flowering plants pollinated by birds may also be compromised. Due to the decline in the avifauna, there is a widespread failure

Table 1 Percentage of study sites on mainland New Zealand where pollination is inadequate (pollination index < 50%) in bird-pollinated New Zealand plants

Species	Sites with PI < 50% (<i>n</i> sites)	Source*
<i>Peraxilla tetrapetala</i>	69% (29)	1
<i>Peraxilla colensoi</i>	30% (10)	1
<i>Rhabdothamnus solandri</i>	100% (2)	2
<i>Fuchsia perscandens</i>	100% (2)	3
<i>Sophora microphylla</i>	55% (11)	2
<i>Fuchsia excorticata</i>	22% (18)	2
<i>Alepis flavida</i>	0% (1)	4

*Sources: Robertson et al., 1999; this paper; Montgomery et al., 2001; Ladley et al., 1997.

of bird-pollination mutualisms on the New Zealand mainland. Some species, in particular the mistletoes (*Peraxilla* spp.), are entirely reliant on reproduction by seed (Robertson et al., 1999). It needs to be stressed that the effects of falls in seed production from such causes are not immediately obvious because most woody plants are long-lived; but ultimately they can lead to serious shifts in vegetation composition.

5 Current status of dispersal mutualisms

In several ways, seed dispersal seems to be less at risk than pollination. There are more widespread species of seed-dispersing birds on the mainland (New Zealand pigeon, tui, bellbird, whitehead, silvereye, European starling, Eurasian blackbird, song thrush, common myna) than pollinating birds (tui, bellbird, silvereye, European starling). Although the dispersal of seeds (> 1.4 cm diameter) of large-seeded trees may be limited to the New Zealand pigeon, which only it can swallow, only six tree species are so affected (Clout and Hay, 1989). Introduced mammals such as brush-tailed possums (*Trichosurus vulpecula*) may also disperse some large-seeded fruits (Williams et al., 2000).

Work on seed-disperser services to plants on the mainland shows that while dispersal of some fruiting plants (*Peraxilla* spp., *Alepis flavida*, *Tupeia antarctica*, and *Ileostylus micranthus*) is adequate in most seasons (Ladley and Kelly, 1996), it has been limited in others by the decline in the numbers of native birds. Comparisons for *Pittosporum crassifolium* between mainland sites near Auckland where only the tui is present and an offshore bird sanctuary (Tiritiri Matangi Island) where all extant native bird dispersers are abundant shows that, despite an equivalent visitation rate by birds, seed dispersal is significantly lower on the mainland (20%) than on the sanctuary (94%). This reflects the inability of introduced bird species at the mainland site to effectively disperse the seed. Similar studies of *Fuchsia excorticata* and *Rhopalostylis sapida* near Wellington also show that a larger proportion of fruits fall undispersed from plants on the mainland than on a neighboring bird sanctuary, Kapiti Island (McNutt, 1998).

Some plants appear able to regenerate from undispersed fruit in the vicinity of the parent (Burrows, 1994; Bell, 1996), while others may not (Ladley and Kelly, 1996; Trass, 2000). Without knowing its frequency, we cannot fully evaluate the consequences of poor dispersal service.

6 Restoring mutualism service

Pollination and dispersal services may be restored on the New Zealand mainland if the representation and numbers of key bird species can be raised. In the last decade, intensive control of introduced mammal pests, especially brush-tailed possums, stoats (*Mustela erminea*) and ship rats (*Rattus rattus*), has frequently increased native bird numbers, including the tui, bellbird and New Zealand pigeon (James and Clout, 1996; Innes et al., 1999). Sustained

control of mammal pests is difficult and expensive, and currently confined to areas under 6000 ha (King, 1984; Saunders and Norton, 2001); but options are widening rapidly, including the use of mammal-proof fences (Clapperton and Day, 2001).

7 Conclusions: birds as keystones in New Zealand?

Although Clout and Hay (1989) have argued that pollination failure was likely to have a much less serious effect on the New Zealand flora than seed dispersal failure, it is now clear that pollination failure is a widespread problem for many native plants. The New Zealand temperate flora was unusually reliant on avian mutualists, and severe reductions in the avifauna are having downstream effects on plants. That both pollination and dispersal are continuing to function on the mainland is largely due to three surviving endemic species: tui, bellbird and New Zealand pigeon. Of these, the first two act as both pollinators and dispersers, and despite their low biomass per hectare, are crucial for continued ecosystem function. They could justifiably be called keystone species, and their continued protection is probably necessary to prevent large-scale, long-term changes in the surviving native forests of New Zealand.

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S04-4 The role of birds in seed dispersal and its consequences for forest ecosystems

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Abstract In tropical forests, most trees have fleshy fruits adapted to animal dispersal; and the important role that birds especially play in their dispersal is well documented. Few studies, however, have so far addressed the question of whether declining bird species richness, whatever the cause, leads to changes, even breakdown, in seed dispersal and plant regeneration processes. In this paper we present a comparative approach to this question by comparing seed dispersal in two closely related tree species of the genus *Commiphora* (family Burseraceae) in two areas with disparate richness in avian frugivores: South Africa and Madagascar. In South Africa, where frugivore diversity is high, relatively high numbers of bird species (12) dispersed seeds leading to high dispersal percentages (70.8%). Consequently, seedlings established away from parent trees, producing an evenly dispersed distribution in the adult tree population. But in Madagascar, which is strikingly depauperate in avian frugivores, few bird species (3) dispersed seeds, leading to very low dispersal percentages (7.9%). Consequently, seedlings established close to and under parent trees, resulting in a clumped distribution of adult trees. Secondary dispersal by ants was also markedly different between the two sites, with high dispersal (47.9%) in Madagascar and no dispersal in South Africa. These results indicate that bird species richness influences seed dispersal and seedling establishment, and thus might have far-reaching consequences for the floristic composition and structure of ecosystems. Furthermore, our studies show the need for broad ecological approaches into the vectors of seed dispersal, as other processes, e.g., secondary dispersal, might also be important for forest regeneration.

Key words Bird dispersal, Bird species richness, Mutualistic plant-animal-interactions, Regeneration, Seedling establishment

1 Introduction

The most famous and frequently cited example of mutualistic interaction between a frugivorous bird and its fruit plant is that of the dodo (*Raphus cucullatus*) and the calvaria tree (*Sideroxylon majus*). The dodo, once native to Mauritius but extinct by 1681, was said to play an integral role in the dispersal of calvaria seeds. Temple (1977) even went so far as to suggest an obligate mutualism between dodo and tree, thereby explaining the failure of the tree to regenerate by the dodo's extinction. This example of obligate mutualism has appealed to many ecologists and has long become textbook dogma exemplifying tight ecological interdependence among species. Yet there is little evidence that obligate mutualisms in seed dispersal really exist. Although more than 90% of all tree and shrub species in tropical forests develop fleshy fruits adapted to animal dispersal (Howe and Smallwood, 1982), interactions between seed dispersers and plants are in general less tight than, for example, those between pollinators and plants. Rather, they are rather diffuse and nonspecific: seeds of a given plant species are commonly dispersed by a variety of animals (Coates-Estrada and Estrada, 1988; Fleming and Williams, 1990). With such diffuse interactions, the question arises

whether seed dispersers have the potential to exert influence on their interactive partners, the plants themselves.

Many studies indicate that worldwide habitat loss and fragmentation lead to a decline in bird species richness (see review in Turner, 1996; Brooks et al., 1999). It is also known that dispersal mutualists such as birds are important for seed dispersal, for without them seedling recruitment is limited due to the high mortality in non-dispersed seeds that merely fall beneath parent trees (Janzen et al., 1976; Augspurger, 1983; Howe et al., 1985). However, understanding of the link between bird species richness and its consequences for forest regeneration is still meagre. Few studies have addressed the consequences of disperser declines for plant populations, although some possible scenarios have been presented (e.g., Howe, 1984; Bond, 1995). Pizo (1997) found that local bird species richness determined the frugivore assemblages of fruiting trees, with a higher number of more reliable and efficient bird species visiting trees and dispersing seeds in a large forest site than in a small forest fragment. Santos and Telleria (1994) also showed in a comparison of large and small forest sites that a low number of dispersal agents at the small sites, both in species and abundance, led to a reduction in seed transfer and seedling

establishment in *Juniper* trees.

At the community level, Cordeiro and Howe (2001) found a decline in frugivorous birds and primates with decreasing site-fragment size in the Eastern Usambara Mountains in Tanzania. When relating this to seedling recruitment, the density of regeneration in 31 animal-dispersed tree species was found to increase with patch size, with highest numbers in large and lowest numbers in small fragments. In contrast, recruitment of wind- and gravity-dispersed trees was unaffected.

We conducted comparative studies in South Africa (high frugivore richness) and Madagascar (low frugivore richness) to investigate whether frugivore richness influences the seed dispersal system of tree species and whether this has consequences for seedling establishment and the spatial distribution of seedlings and trees (also Bleher and Böhning-Gaese, 2000; Bleher and Böhning-Gaese, 2001). For this we screened the seed dispersal system of two related tree species: *Commiphora harveyi* in Oriibi Gorge Nature Reserve, Natal, South Africa, and *C. guillaumini* in Kirindy Forest on the west coast of Madagascar. Both have similar, bird-dispersed fruits.

2 Results

2.1 Seed dispersal by birds

Corresponding to high bird diversity in South Africa, 15 frugivore species visited *Commiphora* trees at the South African site, 12 of them contributing to seed dispersal (Table 1; Bleher and Böhning-Gaese, 2000; Bleher and Böhning-Gaese, 2001). In Madagascar, with low avian diversity, only 6 frugivores visited the trees at our site there (Table 1, Bleher and Böhning-Gaese, 2000; Bleher and Böhning-Gaese, 2001). Only 3 Malagasy frugivores dispersed *Commiphora* seeds, the primary contributor (lesser vasa parrot, *Coracopsis*

nigra) moreover being a seed waster which dropped most of the seeds to the ground. As a result of these disparities, we found that 70.8 % of all seeds were dispersed per tree in South Africa but only 7.9 % in Madagascar (Table 1; Bleher and Böhning-Gaese, 2001).

2.2 Secondary seed dispersal by ants

Commiphora seeds at the Malagasy study site were dispersed secondarily by ants (47.9% of all seeds). However, seeds were not carried any great distance, and their dispersal contributed little to seedling establishment in comparison with those dispersed by birds (Böhning-Gaese et al., 1999; Böhning-Gaese and Bleher, 2000). At the South African site, in contrast, there was no seed dispersal by ants (Voigt et al., 2002). Poor ant dispersal in South Africa is due to a lack of potential dispersers, low ant activity and few aggressive interspecific interactions among ant species (Voigt et al., 2002).

2.3 Seedling establishment

The differences in bird species numbers and dispersal percentages between the two sites translated to differences in seedling distribution and survival. At the South African site, where most seeds were dispersed, seedlings were found mostly away from parent trees: median distance 21.1 m. At the Malagasy site, however, where most seeds fell under parent trees, most seedlings were found there: median distance 0.9 m (Bleher and Böhning-Gaese, 2001). Moreover, although seedling establishment per hectare was much the same at both sites, survival probability for first-year seedlings differed. In South Africa, 36% of all seedlings survived the first year compared to only 15% in Madagascar (Bleher and Böhning-Gaese, 2001).

2.4 Tree distribution

Our field data using the T-Square-method indicate a

Table 1 Primary seed dispersal by birds, secondary dispersal by ants, seedling distribution, survival probability of first year-seedlings, and distribution of adult trees of the genus *Commiphora* at two study sites in South Africa and Madagascar

	South Africa	Madagascar
Primary dispersal by birds		
Bird frugivore richness	high (14)	low (4)
Bird species visiting trees	15	6
Bird species dispersing seeds	12	3
Percentage of seeds dispersed per tree	70.8%	7.9%
Secondary dispersal by ants		
Potential ant dispersers (assumed from seed size)	absent	present
Ant activity	low	high
Percentage of seeds secondarily dispersed per tree	0%	47.9%
Seedling establishment and tree distribution		
Seedling distribution	away from parent	under parent
Seedling survival	high (36%)	low (15%)
Tree distribution	uniform	clumped

Data from Böhning-Gaese et al., 1999; Böhning-Gaese and Bleher, 2000; Bleher and Böhning-Gaese, 2001; Bleher et al., 2002; Voigt et al., 2002.

rather uniform distribution of the tree populations at the South African study site in contrast to a clumped distribution at the Malagasy site (Bleher and Böhning-Gaese, 2001). A computer simulation model evaluating the influence of different factors such as dispersal distance, tree density, breeding system and seedling distribution on the spatial distribution of tree populations confirmed the importance of dispersal distance. This, in turn, can be traced back to the presence/absence of animal dispersers (Bleher et al., 2002).

3 Discussion

Animal-plant mutualisms are usually not as tight as suggested by the example of the dodo and the calvaria tree. However, the results of our comparative studies in South Africa and Madagascar indicate that bird species richness does affect seed dispersal, which has carry-on effects on plant life cycles (Bleher and Böhning-Gaese, 2001). Therefore, bird dispersers have a potential influence on their interactive partners, even though the extinction of frugivorous birds might not lead to immediate extinction cycles in plant communities as predicted by various scenarios (Howe, 1984; Bond, 1995)

Although bird diversity is of concern worldwide, very few studies have examined quantitatively the effect of bird species richness on seed dispersal and regeneration of plant populations. The scarcity of relevant studies lies in difficulties in approach: an experimental approach has to be excluded from an ethical point of view; and comparative approaches using continuous forest and forest fragments often face the problem of finding adequate sample sizes as well as standardized sites, i.e., fragments not influenced by complicating factors. Therefore, our cross-continent approach of comparing sites or continents with disparate species richness might be a useful alternative.

The island of Madagascar is depauperate in frugivorous birds in comparison with other tropical areas, and lemurs appear to play a prominent role in seed dispersal instead (Scharfe and Schlund, 1996; Goodman et al., 1997; Dew and Wright, 1998). Historical extinction does not appear to be the reason for the poor frugivorous avifauna in Madagascar (Langrand, 1990; Goodman and Rakotozafy, 1997). Rather, it may be linked to reduced diversity in species of *Ficus* (Goodman and Ganzhorn, 1997), which are a keystone resource for frugivores in most tropical forests (e.g., Terborgh, 1986; Bleher et al., 2003).

Although birds seem to play a crucial role in the dispersal of plants, with consequences for forest ecosystems such as shown in our studies, other factors and processes have to be taken into consideration as well. Such factors are abiotic (e.g., light, moisture) as well as biotic (e.g., secondary dispersal, seed predation). Secondary dispersers, for example, can alter the pattern of seed dispersal as shown by one of our studies (Böhning-Gaese et al., 1999). Comparative studies across sites and anthropogenic deconstruction experiments, based on broader perspective

of plant-animal-interactions, might “close the dispersal loop” (Wang and Smith, 2002) and give us a better understanding of the long-term consequences of animal species richness for plant populations.

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Symposium 06 Macroscopic and microscopic evolutionary perspectives on feathers

Introduction

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Feathers receive little attention from most ornithologists, yet a few of us have studied them for a long time. In my experience, the first feather symposium at an International Ornithological Congress was that organized by Alan Brush at the 1974 meeting in Canberra. Since then, reports on feathers have been presented at three Congresses in symposia, lectures, and posters. The subject of most interest at these meetings has been plumage color, i.e., the mechanisms by which it is produced and the functions that it serves. Other continuing themes have been the synthesis and structure of feather keratin, the structure and functions of feathers, and the evolution of feather proteins, feathers, and flight.

There have also been reports on feather development and on bacterial degradation of feathers. Several of those subjects are included again in this symposium. Yet here new ideas and findings about the origin, evolution, and ecology of feathers are presented as well. Such subjects are far beyond what we could have imagined in 1974.

Despite these advances, we still have much to learn about feathers. Here are just a few unanswered questions for future study:

- How did the feather follicle and feather muscles originate in ancestral reptiles?
- Do the different structural types of feathers differ in their keratin? If so, what do these differences suggest as to the ancestral structure of feather keratin and the feathers that it formed?
- The molecular structure and properties of keratin vary in different parts of a feather. Are these variations related to the functioning of the feather and how?
- How do barbules work? In particular, what keeps downy barbules from getting entangled? Our understanding of barbule mechanics is still based on Sick's excellent study, but that was 65 years ago. To my knowledge, little has been done to advance our understanding of barbule mechanics using scanning electron microscopy.
- How did filoplumes evolve? What is their phylogenetic relationship to other kinds of feathers?
- How is the morphology of feather muscles related to the operation of feathers for flight, temperature regulation, display, and other functions?
- What holds a feather in its follicle? Constriction of feather muscles around the follicle may not be the whole answer. Tissue sections sometimes show what appear to be connections between the follicular lining and the outside of the calamus.
- The arrangement of feather tracts on the body differs widely among groups of birds and has been used as a taxonomic character. Do these differences in pterylosis have any functional significance, such as facilitation of heat radiation from the skin or movement of body parts or feathers?
- What is the function of uropygial gland secretion? Experiments are needed to determine whether it keeps keratin supple, contributes directly to waterproofing, and/or has antibacterial properties?
- The chemical composition of uropygial gland secretion differs among groups of birds. Is there any functional significance to these differences?
- The feathers of many birds, especially herons and pigeons, produce a fine powder. Its role has been debated, but never tested. Does it waterproof feathers, clean them, or have a visual effect?
- In a few birds, certain feathers appear to secrete a greasy or waxy substance. What is the purpose of this secretion? More fundamentally, how is keratin synthesis in these feathers transformed to produce this greasy material?
- How is the structure of each and every feather on a bird genetically encoded, bearing in mind that feathers vary over the body and that their constitution ranges in scale from overall macro-shape and -size to the ultramicroscopic and molecular?
- As if that were not complex enough, many follicles produce feathers of different form and color in suc-

cessive molts, and may take up to seven years to produce the definitive adult feather. How are these changes and the timing encoded?

- Lastly, how are genetic instructions carried out in the follicle as a feather grows? Since this question addresses a fundamental problem in cellular differentiation, it should be of interest to all develop-

mental biologists. Here the study of feathers finds application beyond ornithology.

These are just some of the questions about feathers that I believe should be investigated. Already some of the answers are forthcoming in this symposium; as for the rest, we can look forward to them at future meetings and in future publications.

S06-1 Follicles and the origin of feathers

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Abstract Feathers evolved in the mid- to late-Jurassic and first appeared in the fossil record on *Archaeopteryx* (150 MYA). All feathers are constructed from a family of closely related phi-keratin proteins. The structural genes for these proteins exist as a moderately repeated, tandemly repeated, subset of beta-keratin genes. The mechanisms underlying the novel appearance of feathers are based in their development. A phylogeny for feathers based on morphology and molecular information indicates that the most likely common ancestor was a simple, tubular epidermal filament derived from a conical tubercle. The formation of the follicle followed. The developmental programming underlying the rapid appearance and diversification of feathers was modular and involved genetic and morphological duplication. These mechanisms account for the appearance and function of the follicle, the most basic product of which would be an unbranched, tubular structure of phi-keratin. Further duplication events and regulation of growth rates led to the branched structure of feathers and to their rapid diversification. While ontogeny does not recapitulate evolution, it can account for both the basic morphological constraints and phenotypic variation of feathers. Because this model is sufficient to account for all features of the feather character it is not necessary to invoke a functional interpretation for feather evolution.

Key words Feather, Evolution, Phylogeny, Morphology

1 Introduction

Extensive evidence now supports the hypothesis that modern birds are derived from a sister group that includes theropod dinosaurs (Padian and Chiappe, 1998). The presence of feathers is an important element of this argument (Prum and Brush, 2002). There is evidence for derived feathers, formally the quintessential character of birds, in advanced maniraptorian dinosaurs (Prum, 2002). Feathers have their origin deep within theropod dinosaurs and a primitive feather structure occurs in the even more basal coelurosaurians (Chen et al., 1998). Undoubtedly feathers evolved in dinosaurs prior to the appearance of *Archaeopteryx*, the oldest bird in the fossil record (150 MYA), and the presence of feathers in these primitive taxa provides essential clues to feather origins. The sudden appearance of such a novel feature also poses questions regarding mechanisms (Brush, 1993, 1996). In this essay I therefore focus on the earliest patterns in ontogeny, especially that of the presumptive feather: my intent is to relate early ontogenetic processes to evolutionary events.

2 Background factors underlying feather evolution

Feathers are a morphologically diverse group of epidermal appendages. The modern contour feather with pennaceous, symmetrical vanes, a hollow keratinous rachis, and branching, hollow barbs and barbules is structurally complex; but it is not the only feather type evident on fossil dinosaurs and only one of many alternative phenotypes on

modern birds. Such complexity and structural diversity implies functional diversity as well. Phenotypic diversity originates in the earliest phases of ontogeny and may be responsible for the emergence of evolutionary novelties (West-Eberhard, 1989; Brush, 1993). Regardless of their morphology, all feathers are produced in a follicle. This singular structure is capable of generating the entire spectrum of feather phenotypes present over the lifetime of a single bird.

Feathers are not simply transformed reptilian scales. That is, an archaeosaurian scale was not transformed over time into contour feathers to enable flight as has been proposed (Feduccia, 1995, 1996; see also Padian and Homer, 2002). Rather, the earliest ontological processes were modified through variation and selection to produce a unique structural element (Prum, 1999). Specifically, a simple tubular, unbranched filament, composed of ϕ -keratins (=feather ϕ -keratin) and produced in an epidermal follicle, would qualify as a feather. Structures that meet all these criteria exist in many forms on modern birds and, as far as is known, describe the filaments on *Sinosauropteryx*, a coelurosaurian dinosaur (Chen et al., 1998; Brush, 2000). Simple filaments and more complex pennaceous feathers have been found on various dromaeosaurs (e.g. Xu et al., 2001) and, of course, were present on *Archaeopteryx*. The processes of development and growth are plastic enough to account for a range of functions and to generate the vast structural complexity of feathers observed in living birds (Prum and Brush, 2002).

The evolution of feathers and their attendant mor-

phological diversity is linked closely to early ontogenetic events in the epidermis. The properties of symmetry, structural and genetic redundancy, and timing played major roles. Clearly, the changes in organization had a high potential to produce diverse morphological phenotypes (Wagner and Schwenk, 2000). The new organization generated numerous phenotypes, as evidenced by both the diversity in the fossil record and the plumage of living birds. Duplicated genes support rapid changes in patterns of protein synthesis, fine-tuning of structure, and ultimate adaptive potential (Brush, 1993, 2001). An expanded 'genetic repertoire' that involves multiple gene families generates variation leading to new functions. The processes impinge on the squamous layers of the early epidermis and all occur widely in vertebrate development.

What changed is geometry and control, for example tissue folding (Oster and Albrech, 1982). The basic, but static, features of epidermal morphology, histology and cytology are known. The interactions among signaling and synthetic pathways, and the timing and effects of messages among cells and between tissue layers, are essential to the processes that regulate differentiation and tissue specialization. These are, only now, becoming understood (Brush, 2000; Prum, 2000). Further, evolutionary changes are not entirely predictable from the descriptive information derived in classical embryology. Development of a follicle was key to the origin of feathers, and what occurs in the tissue before there is visible morphological evidence for change can be crucial. It is not coincidental that the earliest fossil feather matches the simplest feather phenotype on extant birds.

3 Feather ontogeny

The presumptive feather begins as a flat sheet of cytologically uniform cells. The distribution of the placode primordia is determined by the action of a series of cell adhesion molecules such as Cell Adhesion Molecules (CAM) and β -Calhedrin (Chuong et al., 2001). These molecules originate in the underlying mesenchymal cells. All feathers, regardless of their location or morphology, begin as a placode. Placode cells undergo rapid multiplication and increase in size. This hypoplasia produces morphological changes, such as tissue folding of the cell sheet, that are produced by a combination of internal physical forces driven in part by the cytoskeletal proteins, apoptosis and additional external signals. Harris et al. (2002) have demonstrated that Sonic hedgehog (*Shh*), a member of the TGF β family of growth factors, and Bone Morphogenetic Protein 2 (*Bmp 2*) are active at the early stages and are important in timing events that establish the polarity of the placode. Minimally, they appear to signal the proliferation and differentiation of placode cells. Further morphogenesis is also influenced by factors such as β -catenin. Simultaneously, cellular differentiation begins with the production of Φ -keratin mRNA.

Early ontogeny of the feather follicle is essentially similar in all avian species (Starck, 1982). It is independent

of ultimate feather structure and whether the species is precocial or altricial. The derived condition is one in which contour feathers group in geometric arrays, the pterylae. The first primordia appear in the presumptive dorsal feather tract, followed quickly by all pterylae. The early follicle has features important to subsequent growth and form. Papilla display radial symmetry and internal redundancy. Consequently, a combination of cellular differentiation and apoptosis leads to regionalization into ramogenetic zones, the areas that produce the barb (Prum, 1999). The long axis of the barbs is generated under the control of the *Hox* genes, various growth factors (e.g., TGF- β , FGF) and BMP which act as switches in the protocols, promote apoptosis, and control a variety of genes related to different cell types. Together this activity sculpts the overall tissues. Specialized feather β -keratin protein synthesis is initiated at this point. The resulting spectrum of forms are generated by the internal physical properties of cell aggregates and controlling morphogenetic molecules (i.e., β -catenin). The papilla then elongates, the dermal pulp forms and the collar invaginates (Prum, 1999).

At this stage the presumptive feather has undergone compartmentalization. A module has formed that is essentially separated from the surrounding tissue by protein sheaths that contain alpha- and beta-keratins other than ϕ -keratin. The follicle has become a functional unit with self-contained structure and activity. It is symmetric and relies on the existence of reiterated structural units, new patterns of genetic regulation, and operational molecular gradients. Within the module, changes in molecular level regulatory events are added, deleted, or altered as the result of genomic activity. Modular organization permits enormous latitude in the developmental routines that will, in turn, strongly influence phenotype. Its uniqueness encourages selection to act on nonlethal phenotypic variation. This is apparent in even the first generation of feathers that differ according to location on the body surface.

4 Factors affecting feather ontogeny

Experimental manipulation has shown that the phenotypes of skin appendages are dependent on messages from the mesenchyme (reviewed in Sawyer et al., 2000). Structures at some stage may be interconvertible. Once cell proliferation is initiated the tissue is committed to producing an appendage. Levels of retinoic acid, which can convert presumptive scale to feather, can influence the outcome, however. Molecules such as N-cadherin can influence symmetry of the placode or follicle and subsequent morphology. Differential patterns of protein synthesis are associated with different phenotypes both within and between feathers. This, too, can be under direct or indirect genomic control.

Changes in gene expression and timing, the emergence of a module in the epidermis, redundancy and symmetry, all modify ontogenetic protocols and influence the phenotype. Rather than manipulate the transformation of a pre-existing scale, they provide the variation necessary

in the earliest stages of development to create alternative pathways for basic morphological change (Carroll et al., 2001). Here a branched, tubular structure rather than a flat plate holds the potential for production of phenotypic variety. The earliest stage of the follicle, with the complex folding and invasion of mesodermal tissue, is sufficient to produce a single filament. This matches the filaments on coelurosaurian dinosaurs (e.g., *Sinosauropteryx*), and is presumably the most primitive feather. Diversification in shape, size, and degree of branching followed.

5 Conclusions

The appearance of the follicle involved tweaking existing morphogenetic processes and employing an obscure family of genes for proteins with the ability to form filaments. The proteins were related chemically to the larger group of beta-keratin proteins and, along with sequences and conformational differences, occurred as multiple-tandem repeats. Changes in both time and space of gene activity accommodated the appearance of a newly organized appendage. The mechanisms that produce and break symmetry are tied to other groups of genes which may have variable functions associated with different functional pathways. Metaphorically, the placode generates the blueprint for the production of feathers; and the follicle provides the machinery of fabrication and selection for morphological diversity.

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S06-2 Origin and early evolution of feathers: evidence from the Early Cretaceous of China

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Abstract Discovery of about a half dozen different feathered dinosaurs from the Early Cretaceous of China supports the currently popular view that some dinosaurs were feathered, implying that feathers were initially developed not for flight but for other purposes, such as thermoregulation or display. The presence of arboreal dinosaurs such as *Microraptor*, *Sinornithosaurus* and *Epidendrosaurus*, which are generally believed to be the closest relatives of birds, provides not only important evidence for the arboreal hypothesis of the origin of avian flight and for our understanding of the life style of the ancestors of birds, but also sheds new light on the evolution of feathers. From current evidence, we postulate that protofeathers evolved through a stage when they were used for balance both in trunk-climbing, and in jumping and gliding between tree branches. If the homology of integumentary appendages in non-theropod archosaurs to feathers is established, then the most primitive feathers might have a much earlier origin and wider distribution than is thought today. Early birds from the Early Cretaceous of China also provide evidence for the origin of the alula, a novelty missing from the most basal birds. The alula has, however, been found in all known enantiornithines and ornithurines, indicating that this important structure was already present in birds by the Early Cretaceous.

Key words Feather, Origin, Dinosaur, Bird, Early Cretaceous, China

1 Introduction

It is widely believed that the fossil record, as so far known, has little bearing on the origin of feathers because the oldest known bird, *Archaeopteryx*, already possessed feathers nearly identical in structure to those in modern birds. As a result, hypotheses concerning the origin of feathers have been either purely speculative or based simply on developmental models. This circumstance has changed significantly in the past few years mainly because of discoveries of feathered dinosaurs from the Early Cretaceous in western Liaoning Province, northeast China. Discoveries of early birds from those same beds in the last decade have been equally dramatic. While significantly increasing our knowledge of the early radiation of birds and the evolution of flight, these fossils also contain important information about the early evolution of feathers.

Dyck (1985) has pointed out that the evolution of birds hangs on three questions. Why did feathers evolve, and how? How and with which associated mode of life did flight evolve? And from which reptilian group did birds originate? We would further argue that the evolution of avian flight itself hangs on the same three questions.

Answering Dyck's first question will become a lot easier only with good resolution of the second and third questions. Concerning the third, which is arguably both the most critical and debatable, the balance of current evidence indicates that birds are probably derived from a group

of small theropod dinosaurs (Sereno, 1999). Although paleontologists have generally accepted the dinosaurian origin of birds, some doubt still exists. We will not enter that debate here, but, assuming a dinosaurian origin, will focus instead on reviewing the recent discoveries of feathered dinosaurs and their implications for the origin of feathers.

The second question is also critical because the modes of life of the ancestors of birds are important not only for elucidating of the origin of flight, but also the origin of feathers. We show here how arboreal theropods help us understand the role of feathers in the gliding and jumping stages of flight.

2 Feathers and function in dinosaurs

Since the mid 1990s, six different dinosaurs have been reported with feathers, all from the Early Cretaceous Jehol Biota of western Liaoning, northeast China (Chen et al., 1998; Ji et al., 1998; Xu et al., 1999a; Xu et al., 1999b; Xu et al., 2000). All these taxa are referable to coelurosaurian theropods, and comprise *Sinosauropteryx* (Compsognathidae), *Beipiaosaurus* (Therizinosauridae), *Caudipteryx* (Oviraptoridae), *Sinornithosaurus* (Dromaeosauridae), *Microraptor* (Dromaeosauridae) and *Protarchaeopteryx* (Coelurosauria fam. indet.).

Among these taxa, *Sinosauropteryx*, a basal coelurosaur, was the first recognized as having protofeathers or feather-like integumentary appendages

(Chen et al., 1998). These appendages are generally fiber-like, and are distributed mainly on the head, neck, back and tail region of the impression. Lacking distinct branching and a rachis, these structures have generated extensive discussion and have been considered by some to represent collagenous fibers (Feduccia, 1999). Currie and Chen (2001) have since redescribed the fossils and record the presence of simple branching feathers, with rachis. Our investigation of their specimens, as well as further undescribed material, fails to support their interpretation, even though the integumentary appendages of *Sinosauropteryx* and those on the head and pectoral region of the early bird, *Protarchaeopteryx*, are remarkably similar (Fig. 1). Additional and better-preserved material of *Sinosauropteryx* is needed to determine whether or not it possessed branching feathers. But if it does, then the feather-like structures in its crest and in other dromaeosaurs provides evidence for the display hypothesis of the origin of feathers.

Beipiaosaurus, a medium-sized therizinosaurid theropod, shows preserved integumentary appendages resembling those of *Sinosauropteryx* (Xu et al., 1999a). According to our observations, they appear to be fiber-like and unbranched. It is notable that, in this dinosaur, such structures are associated with the forelimbs and the hindlimbs. In particular, the filaments are best preserved near the ulna, almost perpendicular to the bone, suggesting the precursors of secondary flight feathers of birds. Even

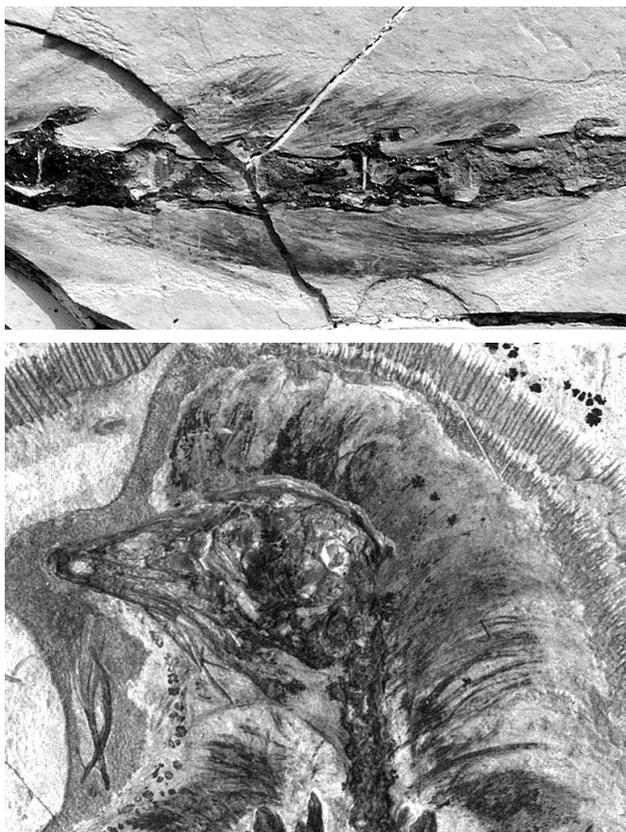


Fig. 1 Protofeathers associated with the tail of *Sinosauropteryx* (top) compared to the crest of the enantiornithine bird, *Protopteryx* (bottom)

so, the existence of branching feathers in this dinosaur will remain unclear without better fossil material.

Caudipteryx and *Protarchaeopteryx* are two bird-like fossils that bear impressions of primitive feathers (Ji et al., 1998). *Caudipteryx* is generally accepted as an oviraptorid (Sereno, 1999; Zhou and Wang, 2000; Zhou et al., 2000); and *Protarchaeopteryx*, although its phylogeny has not been clarified, is generally considered a coelurosaurid. Fossils of both taxa preserve compelling evidence of branched feathers. *Caudipteryx* is also notable for its fan-shaped tail feathers, and possessed feathers attached to the wing and the rest of the body. All feather impressions have distinctive barbs and a rachis; and the vanes of the forelimb feathers are symmetric as in flightless birds (Fig. 2).

Dromaeosaurids are usually held to be the closest relatives of birds, and whether taxa of this group have feathers has undoubtedly been an important question for paleontologists. *Sinornithosaurus* was the first reported with feather-like integumentary appendages (Xu et al., 2000). A later more detailed study of its “feathers” led Xu et al. (2001) to interpret these appendages as compound structures composed of multiple filaments rather than simple, solitary fibers. Two types of branched protofeathers were recognized, one of filaments fused basally in a single tuft to a calamus and comparable to neoavian natal down feathers, and the other of basally joined filaments in series along a central shaft, comparable to barbs along a rachis in a pennaceous feather (Xu et al., 2001). More specimens are needed to confirm the presence of these two types of primitive feathers.

Recently, a new dromaeosaur possibly referable to *Sinornithosaurus* has been reported with branching feathers nearly identical to those of modern birds (Norell et al., 2001). What is particularly significant about the new dromaeosaur is the discovery of elongated feathers attached to the hindlimbs which could only be used for gliding. It indicates that *Sinornithosaurus* was an arboreal animal in spite of its large size in comparison with other early birds.

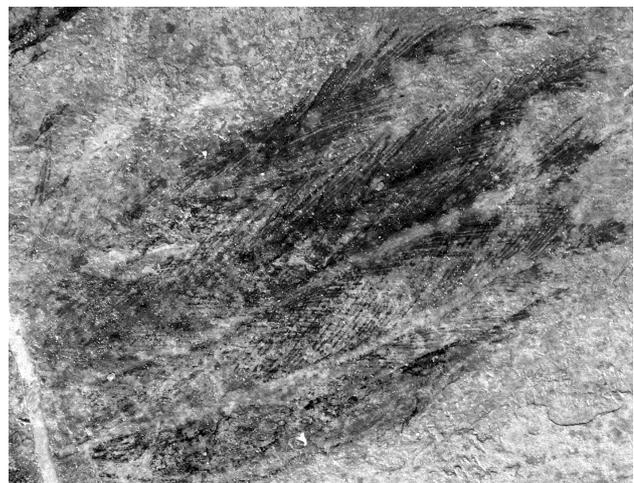


Fig. 2 Branched feathers associated with the forelimb of *Caudipteryx*

This is consistent with the earlier conclusion that *Microaptor*, the smallest dinosaur and the second dromaeosaur reported with protofeathers, was also arboreal, judged by its toe and claw proportions (Xu et al., 2000).

It is also noteworthy that a recently described coelurosaur with integumentary appendages, *Epidendrosaurus*, has unambiguous arboreal-adapted features in the foot (Zhang et al., 2002). More importantly, the beds bearing this fossil are probably of Late Jurassic age, earlier than for all other known feathered theropods from the Jehol Biota. It provides even more compelling evidence for the arboreal hypothesis of the origin of avian flight (see Ostrom 1986, for contrary view), as well as the jumping/balance stage in the evolution of feathers.

3 Feathers in early birds

Although the earliest bird, *Archaeopteryx*, already possessed modern feathers (including asymmetric flight feathers), the tail feathers of the Early Cretaceous birds *Protopteryx* and *Confuciusornis* are proximally undifferentiated and only branched into barbs at the distal end. They would appear to represent a stage from which elongated scales evolved into an early form of feathers (Zhang and Zhou, 2000). Such a scenario for feather evolution, however, is different from that arising from the dinosaur evidence, which suggests the presence of branching (barbs) prior to the evolution of the rachis (Xu et al., 2001; Zhou and Zhang, 2001).

Another significant step in feather evolution is the appearance of the alula, which is attached to the first manual digit and serves primarily for balance during slow flight or takeoff. The most basal birds such as *Archaeopteryx*, *Jeholornis* and *Confuciusornis* all lack an alula. *Sapeornis* probably lacks such a derived structure too, but there is currently no conclusive evidence. A number of Early Cretaceous birds do, however, have an alula, including the Spanish *Eoalulavis* (Sanz et al., 1996) and *Eoenantiornis* (Hou et al., 1999). The most primitive enantiornithine bird, *Protopteryx*, represents the only known bird with an alula associated with an unreduced first manual digit (Zhang and Zhou, 2000). Alulas are also present in Early Cretaceous ornithurine birds.

4 Feather-like structures in other archosaurs

Theropod dinosaurs are not the only non-avian fossils from the Early Cretaceous of Liaoning, China, that have integumentary appendages resembling the feathers of birds. One is an ornithischian dinosaur, *Psittacosaurus*, which has bristle-like integumentary appendages restricted to the proximal sector of the tail. Compared to the feathers of theropods, they are longer, more rigid and much thicker. They are not branched, but cylindrical and possibly tubular, and are anchored deeply in the skin, possibly for display (Mayr et al., 2002).

The other archosaur group that has preserved feather-

like integumentary structures is the Pterosauria. Most notable among them is the recently discovered *Jeholopterus*, which belongs to a distinctive, short-tailed family of rhamphorhynchoid pterosaurs, the Anurognathidae (Wang et al., 2002). This pterosaur has long, flexible and unbranched hair-like filaments covering the entire body. As in the case of *Psittacosaurus*, the data so far neither support nor deny a homological relationship between these structures and the filamentous protofeathers of birds and theropods.

The recent suggestion that the long “scales” of the archosaur *Longisquama* are protofeathers has stimulated renewed debate: a majority of reviewers, nevertheless, seem to reject the suggestion (Reisz and Sues, 2000; Stokstad, 2000; Prum, 2001; Unwin and Benton, 2001; see also Zhou and Zhang, 2001b for a detailed discussion).

5 Discussion

Recognition of unambiguous feathers on an indisputable dinosaur is the key to answering the question of whether dinosaurs were ever feathered. The discovery of modern feathers on the fossils of various theropod dinosaurs seem to have resolved the issue. Dinosaur feathers are a fact for many paleontologists, but there are exceptions. Thus, Feduccia (1999), Jones et al. (2000), Maryanska et al. (2002) and Lü et al. (2002) have all suggested that *Caudipteryx* and other oviraptorids are secondarily flightless birds. Even so, Xu et al. (2002) concluded that *Caudipteryx* is a dinosaur not a bird, based on the study of a new basal oviraptorid. Could dromaeosaurs also be flightless birds? Some paleontologists seem ready to consider such an interpretation seriously (L. D. Martin, pers. comm.).

In the absence of compelling evidence against a close relationship between birds and dinosaurs, the issue of the origin of avian flight and feathers has to be discussed within the framework of a dinosaurian origin for birds. Discovery of arboreal dromaeosaurs with feathers along the whole body, especially the hindlimbs, provides strong evidence that, at least at some stage in feather evolution, feathers were used for balance and gliding in the ancestors of birds. Display or thermoregulation may have been the initial selective force leading to the appearance of feathers, but it was aerodynamic adaptation that finally developed feathers for flapping flight in birds. More advanced structures such as the alula, which was undoubtedly adapted to modern styles of flapping flight, evolved only at a later stage in avian evolution.

Our understanding of the evolution of feathers is still far from complete. It could be that the integumentary homologs of avian feathers are indeed present not only in theropods but also in a more inclusive archosaur group, including core dinosaurs and pterosaurs. If so, we should not be surprised if more such animals are discovered with unbranched protofeathers or feather-like structures in the future.

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S06-3 The theropod origin of feathers: congruence between development, paleontology, and phylogeny

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Abstract Progress on the evolutionary origin of feathers has been hampered by conceptual problems and by the lack of primitive feather fossils. Recently, both limitations have been eliminated. A new developmental theory proposes that feathers evolved through a series of novelties in developmental mechanisms of the feather follicle and feather germ. Recent analyses of the integumental appendages of theropod dinosaurs from the early Cretaceous Liaoning formation of China (~124 million years ago) have confirmed that these integumentary structures share several unique features with avian feathers: multiple filament structure, branching at the base, and serial branching. In combination with robust phylogenetic evidence supporting the theropod origin of birds, the details confirm that these integumentary structures are homologous with avian feathers. The discovery of primitive and derived fossil feathers on a diversity of coelurosaurian theropod dinosaurs documents the evolution and diversification of feathers in non-avian theropods before the origin of birds and before the origin of flight. The morphologies of these primitive dinosaur feathers are exactly congruent with the predictions of the new developmental theory. The aerodynamic theory for the origin of feathers is falsified, but other proposed functions remain developmentally and phylogenetically plausible. Feathers are inherently tubular structures. Whatever their initial function, they evolved by selection for a follicle that would grow an emergent tubular appendage.

Key words Feather, Evolution, Theropod, Fossil

1 Introduction

Despite more than a century of research, the evolutionary origin of feathers has long remained a mystery (Prum and Brush, 2002). Progress was hampered by two long-standing problems: the lack of primitive, fossil feathers, and the limitations of conceptual models of feather evolution. The earliest and most basal bird fossil, *Archaeopteryx lithographica* from the Late Jurassic, exhibits entirely modern feathers that are indistinguishable from those of extant birds. So, traditionally, paleontology has contributed little so far to the debate on how feathers evolved. The conceptual problems arose largely from the adoption of inappropriate concepts of the primitive feather, for example the interpretation of feathers as elongate scales, as well as unproductive approaches to the study of macroevolution and speculative assumptions that feathers evolved for a specific function, such as flight.

These traditional problems have been eliminated by recent advances in the developmental biology of feathers (Prum, 1999; Harris et al., 2002), and by fortuitous discoveries of feathered, non-avian, theropod dinosaurs from the early Cretaceous Yixian formation of Liaoning, China, summarized in Prum and Brush (2002). Together, these studies document the origin and diversification of feathers within carnivorous, bipedal theropod dinosaurs before the origin of birds or the origin of flight.

2 The feather origin problem

The origin of feathers, conceptually, exemplifies the more fundamental questions raised by the origin of evolutionary novelties. Evolutionary novelties are derived structures that have no homologs, or antecedent structures, in ancestral or related organisms (Müller and Wagner, 1991). Evolutionary theory provides a robust understanding of the evolution of minor or continuous variations in organismal size and shape. But where do entirely novel structures, such as digits, limbs, eyes and feathers come from?

Understanding the evolutionary origin of feathers has been hampered by several common conceptual problems. First among these is the neo-Darwinian view of *macroevolution* as merely *microevolution* writ large. Since 1960s, biologists have theorized that novelties originated through a series of small, micro-evolutionary stages, each of which is ecologically, functionally, and selectively plausible. Since such adaptive micro-evolutionary approaches never focused specifically on what is *genuinely* novel about the two transformational end points, they are unlikely to contribute to a realistic understanding of the origin of novel structures.

A favorite micro-evolutionary theory for the origin of feathers has been that planar feathers evolved from elongate scales through natural selection for flight within an-

central birds. Such theories have a persistent flaw which was first pointed out in the 19th century (Davies, 1889), but which has been ignored for most of the last century (Prum, 1999; Prum and Brush, 2002). That error is the assumption that the two planar surfaces of a scale develop from the top and bottom of the initial epidermal outgrowth that forms the scale. In actual fact, however, the two planar surfaces of a pennaceous feather are created by the *outer* and *inner* surfaces of the tubular feather germ only after the feather emerges from its cylindrical sheath. The planar surfaces of an elongate scale and a pennaceous feather are not, and could not have been, homologous. Feathers could never have evolved by elongation and division of a planar scale. The unchallenged persistence for most of the 20th century of the flawed concept of the primitive feather as an elongate scale has contributed greatly to the delay in achieving an understanding of the origin of feathers.

3 The developmental theory

An alternative approach to the study of the origin of feathers posits that the detail of feather development can be used to reconstruct plausible antecedent feather morphologies (Prum, 1999). It maintains that any theory of the origin of feathers should also provide a complete and consistent theory of the evolution of the complex mechanisms of feather development. This alternative “developmental” theory of the origin of feathers is based entirely on the hierarchical details of how feathers grow, and provides a detailed, testable model of the evolutionary origin and diversification of feathers.

The developmental model hypothesizes that the first feather (Stage I) originated with a tubular elongation of the placode and the first feather follicle, a cylindrical epidermal invagination around the initial feather papilla. Subsequent feather diversity evolved through a series of derived developmental novelties within the ring-shaped epidermal collar of the follicle that generates the tubular feather germ. After the origin of the tubular feather germ came the differentiation of the tubular epidermis into the barb ridges that generate the barbs (Stage II). The model proposes two alternative stages next: (1) the origin of helical growth and the rachis (Stage IIIa), or (2) the origin of barbule plate differentiation (Stage IIIb). Evolution of both of these developmental novelties established the capacity to grow both the branched structure of modern feathers (Stage IIIa+b). The origin of differentiated distal and proximal barbule plates followed (Stage IV).

This hypothesized series of five developmental novelties predicts an explicit transition series in the morphologies of the feathers grown from such follicles. Stage I follicles would produce an unbranched, hollow, tubular feather. A Stage II follicle would produce a tuft of barbs fused ba-

sally to the calamus. A Stage IIIa follicle would grow a feather with a rachis (formed by the initial fusion of feather barbs on the anterior side of the follicle) and a series of fused barbs. A Stage IIIb follicle would produce a tuft of barbs from which barbules branched. Stage IIIa+b follicles would grow the first bipinnate (double-branched) feathers with a rachis, barbs, and barbules. In the absence of differentiated barbules, a Stage IIIa+b feather would be diffusely pennaceous, i.e. lack a coherent vane. Stage IV follicles would grow a pennaceous feather with a coherent vane produced by the interlocking of the differentiated hooks and grooves of the distal and proximal barbules of neighboring barbs.

4 Support for the developmental model and theropod origin of feathers

Support for the developmental theory of feather origins comes from the hierarchical nature of feather development itself (Prum, 1999) and the diversity of feathers among extant birds (Prum, 1999). Furthermore, exciting new molecular data from the developmental biology of feathers (Harris et al., 2002) now corroborates both the morphologies and the sequence of the first three stages predicted by the developmental model (Prum, 1999).

The last decade has also produced startling new paleontological discoveries from the early Cretaceous (~124 million years old) Yixian formation in Liaoning Province, north China, yielding a diversity of theropod dinosaur fossils with well-preserved integumentary structures. These discoveries have produced a revolution in our understanding of the origin and evolutionary history of feathers. Feathers first appeared in a lineage of coelurosaurian theropod dinosaurs and diversified into essentially modern structural variety within subsequent lineages of non-avian theropods (Zhou, 2003). Among the numerous feather-bearing theropod dinosaur lineages, one particular group evolved the ability to fly with the feathers of its specialized forelimbs and tail: the birds.

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S06-5 Selection for feather structure

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Abstract We focus here on possible selection pressures that acted on the protofeather to create the structural complexity and diversity of modern feathers. The need for water repellency may have influenced the spacing and structure of barbs and barbules. Thermodynamics may have been critical to the development of downy barbs and the subsequent formation of semiplumes and down feathers. Aerodynamics probably influenced the twisting of barbules that provides for the overlap of adjacent barbules and the resistance of the vane of flight feathers to air flow. Air pressure may also have selected for the elliptical, cross-sectional shape of the ramus, since such a shape would reduce the tendency of the barb to rise into the low pressure over the dorsal surface of the flight feather. Because the elliptical shape would resist bending, it would also reduce material fatigue from repeated flexing. Resistance to abrasion by airborne particles would favor larger feather parts and increased strength of the protofeather. Melanin deposited in the keratin increases its strength and increases the thickness of the cortex of the ramus of the barb and of the rachis. While these selection pressures have been invoked as affecting modern feathers, their potential importance to the evolution of feather structure has been largely overlooked. We briefly discuss new data on ectoparasites and feather-degrading bacteria which suggest that both parasites and bacteria have had a long association with feathers and may have selected for the deposition of melanin and the thickening of the cortex among birds inhabiting humid environments. Ultraviolet damage to feathers is almost unstudied, and damage from icing has been mentioned only anecdotally. Exploring selection pressures that act on modern feathers may be key to understanding the evolution of feather structure and diversity.

Key words Feather, Evolution, Selection, Feather structure, Feather diversity

1 Introduction

To understand the evolution of feathers we must answer two related, but different questions: how the protofeather originated and how it evolved into the structural complexity and diversity of modern feathers. The most primitive feathers are filamentous structures projecting from the integument of *Sinosauropteryx*, a basal coelurosaur (Chen et al., 1998; Zhou, 2006), and *Beipiaosaurus*, a therizinosaurid theropod (Xu et al., 1999). The integumentary appendages of both dinosaurs are single filaments. Such structures correspond to stage I in the evolution of the feather as predicted by Prum (1999) and Prum and Brush (2002).

Attention so far has focused on the evolutionary origin of feathers (Feduccia, 1999; Prum, 2002; Zhou, 2006), and on mechanisms by which the structure and form of modern feathers evolved (Prum, 1999; Prum and Williamson, 2001), with but little attention to the selection pressures that shaped that structure and diversity. With the appearance of protofeathers (Xu et al., 2001; Zhou, 2006), an array of biotic and abiotic pressures began to select for particular modifications to their filamentous structure. Like the reptilian skin and scales that preceded this evolutionary novelty, the protofeather needed to resist abrasion, degradation by bacteria and consumption by ectoparasites. Similarly, ex-

posure to the damaging effects of ultraviolet radiation necessitated a structure that could resist UV-damage and protect sensitive underlying tissues. As protofeathers enlarged, they needed to be flexible so as to move with the limbs, but also resilient in order to recover their position and shape. These and other pressures could not have acted until the original feather appeared. Some of these pressures acted in concert, for example resistance to abrasion, feather-degrading bacteria and ectoparasites. Others acted in opposition, for example flexibility versus resiliency. But over time these actions and interactions selected for the structural complexity and diversity of modern feathers.

Accordingly, we review here those selection pressures we believe played a role in the evolution of complex and diverse modern feathers from filamentous protofeathers and summarize the supporting data. The discussion is based necessarily on evidence from modern feathers. We realize that selection on protofeathers may have been different from that on modern feathers, but we are convinced that a better understanding of selection on modern feathers will lead to new insights concerning the evolution of feather structure and diversity generally. To set the stage, we summarize structure and diversity in modern feathers.

1.1 Brief review of feather structure and diversity

Modern feathers include contour feathers,

semiplumes, filoplumes, bristles, down, those with and without aftershafts and come in a bewildering array of colors and shapes. All have a basal calamus that is anchored in a follicle below the surface of the skin. All have a central structure from which branches, the barbs, extend; and the barbs have secondary branches, the barbules. Growth patterns are similar and all growing feathers are enclosed temporarily in a sheath. There the similarity ends. Contour feathers and semiplumes have a central shaft, the rachis, flanked by barbs that form a flat vane on either side of the rachis. Flight feathers and coverts have barbs that interlock rigidly, whereas body contour feathers have barbs that interlock weakly; and semiplumes have barbs that do not interlock at all. Filoplumes have a rachis that thickens distally and ends in a tuft of 1–6 short barbs. Bristles have a stiff tapered rachis and a basal tuft of barbs. Most down feathers have flexible barbs and barbules that extend directly from the calamus to form a loose tangle that entraps air. However, some down feathers, especially those of waterfowl, may have a rachis that is as long as the longest barbs. With this brief sketch of the structural diversity of feathers we can now ask what are the selection pressures acting on feathers that might account for their evolution from primitive filaments to the complex, diverse structures described above.

2 Selection pressures

2.1 Water repellency

Theropods had protofeathers that were thin filaments, some of them branching in a pattern similar to the open pennaceous feathers that cover the bodies of modern birds. These fibers were 30–40 mm long, but less than 0.5 mm in diameter and possibly as little as a 0.1 mm in diameter. When such long, thin filaments were struck by raindrops they would not have had the mechanical strength to resist the forces exerted by the surface tension of the water droplet and would have adhered to each other in clumps, such as seen in wet fur. Such clumped filaments would be less able to shed further rain and would provide reduced insulation. In addition, the water that clung to the coalesced bundles of fibers would conduct heat away from the body. Thus rain would have wet a body covering of branching, filamentous protofeathers, which would have lost their ability to shed additional water and their ability to insulate.

Both problems can be eliminated by evolving a structure that resists the forces of surface tension. One way to do this is to arrange the filaments so that the distance between them remains constant despite the presence of water droplets and the forces of surface tension (Cassie and Baxter, 1944). On contour feathers, barbules from adjacent barbs link to each other and maintain relatively constant spacing between barbs. Furthermore, the barbules and barbs of overlapping feathers (e.g. coverts, body feathers) maintain an open porous structure such as envisioned by Cassie and Baxter who point out "... it is surprising how closely the structure of feathers conforms with the theoretical requirements for water-repellency."

Rijke (1970, 1987, 1989) developed a model for water repellency based on the model for porous surfaces developed by Cassie and Baxter (1948) and Cassie (1958) for textiles. However, Elowson (1984, 1987) found that the vane of a modern feather is considerably more complex and variable than the geometry of the textile model, that the model's predictions were not met, and that the spacing of barbules appeared to influence the shape of droplets more than the spacing of barbs. The open branching structure of protofeathers described by Xu et al. (2001) and modeled by Prum and Williamson (2001) may more closely approach the conditions assumed by the textile model. Possibly water repellency shaped the early or later evolution of feather structure.

2.2 Resistance to water penetration

When a bird floats on the surface of the water or dives beneath it, pressure may force water between the barbs. Mahoney (1984) showed significant differences in the penetration of water into the plumage of different aquatic species. She and Rijke (Rijke et al., 1989) calculated and measured penetration on isolated feathers and found that spacing of the barbules was an important factor in limiting water penetration whereas spacing of the rami of the barbs was critical to shedding rain drops. Water penetration under pressure is critical to water birds whereas water repellency is critical to water birds and terrestrial birds alike. Furthermore, water penetration and water repellency select for different structural adaptations in the feather. The relative contributions of each to the evolution of feather structure is open to exploration.

2.3 Damage from freezing

Water that freezes after penetrating the network of barbs and barbules can bind feathers together and cause barbs to be ripped from the rachis when a bird moves, thereby pulling the feathers apart as, for example, when opening a folded wing in the morning after a night of sleet (pers. obs.). How the feather can evolve to minimize such damage and how important such damage is to birds are unknown. The topic is unstudied.

2.4 Durability

We do not know whether protofeathers grew continuously or reached a predetermined length after which the follicle became quiescent and growth ceased until the follicle resumed activity and a new protofeather replaced the old. In either case, the filament had to be sufficiently durable to resist wear so that the organism could maintain a functional coat. Durability of the filaments and simple branching structures evident in the early fossils is unknown, but selection should have favored resistance to abrasion by airborne particles.

Particulate abrasion has been measured experimentally for feathers by Burt (1986) who used an aerodynamic model to predict which areas of a flying bird receive the most intense particulate abrasion. Melanic feathers, which

are the most resistant to particulate abrasion, occur disproportionately often in those areas (most notably the wing tips) predicted by the aerodynamic model (Burt, 1986). The cortex of the rachis and of the ramus is thicker when melanin is present than when not (Voitkevich, 1966), and melanic keratin has greater tensile strength than non-melanic keratin (Bonser, 1993, 1995).

Recent isolation of feather-degrading bacteria from the plumage of wild birds raises the possibility that bacteria, which can be seen associated with feather impressions of fossil birds (Davis and Briggs, 1995), may have catalyzed selection for characteristics that resisted bacterial degradation. Feathers with melanin degrade more slowly than those that lack melanin (Goldstein et al., 2004). Furthermore, Burt and Ichida (2004) have shown that the darker color of song sparrows (*Melospiza melodia morphna*) from the humid forests of the Pacific northwest of USA is associated with a somewhat higher incidence and more active strain of feather-degrading bacteria (*Bacillus licheniformis*) than in the pale song sparrows (*M. m. fallax*) of arid southwestern USA. Here again, the presence of melanin is associated with greater cortical thickness. Other structural differences between feathers with more or less melanin have not been studied.

2.5 Resilience

The rachis, rami, and barbules will bend as the feather moves through the air, as it interacts with neighboring feathers when limbs, head and neck move, and as feathers brush against grass, twigs, and other objects in the environment. How far can the feather bend without breaking? How does the structure of the feather respond to repeated bending?

Flexibility can be advantageous. Slight bending of the tips of the primaries reduces wing tip vortices in soaring birds such as vultures, increasing the efficiency of the wing at slow speeds. Similar bending of the coverts into the airstream over the wing creates the micro-turbulence that helps to hold the laminar flow of air close to the wing at slow speeds and steep angles of attack. In both these cases, limited bending of the feather into the airstream of a flying bird is essential to the function of the feather. Too much bending would create excessive turbulence and reduce aerodynamic efficiency.

The square cross-sectional shape of the rachis with its thickened dorsal and ventral cortex suggests selection for limited flexing of the feather in dorsal and ventral directions, the very directions in which the primaries and coverts would flex into the air stream. The elliptical cross-sectional shape of the ramus, reinforced dorsally and ventrally, permits bending toward the tip or base of the feather, but restricts bending above or below the plane of the vane of the feather. What selection pressures favored flexibility in certain directions and not others? Can we infer selection acting on the primitive open structure hypothesized by Prum and Brush (2003) from measurements on modern feathers?

2.6 Ultraviolet damage

As the outermost covering, protofeathers and modern feathers were and are exposed to solar radiation. Bergmann (1982) provided qualitative evidence that ultraviolet radiation damages feathers, but quantitative evidence for relating exposure to damage is lacking. Also lacking is evaluation of ultraviolet damage to differently structured and colored feathers. Melanin is present more often in the dorsal cortex of the rachis, rami, and barbules than in the ventral cortex. Is melanin distribution an adaptation to limit ultraviolet damage to feather structure? Is thickening of the dorsal cortex of the rachis and rami an adaptation to reduce potential ultraviolet damage to the feather? If we can document how modern feathers resist damage from ultraviolet radiation, that may help us understand the role played by ultraviolet light in the evolution of modern feathers from protofeathers.

Adaptations of the feather may not be limited just to preserving structural integrity. The feather may shield underlying tissue from ultraviolet radiation. The open structure of the primitive feather, as hypothesized by Prum and Brush (2003), would be a poor shield and closure of the structure would be strongly selected by the need to absorb potentially damaging UV-radiation.

2.7 Thermodynamics

Regal (1975) makes a strong case for the evolution of feathers as insulation to prevent heat loss. Indeed, the filamentous structures found on theropod dinosaurs and postulated by Prum (1999, 2002), Prum and Williamson (2001) and Prum and Brush (2002, 2003) as stage 1 in the evolution of feathers would have trapped air among the many overlapping filaments. The multiple barbs extending from a calamus or the branches extending from a rachis would have improved the ability of the primitive feather to capture warm air near the body of protobirds. Additionally, the air-filled structure of the feather is ideal for reducing conduction of heat through the feather itself, as pointed out by Dyke (1985) in his discussion of feather evolution. Thus the form of primitive feathers and their internal structure could have been selected for their thermodynamic advantages. Protofeathers could have helped retain metabolic heat, thereby increasing the efficiency of energy conversion in a small active organism. Alternatively, they could have helped protect the organism from overheating in warm, sunlit, but breezy conditions (Walsberg, 1982).

Thermodynamics may explain evolution of multiple barbs (down) or the open branching structure (semiplume), but there seems to be no thermodynamic advantage to the closed branching structure of contour feathers. However, selection based on thermodynamic requirements would seem to provide strong reasons for the origin of filamentous protofeathers and for their elaboration into structures with multiple branches.

2.8 Aerodynamics

Much has been written about the role of aerodynam-

ics in the origin of birds and feathers. If we accept the developmental model for the origin of feathers, then aerodynamics has no role to play. Novel changes in the integument resulted in the evolution of a papilla surrounded by germinal tissue that produced a hollow tubular structure such as seen in *Sinosauropteryx* (Chen et al., 1998; Zhou, 2006) and *Beipiaosaurus* (Xu et al., 1999). Such structures are not aerodynamic. Not until the open branching stage of development did the feather reach a point at which selection for aerodynamics might have played a role in selecting for the closed structure that characterizes modern remiges.

However, several characteristics of feathers are ideally suited for flight. Feather keratin is lighter than the keratin that covers the bill and feet. The tubular structure of the rachis and rami of barbs is light but strong, and more resistant to bending than a solid rod of the same weight. The elliptical shape of the rami allows the barbs to flex only toward the tip of the feather and the thickened dorsal and ventral surfaces of the rachis allow only slight lifting of the feather tip into the airstream above the wing. The slight lift creates a thin layer of turbulence over the wing, which helps hold the laminar flow of air on the wing at slow speeds. Such control of the airflow enables the bird to lower its stalling speed and thereby maneuver and land at low, safe speeds.

The remiges and rectrices of many birds are further modified so that each feather has an airfoil shape that contributes to lift and propulsion. These changes must have occurred after the feather had become a closed branching structure, stage 4 in the scheme laid out by Prum and Brush (2003), but when? Could earlier, more open stages in the evolution of the feather have conferred advantages on a gliding protobird?

3 Conclusions

Protofeathers were probably unbranched, tubular structures such as found on several of the Chinese fossil theropods and predicted by Prum and Brush (2003). Selection for the origin of such filaments was probably thermodynamic, but may also have been protection from ultraviolet radiation or rain. Once this tube of keratin came into existence, it became subjected to selection to improve its thermodynamic properties, to better shed rain, and to better shield the underlying skin and organs from harmful radiation. These pressures could have favored the evolution of a branching structure. Selection to resist abrasion, brushing against stationary objects, degradation by microorganisms, and consumption by lice and mites would have influenced the shape and reinforced the structure of the protofeather.

At some point, the primitive feather evolved into a branched structure, at which time its evolution as an aerodynamic appendage could begin. Were tubular protofeathers made of β -keratin, or did incorporation of a light, strong keratin occur during evolution of an aerodynamic appendage? Bristles and filoplumes have sensory and pro-

tective functions (Gill, 1994); but were such functions critical to their evolution? We are now beginning to understand the origin of feathers, but we are barely on the threshold of understanding the selective pressures that account for the evolution of the structure and diversity of modern feathers. Exploration of such pressures acting on modern feathers may provide insight into the pressures that transformed the ancient protofeather into the structurally and functionally diverse feathers of today.

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S06-6 Conclusion

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1 Review

This symposium addresses several important topics. That with the highest public profile is the question of whether feathered dinosaurs existed. Both Zhong-He Zhou and Richard Prum agree that dinosaurs did indeed have feathers. My personal view is that, because in some dinosaurs we see large feather-like structures which resemble avian feathers as much as the large feathers of *Archaeopteryx*, we must conclude that these dinosaurian features are homologous with avian feathers. A difficulty with this view is the apparently plumulaceous nature of the small body feathers in dinosaurs, which suggests that among theropod dinosaurs there were diverse integumental appendages, some of which may not be homologous with avian feathers.

Another important topic concerns the evolutionary origin of feathers. Dominique Homberger, Alan Brush and Richard Prum brought new ideas and new emphases to this issue. Homberger, in an oral, unsubmitted, advanced the new hypothesis that the evolution of feathers is linked functionally with streamlining of the body; a abstract is published in the Abstract Volume for the Congress. Brush and Prum argue that the evolution of feathers passed through stages resembling those of the developing feather. An important plank of their developmental hypothesis is the novel appearance of the follicle from which the unbranched tubular protofeather grows.

This developmental hypothesis has strengths and weaknesses. One weakness is that it does not address function. Function is such an integral part of evolutionary thinking that we need to incorporate it in any reasonably complete theory of the evolution of feathers. A strength of their hypothesis is that it integrates biochemical, genetic, developmental and morphological data. The work of Brush and Prum represents a significant contribution to the understanding of feather evolution.

2 Prospect

I wish to emphasize in these concluding remarks that there are basic questions concerning modern feathers which have not been answered today. I will give two examples.

The first pertains to the fact that the most characteristic feature of modern contour feathers in birds is their high regularity. A very high number of barbules are spaced regularly along the barbs, which in themselves are spaced regularly along the rachis. In a belly feather of an Arctic Tern, approximately 3 1/2 cm long, the number of pennaceous barbules is about 90 thousand. Despite this striking complexity, no generally accepted theory for its functional significance exists. My second example is the frequently stated hypothesis that links feather evolution with thermal insulation, and has a flaw that is rarely pointed out. Judged from modern feathers and the fossil evidence presented by Zhou, open pennaceous feathers probably evolved before downy feathers: such feathers insulate poorly.

Other examples of unresolved issues could be given, some of them noted by Peter Stettenheim in his introduction. We need basic, thorough studies of modern feathers, along with studies of the fossil record that will deepen our understanding of modern feathers and their functioning and perhaps also their evolutionary origin.

The contributions of Homberger and Burtt exemplify the type of studies I advocate. Both provide new data and lead to the formulation of new hypotheses. Thus Homberger, in her penetrating study of the functional microanatomy of the feather-bearing integument, suggests that the depressor feather muscles, which are unique to birds, play a role in streamlining the body during flight. Burtt, in his thorough and inspiring study of the relations between feathers and feather-degrading bacilli, puts forward the idea that dark feather development may reflect a response to the greater potential for bacterial degradation in humid climates. Both these studies stress the variety of selection pressures acting on feathers. To quote Jed Burtt: "We need to think broadly and creatively about the selection pressures acting on feathers to understand their past and continuing evolution."

Although much work remains to be done in feather science, there is no need to hurry. Feathers have existed on our planet for more than 150 million years. They have so far been studied scientifically for no more than 150 years. Let us continue the work.

Symposium 07 Key issues in the conservation of sites important for birds

Introduction

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Central to adequate land-use planning is the identification and conservation of sites of exceptional importance for biodiversity. This is crucial because such sites cannot be replaced once they are lost to development, i.e., they represent “critical natural capital”. The Important Bird Area (IBA) program of BirdLife International is a worldwide project aimed at identifying and conserving important sites using birds as flagships. By 2001, over 8 000 IBAs had been identified and documented, including 4 000 in Europe, 500 in the Middle East and Central Asia, 1 250 in Africa, 1 500 in Asia generally, 1 500 in the Americas, and 5 in the Pacific. For each site, data is collected by standardized methods that details geography, birds, habitats, land-use, threats and protection. This is stored, analyzed and reported with purposely-built computer software “The World Bird Database”.

To date the IBA program has produced a very large body of conservation advocacy and action at national levels. These include the establishment of local site support groups, the creation and management of new protected areas, the establishment of integrated conservation and development projects for key IBAs, and the strengthening of national legislation. At regional levels, especially within the European Union, more and more IBAs are being designated for protection under international agreements and conventions. Globally, the importance of IBAs has been recognized by the World Bank in their Critical Natural Habitats operational policy, and by the Global Environment Facility in its own strategy. The IBA program is undergoing exciting broadscale development from the identification and documentation of sites to action, advocacy and monitoring. This symposium brings together speakers from four conti-

nents and presents recent experience with and current thinking on key issues involving site identification and prioritization, site monitoring, and local community involvement. Included is an update on the Asian IBA program and an analysis of the situation in China.

The influence of the IBA program is helped by its criteria for operations which are objective and globally agreed as well as being applicable and implementable at national levels. There is growing evidence that the IBA program identifies many sites of wider importance for biodiversity, though not, of course, all of them. The purpose of the program is to promote effective conservation, though this symposium focuses mainly on the scientific aspects, particularly the need for effective monitoring.

Given the scarcity of resources, thought has been given to the development of effective monitoring methods that are simple to do and focused on the most pressing priorities. Only on such a basis will monitoring programs be sustainable in the longer term. Outputs need to be targeted at clear constituencies if they are to achieve real impact. Development and refinement of approaches will be an iterative process. Ornithologists understand increasingly that conservation is only partly a scientific activity. Every bit as important is the social and political stage on which the science plays. It is a common thread running through the contributions in this symposium.

All presentations are reported here except the first paper by Leon Bennun, “Site identification and prioritization”, which was drawn from African experience in establishing Important Bird Areas and given as an oral. An abstract of it is published in the Abstract Volume for the Congress.

S07-2 Inventory of sites important for birds in Asia

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Abstract The Important Bird Area program in Asia was launched at the first Pan-Asian Ornithological Congress, Coimbatore, India in November 1996. Since then several international and regional workshops have been held. Almost all countries in Asia are working on identifying IBAs and compiling information. More than 2 000 sites have been nominated so far, and a summary book focusing on the status and conservation needs for maintaining these sites is to be published in mid-2003.

Key words Important Bird Areas, Asia

1 Introduction

The Important Bird Area (IBA) program for Asia is a conservation project of BirdLife International. It was launched at the first Pan-Asian Ornithological Congress, Coimbatore, India, in November 1996, when the compilation of the BirdLife International Asian Red Data Book was underway (1995–2001).

2 Structure and procedures

Since the launch of the Asian IBA program, a series of international and national workshops have been held for instruction of the IBA criteria, discussion of potential IBAs and the building of a network of compilers:

- Tokyo, Japan (October 1997): International workshop.
- Genting Highlands, Malaysia (February 1998): Workshop for Malaysia, Singapore and Indonesia.
- Irkutsk, Russia (March 1998): Workshop for Russia.
- Phnom Penh, Cambodia (March 1998): Workshop for Cambodia.
- Changhwa, Taiwan (August 1998): Workshop for Taiwan.
- Bangkok, Thailand (November 1998): Workshop for Thailand, Laos, Cambodia and Myanmar.
- Beijing, China (December 1998): Workshop for Mainland China and Hong Kong.
- Ulaanbaatar, Mongolia (July 1999): Workshop for Mongolia.
- Seoul, South Korea (August 1999): Workshop for South Korea.
- Bogor, Indonesia (August 1999): Workshop for Indonesia, Philippines, Singapore and Thailand.
- North-western India (September 1999): Workshop for India.
- Ulaanbaatar, Mongolia (October 1999): Workshop for Mongolia.

- Genting Highlands, Malaysia (October 1999): International workshop.
- Penang, Malaysia (August 2001): Workshop for Malaysia, Singapore and Brunei.
- Yangon, Myanmar (December 2001): Workshop for Myanmar.

IBA workshops were also held concurrently with Red Data Book workshops in the Philippines in 1995 and 1996, before the Asian IBA Program was officially launched.

More than 200 ornithologists and conservationists have participated in these workshops. With the exception of several countries with which BirdLife International has not yet developed contacts, the IBA data have been collected by BirdLife partners and affiliates, and by participants in the workshops.

The overall progress of IBA compilation in Asia is coordinated by the Wild Bird Society of Japan (BirdLife partner in Japan), which is also the major fund-raiser for the IBA Program in eastern Asia. The Royal Society for Protection of Birds (BirdLife partner in the United Kingdom) is coordinating and providing funds for IBAs in South Asia as well. BirdLife Asia Division Program Offices in Bogor and Hanoi are coordinating the compilation of IBAs in Indonesia, Philippines, Malaysia, Singapore, and Vietnam. The BirdLife Vietnam Program Office has also undertaken a thorough revision of IBAs in Indo-China.

3 Results

Most countries have finished the first stage of producing preliminary lists of IBAs. To date, 2 114 IBAs have been identified in Asia (Table 1), covering a combined area of probably over 2 000 000 km². This represents at least 7% of the total area of Asia, excluding Central Asia and the Middle East which have their own IBA programs. The size of IBAs varies from 337 920 km² (Changtang Plateau, Tibet),

which is slightly larger than Vietnam) to 4 ha (Okhla, India) and 200 m² (Camp O'Donnel, Philippines). About 40% (841 sites) of IBAs in Asia receive no protection in any form at all, while many of the remainder are not fully protected or properly managed.

4 Discussion

Compilation of IBAs in Asia is ongoing, and their numbers and total area are expected to increase. A synopsis summarizing the first stage of the IBA program will be published in 2003. But it will take several more years to publish

a full inventory of Asian IBAs comparable to those for Europe (Heath and Evans, 2000) and Africa (Fishpool and Evans, 2002). However, two IBA inventories have been published, for the Philippines and Taiwan, and others (e.g., for Nepal) are in preparation.

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Table 1 Number of IBAs identified in Asia as of August 2002 (Figures subject to change)

Country or territory	Number of IBAs (number protected in parenthesis)	Area of IBAs (ha)
Russia (east of the Yenisey River)	124 (53)	>1 277 520
Mongolia	32 (13)	>2 698 794
Japan	193 (115)	>556 143
North Korea	33(25)	262 882
South Korea	37(20)	101 882
China (Mainland)	422 (277)	109 128 761
China (Taiwan)	53 (32)	652 677
China (Hong Kong)	2 (2)	>3 150
China (Macao)	1 (1)	80
Vietnam	65 (28)	>1 619 052
Lao PDR	44 (31)	?
Cambodia	39 (14)	?
Thailand	72 (56)	5 125 753
Myanmar	52 (17)	8 030 300
Pakistan	64 (47)	4 089 043
Nepal	25 (15)	2 521 400
Bhutan	14 (11)	>997 800
India	313 (198)	>6 844 913
Bangladesh	23 (9)	108 262
Sri Lanka	112 (96)	>325 898
Maldives	1	?
Malaysia	70 (51)	3 777 700
Singapore	4 (4)	>2 545
Brunei	?	?
Philippines	117 (65)	>2 189 722
Indonesia	202 (93)	21 491 689
East Timor	?	?

S07-3 Monitoring important bird areas in Africa: prospects and challenges

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Abstract We address the monitoring of sites important to the conservation of birds globally within the context of our African experience. The Important Bird Areas process has been used to designate such sites. We describe a model site-monitoring process developed in eastern and southern Africa, drawn from a rationale for monitoring, the variables to be measured, monitoring techniques, coordination and long-term sustainability. The need for monitoring is reviewed. In Africa, there are insufficient resources to monitor a wide array of variables in all the IBAs, or even the highest-priority IBAs, in every country. It is necessary to select priority variables that indicate habitat and species status, as well as potential human influences and conservation responses. Within this “pressure-state-response” framework, variables can be selected by ranking their feasibility (ease of use and cost-effectiveness), and their utility (value of information collected). A two-level approach of “basic” monitoring at all sites and “detailed” monitoring at a subset of sites allows effort to be scaled according to capacity. This process should provide the means for comparing a range of sites within countries and between countries regionally. It should delineate large-scale trends, while helping to build the capacity of individual organizations through sharing experience. Effective linkages to conservation action are essential if monitoring is to be useful, requiring appropriate institutional structures. There are also needs, largely unmet at present, for national and regional coordination, data analysis and long-term data storage.

Key words Site monitoring, Field techniques, IBA, Africa

1 Introduction

The Important Bird Area (IBA) conservation program of BirdLife International is unique in using agreed, objective criteria for site selection that are applied nationally using information collected locally. It employs birds as the primary indicators and is global in scope. Identification and documentation of the sites leads on to conservation planning, advocacy, intervention and monitoring. This paper outlines the development of an IBA monitoring program in Africa applicable at site, national, continental and global levels by the BirdLife International Africa Partnership. The approach was developed initially by Nature Kenya and later adopted and refined by the BirdLife Africa Partnership (Bennun, 2000a,b; Mutekanga, 2000; Ngeh, 2001).

Monitoring involves repeated collection of information over time, in order to detect changes in one or more variables of concern. There are different levels at which data can be systematically collected at a site. Survey is one, comprising a set of standardized observations. Surveillance is another, comprising a series of standardized surveys over time. Narrowly defined, “monitoring” means surveillance that is carried out with specific objectives, usually to detect departures from a standard set. Here we use monitoring more broadly, and include “surveillance” in it. Monitoring has another specialized meaning in the context of project design; but this paper deals only with monitoring of sites, not project outputs.

2 The need for monitoring and coordination

The approach in IBA monitoring is to “think global and act local”. It means that information collected is collatable and comparable at the levels of the site, nation, continent, and globe (Figs. 1, 3). Its purpose is to determine current biodiversity trends and status, and to assess the impact of conservation activities at each of these levels and so serve as an early warning of impending changes. This implies that a monitoring system must contain effective feedback loops into policy, legislation and management actions at each level. Such a system, in sum, should be designed to provide an efficient framework for conserving biodiversity and the life sustaining properties of the Earth (Fig. 1). It should be noted, however, that in such monitoring schemes, not all indicators will be able to be monitored by any single organization, e.g., the BirdLife Partner NGO; usually a consortium of institutions will have to be involved (Fig. 3; Bennun, 2002).

Successful regional coordination of national IBA monitoring allows an unprecedented synthesis and overview of the threats to biodiversity, biodiversity status and conservation responses across Africa. It provides, moreover, a very powerful tool for international conservation advocacy and fund-raising. Such a level of cooperation in Africa serves to continue the process of building the capacity of individual organizations, through sharing experience and technical expertise (Fig. 3).

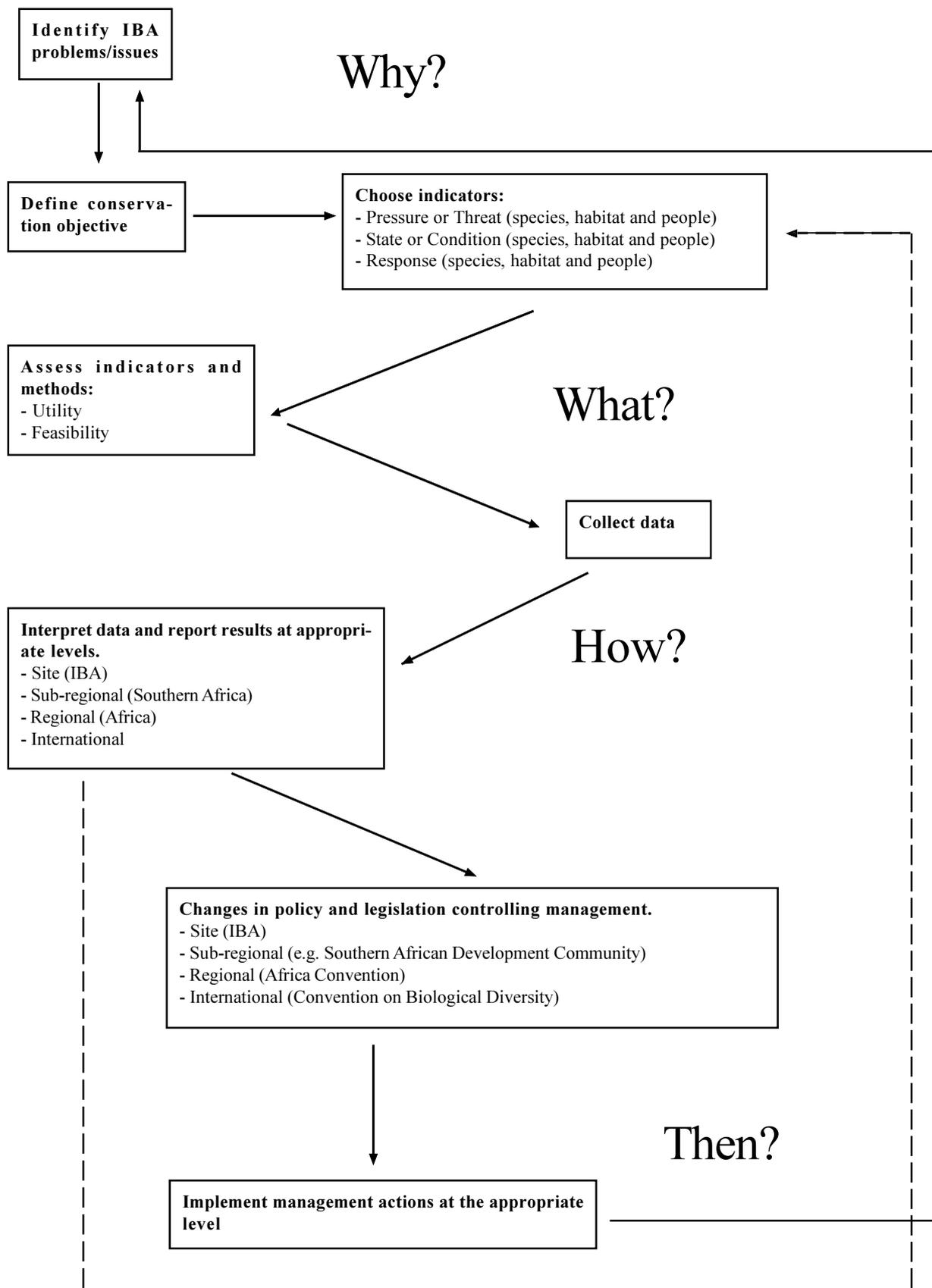


Fig. 1 Simplified steps in designing a monitoring scheme (adapted from Bennun, 2002)

3 Classification of indicators

The IBA conservation program aims to identify and protect a global network of sites critical for the long-term viability of naturally occurring bird populations, across the range of those bird species for which a site-based approach is appropriate (Fishpool and Evans, 2001). IBAs are selected on the basis of the birdlife occurring in them, the objective being to manage the sites to conserve their bird populations. The indicators selected for monitoring should be appropriate to this objective (Fig. 1).

Many indicators are open to selection. The BirdLife International Partnership in Africa and Europe, as well as the Convention on Biological Diversity, order them within a “pressure-state-response” indicator framework (Callaghan, 2000, 2001; Bennun, 2002) (Fig. 2). Conservation is usually approached at either the habitat (landscape), site (IBA) or species level. These three levels inter-link closely (Fig. 2). Sites are selected using species, and from landscape features containing particular habitats that are connected (or isolated) by the surrounding matrix. Thus, a site (IBA) monitoring program is likely to incorporate habitat and species indicators (Fig. 3). Another category of indicators concerns people (Fig. 3). Each of the indicators within the “pressure-state-response” framework can thus be categorized further to involve species, habitat or people. A summary of the following indicators is found in Bennun (2002).

3.1 Pressure (threats)

Pressure indicators identify and track the major threats to IBAs. Examples include the rate of grassland conversion to crop-agriculture (habitat), applications to prospect and mine (people), number of birds hunted (species), and human population growth (people).

3.2 State (condition)

Indicators of state concern changes in site condition and biodiversity value. Examples of site condition indicators (habitat) include forest canopy height, grass cover or

dead wood density. Examples of biodiversity value indicators (species) include threatened species populations or species richness.

3.3 Response

Response indicators identify and track conservation actions. Examples include a change in legal conservation status (people), reduction in the rate of decline in the population or re-introduction of a threatened species (species), and reduced conversion of grasslands to crop-agriculture or establishment of Site Support Groups (people).

To illustrate the integration of these indicators by means of an example: Owunji (2001) assessed changes in the avian communities of Budongo Forest Reserve after 70 years of selective logging. Assessing the avian communities involves screening both state (condition) and response indicators. Establishing the effects of selective logging on the forest structure, and consequently impacts on the avian community, in turn analyses a pressure (threat) indicator. Together, the appropriate indicators of pressure, state and response meet the overall monitoring objectives of detecting threats (pressure), determining which interventions to implement (response), assessing their effectiveness (state), making appropriate changes to interventions (response), and tracking overall biodiversity status (state). As this is a site-monitoring (IBA) framework, it is not necessary to always have a habitat, species and people indicator for each of the categories: the most appropriate indicators will depend on the circumstances (Fig. 2).

4 Selecting the most appropriate indicators

In Africa, there are insufficient resources to monitor a wide array of indicators in all the IBAs, or even the highest-priority IBAs in every country. There is therefore a need to select priority variables and indicators within the “pressure-state-response” framework (Fig. 2). Many monitoring schemes are over-ambitious, designing indicators that may be informative but require very expensive and time-consuming data collection. Such schemes cannot be sustained. It is far better to collect basic data reliably over many years than to adopt a more ambitious scheme that soon falls apart (Bennun, 2002).

Indicators should be scientifically credible, simple and easily understood, and quantify information so that its significance is clear (SBSTTA, 1999). Finding indicators that fulfil all these requirements is not easy. The approach currently in use within the BirdLife Africa Partnership ranks indicators against their utility or value for monitoring, regardless of expense and other factors, and their feasibility or practicability in terms of expense and logistics for collecting data (Bennun, 2000a,b; Mutekanga, 2000; Ngeh, 2001).

At a national level, this system can be used to ensure selection of the most effective indicators (Bennun, 2000). At subcontinental and continental level, it has been used to determine which indicators are used by all, some or a few NGOs (Mutekanga, 2000). Indicators do not need to be completely

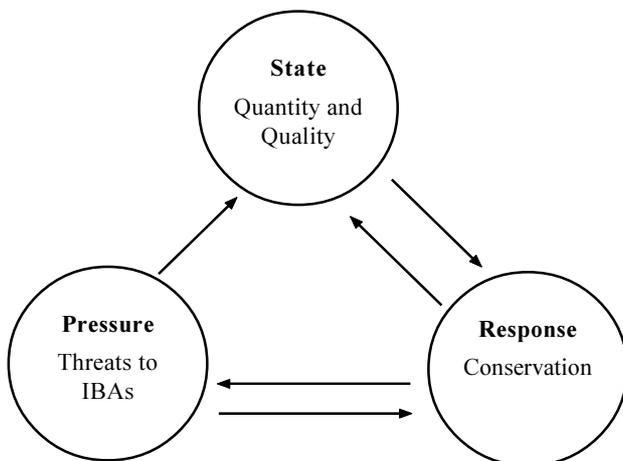


Fig. 2 The relationship between indicators of pressure, state and response (from Bennun, 2002)

standardized across sites and countries; for basic monitoring, they can vary so long as they are appropriate for making an overall rating of change. Indicators for detailed IBA monitoring can vary too, depending on the nature of the site and the conservation issues, as long as the links between monitoring and site conservation objectives are made.

5 Monitoring and prioritization of conservation action

Large changes in the condition of an IBA — the drain-

age of a wetland for example — are reasonably easy to appraise, and form the foundation of basic IBA monitoring. A decline in the population of a threatened species or other subtle changes in the biodiversity value of an IBA are much more difficult to assess and, practically, can only be measured at a very small number of IBAs. Such variables form the foundation of detailed IBA monitoring (Bennun, 2002).

5.1 Basic IBA monitoring

This procedure should be undertaken for all IBAs everywhere. Ideally, it involves an annual assessment of

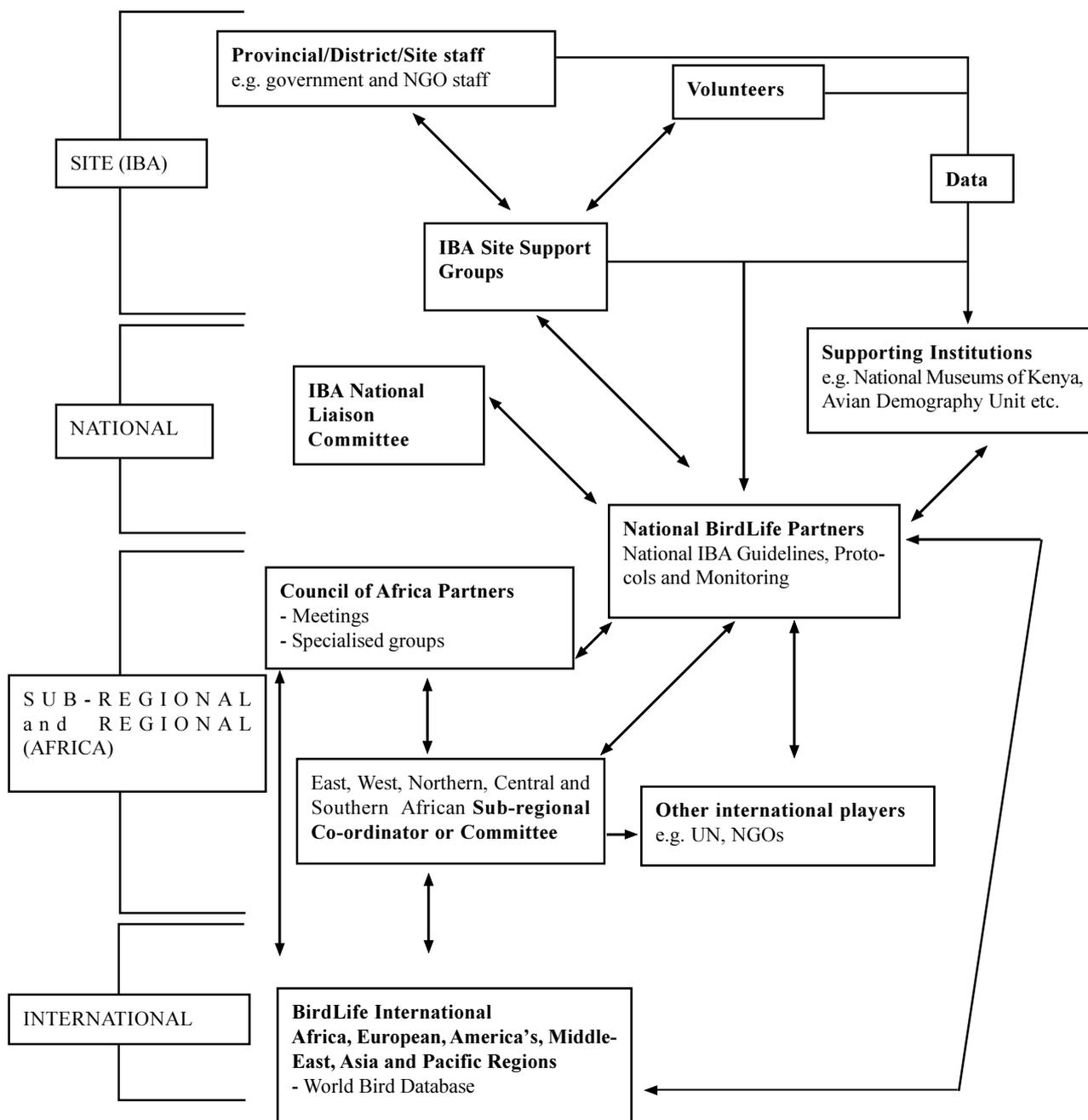


Fig. 3 Co-ordination and information flow between various components and levels of BirdLife International focused on Africa

Adapted from Bennun, 2000b; Mutekanga, 2000.

each IBA against indicators of pressure (threat), state (condition) and response. If annual monitoring is not possible, then a longer but regular time-scale (e.g., every two or three years) should be set. The actual indicators that are used can vary from IBA to IBA, and country to country, so long as they are appropriate for making an overall rating. Information on particular IBAs is submitted on simple forms by those with recent personal knowledge of the site, such as its management authority or conservation project staff, site support groups, researchers or birdwatchers. The data required are simple and mainly qualitative, and can be scored to give an overall rating for each site.

Data collection forms may vary in their structure and level of detail. The form should be designed to fit local needs in particular countries. As well as being used in annual assessments, such forms can capture valuable information from ad-hoc visits to the IBA at any time. This information is compiled and added to whatever is already available centrally. From the compiled information, the national IBA monitoring coordinator assesses overall improvement or deterioration at the IBA once a year, and rates each to cover pressure, state and response (Bennun, 2002).

An annual IBA status report, produced regularly and on time, is a potentially powerful conservation tool. It is important to have an accepted, predictable recording system that can be sustained into the future, without constant delays and lapses. The national IBA status report is forwarded to the BirdLife secretariat for regional compilation (Fig. 3).

5.2 Detailed IBA monitoring

Ideally, detailed monitoring should take place at all IBAs annually. Realistically, however, it only takes place in a subset of priority sites, and then not in all countries in Africa. This is because detailed monitoring is substantially more expensive and time-consuming than basic monitoring. The number of IBAs that can be covered will depend on available resources, and some countries find that only basic monitoring is possible (Bennun, 2002). IBAs for detailed monitoring should be carefully selected to include those where this approach will be both most useful and most feasible. Although all IBAs are, by definition, of high priority for biodiversity conservation, some are more immediately threatened and some are richer than others. One method for setting priorities among IBAs to target effort where it is most urgently needed combines the two axes of threat and importance: see Bennun and Njoroge (1999) for its application in Kenya. Other filters to use are the presence/absence of ongoing conservation projects, particular threats that need to be tracked, and the presence of people who can monitor. Such procedures for prioritizing action amongst IBAs has also been adopted in several other African countries (Ethiopia, Uganda and South Africa) (Evans, 2000).

Detailed monitoring is likely to focus mainly on indicators of state, e.g., the condition of the site and its biodiversity value. However, detailed assessment of pres-

sure and response is sometimes appropriate as well. Indicators need to be carefully selected so that the monitoring can inform site management. When monitoring numbers of a threatened bird, for example, it is probably useful to monitor its habitat as well. Such indicators might also be assessed during basic monitoring. In these instances, the difference between basic and detailed monitoring is likely to be in levels of precision and accuracy.

Detailed monitoring can benefit from shared information about techniques, and it is desirable for the same methods and indicators to be used wherever possible. Even so, and providing that they give useful information about trends, there is no rigid requirement for indicators to be standardized across the IBA network, as they must respond to local needs (Bennun, 2002). For project sustainability, detailed monitoring should be kept as simple, robust and inexpensive as possible, and integrated into the site action plans of site management authorities and Site Support Groups.

6 Coordination and communication

Project sustainability is a key problem for IBA monitoring in Africa. This makes it necessary to institutionalize monitoring (basic and detailed) as far as possible, keep techniques simple and inexpensive, and take on only those that can be kept going. Basic monitoring is difficult enough to implement, and detailed monitoring must be carefully and cautiously planned (Bennun, 2002). An effective institutional structure is essential. These vary from country to country according to national circumstances, especially the local history of bird monitoring. Figure 3 illustrates the information exchange between various structures and levels of the BirdLife International African Partnership that results from institutionalization.

A common key gap at national level is coordination (Bennun, 2002). Experience has shown that there must be a designated National IBA Monitoring Coordinator, irrespective of physical location or employment status. Fig. 3 illustrates the components involved in coordinating the collection, analysis and distribution of IBA monitoring results at site, national, continental and global levels for Africa. A key gap at the continental and global levels is the current absence of Continental and Global IBA Monitoring Coordinators within the BirdLife Africa Division and BirdLife International Policy and Advocacy Division respectively. At the global level, all IBA and species monitoring results are entered, stored and analyzed in BirdLife International's World Bird Database.

7 From monitoring results to action

Data from monitoring must be used to improve the management of an IBA; that is the purpose of collecting them (Bennun, 2002). Through its structure of national organizations operating at grassroot levels, and regionally linked, the BirdLife International Partnership is ideally situated to achieve this unprecedented task in Africa. If the framework is used consistently, it will be possible to sum

data across levels to produce credible, high-quality analyses that can inform advocacy and management at the national, continental and international levels.

Audiences need to be considered carefully, and reports targeted accordingly. It may be appropriate to provide a detailed technical report for IBA managers, yet only a readable summary for higher-level decision-makers such as Government Ministers and executives of the Southern African Development Community (SADC). The summary for a Government Minister may focus on the status of IBAs in one country only, while a summary for a meeting of the SADC would include information on all the IBAs in its region of interest. Separate, clearly targeted reports are necessary for multilateral environmental agreements such as the Convention on Biological Diversity, Convention on Wetlands of International Importance (Ramsar) and Convention on the Conservation of Migratory Species of Wild Animals (Bennun 2002).

If monitoring identifies a conservation problem, a process needs to be in place that allows action to be taken. It is important to develop clear routes for taking action. This is an area where the IBA National Liaison Committee or specific Site Support Group has potential to play a very valuable role (Figs 1 and 3).

At both regional and global levels, implementing this framework should allow the BirdLife Partnership to learn lessons about the approaches that work best for conserving IBAs across Africa (Figs 1 and 3). These lessons need to be documented, analyzed, interpreted and published — and imported into strategies for site conservation. This is the task of the BirdLife International secretariat, particularly its Africa Division (Fig. 3). Initiating and maintaining monitoring requires substantial investment in a national African network (Fig. 3). Much of the work will have to be done through the personal interest, commitment and good will of volunteers, who need support and motivation. Ignoring this reality may prove fatal for the long-term prospects of the monitoring scheme.

8 Conclusion

Developing an effective IBA monitoring program is not a simple task. To work, it must be sustainable, practical

to implement, flexible, repeatable over time, and respond to local conditions and needs. The data that it gathers, moreover, must have the capacity to improve the management of an IBA. The BirdLife International Partnership is in the process of developing and implementing national IBA monitoring throughout Africa. Its organizations there are currently directing most of their resources towards coordinating national IBA monitoring programs and solving the problems associated with long-term data storage and processing for the future. We envisage that the Partnership will be able to report positively on the establishment of national IBA monitoring and conservation frameworks across Africa within the next four years.

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S07-4 Local community involvement: the role of the IBA program in Mexico

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Abstract The IBA program in Mexico began in 1996 as a cooperative effort. First and second phases involved two sets of collaborators: first, academics with knowledge of birds and their habitats, and secondly, governmental agencies concerned with managing biodiversity and its conservation. Using information and facilities from the two sets, we compiled a directory of important areas for bird conservation with three products: a printed book, a database and a geographical information system. This was the first phase. The second phase involved promotion of local conservation action in priority sites designated by a number of regional workshops. These initiatives evolved in concert with a North American Bird Conservation Initiative (NABCI), which in Mexico adopted the IBA program as its implementation tool. International participation here has strengthened local conservation action by developing pilot cooperative conservation projects that involve all parties (i.e., local people, international players) in identifying needs and goals and in finding ways to overcome challenges.

Key words Important Bird Areas, Prioritization, Local communities, Ecotourism, Mexico

1 Introduction

The Mexican avifauna is particularly diverse, with 1050 species in 468 genera, 79 families and 22 orders (AOU, 1983; Escalante et al., 1992; Howell and Webb, 1995). Mexico, moreover, is the country through which more than half of the migratory birds of North America pass. Around 100 species, representing 10% of the national avifauna, are endemic. The areas of highest endemism are, in order of importance, (i) the tropical dry forest of the Pacific slope, (ii) the arid and semiarid areas of the center-north and, (iii) the temperate forests of the Sierra Madre del Sur and the Eje Neovolcánico Transversal (Escalante et al., 1993; Arizmendi and Ceballos, pers. obs.).

Birds in Mexico, like other groups of vertebrates, are subject to strong pressures that threaten their survival. These pressures affect all the species, but especially those restricted in distribution. The main threat that they face today is habitat loss. The conservation of natural populations of plants and animals necessarily depends on maintenance of the habitats in which they have evolved and can breed and survive. Thus perhaps the highest priority for biodiversity conservation is the protection of habitats and areas that will ensure sustainability not only of birdlife but also all other components of the ecosystems.

The number of bird species under threat in Mexico has increased in recent decades. Thus, in 1979, Aguilar-Ortiz (1979) reported that 31 species were at risk of extinction. Soon after, the International Council for the Conservation of the Birds (King, 1981) raised the number to 35. More

precise information then caused the International Council for the Preservation of Birds (CIPAMEX, 1989) to increase this to 117 species, of which 35 were considered in danger of extinction, 27 as threatened and 55 as prone to extinction. In recent reviews (Collar et al., 1994; IUCN, 1996), 76 species are considered globally threatened; and in the last revision of BirdLife International (2000), 70 species are so listed.

Yet, despite the threats to such a diverse bird fauna, conservation action was limited and uncoordinated until 1996. Then an Important Bird Areas program was initiated in Mexico as part of a trilateral project between Mexico, USA and Canada within the framework of the North American Free Trade of Commerce Agreement (NAFTA). The main aim of the Important Bird Areas (IBA) program is to identify and conserve areas of global importance for bird conservation.

2 Methods

As a first step in the Mexican program, a steering committee was formed to oversee the activities of a coordinator. Representatives from both academia and government formed this committee to ensure the involvement of both sectors and towards integrating the program into governmental agendas and areas of interest. The next step involved experts who knew the regional bird fauna and its habitats. These were brought together at one national and eight regional workshops between 1996 and 1999 to identify all potential IBAs in Mexico.

The national workshop comprised experts representing different regions of the country. Each had been nomi-

nated by his or her own regional collaborators. This was accompanied by a communications campaign that produced a printed bulletin outlining the aims of the program and the criteria used to identify IBAs. It was sent to a wide list of persons and organizations known to be concerned with wildlife conservation in Mexico. At the national workshop, 170 initial IBAs were identified using standardized IBA criteria. This meeting was then followed by the eight regional workshops to review and refine the IBA directory with a wider regional representation of experts, including students and local naturalists.

To reinforce governmental involvement and improve coordination, we invited the governmental institution Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) to design a database and to prepare maps with the same system used for other biodiversity databases generated in Mexico. The database and maps were compiled after the first phase of involvement and then revised (i.e., maps were replotted at a finer scale of 1:250 000) during subsequent regional workshops.

3 Results

These initiatives produced a directory of 230 IBAs (Fig. 1) representing more than 22 000 records of 1 038 species of birds (96% of all species in Mexico, after AOU, 1983). Additionally, they ensured that all globally threatened species identified in Mexico by BirdLife International (2000) were covered by the IBA network. Of the 100 species endemic to Mexico, all were included in at least IBA. This information is now published in hard copy (Arizmendi and Valdelamar, 2000) and on the internet (<http://www.conabio.gob.mx>), as well as stored in a database.

4 Discussion

4.1 The prioritization exercise

Implementing necessary conservation actions in all IBAs was not possible. Because of that, we decided to develop regional criteria for prioritization. During the workshops, we scored each IBA in each region for its bio-

logical diversity, presence of endemic species and opportunities for conservation, judged by institutional presence and attitudes of local people. It resulted in 16 IBAs being identified as high priority areas for bird conservation (Fig. 2). Protection of all 16 IBAs conserves 805 species (over 75% of the Mexican avifauna), 55% of Mexico's globally threatened species (BirdLife International, 2000), and 81% of endemic Mexican species.

Mexico nevertheless has a responsibility to conserve all Mexican endemics and to ensure conservation of all species considered globally threatened. To achieve this, we implemented a prioritization exercise based on species. Using lists of endemic Mexican birds (Escalante et al., 1993) and globally endangered species (Birdlife International, 2000), we searched for fewest areas covering all such species in the IBA network, adding a further 19 IBAs to the original high priority 16.

4.2 Local community involvement

The first Mexican IBA selected was El Carricito del Huichol, one of the few intact remnants of old-growth pine forest on the western coast of Mexico. This area has been a focus of attention for CIPAMEX since 1997. Our particular goal here was to promote conservation by developing a management plan that would enable local landowners (private and indigenous) to make a living from their lands without damaging the environment. Several steps have already been taken, including the construction of a field station where both scientists and tourists are welcome to carry out research or bird watch. The project grew so fast that in 1998 a new NGO, Bosque Antiguo AC, was formed to manage the area.

More recently, a second, sister IBA, Sian Ka'an in the Yucatan Peninsula, was established in cooperation between Panama, Mexico and Canada. This project is developing bird-based ecotourism as an alternative to economic development in the area. To this end, Amigos de Sian Ka'an, together with the director of this biosphere reserve and CIPAMEX, conducted training workshops for two local communities to produce local nature guides. Trails for bird watching are being built as well. Promotion at the national level is provided by



Fig. 1 Important Bird Areas in Mexico



Fig. 2 Priority IBAs in Mexico

CIPAMEX, and at the international level by our Canadian partner, the Canadian Nature Federation.

Conservation plans developed by ornithologists, academics and local people are being put into effect in three further IBAs: Marismas Nacionales, Sierra de Arteaga and Cuitzeo. At another site, a biosphere reserve that already has a management plan, a series of bird-oriented activities concerned with environmental education are being undertaken as well.

4.3 International community involvement

Out of these processes, a broader initiative grew: the North American Bird Conservation Initiative (NABCI) which has as its aim the promotion of bird conservation in Mexico, USA and Canada with all tools available to all three countries. Both IBAs and Bird Conservation Regions (BCRs) were agreed as the implementation units for determining major bird conservation regions under this program. A trilateral committee identified birds of common concern, including migrants shared between the countries and shared endemics in IBAs and BCRs. These birds are used as linkages for coordinating international effort for bird conservation. Endemic Bird Areas (EBAs), where migrants from Canada and USA winter (Blanchet, 2002), were an important criterion in the choice of regions.

Three BCR regions containing several IBAs were chosen in Mexico. One is the Yucatan Peninsula, which includes three IBAs (two biosphere reserves and one national park), and many migrants mainly from the east of the continent. The second, El Triunfo biosphere reserve, is an area of high concentration of migrants from the center and west of the continent. The third is the grasslands of northern Mexico where there is a high concentration of endemics. All three regions are EBAs and contain a considerable number of threatened birds.

These three pilot regions will be developed under the NABCI program as participative projects where both local people and international participants will have opportunities to develop cooperative projects which have both international strength and the involvement of local people. Planning will be finished in 2003, and the three pilot projects implemented soon after.

5 Conclusions

In Mexico, we view the involvement of people at dif-

ferent levels as a key issue, and the only route to success for conservation programs. Both IBA and NABCI programs are now in the minds of many people, including government. However, this is only a first step, and the next challenge will be to put this entire framework into action in ways that will achieve long-lasting bird conservation.

To achieve these goals, establishment of each IBA will have to be approached separately, as each one faces different problems and opportunities. For that reason, we are planning to develop NABCI demonstrative or pilot projects in three very different regions of the country. These projects will address the challenges and opportunities in each site, using the experience and talents of both local people, local and federal government and international participants.

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S07-5 Conservation of sites important for birds in China

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Abstract As one of the mega-diversity countries of the world, China supports about 1 300 species of birds, including 87 globally threatened species and a large number of endemic species. The work of 12 ornithologists during 1998–2001 identified 422 Important Bird Areas (IBAs) in mainland China, while future surveys of the more remote areas in Yunnan, Sichuan, Fujian and Tibet will no doubt lead to the identification of more. Most IBAs identified so far hold significant numbers of globally threatened species and restricted-range species, while about 24% of the sites support large concentrations of congregatory species, especially waterbirds. The main threats to these sites are habitat loss due to deforestation and agricultural intensification, over-exploitation of natural resources and pollution. Conservation of these sites is considered essential for the preservation of birds and other biodiversity in China. This work needs effective collaboration between the Chinese Government and conservation organizations, such as BirdLife International. Although a large number of IBAs have been protected nationally, further effort is needed to protect those not yet included in the reserve system. In addition, adequate training of reserve staff is essential.

Key words Important Bird Areas, Threatened species, Conservation, China

1 Introduction

The Important Bird Area (IBA) program of BirdLife International is a worldwide cooperative project aimed at identifying, monitoring and protecting a network of critical sites for birds globally, and to use birds as flagships in biodiversity conservation. Documentation of IBAs and their subsequent protection has, in particular, proven to be an important conservation tool in Europe (Heath and Evans, 2000). Such work is even more important in developing countries, where the number of threatened species is greater and threats are more acute (Zheng and Wang, 1998; BirdLife International, 2000, 2001).

China is a large country in East Asia, with a land area of 9.6 million km² and sea area of 4.73 million km². A complex geological history and varied natural environments make China one of the 12 “megadiversity countries” in the world (McNeely et al., 1990). It supports a high diversity of plants, animals and microorganisms. So far, over 30 000 species of seed-plants and 6 300 species of vertebrates have been recorded (SEPA, 1998). Crossing two zoogeographical realms, the Palaearctic and Oriental, China is also particularly rich in birds. Some 1 300 species of birds have been recorded in the country, including nearly 100 endemic or near-endemic species (Cheng, 2000; Zheng, 2002).

China holds 20% of the world human population and has over 7 000 years of agricultural history. With the human population continuing to increase over the past 50 years, a large proportion of the natural habitats for birds has been turned over to farmland and towns. As well, over-hunting,

illegal poaching and the wide use of pesticides have been caused declines in many species (SEPA, 1998). As a result, more and more species are threatened with extinction. 87 species of birds in China are listed as globally threatened in the Asian Red Data Book, comprising five Critically Endangered, twelve Endangered and 70 Vulnerable (BirdLife International, 2001). One is also Conservation Dependent, 45 are Near-threatened and one is Data Deficient. Conservation of the avifauna of China is thus of global significance. Given that birds are good indicators of environmental quality, the conservation of IBAs in China will not only benefit birdlife but also improve habitats and contribute to the conservation of ecosystems and biodiversity generally.

The China IBA project is just one part of the Asian IBA program which was launched at the BirdLife Asia Conference in Coimbatore, India, in November 1996. Supported by the Wild Bird Society of Japan, the China IBA project was begun in early December 1998. Its first step focused on producing inventories of internationally recognized sites vital for the conservation of Chinese birds. This paper reports the progress of that work.

2 Methods

Twelve senior ornithologists from all parts of China were invited to work on the project. Several workshops were held up to 2002, identifying IBAs using four standard global IBA criteria:

A1 Species of global conservation concern — significant numbers of a globally threatened species regularly

Table 1 IBAs in China: location, number and size

Region	Area (km ²)	Number of IBAs	Total IBA Area (ha)	IBA area/ Region area
Anhui	139 600	4	51 814	0.37
Beijing	16 808	5	48 160	2.87
Chongqing	82 000	6	127 800	1.56
Fujian	123 800	7	831 429	6.72
Gansu	453 694	16	14 276 470	31.5
Guangdong	212 000	13	75 991	0.36
Guangxi	236 661	38	1 600 617	6.76
Guizhou	176 128	5	112 200	0.64
Hainan	33 920	10	70 529	2.08
Hebei	187 700	6	95 907	0.51
Helongjiang	453 900	33	1 719 609	3.76
Henan	167 000	9	172 256	1.03
Hubei	185 900	7	1 119 967	6.02
Hunan	211 830	20	654 891	3.09
Inner Mongolia	1 183 000	26	7 770 442	6.57
Jiangxi	102 600	3	534 300	5.21
Jiangsu	166 900	6	72 670	0.44
Jilin	187 400	15	919 298	4.9
Liaoning	145 900	14	336 618	2.31
Ningxia	66 400	5	739 400	11.1
Qinghai	721 200	13	10 321 300	14.3
Shaanxi	205 603	14	383 292	1.86
Shanghai	6 341	1	32 610	5.14
Shanxi	156 266	7	75 747	0.48
Shandong	156 700	6	335 700	2.14
Sichuan	485 000	30	2 121 077	4.37
Tianjin	11 305	1	6 000	0.53
Tibet	1 200 000	23	49 914 220	41.6
Xinjiang	1 660 000	42	4 884 400	2.94
Yunnan	394 000	17	8 898 697	22.6
Zhejiang	101 800	20	193 141	1.90
TOTAL	9 631 356	422	108 496 552	11.3

Table 2 Distribution of size-classes of IBAs in China (n=405)

Size (ha)	Number of IBAs	Percentage (%)
<1 000	25	6.17
1 000–5 000	45	11.1
5 001–10 000	56	13.8
10 001–100 000	181	44.7
100 000–500 000	66	36.5
>500 000	33	8.15

Table 3 Frequency of use of IBA criteria for identifying IBAs in China

Criteria	Number of IBAs	Percentage (%)
A1	376	89.1
A2	54	12.8
A3	34	8.05
A4i	31	7.35
A4ii	9	2.13
A4iii	19	4.50
A4iv	22	5.21

For explanation of criteria, see Methods, above.

present, or other species of global conservation concern.

A2 Restricted-range species — presence of a significant component of restricted-range species, the breeding ranges of which define an Endemic Bird Area (EBA) or Secondary Area (SA).

A3 Biome-restricted species — presence of a significant assemblage of the species, the breeding ranges of which are largely or wholly confined to one biome.

A4 Congregations — (i) presence, on a regular basis, of >1% of a biogeographic population of a congregatory waterbird species; (ii) presence, on a regular basis, of >1% of the global population of a congregatory seabird or terrestrial species; (iii) presence, on a regular basis, of >20 000 waterbirds or >10 000 pairs of seabirds of one or more species; (iv) a “bottleneck” site through which at least 20 000 storks (Ciconiidae), raptors (Falconiformes) or cranes (Gruidae) regularly pass or use as stopovers during spring or autumn migration.

This exercise produced a foundation list of IBAs in China. Participant researchers were then allotted series of IBAs, and charged with the responsibility of gathering information from each, to be entered on standardized forms. The required information was sourced from the Asian Red Data Book and other literature, personal knowledge, and from National Wildlife Surveys carried out in China between 1995–2000. With our encouragement, many local researchers provided much useful information. All data were then compiled, translated into English and loaded on to a computerized database designed by the Wild Bird Society of Japan. The IBA for Hong Kong was established by the Hong Kong Bird Watching Society, and that in Taiwan by local researchers there.

3 Results

3.1 Distribution and size of IBAs in China

By the end of 2001, 422 IBAs had been identified on the mainland of China (Table 1). If we include the IBAs in Taiwan (53), Hong Kong (2) and Macao (1), total IBAs for China sum to 478. Xinjiang, Guangxi, Heilongjiang and Sichuan provinces hold the most IBAs, with more than 30 in each (Table 1). Both Shanghai and Tianjin hold only one each. The areas covered by the IBAs vary with region. Aside from a few sites that have not yet been defined accurately, they vary from a few hectares to over 33 million ha. The smallest is Daniao’ao of Longhui County, Hunan Province, which is an important site for passerine migration; during that event, millions of birds pass through it. The largest is the Qiangtang Plateau in Tibet (33 792 000 ha). Compared to province size, Tibet, Guansu and Yunnan have larger areas under IBA designation than other regions. Table 2 shows the distribution of size-classes of IBAs in China. It indicates that 81.2% of the IBAs are between 100 km² and 5 000 km² in area.

3.2 Coverage of IBAs for biodiversity conservation in

China

The 422 IBAs in mainland China cover 1 084 966 km², which is about 11.3% of total land area (Table 1). Among them, 376 hold at least one globally threatened species and 31 are important for waterbird congregations (Table 3). Of the 17 Critically Endangered and Endangered species found in China, 77% occur in at least one IBA (Table 4). Of the 12 Endemic Bird Areas (EBA) identified in mainland China, 52 IBAs are designated within 9 of them.

3.3 Conservation status of IBAs in China

56% of IBA sites are established nature reserves, while the remainder have no protection. The main threats to IBAs are disturbance from human activity (53%), over-exploitation of natural resources (38%), habitat loss due to deforestation (29%) and agricultural intensification (23%). Moreover, surveys of IBAs in established nature reserves found that over 70% of reserve staff lacked the knowledge to manage the sites effectively.

During this first stage of IBA work in China, the outputs and new findings have already had effect. Several new nature reserves have been established at IBAs, and management at existing nature reserves has been improved. For example, the Beidagang Reservoir of Tianjin was set up as a provincial nature reserve in 2001 after 800 oriental white storks (*Ciconia boyciana*) and a large congregation of waterbirds were found there by the researchers from Beijing Normal University. Dongzhai Nature Reserve was also promoted from a provincial nature reserve to a national nature reserve because it was found to hold a viable population of the threatened pheasant, *Syrmaticus reevesii*.

4 Discussion

Although many field surveys have been carried out in China since 1950s, information on the status of birds is missing from many regions, especially from the more remote areas of Tibet, Xinjiang, Yunnan, Inner Mongolia and Fujian (Cheng, 1997; Zheng and Wang, 1998). Further IBAs will doubtless be identified in these regions, from surveys that still need to be done. In the interim, the China IBA data base is being revised year by year as more information becomes available.

The China IBA project is long-term, with identification of IBAs only the first step. Current results can be expected to influence site protection by local and central Government agencies. Conservation of IBAs is not only very important for the survival of the birds, but also of benefit to other wildlife living in them as well. As flagship species, birds are good indicators of the state of the environment (Zheng, 1995), such that protecting IBAs is an important step towards conserving biodiversity as a whole (Bibby et al., 1992).

Monitoring IBAs is a core task for the China IBA project, and it should form the major program of work for IBA compilers over the next five years. For this, effective

Table 4 The number of IBAs in China supporting Critically Endangered and Endangered bird species

Species	English name	Category of threat ¹	Number of IBAs
<i>Fregata andrewsi</i>	Christmas Island frigatebird	Critically Endangered	0
<i>Grus leucogeranus</i>	Siberian white crane	Critically Endangered	33
<i>Gyps bengalensis</i>	white-rumped vulture	Critically Endangered	0
<i>Pseudibis davisoni</i>	white-shouldered Ibis	Critically Endangered	1
<i>Sterna bernsteini</i>	Chinese crested tern	Critically Endangered	0
<i>Anser cygnoides</i>	swan goose	Endangered	79
<i>Arborophila rufipectus</i>	Sichuan partridge	Endangered	7
<i>Ciconia boyciana</i>	oriental white stork	Endangered	60
<i>Gorsachius goisagi</i>	Japanese night-heron	Endangered	0
<i>Gorsachius magnificus</i>	white-eared night-heron	Endangered	10
<i>Grus japonensis</i>	red-crowned crane	Endangered	57
<i>Ketupa blakistoni</i>	Blakiston's fish-owl	Endangered	10
<i>Mergus squamatus</i>	scaly-sided merganser	Endangered	47
<i>Nipponia nippon</i>	crested ibis	Endangered	5
<i>Oxyura leucocephala</i>	white-headed duck	Endangered	5
<i>Platalea minor</i>	black-faced spoonbill	Endangered	13
<i>Tringa guttifer</i>	spotted greenshank	Endangered	7

¹ after Collar et al., 2001

collaboration between the Chinese Government and conservation organizations, such as BirdLife International, WWF and IUCN, is needed. In the national action plan for biodiversity conservation in China, for example, the Government has listed 155 important sites for conserving natural ecosystems (SEPB, 1994). WWF, in turn, has put forward its Ecoregions-based Conservation Strategy in recent years, and nineteen of these are located in China. By working together, these conservation bodies can only be more effective.

In the recent years, the Chinese Government has begun paying more attention to the protection of biodiversity. A series of environmental laws and regulations have been formulated and issued, together with the establishment of over 1 200 nature reserves by the end of 2001. However, with rapid development in most areas, current measures are inadequate. Although a large number of IBAs have been protected nationally, further effort is needed to set aside those not yet included. Habitat destruction, deforestation and agricultural intensification need to be controlled, and over-exploitation of natural resources and disturbance to birds from human activities should be stopped.

To improve the management of nature reserves is another task. At present, many nature reserves have no effective management, because both managers and staff have little or no experience in protecting and maintaining natural areas and resources. Training of reserve staff is yet another essential.

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Symposium 08 Effects of global climate change on birds: evidence and predictions

Introduction

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Global climate change is probably the most important environmental challenge that faces our planet. The Intergovernmental Panel on Climate Change, in their monumental Third Assessment Report published in 2001, reported that global average surface temperature had increased over the 20th century by about 0.6 degree C. The 1990s was the warmest decade and 1998 the warmest year in the instrumental record, since 1861. Furthermore, the increase in temperature in the 20th century is likely to have been the largest of any century during the past 1 000 years. These changes have been accompanied by changes in precipitation patterns, measured decreases in snow cover and ice extent, and increases in sea-levels as ocean heat content has risen. The report concludes that there is strong evidence that most of the warming over the last 50 years is attributable to human activities, and that human influences will continue to change atmospheric composition throughout the 21st century. As a result, global average temperature and sea level are projected to continue to rise, along with considerable changes in precipitation patterns worldwide and increases in the frequency of extreme weather events.

The subject has received little coverage in previous IOCs, but recent publications have already reported probable effects of global climate change on birds in North America, USA, Europe, Central America, Antarctica, and

the Pacific. These effects include (1) earlier breeding, (2) earlier spring migration, (3) changes in breeding performance (egg size, nesting success), (4) changes in population sizes, (5) changes in population distributions, and (6) changes in selection differentials between components of a population. Birds are not only already being affected by global change but can serve as well as important bioindicators readily understood by the general public.

In this symposium we present a series of papers that cover important areas of research in this rapidly advancing field. These include the impact of climate change on the phenology of nesting and migration, how climate change may lead to mismatched timing between different parts of the food chain, the potential impacts of increased incidence of extreme events, changes over different temporal scales in marine ecosystems, and finally a case-study of the impacts of sea-level rise on conservationally important estuarine birds. These papers all present information on how climate change has already affected the ecology of a range of bird species in different situations. Although they attempt to predict how birds will be affected by future climate change, the consequences for the population dynamics, distributions and interactions of bird species with other components of the communities in which they live are still very uncertain and will require much further research.

S08-1 Changes in the phenology of breeding and migration in relation to global climate change

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Abstract The timing of life history events is often critical for the fitness of organisms. Among birds, the timing of events at the start of the breeding season can, for example, determine an individual's chance of obtaining breeding territory and of achieving a level of reproductive success. The timing of migration and egg-laying can be affected by weather conditions, and it has been predicted that climate change could thus have a major impact. Data from a variety of sources strongly suggests that the timing of migration and nesting have already been affected by climate change, and provide some of the strongest early signals of likely impacts from the relatively moderate climate change that has occurred to date. We review information from intensive study sites and extensively gathered data to draw out general patterns, and then briefly consider the potential consequences of such changes for birds.

Key words Phenology, Nesting, Migration, Climate change

1 Introduction

The timing of life history events is often critical for the fitness of organisms. Natural selection tends to act to optimize the timing of these events such that individuals achieve the best chance of passing their genes on to the next generation. Among birds, the timing of events at the start of the breeding season can, for example, determine an individual's chance of obtaining breeding territories (Kokko, 1999) and of achieving a certain level of reproductive success (Perrins, 1970). The timing of migration to breeding grounds and, of egg-laying, is determined by an interaction of endogenous and environmental factors; and key among the latter is the influence of weather conditions (Berthold, 1993). Thus the effect of climate change on these factors could have major impacts on bird populations.

The study of the timing of natural events, phenology, is an area which has attracted much interest not just from scientists but also from amateur natural historians over the last two or three centuries. As a result, many long-term datasets exist which have now begun to be explored, revealing insights into historical phenological changes in relation to climate change (e.g., Sparks and Carey, 1995; Sparks et al., 2001).

Here we review evidence which strongly suggests that the timing of bird migration and nesting has already been affected by climate change. This has occurred despite the relatively modest degree of climate change to date. Such changes currently provide some of the strongest signals of potential impacts of climate change on the natural world. If

components of ecological communities respond at different rates to climate change, these differential responses could lead to "phenological disjunction" between trophic levels, with major consequences for each level and ultimately for the functioning of their ecosystems (Harrington et al., 1999).

2 Timing of breeding

Two main types of investigation have been used to study long-term trends in the timing of breeding in birds: (a) intensive studies, usually of a single species and at a single location by professional scientists; and (b) studies of extensively gathered data, collected by volunteers as part of a monitoring network. The latter can provide the most conclusive evidence of effects from widespread climatic change because the data are often gathered at a national scale. The Nest Record Scheme of the British Trust for Ornithology (BTO) is probably the most studied dataset in this respect. It holds more than a million detailed records of individual nesting attempts collected by volunteer ornithologists from the 1930s onwards (Crick and Baillie, 1996).

Using this dataset, Crick et al. (1997) demonstrated that 51 of 65 species showed a trend towards earlier nesting between 1971 and 1995. The average advancement in the 20 species in which the trend was most marked was 8 d, ranging from 4 to 18 d. These species belonged to no one taxonomic or ecological group; they included shorebirds (*Numenius arquata*), resident insectivores (*Cinclus cinclus*), migrant insectivores (*Anthus trivialis*), corvids (*Pica pica*) and seedeaters (*Fringilla coelebs*). This suggested that a wider environmental factor, such as climate

change, was the likely driver. Forchhammer et al. (1998) re-analyzed examples of data from Crick et al. (1997) to show that laying date trends in *Miliaria calandra* and *Phylloscopus collybita* were related to the North Atlantic Oscillation (NAO), a large-scale atmospheric phenomenon that determines the extent to which western Europe is affected by damp Atlantic or dry continental weather.

Subsequent examination of the BTO's nest record data for 1939–1995 showed that 19 of 36 species (53%) exhibited significant long-term shifts in laying, most of which tended to be curvilinear, becoming later during the period of spring cooling from 1950–1970 and then earlier during the period of warming from 1970 to 1995 (Crick and Sparks, 1999). In 31 (86%), there were significant correlations between laying dates and weather (temperature and precipitation); and of the 17 that showed long-term trends as well, seven (41%) showed no residual trends after weather factors had been included in the regression models. These were among the most common and widespread species in the dataset, and for which the weather variables used were probably most appropriate: *Troglodytes troglodytes*, *Prunella modularis*, *Sylvia atricapilla*, *Phylloscopus trochilus*, *Muscicapa striata*, *Aegithalos caudatus* and *Carduelis chloris*. For the other 10 species, the causes of residual trends could have been inappropriate choice of weather variables (e.g., soil rather than air temperature) or factors unrelated to climate (e.g., land-use change).

For 33 species, data were sufficient for investigating how the distribution of laying dates had changed over time. This we did by screening trends through the interval between the median and the 5th percentile or 95th percentile of the laying date distribution, as measures of the relative lengths of the first and second halves of the nesting season respectively. Significant lengthening of the first half occurred in only eight species, and significant shortening in just one. Similarly, significant lengthening of the second half occurred in only four species, and significant shortening in two. The general lack of significant change suggests that, for most species, changes in the timing of nesting involved a whole shift in the frequency distribution. A few species had increased the length of the nesting season, suggesting that a proportion of individuals could potentially fit in an extra breeding attempt. Unfortunately, individual pairs are not followed within the Nest Record Scheme protocols, a gap that can only be explored further from records of individually marked birds.

The only other major study using such extensive data also shows a general trend towards earlier laying. Dunn and Winkler (1999) analyzed 3 450 nest records from the North American nest record schemes between 1959 and 1991 and found that the laying date of *Tachycineta bicolor* had advanced by an average of 9 days and that the main correlative factor was change in air temperature.

A number of intensive studies at single locations have also demonstrated shifts towards earlier laying in response to warmer spring temperatures in recent years. In Britain,

McCleery and Perrins (1998) showed changes in the average laying date of a population of *Parus major* between 1947 and 1997 to be linked to shifts in spring temperatures. Over the course of their study, temperatures had cooled and then warmed, with associated trends towards later then earlier laying, corresponding with the results of Crick and Sparks (1999). They showed that the relationship between laying date and temperature was the same in cooling and warming phases.

Winkel and Hudde (1997) also found that hatching dates for *Parus major* and *P. caeruleus* had advanced between 1975 and 1995 in northern Germany, in response to warmer springs, and obtained a similar result for *Ficedula hypoleuca*, as have several other studies (e.g., Jarvinen, 1989; Slater, 1999; Both and Visser, 2001) and Przybylo et al. (2000) for the closely related *F. albicollis*. The latter study showed, as well, that the response to warmer temperatures could be explained entirely by individual phenotypic plasticity rather than microevolutionary process. A rare example of a study involving an open-nesting species comes from a very different climatic zone: arid Arizona. There Brown et al. (1999) showed that, in a population of *Aphelocoma ultramarina*, the mean first clutch date had advanced by 10 d between 1971 and 1998, associated with warmer minimum temperatures in the month prior to laying.

Two meta-analyses of data gathered across a large number of studies throughout Europe have explored the generality of the results from these intensive projects. Sanz (2002) found that within and across breeding sites, the laying date of *Parus major* and *P. caeruleus* was related to the winter NAO index, showing that both species tend to lay earlier after warmer, moister winters. Moreover, the rate of change in laying date with respect to the NAO differed geographically but not between species. Visser et al. (2003) analyzed a different set of data for these two species from 14 study sites and found that differences in the degree of advancement may be related to changes in the degree of broodedness (single vs double brooding) in response to climate change.

3 Timing of migration

Studies of the timing of arrival and departure of migrants have derived more from the observations of amateur natural historians than from professional biologists. Some species, particularly *Hirundo rustica*, *Cuculus canorus* and *Ciconia ciconia*, have long been popular subjects of phenological recording in Europe because of their association with spring (e.g., Sparks and Carey, 1995). For the most part, such records are based on the first observation of a species at a particular location in each year. Although such records are subject to error and prone to biases, they have also been shown to be remarkably robust when used within long-term time series with respect to investigations of climate change (e.g., Sparks, 1999; Sparks et al., 2001).

One such dataset that has been analyzed in Britain comes from records collated each year by the network of

County Bird Recorders, who publish annual bird reports for each county. These often include a section of the first and last reported dates for each species of migrant. Mason (1995) analyzed the data for 23 such species in the mid-England county of Leicestershire over a 50-year period from 1942–1991. For eight species he found significant negative correlations between arrival date and spring temperatures. Sparks (1999) investigated the same dataset and compared it with data from the county of Sussex, on the south coast of England, over the period from 1966 onwards. He found that 54 of the 56 species/site series showed a negative coefficient, 22 being significant ($P < 0.05$). The synchrony between records from the two counties was often strong, despite a 250 km spatial separation. Comparisons with spring temperatures in Britain produced 49 negative regression coefficients, of which 19 were significant; only 1 positive relationship was significant.

A network of coastal Bird Observatories around the British Isles collects data that are more systematic. These are manned throughout the migration period and are staffed by skilled volunteers and professional staff who not only catch and ring migrants, but also make daily counts around each observatory. Analyses of data from four such observatories (Sparks, 1999) showed that, of 90 species/site combinations, 68 showed trends towards earlier arrival, of which 29 were statistically significant. Only four of the trends towards later arrival were significant. Similarly, 69 showed negative responses to spring temperatures (13 significant); and no positive relationships were significant. The relationships were stronger if French or Iberian temperatures were used, presumably because these are the conditions experienced by the migrants en route.

Across Europe, similar observations have also been made at fixed ringing (banding) sites. Preeminent among these are the records from the banding station on the Courish Spit on the Baltic Sea. Sokolov et al. (1998) have shown long-term trends in the dates of first capture and mean dates of spring migration for 33 passerine species there between 1959 and 1996. Higher spring temperatures tended to be associated with earlier arrival. In addition, arrival date tended to be more variable for earlier arriving species than later, as has also been found by Sueur and Triplet (2001).

Series of long-term observations from a single locality by independent natural historians, either singly or in groups, are also an important source of information on migration phenology. In Britain, Jenkins and Watson (2000) report on a series of such observations made in Scotland between 1974 and 1999. They found an interesting difference between resident, short-distance migrant species and those that winter in Africa. The latter showed generally weak trends over time (8 out of 14 being negative), whereas almost all (9 out of 10 species) of the short-distance migrants showed trends towards earlier arrival.

Berthold (1990), in a speculative review, suggested that long-distance migrants would suffer detrimental effects

more than short-distance migrants because the initiating conditions on their wintering grounds might not track the changes on their breeding grounds. Indeed, Both and Visser (2001) provide evidence for this from their studies of the trans-Saharan migrant, *Ficedula hypoleuca*. On their study site in the Netherlands, this species has shown no shift towards early arrival; and a trend towards earlier laying with warmer springs has not been sufficient to eliminate an increasing selection differential towards earlier nesting. Interestingly, a long time series gathered in northern Spain showed that 5 of the 6 long-distance migrants there showed significant trends towards later arrival over the period between 1952 and 2000 (Penuelas et al., 2002). These trends could reflect different climatic processes acting on wintering and breeding grounds, though later arrival may be a function of declines in population size, as in *Cuculus canorus* and *Luscinia megarhynchos* (Tryjanowski and Sparks, 2001).

4 Conclusions

There is good evidence from both intensive and extensive datasets that birds are showing trends towards earlier migration and nesting. Overall, the response to per degree C warming is an advance in arrival and nesting of 1–3 days. However, plants and invertebrates tend to respond to equivalent rises in temperature at *c.* 6 day rates, leaving considerable scope for mismatching between birds and their food supplies (e.g., Visser et al., 1998). There is some evidence that earlier springs can result in larger numbers of juveniles in autumn (Sokolov et al., 2000); and Winkel and Hudde (1997) found that fledgling production had increased for *Ficedula hypoleuca* as a result of earlier laying. However, the results of Both and Visser (2001) and the evidence that long-distance migrants respond differently to climate change than short-distance migrants suggests that climate change may pose more threats to long-distance migrants than others.

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S08-2 Mistimed reproduction due to global climate change

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Abstract Climate change may affect the phenology of some parts of food chains more strongly than others, which leads to a disruption of synchronization within food chains. We describe three different methods to assess whether the change in laying date in bird populations has been able to maintain synchronization, illustrated with our own work on great tits (*Parus major*). These show: (1) the date of peak abundance of caterpillars has advanced, but great tits have not started to lay earlier, hence the difference in synchronization between great tits and their prey has increased; (2) selection for early laying has become stronger; and (3) great tits have reduced the incubation period (the time between laying the last egg and first hatching) to speed up their reproduction. Clearly, the change in laying date in the studied great tit population has not been able to match the shifts in underlying levels of the food chain. We offer two hypotheses in explanation, and discuss how they can be tested by manipulating laying date under field conditions and by comparing populations on a large spatial scale. We argue that the lack of advancement of laying date may be caused by a differential change of temperature in early and late spring, rather than an increase in spring temperature *per se*. We also report mistiming in two other species due to correlative disruptions from weather variables, and encourage studies on other systems to find out how general this pattern is.

Key words *Parus major*, Climate change, Phenology, Timing of reproduction

1 Introduction

There is now ample evidence that global climate change affects a wide range of biological systems (Wuehrich, 2001; Walther et al., 2002). One important biological system affected is phenology, particularly the timing of reproduction. For many organisms in the temperate zone, there is only a short period in the annual cycle when conditions are suitable for reproduction. In order to breed successfully, birds need to provide their nestlings with adequate food, which is often only abundant within a short period. The food, in turn, is itself dependent on the development of food or mother plants. Therefore, as other organisms in the food chain set the conditions for reproduction, and as different levels in the food chain may be affected differently by climate change, a multi-trophic perspective is needed to understand the changes in phenology in bird populations. Because there is no *a priori* reason to assume that climate change will affect the phenology of these different levels in the same way, and as the synchronization between these levels is crucial for successful reproduction, we then focus on how climate change affects the synchrony between the different levels in the food chain (Fig. 1).

Birds are adapted to year-to-year variation in the timing of favorable conditions, and hence in the optimal laying date. They have physiological control mechanisms that translate the cues from their environment to a laying date (Visser and Lambrechts, 1999). As the cues vary from year to year, so birds lay at different times. It is important to stress, nevertheless, that a physiological control mecha-

nism should not just cue an optimal laying date in one particular year, but should lead to laying dates which are (close to) optimal for a whole range of years. Natural selection will therefore act not so much on the laying date in a particular year but rather on the whole set of laying dates produced by a genotype, and so the underlying physiological control mechanisms.

It is also important to appreciate that natural selection on these mechanisms will have taken place under a specific set of abiotic variables (e.g., weather pattern). A serious but very often ignored aspect of global climate change is that temperatures have not just simply increased, but have changed in different ways or at different rates in different regions (e.g., wintering versus breeding area) or periods (Walther et al., 2002). Thus, global climate change also disrupts the correlated environmental variables under which physiological control mechanisms have evolved.

2 Is advancement of laying date adequate?

Over the past several decades, an advancement in laying date has been reported for many bird species (Crick et al., 1997; McCleery and Perrins, 1998; Brown et al., 1999; Both and Visser, 2001), although, we stress, not for all populations studied (Visser et al., 2002). For instance, Crick et al. (1997) analyzed data on laying date for 65 British species over the period 1971–1995, and found that the date had advanced significantly in only 20 (31%). One might wonder about the lack of advancement in the other 69%; but our

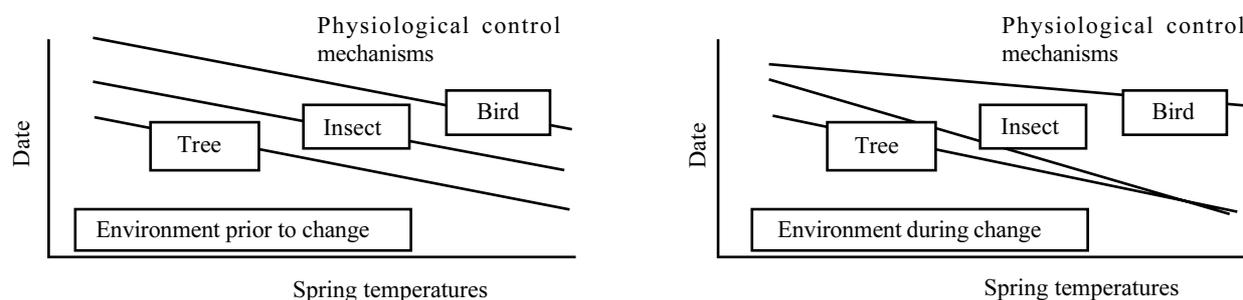


Fig. 1 Schematic responses of different levels of the food chain to climate

The phenology of the different levels is affected differently by climate change. Prior to climate change, the physiological control mechanisms of bud burst in trees, of egg hatching date in insects and of laying date in birds responded equivalently to annual environmental conditions such that the phenology of the different levels in the food chain were synchronized. Climate change alters the relationships between the weather variables that affect different parts of the food chain, destabilizing the pre-adapted physiological control mechanisms, leading to mistimed reproduction in warmer springs.

concern here is whether the advance in the 31% that did shift was sufficient to match the shift in the period of favorable conditions for reproduction. This all important question has rarely been considered so far.

How can it be determined whether a shift in laying date has been sufficient? Three practical procedures may be employed, each illustrated by our own work on the great tit population of the Hoge Veluwe National Park, The Netherlands.

2.1 Comparison of changes in phenology at different levels in the food chain

The synchronization of avian phenology with the phenology of underlying levels in a food chain is an important selection pressure on the timing of avian reproduction (Perrins, 1970). To assess whether shifts in laying date are sufficient, they have to be compared with phenological change in the underlying levels. For example, a primary mediator of the timing of reproduction in many bird species is synchronization of offspring needs with an abundance of food. For great tits in the Hoge Veluwe, the key prey are caterpillars on oak (*Quercus robur*) trees. We have measured caterpillar biomass there from 1985 onwards, and can thus compare changes in the date of maximum food abundance for great tits with changes in laying date. There has been a significant advance in the date of maximum biomass, but great tits have not advanced their laying date (Visser et al., 1998). Hence, the degree of asynchronization (the difference between the food peak and mean date at which the nestlings are 10 days old) has increased: the birds now lay too late to profit fully from the short period in which caterpillars are abundant (Fig. 2).

2.2 Calculating the strength of the selection on phenology

A second method for estimating the adequacy of catchup in the timing of reproduction is to determine whether the strength of directional selection for early laying has changed over time. If advancement of laying date is inadequate, early-nesting birds would be expected to produce increasingly more and better quality offspring than

late-laying birds. This can be quantified by calculating selection differentials. The selection differential for laying date is the difference between (a) the mean date of laying of first clutches weighted for the number of recruits produced per female over the entire season, and (b) the unweighted mean laying date of first clutches. If this value shifts to the negative over time, there is increased selection for earlier laying; early laying great tits will produce more recruits in the following year than late laying birds. For the Hoge Veluwe great tits, there is a clear decrease in selection differentials for laying date (Fig. 2; Visser et al., 1998). In the early years of the study, there was no directional selection (selection differentials around 0) whereas it is now negative, again indicating that the birds, on average, have been laying too late in recent years.

2.3 Monitoring changes in reproductive behavior

The third method investigates changes in bird behavior. Birds may shorten the duration of their reproductive attempt to compensate for laying late. In great tits, selection acts strongly on hatching date, and thus birds may attempt to shorten the time interval between laying and hatching. Laying smaller clutches achieves this, and so does advancing incubation into the laying period, shortening the time to hatching the first-laid egg). The Hoge Veluwe great tits have not changed their mean clutch size (Visser et al., 1998) but they have shortened their incubation period (between laying the last egg and hatching the first) by about 1.5 days (Fig. 2). Although shortening of incubation is an indication that the tits have not advanced their laying date sufficiently, it is not necessarily an indication of mistiming. The birds may reduce their incubation period as part of an adaptive response to reduce mistiming between hatching date and food peak, such as when the fitness costs of laying a few days earlier are higher than the fitness costs of a shorter incubation period.

Another indicator of insufficient advancement in laying date is the within-individual change in laying date from year to year. Birds that have experienced a mismatch between offspring needs and food abundance in one year should shift their laying date in the following year (Grieco

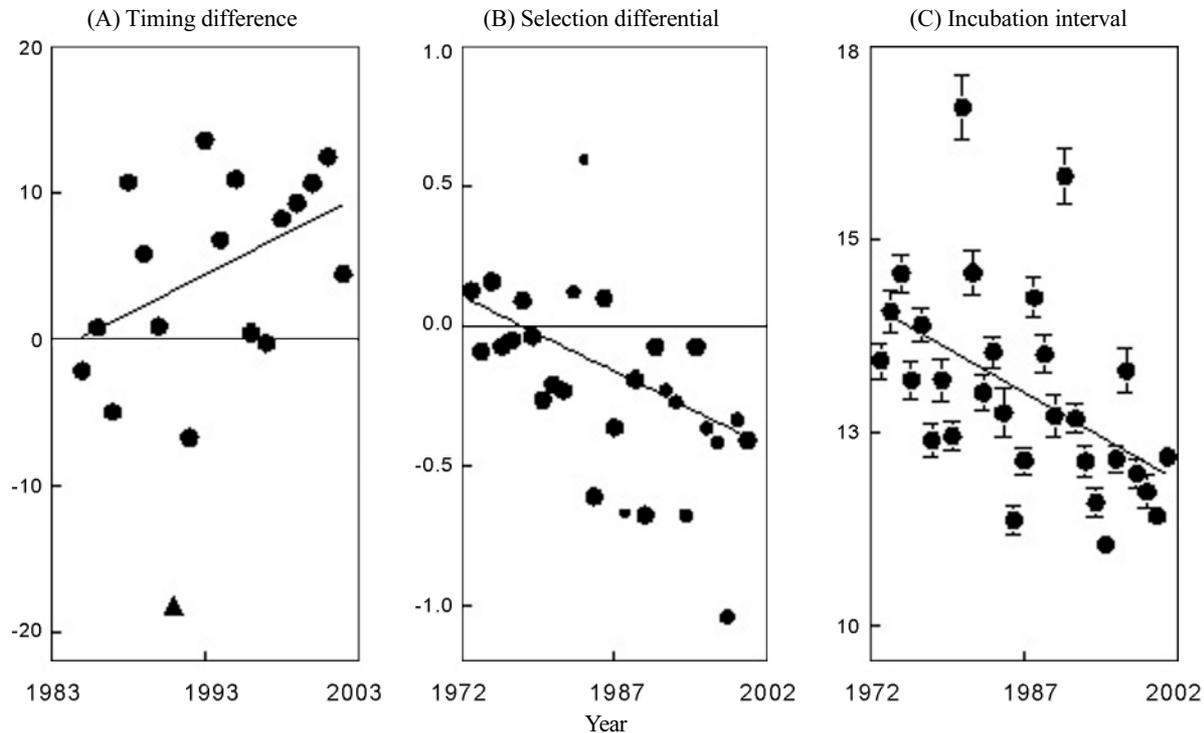


Fig. 2 Mistiming of breeding cycle due to global climate change in a great tit population (Hoge Veluwe, The Netherlands)

(A) The date of maximum food abundance (as measured by frass production of caterpillars) has advanced while the laying date of the great tits has not over 1985–2002, excluding 1991, ($F_{1,15} = 4.15$, $P = 0.06$) (Visser et al., 1998); as a consequence the difference in timing between the date of maximum food abundance and the mean date at which the great tit nestlings are 10 days old has become positive — great tits are too late (▲: a late frost, with damaged the oak leaves). (B) The selection differential for laying date (see text) has become more negative over 1973–2000 ($F_{1,25} = 11.9$, $P = 0.002$); here early-laying great tits tend to produce more recruits than late-laying birds (symbol size indicates the relative sample size for each point). (C) The duration of the incubation period [defined as hatching date of the first egg minus (laying date of the first egg + clutch size), s.e. indicated] has decreased over 1973–2001 ($F_{1,27} = 8.61$, $P = 0.007$); great tits “speed up” reproduction.

et al., 2002). Thus, if the majority of the birds in a population lay earlier than in the previous year, this can also be taken as an indication that their laying in the previous year was, on average, too late.

3 Insufficient advancement of laying date in Hoge Veluwe great tits

3.1 Hypothesis

It is clear that laying date advancement in the Hoge Veluwe great tit population is not keeping up with the advancement of peak caterpillar biomass. Why then has egg-laying not advanced over the years? Involved here are two conditions — one during early spring (time of decision-making) and the other in late spring (selection for synchrony between offspring needs and prey abundance) — which may have changed at different rates. Two hypotheses have been put forward in explanation: (1) Netherlands great tits currently possess a non-adaptive physiological control mechanism for laying; and (2) there are now more severe resource constraints at the time of egg formation (Visser et al., 1998; Stevenson and Bryant, 2000).

The underlying problem for these hypotheses in the Netherlands is that increase in temperature has not been

uniform over the entire spring period. Early spring has not become warmer, while late spring has (Visser et al., 1998). Therefore, the existing correlations between climate variables have changed and hence the physiological control mechanism may no longer be adaptive (cue hypothesis 1). Selection may operate on the control mechanism, given that there is sufficient additive genetic variation, and an advancement of laying date still may occur. Alternatively, due to the lack of increase in early spring temperatures, the food availability for the females during egg production has not advanced and hence there may not be enough resources to lay any earlier without severe fitness consequences (constraint hypothesis 2). Under this scenario, the birds will not be able to advance their laying and hence mistiming will continue.

There are various ways to test these hypotheses. If experimental birds can be manipulated to lay earlier than controls, they would be predicted to do better than under the cues hypothesis and worse under the constraint hypothesis, because then there would be a price to pay for having chicks in the nest at peak caterpillar abundance. It might be reflected in lower post-breeding survival, or even before and during egg laying, when conditions are harsh. The challenge here will be to manipulate birds such that

they have to pay the full costs of egg production (i.e., without supplying them with extra food, etc.). Such experiments are underway at the Hoge Veluwe.

3.2 Generality of the phenomenon

How widespread is the holdup in egg laying in great tits? To assess this we compared populations of great tits across Europe. Climate has not changed uniformly there. In the north and east there has been little or no increase in warming through the spring period, while food chains in the south are much less temperature dependent. Furthermore, only late spring temperatures have risen on mainland western Europe, whereas in Britain there has been a rise in early spring as well. When we compared advancement in laying dates across in 14 regional *Parus* populations, we found significant variation among study sites (Visser et al., 2003). No change was recorded in the north and east, nor on Corsica in the south. Nor could the variation in changes of laying dated in Belgium, The Netherlands and Britain be attributed to differences in spring temperatures across the board. Populations spatially close to each other even differed in the degree of advancement.

A clear correlation with climate change was nevertheless found in a shift in another life-history trait: in populations in which the production of second clutches has declined, there has been no advancement of laying date (Visser et al., 2002). This is evidence that the lack of advancement of laying date on the Hoge Veluwe is related to area or population specific characteristics, and fits in with a general pattern of shift in laying dates across Europe.

4 Discussion

Climate change can lead to a disruption of synchrony through the different levels of the food chain. For the Hoge Veluwe great tits this may be caused by a differential change of temperature in early and late spring, rather than an increase in spring temperatures *per se*. Such disruptions have also led to mistiming in another bird, the pied flycatcher (*Ficedula hypoleuca*) and an important prey species, the winter moth (*Operophtera brumata*). The flycatcher has suffered a change in climate across its breeding grounds but not in its wintering area (Both and Visser, 2001); and for the moth, there has been an increase in spring temperature but no change in the number of days with temperatures below zero during the winter, two parameters which determine winter moth phenology (Visser and Holleman, 2001).

As we found mistiming in all three species that we studied (great tit, pied flycatcher, winter moth), we suspect that this is a very general phenomenon. We wish to encour-

age researchers to look at their own biological systems with this in mind, and to try to use the three different procedures described here to assess responses in changes of laying dates. Only by gathering further more examples will it be possible to determine how general are the patterns described here. Comparing different biological systems is also an important tool towards understanding the shifts in phenology which are becoming so widely observed, a prerequisite to predict how climate change will affect food chains, and thereby biodiversity and ecosystem function.

Acknowledgements J.H. van Balen kept the long-term study on the Hoge Veluwe going for many years, and J. Visser managed the databases. J.M. Tinbergen collected caterpillar biomass data from 1985 to 1992. We thank the board of the National Park “de Hoge Veluwe” for their permission to work within their reserve.

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S08-3 Impacts of extreme climate events on alpine birds

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Abstract With climate change, the frequency and severity of extreme environmental events such as heavy snow fall are expected to increase in north temperate and alpine areas. In a 9-year field study, we evaluated impacts imposed on reproduction in white-tailed ptarmigan (*Lagopus leucurus*) by a year of heavy and persistent snow cover. Under extreme conditions in 1995, all females attempted nesting, but timing was so delayed (mean 18 days) that it did not even overlap with other years. Breeding success in 1995 was the lowest for the study, but survival of adults was normal. Quantifying impacts of extreme climate events on fitness allows refinement of predictions for avian responses to climatic change.

Key words Extreme climatic events, Reproductive success, White-tailed ptarmigan, Quantified impacts

1 Introduction

Patterns of wildlife responses to climate change are emerging from long term monitoring and population data (Crick and Sparks, 1999). A proportion of migratory birds and resident vertebrates now arrive on territories and initiate breeding 1 to 4 weeks earlier than several decades ago (Inouye et al., 2000). Earlier arrival and breeding can result in ecological mismatches if the phenology of different components of food chains do not advance at the same rate (Visser et al., 1998). For example, earlier arrival dates for pied flycatchers (*Ficedula hypoleuca*) in Finland were associated with earlier laying dates, and increases in egg size, clutch size and hatching success over the past two decades (Järvinen, 1994). However, such reproductive investment did not result in improved reproductive success, due to weather events during brood-rearing period later in the season. Thus, potential fitness gains resulting from climate warming need not be realized due to differential changes in climate at different times of the year.

Terrestrial animals in temperate systems regularly experience stochasticity in temperature, wind, precipitation or snow cover that impose seasonal variation in timing of breeding with reproductive consequences (Wingfield, 1984; Hannon et al., 1988). Climate change models predict a general increase in the frequency of extreme weather (IPCC, 2001), with warmer winter temperatures and greater spring snow fall already experienced in western North American and European alpine areas (Diaz and Bradley, 1997).

Ptarmigan are ground-dwelling, herbivorous, tundra grouse with morphological, physiological and behavioral adaptations to survive and reproduce in harsh and unpredictable weather conditions (Braun et al., 1993). In a 9 year

study of alpine white-tailed ptarmigan (*Lagopus leucurus*), we recorded one year (1995) with unusually heavy and persistent snow cover. Here, we evaluate responses and fitness costs imposed on ptarmigan breeding in such extreme conditions, and evaluate the potential impact of increases in the frequency of such events on alpine birds.

2 Materials and methods

We studied white-tailed ptarmigan at 4 alpine habitats in the Colorado Rocky Mountains (3 350–4 250 m a.s.l., 39°34–40'N, 105°35–53'W) from 1987 to 1996. The life history and breeding biology of the ptarmigan, and the field methods used, are detailed in Martin et al. (2000). We located birds using dogs or playbacks of male territorial calls, and captured them with noose poles or nets. All females were taken after they had settled on a territory, and were affixed with radio tags to monitor survival and breeding success. Birds were aged as yearlings (≤ 1 yr) or adults (> 1 yr) based on pigmentation on primaries 8 and 9, after Braun et al. (1993). We recorded survival of breeding birds by thorough checks of study sites and adjacent mountains for marked birds through the summer and the next year.

Data on snow depth were obtained from the Atmospheric Sciences Center, Desert Research Institute, Reno, Nevada, USA. Here we defined a “harsh year” as one of extreme conditions that occurs less frequently than the average life span of individuals that have reached adulthood; such a life span for white-tailed ptarmigan is 3–4 years. Because the timing of snowmelt and laying phenology in 1995 were well outside the normal range of variation for our study, we felt justified in calling it an unusually harsh year (Fig. 1). Thus, we pooled data from the 8 normal years for

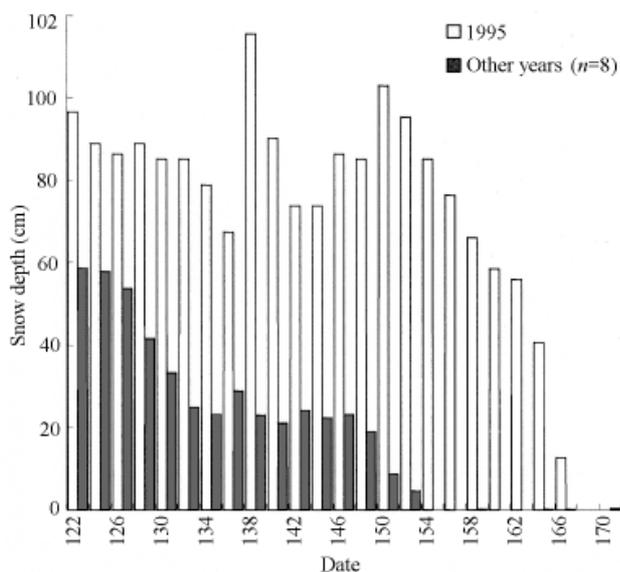


Fig. 1 Snow depths (cm) in May and June (averaged for 2 day periods) near ptarmigan study sites in 1995 (harsh year) compared to average snow depths for other years (normal years: 1987–1989, 1991–1994, 1996)

Depths are averaged for two day periods and measured in an open, non-drifted area at Mount Evans High Altitude Research Station (Stn. # 055797), Colorado, 3 243 m a.s.l. January 1=day 1.

comparison with the harsh year. Statistical significance is reported for two-tailed tests ($P < 0.05$).

3 Results

The spring snow depth in May 1995 was approximately double that in other study years, and snow fall and a deep snow pack persisted until late June, a month later than in “normal” years (Fig. 1). Snow fall was deeper and melted at least 1 week later on our study sites than recorded

on Fig. 1, as the Mt. Evan weather station, from which the recordings came, was located several hundred meters below. Leaf-out in willow (*Salix* spp.), the main spring food of ptarmigan, was also delayed by about 3 weeks in 1995 (pers. obs). Excessive snow fall and delayed melt occurred in all study areas (Martin et al., 2000) and elsewhere in Colorado in spring that year (Inouye et al., 2000).

3.1 Survival and breeding propensity

Virtually all females on our sites obtained mates and bred annually. We determined survival, egg laying dates, clutch size and annual production for about 95% of hens. We expected higher predation on birds in 1995 given that the development of dark nuptial plumage reduced their crypsis in a white landscape prolonged by delayed snow melt. During summer 1995, 5 females (15.6%) died, compared to 11.6% on average in normal years ($n=147$ hens; Braun et al., 1993). Over winter survival of adults after the harsh year was normal (Martin et al., 2000). We expected yearling females to opt out of breeding in 1995 because breeding was delayed beyond the date of re-nest initiation. In 1995, all 32 hens located and radio-tagged on our study sites (including 12 yearlings) initiated clutches. We might have failed to detect birds that had opted out of breeding had they left our sites; but, if this were so, we would then expect fewer breeding pairs in 1995. Breeding densities in that year, however, were above the norm of 26 hens/year. Thus, we have direct and indirect evidence that all female ptarmigan attempted breeding in the harsh year.

3.2 Timing and success of breeding activities

In 1995, first clutches were initiated 18 days later than 7 June, the mean date across all study years (Fig. 2). First clutches in 1995 (5.38 ± 0.19 SE eggs, $n=24$ clutches) were also smaller than across other years (5.94 ± 0.07 , $n=160$; $F_{1,210}=8.65$, $P=0.0004$). Reproductive success in 1995 was

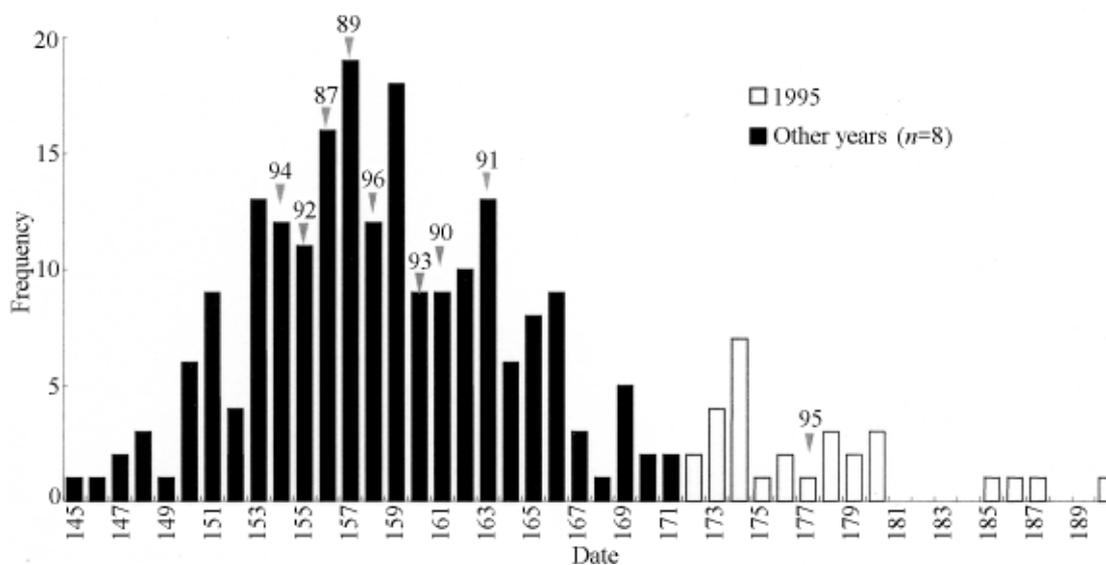


Fig. 2 Initiation dates for first clutches of Colorado white-tailed ptarmigan in harsh (1995) and normal years (1987, 1989–1994, 1996); $F_{1,200} = 270$, $P < 0.0001$

Triangles with year above bar indicate mean annual clutch initiation dates. January 1=day 1.

the lowest of all years, as more than 70% of first clutches failed. Only 3 of 8 adult hens re-nested compared to 83% in other years. No yearlings re-nested.

4 Discussion

It is instructive to examine impacts from the extreme year because increased frequency and severity of extreme events is one predicted consequence of climate warming, especially for high elevation habitats. Despite exceptional delays, no birds opted out of breeding. Proximate responses by ptarmigan to extreme conditions involved adjustments in timing of breeding and fecundity. Over our 8 “normal” years, mean clutch initiation dates varied by 10 days; but in 1995, mean clutch initiation was 14 days later than that in the latest normal year. The harsh year breeding season was also considerably shorter than in normal years. Although they experienced the lowest production recorded, the ptarmigan suffered no increase in mortality in the harsh season or over the next winter. Ground-feeding herbivores may generally resist such extreme weather events, as deeper snow fall in spring may increase access to higher parts of plants. This may differ for insectivorous and granivorous birds, for which harsh conditions often reduce food availability or foraging capacity, so reducing survival of young and adults.

4.1 Impacts of climate variability on avian populations

Reproductive success for birds is often low in harsh years, due to smaller clutches and reduced re-nesting in late years. Delayed snow melt physically constrains nest building for ground nesting birds, and the patches of available bare ground are fewer and smaller, helping predators to detect nests more readily (Martin, 2001). Recruitment of late hatching offspring to natal areas is often lower (Martin and Hannon, 1987). Thus, the consequences of breeding in harsh years may be fewer and poorer quality offspring. It is unclear why female ptarmigan attempted to breed in the harsh year, given their extremely low success. With few survival costs, birds may risk breeding with low benefits, or they may be unable to predict the persistence of harsh conditions.

Increases in climate warming (mean temperature) and extreme weather events may affect animal populations differently, depending on patterns of resource availability and life history traits (Martin, 2001). Their interactive effects are especially complex in sites with strong biophysical gradients, such as alpine or arctic habitats. Food for alpine herbivores may increase with predicted increases in moisture, but advancing treelines will result in smaller, more

isolated patches of habitat that may impede dispersal. In some cases, extreme events later in the spring-summer season may remove potential fitness gains due to advances in breeding phenology associated with climate warming. There may even be a loss of fecundity.

Studies of the impacts of climate variability yield important insights into proximate mechanisms that animals may use to cope with climate change; and they can be used to predict longer term effects of environmental change on behavior, demography and life history. Given their strong biophysical gradients, alpine habitats provide a good system for studying the effects of changing frequencies in extreme climatic events, and alpine animals may function as “canaries” in such research.

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S08-4 The influences of global climate change on marine birds

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Abstract Global climate fluctuates at several temporal scales. For the purposes of this review, we characterize these scales as “cycles”, “trends” and “regime shifts”, as exemplified by ENSO, Global Climate Change and the North Atlantic Oscillation respectively. We investigate whether seabird populations have experienced changes in abundance that correlate with climate variability at each of these scales. There are numerous examples of seabird populations responding to cyclic variation in climate, especially ENSO. Indications so far are that, by virtue of longevity, seabirds recover quickly from declines caused by El Niño. More recently, data have accumulated to demonstrate longer-term changes in populations that correlate with long-term (decadal or more) changes in oceanic climate. While there are clear examples of past regime shifts in the marine ecosystems of the North Pacific, North Atlantic and Antarctic Oceans, these shifts have not yet resulted in major changes in the structure of seabird communities.

Key words Climate change, Climate scales, Seabirds, Community structure, Marine ecosystems

1 Introduction

The earth's atmosphere has warmed by 1°C since 1900, the most of the change having taken place since 1975 (Hayward, 1997; Hughes, 2000). This rate of warming is some ten times higher than any rate of change in the past one thousand years (Hughes, 2000). The increase in temperature has been most pronounced at the poles and decreasingly evident towards the equator, such that mean air temperature has increased by 0.05°C/year since 1945 in the Antarctic Peninsula (Smith et al., 1999). This accelerating trend has been reflected in a warming of the world's oceans (Roemmich and McGowan, 1995); the waters of the California Current have warmed by 0.75°C between 1975 and 1990 (Roemmich, 1992; Roemmich and McGowan, 1995; McGowan et al., 1998). One consequence of increasing sea temperatures is a direct effect on primary productivity through changing patterns of upwelling and advection (Hayward, 1997). Changes in primary productivity then flow up through marine food chains, ultimately affecting populations of upper level predators such as marine mammals and seabirds (Veit et al., 1996, 1997; Montevecchi and Myers, 1997).

In this review, we investigate whether the temperature shifts described above have had demonstrable effects upon populations of marine birds. The scope of our study is limited to responses at the population level, even though there are several studies of phenologic change in seabirds (e.g., Divoky, 1998).

Changes in seabird populations have indeed occurred over the past 30 years or so. However, because of the lag in

population responses to environmental change and buffering by behavioral flexibility and life history patterns, it is difficult to ascribe causes to declines and increases (Morrison, 1986; Montevecchi and Berruti, 1991). Changes in abundance have occurred in response to several climatic scales, so we address them here under three categories that more or less reflect these different spatial and temporal scales. First, there are *cyclical changes* that correlate with periodic changes in climatic variables, especially the ENSO (El Niño-Southern Oscillation). Secondly, there are longer-term changes that to date resemble non-periodic *trends* but which correlate with longer-term climatic change, often referred to as Global Climate Change. Thirdly, there are dramatic *regime shifts* in species composition which have occurred over relatively short periods of time, as evidenced from some marine and limnological studies (Cushing, 1982; Steele, 1998).

2 Cycles

The ENSO cycle has a period of 5–7 years. The most immediate effects of ENSO are evident near the equator, but associated fluctuations develop north and south well into temperate parts of the Pacific and elsewhere (Chelton et al., 1982; McGowan et al., 1998). Cyclical variability in seabird reproduction is evident along the California Current (Ainley et al., 1995, 1996), and as far away as Sub-Antarctic islands in the Indian Ocean (Chastel et al., 1993; Guinet et al., 1998), all of it correlated, with time lags, with the ENSO cycle.

Seabird populations have suffered catastrophic breeding failures, and occasionally substantial mortality of adults, during El Niño events in the Pacific and elsewhere (Barber

and Chavez, 1983, 1986; Boersma, 1997, 1998; Schreiber and Schreiber, 1984; Schreiber, 2002). Generally, these episodes of high mortality have been followed by a return to pre-perturbation conditions in following years such that the long-term viability of affected populations has not been impaired.

3 Trends

3.1 Sooty shearwaters in the California Current

Surface temperatures of the California Current warmed by 0.75 °C between 1949 and 1990, and a significant, 70% decrease in zooplankton abundance followed (Roemmich, 1992; Roemmich and McGowan, 1995). The result of warming surface temperatures and zooplankton decrease is a decline in nutrients at the surface which decreases primary production. Whether the decline in nutrients is due more to decreased upwelling or advection from the north in the California Current is not clear (Hayward, 1997). Upper trophic level predators such as salmoniids and seabirds have declined along with the zooplankton (Fig. 1a; Francis and Hare, 1994; Veit et al., 1996, 1997; Francis et al., 1998). The diets of these predators are similar in the eastern Pacific, consisting primarily of euphausiids, larval rockfish and squids.

Large mobile predators are difficult to census because of the enormous ranges that they cover, making interpretation of what might represent either distributional shifts or population declines difficult. Nevertheless, two pieces of evidence indicate that sooty shearwaters (*Puffinus griseus*) have in fact declined since the 1970s. First, numbers of shearwaters have not shifted elsewhere in the interim according to substantial pelagic surveying, supporting the findings of Veit et al. (1997). Secondly, a significant decline in the breeding population of sooty shearwaters has been found in New Zealand through analysis of Maori harvesting records; and the New Zealand decline is significantly correlated with the decline within the California Current (Lyver et al., 1999). It indicates that the decline in sooty shearwaters is due, at least in part, to a decline in their prey base in the California Current.

3.2 Adelie and chinstrap Penguins in the Antarctic

The sea surface temperatures off the Antarctic Peninsula increased by more than 2°C between 1947 and 1995, resulting in a steady fall in winter ice cover (Smith et al., 1999). During this period, Adelie penguins have decreased while chinstrap penguins have increased (Fig. 1b; Croxall, 1992; Fraser et al., 1992; Loeb et al., 1997; Croxall et al., 2002). Because chinstrap penguins are pelagic and Adelies forage in the immediate vicinity of ice floes, it seems likely that these correlated changes are due to the trend in ice coverage.

3.3 Gannets in the northwest Atlantic

Sea surface temperature off Newfoundland increased by about 0.6°C between 1910 and 1950 (Montevecchi and Myers, 1997). Major changes in commercial pelagic fish

catches in that area reflect this shift. Of particular importance to gannets was the tremendous increase (at 4 orders of magnitude) in the abundance of mackerel through that warming trend. As mackerel are preferred prey for gannets, the nesting population of gannets at Funk Island, off the northern coast of Newfoundland, increased from 0 to 3000 pairs between 1930 and 1970 (Fig. 1c; Montevecchi and Tuck, 1987; Montevecchi and Myers, 1997). It seems likely that the increase of gannets can be attributed directly to the warming of surface temperatures, which permitted a northward expansion of migratory warm-water mackerel into Newfoundland waters.

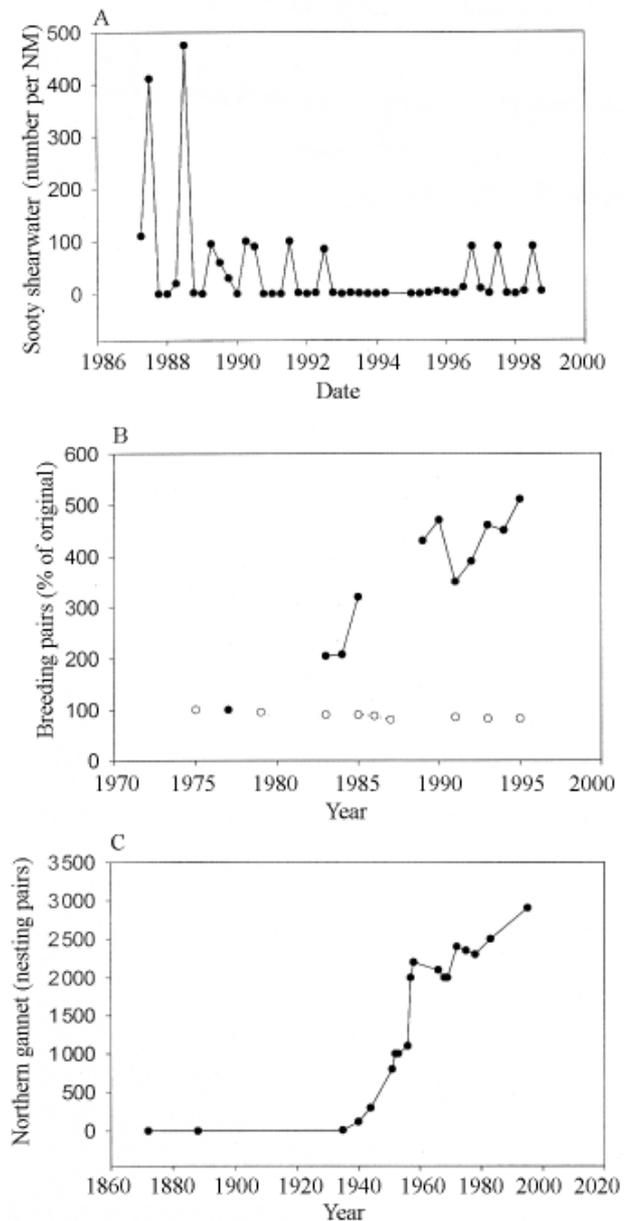


Fig. 1 Population trajectories for (A) sooty shearwater off California, (B) Adelie (open circles) and chinstrap penguins (closed circles) on the Antarctic Peninsula, and (C) northern gannets at Funk Island, Newfoundland

Data for (A) from Hyrenbach and Veit (in press), (B) from Smith et al. (1999), and (C) from Montevecchi and Myers (1997).

4 Regime shifts

The term *regime shift* derives from analysis of nonlinear equations, and its exact meaning in biological terms is open to interpretation (Cushing, 1982; Steele, 1998; Scheffer et al., 2001). In a time series of biological data, it usually means a dramatic change induced by altered physical factors that is not subsequently reversed when the physical factors return to pre-perturbation conditions. Qualitatively, a regime shift implies much more than just a dramatic change in the abundance of a single species, and implicates changes at community level. There have certainly been major, long-term changes in marine ecosystems that have not reverted to former states (Springer et al., 1984, 1986, 1987; Aebischer et al., 1990; Barry et al., 1995; Piatt and Anderson, 1996; Regehr and Montevecchi, 1997; Springer, 1998; Anderson and Piatt, 1999; Croxall et al., 2002). Some of these changes undoubtedly amount to what Scheffer et al. (2001) describe as regime shifts. What is less clear is whether changes recorded at the level of seabird communities represent what can be called a regime shift.

Nevertheless, what surely qualifies is the abrupt change in ecosystem state in the north Pacific in about 1977 (Francis et al., 1998; Scheffer et al., 2001). This abrupt, so far un-reversed shift involves diverse taxa, from phytoplankton to birds. Yet, while changes in seabird reproductive rates coincided with it (Piatt and Anderson, 1996; Springer, 1998), seabird community structure remained little affected. For example, the ranking of seabird abundance did not change among species in 1977, the year of the shift. A similar regime shift initiated by substantial climatic change occurred in the north Atlantic Ocean around 1980, with impacts on phytoplankton, zooplankton, fish and kittiwake reproduction (Aebischer et al. 1990). Yet again as in the north Pacific, no substantive change in seabird community structure seems to have occurred. It is possible that seabird communities have been selected to withstand such perturbation, even at the long-term, decadal scale, the coarsest scale of temporal resolution so far found.

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S08-5 A methodology for predicting the impact of sea level rise on shorebirds (Charadrii) in estuaries

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Abstract Mean sea level has been rising around Britain and the North Sea region over the past century and is predicted to rise more over the next century as a result of global climate change. Britain is internationally important for the large numbers of shorebirds (Charadriiformes) that winter on its estuaries, a habitat that will be directly affected by rising sea levels. The BTO has developed models for estimating estuarine shorebird densities from measurements of estuarine geomorphology predisposed to predict how sea level rise may affect shorebirds. A methodology integrating these models with digital elevation models, coastline management plans and predictions of sea level rise was explored using two case study estuaries. The studies suggest that the densities of shorebird species favoring muddy sediments will decrease as sediments become increasingly sandy under management scenarios that allow land behind existing sea defenses to be reclaimed by the sea. However, where changes in estuary shape become great enough to bring about this shift, the associated increase in area more than compensates for the assumed degradation of habitat and such that numbers of shorebirds may be accommodated overall.

Key words Climate change, Waders, Habitat change, Modeling

1 Introduction

Mean sea level has been rising by approximately 1 mm yr⁻¹ around Britain and in the North Sea region over the past century (Shennan and Woodworth, 1992; Nydick et al., 1995), and is predicted to rise further over the next century as a result of global climate change. Britain is internationally important for the shorebirds (Charadriiformes) that winter on its estuaries (Cayford and Waters, 1996; Rehfish et al., 2003), a habitat that will be directly affected by rising sea levels.

Within estuaries, sediment particle size and salinity influence invertebrate abundance and availability to foraging shorebirds (Goss-Custard et al., 1977; Quammen, 1982) and, therefore, shorebird distribution (Goss-Custard et al., 1991; Yates et al., 1993; Rehfish, 1994). Consequently, such environmental variables can be reliable descriptors of shorebird densities within an estuary (Goss-Custard and Yates, 1992; Yates et al., 1993). The nature of intertidal sediments is largely a consequence of wave action, currents and tide (Yates et al., 1996); and consequently, both the quality and quantity of estuarine habitat available to shorebirds is in part a function of estuary shape.

In Britain, the majority of estuaries (88%) have been modified by the construction of sea defenses which claim former intertidal habitat for agriculture (Davidson and Evans, 1986). These are all being affected by changing sea level. Given an adequate supply of suspended material in the water column, it is expected that natural processes leading to the deposition of intertidal sediments will continue to track

changes in sea level and realignments of sea defenses.

The British Trust for Ornithology (BTO) and Center for Ecology and Hydrology (CEH) have developed generalized linear models (GLMs — McCullagh and Nelder, 1989) that predict estuarine shorebird densities on British estuaries from measurements of estuary morphology and location (Austin et al., 1996; Austin and Rehfish, 2003). These geomorphological variables are based on readily obtained parameters such as mean estuary width, length of channel, mouth width and intertidal area, full details of which can be found in Austin and Rehfish (2003). The models are predisposed to predict how shorebird numbers may be affected by changes in the shape of estuaries due to managed or unmanaged responses to sea level rise. The models make it possible to compare and contrast how various scenarios of estuary realignment are likely to maintain the present populations of wintering shorebirds, in compliance with international agreements encompassed by the Birds Directive (79/409/EEC).

2 Aims

In this paper we describe and apply a method that makes it possible to assess how rising sea levels may affect populations of shorebirds wintering on the estuaries of Britain and elsewhere.

3 Methods

The methodology described was developed using data from two British case study estuaries, the Deben

(52°03'N, 1°21'E) and Duddon (54°10'N, 3°16'W), chosen to represent extremes of historical land claim, proposed future management of sea defenses, habitat characteristics, and shorebird population. Estimates of relative sea level rise under various scenarios by the United Kingdom Climatic Change Program (UKCIP98; Hulme and Jenkins, 1998) were derived from estimates of sea level rise for Britain and Ireland (Austin et al., 2001) using the ESCAPE model of Hulme et al. (1995) which calculates sea level rise for a given level of warming after allowing for vertical land movements in the North Sea region and Great Britain (Shennan and Woodworth, 1992).

Determining how the shape of an estuary may change with sea level rise requires high resolution, accuracy and precision elevation data for land above the current high water mark. Data collected by the airborne Light Detection and Ranging system (LIDAR) that records elevation to 10 cm precision at a 2 m × 2 m spatial resolution were obtained from the Environment Agency, National Center for Environmental Data and Surveillance, and processed within the ArcView Geographical Information System (GIS; ESRI, 1999) to derive digital elevation models (DEMs) for land up to 2 m a.s.l. surrounding each estuary.

Potential sea defense management plans for the case study estuaries were also obtained from the Environment Agency (Environment Agency, 1998, 1999). These plans detail how various compartments (areas of land which can be managed as a unit) would be managed. The management strategies were then incorporated into the GIS, and, in combination with the DEMs, used to assess how the shape of the chosen estuaries might be expected to develop both with and without intervention. This procedure was carried out for each of ten, 20 cm incremental increases in mean high water spring (MHWS) tidemark, from a baseline set of current values taken from the Admiralty Tide Tables (UKHO 1999). Values for the geomorphological variables required by the bird models were extracted for each incremental rise of sea level for each management scenario.

Models that explained a substantial proportion of the variation in bird density (Austin et al., 1996; Austin and Rehfish, 2003) were available for five species (*Haematopus ostralegus*, *Calidris canutus*, *Calidris alpina*, *Numenius arquata*, *Tringa totanus*) that together account for over 90% of the shorebirds overwintering on British estuaries (Cayford and Waters, 1996). These models were then used to predict the densities of these species in each estuary for each incremental rise in sea level under each management scenario. Density predictions for the present were compared to contemporary data obtained from the Wetland Bird Survey (WeBS), in order to assess the applicability of the models for each site.

4 Results

The predictions of baseline shorebird numbers at present were similar to recent WeBS counts for both estuaries, suggesting that the models were performing reli-

ably in each case. Under the UKCIP98 high scenario, the ESCAPE model predicted a maximum increase in relative mean sea level of 78.4 cm for the Deben and 67 cm for the Duddon by around 2050. The management plans for both estuaries equate to a “hold the line” policy for all land compartments vulnerable to sea level rise exceeding these predictions by a factor of three or more. Consequently, if these management proposals are followed, the parameters in the bird density models will not change. If sea-level rise remains within current predicted values by 2050, then this would also be true under a policy of no intervention (a management option not currently envisaged).

Without managed intervention, current sea defenses and local topography on the Duddon would still prevent substantial change in estuary shape unless sea levels exceed the predicted values by a factor of three or more, notwithstanding a slight upward trend predicted in both the densities and numbers of both *Haematopus ostralegus* and *Calidris canutus* beyond a rise of 100 cm. A policy of non-intervention on the Deben, however, would result in sufficient change to estuary shape to affect shorebird densities if relative sea level were to increase beyond 90 cm, when existing sea defenses would be unable to prevent inundation of large areas of the lower reaches. Beyond this level, the models predict decreasing densities of *Tringa totanus* and *Calidris alpina*, increasing densities of *Haematopus ostralegus*, and stable densities of *Numenius arquata*. However, the numbers of *T. totanus*, *C. alpina* and *H. ostralegus* that the estuary could support would all increase, due to the associated gain in area that would more than compensate for reduction in habitat quality. For example, given a rise of up to 150 cm, estuary carrying capacity for the three species could increase by up to 100%. *H. ostralegus*, *T. totanus*, *C. alpina* and *N. arquata* account for about 70% of shorebirds that currently overwinter on the Deben.

5 Discussion

Assuming that mean high water spring mark will rise in line with mean sea level rise, substantial changes in the shape of both case study estuaries are unlikely, even under the UKCIP98 High scenario for climate change. For the Low, Medium-Low and Medium-High scenarios, the rise predicted for both estuaries is such that existing sea defenses are unlikely to be compromised in the next 50 years. However, extreme tidal events such as those that result from low barometric pressure, seiches, onshore winds and storm surges (UKHO, 1999) may well overrun those defenses with increasing frequency as sea level rises. Low barometric pressure and seiches may raise tide heights by up to 30 and 100 cm respectively above normal. Storm surges, particularly those caused by strong and sustained northerly or north westerly winds, may, in extreme cases, raise sea level temporarily by as much as 2 m in the North Sea. Smaller maxima, currently in the region of 60 to 90 cm, occur several times per year; and when these events coincide with high water equinoctial spring tides, extremely high tide levels can result.

The UKCIP98 scenarios predict that mean wind speed will increase and extreme wind events become more frequent. This should increase the strength and frequency of storm surges. An increased frequency of flooding may affect the viability of current land use, which, in turn, could affect future management proposals.

As sea level rises, a general pattern of change to estuarine habitats, and thus shorebird populations, might be expected. Where management scenarios seek to retain current intertidal habitat, the parameters used by the shorebird density models, and thus the resulting predictions, will remain unchanged. Where there is scope for realignment of sea defenses, changes in shorebird densities would be predicted with change of estuary shape. In Britain and much of Europe, estuary realignment will, in practice, often equate to abandoning land formerly claimed for agriculture from the intertidal zone. This will generally result in estuaries becoming wider and more exposed to wave action, producing sandier sediments (Yates et al., 1996). Consequently, they would support lower densities of such mud-preferring species as *Tringa totanus* and *Calidris alpina* than at present, and higher densities of such species as *Haematopus ostralegus* which favor sandier sediments (Austin et al., 1996).

The change in the nature of sediments brought about by increased estuary width will be driven principally by increased fetch, that is, the distance over which wave energy builds before breaking on the shore. Increased wave action would serve to keep finer particles suspended in the water column before being flushed from the estuary, leaving behind an increasingly sandy substrate (Yates et al., 1996). Offshore sea defenses designed to reduce wave action and to protect an estuary from tidal surges would counter this effect. As a result, estuaries might increase in area yet remain muddier than expected. In such circumstances, the densities of shorebirds favoring muddy sediments would be expected to be higher than predicted by the models, while increases in those preferring sandy substrates would be less.

The case studies suggest that while habitat quality will fall for the majority of shorebirds, estuary enlargement may well offset it. On estuaries historically subject to land reclamation, shorebirds may gain a windfall increase in habitable area wherever current sea defenses are breached or intertidal management realigned. Where reclaimed areas have been urbanized or industrialized or is at a premium for agriculture, however, there is probably little scope for managed realignment. Moreover, where estuaries are confined by hard natural features, changes in estuary shape or area are likely to be negligible. The impact of sea level rise on shorebirds can, therefore, be expected to differ between regions, depending on geology, isostatic realignment and historical land claim.

A methodology for predicting the effects of sea level rise on estuarine shorebirds has been demonstrated here for two estuaries. In Britain, many estuaries are surrounded

by low lying land vulnerable to sea level rise, much of it previously reclaimed for development. The ultimate fate of such land will depend largely on socio-economic factors that will either retain its integrity or manage it by realigning existing sea defenses. This must be balanced against Britain's obligations as signatory to international agreements that require maintenance of areas designated for bird and habitat conservation (Stroud et al., 2001). The methodology described here offers an empirical approach for the assessing and comparing the impact of sea defense management on governmental obligations to conserve internationally important bird populations sustainably. Such a methodology has potential for application to other sites globally, wherever predictions of the effects of managed realignment are needed. Its outcomes may offer conservation opportunities for mitigating loss of habitat in situations where options for managed realignment are limited.

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Symposium 09 Photoperiodism: mechanisms and adaptations

Introduction

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Seasonal reproductive cycles in birds result from interactions between endogenous cycles and exogenous factors, in particular photoperiod. This symposium examined photoperiodic phenomena as they affect biological cycles in birds. In the first oral paper, the late Eberhard Gwinner focused on the role of endogenous circannual rhythmicity and its modification by photoperiodic response to ensure that seasonal biological cycles are matched optimally to environmental conditions. Notwithstanding differences from mammals, it seems likely that pineal secretions of the hormone melatonin mediate photoperiodic information for the basic circannual control system. In a second oral paper, Michaela Hau reviewed the growing evidence for photoperiodic influence in circannual cycles in low latitudes where day-length undergoes little seasonal change. Interaction is complex and varied by species-specific thresholds to photoperiodic response, as well as environmental (food availability) and social cues. Information about how neuroendocrine systems mediate interactions between non-photoperiodic factors and day-length is needed. The third

oral paper from Alistair Dawson addressed the role of day-length in the physiological control of molt. He detailed the influence of long and decreasing photoperiods in initiating and hastening the molt processes, and concluded that secretion of prolactin, thyroid hormones and testosterone were implicated in complex but as yet unexplainable ways. Abstracts of these papers are published in the Abstract Volume of the Congress.

Only the last two papers were submitted as full papers for publication and these are now presented here. Ongoing research in all fields covered by this symposium will continue to resolve questions for understanding the bases of photoperiodism and the physiological and life history consequences of photoperiodic responses. This understanding, in turn, has wider application in such issues as the conservation and management of threatened/endangered species, problems related to captive breeding of individuals taken from wild populations, and adaptations to global warming.

S09-4 Molecular neuroendocrine mechanisms controlling photoperiodically regulated release of gonadotropin releasing hormone

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Abstract Change in photoperiod is a key proximal factor timing seasonal breeding at higher latitudes. Photoperiodic information is transduced in the neuroendocrine system to regulate the secretion of neuropeptides, gonadotropin releasing hormone-I (GnRH-I) and a vasoactive intestinal polypeptide, which respectively regulate the release of luteinizing hormone (LH) and prolactin. The initiation of photoinduced LH secretion is closely associated with an increase in hypothalamic GnRH mRNA, suggesting that an early event in the photoperiodic reproductive response is an increase in GnRH gene transcription. In many photoperiodic species, seasonal breeding is terminated by the development of absolute or relative photorefractoriness. Absolute photorefractory birds become unresponsive to very long days, including continuous light, while relative photorefractory birds become unresponsive to spring-like day lengths but remain responsive to very long days. The development of both absolute and relative photorefractoriness is associated with decreased plasma LH and increased plasma prolactin. Photorefractoriness develops for prolactin secretion in absolute photorefractory birds but not in relative photorefractory quail, *Coturnix*. Prolactin treatment depresses GnRH-I and LH beta mRNAs. It is suggested that the development of absolute and relative photorefractoriness may be initiated by increased plasma prolactin, and that increased prolactin maintains relative, but not absolute photorefractoriness.

Key words Gonadotropin releasing hormone (GnRH), Luteinizing hormone (LH), Photorefractoriness, Photoperiodism, Prolactin, Seasonal breeding

1 Introduction

Reproductive function is controlled by neuroendocrine responses to environmental stimuli that are integrated in the brain to increase or decrease the secretion of gonadotropins and prolactin from the anterior pituitary gland (Sharp et al., 1998). Of the many environmental factors that influence reproductive neuroendocrine function, the most extensively investigated is photoperiod (Nicholls et al., 1988; Sharp, 1996; Ball and Hahn, 1997; Hahn et al., 1997; Dawson, 1999; Dawson et al., 2001; Sharp and Blache, 2003). An example of the pattern of seasonal photoinduced changes in concentrations of plasma luteinizing hormone (LH) and prolactin in many photoperiodic birds is provided by the Svalbard ptarmigan, *Lagopus mutus hyperboreus* (Fig. 1A).

This bird breeds in the high Arctic where day length is continuous from May through August, and nights are continuous from November to January. Concentrations of plasma LH and prolactin increase when the threshold of critical day length increases above about 12 h, and remain high during the brief breeding season (Stokkan et al. 1988). A supplementary environmental factor — the availability of nests sites uncovered after the snow melts — determines the precise timing of onset of breeding in June/July (Stokkan et al., 1986). The breeding season is terminated by the development of absolute photorefractoriness, defined as insensitivity to photostimulatory day lengths, including con-

tinuous light (Nicholls et al., 1988; Sharp, 1996). The development of reproductive photorefractoriness is characterized by a steep fall in plasma LH when plasma prolactin values are maximal (Fig. 1A). After concentrations of plasma LH have begun to fall, plasma concentrations of prolactin also drop, demonstrating the development of absolute photorefractoriness for prolactin secretion too (Fig. 1A).

A less common type of annual breeding cycle is found in the European quail, *Coturnix coturnix coturnix* (Fig. 1B). Concentrations of plasma prolactin and LH increase after day length increases above about 12 h, and are high during the breeding season. Plasma LH begins to decrease in the fall when day-length is shortening but still above 15 h, followed by a drop in plasma prolactin in September/October when day length falls below 12 h. European quail therefore terminate breeding in the fall when day length is still longer than that required to stimulate breeding in the spring, but remain in breeding condition indefinitely if exposed to very long photoperiods (Boswell, pers comm.). This form of photorefractoriness is termed “relative” photorefractoriness. In the closely related and similarly responsive Japanese quail, *Coturnix coturnix japonica*, the development of relative photorefractoriness is demonstrated by the rapid decrease in plasma LH and gonadal regression that follows a reduction in the photoperiod to a 13 h day (Robinson and Follett, 1982; Follett and Pearce-Kelly, 1990).

2 The pathway for photoperiodic signal transduction

Light is detected by an extra retinal photoreceptor and the light signal is transmitted to a biological clock that measures day length using a circadian mechanism (Dawson, 1999; Dawson et al., 2001). Photoperiodic birds do not require the pineal gland nor the eyes for photoperiodic signal transduction (Wilson, 1991). Integrated photoperiodic information from the biological clock is transmitted to neurons synthesizing the neuropeptides, gonadotropin releasing hormone-I (GnRH-I) and vasoactive intestinal polypeptide (VIP), which respectively control the synthesis and secretion of gonadotropins and prolactin from the anterior pituitary gland (Sharp et al., 1998). The anatomical location of the extra retinal photoreceptor and biological clock is unknown, but a substantial body of information is available about the anatomical position of GnRH-I and VIP neurons (Teruyama and Beck, 2000, 2001). Photoperiodic information might be transduced via neural inputs to GnRH-I/VIP neurons at two sites: to their terminals in the median eminence and basal hypothalamus and/or to their cell bodies. It is predicted that neural inputs to terminals stimulate/inhibit GnRH-I/VIP release, while neural inputs to cell bodies stimulate/inhibit GnRH-I/VIP gene transcription.

3 Photoinduced GnRH-I gene transcription and GnRH-I release

The Japanese quail provides a model for determining

whether photoinduced GnRH release is initiated by an increased release from GnRH terminals independently of a change in GnRH gene transcription. The Japanese quail and the domestic chicken are the only photoperiodic birds in which there are assays available to measure GnRH mRNA (Dunn et al., 1996; Dunn and Sharp, 1999; Baines, 2001). When sexually inactive photosensitive Japanese quail are transferred from short to long days, photoinduced GnRH release and LH secretion is initiated 20 h after dawn on the first long day (Perera and Follett, 1992). Increase plasma LH 20 h after dawn is associated with an increase in hypothalamic GnRH mRNA (Baines, 2001), suggesting that photoinduced reproductive function may be initiated by increased GnRH-I gene expression.

However there is also evidence that photoinduced GnRH release in quail is associated with increased neural activity in the median eminence and basal hypothalamus, suggesting that photoinduced GnRH-I release is also controlled at GnRH neuronal terminals (Meddle and Follett, 1997). This conclusion follows from the finding that the increase in LH release 20 h after dawn is preceded by an increase in the visible number of cells with increased fos immunoreactivity in the basal hypothalamus and median eminence. Fos is the protein product of an immediate early gene *cfos*; and Fos immunocytochemistry is widely used by neurobiologists to identify neurons and glial cells showing environmentally induced changes in gene transcriptional activity.

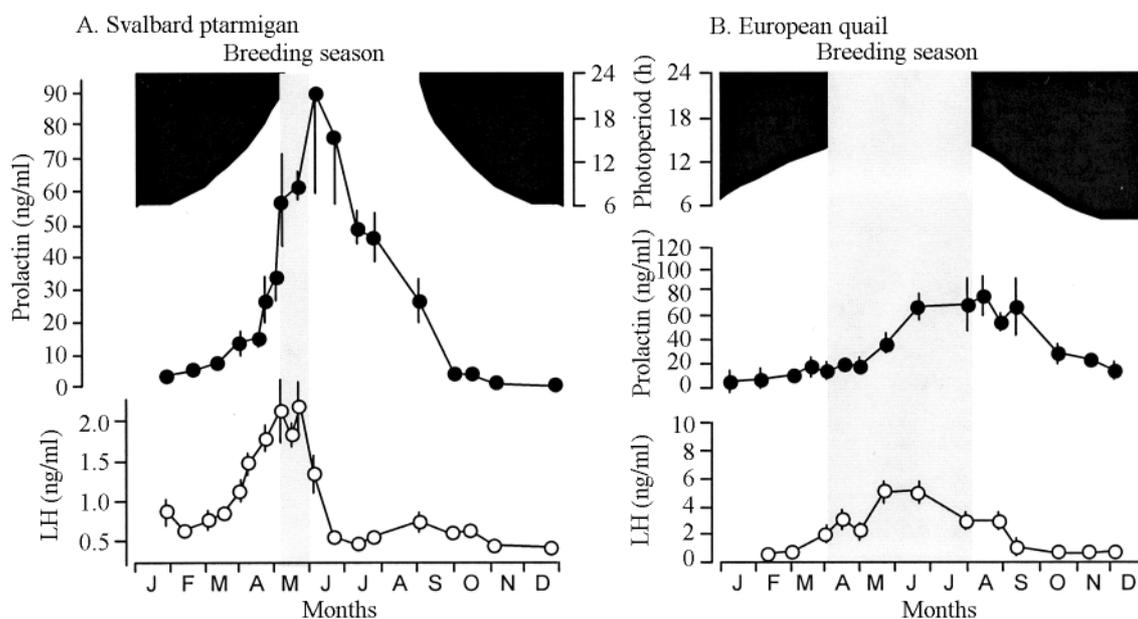


Fig. 1 Changes in concentrations of plasma prolactin and luteinizing hormone (LH) in response to seasonal changes in photoperiod in birds which terminate seasonal breeding by A), the development of absolute photorefractoriness (Svalbard ptarmigan, *Lagopus mutus hyperboreus* breeding at 80°N — data from Stokkan et al., 1988) or by B), the development of relative photorefractoriness (European quail *Coturnix coturnix* breeding at 51°N — data from Boswell et al., 1993, 1995). Observations on Svalbard ptarmigan were made on captive birds exposed to simulated seasonal changes in photoperiod: captive birds came into breeding condition earlier than in free-living birds, which breed in June (Stokkan et al., 1986). Observations on European quail were made on captive birds exposed to natural light: breeding occurred at the same time as in free-living birds (Cramp and Simmons, 1980).

4 Photo-inhibited GnRH-I gene transcription and GnRH-I release during development and maintenance of photorefractoriness

The development of reproductive photorefractoriness is thought to be a consequence of a progressive development of photoinduced inhibitory inputs to GnRH neurons (Parry and Goldsmith, 1993; Sharp, 1996; Dawson, 2001). If the development of photorefractoriness is initiated by an inhibition of GnRH release, it is predicted that photoinduced gonadal regression will be associated with maintained or increased basal hypothalamic GnRH peptide. Alternatively, it is also possible that the development of reproductive photorefractoriness is a consequence of decreased GnRH transcription and GnRH synthesis. If this hypothesis is correct, it is predicted that the onset of photorefractoriness will be preceded by a decrease in hypothalamic peptide and in GnRH mRNA.

The first of these hypotheses has been investigated by measuring changes in the amount of GnRH peptide in the basal hypothalamus in captive male European Starlings during the development of absolute photorefractoriness (Dawson et al., 2002). The development of absolute photorefractoriness, marked by rapid testicular regression after 4–6 weeks exposure to long day lengths, was associated with maintained basal hypothalamic GnRH peptide content. It is therefore concluded that the *initiation* of absolute photorefractoriness is caused by an inhibition of GnRH release. However, the *maintenance* of absolute photorefractoriness after complete testicular regression was associated with a 115-fold decrease in hypothalamic GnRH peptide content (Dawson et al., 2002). The maintenance of absolute photorefractoriness may therefore be a consequence of inhibited GnRH gene transcription. Methodology has not been developed to investigate this inference.

The availability of an assay to measure GnRH mRNA in Japanese quail makes it possible to determine whether the development of relative photorefractoriness in this species is associated with a change in hypothalamic GnRH mRNA. In a study reported by Baines (2001), the amount of GnRH mRNA in the hypothalamus of long term relatively photorefractory quail, in full breeding condition, was significantly lower than in breeding, fully photosensitive birds of the same age. The relatively photorefractory quail had been maintained on 18 h light per day for 67 weeks, while a fully photosensitive subgroup had been created by transferring birds first to 8 h light per day for six weeks to break relative photorefractoriness, and then returning them to 18 h light/day for 3 weeks to recover full breeding condition. No difference was found in the concentrations of plasma LH in the either quail group. This observation suggests that relative photorefractoriness associated with prolonged exposure to long days is maintained by decreased GnRH gene transcription. Further work is needed to confirm whether the development of relative photorefractoriness is

associated with decreased GnRH mRNA.

5 Does prolactin play a role in the development of photorefractoriness?

There may be a causal relationship between the fall in plasma LH and increased plasma prolactin at the end of the breeding season in birds that terminate breeding by developing absolute or relative photorefractoriness (Figs. 1A and B). This hypothesis is consistent with the finding, in the starling, that immunosuppression of photoinduced prolactin release slows the rate of development of reproductive photorefractoriness (Dawson et al., 1998). The decrease in hypothalamic GnRH peptide content following the onset of photoinduced testicular regression is associated with peak values in plasma prolactin (Dawson et al., 2002). Is this association causal? Although no studies have been done in the starling, observations in the Japanese quail suggest that prolactin may depress GnRH neuronal function (Baines, 2001). Hypothalamic GnRH mRNA was significantly depressed in photosensitive Japanese quail injected twice daily for six days with prolactin, compared with vehicle-injected control birds, after transfer from short to long days. This observation suggests that increased plasma prolactin inhibits GnRH gene expression

The decrease in hypothalamic GnRH mRNA in quail treated with prolactin is associated with a decrease in plasma LH (Baines, 2001). This relationship may be causal. However, it could also be that prolactin acts directly at the level of the anterior pituitary gland to inhibit LH synthesis and release. This view is supported by observations *in vitro* using dispersed turkey pituitary cells (You et al., 1995). The addition of GnRH to turkey pituitary cell culture stimulates LH beta mRNA production and LH release. If prolactin is added with GnRH to the culture medium, the stimulatory effects of GnRH on LH beta mRNA and LH secretion are inhibited. Increased plasma prolactin at the end of the breeding season could therefore initiate relative or absolute photorefractoriness by acting through both the hypothalamus and the anterior pituitary gland to suppress GnRH and LH synthesis

6 Mechanisms responsible for relative and absolute photorefractoriness

It has been suggested that relative and absolute photorefractoriness differ in as much as relative refractoriness involves an inhibition of GnRH release without effect on GnRH synthesis and, by implication, GnRH gene expression, whereas absolute refractoriness involves inhibition of both GnRH release and synthesis (Hahn and Ball, 1995; Ball and Hahn, 1997; Dawson et al., 2001). The observation that GnRH mRNA is depressed in long term relatively photorefractory quail is not consistent with this hypothesis (Baines, 2001). A difference between the mechanisms underlying the two types of photorefractoriness may be found in the role of plasma prolactin in suppressing GnRH and LH beta gene expression. Increased plasma prolactin is associated with both develop-

ment and maintenance of relative photorefractoriness, at least in quail, but only with development in absolute photorefractoriness (Figs. 1A and B). Thus it is proposed that relative photorefractoriness is initiated and maintained by increased plasma prolactin, whereas absolute photorefractoriness is only initiated by it.

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S09-5 Gonadotropin-inhibitory hormone in birds: possible modes of action

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Abstract Gonadotropin inhibitory hormone (GnIH) inhibits gonadotropin release *in vitro* in a dose-dependent manner (Tsutsui et al., 2000). In the present study, we investigated the relative neural distributions of GnRH and GnIH, and *in vivo* activity of exogenous GnIH in song sparrows (*Melospiza melodia*) and house sparrows (*Passer domesticus*). Using immunocytochemistry (ICC), GnIH-containing neurons were localized in both species in the paraventricular nucleus, the GnIH-containing fibers emanating from those neurons to multiple brain locations, including the median eminence and brainstem. Double-label ICC with light microscopy and fluorescent ICC with confocal microscopy indicate a high probability of co-localization of GnIH and GnRH (-I and -II) neurons and fibers within the avian brain. Thus, GnIH might be acting at the level of the hypothalamus as well as at the anterior pituitary to regulate gonadotropin release. In an *in vivo* experiment, cGnRH-I alone or a cGnRH-I/GnIH cocktail was injected intravenously into song sparrows. Blood was collected at 2, 5 and 10 minutes post-injection. GnIH rapidly (within 2 minutes) attenuated the GnRH-induced rise in plasma luteinizing hormone. As GnRH-II is involved with regulation of reproductive behaviors, GnIH may play a role in regulating them as well. In sum, GnIH is (1) present in photoperiodic songbird species, (2) has the potential to regulate gonadotropin release at more than one level, and (3) might also be involved in the regulation of reproductive behaviors.

Key words Rfamide function, GnRH, GnIH inhibition, Songbird, Photoperiodism

1 Introduction

The recent discovery of a vertebrate hypothalamic peptide that, in a dose-dependent manner, directly inhibits LH release from cultured pituitary glands *in vitro* has provided the potential for new insights into the regulation of gonadotropin release, and could profoundly enhance our understanding of the mechanistic basis for the timing of reproduction (Tsutsui et al., 2000). This inhibitory peptide, named gonadotropin-inhibitory hormone (GnIH), is a potential direct regulator of gonadotropin release *in vivo*. In this paper, we focus on the distribution and gonadotropin-inhibiting activity of the GnIH protein, establishing its presence in the songbird brain and its distribution relative to chicken gonadotropin-releasing hormone-I and -II (cGnRH-I and -II).

Photoperiodic animals rely on the annual cycle of changing photoperiod to restrict their reproductive activity to the most opportune time of year (Rowan, 1926; Nicholls et al., 1988; Wilson and Donham, 1988; Bronson, 1989; Dawson et al., 2001). In most photoperiodic bird species, changes in reproductive activity are dependent upon, but not directly proportional to, changes in photoperiod. During short photoperiods of winter and early spring, birds are

photosensitive and GnRH is secreted at a low level such that the gonads remain in an immature state, or mature slowly. As photoperiod increases, *photostimulation* occurs, resulting in increased GnRH secretion, full gonadal maturation and breeding. Even though long days continue, however, the breeding season ends abruptly with a profound termination of GnRH release from the hypothalamus, followed by a decrease in synthesis as well (Dawson et al., 1985; Foster et al., 1987; Hahn and Ball, 1995; Reinert and Wilson, 1996; Cho et al., 1998; Deviche et al., 2000). This non-breeding, or “*photorefractory*”, state is caused directly by long photoperiods and, in many species, is maintained indefinitely unless the birds experience a period of short days once again. Thus, long days cause not only reproductive maturation but also regression to a prepubertal state, in sequential order (Bentley et al., 1997). This pattern of puberty and reverse puberty in response to changes in photoperiod is shown in many avian species, including song sparrows, *Melospiza melodia* (Wingfield, 1993).

Based upon research by Tsutsui and co-workers (Tsutsui et al., 2000; Satake et al., 2001), we predicted that, as is the case for GnRH, GnIH is important for the timing of reproduction in all photoperiodic bird species. Thus the aims of the present study were, first, to establish the pres-

ence of GnIH in the brains of species of two families of songbirds (song sparrows, Emberizidae, and house sparrows, Passeridae); secondly, to determine the neuroanatomical relationship of GnIH with GnRH; and, thirdly, if GnIH is present in the brains of song sparrows, to determine whether or not it had gonadotropin-inhibiting capability. The experiment by Tsutsui et al. (2000) demonstrated inhibition of *baseline* LH release from cultured anterior pituitary glands by GnIH. The incubations in that experiment lasted for 100 minutes before medium was collected and gonadotropins measured. If GnIH plays an active role in modulating gonadal growth, or in inhibiting gonadotropin release either during the breeding season (for temporary cessation of breeding as a result of adverse environmental cues), or at the end of the breeding season (to hasten gonadal regression), then it must inhibit LH release *in vivo*. In addition, it must inhibit LH release from *stimulated* pituitary, rather than from the baseline release *in vitro*.

2 Materials and methods

All procedures were performed in accordance with the NIH Guide for the Care and Use of Laboratory Animals, and with the approval of the University of Washington Institutional Animal Care and Use Committee.

2.1 Neuroanatomical distribution of GnIH protein in song sparrows and house sparrows

For immunocytochemistry (ICC), two males and two females of each of song sparrows and house sparrows (*Passer domesticus*) were used. Birds were terminally anesthetized with an intramuscular injection of 7.5 mg sodium pentobarbital, and perfused transcardially with 0.9% heparinized saline (150 IU/10 ml), followed by 4% paraformaldehyde in 0.1 mol/L phosphate buffer-saline, pH 7.4 (PBS). Brains were extracted, post-fixed for 2 hours in the same fixative at 4°C and cryoprotected overnight in PBS containing 30% sucrose. Sagittal or coronal sections (50 µm) were taken throughout the whole brain and collected into PBS. Immunocytochemistry for GnIH was then performed. Sections were washed three times in PBS, background immunoreactivity blocked overnight using 2% normal goat serum (NGS) in 0.2% PBS-T (PBS + Triton X-100), and then incubated in primary antibody (rabbit anti-GnIH) at a concentration of 1:1 000 in 0.4% PBS-T. Three subsequent washes in 0.2% PBS-T were followed by incubation for 1 hour in biotinylated goat anti-rabbit IgG (1:1 000 in 0.2% PBS-T) and another set of washes. Sections were then incubated for 1 h in avidin-biotin complex (ABC; Vectastain Elite Kit, Vector Labs). The resulting complex was visualized using 0.03% 3,3'-diaminobenzidine (DAB) intensified with 0.15% nickel sulfate. Alternately-collected pre-absorption control sections from one brain were processed in the same immunocytochemistry run as the experimental sections. In the only modification to the protocol above, sections were incubated in synthetically-produced GnIH peptide at a concentration of 20 µg/ml concurrently with the primary antibody, instead of primary antibody alone.

2.2 Double-label fluorescence immunocytochemistry and confocal microscopy

House sparrow brain tissue (paraformaldehyde perfused, 40 µm coronal sections) was processed for double-label immunocytochemistry. Immunocytochemistry for GnRH was performed first. The protocol used was similar to the protocol for GnIH ICC above, with the following changes. First, sections were washed, incubated in 0.3% H₂O₂ for 30 minutes, and washed again before background immunoreactivity was blocked with NGS. Secondly, the primary antibody used was rabbit-anti chicken GnRH (HU60H; kindly donated by Dr. H. Urbanski) at a concentration of 1:10 000 in 0.2% PBS-T. This antibody detects cGnRH-I and -II. The secondary antibody used for GnRH was goat anti-rabbit IgG conjugated to the fluorophore, Alexafluor 488 (Molecular Probes, Inc.), and that for GnIH was goat anti-rabbit IgG conjugated to Alexafluor 568. Images were collected using a Biorad MRC 600 confocal microscope, and processed using NIH Image, Image J (NIH) and Adobe Photoshop 6.0.

2.3 *In vivo* demonstration of active and rapid inhibition of LH release by exogenous GnIH

Photorefractory male song sparrows ($n=7$ per group) were used for this experiment. Photorefractory birds were used so that we could control the amount of GnRH given to each bird, thereby eliminating any confounding effects from endogenous GnRH. The pituitary gland of photorefractory birds remains responsive to exogenous GnRH even though little or no endogenous GnRH is released in this reproductive condition (Nicholls et al., 1988; Wingfield et al., 1979). Group I (control) was given an i.v. injection (into the right jugular vein) of 10 ng GnRH in 20 µl physiological saline. Group II (experimental) was given an i.v. injection of a mixture of 10 ng GnRH plus 1000 ng GnIH in 20 µl physiological saline. Blood samples were taken from the alar vein at 2, 5 and 10 min. after injection. This protocol has been used previously to demonstrate rapid gonadotropin-releasing activity of GnRH in songbirds (e.g., Wingfield et al., 1979; Wingfield and Farner, 1993). Plasma was assayed for LH using the homologous chicken LH radioimmunoassay (RIA) (Follett et al., 1972), and validated for songbirds (Dawson and Goldsmith, 1982). Included in the RIA were samples of known LH concentration spiked with 1 000 ng GnIH to check for cross-reactivity with the LH antiserum. No such cross-reactivity was detected in this assay (data not shown). All samples were run in duplicate in a single assay.

2.4 Statistical analysis

Assay data were analyzed by repeated measures analysis of variance (ANOVA), with injection type as a between-subjects factor and time as a within-subjects factor, followed by Fisher's PLSD for *post-hoc* analysis.

3 Results

3.1 Neuroanatomical distribution of GnIH protein in song sparrows and house sparrows

Dense populations of GnIH-ir neurons were found only in the paraventricular nucleus (PVN) of the hypothalamus in all subject birds, regardless of sex or species. These GnIH-ir neurons tend to be bipolar or tripolar (Fig. 1). No GnIH-ir neurons were detected elsewhere in the brain. Furthermore, pre-absorption control sections exhibited no immunoreactivity (Fig. 1F). Thus we are confident that the antibody is specific for the GnIH peptide in songbirds.

In addition to dense immunoreactivity in the population of neurons within the hypothalamus, there are extensive networks of branching beaded fibers emanating from those cells, presumably transporting GnIH. Some of the fibers extend to terminals in the ME, consistent with a role for GnIH in pituitary gonadotropin regulation. In both sparrows, other fibers extend through the brain caudally at least as far as the brainstem and possibly into the spinal cord, consistent with multiple regulatory roles for GnIH.

3.2 Double-label fluorescence immunocytochemistry and confocal microscopy

Confocal microscopy indicates that the cGnRH-I and GnIH proteins are in extremely close proximity to one another, and fibers of each are probably in contact, although electron microscopy and/or tract-tracing will be necessary to determine this conclusively. Close inspection of each area indicates close proximity of GnIH fibers to the cGnRH-I neurons and fibers in the pre-optic area (POA). Presumably these fibers project rostrally from the GnIH neurons in the PVN. The PVN also contains cGnRH-I fibers which pass directly through and in close proximity to the population of GnIH neurons and fibers as they project to the ME. It is apparent that GnIH-ir fibers are also in close proximity to cGnRH-II neurons in the midbrain (data not shown). Pre-

sumably these fibers also emanate from the GnIH-ir neurons in the PVN, but again, this was impossible to discern definitively from the present study. Figure 2 indicates colocalization or extremely close proximity of the cGnRH-I and GnIH peptides in fiber terminals in the ME, with both wavelengths being emitted from the same location. Note the clear separation of immunoreactivity for GnIH and cGnRH-I in fibers dorsal to the ME, where each emits in a separate wavelength.

3.3 *In vivo* demonstration of active and rapid inhibition of LH release by exogenous GnIH

The LH data from the injection experiment are shown in Fig. 3. Analysis of variance indicated a significant interaction of time and injection (ANOVA: $F=7.293(1, 16)$; $P=0.006$), allowing for *post-hoc* analysis to highlight time points at which injections had different effects. At 2 minutes post-injection, birds injected with GnRH alone had higher plasma LH at 2 minutes than at 10 minutes (Fisher's LSD: $P<0.001$). Birds injected with the GnRH/GnIH cocktail also had elevated plasma LH at 2 minutes post-injection (Fisher's LSD: $P<0.05$), but this increase was much attenuated compared to that in the control group (Fisher's LSD: $P<0.05$). The difference in plasma LH concentration between the two groups was no longer evident at 5 minutes and 10 minutes post-injection, by which time plasma LH had returned to baseline values in both groups.

4 Discussion

The aims of the present study were to determine the presence, distribution relative to GnRH, and gonadotropin-inhibiting capability of GnIH in the brains of two sparrow species, both of which are highly photoperiodic. The data

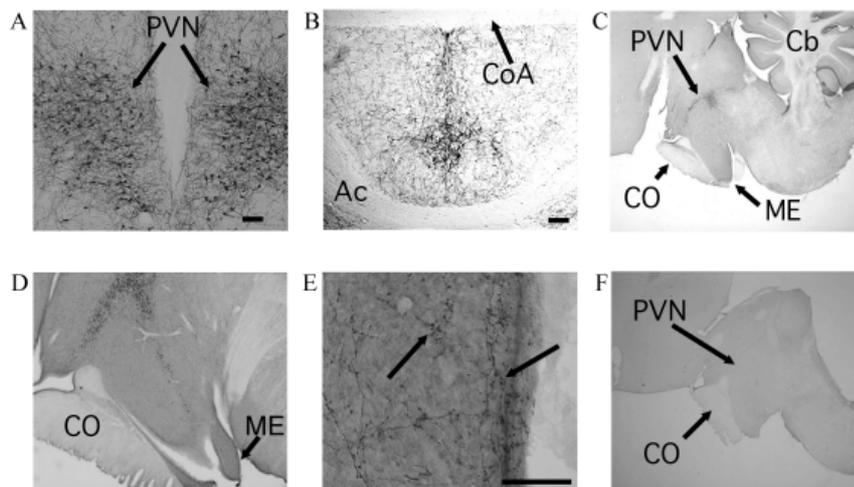


Fig. 1 A. coronal section from male song sparrow brain with dense bilateral populations of GnIH neurons and fibers in the PVN; B. coronal section from male Song Sparrow brain with bilateral population of GnIH neurons and fibers in the caudoventral PVN, extending towards the ME; C. sagittal section from female song sparrow brain with dense GnIH immunoreactivity in the PVN; D. higher magnification of C; E. GnIH fibers and terminal fields in the ME; F. sagittal section from female song sparrow brain with the antiserum preincubated with a saturating concentration of GnIH peptide (preabsorption control)

Acronyms: Cb = cerebellum, CO = optic chiasm, CoA = anterior commissure, ME = median eminence, PVN = paraventricular nucleus. Note the total lack of immunoreactivity in subfigure F. Scale bars, 100 μm .

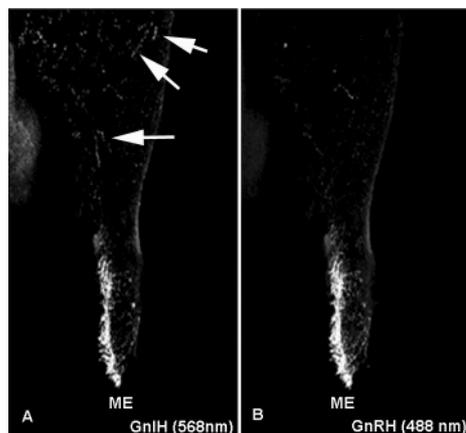


Fig. 2 Separated confocal images of the median eminence of a sparrow brain showing emission of the two fluorophores in different wavelengths

Subfigure A shows emission from the GnIH-ir fibers, and B shows emission from GnRH-ir fibers. The median eminence is visible in both wavelengths, indicating probable co-localization of GnIH and GnRH, or at least extremely close proximity of the two peptides at the terminal fields. Arrows indicate fibers of each peptide that are not co-localized. Images depict the same 0.5 mm plane.

clearly demonstrate that GnIH is present in abundance in the hypothalami of both sparrows. It appears that there are greater numbers of GnIH-immunoreactive neurons in them than in quail hypothalami, although a direct comparison was not performed (but see Tsutsui et al., 2000). It is unclear yet whether the presence of GnIH in the brainstem is unique to sparrow species or songbirds in general, or whether it occurs in non-songbirds as well. The presence of beaded fibers containing, and presumably transporting, GnIH in multiple brain areas is consistent with the likelihood that this dodecapeptide plays multiple roles in the regulation of physiology and behavior, as is the case for GnRH (Millar et al., 1987).

Double-label ICC and confocal microscopy indicate that GnRH and GnIH proteins may be in contact with one another at the level of the hypothalamic neurons, as well as at the fiber level in the hypothalamus, and at the terminal fields in the ME (with the caveat that we have not shown synapses between the two types of neuron and fiber). This observation invokes the question of the mode(s) of action of GnIH. It is as yet unclear how GnIH exerts its effects in terms of receptor binding and downstream processing, or of competition with GnRH for binding sites; nor is it known exactly where GnIH is acting. It may be that GnIH only acts at the level of the anterior pituitary gland (Tsutsui et al., 2000). Alternatively, GnIH could act by inhibiting GnRH release from GnRH fiber terminals in the ME, in addition to acting at the level of the pituitary. The histological data presented here raise the possibility of inhibitory/modulatory action at multiple levels and over different time-frames. In addition, our data indicate that GnIH is likely to act upon cGnRH-II neurons, as identified by their neuroanatomical location and typical “stubby” appearance. In this way, GnIH

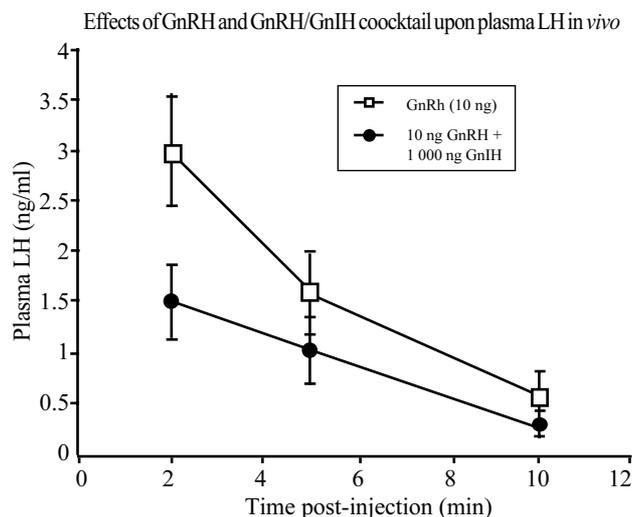


Fig. 3 The effects of intra-jugular injection of GnIH on GnRH-elicited LH release in photorefractory male song sparrows

Note that plasma LH was lower in the GnRH + GnIH group than in the control (GnRH alone) group at 2 minutes post-injection.

has the potential to affect reproductive behavior in addition to gonadotropin release, as exogenous cGnRH-II affects copulation solicitation in estrogen-primed songbirds (Maney et al., 1997).

The results from the injection experiment confirm previous data that GnRH rapidly elicits LH release from the song sparrow pituitary *in vivo* (Wingfield et al., 1979; Wingfield and Farner, 1993). More pertinent to the present study is that the data clearly demonstrate *rapid* (within 2 minutes) reduction by GnIH of this GnRH-elicited LH release. It is possible that in both groups of song sparrows, plasma LH may have increased faster and further than indicated in the first 2 minutes post-injection, but such an effect was not detectable within this experimental paradigm. Even were this to be the case, we would predict that GnIH would attenuate the rise in LH equally as rapidly as GnRH elicits it. The most parsimonious explanation for the rapid attenuation of a GnRH injection-elicited LH rise by GnIH is its action upon the pituitary gland, but this does not negate the possibility of inhibitory action at multiple levels and over different time-frames (see above). Overall, these data confirm the previous *in vitro* demonstration of gonadotropin-inhibitory activity by GnIH (Tsutsui et al., 2000), extending those findings to *in vivo* activity.

It remains to be seen what environmental factors elicit GnIH release in song sparrows and house sparrows, and what the complete range of physiological and behavioral effects of GnIH might be. Data herein indicate potential modulation of activity of the HPG axis, which is primarily under photoperiodic control in these species. The fact that GnIH can affect pituitary gonadotropin release *in vitro* and *in vivo* suggests that at least one function of GnIH might be rapid-time regulation of gonadotropin release within the broader time-frame of the breeding season. In other words, GnIH might act to fine-tune the timing of onset of breeding.

One might envisage increased GnIH release during periods of stress (induced, e.g., by inclement weather), whereby birds could temporarily cease reproductive activity without complete regression of the reproductive system. Moreover, action of GnIH in multiple areas of the brain might allow for direct regulation of reproductive behaviors in response to environmental cues/stressors. GnIH might well also act within a longer time-frame. It is possible that GnIH content and release is regulated seasonally within the photoperiodic system. If this is the case, then GnIH may play a primary role in timing the annual reproductive cycle in songbirds, specifically in terminating the breeding season (photorefractoriness).

In summary, the data present the first demonstration of the presence of GnIH in the brains of two families of songbirds, and its potential for regulating GnRH at multiple levels. This finding builds upon growing evidence of the importance of RFamide peptides in regulatory functions within the vertebrate brain. Even though the discovery of a gonadotropin antagonist is in itself significant to reproductive biology (Tsutsui et al., 2000), the action of RFamide peptides appears not to be limited to neuroendocrine activity.

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Symposium 10 Demographic responses to habitat fragmentation: contrasts across space and time

Introduction

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Among anthropogenic forces pressing in on the natural world of birds, none has had more drastic effects than the loss and fragmentation of habitat. This symposium steps beyond first-order descriptions of avian occurrence and abundance to examine underlying demographic responses to fragmentation, bringing together research that examines survivorship, reproductive success and/or dispersal across the globe. The first four papers addressed issues arising out of fragmentation in Southeast Asia, the tropics of Africa and South America, boreal Europe and the temperate northern hemisphere. Navjot Sohdi took a broad-brush, experimental approach to determining the effects of rainforest fragmentation and disturbance on the demographics of Southeast Asian birds. Harri Hakkarainen and co-workers (oral presentation only) focused on the effects of boreal forest fragmentation on sex ratios in the creeper *Certhia familiaris*, finding that quality of habitat and its fragmentation by changes in habitat structure biased sexes in reared broods; males suffered more than females from perturbation. Luc Lens and Erik Matthysen (oral presentation only) examined variation in survival, estimated from individual mark-recapture histories, across seven Kenyan forest species

(*Zosterops sylvanus*, *Turdus belleri*, *Andropadus milanjensis*, *Phyllastrephus cabanisi*, *Pogonocichla stellata*, *Phylloscopus ruficapillus* and *Nectarinia olivacea*) that differ in their ability to disperse between isolated forest fragments. Abstracts of the two oral papers are published in the Abstract Volume of the Congress.

Shelley Hinsley and co-workers compared the consequences of habitat fragmentation for woodland birds between Europe and North America. They found that habitat fragmentation may reduce habitat quality due to changes in bird community structure, a lack of resources and increased exposure to poor conditions, resulting in reduced breeding success, increased costs of rearing young, delayed molt and reduced survival. In the concluding paper, Mikko Mönkkönen and co-workers considered demographic responses to habitat fragmentation across space and time. The underlying conclusion to be drawn from their review is that it is the population, rather than species or individual, which is affected demographically by changes in landscape and community structure arising from fragmentation, and thus focal in determining conservation strategies and resolving species management.

S10-1 Effects of rainforest fragmentation and disturbance on the demographics of Southeast Asian birds

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Abstract Southeast Asia is currently subject to one of the highest rates of deforestation in the world. The consequences are poorly understood. Accordingly, I review my recent work on the effects of forest fragmentation and disturbance on the demography of Southeast Asian birds. Studies using indirect demographic measures (age structure, sex ratio, recapture rates, presence of ectoparasites and fault bars) found that such variables did not differ among monitored populations in intact and fragmented/secondary forests. However, more individuals had fault bars in forest fragments and more recaptures were recorded in intact continuous forest. Artificial nest predation experiments showed that bird populations in primary forests generally suffered less from depredation than those in secondary forests. Overall, information available on the demographics of Southeast Asian forest birds remains poor; yet it is vital for enhancing knowledge of regional avian ecology and effective regional conservation.

Key words Body condition, Conservation, Habitat fragmentation, Mist-netting, Parasitism, Reproductive success

1 Introduction

Deforestation of Southeast Asian rainforests has reached unprecedented levels with an estimated 1% of forests cleared annually (Achard et al., 2002). Because of it, most tropical rainforests now survive in small patches (remnants or fragments) or as disturbed forest (e.g., secondary forest). As a result, a considerable number of endemic bird species are threatened with extinction (Casteletta et al., 2000). Now more than ever, monitoring of birds in the remaining rainforests is urgently needed so that plans can be devised to preserve them. Additionally, documentation of reduced avian diversity and abundance in remnant and disturbed forests is crucial for arguing for the protection of large undisturbed tracts of forest. Towards providing this information, I review here my current work on the effects of forest fragmentation and disturbance on the demography of the Southeast Asian avifauna.

2 Materials and methods

2.1 Mist-netting

Because tropical birds are generally long-lived, relatively precise demographic data can be obtained by monitoring marked individuals over several years. In Southeast Asia, however, such data are often difficult to collect because study sites can be logged before the completion of a study. For breeding data, moreover, nests are particularly difficult to find in rainforests because of the ease of concealment; and birds may breed throughout the year, making statistically interpretable data difficult to collect.

Due to such constraints, I resorted to collecting data on body condition, age structure, sex ratio and recapture frequency from mist-netting instead, based on the assumption that these parameters would be indicative of avian reproductive success and survival. I also collected data on various surrogates for body condition (e.g., parasite load). Two forest fragments in Singapore were sampled and the data compared with those from two intact primary forests in Sarawak on Borneo. The two fragments in Singapore, Nee Soon and MacRitchie forests, are located in the central water catchment area (1°22'N, 103°48'E; Fig. 1), and cover 937 and 483 ha, respectively. The two continuous forests in Sarawak, the Matang Wildlife Sanctuary (hereafter Matang; 1°48'N, 110°00'E) and Gunung Gading National Park (hereafter Gading; 1°48'N, 109°52'E) cover 2 230 and 4 196 ha, respectively (Fig. 1). Because they are in the same biogeographic region (Greater Sundas), both Singapore and Sarawak harbor similar forest types and bird communities.

In all four sites, I conducted mist-netting between March and November 1998. The total net-hours were 1 442, 1 413, 1 566 and 1 661 in Nee Soon, MacRitchie, Matang and Gading, respectively. All captured individuals were identified, measured, banded and released. Captured individuals were sexed by plumage coloration where possible, aged at < 1 or > 1 year based on skull pneumatization, and weighed. A bird was considered recaptured if it was caught again during any of the subsequent mist-netting sessions excluding those within the same month. I determined the presence of ectoparasites (chewing lice, suborder Mallophaga) by carefully examining the right wing against

sunlight. Parasitic prevalence is predicted to be high in lower quality habitats (Sodhi, 1995). The presence of fault bars was determined by carefully examining the tail against sunlight. Fault bars are thought to result from nutritional stress during feather growth, and are considered reliable indicators of body condition (Steeger and Ydenberg, 1993). Only resident bird species were recorded and compared. Comparisons were usually made at the community/population level (e.g., for sex ratio), but when sample sizes permitted, variables were compared across three particular species: little spiderhunter (*Arachnothera longirostra*), short-tailed babbler (*Malaccocincla malaccensis*) and chestnut-winged babbler (*Stachyris erythroptera*). Further details of the study sites and methods are given in Sodhi (2002a).

In Java, I gathered further data in Linggoasri (109°30'E, 7°00'S), which is located in the Dieng mountains (Fig. 1). The total area of continuous forest in the Dieng Mountains covers 25 500 ha, and is one of the last remaining lowland rainforests in Java. The four monitoring sites comprised (1) a selectively-logged tract of primary lowland/submontane forest at least 80 years old, 30% of which had been logged illegally, (2) two young secondary lowland forests clear cut in 1998, and (3) a pine (*Pinus merkusii*) plantation planted in 1952. Mist-netting was carried out at all sites between April and July 2001. Total net-hours were 825, 900, 941 and 770 in the primary, two secondary and pine forest sites, respectively. The same variables were recorded as in the Singapore and Sarawak programs.

2.2 Artificial nest predation experiments

Because actual predation events are difficult to observe, I used artificial nest experiments to compare predation pressure among sites. Artificial nest predation experiments were conducted in August 1996 in five forest fragments in Singapore state. Two sites were in primary forest, two in secondary forest, and the fifth was located in an abandoned rubber (*Hevea brasiliensis*) plantation. In an experiment to screen ground-nest predation, one chicken

(*Gallus gallus*) egg and one plasticine egg were placed together at each station. The eggs were simply placed on the open ground without any attempt to create an artificial nest. Experimental nest stations were checked on day 8. Nests were considered attacked on if an egg was missing, or if the chicken egg was cracked, pecked or smashed, or if the plasticine egg showed bite-marks. More details of this procedure can be found in Wong et al. (1998).

Because nest placement can affect predation (Yahner and Scott, 1988), I conducted additional experiments in Singapore in May and June 2000. These were carried out in two tracts of primary forest, two of secondary forest and two of woodland (abandoned rubber plantations). The egg of one Japanese Quail (*Coturnix japonicus*) and one plasticine egg were placed together in an artificial cup nest (15 cm in diameter × 5 cm high) secured by wire fasteners in shrubs or trees at a height of 1 m. In June 2001, I conducted similar experiments in Linggoasri, Java. There artificial arboreal nests were placed in a primary forest, a young secondary forest and a pine plantation. All artificial nests were checked after eight and four days in Singapore and Java, respectively.

Previously, Cooper and Francis (1998) performed artificial nest predation experiments in Pasoh, Peninsular Malaysia (2°58'N, 102°17'E). They placed experimental ground nests containing two quail eggs in the interior of unlogged and logged forest and on the edges. Their stations were checked on days 2 and 5.

3 Results

3.1 Fragments (Singapore) versus continuous forest (Sarawak)

For all species combined, bird recaptures were at least 18% higher in Gading than in other sites ($\chi^2 = 8.35$, $df = 3$, $P = 0.04$). However, for the little spiderhunter ($\chi^2 = 9.7$, $df = 2$, $P = 0.008$) and short-tailed babbler ($\chi^2 = 6.75$, $df = 2$, $P = 0.03$), recaptures were still higher by 24% and 34% respectively in MacRitchie and Gading. Neither the proportion of adults nor sex ratios differed among sites ($P > 0.11$), either for all species combined or individual species. Similarly, body mass of the little spiderhunter and short-tailed babbler did not differ among the sites ($P > 0.06$). However, chestnut-winged babblers were 1 g heavier, on average, in Nee Soon than MacRitchie (Mann-Whitney $U = 21$, $df = 8$, 14 , $P = 0.02$). For all species combined, the load of ectoparasites did not differ among sites. At least 39% more short-tailed babblers carried parasites in Nee Soon than in other forests ($\chi^2 = 7.73$, $df = 2$, $P = 0.02$). However, 55% more chestnut-winged babblers were parasitized in MacRitchie than in Nee Soon ($\chi^2 = 7.49$, $df = 1$, $P = 0.006$). Overall, at least 15% more individuals had fault bars in MacRitchie than other forests. Similarly, at least 40% and 52% more little spiderhunters and short-tailed babblers, respectively, had fault bars in MacRitchie than in other forests ($P < 0.01$). For sample sizes and further comparative details, see Sodhi

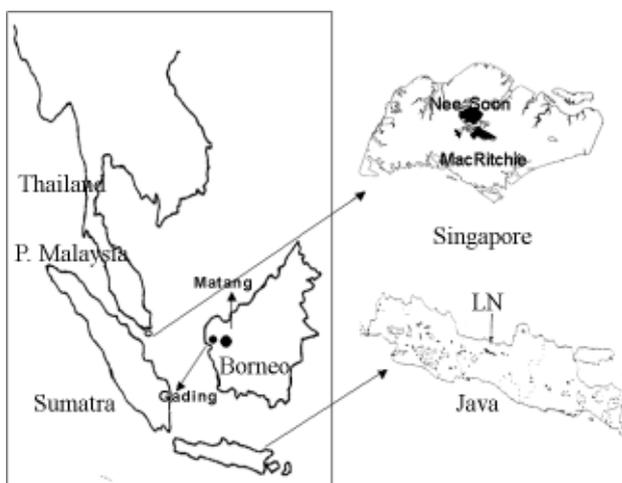


Fig. 1 Map of Southeast Asia showing the study sites
LN = Linggoasri.

(2002a).

3.2 Forests of central Java (disturbed versus undisturbed)

Because very few individuals were captured in the pine plantation, only the results for the primary and two secondary forest sites are compared here. Little spiderhunters were recaptured at least 12% more times in primary than the secondary forests ($n \geq 6$); and at least 17% more adult little spiderhunters were recorded in primary forest ($n \geq 6$). However, these and other differences were not statistically significant ($P > 0.05$).

3.3 Artificial nest predation

In Singapore, 80% of 328 set ground nests were predated, but one primary forest site suffered at least 12% less predation than other fragments ($P = 0.01$). Sixty-two percent of the arboreal nests ($n = 110$) were depredated. However, there was no difference in predation among forest types ($\chi^2 = 3.12$, $df = 5$, $P = 0.68$). In Java, only 10% of 105 set arboreal nests were predated. Predation was 20% less in primary forest than secondary forest sites. However, the same proportion (3%) of nests was predated in primary and pine forests. After five days in Pasoh, Cooper and Francis (1998) recorded that at least one more nest had survived within unlogged forest than in logged forest interior and forest edge.

4 Discussion

For all the species combined, as well as the short-tailed babbler, Gading produced the highest recapture rates. It is possible that higher recaptures in the larger forest tract imply low mortality or greater site fidelity, but they can also be affected by resource distribution. Chestnut-winged babblers were heavier in Nee Soon and carried a low parasitic load there. Body mass has been shown to be negatively correlated with parasitism in birds (Paperna and Smallridge, 2002). However, such a relationship was not apparent for the other species. This suggests that species may differ in how body mass affects their susceptibility to parasitism. The highest occurrence of fault bars in MacRitchie may indicate that the bird community there was more resource-limited than elsewhere; it is possible that habitat quality was poorer, at least for some bird species. One possible factor depressing habitat quality for birds in MacRitchie could have been high anthropogenic disturbance from army and other exercises.

As for Singapore and Sarawak sites, more recaptures were recorded in the primary forest tract on Java, and this forest contained more adult little spiderhunters too. These differences, however, were not statistically significant, probably due to small sample sizes. They do suggest, nevertheless, that habitat quality in primary forest is higher, a likelihood supported by lower predation of artificial nests there than in at least one of the secondary forests.

Artificial nests, both ground and arboreal, experienced

heavy predation pressure in Singapore. Singapore has been severely deforested, with less than 5% of the native forest cover remaining. In this heavily developed island, forest birds suffer because of infiltration of nonnative generalized predators (e.g., feral cats, *Felis catus*) from surrounding suburbia. Other small predatory mammals, e.g., squirrels, are also often in high numbers in forest fragments due to the loss of mesopredators. It is not surprising then that at least one of the primary forest sites suffered less ground nest predation than those in secondary and plantation forests. Similarly in Pasoh and Java, nest predation in more pristine forest was lower. Although the artificial nest experiments may not realistically reflect natural nest predation rates (Haskell, 1995), they nonetheless indicate here that less disturbed sites suffer less nest loss than more disturbed sites.

I conclude by repeating that information on the ecology of Southeast Asian forest birds is poor (Sodhi, 2002b). More data on their demographics are needed to enhance ecological understanding and to understand and predict the effects of heavy deforestation.

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S10-4 Consequences of habitat fragmentation for birds: comparison between Europe and North America

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Abstract Much semi-natural habitat in Europe and North America now exists as small patches in landscapes dominated by agriculture, industry or urban sprawl. European landscapes, such as in eastern England, have existed in this state for a much longer period of time (> 1 000 yrs) than landscapes in the central United States (< 200 years). We compare the population and community responses of birds in small woodland patches in agricultural landscapes in eastern England and central US (Ohio), focusing on the family Paridae. In both England and the US, decreased reproductive success in small woods was observed, but differing causal mechanisms may be involved. Decreased food supply and increased foraging costs due to greater travel distances between patches may result in chick loss, reduced fledging weights and, therefore, reduced recruitment in England. The main cause of low reproductive success in our study in the US, however, was interspecific nest-site competition in relation to wood patch structure. Parental time and energy budgets may also be adversely affected by increased exposure to poor weather conditions in small woods. Birds in small English woods bred later than pairs in large woods, possibly due to microclimatic effects on vegetation development and invertebrate availability. Molting and breeding are both energetically costly and are usually separated in time; therefore, late breeding is followed by late molting. Late molting is associated with lower overwinter survival and subsequent breeding success, which may result from poorer plumage quality in late-molting birds. In the US, lower survival rates were also detected in small woods, especially those without supplemental food. These locations also contained birds with narrower feather growth bars, indicating lower nutritional condition. Habitat fragmentation may therefore reduce habitat quality due to changes in bird community structure, a lack of resources and increased exposure to stressful conditions, resulting in reduced breeding success, increased costs of rearing young, late molting and reduced survival. Our results suggest that there are generalities to be drawn in landscapes where habitat patches are small, despite differences in time since fragmentation.

Key words Feather quality, Habitat fragmentation, Reproductive success, Survival, Woodland birds

1 Introduction

The consequences of habitat fragmentation for the persistence of native species (e.g., Fahrig, 2002) and for current worldwide declines in biodiversity (Heywood, 1995) are the focus of much current concern. A neglected aspect of this phenomenon is the extent to which organisms may have adapted evolutionarily to habitat fragmentation. Due to such adaptation, one might expect that negative effects associated with fragmentation should decrease with time since fragmentation. Accordingly, we compare responses to forest fragmentation by one group of woodland birds, family Paridae, in midwestern USA (Ohio) and eastern England (Cambridgeshire). Today landscapes in these regions resemble one another with their islands of woodlands in a matrix of row-crop agricultural land, yet those in Europe have been fragmented for over 1 000 years longer (Rackham, 1986). The comparative studies herein were conducted without recourse to common methodology, so close comparisons of the same variables measured in the same way are not possible. Instead, we probe more diffusely for findings

that might suggest increased adaptation to fragmentation, as evidenced by greater reproductive success and survival among the parids of England than in Ohio. Both sites are the scenes of continuing long-term demographic studies of parids and other species, from 1990 in Cambridgeshire and from 1995 in Ohio.

2 Methods

In Cambridgeshire, reproductive success in great (*Parus major*) and blue (*P. caeruleus*) tits has been studied since 1993 using nest boxes (total *c* 170) located in up to 45 woods of different sizes (0.1–157 ha). Boxes are checked at approximately weekly intervals; the components of breeding success recorded are given in Table 1. Relationships between these variables and woodland area were investigated using mixed linear models incorporating both fixed and random effects. Only data from first broods and first breeding attempts were used. Full details are given in Hinsley et al. (1999).

To measure survival, turnover of individual breeding

Table 1 Breeding performance of great and blue tits in a 1-ha woodland compared to that in a 150-ha woodland

Variable	Great tit	Blue tit
Timing of laying (1st egg date)	7 days later	8 days later
Clutch size	same	same
Number of young at 11 days	-1.2	-1.8
Mean mass of young, g	-1.4	same
Total mass of young, g	-30.0	-22.5
Number fledged	-1.4	-2.4

The difference due to woodland area was estimated from linear mixed models based on tit performance in 5 breeding seasons (1993 to 1997) in Cambridgeshire, England. Mass of nestlings was measured at day 11 post-hatching (Hinsley et al., 1999).

birds in a maximum of 16 small woods (0.51 ± 0.27 ha) was estimated for several species from color-banding (Table 2). All adult breeders of the target species were color-banded each year and their presence/absence noted in subsequent years. Full details are given in Hinsley et al. (1994).

To compare the timing of molt in large and small woods, post-nuptial primary molt scores of great and blue tits were recorded as a matter of routine during various aspects of the long-term study. Molt scores were recorded by the standard procedure of the British Trust for Ornithology (Ginn and Melville, 1983). Full details are given in Hinsley et al. (2003).

To assess feather quality, the effects of molt rate were investigated by increasing its speed in an experimental group of European starlings (*Sturnus vulgaris*) in comparison with a control group which molted more slowly. Rate of molt is increased by shortening photoperiods, and thus different rates were achieved by exposing the groups to either long (slow molt) or shortening (fast molt) days. The characteristics of resulting primary feathers are shown in Table 3. Full details are given in Dawson et al. (2000). Details of the study area can be found in Hinsley et al. (1995).

3 Results

3.1 Reproductive success

Between 1993 and 2002, great and blue tits in England bred earlier and fledged more young in large (27–157 ha) than in small (0.1–1.1 ha) woodland patches. Furthermore, great tits in small woods reared lighter young. These differ-

ences are highlighted in a comparison between production in 1 ha and 150 ha woodlots that was based on the models of trends in components of breeding success/woodland area for the years 1993 to 1997 (Hinsley et al., 1999; Table 1).

In Carolina chickadees (*Poecile carolinensis*) in Ohio, the probability of a nest fledging successfully was a positive logistic function of woodlot size, with an inflection point at 6.8 ha. In woodlots of < 6.8 ha and > 6.8 ha, respectively, 30% and 72% of nests fledged successfully. A manipulative experiment demonstrated that chickadee reproductive success was lower near a woodland edge and, furthermore, that chickadees preferred to nest in woodlot interiors when given a choice (Doherty and Grubb, 2002a). As the edge-to-interior ratio is greater in small than in large woodlots, the increased nest failure near edges could have accounted for the difference in nest success in small and large woodlots. The cause of chickadee nest failure came predominantly from nest site competition with house wrens (*Troglodytes aedon*), a well-known forest-edge species.

3.2 Survival

In England, individuals of several songbird species disappeared from small (0.51 ± 0.27 ha) woodlands at a rate considerably higher than mortality rates reported in the literature (Hinsley et al., 1994; Table 2). While the divergence from published rates was not extreme in the two species of tits, winter wrens (*Troglodytes troglodytes*), European robins (*Erithacus rubecula*), and chaffinches (*Fringilla coelebs*) underwent almost complete annual turnover in the study plots, a far higher rate than previously reported. Turnover rates in color-marked

Table 2 Percentage loss of banded birds between 1990 and 1991 from small woodlots in Cambridgeshire, England, compared to published mortality estimates (Hinsley et al., 1994)

Species (<i>n</i> = number of woodlots)	% loss in small woodlots	Published annual mortality estimates
great tit (<i>n</i> = 16)	67	50 ¹
blue tit (<i>n</i> = 14)	58	70 ¹
winter wren (<i>n</i> = 16)	96	63 ²
European robin (<i>n</i> = 15)	95	62 ³
chaffinch (<i>n</i> = 13)	85	33 ⁴

¹ Perrins (1979); ² Hawthorn and Mead (1975); ³ Lack (1965); ⁴ Newton (1972).

Table 3 Quality of primary feathers of European starlings in relation to rate of molt measured experimentally in Cambridgeshire, England

Parameter	Fast molt	Slow molt
Duration of molt (days)	73	103
7th primary, fresh mass (mg)	51.7	55.6
9th primary, mass after 9 months' wear (mg)	57.2	71.1
Rachis keratin hardness (kg/mm ²)	10.0	12.3
Deflection under standard load (mm)	16.7	13.2
8th primary, Young's modulus (Gpa)	2.6	2.3

Rate of molt was manipulated by exposing birds to different photoperiods (constant long days = slow molt; shortening days = fast molt, from Dawson et al., 2000).

birds were up to 167% greater than estimates of species presence/absence based on an annual census of breeding birds. In other words, although all species were present in the second year, nearly all the individuals were new birds.

In Ohio, annual survival of adult chickadees across a sample of 47 woodlots varied from about 40% in very small woodlots with no supplemental food to about 65% in large woodlots that contained supplemental food in the form of permanent bird feeders (Fig. 1). Similar trends were recorded in the tufted titmouse (*Baeolophus bicolor*), white-breasted nuthatch (*Sitta carolinensis*) and downy woodpecker (*Picoides pubescens*) (Doherty and Grubb, 2002b). The importance of adequate winter nutrition and shelter was further emphasized by the finding that rate of energy expenditure in free-ranging chickadees was greater in winter than during breeding (Doherty et al., 2001).

3.3 Timing of molt and feather quality

Analysis of molt scores from great and blue tits showed that, on average, molt was delayed by about 8 days in small woods compared to large woods (Hinsley et al., 2003). This matched differences found in timing of breeding

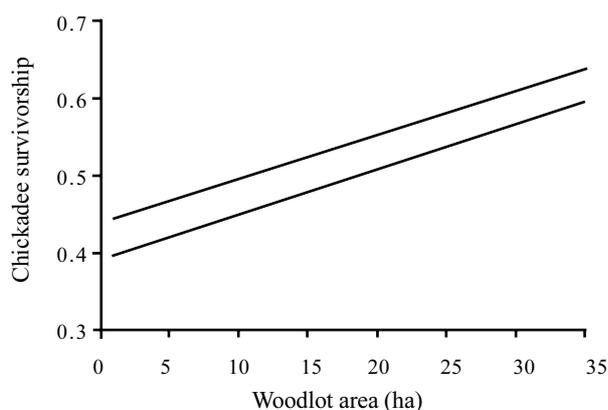


Fig. 1 The calculated relationship between woodlot size and annual survivorship of adult Carolina chickadees in an agriculture landscape in Ohio, USA

The upper and lower curves, respectively, indicate survival in woodlots with and without supplemental food in the form of winter-long bird feeders (Doherty and Grubb, 2002b).

(Table 1). Although we have no information about the effects of timing of molt on tit feather quality, later-molting starlings showed a reduction in quality as a result of molting faster. Faster-grown primary feathers had less mass, were composed of softer keratin, were more prone to wear and were more flexible (Dawson et al., 2000, Table 3). However, Young's modulus, which depends on the structure of feather keratin (Bonser and Purslow, 1995), did not vary with rate of molt, suggesting that the measured differences were due simply to a shortage of keratin in the faster-grown feathers.

4 Discussion

In both Cambridgeshire, England and in Ohio, reduced reproductive success was found in small woodlots. Possible causes include diminished food supply, increased foraging costs, especially if birds incur increased travel costs from foraging in more than one woodlot (Hinsley, 2000), and, in Ohio, interspecific nest-site competition. Nest-site competition was not a significant factor in England, but nest losses due to predation were more common in larger woodlots. This was probably because predators such as the grey squirrel (*Sciurus carolinensis*), which is also affected by fragmentation (e.g., Fitzgibbon, 1993), were less common in small woodlots and/or because nestboxes were too few to create an active search response. Thus, nest failure in relation to woodlot size is more complex than the often assumed scenario of greater losses in smaller patches due primarily to predation (also Friesen et al., 1999; Huhta et al., 1998).

In both England and Ohio, low survival (indexed by lower persistence) was recorded in small woodlots. One possible cause may be the increased exposure to cold and windy winter weather in smaller woodlots, and hence increased energy expenditure (Doherty et al., 2001). Birds in small English woods bred and molted later than those in large woodlots. Molting later after the summer solstice exposes birds to shorter days and hence they molt faster (Morton and Morton, 1990). As demonstrated for starlings, faster molting can reduce feather quality (Dawson et al., 2000). Although we did not investigate the thermoregula-

tory ability of European starlings in relation to rate of molt, work by Nilsson and Svensson (1996) showed that late breeding (and hence presumably, late molting) blue tits had higher thermoregulatory costs in winter than earlier breeders, and suffered higher overwinter mortality.

In Ohio, birds in small woodlots without supplemental food had the lowest survival rates. In winter, this same category of birds also grew induced feathers with the narrowest growth bars, indicating poor nutritional condition (Grubb, 1995). Such reduced nutritional condition may have resulted from food shortage coupled with high winter metabolic rates. Hence slow feather growth-rates in small woodlots may result from nutritional/energetic constraints.

In conclusion, our data from the two continents indicate that, despite differences in time since fragmentation, there are some generalities to be drawn in landscapes where habitat patches are small. We found no evidence for adaptation to fragmentation, judged by the recorded declines in breeding success with woodlot size in both studies. Survival in Ohio chickadees was influenced by supplemental food in relation to woodlot size, and it is likely that such an effect also operates in England. Up to 75% of householders there provide some food for birds in their gardens, and blue and great tits are recorded at nearly 100% of feeders monitored by the BTO Garden Bird Feeding Survey (Glue, 2002). Causes for the deleterious effects of fragmentation may differ in detail, but in general, lack of resources (especially food) and exposure to inclement weather are basic elements. We anticipate tightening future comparisons by coordinating our methodologies.

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S10-5 Demographic responses to habitat fragmentation

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Abstract Destruction of natural habitats involves two different, commonly simultaneous changes in the landscape: habitat loss and habitat fragmentation. Fragmentation effects can compound the negative effects of habitat loss on bird populations. We provide an analytic overview of numerical and demographic responses in bird populations to habitat fragmentation. We also survey measurements that can be taken from populations to help reveal key mechanisms behind bird responses to habitat fragmentation. We conclude that studies on demographic responses of birds to habitat fragmentation would be more effective if based on measures that are selected beforehand to distinguish among mechanisms and which can be taken with ease. Finally, we review relevant literature to evaluate what has been measured. Nesting success is the most frequently taken measurement, reflecting the recent emphasis on nest predation and parasitism in fragmentation studies. In contrast, we found no study where the relationship between population sex ratio and habitat fragmentation has been examined. Far-reaching conclusions cannot yet be made because of publication bias and nonrandom selection of species and landscapes for studies.

Key words Fecundity, Nest success, Patch size effect, Reproductive output, Survival

1 Introduction

Recent rates of extinction of known animal and plant species, from diverse environments in diverse regions, are 100 to 1000 times greater than their prehuman levels. The prime reasons for this decline are indisputably anthropogenic (Pimm et al., 1995), in which habitat loss and fragmentation are preeminent factors (Rappole, 1996).

Destruction of natural habitat involves two different, generally simultaneous changes in the landscape. One, and perhaps the more important, is the loss of original habitat via proliferation of disturbed and man-made environments (Pimm et al., 1995; Schmiegelow and Mönkkönen, 2002). The other, which invariably accompanies habitat loss, is the decrease in patch size of habitat remnants. Patch size reduction translates into increased exposure at patch edges and increasing levels of patch isolation (Andrén, 1994).

It is important to distinguish between the effects of pure habitat loss and fragmentation. When habitat is lost from the landscape, the individuals inhabiting it are lost too, resulting in population declines. In circumstances of habitat loss alone, without fragmentation effects, there is a linear relationship between the number of individuals and the area of habitat, so that the density of individuals per unit area remains constant. Fragmentation effects (patch size reduction and isolation) can exacerbate the effects of pure habitat loss, potentially producing even greater population declines (Andrén, 1994; Bender et al., 1998). This may ultimately result in population extinction even if suitable habitat still remains. Major declines in species richness

follow, at least in tropical (Gascon and Lovejoy, 1998) and temperate (Donovan and Flather, 2002) regions.

We have indirect evidence on numerical responses of birds to habitat fragmentation through numerous studies of patch size effects, all of which point to reduced density in small patches. Bender et al. (1998) and Connor et al. (2000) reviewed such studies, the former concluding that patch size effects were strongly negative for bird species associated with habitat edge (decreased densities with increasing patch size), but strongly positive for bird species specialized to habitat interiors (increased densities with increasing patch size). This indicates that for interior species, declines in population size resulting from habitat fragmentation will be greater than predicted from simple habitat loss alone. Several studies have also shown that avian numerical responses to patch size effects are sensitive to landscape context, i.e., the type of disturbed habitat in which patches of original habitat are embedded (Mönkkönen and Reunanen, 1999; Norton et al., 2000; Ricketts, 2000).

Despite wide knowledge of the numerical effects of habitat loss and fragmentation on bird populations, our understanding of the mechanisms causing these responses is far more limited. Proper understanding of such mechanisms is crucial because only then can we start taking effective steps to remedy the negative effects of fragmentation. In this paper, we provide a flowchart linking landscape changes to demographic and numerical responses. We then proceed with an analytic survey of the measurements that can be taken from populations to help reveal key mechanisms behind responses to habitat fragmentation. Finally, we review

the existing literature to evaluate what has been measured.

2 From habitat fragmentation to demographic effects to abundance patterns

We address here true fragmentation effects, i.e., changes in bird populations resulting from patch size, patch isolation and patch-edge effects. We do this because habitat loss alone does not result in changes in the demographic parameters of populations. Accordingly, we focus on three different demographic components: (i) annual survival rate, (ii) fecundity (or clutch size), covering total investment by a female or a pair in the clutch during one breeding attempt, and (iii) reproductive output or nesting success, i.e., the rate or probability with which fecundity is transformed into independent offspring.

Mechanisms affecting these components fall into three categories. First, predation upon adult birds and their offspring (nest predation) may have a strong impact on population demography, particularly annual survival and nesting success. Several studies have shown that landscape change can result in dramatic changes in predator species assemblages, overall density of predators and predation pressure on birds and their nests (Andrén, 1992, 1995; Bayne et al., 1997). Secondly, habitat fragmentation may in many ways affect the availability of critical resources such as food. According to the “resource concentration hypothesis” (Root, 1973), there is a greater concentration of critical resources in larger habitat patches, resulting in higher population densities of consumers. Thirdly, fragmentation may disrupt functional connectivity in the landscape, causing problems for dispersal and movement. For example, some patches in the landscape may become unreachable if too isolated from other patches, thereby lowering the chances of meeting and pairing success (Cooper and Walters, 2002).

We argue that avian numerical responses to fragmentation stem mostly from the above demographic components. If survival, fecundity and/or nesting success

are negatively affected by fragmentation, population size will certainly decline more than would be expected from habitat loss alone. Numerical responses may also result from demographic effects anticipated by birds themselves, for example in cases where they respond adaptively to landscape changes by deserting small habitat patches. It is important to distinguish between population-level and individual-level mechanisms here, even though their effects are commonly parallel (Andrén, 1994). Individual responses can be seen as proximate processes, while population responses are ultimate and more directly linked to population persistence.

3 Measurements and mechanisms

There are several alternative ways, both direct and indirect, of measuring each of the components of population demography. Individual survival can be measured directly by mark-recapture or indirectly through annual turnover of individuals. Fecundity can be measured directly by clutch size or indirectly by the timing of nesting, which is related to clutch size (Godfray et al., 1991). Pairing success and population sex ratio are also important components of fecundity. Moreover, rates of nest predation and parasitism, as well as the number of fledglings and their quality, are further measurements associated with nesting success. Such measurements can also be divided into those that are taken from adult birds (e.g., survival, pairing success, sex ratio) and those taken from nests (e.g., clutch size, rate of nesting success).

The mechanisms listed above also have both direct and indirect effects on population demography and on the measurements we take from populations. For example, predation directly affects annual survival, but may indirectly influence sex ratio or age structure if predation is either sex- or age-biased. Nest predation has direct effects on both nest success rate and population age structure, and may indirectly affect site fidelity as well, thereby modifying annual turnover in local populations.

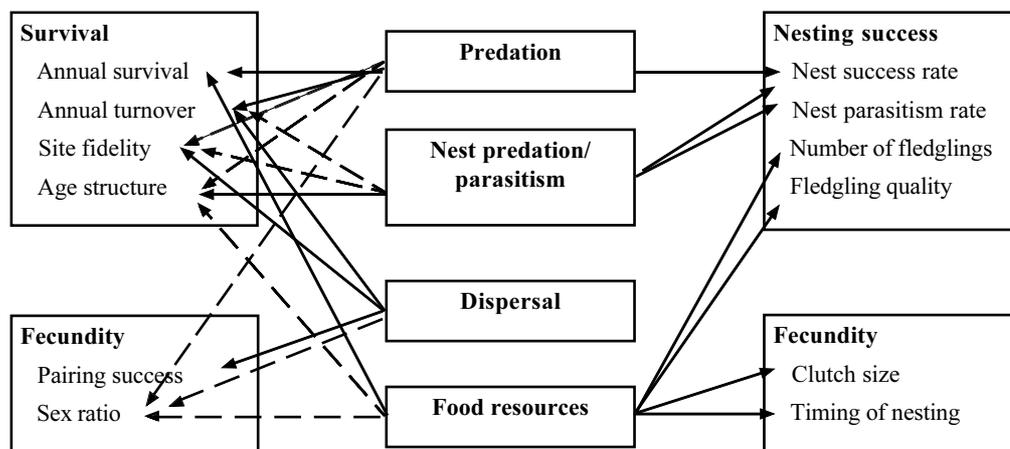


Fig. 1 Measurements of bird population demography that can be taken from adult birds (left) and nests (right). Mechanisms are itemized in the middle of the diagram against direct (solid arrow) and indirect (dashed arrow) effects on measurements.

One potentially important message emerges from the direct and indirect links between mechanism and measurement. It is embodied in Fig. 1, which suggests that a clearer understanding of important processes affecting population demography can be gained from inspecting nests. Here the mechanisms that may be considered putative factors for demographic change in measurements that can be taken from nests are narrowed, as a rule, to one.

The various measurements can be ordered according to their ease of acquisition. It is relatively easy to assess population densities, because of which much is already known about numerical responses. Unfortunately, measurement of density alone does not allow us to draw conclusions about the mechanisms causing numerical responses. Pairing success, timing of nesting and fecundity (clutch size) are also relatively easy to measure because they only require one or several observations. Nest success and fledgling quality (e.g., mass, growth rate and body condition of fledglings) do require more detailed monitoring of nests, but are still more easily taken than those that require the capturing of adult birds one (sex ratio, age structure data) or more (annual survival, site fidelity data) times. Fledgling quality reflects the effects of resources but is only slightly, if at all, affected by predation.

We conclude that most effective and efficient studies on demographic responses to habitat fragmentation in birds are those that have used measurements that can be taken most easily, with the caveat that planning should be undertaken beforehand to select those measures that distinguish among mechanisms. A good combination of non-experimental measurements would be pairing success, nest success rate and fledgling quality monitored simultaneously. Here pairing success is likely to be affected only by dispersal; and nest success and fledgling quality can be used to distinguish between the effects of predation and resources. Other similarly optimal combinations can be found by inspecting Fig. 1.

4 Literature review of demographic response to fragmentation

We conducted a literature search in the BIOSIS database for studies dealing with forest bird responses to habi-

tat fragmentation. For this, we used a combination of keywords given in Fig. 1 and included only studies dealing with forest fragmentation and demographic responses of birds in natural environments. All studies using artificial nests sites were thereby excluded. Two types of studies were found: those that provided data on demographic responses to variation in patch size, and those that compared bird demography in fragmented vs. unfragmented landscapes. For the purposes of this review, we pooled both types of studies. Altogether, 36 studies were found, with information on responses for 80 species. By *response* we mean one measurement (e.g., clutch size) for one species. Some studies provide data on one measurement for several species, while others gave information on a combination of measurements for one species population.

On average, measurements given for populations were scarce (mean = 1.4 measurements). Thus no firm conclusions about causal mechanisms for observed patterns could be made because, as we have shown, several measurements are needed to distinguish among mechanisms. Moreover, no studies on the relationship between sex ratio and habitat fragmentation were found (Table 1). By and large, the most frequently measured parameter was nest success. This probably reflects the popular belief that nest predation and parasitism are the primary causes of demographic change in fragmented landscapes. It is notable that almost two thirds of the studies found that fragmentation had either no effect on nest success (54% of cases) or was positive, i.e., nest success increased with increasing fragmentation (12%). No study detected a significant effect on clutch size, but other fecundity-related measurements, particularly pairing success, were found to be affected more frequently.

Dispersal was also implicated as an important mechanism because dispersal-related measurements (direct dispersal, pairing success) were found to be more frequently influenced by fragmentation than, for example, resource related measurements such as clutch size or fledgling quality. Such conclusions, however, may be premature because the data that we reviewed could have been biased in at least two ways. First, there could have been publication bias, whereby only papers submitting significant results were accepted for publication. Secondly, and perhaps more importantly, researchers may have selected species and

Table 1 Frequency of the responses of species of forest birds to habitat fragmentation according to a compilation of published studies

Fragmentation effect	Pairing success	Nest timing	Clutch size	Nest success	Fledgling quality	Sex ratio M/F	Age structure A/J	Annual survival	Dispersal
Negative	8	3	0	9	3	0	1	4	7
No effect	4	7	10	14	4	0	1	2	0
Positive	0	0	0	3	0	0	0	0	0
Number of studies	11	8	8	19	6	0	2	3	5

The demographic variables given from left to right are in order of decreasing ease of measurement. Each cell records the number of cases where effects were found. The bottom row gives the number of studies furnishing information for each demographic parameter. Note that the numerical results in each column may exceed the sum of studies because each study may provide more than one estimate.

measurements expected to reveal significant results, thereby creating their own bias. Thus, the species selected for expensive studies of dispersal were not chosen randomly. That all seven recorded cases in our review revealed that fragmentation had a significant, negative effect on dispersal should thus come as no surprise.

5 Discussion

Even though much is known about the numerical responses of birds to habitat fragmentation, we lag far behind in our understanding of the mechanisms involved and can therefore provide little knowledge on how to remedy impacts on populations at the landscape level. A good starting point for research to address this gap would be to focus on simple and readily measurable parameters such as pairing success, nest success and fledgling quality. To provide more robust assessments of demographic mechanisms, we propose that future studies should take an analytical approach to mechanisms and related measurements by repeating an exercise, such as that depicted in Fig. 1, which would pinpoint key variables. Assuming that each measurement has a cost, one should try to find a combination of measurements capable of distinguishing among such putative mechanisms as predation, resource availability and dispersal.

We also have very little understanding of adaptive responses to habitat fragmentation. For example, life-history theory (e.g., Stearns, 1992) and a large body of empirical research (e.g., Reznick et al., 2000) suggest that there are trade-offs among demographic traits. Allocation of more resources to one particular activity, such as reproduction, will result in less time and energy for other activities, for example, improvement of individual survival. The ultimate impact of habitat fragmentation on population viability is the result of not only changes in demographic parameters related to survival and reproduction but also in their trade-offs. This stresses the point that it is important to study all parameters affecting population demography (survival, fecundity and nest success) simultaneously if a sound, holistic understanding of population viability prospects in fragmented landscapes is to be achieved.

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Symposium 11 Forest management and conservation of Galliformes

Introduction

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Many species of Galliformes live in forested habitats. As mainly ground-feeding and -nesting species of some size, they are unusually sensitive to understory fragmentation and habitat fragmentation from timber harvesting, as well as hunting. There is a long tradition of research on these species in China; and this symposium reviews some of what is known, both from there and elsewhere, about the ecological requirements of Galliformes in forested habitats, many of which are under threat.

Further, the symposium illustrates how this knowledge has been used for conservation at various scales. In the case studies selected, the reliability of the knowledge base is assessed, gaps revealed, conservation actions identified and tested, and future research directions suggested. It begins with an assessment by Philip McGowan of the forest protected area network for the conservation of all phasianid species in east Asia, followed by Daniel Brooks

with an analysis of hotspots for cracid distribution in tropical America. At landscape level, Yue-Hua Sun and colleagues assess the effects of habitat fragmentation on the Chinese grouse as a basis for making recommendations for its conservation.

The final two papers were submitted as orals only. One, from John Carroll, reviewed approaches to the management of species and sites from the perspective of harvesting, using as examples the ring-necked pheasant (*Phasianus colchicus*), bobwhite quail (*Colinus virginianus*) and wild turkey (*Meleagris gallopavo*). The other, from Dai Bo and Simon Dowell, presented a study of habitat use by the endangered Sichuan partridge (*Arborophila rufipectus*) towards designing forest managing policy that will enable the partridge to survive. Abstracts of these two papers are published in the Abstract Volume for the Congress.

S11-1 Is the current protected area system adequate to support viable populations of forest Galliformes in eastern Asia?

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Abstract The Galliformes are one of the most threatened of avian orders; more than 25% of their species are considered at risk of extinction compared with 11% of all birds. Direct exploitation is believed to be the main reason for this substantially higher level of endangerment. Using additional and recently collected locality data from east Asian protected areas, analysis here revises an earlier study in 1999 that assessed the degree to which the existing protected area network in eastern Asia covered the 101 species of grouse, partridges and pheasants endemic to that region. A network of important protected areas is identified that secures each species in a minimum of three protected areas, our preset target. China and India are key countries in this network, and Malaysia and Indonesia are important for Sundaic tropical forest species. Many of the protected areas are irreplaceable because they alone contain the most under-represented species. Indeed, some species, including some of the region's most threatened Galliformes, occur entirely outside protected areas or in just one or two, such as the Sichuan hill partridge and Edwards' and Vietnamese pheasants in central Vietnam. Although the present network is likely to prove crucial for the survival of these species, it is not sufficient on its own because of shortcomings in species representation, the size of individual protected areas, and their connectivity.

Key words Galliformes, Asia, Protected areas, Pheasants, Partridges, Grouse

1 Introduction

A quarter of Asia's bird species are of global conservation concern, being listed as threatened, near-threatened or data deficient in the 2000 IUCN Red List (Hilton-Taylor, 2000; also BirdLife International, 2000). Habitat loss is thought to be the overwhelming threat facing these species, as forest clearance is now widespread, leaving forests severely fragmented almost everywhere, including the Himalayas, much of China, and the Sundaic forests of South east Asia. Such fragmentation splits populations of forest specialists, leading to isolation of subpopulations, decline and an increased probability of extinction.

Amongst the most threatened of Asia's bird groups is the order Galliformes. There are 112 species in continental eastern Asia, 99 of which are endemic and another two centered in the region. Globally, 25% of all Galliformes are threatened (Hilton-Taylor, 2000), and 35% of the eastern Asian species are at risk. Of special concern are the pheasants, with 24 of the 50 Asian species threatened and a further nine near-threatened. The reason for such heightened endangerment appears to lie in the additional threat posed by hunting (McGowan, 2002), such that the combined impacts of habitat loss and hunting place the long term survival of many of these species in the balance.

Mitigating these pressures to ensure that the threat-

ened Galliformes of Asia have a future requires a range of conservation measures. One fundamental requirement is a network of well-managed protected areas that are devoted primarily to maintaining biodiversity. McGowan et al. (1999) documented what is currently known about the representation of Galliformes in east Asian protected areas, paying particular attention to the large number of endemic species. The study also identified a network of protected areas that would make a considerable contribution towards the conservation of the Galliformes, provided that they were managed properly. Since then, additional field surveys have yielded much new distributional information, and in some cases, new protected areas have been created or their status assessed. Because strategic conservation recommendations need to be based on current and accurate distributional information, this paper sets out to update the analysis carried out by McGowan et al. (1999) by (1) reassessing the representation of endemic regional Galliformes in east Asian protected areas, and (2) revising the near-minimum network of protected areas required to include each species in three protected areas wherever possible. As the emphasis of this symposium was to provide information on Chinese Galliformes and to draw upon international experience to help in their conservation, the representation of Galliformes in protected areas in China is highlighted.

2 Methods

To allow direct comparison with previous work, methods were as detailed in McGowan et al. (1999). Additional species locality information was obtained from reports by fieldworkers to the World Pheasant Association, the Pheasant Specialist Group and the Partridge, Quail and Francolin Specialist Group. In addition, BirdLife International kindly provided the database used to generate distribution maps and locality lists for their recent assessment of the threat status of Asian birds, *Threatened Birds of Asia* (Collar et al., 2001).

The protected areas included in this analysis were those assigned IUCN management categories I–IV (IUCN, 1994), with primarily biodiversity conservation objectives. In compiling the near-minimum network, we again set a target to include each species in at least three protected areas. Some species, however, were present in as many as three protected areas. Those protected areas that did contain such suites of poorly represented species were termed ‘irreplaceable’, as they had to be included in the network to avoid reducing representation further. The algorithm used for selecting the remainder of the protected areas (termed ‘others’) is given in McGowan et al. (1999).

3 Results

3.1 Summary statistics

Eleven species with main distributions outside eastern Asia were first discarded from the analysis: *Ammoperdix griseogularis*, *Coturnix japonica*, *Coturnix ypsilophora*, *Falcipecten falcipecten*, *Lagopus lagopus*, *Lagopus muta*, *Lyrurus tetrix*, *Perdix perdix*, *Tetrao parvirostris*, *Tetrao urogallus*, *Tetraogallus altaicus*.

For the 101 species remaining (99 east Asian endemics and two with core ranges in east Asia), we collated more than 6 000 records, including more than 3 000 from China. From this dataset, 1 127 species records were extracted and from 399 protected areas. In China, there were 225 records

from 104 protected areas. Nine of the species involved are Chinese, and all except *Arborophila atrogularis* are endemic to that country. 21 species were recorded from fewer than three protected areas (Table 1), five of which are still not known to occur in any protected area. Of those 21, 13 inhabit forest, 10 of which are probably forest specialists and globally threatened.

3.2 Significant changes from McGowan et al. (1999)

The most significant novelty from the present survey was the finding of *Arborophila rufipectus* in a protected area. Changes among other poorly represented species, all positive, were: *Polyplectron germaini* present in three protected areas, *Arborophila cambodiana* in three, *Arborophila gingica* in five, and *Lophophorus sclateri* in three.

3.3 Near-minimum network

Using the guidelines established by McGowan et al. (1999), the near-minimum network produced a set of 86 protected areas that gave the best possible representation of species in protected areas based on the available data. The network comprised 44 irreplaceable protected areas and 42 others (Table 2).

4 Discussion

Since 1999, there has been only minor improvement in the representation of endemic east Asian Galliformes in protected areas. This may be significant for several individual species, notably *Arborophila rufipectus*, but there is still much cause for concern because of the many species still represented in fewer than three protected areas. The ten species currently believed to be forest specialists seem to be most at risk.

For the five species outside all protected areas, the message is mixed. Thus the status of *Perdica manipurensis* is of real concern, as this species has not

Table 1 Species currently known from fewer than three protected areas of IUCN management categories I–IV in eastern Asia

Number of protected areas per species		
0	1	2
* <i>Crossoptilon harmani</i>	* <i>Alectoris magna</i>	* <i>Arborophila atrogularis</i>
<i>Ophrysia superciliosa</i>	<i>Arborophila davidi</i>	<i>Arborophila rubrirostris</i>
<i>Perdica manipurensis</i>	<i>Arborophila merlini</i>	* <i>Perdix dauurica</i>
<i>Polyplectron schleiermachersi</i>	* <i>Arborophila rufipectus</i>	<i>Polyplectron chalcurom</i>
<i>Syrnaticus soemmeringii</i>	* <i>Chrysolophus amherstiae</i>	* <i>Tetraogallus tibetanus</i>
	* <i>Crossoptilon crossoptilon</i>	
	<i>Lophura edwardsi</i>	
	<i>Lophura hatinhensis</i>	
	<i>Lophura imperialis</i>	
	* <i>Perdix hodgsoniae</i>	
	<i>Polyplectron napoleonis</i>	

* denotes species occurring in China.

Table 2 The number of protected areas in the near-minimum network in each country or territory

Country /Area	Irreplaceable sites	Others	Total
Bhutan		1	1
Cambodia	2	1	3
Mainland China	16	15	31
India	7	11	18
Indonesia	8	0	8
Laos			
Malaysia	3	6	9
Nepal	1	1	2
Pakistan		1	1
Philippines	1	0	1
Sri Lanka		3	3
Taiwan, China	3		3
Thailand		3	3
Vietnam	3	0	3
Total	44	42	86

The terms "Irreplaceable sites" and "Others" are defined in the text.

been recorded anywhere, let alone in a protected area, since the 1930s (Fuller et al., 2000); it may already be extinct. In contrast, *Crossoptilon harmani* seems likely to occur in some protected areas in its remote range, but even if not, it is probably well protected around Buddhist monasteries (Lu Xin, pers. comm.).

The size of the near-minimum network has increased from 82 to 86 since 1999. The additions contain the least well-represented species, and are Laojunshan Nature Reserve in China (Dai Bo and Dowell, oral paper in this symposium), and Virachey and Bokor National Parks and Snoul Wildlife Sanctuary, all in Cambodia (Setha and Bunnat, 2000).

Concerning the adequacy of the network of protected areas in China, current data indicate that China has the greatest number of protected areas globally important for Galliformes. There are 31 Chinese protected areas in the near-minimum network. Because so many species are endemic to China (Fuller and Garson, 2000; Fuller et al., 2000), its protected areas will always be very important at a global level. To determine which protected areas are the more important, however, there is an urgent need for better information on the occurrence of Galliformes within them. Data presented here (204 records from 112 protected areas) indicate an average of two species per protected area, clearly an underestimate. The skew appears to result from a focus on particular individual species, such as Temminck's tragopan, *Tragopan temminckii* (Li, 1991), instead of general surveys.

The list of protected areas from which this species has been recorded is comprehensive, but information on other species that might occur in them is not. This needs to be remedied; it seems probable that the information exists and has only to be collated.

It is not just presence in a protected area that is important, but whether or not the populations there are viable. This is especially true in China, where many protected areas include significantly altered habitats, such as those resulting from forestry operations undertaken before the site was declared protected. Data are available on habitat use by a range of pheasant and partridge species in some of these areas, and these now need to be used to determine population viability, both in China and elsewhere. Information on habitat use can also be used to ensure that management of forests in protected areas is appropriate for threatened species.

The size of many of the protected areas has been determined by administrative or geographical considerations, rather than the need to accommodate populations of viable size. As a result, many protected areas are likely to be too small to hold adequate populations of target species. Therefore, the potential for connecting the most important sites with corridors of habitat must be investigated as a matter of urgency.

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S11-2 The utility of hotspot identification for forest management: cracids as bioindicators

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Abstract Diverse species of large forest-dwelling vertebrates can serve as bio-indicators of forest quality. In the Neotropics, forest-dwelling game mammals have often been used as the model because their presence/absence can identify forest integrity and sustainability of game harvest together. Species such as ateline primates are often the first to disappear when forest is degraded and population harvest is beyond sustainable limits. In South America, one of the few groups of birds that can also serve in this way is the family Cracidae. This is especially true for curassows and guans, which are typically associated with pristine forest, and also provide a highly preferred source of protein for rural hunters and Amerindians. Determining where these species reach peak diversity in sympatry (i.e. hotspots) is a means of identifying and prioritizing regional forest conservation. In this study, I identify cracid hotspots by comparing equal blocks of regional map quadrats. The location of these hotspots is then compared with current regions identified in the Cracid Action Plan of Birdlife International and FAO. Hotspot analysis is a contemporary paradigm in modern conservation biology because of its usefulness in determining priorities for regional forest conservation.

Key words Cracidae, Hotspot analysis, Primary forest, Priority regions

1 Introduction

Neotropical game mammals that are terrestrial are often used as bio-indicators of forest quality and sustainability of harvest (Bodmer, 1997). Such species, all vulnerable to local extinction by forest destruction and non-sustainable harvesting, include the ateline primates (spider and woolly monkeys) and the bird families Psophiidae (trumpeters) and Cracidae (Brooks, 2001). The latter group, the cracids, are the most threatened family of birds in the Americas, and include 12 species of chachalacas (*Ortalis*), 24 species of guans (15 in the genus *Penelope* and the remainder in five other genera) and 14 species of curassows in four genera (Brooks and Strahl, 2000).

Most cracids depend on undisturbed, often primary, forest. In this category are four species (34%) of chachalacas, eight (54%) of *Penelope* guans, five (45%) of other guans, and all curassows (100%), totalling 31 species (62%) of cracids. Other cracids, however, can use secondary habitat, including eight species (66%) of chachalacas, seven (46%) of *Penelope* guans, and four (55%) of other species of guans, totalling 19 species (38%) of cracids (Appendix 1). Even so, most cracids, especially curassows, are associated with and dependent on pristine habitat. These species, moreover, have been much used as a traditional source of preferred protein (Brooks, 1999). Consequently, half of the 50 species are threatened or endangered.

The objective of this study, then, was to assess the utility of cracid hotspots for determining priorities for for-

est conservation in the Neotropics. Hotspot analysis is a procedure for identifying and prioritizing regional habitat conservation by comparing species richness among equal blocks of regional map quadrats (Mittermeier et al., 1998).

2 Methods

I compared equal blocks of regional map quadrats to identify hotspots of species richness at 6 group levels: 1) chachalacas, 2) *Penelope* guans, 3) other guans, 4) curassows, 5) all cracids, and 6) cracids dependent upon undisturbed forest. I then compared the resulting hotspot locations with regional priorities for forest conservation in the Cracid Action Plan (Brooks and Strahl, 2000), and assessments of globally threatened birds (Birdlife International, 2000) and threatened and degraded forests (FAO, 2000).

3 Results

Diversity for the groups of *Penelope* guans, all cracids, and cracids dependent upon undisturbed forest reached peak species richness in the region of southwestern Colombia and Ecuador.

Chachalacas were the only group with a hotspot in Central America, in the region of the southern Mexican isthmus. The “other guans” group peaked in southeastern Peru, where Andean and Amazonian forests interface. Curassows reached peak diversity in western Amazonia, a somewhat surprising result in light of the greater uniformity of habitat in the Amazon basin than on the slopes of the Andes.

Table 1 Conservation priorities, by nation, for the Cracid Action Plan (Brooks and Strahl, 2000), Birdlife International (2000) and FAO (2000)

Rank	CAP	BL	FAO (2000)		
			Total forest cover (ha)	Forest cover loss 1999–2000 (ha/yr)	Forest cover change 1999–2000 (%/yr)
1	Brazil	Brazil	Peru (65 215 364)	Mexico (–630 574)	El Salvador (–4.6)
2	Colombia	Colombia	Mexico (55 205 278)	Argentina (–285 111)	Belize (–2.3)
3	Peru	Peru	Bolivia (53 068 062)	Peru (–268 794)	Guatemala (–1.7)
4	Mexico	Mexico	Colombia (49 601 300)	Venezuela (–217 539)	Panama (–1.6)
5	Bolivia	ND	Venezuela (49 506 000)	Colombia (–190 470)	Ecuador (–1.2)
6	Ecuador	ND	Argentina (34 648 222)	Bolivia (–161 075)	Mexico (–1.1)

CAP = Cracid Action Plan, BL = Birdlife International, FAO = Food and Agricultural Organization

Table 2 Regional priorities for CSG (Brooks and Strahl, 2000) and Birdlife International (2000) = BL

Rank	CSG	BL
1	Santa Marta mountains, Colombia	Atlantic forest
2	Colombian Pacific and Andean slopes	northern Colombian Andes
3	northern Andean foothills and cloud forest (Venezuela–Bolivia)	no data
4	Mexican highlands and cloud forest	no data

4 Discussion

Southwestern Colombia and Ecuador harbor the highest diversity of forest-dependent cracids, a region that was also the primary hotspot for other groups, including *Penelope* guans and all cracids. Comparative data from the Cracid Action Plan (Brooks and Strahl, 2000; Birdlife International, 2000; FAO, 2000) are provided in Tables 1 and 2. Rankings by Brooks and Strahl (2000) and Birdlife International (2000) place southwestern Colombia only second for both county and region (Table 3). Brooks and Strahl (2000) also ranked Ecuador second regionally and sixth by country (Table 3). Birdlife International (2000) did not in-

Table 3 Ranked comparison of southwestern Colombia/Ecuador hotspots with other regional priorities

Criteria	SW Colombia	Ecuador
CAP — Country	2	6
CAP — Region	2	2
BL — Country	2	ND
BL — Region	2	ND
FAO — total forest cover	4	ND
FAO — forest cover change	5	ND
FAO — % forest cover lost	ND	5

CAP = Cracid Action Plan, BL = Birdlife International, FAO = Food and Agricultural Organization

clude Ecuador at all, and their criteria only ranked two regional priorities and four country priorities (Table 3). FAO (2000) ranked Colombia within the top five countries for categories of both total forest cover and forest cover loss, and placed Ecuador fifth for percentage of forest cover change (Table 3).

Cracid hotspots of secondary importance include the southern Mexican isthmus (chachalacas), southeastern Peru (other guans), and western Amazonia (curassows). Here conservational priorities in Brooks and Strahl (2000), Birdlife International (2000) and FAO (2000) are more appropriate. Brazil, Peru and Mexico (Table 1) were all ranked high in priority by Brooks and Strahl (2000) and Birdlife International (2000). Peru and Mexico are ranked highest by FAO (2000) for total forest cover and loss, and Mexico sixth for forest cover change (Table 1). It should be noted, moreover, that the smaller countries have suffered higher proportions of forest destruction by virtue of their smaller relative size.

Thus, cracid diversity hotspots are linked generally to prioritized regional and geopolitical units for conservation, and consequently could serve as good bio-indicators for forest management. Moreover, while the hotspots are not necessarily concordant with the highest ranks of conservation need according to other criteria, they are still important indicators for forest management involving a suite of factors.

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Appendix 1

Habitat type required by cracids

(a) Species of cracids dependent upon undisturbed habitat:

1. Chachalacas: *Ortalis erythroptera*, *O. wagleri*, *O. poliocephala*, *O. superciliaris*

2. *Penelope* guans: *Penelope barbata*, *P. ortoni*, *P. dabbenei*, *P. purpurascens*, *P. albipennis*, *P. pileata*, *P. ochrogaster*, *P. jacucaca*

3. Other guans: *Pipile cujubi*, *P. jacutinga*, *Chamaepetes unicolor*, *Penelopina*, *Oreophasis*

4. All curassows: *Nothocrax*, *Mitu tomentosa*, *M. salvini*, *M. tuberosa*, *M. mitu*, *Pauxi pauxi*, *P. unicornis*, *Crax rubra*, *C. alberti*, *C. daubentoni*, *C. alector*, *C. globulosa*, *C. fasciolata*, *C. blumenbachii*

(b) Species of cracids that can use secondary habitat:

1. Chachalacas: *Ortalis vetula*, *O. cinereiceps*, *O. garrula*, *O. ruficauda*, *O. canicollis*, *O. leucogastra*, *O. guttata*, *O. motmot*

2. *Penelope* guans: *Penelope argyrotis*, *P. montagnii*, *P. marail*, *P. superciliaris*, *P. perspicax*, *P. jacuacu*, *P. obscura*

3. Other guans: *Pipile pipile*, *P. cumanensis*, *Aburria*, *Chamaepetes goudotii*

S11-3 Habitat isolation and fragmentation of the Chinese grouse (*Bonasa sewerzowi*) at Lianhuashan Mountains, Gansu, China

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Abstract The habitat (altitude 2 600–3 600 m) of the Chinese grouse in the Lianhuashan Mountains of Gansu province comprises a mixture of conifers for cover and deciduous trees (willow, birch) for food. Logging of virgin forest in this area over the past 30 to 40 years has destroyed much of the coniferous forest. Using digitized SPOT satellite images, we mapped the surviving distribution of the forest, the key habitat of the Chinese grouse. The population of the Chinese grouse there is isolated from others elsewhere and has now been broken into two subpopulations. Within a study area of 120 000 ha, we found 77.3% of forest patches to be smaller than 10 ha, indicating a high level of habitat fragmentation. From a survey of 31 forest patches, we found that grouse only occupied tracts larger than 100 ha and closer to one another than 600 meters. On this basis, proposals have been put to local government to protect the whole habitat of this isolated population.

Key words Chinese grouse, Habitat fragmentation, Conservation

1 Introduction

The endemic Chinese grouse (*Bonasa sewerzowi*) inhabits isolated remnants of the coniferous mountain forests of Gansu, Qinghai, Sichuan, Yunnan and Tibet (Sun, 2000). The decline and increasing fragmentation of this endangered species is being caused by natural aridity and the effects of agriculture, logging and deforestation on mountain forest (Zheng and Wang, 1998). Habitat fragmentation, beyond that of habitat loss, has apparently had greater negative effects on its survival than for mammal species (Andrén, 1994). As the hazel grouse (*B. bonasia*), the species most closely related species to the Chinese grouse, is exceptionally sensitive to habitat isolation and habitat fragmentation (Åberg et al., 1995; Saari et al., 1998), we set out to determine the status of the Chinese grouse in the Lianhuashan Mountains at landscape scale.

Remote sensing is a powerful and accurate tool for assessing wildlife habitat, particularly for large areas where access is difficult. In this study, we used satellite imagery to determine the distribution of the Lianhuashan conifer forest, a habitat considered primary for the Chinese grouse.

2 Study area and methods

The study area in the Lianhuashan Mountains (34°45'–35°06'N, 103°27'–103°51'E) in Gansu Province, west China, includes the Lianhuashan Nature Reserve and parts of the Yangsha and Yeliquan forestry farms in the counties of Kangle, Lintan and Zhuoni. Forests there occur on northern and some northeast and northwest slopes at altitudes between 2 600 m and 3 600 m a.s.l. On the dry, insolated southern slopes, only shrub and grass grow. The forests

are dominated by fir (*Abies fargesii*), spruce (*Picea asperata*), birch (*Betula* spp.) and many kinds of willow (*Salix* spp.). The yearly temperature in the Lianhuashan Nature Reserve ranges from a mean low of –27.1°C to a mean high of 34°C. Except in the Lianhuashan Nature Reserve, the forests in this area had been selectively logged for 30 to 40 years until 1998, when the Chinese government stopped logging in virgin forests in Gansu and Sichuan.

The TM-satellite picture, taken on 8 December 1996 (ground area: 185×185 km²) was used to assess the external isolation of the study area. For determining the extent of internal fragmentation, we used a SPOT image taken on September 1998, with a ground area of 60×60 km². ERDAS IMAGIE 8.4 was used for analyzing it. As all mating and nesting territories for the grouse were found to be confined to spruce-fir forest mixed with deciduous trees, mainly willow and birch (Sun and Fang, 1997; unpublished data), we selected conifer forest as the key indicator habitat for survival and reproduction. In an area of about 120 000 ha, all conifer forest patches bigger than 2 ha were numbered and mapped. In spring 1999 to 2001, we then went to 31 larger forestry tracts to survey for Chinese grouse, assisted by local forestry maps, topographic maps of 1:50 000 and GPS.

To determine presence, we searching mainly for droppings under possible night-roosts in conifer trees, as the grouse usually roost in conifers in winter and spring (Klaus et al., 1996) and defecate many times (more than 30 droppings/night). We also used other methods, such as direct observation and the finding of dusting and nesting sites.

3 Results and discussion

3.1 External isolation

Combining the forest distribution map for Gansu and TM satellite imagery showed that the population of Chinese grouse in the Lianhuashan Mountains is isolated from all others. At its eastern limits there, it is separated by about 120 km from its nearest neighboring population to the west in Xunhua County, Qinghai Province. Although patches of logged forest remain in between, no grouse have been recorded in them. The nearest population to the north is found in the Liancheng Nature Reserve in Yongdeng county of the Qilianshan Mountains, some 200 km away; no forest has been left in between. The nearest population there lives on the Kache and Muer forestry farms in Zhuoni (Jone) county, separated by 30 km and 10 km, respectively, of unforested mountains.

3.2 Internal fragmentation

Within a proscribed study area of 120 000 ha, 1 762 forest patches larger than 2 ha were determined from the SPOT satellite image (Fig. 1). Of these, 1 362 (77.3%) were smaller than 10 ha, and only 31 were larger than 100 ha, indicating a particularly high level of fragmentation.

3.3 Survey of Chinese grouse

Of the 31 larger (>100 ha) forest patches checked in the spring of 1999 through 2001, Chinese grouse were found in only 16. They were present in patches that had been subject to cut over rates of up to 60% of trees, but only in low numbers. Grouse also only occupied tracts that were closer to one another than 600 meters. No grouse were found in the 5 forest patches between the two subpopulations in the Lianhuashan Nature Reserve and on the Yeliguan Forestry Farm.

3.4 Recommendations for conservation

Our studies of the Chinese grouse in the Lianhuashan Nature Reserve since 1995 show that population density

has been stable through the subsequent five years (Sun et al., 2003). Because of this, the Lianhuashan Nature Reserve has great conservation value for the species and other regional wildlife and, partly due to our efforts, was upgraded to a national reserve in 2002. Although the reserve is linked to the Yeliguan Forestry Farm (and the other local grouse population) by a forest corridor, that corridor is less than 1 km wide, locally broken and contains no grouse. The local management plan should attend to plantings that will improve connectivity between the two forested areas.

Many other endemic birds occur in the conifer forests of the Lianhuashan Mountains. Examples are the blood pheasant (*Ithaginis cruentus*), blue-eared pheasant (*Crossoptilon auritum*), chestnut-throated partridge (*Tetraophasis obscurus*) and snowy-cheeked laughing-thrush (*Garrulax sukatschewi*). Our study also recorded the Sichuan wood owl (*Strix davidi*) there (Sun et al., 2001). For them, the Chinese grouse may served as an umbrella species for protection. As a next step, we recommend that the Lianhuashan Nature Reserve should be enlarged to cover the whole conifer forest in the Lianhuashan Mountains.

In October 1998, the Chinese government stopped the logging of virgin forests in Gansu and other provinces. Despite this, local people are still continuing to log extensively and illegally in the Lianhuashan Mountains. We strongly recommend that the local government should take action to stop this and pay better attention to forest management.

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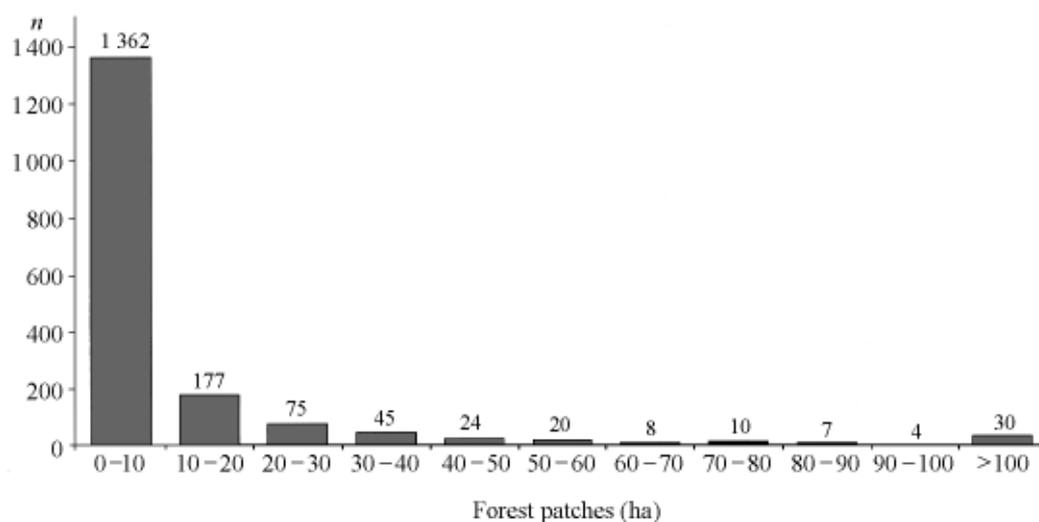


Fig. 1 The number (shown above the columns) of conifer forest patches in categories of patch size in the Lianhuashan Mountains, Gansu Province, west China

Forest patches bigger than 2 ha were determined from SPOT satellite imagery.

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Symposium 12 Migration and conservation of cranes and storks

Introduction

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Large migratory wetland birds such as cranes and storks are threatened in many parts of the world. Knowledge of breeding and wintering habitat and of migration routes and stopover points are crucial for the conservation of these birds. Recently, cranes and storks have begun to be tracked by satellite, which has facilitated the collection of much new and accurate information about their migration routes, information that could never be obtained from routine ringing recaptures. This symposium reviews recent studies and the present state of knowledge of the migration

and conservation of several indicator species of cranes and storks, focusing on newly developed research technologies and Asian taxa that are poorly known. More specifically, the contributors concentrate on four aspects of migration and conservation: (1) the satellite tracking of migration, (2) ecological requirements in staging and wintering areas, (3) satellite imagery in the identification and mapping of habitat, and (4) the application of basic migration research to conservation.

S12-1 Satellite-tracking the migration of cranes and storks

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Abstract We satellite-tracked demoiselle (*Anthropoides virgo*), red-crowned (*Grus japonensis*), Siberian (*Grus leucogeranus*), and white-naped (*Grus vipio*) cranes and the oriental white stork (*Ciconia boyciana*) between their breeding and wintering grounds in Asia. With the aid of helicopters, birds for tracking were captured after baiting with wheat coated with the oral tranquiliser alpha chloralose. Platform transmitter terminals were then attached to them with a harness system. Cranes tended to make one long and several shorter stops on migration, and covered considerable distances between rest stops. Storks made much shorter daily flights and rested for longer. Cranes and storks breeding in far eastern Russia used several common resting and wintering sites, notably Bohai Bay and the Yellow River delta in China, the Korean Demilitarized Zone, Lake Khanka in Russia, and Poyang Lake, the Qiqihar Baicheng area, the Three Rivers Plain and Yangcheng Nature Reserve in China. Threats to resting and wintering sites are diverse, from development, human disturbance, hunting, mining, pesticide use, and pollution. We emphasize the need to protect habitats used by these species over the entire course of their migrations, and for continued research into and mitigation of the many threats to their survival.

Key words Migration, Asia, Cranes, Storks, Satellite tracking, Conservation

1 Introduction

In recent years, the study of animal movements has been greatly enhanced by the development and application of satellite-tracking technology. Satellite tracking allows relatively precise monitoring of animal positions from remote locations. The technique has enabled progress in the study of bird migration otherwise impossible from the use of more conventional methods, such as ringing (e.g. Berthold et al., 2001a), and it has been applied to a variety of bird species over the last 15 years.

In Asia, avian research incorporating satellite-tracking has been in operation for about 10 years (Higuchi et al., 1991; Higuchi et al., 1992). This approach is especially applicable to Asia, because of its vast area, sensitive political environment, and urgent conservation problems. Wetland conservation is particularly pressing due to the extremely rapid conversion of these habitats to agriculture and industry (APMWCC, 2001). Because cranes (Gruidae) and storks (Ciconiidae) tend to be wetland-dependent, loss and degradation of wetland habitats render these birds vulnerable to extinction. At the same time, limited knowledge of their requirements hampers initiatives for their conservation. Consequently, the goal of our ongoing research is to identify the migration routes, migration patterns and habitat use of threatened cranes and storks in Asia.

In this paper, we briefly review recent research involving the demoiselle crane (*Anthropoides virgo*), red-

crowned crane (*Grus japonensis*), Siberian crane (*Grus leucogeranus*), white-naped crane (*Grus vipio*), and oriental white stork (*Ciconia boyciana*). Except for the demoiselle crane, these species are listed as globally vulnerable, endangered or critically endangered (IUCN, 2000).

2 Materials and methods

Birds were first captured on their breeding or wintering grounds using helicopters and by distributing wheat coated with the oral tranquiliser alpha chloralose (Kanai et al., 2000). Captured birds were marked with leg bands or neck rings, and saddled with satellite transmitters as described in Nagendran et al. (1994); transmitters were secured by teflon ribbon transmitter harnesses. The transmitters (Platform Transmitter Terminals, PTT) were made by NTT Corp. (Japan), Toyo Communication Equipment Co. (Japan), and Microwave Telemetry (USA) and weighed 30–80 g, about 1%–2% of body weight (Higuchi et al., 1996; Higuchi et al., 1998).

PTTs were set to cycle 6 hours on and 12 hours off. Location data were received by and accessed from ARGOS satellites, which categorized them into Location Classes 0–3 and A, B, and Z. We used classes 0–3 in analyses; accuracy of location increases from classes 0 through 3 (Keating et al., 1991; Service ARGOS, 1994). Due to the potential inaccuracy of class A, B and Z data, we only considered these locations when points fell on migration pathways determined from classes 0 through 3.

Satellite-tracking was also complemented by some local ground-based studies of tracked birds. Such work included observational studies and investigations of local movements in tracked birds on their staging areas in China, and their wintering grounds in China, Korea, Japan, and India.

3 Results

3.1 Demoiselle crane

In 1995, we satellite-tracked the partial migrations of 11 cranes, and the complete migrations of another four. Complete migration routes were monitored from crane breeding sites at Har Us Lake in Mongolia and Kopa in Kazakhstan to wintering sites in northern India (Fig. 1; Kanai et al., 2000). The cranes spent 18–35 days ($\bar{x}=25.75$, $SE=4.05$) migrating 2 710–3 332 km ($\bar{x}=3 031$, $SE=171$), and rested at 7–9 locations ($\bar{x}=8$, $SE=0.41$) for 1–20 days en route. One rest period extended for 9–20 days but the remainder lasted only a day.

3.2 Red-crowned crane

In 1993–1994 and 1998–1999, complete migration routes were tracked for 11 cranes from their breeding

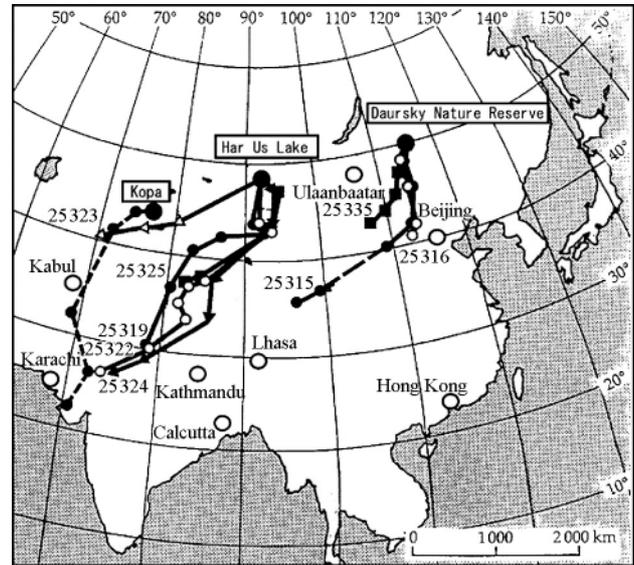


Fig. 1 Satellite-tracked migration routes of demoiselle cranes captured in Kazakhstan, Mongolia, and far eastern Russia
From Kanai et al. (2000).

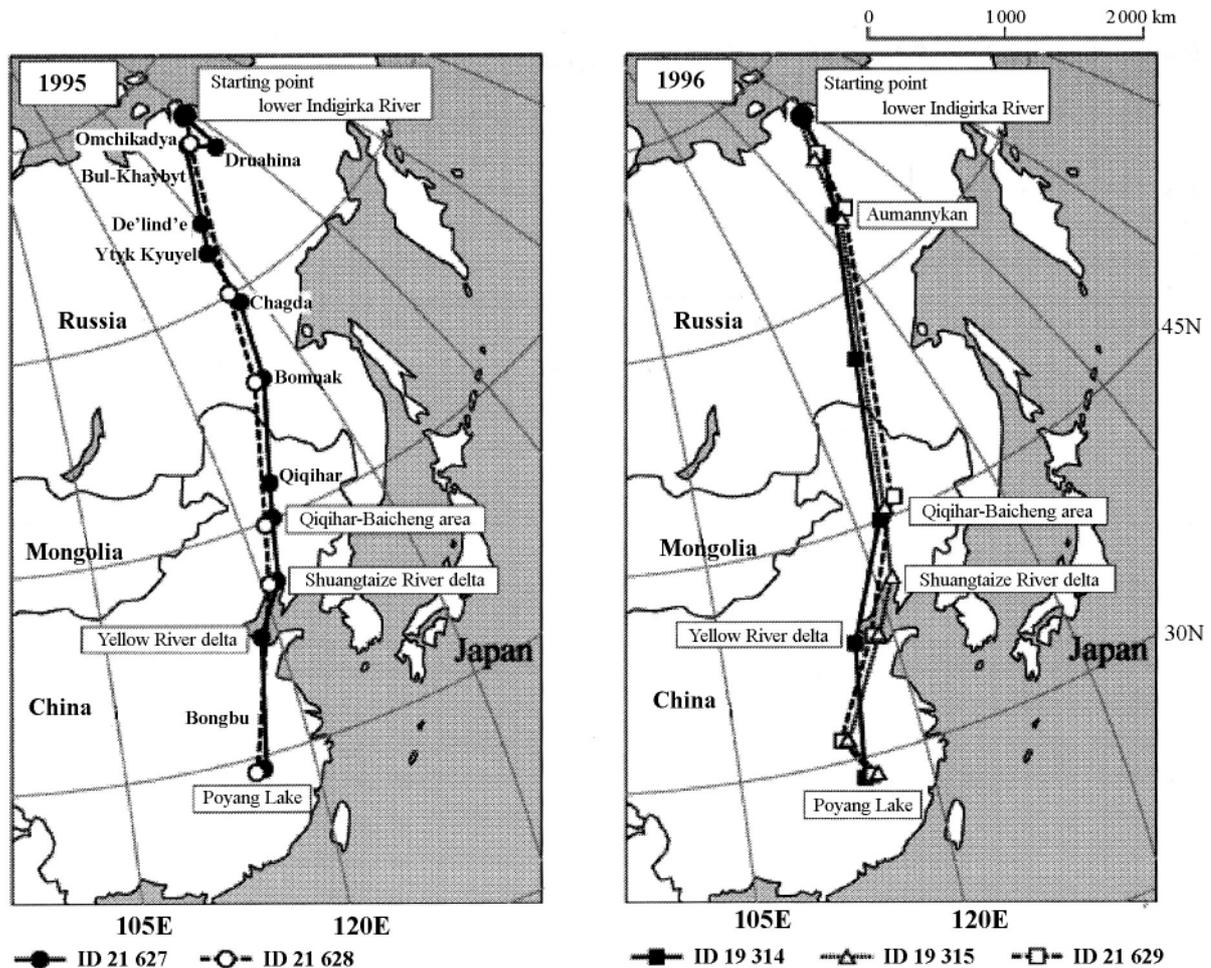


Fig. 2 Complete migration routes of five Siberian cranes satellite-tracked from north eastern Siberia
From Kanai et al. (2002).

grounds on the Amur River in Russia and another 7 from Lake Khanka on the border of Russia and China (Higuchi et al., 1998; Tamura et al., 2000). Birds migrating from the Amur covered 1 626–2 509 km ($x=2\ 073$, $SE=122$) in 3–39 days ($x=22$, $SE=5$), and birds from Lake Khanka 871–948 km ($x=874$, $SE=19$) in 3–9 days ($x=5$, $SE=1$). Amur cranes took 0–3 ($x=1.6$, $SE=0.6$) rest stops of 3–37 days each ($x=16$, $SE=7$) in 1998–1999. Sites around Liaodong and Bohai Bay and the Yellow River delta (China) are important stopover grounds for cranes from the Amur. Lake Khanka cranes rested around the Tumen River (Russia) and at Odaejin-nodonjagu (North Korea). Wintering sites were Yangcheng Nature Reserve (China) and the Korean Demilitarized Zone (DMZ), where extensive local short-term movements occurred (Higuchi et al., 1998).

3.3 Siberian crane

In 1995–1996, we tracked the partial migrations of 11 critically endangered Siberian cranes and the complete migrations of another 5, from their breeding area in Yakutia, Siberia, to their main wintering area at Poyang Lake in China (Kanai et al., 2002). The cranes took some 41 to 60 days ($x=50$, $SE=4$) to migrate 4 903–5 586 km ($x=5\ 313$, $SE=117$) between their breeding and wintering areas (Fig. 2). They stopped over from 1 to around 30 days ($x=3$, $SE=0.3$) en route; most rests lasted no more than a day, but several were longer. The most important rest sites were the Aumannykan area in Russia, and the Qiqihar Baicheng area, Shuangtaizi River delta and Yellow River delta, all in China.

3.4 White-naped crane

Since the early 1990s, the complete migration of 20 cranes and the partial routes of another 11 have been tracked from their breeding sites in far east Russia (16 birds) and one of their wintering sites in Izumi, Japan (15 birds) (Higuchi et al., 1996; Higuchi et al., submitted). The post-breeders from Russia spent 8–68 days ($x=38$, $SE=6$) migrating 2 205–2 897 km ($x=2\ 558$, $SE=63$), with 4–12 ($x=8$, $SE=1$) stopovers on the way. They spent 1–52 days ($x=6$, $SE=1$) at stopover sites, where most birds took multiple short but only one long rest. Important stopover sites included Bohai Bay and the Yellow River delta, the Three Rivers Plain and Tianjin, all in China, as well as the Korean DMZ and Lake Khanka. Most birds wintered at Izumi and around Poyang Lake.

When white-naped cranes migrated from Izumi, it took them 17–85 days ($x=44$, $SE=8$) to travel 1 820–2 728 km ($x=2\ 278$, $SE=90$) to their breeding areas on the Three Rivers Plain and in Zhalong Nature Reserve near Qiqihar, China. On migration, these birds spent 1–53 days ($x=9$, $SE=2$) at 1–9 ($x=5$, $SE=1$) stopover sites. Most birds made only one longer stopover. Important rest sites were around the Korean DMZ (Cholwon, Panmunjom), Lake Khanka, Kumya and Sonbong (Fig. 3).

3.5 Oriental white stork

The partial migrations of four storks and the complete migrations of another nine captured in the Amur region,

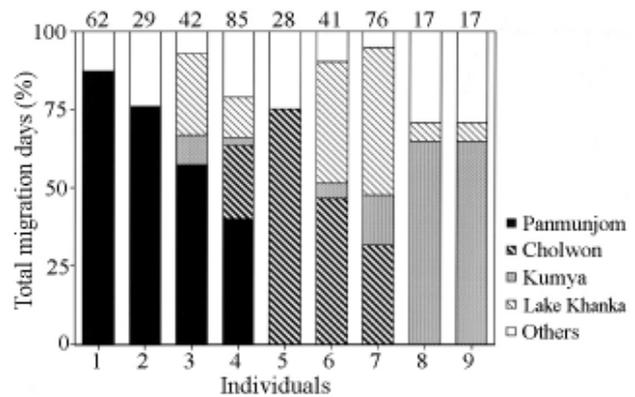


Fig. 3 The percentages of total migration days that nine white-naped cranes spent resting at four important stopover sites when tracked in 1992 and 1993

Numbers above columns=total migration days for each crane. Columns 8 and 9 represent a family that migrated together; other birds migrated separately. From Higuchi et al. (1996).

Russia, were tracked in 1998–2000 (Higuchi et al., 2000; Tamura et al., 2000). Eight of the nine storks wintered on the Yangtze River floodplains, including Dongting, Poyang, and Shenjin Lakes, and moved around between wintering sites. One stork, however, unexpectedly wintered southwest of Beijing (Shimazaki et al., 2004). On leaving their natal areas, storks flew 2 455–3 208 km ($x=2\ 759$, $SE=86$) over 60–117 days ($x=103$, $SE=6$), stopping at 3–6 rest sites ($x=4$, $SE=0.1$) on the way to their wintering grounds on the Yangtze plain and spending 2–68 days ($x=20$, $SE=3$) at these sites. Oriental white storks tended to take longer breaks at several staging sites and make shorter daily flights than the cranes. Migrating storks followed river drainages (including the Amur/Heilongjian, Nenjiang, Diaqinhe, Liao, Luanhe, Shuangtaizi and Yangtze Rivers), and used Bohai Bay heavily (Higuchi et al., 2000; Shimazaki et al., 2004).

4 Discussion

Our research demonstrates that satellite-tracking is effective in monitoring the long distance movement of migratory wetland birds, and can be used to identify previously unknown migration routes, staging areas and stopover sites. Further, the combination of this technique with others, such as remote sensing and simulation modeling (Tamura et al., 2000; Shimazaki et al., 2004), provides sophisticated technology for application to conservation issues.

The species of cranes that were tracked appear to have similar migration strategies. All tended to travel as far as they could in the shortest time possible. Habitats along the migration pathways of demoiselle cranes are rather inhospitable, probably rendering stopovers unviable (Kanai et al., 2000). However, the migration routes of other species traversed less extreme habitats, suggesting that rapid migration with few stops is strategic rather than necessary. In contrast, the oriental white stork flew much shorter distances between stops, and rested for consistently longer

periods than the cranes. This key difference in strategy could be correlated with the tendency of cranes to store fat, while storks may not (Berthold et al., 2001b). If this is the case, oriental white storks may be especially sensitive to the destruction of stopover sites along their migration routes, because it limits their food resources.

Given that the species we tracked are obligate wetland birds, it is not surprising that we have recorded more than one species using the same wetland areas. Bohai Bay, in particular, appears to be a critical habitat for the birds we studied, and all species except demoiselle cranes made extensive use of this area when migrating. Other areas that are similarly important are locales along the Amur River and at Lake Khanka, the Korean DMZ, Poyang Lake, the Qiqihar area, the Shuangtaizi River including the delta, the Three Rivers Plain, and the Yellow River delta.

Common use of particular sites by multiple species of wetland birds is to be expected, based on the tracking of major migration flyways across Asia. Recognition of such flyways has led to their being advocated as useful management units for conservation purposes (APMWCC, 2001). However, because many sites were used by each species alone in our study, and because of potential differences in migration strategies, species-specific protection measures must also be taken into account with migration networks. Regardless of whether migrating birds gravitate to flyways, it is necessary to treat migration routes as a network of functionally connected sites. If any one site is lost from the network, birds may be unable to complete their migrations successfully.

There are numerous threats to important sites used by migrating cranes and storks in east Asia. Our study identified the Korean DMZ, in particular, as critically important. Although currently secure and including some protected areas, development and human disturbance associated with reunification of the two Koreas has the potential to degrade the region generally. The Three Rivers Plain in China is another particularly important yet sensitive area, where development appears to be continuing apace with little provision for conservation.

Those reserves that are established may be insufficient to protect birds. This may be because the birds frequent sites outside the areas designated to protect them, as at Lake Khanka and Poyang Lake (Higuchi et al., 2004), or because enforcement of protective regulations is altogether inadequate (Chong et al., 1994; Higuchi et al., 2004; Kanai et al., 1994; Scott, 1989). Upstream disturbances must also be considered, particularly the damming of wetland feeder streams. The Three Gorges dam currently under construction on the Yangtze River will bring massive changes in upstream water levels, as well as greatly affecting downstream flows. Although our study species do not occupy areas around the dam, they will probably be affected by changing hydrologic regimes downstream and disruption of food bases.

The diversity and severity of conservation issues,

combined with relatively sensitive political and economic situations and a huge spatial scale, render conducting scientific research and conservation in Asia difficult. However, addressing the conservation challenges in this region can be greatly facilitated by applying satellite-tracking to long-distance migrant birds. Beyond technical and logistic difficulties, the greatest challenge lies in applying research results to achieve practical and effective conservation outcomes. As the migration routes of large wetland birds become known around Asia, the greatest obstacle to their preservation will not be lack of knowledge but lack of human action in conservation.

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S12-2 Conservation measures based on migration research in white storks (*Ciconia ciconia*, *Ciconia boyciana*)

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Abstract For over a decade, we have been using satellite tracking to study the migration of white storks (*Ciconia ciconia*) along their eastern migration route from Europe to southern Africa. About 120 individuals have been monitored by satellite-tracking to determine the route of the journey, choice of staging areas and overwintering patterns. Satellite-tracking not only confirmed migration routes formerly elucidated by ringing but also enabled us to detect new routes to western Sudan and Chad and identify large staging areas in this region. The most important results of the tracking are the identification of 15 major staging areas during migration and wintering, for which specific conservation measures are being implemented in a “stepping-stone” project in accord with the Bonn Convention. We have also investigated the migration physiology and stopover-site ecology of the storks. Because storks migrate to northeastern Africa with minimal fat stores and very low food intake, resting areas on this sector of their route, are currently in greater need of protection than feeding grounds. In a second, smaller study, oriental white storks (*Ciconia boyciana*) are being tracked from Siberia to locate their overwintering grounds in China, and identify and implement appropriate conservation measures for this species.

Key words White stork, *Ciconia ciconia*, Oriental white stork, *Ciconia boyciana*, Migration, Satellite-tracking, Conservation

1 Introduction

In 1991, when sufficiently small mini-transmitters became available, we applied the method of satellite-tracking to investigate the migration of the white stork (*Ciconia ciconia*). Since then, we have been investigating the flight path and timing as well as the staging ecology of this species (Berthold, 2001). We have concentrated mainly on the “eastern” storks, i.e., those that migrate from the eastern and east-central parts of Europe through Israel to eastern Africa. The main aims of our study were (1) to compare data based on satellite tracking with those obtained by 100 years of stork ringing, (2) to elucidate migration, staging and wintering strategies using satellite-tracking and the white stork as a model species as much as possible, and (3) to provide basic biological data for the development of conservation measures for this endangered species.

Even in the earliest years of the study, the multitude of transmitted coordinates allowed us to answer, for the first time, questions about migration speed, distance covered per day, choice of resting sites and much more (van den Bossche et al., 2002). On the basis of these data, we gradually developed a picture of white stork migration that was considerably more precise than could ever have been gained from analyses of ring recoveries, even after 100 years of ringing activity (Berthold et al., 2000). Exact evaluation of the many coordinates derived from various places along

the eastern route, from Europe into the Sudan, revealed clearly the most important staging areas of these storks.

These results have been incorporated into a so-called stepping-stone project — a special agreement within the Bonn Convention. The stepping-stone project aims to increase the number of conservation areas along the bird migration routes between Europe and Africa, in order to allow the traveling birds to rest undisturbed and to provide them with food where necessary (Müller-Helmbrecht and al-Janabi, 1999).

2 Methods

Our satellite tracking studies were based on the ARGOS system, and mini-transmitters were obtained from Microwave Telemetry, USA. Most of the storks were equipped with 35 g solar-powered mini-transmitters. Fat deposition in white storks was quantitatively investigated in a pilot study based on Magnetic Resonance Imaging (MRI). For technical details, trapping procedures of storks, analyses of basic ARGOS data and MRI techniques, see Berthold et al. (2001).

3 Results and discussion

3.1 Satellite-tracking

We have now monitored 120 white storks by satellite tracking. Figure 1 shows the migration routes of 30 eastern

storks reconstructed from satellite location data. The great majority of the eastern storks start their migration in August, between the beginning and middle (juveniles) or middle and end (adults) of the month. They fly southeast, reaching the Bosphorus after an average of 10.2 ± 2.7 ($n=47$) days, Israel after 15.0 ± 2.6 ($n=41$) days and the northern Sudan after 20.3 ± 3.5 ($n=41$) days (Kaatz, in prep.). From there about half of the birds continue southwards into staging areas southeast of Khartoum already identified from ringing (Berthold et al., 2001). The rest travel to southwest, into western Sudan and Chad. Because no ringing recoveries had ever come from these areas, it was left to satellite-tracking to find them (Berthold et al., 2001). It is vital that these areas are included in future conservation planning for the storks.

The first substantial pauses for rest along these two routes are made at sites reached after about three weeks, when the storks have traveled c. 5 000 km to eastern Sudan or c. 5 500 km to western Sudan and Chad. The time spent in these regions presumably depends on the food supply; birds rarely overwinter there. Most storks then depart again in November or December, flying over Uganda to Kenya and Tanzania and in many cases even further, along a very narrow migration corridor into southern Africa (Fig. 1).

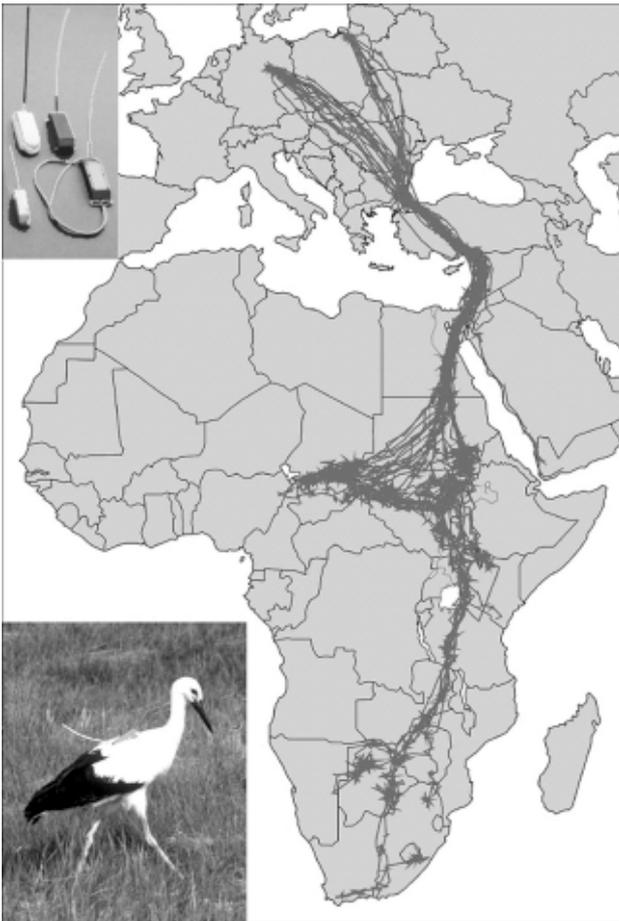


Fig. 1 Migration routes of 30 white storks from central and eastern Europe, as determined by satellite-tracking. From Berthold et al. (2000). Inset: satellite transmitters before (above) and after (below) deployment on white storks.

3.2 Stopover sites

The most important — and as yet largely unprotected — areas used by the storks for overnight and longer stopovers along the eastern migration route are shown in Fig. 2. From north to south, these are (1) the regions before and after the Bosphorus crossing in Turkey, (2) the northern shore of the Gulf of Iskenderun, (3) an area often disturbed by duck hunting east of Damascus in Syria, (4) the Bet She'an Valley in Israel, and (5) the regions before and after the crossing of the Gulf of Suez in northern Egypt. However, evaluation of the satellite data has revealed further stopover concentrations along the migration routes in central and southern Africa. The recently discovered resting sites in western Sudan and Chad (6–8) are particularly important for relatively long sojourns, as are the known regions in eastern Sudan (9,10). In Tanzania, the Serengeti serves as winter quarters in some years, but is usually used only for brief rests on the outward and homeward journeys. Southeast of the Serengeti, our satellite-tracking data have revealed a frequently used resting site east of Tabora (11).

Conservationists in Tanzania are currently working to have the region east of Tabora placed under protection.

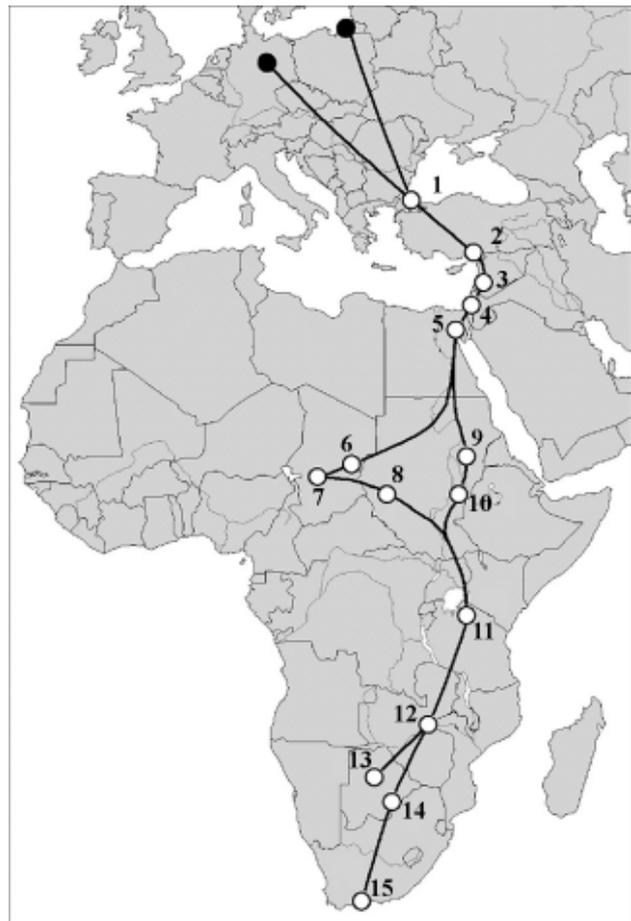


Fig. 2 Stopover and resting places used by migrating white storks

At the border between Zambia, Zimbabwe and Mozambique there is another clumping of coordinates, indicating a further crucial rest area (12). On several occasions we have lost contact with transmitter-bearing storks in this area, presumably because they have succumbed to hunting. Because the migration corridor is particularly narrow in this region, conservation measures are urgently needed there. The staging areas for relatively long sojourns in southern Africa are either in protected areas, such as the Okavango Delta in Botswana (13), or cultivated fields (14,15) where the storks are welcome because of the large quantities of insect pests that they eat.

3.3 Ecophysiological studies

Until recently, little was known of stork behavior in staging areas, patterns of weight change and extent of fat reserves during migration. Studies of behavior in staging areas conducted over three years by M. Kaatz on the route from breeding areas in northeastern Germany and Poland to Turkey, and over five years in Israel by van den Bossche et al. (2002), have produced much data on the availability and intake of food. To obtain data on weight changes and fat deposition over an entire year, moreover, we kept 12 hand-reared white storks from the eastern population in large aviaries and simulated the photoperiod at their natural winter quarters during the boreal winter. Food (day-old chickens, fish and insects) was provided daily ad libitum. The birds were weighed once a month, and their fat content measured by Magnetic Resonance Imaging, MRI (Fig. 3). By this method, the cutaneous/subcutaneous and visceral fat stores can be quantified with high precision (Berthold et al., 2001). Data from the experimental birds were then com-

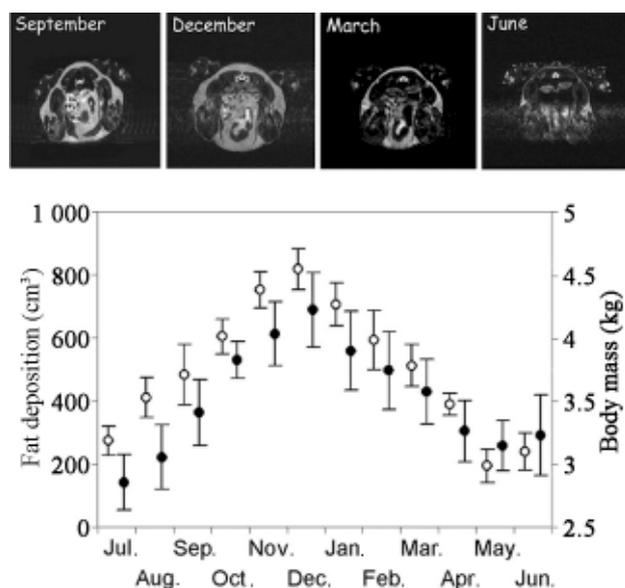


Fig. 3 Magnetic resonance imaging of white storks

Upper: virtual dorsoventral cross section at the level of the proventriculus and gizzard. Lower: annual cycle of body weight (black dots, means and standard deviations) and of abdominal fat deposition (white circles) in experimental white storks. From Berthold et al. (2000).

pared with values from larger samples of wild storks obtained in eastern Germany and Israel.

The most important results of this research is as follows. White storks have meager fat reserves when they begin their outward migration in August, starting with a breeding-period weight of $3\,365\text{ g} \pm 382$ ($n=23$). During the outward journey, very little food is consumed, until the birds pause for a fairly long time on the main staging areas in the Sudan and Chad. As comparative body-weight data for resting storks in Israel show, the migrating white storks lose weight on the trip from breeding grounds to northeastern Africa by as much as 15 % of body mass. During their main overwintering period between November and January, our test group attained the highest fat-deposit values, weighing to $4\,253\text{ g} \pm 280\text{ g}$. Very few comparative findings are available from the field for this period, but what little data there is also indicates considerable fat deposition (Berthold et al., 2001). We interpret this as an adaptation to the extremely variable and unpredictable overwintering conditions in Africa. By the time of spring migration northwards, the fat-deposit and weight values in our experimental captive birds had fallen again to the same levels as at the onset of autumn migration.

This unusual mode of migration — traveling largely without fat reserves or food intake until arrival in northeastern Africa — has the following implications for the step-



Fig. 4 Migration routes of two oriental white storks (solid line and dashed line) from their breeding grounds in Russia to their wintering area in China, as determined by satellite-tracking

From van den Bossche et al. (2001).

ping-stone project. Along the migration routes to North Africa, conservation areas that mainly provide places to rest are sufficient, as the storks do not need any special feeding grounds. Resting areas that are safe, however, are urgently needed. Rest areas must be free of disturbances that would cause storks, migrating with minimal energy reserves (which may be favorable for their gliding flight), to lose what reserves they do have to complete migration successfully. The major staging areas in Africa (Sudan, Chad, southern parts as far as South Africa), moreover, are where special feeding grounds must be provided as well. This is a difficult task, and partly outside of the frame of the Bonn Convention; it will require extra, special effort.

3.4 Satellite tracking oriental white storks

We are also using satellite-tracking to study the migration of oriental white storks in Asia. The main goal of this project is to track transmitter-bearing birds that breed in Siberia in order to find out where they winter in China and how they can be protected there (van den Bossche et al., 2001). Results so far show that Lake Poyang in Jiangxi province is an important overwintering region. The fact that the eight tracked individuals constantly wander around at winter quarters suggests that the food supply in this region may be inadequate, requiring the storks to search around

continuously (Fig. 4; van den Bossche et al., 2001).

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S12-3 Changes in red-crowned crane (*Grus japonensis*) habitats in Yancheng Nature Reserve in the last 20 years

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Abstract Over the last 20 years we studied changes in winter habitat use by red-crowned cranes *Grus japonensis* at Yancheng Nature Reserve, China. The number and distribution of red-crowned cranes, as well as habitats occupied, were recorded. In the 1980s, the birds occupied almost all tidelands in the Reserve, but by the early 1990s had become confined to middle and southern sectors, and then, in the late 1990s, to the center itself, the core area of the Reserve. Currently, more than 70% of cranes occur there and in its surrounds, over an area of about 200 km². Over the past two decades, habitats used by the cranes have changed from original wetlands (1980s) to artificial and semi-artificial wetlands (1990s) and now artificial wetlands, semi-artificial wetlands and wheat/paddy fields (1999–2000). Wheat/paddy fields began to be used by the cranes in 1995, and by the winter of 2000 were occupied by nearly 40% of the Reserve's total population. Changes in habitats and habitat use are due to large-scale development of the tidelands. We consider that, with suitable management, artificial wetlands are a viable alternative to natural wetlands for red-crowned cranes at winter quarters.

Key words Red-crowned crane, *Grus japonensis*, Habitat change, Habitat use, Yancheng Nature Reserve, China

1 Introduction

The red-crowned crane (*Grus japonensis*) is an endangered species endemic to North-East Asia, where it survives in a migratory continental population and a resident non-migratory population in Japan (Meine and Archibald, 1996; BirdLife International, 2001). Its present population stands at 2200, of which about 1 600 belong to the migratory population (Chan, 1999). Yancheng Nature Reserve in China is one of its most important wintering grounds: nearly 1000 birds have been wintering there in recent years, more than half of the migratory population.

Due to the sedimentation of silt carried by the Yangtze River, the tidelands at the southern part of Yancheng Nature Reserve extend eastward to the sea, creating large expanses of natural wetlands that are good habitat for red-crowned cranes (Ma et al., 1998). Over the last two decades, however, simultaneous pressure from a growing human population and an urgent need for land resources has led to both reclamation of tidelands and concomitant development in the Reserve. Intensive exploitation of the tidelands continues to destroy the natural wetlands, formerly the main habitat of the red-crowned crane (Ding and Zhou, 1982). Because the rate of land reclamation is much faster than natural tideland expansion, the area of natural wetlands continues to diminish. The changes in land use have already affected the crane and its habitat seriously (Ma et al., 1998), because of which Reserve managers need to know

how to conserve the crane as the tidelands are developed.

Accordingly, this study aims to (1) understand how the changes in habitat have affected the distribution and habitat use of the red-crowned crane at Yancheng Nature Reserve, (2) analyze the effects of development activities on the cranes, and (3) provide conservation strategies for sustaining the crane in the future.

2 Materials and methods

2.1 Study area

Yancheng Nature Reserve is located in the central part of the eastern tidelands of China, between 32°34'N and 34°28'N, and 119°48'E and 120°56'E. The coastline of the Reserve is 584 km long and the total area covered is about 4 530 km². The major conservation targets of the Reserve are management of the red-crowned crane and other waterbirds, together with their habitats.

The tidelands are important for the crane. Coincident with the natural expansion of the tidelands, the vegetation shows successional sequence. Its pioneer plant is *Suaeda salsa*, changing to *Aeluropus litoralis* in a transitional zone to the climax community of *Imperata cylindrica* and *Phragmites communis* (Ma et al., 2000). In recent years, *Spartina alterniflora*, an introduced species from America, has spread rapidly and now covers large areas. An abundant zoobenthos (crabs, snails, clamworms) and aquatic

animals (fishes, shrimps) provide food resources for the crane (Liu, 1990).

2.2 Bird counts

Every October, red-crowned cranes arrive on the Reserve from their breeding grounds, and remain until March. Bird counts were conducted in every December or January over the last two decades when the numbers and habitats of cranes are stable. To cover the entire area of the Reserve, two to four groups of observers conducted counts simultaneously, using 30× telescopes. The numbers and habitats occupied by cranes were both recorded, and the point location of cranes marked on landuse maps (1:10 000). After 1997, the locations of cranes were determined by GPS.

2.3 Habitat analysis

Following Ma et al. (1999), the major habitats of red-crowned cranes were classified into six types: saltworks, aquacultural ponds, reed lands, grassy tidelands, beaches with salt-living wormwood, and wheat/paddy fields. The number of cranes in each habitat type was recorded. All habitats used by cranes were regrouped into four further types to add a historical dimension: natural wetlands, semi-artificial wetlands, artificial wetlands, and wheat/paddy fields. They are categorized as follows: (1) natural wetlands, formed naturally and without disturbance from human activities, (2) semi-artificial wetlands, formed naturally but affected by human activities, such as reed-harvesting, and catching of crabs, mollusca and gastropods, (3) artificial wetlands, converted from other types of land use into wetlands and dominated by human activities, such as fishponds and aquaculture, and (4) wheat/paddy fields, which are uncultivated after harvest and through the winter, and available to cranes for foraging then. In these fields, the cranes forage for seeds and malts.

Landuse data for the Reserve were collected from local government sources. Satellite imagery (Landsat5 TM) of the Reserve was also examined in 1984, 1992 and 2000 to map landuse conditions in the Reserve. The area of developed land and the location of developments on the tidelands were also determined then; the area of developed tidelands was calculated using Arcview GIS version 3.2 (ESRI 1999).

3 Results

3.1 Changes in numbers of red-crowned cranes

In the early 1980s, only about 400 red-crowned cranes were recorded in the Reserve. In the two decades since then, their numbers have, despite fluctuations, increased gradually. In the winter of 1996, their numbers reached 1 020, the largest number yet recorded. Since then, numbers have remained stable at about 800–1 000.

3.2 Changes in distribution of red-crowned cranes

Significant changes have occurred in the distribution of the cranes over the past two decades. In the early 1980s,

cranes could be found in most parts of the Reserve, although their numbers were low. From then on, they began to become concentrated in southern sectors. In the early 1990s, most cranes occurred in central and southern parts which, from 1985 to 1996, held 40% of the population; cranes in the north occurred only at saltworks. By the late 1990s, all had become concentrated in the central part of the Reserve, that is, the Reserve's core area. In the winter of 2000 and 2001, more than 70% of cranes were present in the core and surrounding regions, within an area of about 200 km² and covering about 4% of the total area of the Reserve.

3.3 Changes in habitat use by red-crowned cranes

In the early 1980s, the main habitats used by cranes were grassy tidelands and beaches with salt-living wormwood. Nearly 80% of cranes were recorded in these two types of habitats. The number of cranes on beaches with salt-living wormwood decreased in the 1990s, and those on grassy tidelands decreased similarly after 1996. In the winter of 1995, three cranes were recorded in wheat fields. This was the first time that cranes were found selecting farmland as habitat. In the winter of 1996, the number of cranes recorded there increased to 95, to about 10% of the total crane population. In the winter of 1999 and 2000, wheat/paddy fields finally became important habitats for cranes. In these two years, 37.2% and 38.1% of the total crane population, respectively, was recorded there. Some cranes searched for wheat seeds and malts in wheat fields, while others foraged by gleaning in harvested paddy fields.

In 1982, natural wetlands were the major habitats of red-crowned cranes, with 61% of cranes recorded there. In the late 1980s, this changed to artificial and semi-artificial wetlands. Thus, in 1988, about 47% of cranes were recorded on natural wetlands while the remainder, more than half, selected artificial and semi-artificial wetlands. In the winter

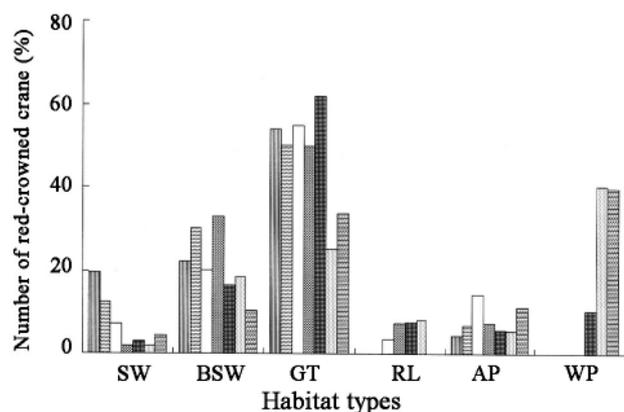


Fig. 1 Habitat use by red-crowned cranes in Yancheng Nature Reserve, showing % of total crane population in each habitat type in different years

SW = saltworks, BSW = beaches with salt-living wormwood, GT = grassy tidelands, RL = reed lands, AP = aquacultural ponds, WP = wheat/paddy fields. Column legend for different years: vertical lines = 1982, diagonal dashes = 1985, open bars = 1988, shaded bars = 1993, cross-hatched bars = 1996, stippled bars = 1999, horizontal lines = 2000.

of 1995, 564 cranes were recorded on artificial and semi-artificial wetlands, about 71% of the total crane population in that year. Since 1999, artificial wetlands, semi-artificial wetlands and wheat/paddy fields have become the major habitats for cranes; only about 10% of cranes are now recorded in natural wetlands. These shifts in habitat use are shown in Fig. 1.

3.4 Changes in land use in the Reserve

Tidelands in the Reserve have been reclaimed and developed over the past two decades. In the early 1980s, development was concentrated in the north, where more than 50% of the tidelands were converted to saltworks and farmlands in Xiangshui and Binhai counties (Fig. 2). At that time, most of the tidelands in the central and southern parts of the Reserve remained in natural condition. From the mid 1980s, however, large-scale development began in central sectors, particularly in reed beds and aquacultural ponds.

Then, the southern parts of the Reserve became subject to development, and by 2000, about 75% of the tidelands had been reclaimed for exploitative development. Currently, the natural wetlands in the Reserve remain as beaches with salt-living wormwood, exposed tidelands and other areas with little human disturbance. Due to harvesting, most of the reed beds and grassy tidelands have become semi-artificial. The percentage of Yancheng Nature Reserve that has been subjected to development is shown in Fig. 2.

4 Discussion

Due to the deposition of silt and human activities on the tidelands, the environmental conditions of Yancheng Nature Reserve have continued to change during the past two decades. The distribution of red-crowned cranes in the Reserve follows these changes. In the 1980s, the natural wetlands in the northern part of the Reserve gradually disappeared due to development. Because of the sedimentation of silt on tidelands in the southern sector, large areas

of new tidelands formed there rapidly. Though some development began there as well, large areas still remained to provide natural wetlands for cranes; and the cranes moved there accordingly. After the mid-1990s, large-scale development in the southern sector reclaimed large areas of natural wetlands, changing them into farm lands. The loss of natural wetlands and intensive human disturbance then caused the cranes to move to the central parts of the Reserve.

Although development has now begun in this core area, its relatively low intensity has not disturbed the cranes much. Moreover, most development there is concerned with establishing artificial wetlands, such as aquacultural ponds and waterfowl lakes, which provide habitat for cranes. Human-provided foods may also be important to the cranes there (Lu, 1998). More than 100 cranes are now commonly recorded foraging for food provided to them daily at artificial feeding sites. Artificial feeding is important for maintaining a stable population of red-crowned cranes in the core area of the Reserve, especially later in the winter, when natural food resources become depleted. Due to large scale of tideland reclamation and development elsewhere, human-provided foods help to maintain stable populations of cranes over the rest of the Reserve as well.

This study shows that artificial wetlands, semi-artificial wetlands and wheat/paddy fields have now become the major wintering habitats of red-crowned cranes, and that human-provided foods are an important resource supplement. This situation is similar to that in Japan, where red-crowned cranes depend on artificial wetlands and human-provided foods (Ohsako, 1994). Nevertheless, we conclude that the habitat changes for red-crowned cranes in Yancheng Nature Reserve reveal that development has had serious effects on their feeding ecology, and that their natural wetland wintering habitat has been largely lost in the past two decades.

By foraging in wheat fields, red-crowned cranes are

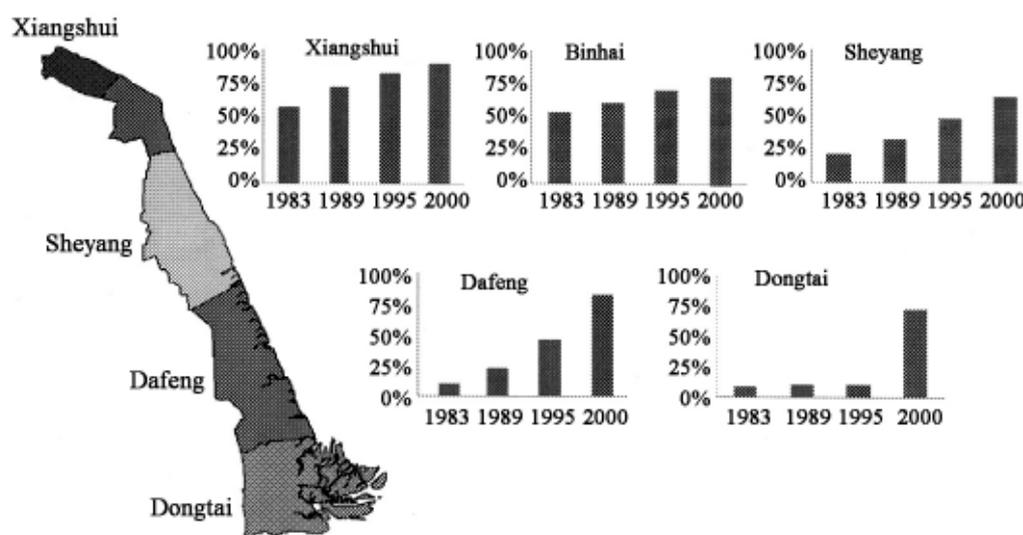


Fig. 2 Developed area (%) of tidelands in Yancheng Nature Reserve

further threatened by agrochemicals and pesticides. Every year from 1996 onwards, cranes have been found poisoned from eating treated seeds or malts in wheat fields. Poisoned cranes have also been found frequently at other wintering grounds and stopover sites (Ma et al., 2000). Conservation measures should be taken by the Reserve and local government to allay these threats.

Although the development of tidelands has had serious effects on the red-crowned crane and its habitats, it has also brought enormous economic benefit to the local communities (Ma, unpubl.). How to manage the relationship between economic development and the conservation of red-crowned cranes is an important issue facing Reserve managers and local government (Ma et al., 1998). In the interim, we conclude that artificial wetlands, such as aquacultural ponds, should be considered as having significant potential in the Reserve, economically and for the cranes. Scientific management should also be undertaken to limit disturbance to artificial wetlands coincident with human activities, and to provide abundant food resources for red-crowned cranes.

Acknowledgements We thank Yancheng Nature Reserve for facilitating our field investigation and Dr. Masayuki Tamura for providing satellite images of the Reserve. This study was supported financially by the International Crane Foundation and the UNESCO Young Scientist Award.

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S12-4 Distribution of red-crowned cranes, *Grus japonensis*, in the Cholwon Basin, Korea

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Abstract Distribution patterns and wintering populations of red-crowned cranes (*Grus japonensis*) were studied in the Cholwon Basin near the DMZ (Demilitarized Zone) on the Korean Peninsula from 1992–1998. Study areas were located at 38°5'N, 127°3'E in the administrative districts of WolChong-ri, Taema-ri and Hagal-ri. They comprised mainly rice paddies and harvested grain fields (rice stubble). These are the principal habitat types used by red-crowned cranes during their spring and autumn migrations, as well as when wintering. I developed habitat indices based on digital models constructed from environmental factors such as elevation, slope and habitat patch size. These indices were then used to relate patterns of occurrence of red-crowned cranes to habitat types. The spatial distribution of cranes differed between years. Variation in slope and elevation affected the horizontal visibility of wintering cranes. Habitat use indices were correlated positively with elevation and negatively with slope and distance between feeding and roost sites. Wintering cranes preferred to inhabit areas with less variability in slope and at higher altitudes to maximize horizontal visibility.

Key words Red-crowned crane, *Grus japonensis*, Horizontal visibility, Habitat use, Disturbance, DMZ, Korea

1 Introduction

Among the fifteen species of cranes, seven species — red-crowned crane *Grus japonensis*, white-naped crane *Grus vipio*, hooded crane *Grus monacha*, sandhill crane *Grus canadensis*, Siberian white crane *Grus leucogeranus*, Eurasian crane *Grus grus*, and demoiselle crane *Anthropoides virgo* — have been recorded on the Korean peninsula (Austin, 1948; Pae and Won, 1994; Pae, 1994; Pae et al., 1995, 1996), especially near the DMZ (Demilitarized Zone). The DMZ was established after the Korean war in 1953. No humans are allowed to enter it for military reasons. Consequently, the DMZ has functioned as an undisturbed nature reserve between North and South Korea ever since. Since the 1970s, agricultural activities have been permitted in the Civilian Control Zones (CCZ) on the southern boundary of the DMZ, and agriculture is established in areas adjacent to it. An abundance of rice remaining after harvest, access to safe refuge areas in the nearby DMZ and little human disturbance in the winter, have enabled wildlife, including cranes, to concentrate in these areas (Koo, 1986; Won, 1981a, b, 1988).

The three species of cranes that winter in Korea — red-crowned, white-naped and hooded cranes — have been designated as Natural Monuments, and their major wintering site, Cholwon Basin, has been designated as Natural Monument No. 245. Cholwon is the only area where both red-crowned and white-naped cranes winter, and Cholwon is the southern limit of red-crowned crane wintering grounds on the Korean peninsula.

Wintering red-crowned cranes have been placed in a very difficult situation by the recent development of lands near the DMZ. Despite this, the wintering population has increased steadily since 1992 through 1998. I studied the cranes at their wintering sites around Cholwon, near the Korean DMZ. Study areas at Cholwon were located at 38°5'N, 127°3'E in the administrative districts of WolChong-ri, Taema-ri and Hagal-ri (Fig. 1). The aim of my study was to clarify the relationship between physical geographic characteristics and distribution patterns of red-crowned cranes, which may ultimately contribute to their protection and management.

2 Materials and methods

I divided the study area into eight patches to conduct censuses. Each patch (site) was named using initials of the appropriate administrative district or facility. The distribution patterns of migrant or wintering red-crowned cranes in relation to habitat were obtained from habitat-use indices modified from Alisauskas et al. (1988). The number of cranes was recorded daily in each patch and the data converted into habitat-use indices, in terms of percentage occupation. Habitat-use data were arcsin-transformed for analysis (Sokal and Rohlf, 1981), and habitat-occupation indices produced from the following formula

$$H_i = (N_i S_i) / (\sum N_i S_i) \times 100,$$

where H represents the habitat-use index value, N_i = number of observations at each site (i) and S_i = mean number of cranes/number of observations at each site (i).

Cranes are tall birds, which become aware of approaching threats and disturbances mainly through sight. In the absence of food restriction, their wintering distribution may be influenced by the extent of their horizontal line of sight, which is defined as the straight-line distance to the nearest obstruction greater than 1 m in height (Ambruster, 1990). The study area was located near the DMZ which is subject to strict military regulation and where few buildings and obstructions are permitted. Therefore, topographical slope and elevation are the main factors affecting horizontal visibility. For this reason, a National Geography Institute map (1:50 000) was digitized, and from it the size of each study patch and its variations in slope and elevation were determined using the Spatial Analyst extension of ArcView GIS (ESRI 1999). The area of each observation site, distance from roosting sites and refuges in the DMZ, and variation in slope and elevation were calculated in meters. Distribution patterns were obviously affected by construction of a new road in 1995–1996. Therefore, two different temporal patterns (less disturbed, 1992–1994; more disturbed, 1996–1998) were compared by habitat-use indices to allow for disturbance, and analyzed for correlations with elevation, slope, and distance from roosting sites and refuges in the DMZ. Habitat-use data were acrsin-transformed for analysis (Sokal and Rohlf, 1981).

3 Results

3.1 Elevation and slope analysis

In the Cholwon basin, 29.4% of land is in the 150–200 m above sea level range, and 34.3% between 200–250 m. The average elevation of my study area is 250 m, with a range of 50–300 m between patches. The Ice Cream Mountain site (ICM) is the highest location, at 228.8 ± 13.2 m a.s.l., and the

Chungto-Dong site (CTD) the lowest, with an average elevation of 173.6 ± 10.0 m. Variation in elevation also affects slope. 45% of the study area is 0–3 % in slope, and another c. 50% <5%. Among the study sites, however, slopes were relatively low: Cholwon Station (CWS) $0.3\% \pm 0.6\%$, ICM $1.0\% \pm 1.6\%$, White Horse Monument (WHM) $1.4\% \pm 2.2\%$ and the Meteorological Observatory (MO) $1.7\% \pm 2.1\%$.

If cranes prefer locations of higher elevation and relatively low variation in slope to increase horizontal sight, CWS should be the most preferred area, followed by ICM, WHM and MO; and Sangto-Dong (STD), Chungto-Dong (CTD) and Taejo-Dong (TJD), which have relatively high variation in slope, should be least preferred. These predictions were largely borne out (Table 1).

3.2 Changes in habitat use

Habitat use changed between 1992–1994 and 1996–1998, before and after road construction (Table 1). In 1992–1994, cranes used ICM more than other study sites. CTD was the second most used area, closely followed by CWS and MO. In 1996–1998, ICM was still the most used area, but the differences in percent use of ICM compared to the next most used habitats were much greater. WHM and MO followed ICM as the second and third most used habitats. CWS and TJD are especially close to the newly constructed road, and were more affected. Yet, although road paving also crossed ICM, its habitat use increased more than two-fold. Habitat use across sites showed no significant correlation with patch size in 1992–1994 ($r=0.385$, $P > 0.05$), but was correlated in 1996–1998 ($r=0.475$, $P < 0.05$).

3.3 Horizontal visibility and correlations with elevation and slope

Habitat-use indices were positively correlated with

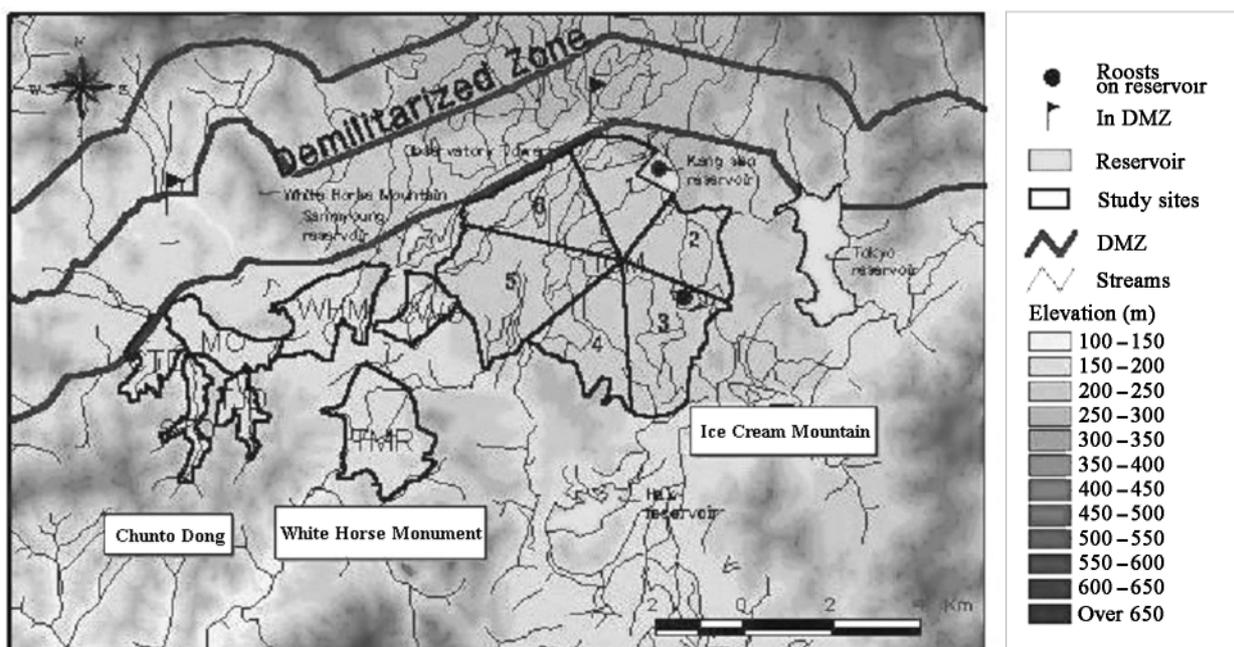


Fig. 1 Map of study area

elevation, and negatively correlated with slope and distance between feeding sites and roost sites (Table 2). Before road construction in 1992–1994, habitat use was not significantly correlated with elevation, slope or distance between roosting and feeding sites. After road construction, however, it was correlated positively with elevation and negatively with slope variation and distance between feeding sites and roosting sites in the DMZ. Roost 1 and Roost 2 were both located in the DMZ. Distances between feeding and roosting sites were 8–11 km for Roost 1, and 2–5 km for Roost 2. Habitat use decreased with increasing distance from Roost 2. Wintering cranes often appeared to gather near the DMZ boundary for safety.

4 Discussion

The differences in distribution patterns between less (1992–1994) and more (1996–1998) disturbed periods were evidently influenced by horizontal visibility, disturbances from the road, and the distance between roosts and feeding sites. Shenk and Armbruster (1986) consider that horizontal visibility and roost site characteristics (see below) are important for the safety of cranes. Horizontal visibility is represented by the straight-line distance to the nearest obstruction greater than 1 m in height, or over 5.6% in slope (Armbruster, 1990). Thus it is affected by variation in slope and elevation. Consequently, sites of less variable slope and higher elevation should enhance horizontal visibility.

Table 1 Changes in habitat use by migrant and wintering red-crowned cranes in Cholwon between 1992–1994 and 1996–1998

Study sites	Habitat occupation (%)	
	1992–1994	1996–1998
ICM (Ice Cream Mountain)	30.3	70.9
CWS (Cholwon Station)	15.6	1.6
WHM (White Horse Monument)	12.1	13.2
TMR (Taema-Ri)	0.9	0.9
TJD (Taejo-Dong)	8.3	0
STD (Sangto-Dong)	1.6	0.5
CTD (Chungto-Dong)	17.5	0.3
MO (Meteorological observatory)	13.7	12.6
Total	100.0	100.0

Table 2 Spearman rank correlations between habitat use and elevation, slope and distance between roosts and study sites in red-crowned cranes

Habitat use	Elevation	Slope	Roost 1	Roost 2
1992–1994	0.393	–0.326	0.189	–0.521
1996–1998	0.684*	–0.787*	0.323	–0.811**

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

Roost 1 and Roost 2 are located in the DMZ, at different distances from crane feeding sites.

Forty five percent of my study area was at 0–3% in slope. Habitat use of ICM, WHM and MO increased, as expected, due to their relatively slight slope and high elevation. The average slope of CWS is 0.3%, which offered the best wintering ground in terms of horizontal visibility.

Characteristics of roost sites thought to be advantageous to cranes, other than horizontal visibility, include the absence of predators and human disturbance. After road construction, all wintering sites in the study area were fragmented into small patches, reducing buffer zones to disturbance. The newly constructed road actually ran across the middle of the much used CWS site. Because disturbances such as roads may be critical, those created by the road, together with reduction in feeding area, may cause wintering cranes to behave in a density dependent manner. That distance between roosting and feeding sites also affects crane distribution was supported in my study as well, with the finding that roost distance was correlated negatively with habitat use. Migrant or wintering cranes in Cholwon prefer feeding grounds close to the DMZ, so they can use the DMZ as a refuge when they were disturbed.

In terms of protecting areas for the management of cranes in Cholwon, suitable habitat can be determined on the basis of habitat characteristics such as horizontal visibility, disturbance, and the availability of refuges for roosting.

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S12-5 Investigation of the migration routes and habitats of red-crowned cranes and oriental white storks using satellite tracking and remote sensing

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Abstract The movements and habitats of red-crowned cranes (*Grus japonensis*) and oriental white storks (*Ciconia boyciana*) were studied in East Asia using two kinds of satellite-based observation techniques: satellite tracking and remote sensing. A satellite tracking system (Argos) was used to automatically obtain bird location data. Satellite remote sensing was used to investigate land-cover types and environmental conditions of habitat. Bird movements and habitat occupation patterns at breeding sites in the Amur River basin are recorded. Migration routes and important habitats for stopovers and wintering are identified in China. Investigation of habitat occupation patterns in China showed that both focal species used farmlands more frequently than wetlands.

Key words *Grus japonensis*, *Ciconia boyciana*, Habitat type, Migration, Satellite tracking, Remote sensing, Amur River basin, China

1 Introduction

Wetlands that support migratory birds are disappearing at a rapid rate all over the world due to human activity and development (Mitsch and Gosselink, 1993). Such deterioration has made a number of these species vulnerable to extinction. For their conservation, there is an urgent need to inventory the present situation to understand the relationships between ecosystem and patterns of habitat occupation by the birds.

In this study we focus on two endangered species, the red-crowned crane (*Grus japonensis*) and the oriental white stork (*Ciconia boyciana*), both of which inhabit wetlands in east Asia. Threatened by anthropogenic development, they have decreased greatly in numbers over the last several decades; according to current information, their present populations are estimated at about 2 000 and 3 000, respectively (Higuchi, 1998; Litvinenko, 1999). Because these birds are at the top of wetland food chains, protecting them from extinction requires conservation of entire wetland ecosystems. They are, in a real sense, indicators of the condition of natural wetlands and the effectiveness of wetland conservation.

In order to investigate the movements and habitat

requirements of the two cranes, we employed two satellite-based observation techniques: satellite tracking and remote sensing. A satellite tracking system (Argos) was used to obtain bird location data automatically, from which migration routes, movements within local habitats, and important places for breeding, stopover and wintering could be identified. Satellite remote sensing techniques were used to investigate the distribution and environmental conditions of wetlands. Satellite images are useful for observing ground surface conditions over large areas or in areas otherwise difficult of access, such as wetlands. We also combined satellite tracking and remote sensing to analyze relationships between wetland ecosystems and patterns of habitat occupation from 1998–2000.

We first describe bird capture sites and satellite tracking data, and present analyses of bird movements and land-cover conditions in the Amur River basin. Then we analyze bird movements and land-cover conditions in China.

2 Methods, results, discussion

2.1 Capturing birds and using Argos terminals

In each July from 1998 to 2000 we deployed small platform transmitter terminals (PTTs) on 12 adult red-

crowned cranes and 23 fledgling oriental white storks on their breeding grounds in wetlands along the Amur River in Far East Russia (Fig. 1). Their migration routes to wintering sites in China were then tracked with the Argos system. Fourteen birds (5 red-crowned cranes, 9 oriental white storks) were successfully tracked over the complete journey, and the other 21 birds (7 red-crowned cranes, 14 oriental white storks) for part of the route (Table 1). The accuracy of Argos location data is indicated by the location classes in Table 2. Only data in location classes greater than or equal to 1 were used, so that the standard deviation error for any estimated point location was less than 1 km. Of a total of 4 314 such point locations, 72% were used in our analyses.

2.2 Bird locations, movements and land-cover conditions in the Amur River basin

To analyze bird movements and land-cover conditions in the Amur basin, we used Landsat/TM imagery with a ground resolution of 30 m. Bird location data were overlaid on the TM images and movement patterns tracked. In 1998, all birds tracked kept to within a relatively small area of about 10–15 km in diameter, but in 1999 moved about locally within the Amur basin to a scatter of locations. We ascribe the differences to variations in food supply caused by weather conditions.

From Landsat/TM images, we classified the land-cover of the Amur basin into six types: water, wetland 1, wetland 2, wetland 3, farmland/soil, and woods. Wetland 1, the wettest part of the wetlands, comprised water-covered reed, grass and sedge vegetation. Wetland 2 was of moderately

wet sedge- and grass-land. Wetland 3 was still drier and dominated by lowland grasses. The land-cover type “woods” included both woods in wetland areas and forests in mountainous areas. Fig. 2 shows classified land-cover in the Arkhara area of the basin.

Overlays of bird location points were then translated into land-cover use by the cranes and storks: see Fig. 3 for the Arkhara lowland in 1998–2000. The distribution of location points may be affected by several factors, such as competitive interaction among species, ground conditions, and year-to-year differences in weather. The total percentage of locations in wetland areas (wetland 1–3) are 79.5% for red-crowned cranes and 77.6% for oriental white storks (Fig. 4). Thus the breeding populations of both cranes and storks in the Amur basin are centered in the wetlands of the Arkhara lowland. Because the natural conditions of wetlands are well preserved on the Russian side of the Amur River basin, we conclude that there are sufficient food resources and available habitat there for effective conservation of populations of both cranes and storks.

Table 2 Accuracy categories for the Argos system

Location class	Estimated accuracy
3	< 150 m
2	150–350 m
1	350–1 000 m
0	> 1 000 m
A	no estimate of location accuracy
B	no estimate of location accuracy
Z	invalid locations

Table 1 Number of captured and successfully tracked red-crowned cranes and oriental white storks

Species	Status	1998	1999	2000
Red-crowned crane	captured	6	6	–
	successfully tracked	3	2	–
Oriental white stork	captured	6	6	11
	successfully tracked	2	3	4

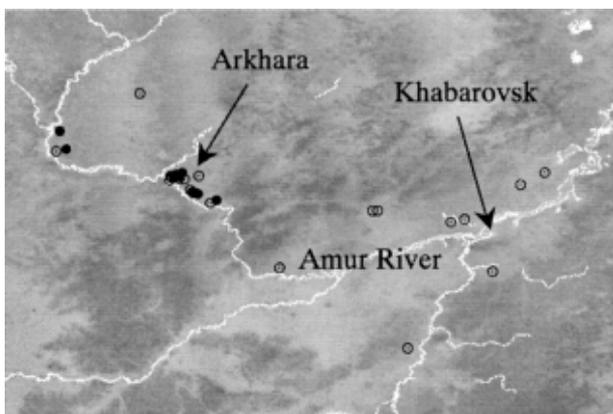


Fig. 1 Capture locations of red-crowned cranes (filled circles) and oriental white storks (open circles) on breeding grounds in the Amur River basin

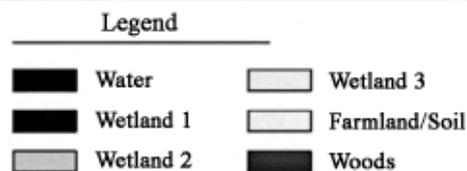
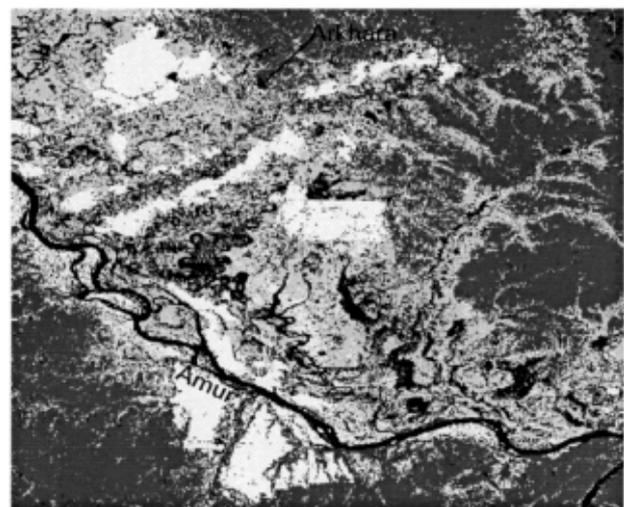


Fig. 2 Land-cover map of the Arkhara lowlands in the Amur basin produced from a Landsat/TM image and showing habitat types described in the text

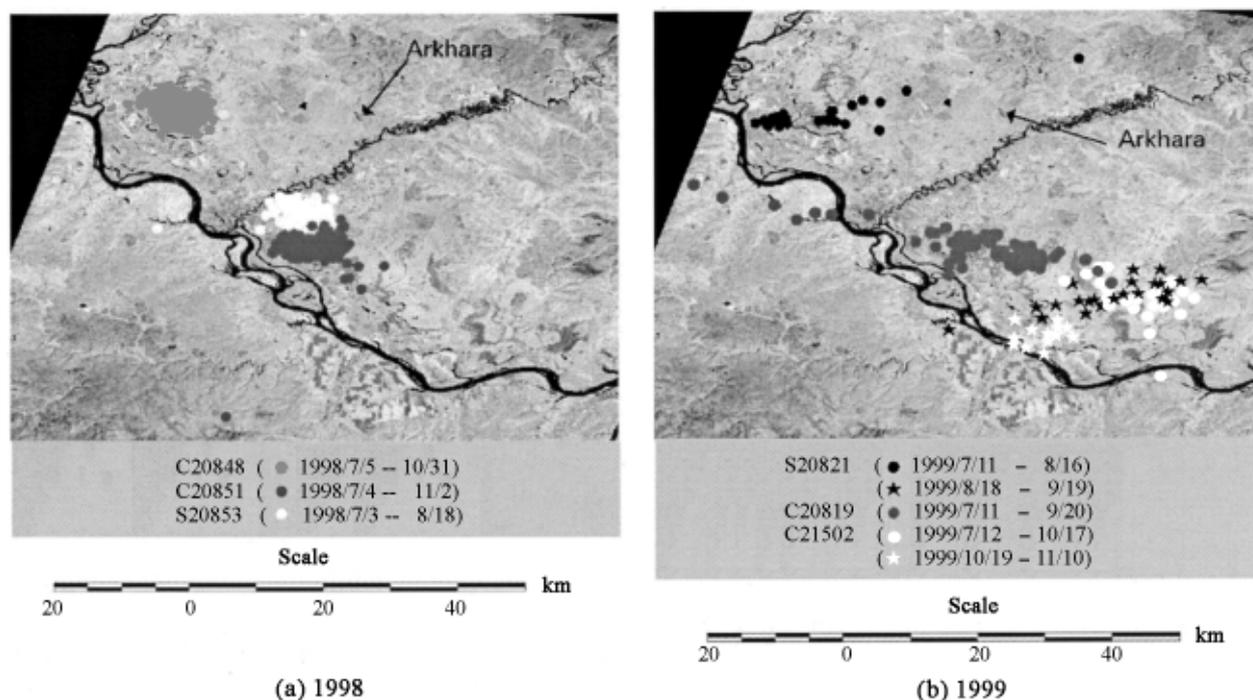


Fig. 3 Bird locations in the Arkhara lowland

Bird identification numbers starting with “C” indicate red-crowned cranes and those with “S” indicate Oriental white storks.

2.3 Bird locations, movements and land-cover conditions in China

In order to identify both bird migration routes and important habitats in China, bird location data were overlaid on NOAA/AVHRR satellite images, which had a ground resolution down to 1 km. Figs. 5 (a) and (b) show record location points along migration routes from 1998 to 2000 for cranes and storks, respectively. After leaving breeding grounds on the Amur basin, both species use two main corridors in northeast China, one along the Nen River basin and the other along the Songhua River basin, to the coast of Liaodong Bay. From Liaodong Bay, they then fly along the coast of Bohai Bay to the Yellow River delta, there to split, the cranes moving to Yangchen Beach in 1998 and 1999 and the storks to the Wuhan Lakes in 1998 and Poyang Lake in

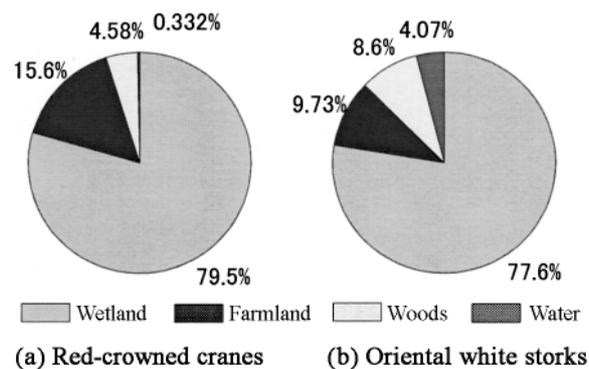


Fig. 4 Percentage habitat use by red-crowned cranes and oriental white storks on breeding grounds in the Arkhara lowlands, Amur basin

Table 3 Important sites for red-crowned cranes and oriental white storks in east Asia

Species	Site	Longitude (°)	Latitude (°)	Environment	Usage
Red-crowned crane	Amur River basin	127.6–130.4	49.0–50.1	inland	breeding
	Liao River delta	121.8	41.0	coastal	stopover
	Yancheng beach	119.9–120.8	33.0–34.4	coastal	wintering
	Han/Imjin estuary	126.6	37.6	coastal	wintering
Oriental white stork	Amur River basin	127.6–135.5	47.8–50.9	inland	breeding
	Nen River basin	122.3–126.6	44.9–49.0	inland	stopover
	Songhua River basin	128.5–132.7	46.0–47.7	inland	stopover
	Ussuri River basin	134.1	47.3	inland	stopover
	Liao River basin	122.4	42.9	inland	stopover
	Bohai Bay coast	117.5–119.2	38.6–39.6	coastal	stopover
	Yellow River delta	117.8–118.9	37.7–38.2	coastal	stopover
	Shengjin Lake	116.4	30.0	inland	stopover
	Poyang Lake	116.1	29.1	inland	wintering
	Wuhan Lakes	113.8	30.3	inland	wintering

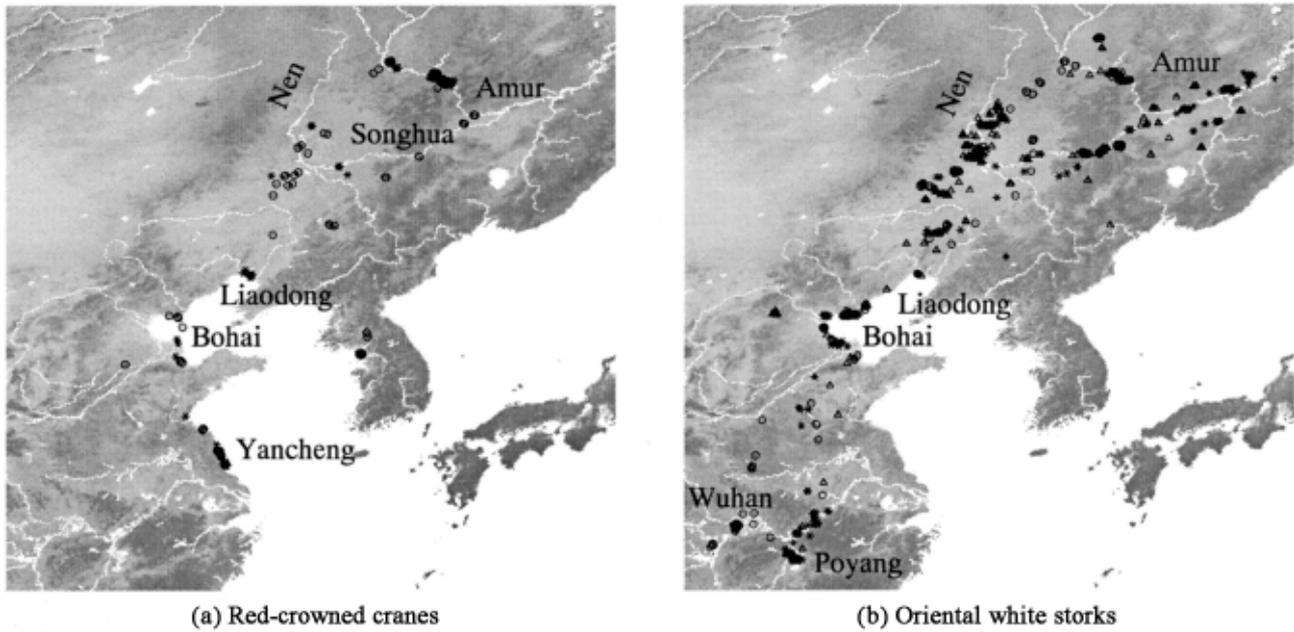


Fig. 5 ARGOS location points of migrating red-crowned cranes and oriental white storks, showing migration routes. Circles: 1998; asterisks: 1999; triangles: 2000.

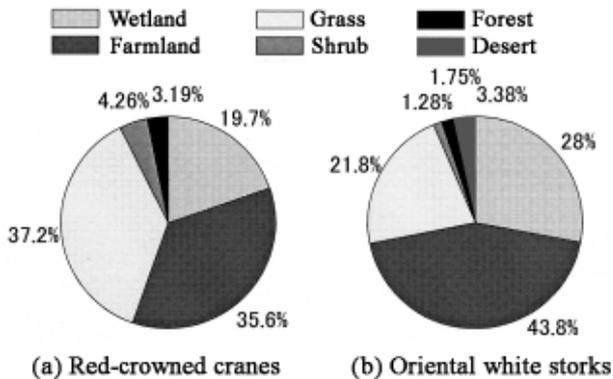


Fig. 6 Percentage of habitat use by red-crowned cranes and oriental white storks on migration stopovers and wintering grounds in China

1999 and 2000. Important stopover habitats used for more than 10 days at a time are listed in Table 3. The storks used more staging areas than red-crowned cranes and so took longer to reach wintering quarters (average 103 days) than the cranes (average 13 days). At winter quarters, the storks also moved around locally more than the cranes.

Bird location data overlaid on land-cover types in China, assessed from NOAA/AVHRR images, produced land use patterns shown in Fig. 6. Both species used farmlands more than wetlands. The percentages of location points in wetlands were 19.7% for cranes and 28.0% for storks, in contrast to wetland occupation at breeding grounds in the Amur basin. It seems likely that the birds are forced to visit farmlands to find food because much of the wetlands in coastal China has disappeared under agricultural and industrial development. Prolonged use of farmlands may be dangerous for the birds due to competition with local people

for food resources, hunting and pesticides.

3 Conclusion

By combining satellite tracking, which allows automatic tracing of bird movements over a wide area, and remote sensing, which enables regular assessment of the condition of bird habitats, we analyzed the relationship between the movements of red-crowned cranes and oriental white storks in east Asia and the habitats used. The major results are as follows. Movements around breeding sites in the Amur River basin vary from year to year, probably due to differences in food conditions caused by variation in weather. Both species prevailingly use natural wetland areas there, but mainly farmlands at stopovers on migration to winter quarters, perhaps now constrained by loss of wetlands in China due to development. Both species also migrate along common and split flyways, using two migration corridors in northeast China to Liaodong Bay, then traveling together along the coast to the Yellow River delta where they split, the cranes going mainly to Yangchen Beach and the storks to Wuhan Lakes and Poyang Lakes for the winter in different years. Further research is needed into the effects of wetland reduction in China on the survival prospects of both crane and stork.

Acknowledgements We express our gratitude to NASDA (National Space Development Agency of Japan) for providing Landsat/TM images, and to Dr. Buheosier of the Institute of Remote Sensing Applications, Chinese Academy of Sciences, for providing land-cover thematic images of China. This research was supported by the Global Environment Research Fund of the Ministry of the Environment, Japan.

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Symposium 13 Mating patterns and ecology

Introduction

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Ecology has a long-standing tradition in explaining the evolution of social mating systems. Earlier studies have shown that the social mating system of a population is determined primarily by the ability of individuals to control access to mates. Such control is, in turn, determined by whether mates and/or critical resources are economically defensible or not, depending on their spatial and temporal distribution. However, extra-pair fertilizations, i.e. matings outside the social pair bond, have turned out to be widespread among birds. The genetic mating system of a species is therefore rarely the same as the social mating system. To date, most studies of genetic mating systems have focused on aspects of sperm competition, such as the reproductive anatomy and physiology of males and females, paternity assurance behaviors, and the costs and benefits of multiple matings. Nevertheless, ecological factors can also influence the occurrence of extra-pair fertilizations, for example by affecting the opportunity for extra-pair copulations.

In this symposium, we review the current knowledge

of the interactions between ecology and genetic mating systems in birds. In particular, we examine how habitat structure and quality, as well as breeding dispersion, density and synchrony, may influence extra-pair behaviors and fertilizations. Two of the four papers, which centered on the effects of food availability on breeding synchrony, copulation behavior and paternity in the house sparrow and lesser gray shrike, were unavailable for publication. Their abstracts are published in the Abstract Volume of the Congress.

Of the two that are published here, the first, by Donald Blomqvist, Herbert Hoi and Ingrid Weinberger investigates the interaction of habitat structure, paternity guarding and extra-pair paternity across the class Aves, finding that increased habitat density facilitates extra-pair copulations and that paternity guarding may take more than one form. The second, from Arild Johansen and Jan Lifjeld, explores climatic influences on extra-pair paternity in Norwegian Bluethroats, finding that EPP is facilitated by warmer temperatures at peak fertile periods. These papers should stimulate further studies linking ecology with extra-pair behavior.

S13-1 To see or not to see: the role of habitat density on the occurrence of extra-pair paternity and paternity assurance behaviors

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Abstract Several ecological factors have been thought to influence opportunities for extra-pair copulations. Based on an extensive literature survey, we tested the hypothesis that female birds can escape more easily from paternity guards in closed, i.e. visually occluded habitats. Assuming that occurrence of paternity assurance behaviors reflects an increased risk of cuckoldry, we predicted that both extra-pair paternity (EPP) and paternity guarding (mate guarding or frequent within-pair copulations) should be more frequent among species breeding in habitats with reduced visibility. As predicted, we found that species breeding in closed habitats had higher EPP rates than those breeding in more open habitats. Mate guarding was also more frequent in closed habitats, but not high copulation rates. These relationships, however, were influenced strongly by taxonomic position, particularly by differences between passerines and non-passerines, implying that phylogeny and traits associated with it play an important role in explaining the occurrence of EPP and paternity guards.

Key words Habitat density, Extra-pair paternity, Paternity guards, Comparative analyses

1 Introduction

Molecular genetic methods have demonstrated that extra-pair copulations (EPCs) and fertilizations are frequent among birds. Thus, even if most birds are socially monogamous (e.g., Mock and Fujioka, 1990), genetic monogamy is a relatively rare phenomenon. Indeed, less than 25% of the socially monogamous species studied to date are truly genetically monogamous (Griffith et al., 2002). It is still unclear, however, what benefits female birds obtain from EPCs, and why there is such marked variation in extra-pair paternity (EPP), both within and between species (reviewed by Petrie and Kempenaers, 1998; Griffith et al., 2002).

Several ecological or socio-ecological factors, such as food supply, breeding synchrony and density, have been thought to influence opportunities for seeking EPCs (e.g., Westneat et al., 1990). If males are widely dispersed, for example, the time and energy costs to females for finding an extra-pair partner may outweigh any potential benefits (Petrie and Kempenaers, 1998). Westneat and Sherman (1997) found that, within species, EPP increased consistently with increasing breeding density. Across species, however, they found no such correlation, leading them to suggest that confounding factors might have caused the disparity. In particular, they proposed that “other ecological factors, such as the openness of the habitat....could have major effects on extra-pair behaviors”, and that “habitat complexity allows females more opportunity to escape from male surveillance....” (Westneat and Sherman, 1997:

211). Similarly, an earlier study by Westneat et al. (1990: 360) suggested that “visually occluded habitats also make mate guarding more difficult and less efficient at preventing EPC”.

We examine the relationships between EPP, paternity assurance behaviors and habitat density. Based on an extensive literature survey, we tested the hypothesis that females are more able to escape male paternity guards in closed, i.e. visually occluded, habitats (Westneat et al., 1990; Westneat and Sherman, 1997). We predicted that both EPP and paternity assurance behaviors should be more frequent among species breeding in closed habitats compared to those breeding in more open habitats, assuming that occurrence of paternity guards reflects an increased risk of cuckoldry (e.g., Birkhead, 1987; cf. Westneat et al., 1990).

2 Materials and methods

2.1 Extra-pair paternity

We searched the Science Citation Index for pre-January 2002 data on EPP rates. In the analyses, we only included data from DNA screening, thus excluding those based on plumage polymorphism, polymorphic enzymes or sex-differences in heritability estimates (cf. Griffith et al., 2002). We also excluded lekking or cooperatively breeding species, for which EPP is either impossible or difficult to define, as well as EPP estimates influenced by experimental manipulations (cf. Griffith et al., 2002).

Our data set included 114 species, representing 46

families and 12 orders. For species provided with more than one estimate of EPP rate (proportion of young sired by extra-pair males), we used the mean value. A complete list of references, with data on frequencies of paternity guards and breeding habitat classification (see below) as well, can be provided upon request.

2.2 Paternity guards

We scored presence / absence of paternity assurance behaviors, including *mate guarding by close following* in males and *frequent within-pair copulations*: for definitions, see Birkhead and Møller (1992). Data were obtained mainly from a review by Møller and Birkhead (1991), complemented with recent case studies. This data set comprised 155 species, representing 52 families and 15 orders.

2.3 Habitat density

For each species, we classified the main breeding habitat as (1) closed (dense forests, reeds and thickets, with much reduced visibility), (2) semi-open (open forests, parks and gardens, with intermediate visibility), or (3) open (seacoasts, pastures and meadows, with full visibility). Using an alternative habitat classification for 77 species (35%, $n = 220$) did not change the results presented here. Data were obtained mainly from standard references such as *The Birds of the Western Palearctic* (Oxford University Press) and *Handbook of the Birds of the World* (Lynx Edicions, Barcelona).

2.4 Statistical analyses

We first examined the relationships between EPP, paternity guarding and habitat density using species data. Since, however, species of close ancestry are likely to share many traits, species values may not be statistically inde-

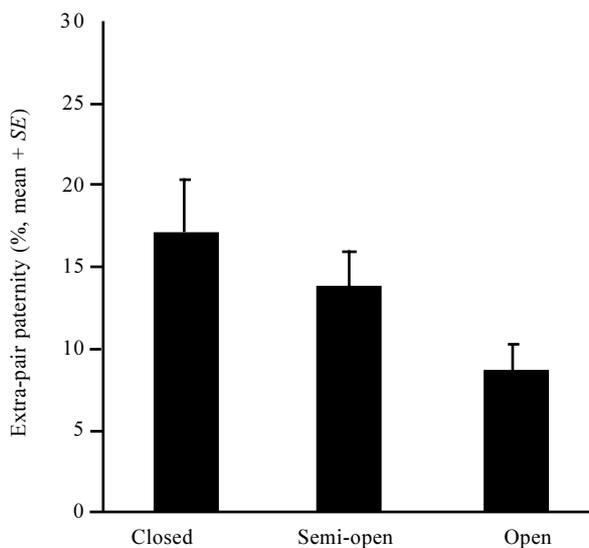


Fig. 1 Frequency of extra-pair paternity (proportion of young) in relation to habitat density (horizontal axis)

Density classifications on the horizontal axis (closed, semi-open, open) reflect presumed visibility in each habitat type. Data from 114 species.

pendent (Harvey and Pagel, 1991). We therefore tried to control for the effects of phylogeny on EPP rate by using the phylogenetic-subtraction method described by Sterns (1983). This procedure removes variation associated with taxonomic similarity from species data, on the assumption that differences among orders, as well as among families within orders, reflect phylogenetic effects.

Since the phylogenetic-subtraction method only corrects for taxonomic-dependent variation in quantitative variables, we examined the presence / absence of paternity guards by first determining the modal habitat type (degree of density) for each order and family. We then tested whether

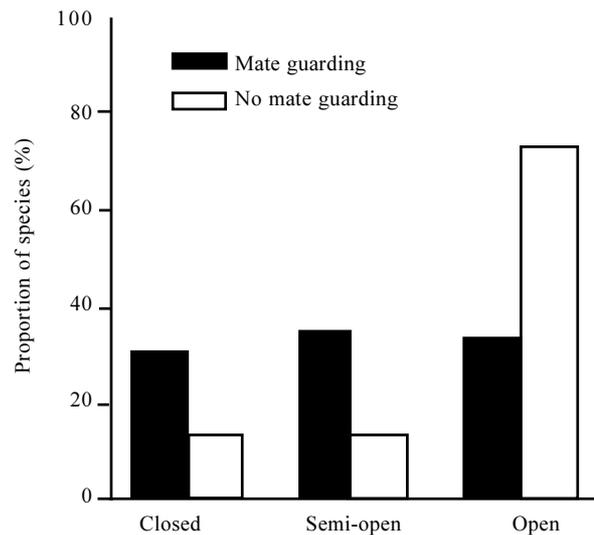


Fig. 2 Frequency of mate guarding by close-following in relation to habitat density (horizontal axis)

Density classifications on the horizontal axis (closed, semi-open, open) reflect presumed visibility in each habitat type. Data from 155 species.

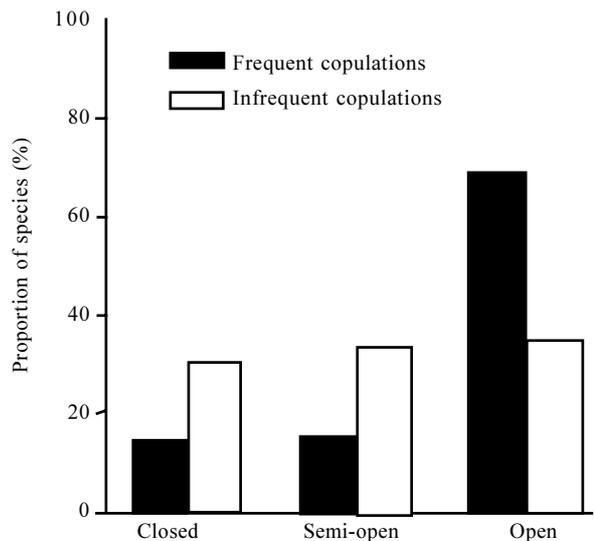


Fig. 3 Frequency of within-pair copulations in relation to habitat density (horizontal axis)

Density classifications (closed, semi-open, open) reflect presumed visibility in each habitat type. Data from 153 species.

the proportion of species showing either mate guarding or frequent copulations differed among habitat types, thus using orders and families as independent sample units.

3 Results

EPP frequency in species breeding in closed habitats was higher than in those breeding in more open habitats (Fig. 1; $P = 0.01$, $n = 114$ species, Kruskal-Wallis ANOVA). We also found a significant association between the presence of paternity guards and habitat structure. Mate guarding was relatively more frequent among species breeding in closed or semi-open habitats than in those breeding in open habitats (Fig. 2; $P < 0.001$, $n = 155$ species, log-linear analysis), whereas the opposite was true for species in which within-pair copulations were frequent (Fig. 3; $P < 0.001$, $n = 153$ species, log-linear analysis).

The above results seem to support our prediction: both EPP and mate guarding (but not high copulation rates) were more frequent among species breeding in habitats of reduced visibility. There was, however, a strong phylogenetic effect as well. When we controlled for taxonomic position, the significant differences in the frequencies of EPP among habitat types disappeared ($P = 0.74$, $n = 114$ species, Kruskal-Wallis ANOVA). So did those for the proportion of species with paternity guards: mate guarding, $P = 0.19$ (orders) and 0.20 (families); frequent copulations, $P = 0.22$ (orders) and 0.50 (families); $n = 13$ orders and 37 families (Kruskal-Wallis ANOVA).

4 Discussion

Species breeding in closed habitats with reduced visibility have significantly higher EPP rates than those breeding in more open habitats. Male mate guarding was also more frequent among species breeding in dense habitats, supporting the idea that such behavior is a response to the risk of cuckoldry (e.g., Birkhead, 1987). On the other hand, frequent within-pair copulations occurred predominantly among species breeding in open habitats. Since the frequencies of EPP were significantly lower in these habitats, this result suggests that copulation rate does not reflect the risk of losing paternity.

Yet such paternity assurance behavior may be more effective in preventing extra-pair fertilizations than is commonly assumed (Møller and Birkhead, 1991). Frequent copulations typically occur in species in which males cannot guard their mates by close following, for example where one of the mates has to guard the nest (review in Birkhead and Møller, 1992). Therefore, this behavior has been interpreted as an alternative but inferior paternity guard (e.g., Møller and Birkhead, 1991). Yet even if frequent within-pair copulations have functions other than ensuring paternity (Møller and Birkhead, 1991), the relatively low frequency

of EPP in species that have it questions whether it really is inferior in paternity guarding.

Our analyses indicate a strong phylogenetic influence in the above patterns. Thus, when we controlled for the effects of taxonomy position, the significant relationship between EPP rate and habitat density disappeared. We conclude that the underlying reason for this result is the considerably higher rate of EPP in passerine than nonpasserine birds (Westneat and Sherman, 1997). Furthermore, passerines in our data set occurred more in closed habitats, and nonpasserines more in the open (D. Blomqvist et al., in prep.). As passerines were biased towards mate guarding and nonpasserines to frequent copulations (D. Blomqvist et al., in prep.), this could also explain why the relationship between paternity guarding and habitat density disappeared when we controlled for taxonomic position.

To summarize, our results support the hypothesis that habitat density affects the frequency of EPP and paternity guarding. Since the phylogenetic-subtraction method may not be the best way to control for the effects of phylogeny (cf., Harvey and Pagel, 1991), further studies are needed to determine whether these eco-behavioral relationships remain after ancestry has been accounted for. Within-species comparisons should also help to clarify the influence of habitat density on variation in EPP and paternity assurance behaviors.

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S13-2 Do weather conditions affect the frequency of extra-pair paternity in the bluethroat (*Luscinia svecica svecica*)?

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Abstract Ecological factors may affect levels of extra-pair paternity (EPP) by influencing the costs and benefits of extra-pair copulation. During a 10-year study of a Norwegian bluethroat population, the frequency of EPP has varied extensively (8%–76% nests with EPP, 7%–33% extra-pair offspring among years). Here, we investigate whether socio-ecological factors (breeding density, breeding synchrony) and weather conditions (ambient temperature, precipitation) during the peak fertile period explain some of the variation in the frequency of EPP. None of the factors assessed were related significantly to the likelihood that a nest would contain extra-pair offspring. Among broods that contained at least one extra-pair offspring, however, ambient temperature was related significantly to the frequency of EPP: broods contained more extra-pair offspring when the temperature was relatively high during the period of peak female fertility. We suggest that there is a direct link between weather conditions and the level of EPP in this population of bluethroats. Environmental conditions are often harsh when the birds start to breed, a large proportion of the ground being covered by snow and night temperatures falling well below zero. It therefore seems likely that there is a trade-off between investment in self-maintenance and extra-pair behavior, which shifts towards self-maintenance when the weather conditions are severe.

Key words Sperm competition, Breeding density, Breeding synchrony, Ambient temperature, Precipitation

1 Introduction

Ecological factors may influence the costs and benefits of extra-pair copulation (EPC) behavior by constraining individual ability to engage in it and / or influencing the availability of potential mates. Studies of the influence of socio-ecological factors on the frequency of extra-pair paternity (EPP), such as breeding synchrony (e.g., Stutchbury, 1998) and breeding density (e.g., Westneat and Sherman, 1997), have been several. However, the potential influence of weather conditions during the fertile period has not yet been explored. Weather conditions may constrain EPC behavior directly by affecting the need to prioritize maintenance, or indirectly by affecting other factors such as breeding synchrony or density that in turn may influence EPC-activity.

In this study, we explore the relationship between the frequency of EPP and breeding density, breeding synchrony and weather variables (temperature and precipitation) in a Norwegian population of the bluethroat (*Luscinia svecica*). EPP occurs frequently in this population, but with considerable annual variation, fluctuating over the course of 10 study years between 7 and 33% of young, and 8 and 76% of broods. Here, we investigate whether ecological factors explain some of the variation in EPP between years, and between broods within years.

2 Materials and methods

Fieldwork was conducted in Øvre Heimdalen, Norway (61°25'N, 8°52'E; 1 100 m a.s.l.), and analyses of paternity were carried out on data from 10 years (1991–2000). In total, 305 broods containing 1568 chicks were analyzed by means of multilocus DNA fingerprinting (1991–1993) and microsatellite typing (1994–2000).

We calculated population synchrony, using the synchrony index proposed by Kempenaers (1993), and local synchrony, defined as the number of females within a radius of 200 m whose peak fertile periods (day-3 to day-0 *day of first egg*) overlapped that of the focal female partly or completely. Local density was defined as the number of territories within a radius of 200 m of the focal territory. Local synchrony and density were calculated only from the year 1995, after we had gained sufficient knowledge of the breeding population.

Data on morning temperature (0800 hours) and daily precipitation was retrieved from Bygdin weather station, situated 12 km southwest of the study site at a similar altitude (1 055 m a.s.l.). For analyses of annual variation, we calculated the annual averages in morning temperature and daily precipitation from 15 May to 5 June, a period that covers the pre-fertile and fertile periods in the local bluethroat population. For analyses of individual variation, we calculated average morning temperature and average

precipitation during the peak of female fertility (day –3 to day 0).

3 Results

3.1 Annual variation

In total, about half (151/305) of the nests contained one or more extra-pair offspring, and 26.3% (412/1 568) of the young were sired by extra-pair males. There was significant variation between years, both in the frequency of nests with EPP (Fig. 1) and in the proportion of EPP within nests (Johnsen and Lifjeld, 2003).

We found no significant correlations between the annual proportion of nests with extra-pair offspring and (1) annual average morning temperature during the pre-fertile and fertile period, (2) annual average precipitation during the pre-fertile and fertile period, (3) annual population synchrony, and (4) annual average local density ($P > 0.14$ for all tests; Johnsen and Lifjeld, 2003). It should be noted that sample sizes were low in these tests ($n = 10$ years).

3.2 Variation between broods

Generalized linear model (GLM) analyses revealed no significant relationships between any of the ecological factors and the frequency of EPP when all broods were included in the analyses (Johnsen and Lifjeld, 2003). Similarly, neither factor was related significantly to the likelihood that a nest would contain EPP, as shown by logistic regressions (Table 1).

There may be several reasons why nests did not contain extra-pair young (see Discussion). Therefore, we repeated the above GLM analyses on the potentially more uniform and comparable fraction of the nests that contained one or more extra-pair offspring. Within this data set, the morning temperature during peak fertility was related significantly and positively to the proportion of EPP (Fig. 2; Johnsen and Lifjeld, 2003), and there was a tendency for a negative relationship between local synchrony and the proportion of EPP (Johnsen and Lifjeld, 2003).

Multivariate GLM analyses on the restricted data set (only broods with EPP), using the four ecological variables, laying date and year as factors, revealed a significant effect from temperature only (Johnsen and Lifjeld, 2003).

Table 1 Logistic regression analyses (controlling for year) of the effect of ecological factors on the occurrence of extra-pair paternity

	<i>n</i>	<i>r</i> ²	<i>P</i>
Temperature	286	0.06	0.68
Precipitation	286	0.06	0.91
Local Synchrony*	190	0.03	0.57
Local density*	195	0.03	0.81

*Data from 1995–1999 only.

4 Discussion

About half the broods in this study lacked EPP, a situation that may arise because (1) females are truly faithful, (2) females do not succeed in obtaining extra-pair fertilizations, and/or (3) the pair males are superior in sperm competition. Whatever the ultimate reason, we could not predict whether or not a female would obtain extra-pair fertilizations from the weather conditions, nor from the socio-ecological situation that she experienced during her period of peak fertility. Earlier studies have suggested that both sexes play active roles in EPCs in the bluethroat (Johnsen et al., 2000; Johnsen et al., 2001). In such species, the occurrence of EPP should depend on the particular interests of, and constraints on, all potential participants (pair male, pair female, one or more extra-pair males; cf. Petrie and Kempenaers, 1998). Our data suggest that socio-ecological circumstances have little or no influence on this.

About half the females in this study engaged in at least one EPC. As indicated above, there may be many rea-

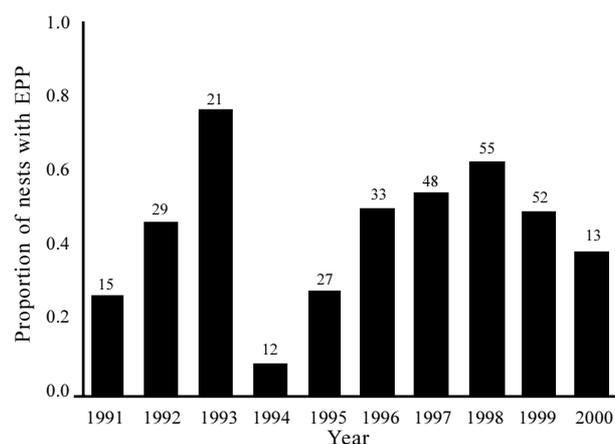


Fig. 1 Annual proportion of nests with extra-pair paternity (EPP) 1991–2000

Numbers above bars represent sample sizes (number of nests).

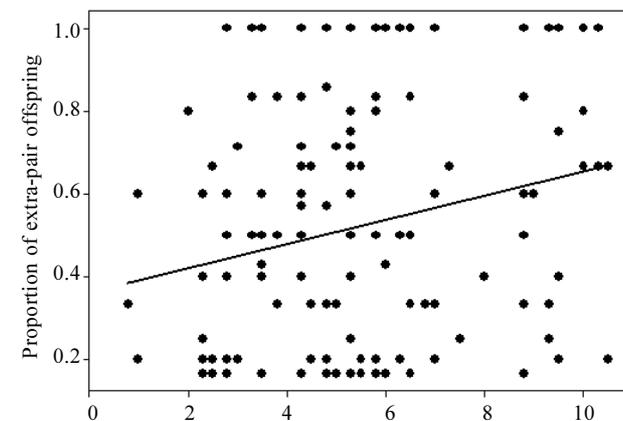


Fig. 2 Relationship between the proportion of extra-pair offspring in nests with mixed paternity and ambient temperature (horizontal axis) during the peak fertile period. The regression line is shown for illustrative purposes.

sons why they did so. Even so, our data suggest that the degree to which they engaged in it was influenced to some extent by weather conditions during the period of peak fertility. When morning temperatures were low, EPP-broods contained relatively fewer extra-pair offspring than when temperatures were higher. There may well be a causal relationship between weather conditions and the frequency of extra-pair encounters in Norwegian bluethroats. The breeding season is initiated very early in the phenological cycle, when large parts of territories are still covered with snow and poor weather conditions may force the birds to spend more time on self-maintenance than to sexual activity.

This study shows that properties of the physical environment may influence levels of EPP by affecting the trade-off between self-maintenance and sexual behavior. We urge investigators of extra-pair mating systems to take weather conditions into account when assessing the frequency of

EPP at the individual and the temporal level.

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Symposium 14 Integrating mechanism and function in bird behavior: how hormones can help

Introduction

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1 Overview

Ever since Tinbergen, behavioral biologists have appreciated that a complete understanding of behavior will require knowledge of its function, causation, evolution, and development. In the past decade, each of these approaches has been highly successful, leading to development in behavioral ecology, behavioral physiology, developmental psychobiology, and comparative biology. However, the development of these subdisciplines has only enhanced the need to integrate proximate and ultimate approaches, a goal that has thus far proved elusive.

While answers to questions regarding the functional/evolutionary significance of behavior in birds are necessarily different from those about how behavior manifests itself within the lifetime of the individual, each approach can strongly benefit the other. Thus knowledge of problems faced by birds in the wild should guide questions posed about causal mechanisms, while knowledge of the limitations and plasticity in causal mechanisms should guide questions posed about the function and evolution of behavior.

This symposium focused on how studies of hormones can help to integrate different levels of analysis of bird behavior and physiology. Hormones are key to understanding behavior at the proximate level because they influence many aspects of the behavioral and physiological phenotype that are important functionally. For example, they act early in development to set a course, interact with other physiological systems such as the immune system, coordinate the expression of secondary sex characteristics, reflect the environment in the stress response and metabolism, and serve to coordinate the timing of reproduction. Hormones are also key to understanding how secondary sex characteristics evolve and how life history evolution can be constrained by trade-offs. Further, they move across generations as maternal effects and so influence phenotypic development in future generations much as genes do. Their effects on behavior, moreover, enable species-specific adaptations to match social systems to their environments.

2 Review of papers presented

In reporting their own hormonal studies, the speakers at this symposium provided outstanding examples of the power of an integrative approach, as follows.

2.1 Integrating steroid synthesis with steroid action

Schlinger, Soma and London summarize fascinating new alternatives to the traditional view of how gonadally derived sex steroids influence expression and development of sexually differentiated behaviors in birds. In particular, they focus on two well studied examples: the roles of testosterone in activating male territorial behavior and estradiol in organizing the vocal control system of oscine songbirds. In recent years, territorial aggression during the non-breeding season was found to be unresponsive to castration but still dependent on sex-steroids in song sparrows. Further, the song system in male zebra finches was found to develop in male castrates and not to develop in females induced to grow testicular tissue. The prevailing paradigm, which asserted that gonadal steroids enter systemic circulation to take effect in brain, often after conversion to estradiol, could not accommodate these findings.

Thanks to the work of Schlinger et al., we may be approaching resolution. They provide evidence that the adrenals secrete a precursor to testosterone and estradiol, DHEA, that circulates and has its effect on aggression in the brain without some of the “pleiotropic effects” we normally attribute to testosterone (e.g., reduced immune function or elevated metabolism). With respect to the song system, estradiol that is produced *de novo* in the brain from cholesterol may have its masculinizing effect *in situ*. These new findings add great depth to our knowledge of how steroids induce behavior without altering our fundamental understanding of steroids as activators of gene expression and determinants of sex differences.

Concerning adaptation and constraint in the evolutionary process, the findings suggest a mechanistic means by which constraints can be overcome. If complex phenotypic characters that evolved under one proximate mecha-

nism can be handed off to another and accomplished with fewer costs (e.g., territorial aggression in the non-breeding season without suppressed immunity), then constraints in the form of physiological trade-offs provide less of a barrier to evolution because the trade-offs themselves are dynamic and change with the seasons.

The findings on sexual differentiation in the song system also help to explain how complex phenotypes of many characters can evolve. By coupling and uncoupling their dependence on systemic steroids, tissues can develop and evolve as modules. One of the most-studied sex differences in birds is copulatory behavior, one that obviously requires close coordination between brain and gonad: if you make sperm, then mount; if you make eggs, then squat. But, as the authors point out, vocal behavior has no necessary connection to gametogenesis, and lineages in which vocal behavior and copulatory behavior are free to evolve independently in males and females have apparently been favored — at least that appears to be the case for the zebra finch. Both types of behavior remain dependent on the same steroid to activate gene expression, but copulatory behavior is plugged into the systemic circulation, while song is freestanding. Only further research will uncover new examples and extend our understanding of how hormone-dependent characters evolve.

2.2 Hormones, sexual dimorphism and mate choice

Elizabeth Adkins-Regan summarizes the important developmental and organizational role played by steroid hormones in producing traits shaped by selection that is natural (with respect to reproduction) and sexual (with respect to successful acquisition of mates). By altering the levels of hormones very early in life, she sex-reversed three attributes: mounting partners in copulation, production of song to attract partners, and opposite-sex partner preference. This indicates that natural steroids establish male-typical or female-typical behaviors.

In quail, natural ovarian estrogens lead to female-typical behavior. Blocking the estrogens leads instead to male-typical behavior, including copulatory mounting and interest in females. If, in zebra finches, genetic females are treated with estradiol when young, they will behave like males by singing and preferring females. This work reveals the epigenetic power of steroid hormones in the organization of the phenotype. By affecting the expression of genes that are usually sex-specific in expression, and thus silent in the other sex, steroid hormones can induce maleness in females or femaleness in males.

Adkins-Regan's fascinating and compelling work on partner preference is especially interesting and raises many new questions: what aspect of typical females appeals to masculinized females and makes them more attractive than typical males? Is it their behavior? Or their silence? Are naturally more masculine females ordinarily attracted to naturally less masculine males as in, for example, the white-throated sparrow?

Her work stresses that attributes which typify one sex can be expressed as modules able to evolve separately. By relying on steroids for organization, including brain-derived steroids that require several enzymatic conversions for synthesis, evolution could favor individuals in which one site in the brain is masculinized or feminized early in development by conversion of a circulating steroid at the site, while another site is left unorganized because it did not express the converting enzyme. Much remains to be learned about how sexual dimorphism evolves, but comparisons of the role of organization in ancestral and derived species that differ in the degree of dimorphism are sure to be informative.

Adkins-Regan also links this research to Reeve and Spellman-Reeve's protected invasion theory, in which the mode of chromosomal sex determination explains why male birds may have evolved to be more dimorphic than male mammals. In birds, males are the homogametic sex, and mutant alleles arising on the Z chromosome would be less likely to be lost when new and rare because they would be present in both sexes. In their model, such protection of rare alleles permits retention of novel forms long enough for them to increase via sexual selection. Organizational actions extend this protection to steroid regulated genes on autosomes.

Much remains to be learned. Almost all that we know about the organizational effects of steroidal hormones on sexual preference, song, and mounting has come from studies of a just a few species, and interesting differences are apparent. Imagine how much more will be learned about these important and fascinating processes as researchers turn to new study systems and employ new tools (see paper by Schlinger et al.).

2.3 Hormone, brain, immune interactions and song

Ball, Duffy, and Gentner assess singing by male European starlings and its impact on females. Their studies exemplify a productive blend of proximate and ultimate explanations for bird behavior. Male starlings sing their songs in bouts, and bout length varies among males. Those singing longer bouts have enlarged vocal control regions in the brain and are preferred by females. The neural basis for the preference is not known, but Ball et al. have shown that immediate early gene expression in the auditory forebrain is greater in females exposed to longer bouts of song. If we were to assume that the variation among males in song and among females in preference had a genetic basis, we would expect selection to favor males that sing longer bouts unless there were balancing costs. If instead variation among males in song is attributable to environmental variation that allows some males to devote more resources to song, we might predict cost-free success for the longer-bout males, but no response to selection.

The results fit neatly with the balancing costs hypothesis. Males that sing longer bouts also have higher levels of plasma testosterone, and males with higher test-

osterone respond less robustly to immune challenges, suggesting costs to attractiveness. However, Ball et al. show that males which sing longer bouts have more robust immune responses to immune challenges. This apparently contradictory finding may be explained by assuming that only good quality males can afford to become attractive by producing high levels of androgens and bearing the costs of immune suppression. Such correlations between hormone, behavior and physiology hold great promise for future studies of selection on correlated characters mediated by hormones; they also pose challenges for those seeking to understand links between health and attractiveness.

2.4 Additional papers

Two other presentations in this symposium addressed the importance of testosterone, each from rarely studied perspectives. Groothuis et al reviewed the wide array of effects, both beneficial and costly, of androgen pro-

duction in young birds, and described several ways in which the chicks can reduce these costs. Further, they showed how parents can adjust androgen production in their chicks to the level needed for social competition via choice of a nest site, so affecting the social context in which young are reared. In the other paper, Sandell et al. reviewed the importance of androgen production in female birds and placed the results in an evolutionary context. They asked whether testosterone in females has similar or different effects to that in males. This is an intriguing question because if testosterone affects similar traits in both sexes, but with beneficial effects in males and detrimental ones in females, the latter may constrain the evolution of testosterone production and its effects in males. These two papers (S14-2 and S14-4) were read as orals and only submitted as abstracts already published in the Abstract Volume of the Congress; they are not repeated here.

S14-1 Integrating steroid synthesis with steroid action: multiple mechanisms in birds

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Abstract Sex steroids of gonadal origin influence avian behavior, anatomy and physiology. There is evidence, however, that sex steroids can be synthesized in non-gonadal tissues and have actions unrelated directly to reproduction. We describe evidence in birds for sex steroid synthesis in the adrenals and brain. The expression and activity of steroidogenic enzymes outside of the gonads creates opportunities for birds to use sex steroids as potent signaling molecules on nonreproductive tissues without disadvantageous activation of reproductive systems.

Key words Steroid hormones, Brain, Aggression, Song, Reproduction

1 Introduction

The sex steroid hormones progesterone (Prog), testosterone (T) and estradiol (E_2) are powerful signaling molecules influencing a wide range of anatomical and physiological systems. These hormones play a significant role in reproduction; and the gonads are the dominant source of these steroids. Upon reaching the circulatory system, they have access to all tissues and then act on cells that express the appropriate steroid receptors and their coactivators. In some cases, sex steroids may act on tissues associated with nonreproductive functions. In these cases, the sex steroids can be synthesized outside of the gonads, principally in the adrenals and in the brain. We propose that the synthesis of sex steroids in these non-gonadal sites is a mechanism for taking advantage of the potency of these hormones, allowing them to be used in nonreproductive contexts without inappropriately activating reproductive tissues. Birds are useful animal models for exploring this hypothesis.

Do birds synthesize sex steroids in non-gonadal tissues, and if so, why? We will present evidence that the avian adrenals and brain can synthesize androgens. We describe two systems involving songbirds in which non-gonadal androgens may have significant actions on the brain to control behaviors that can be expressed independently of such behaviors as copulation which are traditionally associated with reproduction *per se*. In the first system, an inactive androgen may be secreted by the adrenals and then metabolized into active androgens and estrogens in the brain to activate aggressive behavior in winter. In the second system, active sex steroids may be synthesized locally in the developing brain to masculinize some neural circuits. In both of these systems, non-gonadal sex steroids are used as signaling molecules, and their actions are restricted to

neural circuits and behaviors that can be expressed in non-reproductive contexts.

What evidence exists that sex steroids are synthesized outside of the gonads? Steroid synthesis by a tissue can be inferred if removal of that tissue (such as castration) reduces circulating hormone levels. It is possible also to infer synthesis in tissue if the concentration of hormone there exceeds the concentration of that hormone in blood or if the concentration of hormone in the venous output of that tissue exceeds the concentration of hormone in its arterial supply. Direct evidence of steroid synthesis, moreover, can be determined if the tissue itself has the activity or mRNA expression of the enzymes and transporters needed for steroid synthesis.

From such inferences, steroidogenesis is easy to document in vertebrate gonads during periods of reproduction, especially in birds. At this time they express steroidogenic enzymes in large amounts to produce the large quantities of hormone needed to elevate blood levels (e.g., Freking et al., 2000). In cases where steroid synthesis is coupled to local actions, evidence for synthesis is more difficult to document because the amount of steroid produced is small. Often, the best approach for identifying steroid synthesis under these conditions is to use sensitive molecular or biochemical techniques to identify expression or activity of steroid synthetic enzymes (Tsutsui and Schlinger, 2002). It is also important to examine the appropriate animal models at life-history stages when non-gonadal steroidogenic enzymes might be expressed.

Sex steroids are synthesized from cholesterol in the following way. Cholesterol is first transported into mitochondria where it is converted into pregnenolone by the side-chain cleavage enzyme (CYP11A1). Pregnenolone is

then converted into either Prog by the enzyme 3 β -hydroxysteroid dehydrogenase (3 β -HSD) or into the inactive androgen dehydroepiandrosterone (DHEA) by the 17 α -hydroxylase enzyme (CYP17). Androstenedione (AE) is then produced from Prog by the actions of CYP17 or by the actions of 3 β -HSD on DHEA. AE is converted to T by the enzyme 17 β -HSD. And T is converted to E₂ by the enzyme aromatase. These reactions occur in mitochondria and the endoplasmic reticulum. Because they are lipophilic, steroidal products diffuse passively out of cells to affect neighboring cells or distant cells after entering the systemic circulation (Miller, 1988).

Typically, these enzymes are co-expressed in a single cell (as in the testicular Leydig cell) or in adjacent cells within a tissue (as in theca and granulosa of the ovarian follicle). In some cases, however, they can be expressed in different tissues. Thus there can be substantial physical separation of the reactions along the steroidogenic pathway within an organism. For example, estrogens have many important actions on the avian male brain, despite low E₂ concentrations in blood. The T in blood is produced in the testes by action of the synthetic enzymes side-chain cleavage, 3 β -HSD and CYP17 (Freking et al., 2000). Circulating T is then converted into E₂ in the brain by the neural expression of aromatase (see above; Schlinger, 1997). Here we discuss evidence that the avian brain can express other enzymes of the steroidogenic pathway.

2 DHEA and aggression in non-breeding birds

Many birds abandon territories over winter in favor of flocks. In the non-breeding season, the gonads and secondary sex characters (e.g., cloacal protuberance, wattles) are generally regressed, and circulating T and E₂ are usually non-detectable. Some species, however, aggressively defend territories during the non-breeding season, even though plasma T is at basal levels (Soma and Wingfield, 1999). Winter territoriality may be dissociated from plasma T because of the costs of circulating T (e.g., Ketterson et al., 1992). In seasonally breeding birds, sex steroid hormones in general circulation may have particularly high costs during the non-breeding season. The non-breeding season may extend over most of the year and can be a difficult time for birds, especially small birds, because of cold temperatures and reduced food supply (Wingfield et al., 2001). Diurnal species also cannot forage during the long nights of winter. Overall, T treatment has been shown to reduce overwinter survival in songbirds (Dufty, 1989). Many costs of T during the non-breeding season may be energetic: T increases metabolic rate (e.g., Buchanan et al., 2001) and decreases fat stores, which are important for insulation and surviving snow and ice storms during winter. Other costs of T involve suppression of the immune system (Casto et al., 2001). T treatment may also stimulate reproductive behaviors that are inappropriate during the winter (Logan, 1992). During the spring breeding season, in contrast, high levels

of circulating T are useful for coordinating multiple physiological systems in preparation for reproduction.

In song sparrows (*Melospiza melodia*), males are territorial during the breeding season (spring) when plasma T is high. Yet they are also highly aggressive during the non-breeding season (autumn and winter), when plasma T is non-detectable and the testes are completely regressed (Soma and Wingfield, 1999). Furthermore, castration has no effect on non-breeding aggression. Thus, aggression may be independent of sex steroids such as T in autumn and winter. This hypothesis was tested in three field experiments by treating wild song sparrows with the pharmacological inhibitors of aromatase and androgen receptor binding. In particular, blockade of estrogen synthesis by an aromatase inhibitor strongly decreased male aggression in the non-breeding season. The effects of the aromatase inhibitor, however, can be rescued by estrogen replacement (Soma et al., 1999, 2000a,b). These data indicate that sex steroids, particularly estrogens, are important for the expression of aggressive behavior in the non-breeding season, even though plasma levels of sex steroids are non-detectable and castration has no effect.

Subsequent studies have addressed the source of androgen substrate for brain aromatase in the non-breeding season, because plasma levels of aromatizable androgens (testosterone and androstenedione) are basal then. Although Dehydroepiandrosterone (DHEA) is a largely inert androgen precursor, it can be converted locally into active sex steroids within tissues that express the appropriate enzymes. Interestingly, plasma levels of DHEA are elevated in non-breeding song sparrows (Soma and Wingfield, 2001). Further, DHEA concentrations in the adrenals of winter birds are high, suggesting adrenal secretion of DHEA. In a separate experiment, treatment of wild non-breeding males with DHEA increased territorial song and the size of a brain region that controls song behavior (Soma et al., 2002b). DHEA treatment did not, however, stimulate the growth of secondary sex characters such as the cloacal protuberance. These data raise the hypothesis that DHEA is converted into active sex steroids in the brain but not in peripheral tissues. Recent results suggest that DHEA treatment does not inhibit immune responses in sparrows, in contrast to T treatment (N. Owen-Ashley and J. Wingfield, pers. comm.).

Current studies are examining regional and seasonal differences in song sparrow brain aromatase using biochemical and molecular techniques. *In situ* hybridization reveals that aromatase mRNA is highly expressed in the hypothalamus and telencephalon. Interestingly, biochemical measurement of aromatase activity in the avian amygdala (nucleus taeniae) shows that seasonal changes in aromatase activity correspond to seasonal changes in aggression, as in its reduction at molt (Soma et al., 2003). As DHEA has important behavioral and neural effects in songbirds, its metabolism in the song sparrow brain is also under examination. We have designed and validated a biochemical assay to measure its conversion to androstenedione and estrogen by

the sequential activities of 3 β -HSD and aromatase (Vanson et al., 1996; Soma et al., 2002a). Excitingly, the song sparrow brain can convert DHEA to androgens and estrogens, with highest levels of 3 β -HSD activity in the diencephalon and telencephalon. We are now comparing seasonal differences in DHEA metabolism by the brain, with the prediction that it will be highest in the non-breeding season.

Taken together, the data support the novel hypothesis that in non-breeding song sparrows, the adrenals secrete DHEA, which is then metabolized into sex steroids in the brain to maintain aggression. With DHEA instead of T in the circulation, non-breeding song sparrows may circumvent the costs of circulating T, while continuing to provide sex steroids to appropriate neural circuits. A similar mechanism may be operating in a wide variety of species.

3 Neural steroid synthesis in the developing avian brain

Evidence is accumulating that the avian brain may not only metabolize steroids but has the capacity as well to fully synthesize steroids from cholesterol. These “neurosteroids” may influence the development of neural circuits in songbirds. The zebra finch (*Taeniopygia guttata*) is sexually dimorphic in its behavior and underlying neural song circuit. Adult males sing and possess a series of brain nuclei that control song output, but females never sing and lack a functional song system. Studies show that these brain areas can be masculinized by steroids, especially by E₂. Specifically, treatment of females within the first 3 weeks post-hatch masculinizes the neural song system sufficiently to allow them to sing song as adults (Arnold and Schlinger, 1993). The source of these steroids was assumed to be the gonads. Most studies, however, fail to support the idea that the gonads are their natural source.

If males develop their functional song system under the influence of gonadally-derived steroids, then manipulations of gonads should impact the organization of the song system. Contrary to this hypothesis, castration of genetic male zebra finches nine days post-hatch does not block the male pattern of song circuit organization; and induction of functional testicular tissue in genetic females is not sufficient for the development of the male song system (Wade et al., 1999; Arnold and Schlinger, 1993). In addition, it would be expected that circulating levels of steroids would be higher in males than females during the steroid-sensitive period if the gonads were secreting the necessary steroids. No such difference, however, has been measured consistently during the first three weeks of post-hatch development (Arnold and Schlinger, 1993). Further, male and female zebra finch gonads show equal capacity to synthesize androgens based on enzymatic activity and enzyme mRNA levels. The testes do not express the enzyme aromatase in significant amounts, but the ovary does, rendering the testes unable to supply greater concentrations of E₂ to the brain than ovaries (Freking et al., 2000). Therefore, an alternative source must exist for the masculinizing steroids.

Evidence that the brain is the steroid-synthesizing tissue has emerged for the zebra finch song system. Holloway and Clayton (2001) prepared slices of male and female brains from developing birds and cultured them. These slices contained major song areas that are sexually dimorphic in the nuclei and inter-nuclear connections. The normal masculine song nuclei connections were present in male slices but not in female. If a female slice was put in culture with a male slice, however, the male pattern of connections appeared in the female, suggesting that the male slice was secreting a diffusible factor that impacted the female. An assay of the culture media for male and female slices then found the level of estrogen to be higher in that from the male slice. Since the brain is isolated from the gonads, these data not only suggest a sexual difference in the ability of the brain to synthesize estrogens, but also that the brain itself has the capacity to synthesize steroids *de novo*.

Molecular and biochemical techniques have enabled the identification of steroidogenic enzymes in the brain of zebra finches and other avian species. Extensive evidence shows that aromatase is abundant in the zebra finch brain (Schlinger, 1997). Biochemistry has measured levels of 3 β -HSD activity in cultures from developing zebra finch telencephalon (Vanson et al., 1996), as well as in the adult songbird telencephalon (see above). In the zebra finch, highly sensitive RT-PCR has shown the presence of mRNA for CYP11A1, 3 β -HSD, CYP17, and aromatase in developing telencephalon as well (Schlinger et al., 2000). *In situ* hybridization, moreover, confirms the expression pattern of CYP17 mRNA in developing and adult zebra finch telencephalon and other brain areas (London and Schlinger, 2002).

In another avian species, the common quail (*Coturnix coturnix*), evidence for expression in the brain of all steroidogenic enzymes necessary for active steroid synthesis has been shown (Tsutsui and Schlinger, 2002). Taken together, these data suggest that the zebra finch brain will be found to express the complete suite of enzymes necessary to synthesize steroids independently of the gonads. Brain-derived steroids could then act to specifically organize the song system into a functional neural circuit. Song can be used in nonreproductive contexts, so its development is uncoupled from the organization of neural circuits underlying male and female copulatory behavior. In this way, the song circuit can develop in females of those species in which females sing without masculinizing other sex-related events.

Although we have presented evidence for adrenal and neural sex steroid synthesis, further work is required to confirm that the amount of androgen produced is sufficient to influence target sites in the avian brain as we suggest. We predict that additional studies of other bird species at appropriate life history stages will reveal the involvement of non-gonadal sex steroids in other behavioral and physiological systems.

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S14-3 Hormones, sexual dimorphism, and mate choice

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Abstract Sexual selection through mate choice is a major force in the evolution of ecologically relevant behavior in birds. Sexual selection favors behavior, including aspects of mate choice itself, that is different in males and females. How are these differences created during development? What processes produce the adult male and female phenotypes? Many experiments have shown that the organizing actions of sex hormones during critical periods early in development, even before hatching, are an important mechanism for generating adult sex differences in copulatory behavior. Sexually selected behavior such as courtship and mate choice occurs prior to copulation and is not the same behavior as mating itself. Are sex differences in these sexually selected behaviors also produced through organizational hormone actions? Experiments with zebra finches (*Taeniopygia guttata*) have addressed this question by manipulating sex hormone levels in embryonic and nestling birds and then testing them for singing or pairing preference when adult. Female zebra finches treated with estrogen as nestlings, or treated with an estrogen synthesis inhibitor as embryos (so that they develop testes instead of ovaries), prefer to pair with other females instead of males. These results confirm the potential importance of organizational hormone effects on adult mate preference, thereby integrating physiological mechanisms, development, and behavior of known adaptive significance. The organizational concept may also prove valuable in understanding the phylogeny of sexually dimorphic behavior.

Key words Organizational hormones, Sexual selection, Mate choice, Sexual dimorphism

1 Introduction

Many features of birds have evolved through the process of sexual selection, in which conspecifics are the agents of selection. Preference for potential mates on the basis of behavior or appearance is one form of such selection. Mate choice results in the evolution of sexual differences, also called sexual dimorphism. Many elaborate male behaviors such as singing or crowing and courtship displays have evolved because they make the males more attractive to females (Andersson, 1994). Because males and females have different genetic interests and are looking for different qualities in mating partners, mate choice itself is sexually dimorphic. That is, mate choice can act as a selective agent, shaping preferences by selection. In some species, for example those in which males lek, females choose mates but males do not, trying instead to mate with any female that comes near. In other species in which males sing and females do not, females may choose singers as mates while males do choose females, but on a different basis. The most fundamentally dimorphic aspect of mate choice is the preference itself for the opposite sex of the partner: females choose males as partners and males choose females.

These preferences are adaptive; but does understanding their function tell us everything we need to know? We also need to know how they originate and develop, that is, how males and females develop dimorphic mate choice as

they mature. Most of the genome within species, except for the small fraction that determines whether testes or ovaries develop, is much the same in both sexes; yet different behavior develops. How? Sex steroid hormones such as estradiol and testosterone are important mechanisms for expressing sex-limited traits. They regulate gene expression and thus have potential to create sex differences in behavior within a common genome. But both sexes produce both hormones, and in some birds the hormone levels in the blood overlap between males and females, so the answer to the question is still far from complete.

2 Hormone organization and its role in dimorphic sexual behavior

During the twentieth century, research with laboratory mammals led to important discoveries about the sources of sex differences (Arnold, 2002). It showed that gonadal sex steroid hormones are produced during early development, even before birth, and that these hormones organized future sex differences in behavior. Sex hormones are considered to organize behavior when: (1) their action occurs early in development, (2) their action is limited to a critical period, (3) their effect of their action is permanent, and (4) their action establishes the sexual phenotype of an animal's behavior.

Beginning in the 1970's, a number of experiments conducted in two laboratories showed that the mating be-

havior of Japanese quail, *Coturnix japonica*, is hormonally organized (Balthazart and Adkins-Regan, 2002). Quail mating behavior is sexually dimorphic: males mount females, but females never mount another bird. This is not just because males have more testosterone as adults than do females. Even if females are injected with high doses of testosterone they will not mount other females. But if eggs are injected with estradiol before hatching, none of the males will mount when they become adult. They have been turned into females in this behavior. Such a dramatic sex reversal in behavior occurs even at a very low dose, and with a single injection (Adkins, 1979). And if eggs are injected with an estrogen antagonist (estrogen receptor blocker) or estrogen synthesis inhibitor, the females will themselves mount when they are adults; they have been turned behaviorally into males (Balthazart and Adkins-Regan, 2002).

Such effects are permanent and limited to a critical period. A parallel effect has been reported in the zebra finch, *Taeniopygia guttata* (Adkins-Regan and Ascenzi, 1987): young males treated with estradiol failed to mount as adults. Because zebra finches hatch at a less developed stage, the critical period for effecting this treatment is the first week or two after hatching, not pre-hatching. These experiments in two unrelated birds confirm that sexual differences in a behavior closely linked to reproductive success arise from hormonal organization.

Does hormonal organization also create sexual dimorphism in mate choice and other sexually selected behavior such as courtship display and singing? These behaviors are also important for fitness. In Japanese quail, much of the sexual difference in crowing and strutting is due to dimorphism in adult hormone levels. In contrast, difference in interest between the sexes in looking at a female — males are much more interested — is hormonally organized in the same manner as mating itself (Balthazart and Adkins-Regan, 2002). Most other research addressing hormonal organization of mate choice and related behavior has been conducted with zebra finches.

Zebra finches choose their partners at an early age and pair for the life of the partner. Paired males and females spend much time preening each other, sitting in direct physical contact and occupying a nest box together. There are no sexual differences in these behaviors. Instead, the real difference in zebra finches (and other birds) lies in the choice of partner, with males usually choosing females, not males, and females usually choosing males, not females. Pairing preference can be measured both in free-flight aviaries containing a group of birds and in two-choice tests where a subject bird chooses

between a male and a female. A further sex difference related to mate choice in zebra finches is song: males sing, a behavior that is attractive to females, but females never sing. Are such differences in mate choice and singing produced by organizational actions of sex hormones?

Beginning with Gurney and Konishi (1980), several laboratories have shown that female zebra finches injected with estradiol during the nestling period grow up to sing remarkably well and to have male-sized song regions in the brain (Balthazart and Adkins-Regan, 2002). It might seem paradoxical that estradiol, an estrogen, should turn females into males with respect to singing. Such masculinization is not uncommon in studies of hormones and behavior; and, moreover, normal male zebra finches have as much circulating estradiol as females, both as nestlings and as adults (Adkins-Regan et al., 1990).

Can partner preference also be sex reversed by manipulations of hormones at early stages? Adkins-Regan and Wade (2001) carried out an experiment in which finch eggs were injected with a drug (fadrozole) that prevents the formation of estrogens such as estradiol. Females hatching from these eggs had testes or ovotestes rather than the normal single ovary, confirming that, in normal development, estrogen acts to produce the ovary, much as estrogen organizes female mating behavior in normal development in quail (lack of mounting). Fadrozole treated female finches were also sex-reversed in their pairing preference. Here there is another apparent paradox, because estrogen masculinizes singing whereas its inhibiting masculinizes partner preference. Singing and partner preference are likely to have different neural bases, however. Thus hormone manipulations at early stages of growth caused partial or complete sex reversal of behaviors related to mate choice. This supports the hypothesis that hormonal organization creates sex differences in these behaviors in birds.

3 Issues for phylogeny and biology

The hormone organizational concept may be used to address some important comparative and phylogenetic issues in biology. First, among the nearly 10 000 species of birds in the world, there is an enormous range of sexual dimorphism in behavior and appearance. In some species, the sexes look identical to our eyes, and in others very different. The same is true of sexually selected behavior, such as singing. In some species, such as those that duet, both sexes sing equally well. In others such as zebra finches, females never normally sing. Such diversity is thought to

Table 1 Comparison of effects of early treatments on zebra finch behaviors

Treatment	Behavior		
	Singing	Mounting	Partner preference
Estradiol	F→M	M→F	F→M
Estrogen synthesis inhibitor	0	0	F→M

F→M = masculinization; M→F = feminization/demasculinization; 0 = no effect.

be the consequence of the degree and type of sexual selection that has occurred in the evolution of the species. When confronted with it in closely related groups of birds, we can ask whether the hormone organizational concept can help us understand the developmental mechanisms responsible for its evolution.

Wrens of the genus *Thryothorus* wrens are a case in point. Within this genus there is marked variation in singing between the sexes: in some species only males sing whereas in others both sexes do, some duetting (Farabaugh, 1982; Levin, 1996). Males of species in which males alone sing have greater sexual dimorphism in the brain song nuclei (Brenowitz and Arnold, 1986; Nealen and Perkel, 2000). Enough is known about how song system dimorphism develops to be able to envisage, as these researchers have, how a small developmental change, such as in the timing or amount of estrogen action, might result in a shift from sexual monomorphism to dimorphism in singing or vice versa. This example also serves as a reminder that the nervous system and its developmental rules are critical to understanding evolutionary change in behavior.

A second issue is raised by research on zebra finches which suggests that the rules for the hormonal organization of mounting, singing, and partner choice might be somewhat different (Table 1). All three behaviors seem to be organized by sex steroids, but a different pair of results is seen for each behavior. This helps us to understand how such behaviors evolve somewhat independently of one another. Given that females prefer singing males, it would be disastrous for the species if the evolution of singing required a loss of mating (e.g., mounting) behavior in males. Divergent hormonal pathways (developmental cascades) provide the necessary disconnect for changing one behavior without disrupting others. They allow the evolution of diverse degrees and kinds of singing and mate choice without perturbing mating, which must occur. Divergent developmental cascades could also be the mechanistic basis for sex role reversal in birds, as in buttonquail, Turnicidae, in which females sing and are more brightly colored yet still produce eggs that need to be fertilized.

A third issue concerns the evolution of elaborate behaviors in male birds, far more than in male mammals, to attract females, especially potentially costly courtship signals such as the display of the peacock or song of the skylark. Reeve and Shellman-Reeve (1997) have proposed that the potential for evolving to a novel adaptive peak of this kind derives in part from the genetic architecture of the lineage, which differs in birds and mammals. Birds have Z and W sex chromosomes, and males are the homogametic sex; mammals have X and Y chromosomes, and females are the homogametic sex. According to Reeve and Shellman-Reeve's (1997) protected invasion theory, a novel trait will

be less susceptible to extinction in early evolutionary stages if it appears in the ZZ or XX sex, that is, the sex with the two similar sex chromosomes. Sexual selection is usually stronger for males; and in birds, it is the male that has the two similar sex chromosomes. Thus protected invasion theory helps us understand why elaborate males seem to have evolved more often in birds. What does this have to do with hormones? Because they regulate the expression of genes on autosomes to produce sex-limited trait expression, steroids in effect bring these genes under the protected invasion principle.

Hormonal organization is an especially powerful trait expression mechanism because it occurs early in the life of the animal and is permanent. By integrating its study with research and theory on development and behavior, we can achieve greater understanding of the evolution of sexually selected behavior, for which birds are justly famous.

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S14-5 Studies of song behavior in European starlings: interrelationships among testosterone, neuroanatomy and immune function

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Abstract Female starlings pair preferentially with males that produce song organized into long bouts. Females exhibit immediate early gene responses in the auditory forebrain that are biased towards longer bout songs. In male starlings, length of song bout correlates with variation in the volume of two key brain areas controlling song production, the HVC and the robust nucleus of the archistriatum (RA). Length of song bout and song rate are correlated positively with variation in humoral and cell-mediated immunity respectively. Testosterone stimulates female-directed song and the volume of the song control nuclei, but inhibits (perhaps indirectly) immune responses. This hormone is thus positioned as an important endogenous signaling mechanism that coordinates several aspects of male physiology and behavior relevant to reproductive success in starlings.

Key words Brain control, Testosterone, Immune response, European starling

1 The function of male song in relation to female choice

In this paper we review recent studies that interrelate endocrine state, brain mechanisms for song perception and production, features of song, and immune measures in European starlings (*Sturnus vulgaris*), considering first the adaptive significance of male song in that species. Several lines of evidence indicate that male starling song influences female choice. Male starlings paired with a female will increase their rate of singing just prior to copulation (Eens and Pinxten, 1990) and stop singing only after the clutch is complete, whereas unpaired males continue singing throughout the breeding season (Kluyver, 1993; Eens, 1997). In fact, male song output is closely related to different stages in the female breeding cycle. There is a rapid decrease in male singing activity after pairing (Eens et al., 1994; Hindmarsh, 1984), and then an increase 2 to 4 days prior to egg laying, after which song rates remain elevated until the end of the laying period before nearly ceasing altogether (Eens et al., 1994).

Likewise, male song rate is negatively correlated with the date of clutch initiation (Mountjoy and Lemon, 1996; Wright and Cuthill, 1992). The post-pairing period of high song output coincides, moreover, with the presumed fertile period for female starlings (Birkhead et al., 1987), and (albeit roughly) with the most rigorous period of mate guarding for the male (Pinxten et al., 1987). In the field, copulations between starlings are almost always preceded by bouts of male song (Eens et al., 1989; Eens and Pinxten, 1995;

Mountjoy and Lemon, 1996); and when presented with a conspecific female, unmated captive male starlings sing many more song bouts than when confronted with a conspecific male (Eens et al., 1993). The number of songs sung in the nest box also increases significantly with the introduction of a female, both for captive male starlings (Eens et al., 1993) and those in the field (Eens et al., 1994).

Among males, both repertoire size and song bout length are directly correlated with age and mating success (Eens et al., 1991). In the laboratory, moreover, female behavioral preferences can be directly controlled by varying the mean length of male song bouts. That is, females will spend more time listening to long bouts of male song than to shorter ones, and will preferentially track the position of longer bouts coming from different locations (Gentner and Hulse, 2000).

2 Testosterone and male starling song

Like many temperate zone songbirds, starlings are seasonal breeders and exhibit marked seasonal variation in hormone concentrations in the plasma (Dawson, 1983; Ball and Wingfield, 1987). As noted above, song activity peaks just prior to and during the egg-laying period which means that high rates of song roughly correlate with high concentrations of plasma testosterone (T) in field-caught males (Dawson, 1983; Ball and Wingfield, 1987). However, it is not the case that male starlings sing only when breeding. Song can be heard in the fall as well, and even in late summer during molting (Feare, 1984; Eens, 1997). Song in the fall and early winter, in contrast to breeding song, does not

seem to be influenced by the presence or absence of a female. When males held in outdoor aviaries with nest boxes are presented with a female, they do not change their song rates, whereas males housed in similar conditions in the spring increase song rates dramatically (Riters et al., 2000). Experimental studies involving the administration of exogenous T indicate that T does enhance the rate of song production in male starlings but it is specifically female-directed song that is enhanced (DeRidder, Pinxten and Eens, 2000; Pinxten et al., 2002).

3 Variation in the song control system and song behavior in starlings

Starlings, like all songbirds, possess a specialized forebrain circuit involved in the learning and production of song (Brenowitz et al., 1997). Captive studies involving the manipulation of photoperiod, as well as studies of starlings housed in outdoor aviaries experiencing natural fluctuations in photoperiod, indicate that a key forebrain nucleus, HVC, changes seasonally in volume (Bernard and Ball, 1995; Riters et al., 2002). An important nucleus for the control of courtship behavior, the preoptic medial nucleus (POM), also exhibits variation in volume and is largest during the breeding season (Riters et al., 2000). These brain changes are regulated, at least in part, by seasonal variation in testosterone concentration in plasma (Bernard and Ball, 1995;

Riters et al., 2000). Within older birds, the size of the HVC and another brain nucleus involved in song production, the robust nucleus of the archistriatum (RA), correlates with variation in length of song bout (Bernard et al., 1996) — Fig. 1. It is not known whether this intra-specific variation is related to variation in concentration of plasma testosterone. Thus features of male neuroanatomy appear to be driven by behavioral attributes that females use in choosing males.

4 Neural correlates of song perception in female starlings

It was discovered about 10 years ago that conspecific song can induce a marked expression of immediate early genes in the auditory forebrain of male and female songbirds (Mello et al., 1992). In particular, many neurons in the caudomedial neostriatum (NCM) and the caudal ventral hyperstriatum (cHV) show a rapid up-regulation of the immediate early gene ZENK in response to the presentation of conspecific songs (Mello et al., 1992). This gene expression is tuned to the acoustics of particular conspecific song syllables (Ribiero et al., 1998). Interestingly, the genomic response also habituates to the repeated presentation of the same conspecific song (Mello et al., 1995). In starling females, it was found that the number of cells expressing the ZENK protein in the ventral NCM were significantly higher in those females exposed to longer songs, whereas variation in the total duration of song exposure had no significant effect (Gentner et al., 2000). These results suggest that subregions of NCM in female starlings are tuned to variation in male song length. Thus females exhibit biases in gene expression that correlate with song attributes to which they attend when choosing males.

5 Why choose males that sing longer bout songs?

One attractive theory for female choice is that females attend to characters that predict male quality (Andersson, 1994). Recently much work has focused on traits that correlate positively with variation in immune responses as a basis for female choice (Folstad and Karter, 1992). In male starlings, measures of cell-mediated and humoral immunity were assessed via cutaneous swelling responses to T-cell mitogen phytohaemagglutinin and via antibody responses to a novel antigen, keyhole limpet haemocynin. Song rate and length of song bout were positively correlated with cell-mediated and humoral immunity respectively. Thus features of male song chosen by females experimentally do predict variation in immunocompetence (Duffy and Ball, 2002).

6 The role of testosterone

In European starlings it is clear that there is interplay between female choice and various aspects of male behavior, neuroanatomy and physiology. The gonadal hormone T is involved in the regulation of all these aspects of the male phenotype. It stimulates song behavior during the breed-

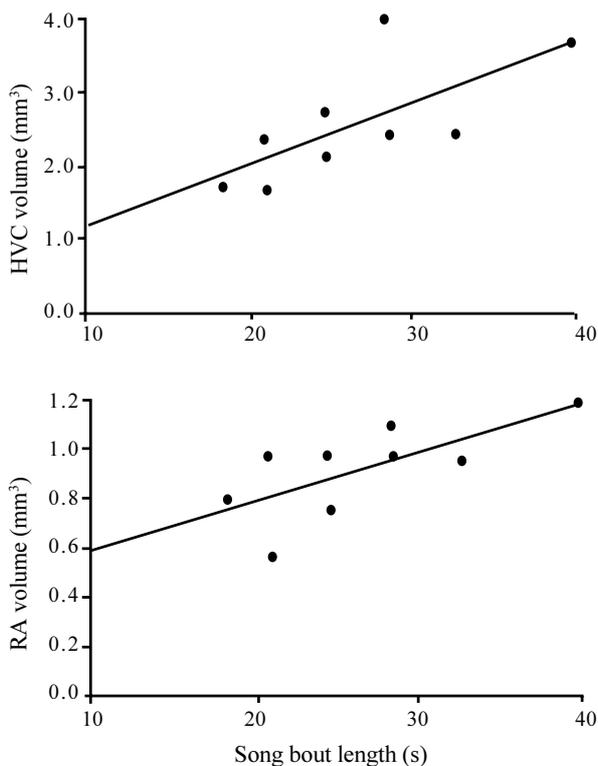


Fig. 1 Scattergrams showing the positive correlation between length of song bout (in seconds) and the volume of song nuclei HVC (top) and robust nucleus of the archistriatum (RA) (bottom) in the brain of European starlings

From Bernard et al. (1996).

ing season (Pinxten et al., 2002) and it promotes the growth of song nuclei such as HVC and RA (Bernard and Ball, 1995). It also inhibits cell-mediated and humoral immune measures, although this may be through increased corticosterone secretion (Duffy et al., 2000). Further studies are needed to assess exactly how this hormone may coordinate the disparate but related aspects of the male phenotype that are so important for reproductive success.

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Symposium 15 Specialization in island land birds

Introduction

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Many island land birds are under threat of extinction today as a result of increased human impact on their environment (Collar et al., 1994). How could such vulnerable species evolve on islands where the physical environment is hazardous and the vital resources limited? Obviously, to persist on islands for a long time, as they must have done so till now, they would have had to be well adapted to island life except against invasive species. It is generally assumed that such adaptation involves flexible use of resources, particularly food resources. There are a number of examples of colonizers becoming generalists (Grant, 1998). We also have clear examples of extreme specialization, such as found among the members of Vangidae in Madagascar (Yamagishi and Eguchi, 1996), Paradisaeidae in New Guinea (Frith and Beehler, 1998) and Callaeatidae in New Zealand (Williams, 1976). These islands are large enough to have the diversity of topography and resources to permit radiation of founding species; but interspecific interactions are unlikely to be the cause of specializations, particularly in New Zealand where species diversity has remained low. It is therefore remarkable that small islands, such as those of the Galapagos and Hawaiian chain, have produced specialized species of land birds to the extent that they have (Grant, 1999).

In this symposium we attempt to identify the evolutionary processes that enable specialization among island land birds. Are there detectable behavioral or ecological characteristics among colonizing land birds that reveal potential for specialization or anti-specialization? Such characteristics include resource partitioning, competitive release, environmental plasticity, individual specialization, density inflation, social tolerance and site tenacity. Key to evaluating these specializations is the issue of how island populations maintain the flexibility required to meet the challenges of changed environment in the face of the specialization needed for effective use of limited island resources.

One possibility is that individuals become adept at exploiting several resources, thereby maintaining flexibility to cope with environmental changes. Another is that individuals, while each specializing on different specific resources (and thereby remaining unskilled and uncompetitive in utilizing others), form a population that maintains flexibility and effective size by exploiting a greater range of resources collectively. This second scenario would see intensification of intraspecific processes, which could lead to degrees of specialization far beyond the flexible use of resources and establish special relationships with limited but reliable resources. Such specialization may then lead on to speciation and adaptive radiation on islands. One difficulty with this hypothesis is that the process specialization needs to happen frequently because occasional hazards will eliminate the majority of skilled individuals.

This symposium focused mainly on the land birds of small islands remote from neighboring continents. In archipelagos, radiation of species is assisted by geographical isolation of founder populations; but on single islands, a tendency to differentiate through efficient use of limited resources is revealed in analyses of specialization.

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S15-1 An overview of feeding specialization and generalization on islands

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Abstract Land birds on small, remote islands sometimes feed in unexpected and diverse ways. Observations such as these have given rise to the idea that islands are difficult to reach; the first lucky colonists to arrive enter a competitor-free environment, to take advantage of extra resources and diversify their diets. They become generalists by responding to new opportunities. They may be driven by natural selection to generalize because resource variety, like bird diversity, is reduced on islands. Species in archipelagos are different. Evolutionary patterns are more complex than on solitary islands, more multidirectional than unidirectional. Some species display generalist behavior while others are impressively specialized. We know most about evolution in archipelagos from the study of two spectacular adaptive radiations: the honeycreepers (finches) in the Hawaiian archipelago and Darwin's finches on the Galápagos islands. Adaptation to feeding in a specialized manner on a narrow range of food resources has been facilitated by strong isolation on the archipelagos and the rarity of colonization by other bird species. Environmental change has played a largely unknown part in creating new niche possibilities. The appearance of behavioral novelties, such as tool-using by the Galápagos woodpecker finch (*Cactospiza pallida*), reflects an unpredictable element in the evolution of feeding specializations. To place feeding specializations and generalizations in an evolutionary context, a phylogeny is needed. This work has only just begun, and presents some stimulating challenges to quantify modern diets and to reconstruct ancestral ones.

Key words Foraging diversity, Specialized beaks, Novel behavior, Phylogeny, Radiations

1 Introduction

Some birds on islands are strange, and do strange things. I shall start with a bird that everyone knows but no one has seen alive: the dodo. It was a pigeon built like a goose without the power of flight. It illustrates three fundamental points about birds on islands: (1) change in feeding niche, (2) morphological trends, in this case towards massive body size and flightlessness, and (3) vulnerability to extinction. Its feeding behavior cannot be observed because it became extinct centuries ago; but contemporary island species do strange things also, and these can be observed today. We can observe tool-using behavior in the woodpecker finch (*Cactospiza pallida*) on the Galápagos islands, or the rolling, breaking and eating of booby eggs by the sharp-beaked ground finch (*Geospiza difficilis*) on the same islands, or, in the very same population, blood-drinking from wounds that the finches inflict at the base of booby wing feathers (Bowman and Billeb, 1965).

Observations such as these and many more, together with island biogeography theory, have given rise to the idea that, for birds, islands are difficult to reach. The first lucky colonists to arrive enter a competitor-free environment, and there take advantage of extra resources and diversify their diets (Grant, 1998). They may start out as generalists (Ricklefs and Cox, 1972), although there seems to be no obvious trend (Schluter, 2000), or they become generalists by responding to new opportunities. They may be driven in

the same direction by natural selection because resource variety, like bird diversity, is reduced. This is especially likely to happen if occasional temporal fluctuations in resources make food-finding difficult at times. More than a century ago, Grayson (1871) made this point when interpreting his surprising finding that hawks, owls and wrens on Socorro in the Revilla Gigedo group of Mexican islands fed largely on land crab meat.

2 Generalists on solitary islands

Species on such islands become generalists in two ways (Grant, 1999). Either all individuals are generalists in the same way (type 1a) or they are specialized in somewhat different ways (type 1b), according to age, sex, beak morphology etc. There is no good theory that tells us when and where to expect each type, probably because factors inherent within species are as important as extrinsic (environmental) factors. Nevertheless, both types of generalists exist.

2.1 Type 1a generalization

Members of this group are exemplified by the white-eyed vireo (*Vireo griseus*) on Bermuda. Crowell (1962) performed a pioneering field study by comparing the foraging characteristics of three bird species on Atlantic island, Bermuda, with their foraging behavior in similar habitats on the North American mainland. By using the information

theory statistic H as a measure of foraging niche diversity, he found that only one of the three species, the vireo, was more generalized in its foraging on Bermuda. Type 1a generalization is expressed by the absence of conspicuous foraging differences among individuals in the island population. The study also produced the insight that niche expansion involves an increase in the use of marginal resources rather than the acquisition of entirely new ones by adoption of new foraging techniques. This may be the usual mode by which niche expansion begins, perhaps by trial-and-error learning and exploitative responses to local foods within the behavioral repertoire of the birds. Later the repertoire changes.

2.2 Type 1b generalization

The alternative type 1b generalization has been described by Jiro Kikkawa and colleagues (1975) in silvereyes (*Zosterops lateralis*) on Heron Island, Australia, and more recently quantified by Werner and Sherry (1987) in a study of the Cocos finch. The distantly isolated Costa Rican island of Cocos is occupied by a single species of Darwin's finch (*Pinaroloxias inornata*) and only three other, and unrelated, species of land birds. By banding 89 individual finches and quantifying their foraging in nine types of probing and gleaning, Werner and Sherry showed that none of them fed in all nine ways. Rather, 62 spent more than 50% of their foraging activity on a single foraging behavior. The finches are individually specialized and, importantly, different individuals are specialized on different food resources or to different ways of exploiting them. The same has been found in some of their Galápagos relatives (Grant, 1999).

Despite these two well-investigated examples, there are very few comparative studies of diet diversity and foraging behavior in island populations and their mainland relatives (Grant, 1964; Morse, 1971; Martin, 1992). Even so, the direct evidence for trends towards diet generalization on islands is complemented by indirect evidence from morphology. Maximum food size is a function of beak size. As beak size increases among populations or species, maximum food size increases faster than minimum food size, with the result that the potential range of food sizes in the diet increases. Birds on islands, especially small species (Clegg and Owens, 2002; Owens et al., this symposium), tend to become larger in beak as well as body size and, by inference, their diets broaden.

3 Generalists and specialists in archipelagos

Species in archipelagos are different. They show no such trends. Evolutionary patterns are more complex than on solitary islands, more multidirectional than unidirectional. Some display generalist behavior while others are impressively specialized. Most is known about evolution in archipelagos from the study of two spectacular adaptive radiations: honeycreepers (finches) in the Hawaiian archipelago and Darwin's finches on the Galápagos islands. The

honeycreeper radiation has been extremely rapid (Schluter, 2000; Fleischer and McIntosh, 2001). From a cardueline finch ancestor, they have diversified morphologically in a manner that not only duplicates a range of passerine morphologies in other families, but also goes beyond them into novel morphological space (Lovette et al., 2002). Darwin's finch morphologies are also diverse; 14 species evolved in the last 2–3 MY, and are much more varied than extant mainland relatives (Sato et al., 1999, 2001; Burns et al., 2002). Diets diversified as well.

For understanding the evolution of diets and foraging niches, a phylogeny is needed. A simple overview of diet evolution can be gained by examining variation in diets across a phylogeny, such as the microsatellite-based phylogeny of Darwin's finches (Petren et al., 1999) or one that is mtDNA-based (Sato et al., 1999). Both show that specialized and generalized diets are interspersed among the lineages, implying multiple evolutionary origins for both.

To improve detail, quantitative data are needed. Diets of the four most recently derived ground finch species have been well characterized on the small Galápagos island of Daphne Major. Two species are specialists and two are generalists, as reflected in their positions on axes of variation of seed size and flower exploitation (Grant and Grant, 1996). Interestingly, one of the generalists, the cactus finch (*Geospiza scandens*), specializes on cactus (*Opuntia*) products when overall food supply declines to low levels (Boag and Grant, 1984). This makes it clear that the generalized diet of the other generalist, the medium ground finch (*G. fortis*), is derived, because the species itself is phylogenetically derived (Petren et al., 1999). In this case, a specialist species has given rise to a generalized one, reminiscent of the trend on solitary islands.

Schluter and colleagues have used more powerful statistical inference procedures to estimate ancestral diets in Darwin's finches and other groups of organisms (Schluter et al., 1997). Results vary to some extent, depending on the algorithm used when transition rates are constrained to be equal or not. The results are also dependent on adequate characterization of diets of all species. In terms of the theme of specialization and generalization, adequate characterization has not yet been realized for any monophyletic group of birds on islands. The analyses, limited by uncertainty, show a way forward but not a destination reached.

Substituting beak sizes and shapes for diet is an alternative to diet analysis for reconstructing ancestral states. Beak morphologies are easier to assess and better known. For example, among the Hawaiian honeycreepers, there are two specialized beak morphologies, one thin and down-curved, the other very deep. The first is a tool for probing flowers for nectar, or cracks and crevices in bark for cryptic arthropods. With its extreme evolution, some aspects of food acquisition and crushing in the basic honeycreeper diet must have been relinquished as new techniques were acquired. The deep blunt beak of the Kona finch (*Chloridops kona*) exemplifies the other bill form. It was

apparently used in a specialized way to crack the hard seeds of *Myioporium* (Perkins, 1903). The deep but narrow and hooked beak of the parrotbill (*Pseudonestor xanthophrys*) is also used to break twigs and small branches to reach cryptic insect larvae by brute force. Similar adaptations are found in mainland avifaunas, and in other island settings as well, reflecting repeated and convergent evolution from different starting points. For example, sickle-shaped beaks are possessed by the neotropical woodcreepers, Dendrocolaptidae (Raikow and Bledsoe, 2000) as well as by one of the vangids, the sickle-billed vanga (*Oriolia bernieri*) on Madagascar (Yamagishi et al., 2002).

In contrast to predictable convergence, the woodpecker finch on the Galápagos represents the idiosyncratic, unpredictable, element in evolution. In its diet, it is similar to the cryptic arthropod-exploiters of Hawaii, such as the extinct akialoa, *Hemignathus obscurus* (Perkins, 1903); but the manner in which it obtains its prey could not be more different. Rather than developing an attenuate, probing bill for grasping prey, its behavior is modified to bring the prey within reach: a twig or cactus spine is used by the bill as a tool to provoke emergence of insect larvae from their galleries deep within branches. Such a change in foraging niche through the acquisition of a new skill is very different from the marginal expansion described by Crowell (1962) and referred to earlier. It also differs from the blood-eating of the sharp-beaked ground finch, which appears to be derived from the more prosaic habit of eating ectoparasitic hippoboscid flies and ticks (Bowman and Billeb, 1965). Rather, it has more in common with egg-exploitation in the ground finch because egg-eating has no obvious antecedents.

How did tool-using behavior arise? According to one explanation, a twig was picked up in the trial-and-error phase of early learning and crudely manipulated, yielding some food reward. Tool-use may have improved through subsequent trials with errors and successes, and other finches may have observed and copied the behavior. Mutation affecting a genetic predisposition to behave in this way is another explanation, with social learning perhaps playing a secondary role. By experimenting with captive young woodpecker finches in the presence of tutors that did or did not use tools, Tebbich and colleagues (Tebich et al., 2001) have supported the second explanation by showing that social learning is not required for the expression and development of tool-using behavior. Trial-and-error learning, nevertheless, occurred during the development of tool-using skills in the experimental birds. This pioneering study opens up new possibilities for examining the evolution of specialized behaviors, both feeding and reproductive, on islands.

Long-term stability presumably facilitates specialization, which is why the strongly isolated Hawaiian and Galápagos archipelagos have more specialists, apparently, than the less isolated Solomon and Bismarck archipelagos (Mayr and Diamond, 2001).

4 The importance of environmental change

There is another, different problem and challenge confronting attempts to understand the evolution of feeding ecology on islands. It lies in reconstructing ancestral environments to place the reconstructed ancestral states of island birds in their correct paleo-environmental context (Grant, 2001). I illustrate the point with a single example. According to allozyme and mitochondrial DNA evidence, Darwin's finches colonized the Galápagos about 2 MYA, possibly as much as 3 MYA, at a time when the archipelago was simpler than it is now (Grant, 1999). As new islands were formed through volcanic activity under modern Fernandina, the number of islands increased and their heights and degrees of isolation changed. Moreover, global, and presumably local, climate changed from hot to cooler, then oscillated back and forth during the last million years of glacial-interglacial dynamics. Sea level fell and rose repeatedly, causing coastlines to expand and contract. Vegetation changed, possibly from Cocos island-like rainforest at all elevations to the seasonally arid vegetation at low elevations and moist forest in the highlands present today.

Throughout this period new species of plants and animals probably invaded and colonized the islands, while others became extinct. The adaptive radiation of Darwin's finches happened in the past and therefore should be interpreted in terms of the past, that is, against this backdrop of strong environmental change. For example, the recently evolved ground finches and tree finches may have evolved only after small hard seeds became abundant under a climate of seasonal aridity at low elevations and the development of *Scalesia* forests in the highlands. Presumably when that happened, some of their predecessors became extinct, for the same reason: a change in the food supply.

It is an open question whether a knowledge of past environments in a changing landscape is merely desirable or essential for understanding the evolution of birds and their foraging niches on islands. To what extent are the features of those birds explicable solely in terms of current adaptive landscapes? What is the residual variation whose explanation has to be sought in past events? I suspect the residual variation is not negligible when we ask why birds feed in some ways and not in others.

5 Conclusions

Generalized and specialized feeding of birds on islands has been reviewed here largely in the context of feeding opportunities arising from food availability. Direct quantitative data on diets are surprisingly scarce, and one obvious need is for more data on a variety of birds on many islands. Another need is for more phylogenetic reconstruction and better methods of analysis to permit stronger inferences about the evolutionary pathways of dietary diversification and change. A third need is to determine how much of the features of island birds is explicable solely in terms of

current adaptive landscapes, and how much requires a knowledge of past events.

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S15-2 Food specialization and radiation of Hawaiian honeycreepers

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Abstract Hawaiian honeycreepers are renowned for adaptive radiation and diet specialization. Specialization arose from competition for the relatively few resources available in this remote archipelago and because arthropod prey sufficient to satisfy nestling protein requirements could only be captured by highly modified bills. Historically, most species fed their nestlings with larvae of the widespread geometrid moth genus, *Scotorythra*; but other invertebrates were important also. Thus the palila, *Loxioides bailleui*, a specialist on potentially toxic *Sophora chrysophylla* seeds, feeds its nestlings on *Cydia* moth larvae found inside *Sophora* seeds. *Sophora* seeds are also fed to the nestlings, and seed availability largely determines the timing and extent of breeding. By this and other means, food specialization contributed to reproductive isolation in *Loxioides* and possibly other honeycreepers. Alien threats to insect prey affect *Loxioides* populations and have hastened the extinction or decline of other specialized Hawaiian birds.

Key words Adaptive radiation, Food specialization, Hawaiian honeycreepers, Moth larvae

1 Introduction

Hawaiian honeycreepers (Fringillidae: Drepanidinae) are renowned both for the extinction crisis that endangers them and for the great diversity of bills that demonstrate so spectacularly their specialization on invertebrates, nectar, fruits, and seeds. Food is provided from among 960 flowering plant species (Wagner et al., 1999), 5 500 insect species, 310 spider species (Nishida, 2002), and about 750 land snails (Cowie et al., 1995), although very few single taxa are abundant throughout the archipelago. For example, the canopies of Hawaiian forests are dominated by less than 15 tree genera, and few of these provide staple food for honeycreepers (Perkins, 1903). Although birds find food on many shrubs and lianas, full trophic relationships are difficult to reconstruct because the feeding habits of many honeycreepers are poorly known and native plant communities, especially at lower elevations, have changed markedly since Polynesian colonization (Burney et al., 2001).

We consider that diet specialization evolved in response to competition for a limited variety of plant and invertebrate resources, and because invertebrate prey could be obtained readily when specialty foods became scarce. Certain Lepidopteran larvae (caterpillars) were accessible to birds whatever their bill shape, and they affected reproduction because they provided essential nutrients for nestling growth. Caterpillars and other easily-captured prey, therefore, were critical to the radiation of nectar, fruit, and seed specialists and to insectivores with extreme bill forms. We illustrate ecological processes involved in the honey-

creepers radiation by examining aspects of divergent natural selection, competition, and reproductive isolation in the palila (*Loxioides bailleui*), the most thoroughly studied species (Banko et al., 2002a). Palilas forage primarily on the seeds of the widespread māmane (*Sophora chrysophylla*, Fabaceae), through which they provide a living example of the evolution and consequences of food specialization.

2 Evolution of Hawaiian honeycreepers

Hawaiian honeycreepers began diverging from a cardueline finch ancestor after the emergence of the oldest large island, Kauai, 5.1 MYA (Fleischer and McIntosh, 2001). Earliest among the species to radiate were seedeaters, including the palila (Fleischer et al., 2001), in contrast to nectar specialists which first appeared 2–3 MYA (Fleischer and McIntosh, 2001). The early prevalence of finch-billed species is not surprising, given the presumed seed-eating habit of their cardueline ancestor.

A diverse array of bill forms demonstrates that many honeycreepers were food specialists. Birds with heavy, conical bills specialized on seeds that required great force to extract or crush; birds with long or short curved bills probed flowers for nectar; and others had bills of various form for extracting invertebrate prey by probing, prying, hammering, and crushing. Not all honeycreepers, however, evolved extreme bills or exploited foods that were difficult to obtain. Some, like the extant *Himatione sanguinea* and *Hemignathus* spp., have relatively short, utilitarian bills that allow them to exploit a variety of foods, including nectar and small, agile arthropod prey (Baldwin, 1953). Of the 57

or more honeycreeper species, 37% had conical, finch-like bills and foraged on seeds that were produced abundantly for many months by widespread plant species (James and Olson, 1991). Heavy-billed birds, such as the palila, specialized on seeds found within hard shells or tough, fibrous coverings. Snails (Mollusca) are also eaten by finch-billed honeycreepers, such as *Melamprosops phaeosoma* (Baldwin and Casey, 1983), and may once have been major prey for other finch-billed species.

Regardless of dietary specialization, honeycreepers relied on caterpillars, especially those of widespread *Scotorythra* spp. (Geometridae), both for nestling and adult survival (Perkins, 1913: clii). Perkins (1903) drew attention to the significance of *Scotorythra* caterpillars for 16 honeycreeper species that represent all foraging guilds and occur on all major islands. Some of the other 958 described native species of Hawaiian moths (Nishida, 2002) were also heavily exploited. For example, the palila relish a native crambid caterpillar (*Uresiphita polygonalis virescens*) found on māmane trees (Perkins, 1903: 436), demonstrating that common caterpillar species 1) may have subsidized bird populations when specialized foods became temporarily scarce, and 2) would have been readily caught by birds with disparate bill forms and foraging behavior.

Scotorythra moths probably originated before Kauai arose from the sea (Heddle, pers. comm.), so preceding the origin of honeycreepers. Their 38 species (Nishida, 2002) were abundant and occurred on many host plants used by foraging birds (Perkins, 1913: cl-clii). Just as caterpillars influence timing and extent of breeding in Darwin's finches on the Galapagos (Grant and Grant, 1989), so *Scotorythra* and other caterpillars may have profoundly influenced honeycreeper reproduction and demography. Not only would caterpillars have provided protein needed by nestlings (Newton, 1973), but their abundance would have subsidized fledglings with poorly-developed foraging abilities as well. Indeed, specialization on nectar and fruit, which are low in protein, might not have evolved had caterpillars or other protein-rich invertebrate prey not been readily obtainable by birds with bills better suited to other foods.

Apart from caterpillars, spiders (Araneida) were also major prey for honeycreepers, especially for the smaller species (Perkins, 1913:xxxii; Baldwin, 1953: 314). Not surprisingly, some honeycreepers depend primarily on caterpillar and spider food, despite their cardueline origin. Those that do are species of *Oreomystis*, *Paroreomyza* and *Loxops*, which have relatively short, narrow bills and were historically among the most common insectivores (Perkins, 1903: 416, 418). Although some species of *Scotorythra* were periodically superabundant (Perkins, 1913: cli) and arthropods generally available year-round (Baldwin, 1953), there may have been highs and lows in prey abundance, the highs coincident with new leaves on host plants (Coley, 1983). Therefore, seeds, nectar, and fruits that were abundant for much of the year should have been attractive, such that not all honeycreepers became strictly insectivorous.

3 Case study in food specialization: the palila

Examining food specialization in the palila provides insight into the adaptive radiation of honeycreepers generally. The bill of the palila is adapted for removing māmane pods from trees and extracting the soft embryos. After biting through the tough stem and while holding the pod with one foot against its perch, the bird bites and pulls sideways to tear apart the pod and expose the seeds (Banko et al., 2002a). Palilas forage in māmane trees >90% of the time, and though seeds are eaten by all age classes, younger birds are initially inept and often select alternative foods provided by māmane or other sources. In addition to seeds, caterpillars found inside māmane pods and on foliage are important sources of protein, especially for nestlings.

Although once widespread in coastal habitats (Burney et al., 2001), palilas are now restricted to upper altitudes. They are concentrated today on the western slope of Mauna Kea, where a substantial elevation gradient results in an altitudinal wave of pod production from higher to lower levels, and so prolonged seed availability (Banko et al., 2002b). Palilas track pod ripening by moving up and down the slopes (Hess et al., 2001). Where the range of elevation is small, pods are available in shorter seasonal pulses, and palila populations there have disappeared or are declining.

Although crambid caterpillars were major prey of palilas a century ago (Perkins, 1903), they are now rare in palila habitat and have been superseded in the diet by caterpillars of *Cydia* spp. (Tortricidae), which are found within māmane pods (Banko et al., 2002a). Parents feed *Cydia* to their young until 3–4 months after fledging, but independent juveniles, which survive at lower frequencies than adults, consume few *Cydia*. Because *Cydia* caterpillars are cryptic within māmane pods, juvenile palilas may be naive at identifying pods that contain the caterpillars. Both māmane seeds and *Cydia* caterpillars are rich in lipid and protein, but the seeds also contain high levels of potentially toxic alkaloids, including cytosine (Banko et al., 2002c). Palilas forage selectively on the pods of particular trees, presumably because their seeds contain lower levels of alkaloids. *Cydia* caterpillars do not sequester alkaloids from māmane seeds and are nutritious and relatively safe for palilas of all ages.

Specialization on māmane pods has limited the palila reproductively, as indicated by slow growth, prolonged parental dependency, courtship feeding, and close correlation between pod availability and breeding effort. Even on a nutritious diet of seeds, flower parts, and caterpillars, nestlings still require 26 days to fledge, possibly because digestion is slower for a seedeater but also because alkaloids are physiologically costly to detoxify. For example, māmane seeds are fatally toxic to house finch (*Carpodacus mexicanus*; Carduelinae) nestlings (Banko et al., 2002c). This suggests that if hybrid nestlings were produced in a speciation scenario, they might not survive their first serving

of māmane seeds: since both sexes feed the brood, the palila parent would eventually deliver a potentially toxic meal.

Nevertheless, hybridization between palilas and other species is unlikely because māmane seeds are fed to females by courting males. If females assess male quality by the alkaloid level of seeds fed to them during courtship, sexual selection and intra-specific competition may have accelerated differentiation and permitted sympatric speciation. At least one extinct species of finch with a bill similar to *Loxioides* was sympatric with the palila on Mauna Kea (H. James, pers. comm.), and *T. persecutrix* co-occurred with the palila on Kauai (Burney et al., 2001).

The availability of māmane pods strongly affects the timing and frequency of palila nesting (Banko et al., 2002a). Annual pod production is highly variable, but when pods are abundant, palilas may nest for over 8 months, many pairs attempting to nest and some attempting two broods. When pods are less abundant or available for shorter periods, the nesting season is abbreviated and fewer pairs attempt to nest or re-nest.

4 Consequences of specialization for conservation

Two-thirds of all endemic Hawaiian bird species and subspecies are extinct (Banko et al., 2001). About half of all taxa disappeared within the last 1 500 years, and 24 vanished after 1825. Thirty-two of the 47 remaining taxa are endangered, and 11 of these have little or no prospect of survival. Avian malaria, avian pox, and introduced rats and feral cats have devastated the Hawaiian avifauna. It is the most specialized species that have become extinct or are seriously threatened; those with more generalized foraging habits, in contrast, tend to be more common. The conservation dilemma for extreme food specialists should be obvious.

Destruction of lowland habitats accelerated the disappearance of forest birds because many trees flowered and fruited at different times in accord with elevation (Perkins, 1903: 393). It prevented birds from tracking food availability along the original, full gradient of elevation. This phenomenon certainly applies to palila populations on the eastern and northern slopes of Mauna Kea, where māmane forests were destroyed at lower elevations by cattle grazing (Banko, 2002b). Because forest still extends over a large range of elevation on the western slope of Mauna Kea, palilas are still able to survive there. Yet it represents only the extreme upper portion of their historic range.

Nearly all other Hawaiian forest birds have become restricted to upper elevations as well, not only because habitats and resources have been destroyed in the lowlands, but also because disease-transmitting mosquitoes are scarce above 1 500 m. Moreover, many species of parasitic and predatory insects were imported to Hawaii a century ago to protect sugar cane and other crops from caterpillar outbreaks. These biocontrol agents and other introduced pests, such as ants, spread rapidly into native forests and

have decimated native caterpillars and other natural invertebrate prey of the birds (Perkins, 1913). *Cydia* caterpillars, for example, are heavily parasitized by four species of wasps, only one of which may be native (Brenner et al., 2002). Similarly, *Scotorythra* caterpillars found on māmane foliage are heavily parasitized by five alien species of wasps and flies (Banko et al., 2002b). The incidence of parasitism is related to elevation, and at higher elevations, where palilas forage and nest more frequently, parasitism of *Cydia* is lowest (Banko et al., 2002b).

5 Conclusions

The variety of potential bird foods in the remote Hawaiian Archipelago was limited, until human arrival, by infrequent colonization by plants and invertebrates. Natural selection nevertheless produced a remarkably divergent range of bill morphologies and food specializations among the honeycreepers. The assortment of foraging opportunities arising from habitat heterogeneity may have partly overcome the potential ecological and evolutionary constraints of a limited resource base on birds. Dynamic geological processes that created the archipelago, and the resulting physiographic diversity of individual islands, influenced the evolution of many Hawaiian taxa (Carson and Clague, 1995).

Competition initially centered on seeds, reflecting the finch ancestry of the honeycreepers and preponderance of species with finch-like bills. Strong competitive pressures are suggested by the specialization of the palila on potentially toxic seeds, and the preference of other finch-billed species for seeds that, although abundant, were difficult to extract. Species probably became reproductively isolated in various ways, such as through song, other behavioral mechanisms, and allopatric differentiation (Grant and Grant, 2002). Specialization on particular foods also isolated species as populations became dependent on the phenology and distribution of preferred resources, especially those which subsidized reproduction or promoted courtship.

Reproductive isolation of the palila, for example, would be difficult to breach by species not adapted to toxic foods, such as māmane seeds. Abundant arthropod prey sustained diet specialization when preferred foods became temporarily scarce or were nutritionally unsuitable for nestlings (e.g., nectar, fruit). *Scotorythra* caterpillars and spiders were key components of the diets of many honeycreepers (Perkins, 1913), probably because they were frequently abundant and could be captured by birds with a bill of any form. From this evidence, we infer that arthropod prey played an important role in the radiation of the honeycreepers. Survival of the extant species depends upon the continued availability of native caterpillars, as well as preferred seed, nectar, and other invertebrate resources.

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S15-3 Fitness consequences of cooperative breeding in the Seychelles warbler

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Abstract Inclusive fitness benefits have been suggested as the selective force behind the evolution of cooperative breeding. Assessing the benefits accrued to individual males and females is crucial to understanding the sex-specific helping behavior observed in many cooperatively breeding species. We investigated the fitness consequences of male and female helping behavior in the Seychelles warbler (*Acrocephalus sechellensis*). Until 1988, the entire world population of Seychelles warblers was confined to Cousin Island (29 ha), where the carrying capacity has been maintained since 1973. Due to intense competition for breeding vacancies, many young become subordinates within a territory and often help by provisioning non-descendent offspring. On high-quality territories, the benefits accrued by subordinates are higher for females than males. Female subordinates remain on their natal territory and obtain higher inclusive reproductive success by helping closely related relatives, by co-breeding within the group, and through experience in parenting. Males often become subordinates on non-natal territories and so do not gain indirect reproductive success by helping. They only rarely gain direct benefits through co-breeding, and do not gain through the eventual inheritance of the territory. The disparity in the benefits gained by each sex may explain why the majority of subordinates are female. It should be kept in mind that the benefits of cooperation may be later offset by competition between same-sex offspring, and that the balance between these forces determines the reproductive value of sons and daughters.

Key words Seychelles warbler, Cooperative breeding, Fitness benefits, Competition, Territory inheritance, Co-breeding

1 Introduction

Evolutionary theory is based on the concept that individuals are selected on their efficiency in translating resources into reproductive success, thereby maximizing their genetic contribution to future generations (Hamilton, 1964; Maynard Smith, 1964). The fitness of an individual is expected to be affected by the decision to disperse or not (Kokko and Sutherland, 1998; Pen and Weissing, 2000a) and, in cooperatively breeding species, by the decision to help or not (Emlen, 1991; Koenig et al., 1992). If helping results in higher fitness than dispersal, individuals should delay dispersal and help. The most common form of cooperative breeding involves a breeding pair that is assisted by offspring from previous broods. Normally juveniles of one sex are more likely to stay and assist with parental care, while the other is more likely to disperse (reviewed in Stacey and Koenig, 1990; Cockburn, 1998).

To test the fitness benefits of delayed dispersal and helping in the field, detailed knowledge of the fitness functions for males and females is required (Leimar, 1996; Lessells, 1998; Lessells et al., 1998; Koenig and Walters, 1999; Pen and Weissing, 2000b). Such data are not available for most species because of several hurdles. First, dispersal is hard to measure because individuals often leave

the study population. Secondly, measuring reproductive output is complicated because individuals may produce young outside the pair bond (reviewed in Birkhead and Møller, 1992), and because complex patterns of cooperative breeding, ranging from non-breeding to shared reproduction with others, also occur (reviewed in Vehrencamp, 2000). In this paper we review the sex-specific fitness benefits of cooperative breeding in the Seychelles warbler (*Acrocephalus sechellensis*). To our knowledge, asymmetry in sex-specific fitness benefits from cooperative breeding has not been properly assessed before.

The Seychelles warbler is an insectivorous bird endemic to the Seychelles islands in the western Indian Ocean. Although warblers can breed independently in their first year, a lack of suitable independent breeding opportunities drives some individuals to become subordinates within a territory (Komdeur, 1992). The Seychelles warbler is an excellent model species to test the sex-specific fitness benefits of helping behavior because of: (i) the presence of female-specific helping (Komdeur, 1996a; Richardson et al., 2002) and male-specific dispersal (Komdeur, 1992), (ii) the ability to measure local dispersal in detail (Komdeur 1992, 2003), (iii) the availability of molecular markers to assess sex, parentage and coefficients of relatedness between in-

dividuals in the breeding group (Richardson et al., 2000, 2001), and (iv) the wealth of long-term data allowing accurate fitness measures for each individual (Komdeur, 2003). The majority of subordinates occur on high-quality territories, so for simplicity sake and to avoid the possible confounding effects of territory quality, we here consider the benefits gained by male and female offspring in high-quality territories only.

2 Materials and methods

2.1 Study populations and data collection

The Cousin Island population of Seychelles warblers (c. 320 birds) has been intensively studied since 1985, while the populations on the islands of Aride (68 ha) and Cousine (26 ha), established in 1988 and 1990 respectively (Komdeur, 1997), have been studied from establishment. From 1985, nearly all birds on Cousin Island have been banded for individual recognition and, since 1993, blood sampled for molecular sex and parentage analyses. Off-island migration by warblers is negligible (0.13%; J. Komdeur et al., unpublished), so birds that have disappeared are considered dead. In each year of the study period, nearly all breeding attempts were monitored and activity by resident birds observed during the nest building, incubation and nestling periods (Komdeur, 1996b; Richardson et al., 2002).

Observations on incubation and food provisioning were made at all breeding attempts to determine the status of the birds within each territory. The primary male and female were defined as the dominant, pair-bonded male and female in the territory, while the term 'subordinate' included all other resident birds over eight months old in the territory. Subordinates were split into three categories: non-helpers, subordinate helpers (non-parents) and subordinate parents. Playing recorded songs at different locations to provoke territorial defence behavior by the focal birds identified territory boundaries. Territory size was assessed using a compass and aerial photographs. Because the warblers are insectivorous, territory quality was expressed in terms of insect prey availability (Komdeur, 1992), a factor that has been assessed on a monthly basis within each breeding season. Territories were classified into three quality categories: low, medium and high (Komdeur, 1992).

To test whether helping by males results in inheritance of the territory, nine territories that contained a breeding pair and a male helper were selected. For each territory, the primary male was removed and translocated to either Aride in September 1988 ($n = 4$) or Cousine in 1990 ($n = 5$) (Komdeur, 1994a). After the removal of the primary male, focal helpers were kept under daily observation until the breeding vacancy was filled.

2.2 Molecular analyses

The sex of each individual within the study populations was determined using a PCR-based genotyping method (Griffiths et al., 1998). Genotypes were identified for individuals in the Cousin population using 14 microsatellite

markers (Richardson et al., 2000). Coefficients of relatedness between individuals were determined using KINSHIP (Goodnight and Queller, 1999) and employed to determine, in terms of genetic equivalents, the exact direct and indirect benefits gained by subordinates (Richardson et al., 2002). Using CERVUS (Marshall et al., 1998), parentage was assigned with high confidence (>90%) to all offspring sampled between 1997 and 2000 (Richardson et al., 2001).

3 Results

3.1 Benefits of helping: difference between the sexes

In the Seychelles warbler, removal experiments showed that, on high-quality territories, the helping behavior of subordinates increased the reproductive success of focal breeding pairs (Komdeur, 1994a). Furthermore, subordinates were more likely both to become helpers and provide more help when they were closely related to the recipient (Komdeur, 1994b). In this study, however, relatedness was estimated from pedigree data which was shown to be inadequate when, a decade later, we found from microsatellite-based genotyping that complex patterns of shared reproduction and/or extra-group paternity occur in the Seychelles warbler (Richardson et al., 2001, 2002).

It was also found that females always become subordinates on their natal territory ($n = 43$), whereas a significant percentage of males (25%, $n = 20$) became subordinates on non-natal territories ($\chi^2 = 8.51$, $P < 0.05$; Richardson et al., 2002). This suggests that the indirect benefits of helping are more important for females than for males. Using microsatellite markers to calculate precise coefficients of genetic relatedness among individuals (Richardson et al., 2000), we found that female subordinates without parentage accurately maximized indirect benefits by preferentially feeding more related offspring, produced by relatives of the female subordinate. On the other hand, the amount of help provided by male subordinates was low and independent of relatedness to offspring (Richardson et al., 2003).

In the Seychelles warbler, unrelated subordinates (born in other groups) do sometimes help (D.S. Richardson, pers. comm.) It suggests that direct benefits, such as improved parental skills or gaining parentage (Koenig et al., 1992; Cockburn, 1998), or territory inheritance (Emlen, 1991; Koenig et al., 1992; Balshine-Earn et al., 1998), are important too. To test whether helping improved the reproductive success of subordinates that later become breeders, we translocated males and females of the same age but with different degrees of breeding experience to the islands of Aride and Cousine. Individuals were categorized as: (i) experienced breeders that had fledged young of their own in a previous year, (ii) experienced subordinates with helping but not breeding experience, and (iii) inexperienced birds that had neither helped nor bred (Komdeur, 1996b).

On the new islands, birds with helping experience paired with an experienced partner produced their first fledgling as fast as experienced breeders, and significantly faster than inexperienced birds paired with an experienced partner

ner (Fig. 1). Females with helping or breeding experience built better nests and spent more time incubating than inexperienced females. During this period no subordinates assisted any of the breeding pairs. Pairs comprising a male with breeding experience and an inexperienced female took four times longer to produce their first fledgling than pairs of a female with breeding experience and an inexperienced male (Fig. 1). This is probably a reflection of a breeding system in which only females build the nest and incubate. Once inexperienced birds had fledged young and so acquired experience, they immediately improved breeding success by producing a second fledgling in the same time as birds with either prior helping or breeding experience (Fig. 1). Environmental effects were minimized in this study because comparisons were made between breeding pairs occupying territories of equal quality.

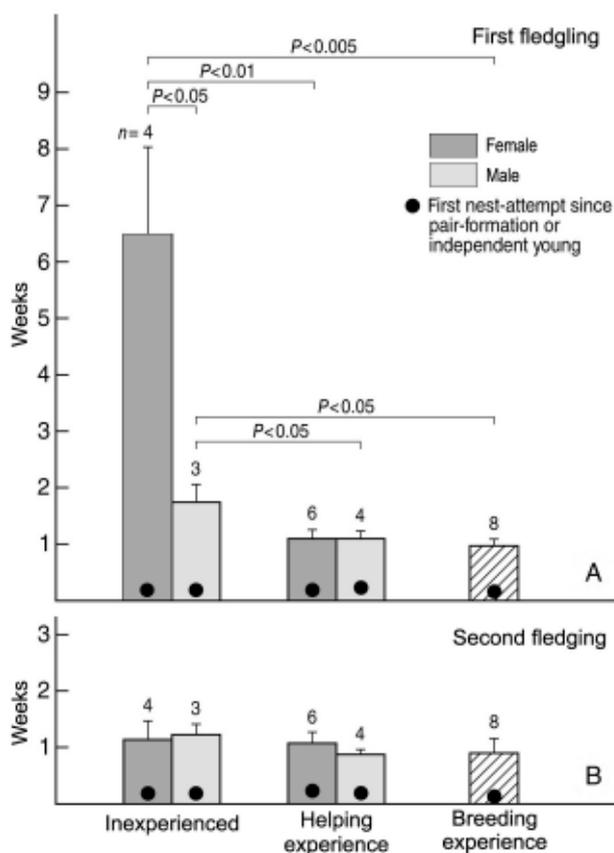


Fig. 1 Comparison of breeding efficiency in Seychelles warblers of differing breeding experience

(A) The number of weeks between pair formation and the production of the first nest and first fledgling on the islands of Aride and Cousine, plotted for male and female birds with different past experience. (B) The number of weeks between independence of first fledgling and the production of a new nest and second fledgling on the islands of Aride and Cousine, plotted for the same male and female birds as in (A) and now experienced breeders. In both cases, the birds were between 3 and 7 years of age, paired with the same experienced breeding partner, and did not receive assistance from helpers. Statistically significant differences determined by Mann-Whitney U tests. Only significant differences are plotted (from Komdeur, 1996a).

Another direct benefit gained by subordinate Seychelles warblers is the acquisition of parentage within the breeding group. Female subordinates often gained parentage within their own group by laying eggs in their mother's nest (44% of 43 female subordinates; Richardson et al., 2001, 2002). Subordinate males also gained direct benefits through parentage within the group (15% of 20 male subordinates), though significantly less often than females (Fisher's exact test, $P = 0.024$; Richardson et al., 2002). Female subordinates gained significantly higher direct breeding benefits (3.3x) than male subordinates, but there was no significant difference for indirect benefits between the sexes (Fig. 2; Richardson et al., 2002). Overall direct benefits were significantly higher than indirect benefits, although this difference was greater in females (Fig. 2; Richardson et al., 2002). None of the subordinate females gained reproductive success through egg dumping in other territories, and none of the male subordinates gained extra-pair fertilizations with females from other groups.

Another suggested benefit of helping is territory inheritance. This may happen in two ways. First, the act of helping in rearing younger siblings could lead to site dominance and, hence, to success when competing for a territory after the death of its owner (e.g., Zack, 1990; Koenig et al., 1992; Balshine-Earn et al., 1998). Secondly, helping can lead to increased size of the family unit and, consequently, to an increase in the size of the natal territory. Large territories may increase the likelihood that the subor-

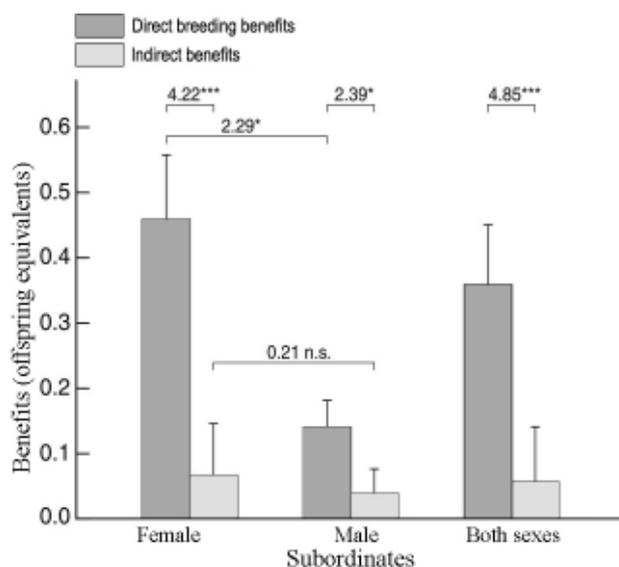


Fig. 2 Fitness benefits of cooperative breeding gained by female and male subordinates in the Seychelles warbler (1997-1999)

Statistical significance assessed by Mann-Whitney Z statistic. Both female ($n = 43$) and male ($n = 20$) subordinates gain significantly higher direct breeding benefits (open columns) compared to indirect benefits (filled columns). Direct breeding benefits are significantly higher in females than in males, but there is no significant difference between the sexes in indirect benefits. Error bars represent one standard error (from Richardson et al., 2002).

dinate will be able to 'bud off' a portion of it as a breeding territory for itself, which might additionally act as a stepping-stone for inheritance (Emlen, 1991).

In the Seychelles warbler, the added presence of male subordinates did not result in an increase in size of the natal territory, and male subordinates that helped never became budders. Because of the absence of a switch between helping and budding strategies, we were able to test whether territory inheritance is entirely the result of helping strategy: male helpers never inherited breeding vacancies after the death of the primary male ($n = 28$; Komdeur and Edelaar, 2001). Moreover, none of these helpers filled any of the nine experimentally created male breeding vacancies that contained a male helper. All male helpers eventually die without having acquired a breeding territory (Komdeur and Edelaar, 2001).

4 Discussion

Inclusive fitness benefits have been suggested as a major selective force behind the evolution of cooperative breeding (reviewed in Cockburn, 1998). One factor that complicates the study of benefits within cooperative breeding systems is the differential in benefits accrued from helping by different individuals in the group (Cockburn, 1998; Heinsohn and Legge, 1999). In systems with subordinates of both sexes, therefore, the benefits of cooperative breeding should be analyzed separately for the sexes. Such differences might in turn help to explain the skewed sex ratios of subordinates often found in cooperative species (West and Sheldon, 2002). The quantification of the direct and indirect benefits accruing to subordinates in cooperatively breeding species has only recently become possible with the advent of powerful molecular techniques that can accurately determine parentage and relatedness within the groups (Burke, 1989; Queller et al., 1993).

The Seychelles warbler is atypical among cooperative breeding birds in that females are much more likely to become subordinates than males. Recorded percentages of subordinates that are female are 88% (Komdeur, 1996a) and 68% (Richardson et al., 2002). Males typically disperse. Our results show that female subordinates gain significantly higher inclusive fitness benefits than male subordinates. Female subordinates remain on their natal territory and obtain higher inclusive reproductive success by helping closely related relatives, by co-breeding within the group, and through improved future parenting ability. Males often become subordinates on non-natal territories and so do not gain indirect reproductive success by helping. They only rarely gain direct benefits through co-breeding, and do not gain through the eventual inheritance of the territory.

The higher inclusive fitness benefits accruing to female subordinates may explain why primary females often skew the sex ratio towards producing female offspring (Komdeur et al., 1997). With female subordinates remaining on the natal territory, the primary female gains both an increase in her own productivity and also indirect benefits

associated with the breeding of subordinate females. The presence of several female subordinates in the group may, however, be a disadvantage to her, because her direct fitness may decline due to competition for food and increased risk of nest failure, mainly from egg breakage due to increased pressure from simultaneous incubation (Komdeur, 1994a). Her indirect fitness may also decline because of increased competition over local breeding vacancies between subordinate female relatives. At this stage, it is in the interests of the group that female offspring should refrain from becoming subordinates and disperse.

The balance between these forces determines whether offspring become subordinates or not. To test the role of cooperation and competition on the fitness of subordinates and their 'decision' to become a subordinate, some subordinate females should be removed from extended families. The shifts in newborn offspring would then have to be compared before and after the manipulations.

There is good evidence that inclusive fitness consequences are higher for female than male subordinates in the Seychelles warbler. The long-term inclusive fitness functions for subordinates and non-subordinates of both sexes, however, should be calculated from molecular parentage analyses and precise coefficients of genetic relatedness, in order to predict under what circumstances males and females should become subordinates.

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S15-4 Large body size in island-dwelling passerines: the roles of insular specialization, niche expansion and ecological release

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Abstract Birds follow the “island rule”, under which small-bodied forms tend to get larger on islands and large-bodied forms tend to get smaller. The traditional explanation for larger island relatives of small-bodied forms is based on ecological release on islands: islands support relatively few species, interspecific competition thus is weak, selection therefore favors niche expansion and ecological generalism, and ecological generalism is facilitated by larger body size. Anecdotal observations that island-dwelling populations sometimes have unusual feeding habits support this. However, important predictions arising from this hypothesis remain untested, namely that (1) island populations will display a greater range of foraging behaviors than mainland populations, and (2) generalist island populations will be made up of individual generalists rather than a diversity of individual specialists. We tested these predictions using the island-dwelling white-eyes (*Zosteropidae*) of the Southwest Pacific region, and the Heron Island population of the Capricorn silvereve (*Zosterops lateralis chlorocephalus*) in particular. Results show that island-dwelling populations of silvereves are indeed consistently more generalistic than their mainland counterparts when viewed *en masse*. Contrary to the generalist foraging hypothesis, however, individual island-dwelling silvereves are actually more specialized than expected by chance alone. Thus generalist foraging and ecological release are not the full explanation for increased body size in these birds.

Key words Niche expansion, Ecological release, Body size, Specialization, *Zosterops*

1 Introduction

Island-dwelling birds have long proved a fruitful source of inspiration to evolutionary biologists and ecologists (MacArthur and Wilson, 1967; Carlquist, 1974; Lack, 1976; Grant, 1998). There are at least two particular reasons for this. First, island communities are often made up of a different mix of species from mainland communities, leading to a string of theories on biogeography and the evolution of biodiversity. Secondly, island-dwelling forms are often different — in terms of morphology, behavior and ecology — from their mainland counterparts. We will focus on the second of these phenomena, using observations and tests on a particular species, the silvereve (*Zosterops lateralis*), to illustrate general patterns in the way island- and mainland- populations differ in ecology and morphology.

In his overview, Grant (Grant, this symposium) stressed the importance of distinguishing between evolutionary shifts in populations on solitary islands versus adaptive radiations in archipelagos, and explained why we might expect to find different patterns and mechanisms in these separate situations. Darwin’s finches of the Galapagos are the classic case of adaptive radiation in archipelago-dwell-

ing birds.

We have been studying evolutionary shifts of the other type, on solitary islands. Our subject populations are, in most cases, the only representatives of their family — the *Zosteropidae* or white-eyes — on the island in question, and may well represent a single colonization event. It is true that in several cases more than one *Zosterops* species occurs on a single island, but even here available evidence suggests that the sympatric species arose through separate colonization events. The evolutionary story that we are exploring, therefore, is very different to that illustrated by Darwin’s finches. We are examining instead the ecological basis of what has been called the “island rule”, with particular emphasis on the role of niche expansion and ecological generalism in promoting morphological evolution on solitary islands.

2 The “island rule” in birds

On first inspection, the literature on morphological evolution on solitary islands might suggest that island-dwelling birds follow a remarkably different pattern of insular evolution from that of other vertebrates, particularly mammals. Mammals follow a general “island rule”, with large

forms evolving towards dwarfism and small forms evolving towards gigantism (Lomolino, 1985). In birds, however, it is generally accepted that there is no general trend for insular shifts in body size (Case, 1978; Grant, 1998). Instead, the general trend among passerine birds is only towards large bills, a trend typically explained as an adaptation towards ecological generalism under “ecological release” (Case, 1978; Grant, 1965, 1998).

Being curious about such a different pattern, we re-examined morphological patterns of evolution in island-dwelling birds by compiling a new database of 110 phylogenetically matched-pairs of species and subspecies, each comprising an isolated island- and a mainland-dwelling form. We then used this database to search for general patterns of morphological change in island birds (Clegg and Owens, 2002).

Contrary to common perceptions, we found no overall tendency for the island birds to have large bills (paired *t*-test: $t = 0.13$, $n = 92$, $P = 0.90$). Instead, we found that island birds, like mammals, followed the “island rule” with respect

to both body and bill size (Fig. 1). For both body size and bill length we found a significant trend for small-bodied species to become bigger on islands and for large-bodied forms to become smaller. Of course, there were exceptions to this rule, causing us to control carefully for a ‘regression effect’. But the overall support for the classic island rule was robust (Clegg and Owens, 2002).

Why has the rule been overlooked in previous analyses on morphological shifts in insular birds? The main reason seems to be bias from a disproportionately large number of passerine species in databases. If we confine our own data set to oceanic island-dwelling passerines alone, we also find a strong trend for increased bill size ($t = 2.0$, $n = 28$, $P = 0.05$); yet this pattern is only half of the island rule. The whole pattern is for both large and small-bodied birds to converge towards a body size of around 100 g, with an independent but parallel island rule for bill size (Fig. 1).

3 The role of niche expansion and ecological generalism

As Grant (Grant, this symposium) points out, the traditional explanation for the island rule is that morphological shifts are adaptations to facilitate ecological niche expansion, with selection favoring generalism because insular populations typically experience relatively weak interspecific competition and a relatively depauperate environment (reviewed in Grant, 1998). In insular passerines, for example, it has often been suggested that larger bill size — and, by extension, larger body size — allows access to a wider range of resources and, ultimately, more efficient generalist behavior (Grant, 1965, 1968, 1998; Carlquist, 1974).

There is abundant circumstantial evidence to support the generalist foraging explanation with respect to morphological shifts in insular passerines. Most strikingly, island populations appear to have wider ecological niches than their mainland counterparts (e.g., Diamond, 1970; Lack, 1976), and there is experimental evidence showing that, in at least one case, such niches are shaped by interspecific competition, or lack of it (Alatalo et al., 1985).

Taken together, these studies make a strong case for associating morphological shifts in island birds with the development of more generalist foraging habits under competitive release. Tests of the generalist foraging explanation remain uncommon, however. Few systematic studies, for example, have compared multiple island with multiple mainland morphologies. Rather, evidence for insular niche expansion has been based largely on qualitative descriptions of habitat use by island forms (e.g., Lack, 1969), on observations of the ecology of island races alone (e.g., Diamond, 1970), or on single mainland-island comparisons (e.g., Alatalo et al., 1985).

In addition to the problem of replication, it has rarely been tested whether apparently generalist island populations are actually made up of individual generalists. An apparently “generalist” population may be made up of individual

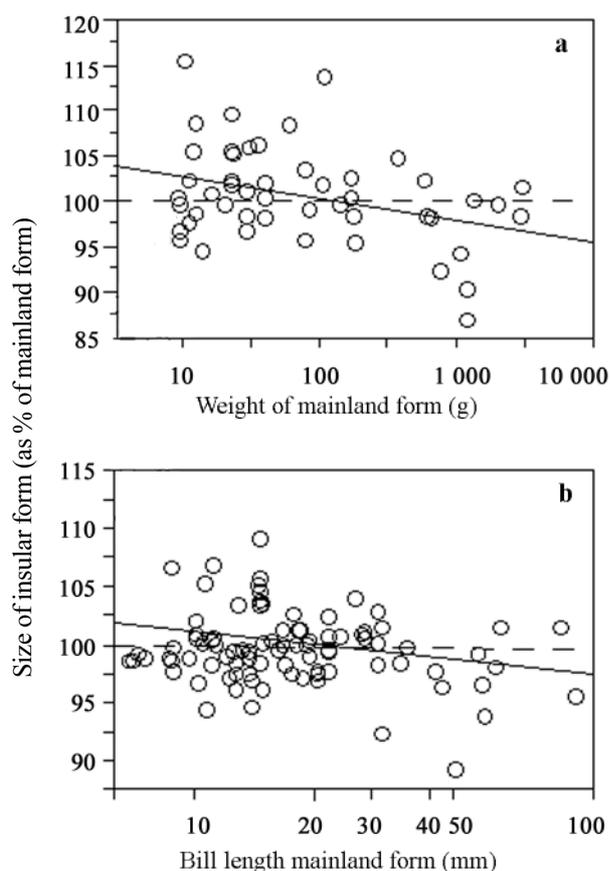


Fig. 1 The island rule in birds

Graphs show the relationship between the size of the mainland form and the relative size of the insular form, with respect to (a) body weight ($r^2 = 0.12$, $n = 51$, $P < 0.01$) and (b) bill length ($r^2 = 0.07$, $n = 92$, $P < 0.05$). In both cases, there is a significant negative relationship, which in the case of the body weight graph crosses the 100% line at approximately 100 g. The lines result from simple linear regression models fitted to log data. See Clegg and Owens (2002) for further details.

generalists or, equally plausibly, of a variety of individual specialists. The distinction between these two types of population has important consequences for understanding how generalist behavior may lead to morphological divergence on islands. If selection for generalist behavior explains the morphological shifts, then individuals should be generalists. If it is found that individuals are, in fact, specialists, then the traditional “niche expansion” explanation for the island rule stands contradicted.

4 A test species: the silvereeye, *Zosterops lateralis*

The family Zosteropidae contains a large number of successful island colonizers (Mees, 1969), many of which have repeatedly undergone insular differentiation in morphology, ecology and behavior. For example, the south-west Pacific members of the silvereeye species complex (*Zosterops lateralis*) have repeatedly invaded islands from the Australian mainland. Many of these isolated populations represent ancient invasions, having diverged into species and subspecies with very distinct phenotypes, while others are more recent and barely incipient species (Mees, 1969; Degnan, 1993). We have therefore made use of this group for a replicated study of island evolution.

One member of the complex — the Capricorn silvereeye *Zosterops lateralis chlorocephalus* — also presents an unusual opportunity to examine niche shifts at the level of individual island-dwelling birds. This race is 40% heavier than its mainland counterpart, with proportionally longer and thicker bill, and has been the subject of a long-term study of behavior and ecology on Heron Island, southern Great Barrier Reef, Australia. The Heron Island population shows strikingly generalist foraging behavior, and its large body size is unlikely to reflect neutral genetic mechanisms such as drift and founder events (Kikkawa, 1980; Degnan, 1993; Clegg et al., 2002a, b). So it was used to test whether population-level generalism is based on individual-level generalism or on a diversity of individual specialists.

5 Are island-dwelling populations more generalist?

We conducted a replicated test of the prediction that island-dwelling populations exhibit a wider range of foraging behaviors than comparable populations on the mainland. We compared the foraging ecology of silvereeyes at five mainland sites with that of silvereeyes at five island sites. The five mainland sites were at Oxley Creek, Brisbane, Queensland (27°32'S, 153°00'E), Mooloolaba, Queensland (26°41'S, 153°08'E), Lamington National Park, Queensland (28°15'S, 153°08'E), Lake Wellington, Victoria (38°06'S, 147°20'E), and Wilson's Promontory, Victoria (39°03'S, 146°24'E). In summer, the race of the silvereeye at mainland sites in Queensland is *Zosterops lateralis cornwalli*, and that in Victoria is *Z. l. westernensis* (Schodde and Mason, 1999). The five island sites are Hobart, Tasmania (42°53'S,

147.20E), Palmerston North, New Zealand (40°21'S, 175°36'E), Chatham Island, New Zealand (44°00'S, 176°30'W), Lord Howe Island, New South Wales (31°33'S, 159.05'E), and Heron Island, Queensland (23°26'S, 151°55'E). The first three of these island populations are of the race *Z. l. lateralis*, while the Lord Howe Island race is *Z. l. tephroleurus* and that on Heron Island *Z. l. chlorocephalus* (Schodde and Mason, 1999).

At each of these sites we quantified the foraging ecology of the silvereeye population in terms of both foraging height and foraging substrate (for detailed methodology, see Scott et al., 2003). We then compared the distribution of foraging activities among mainland and island populations

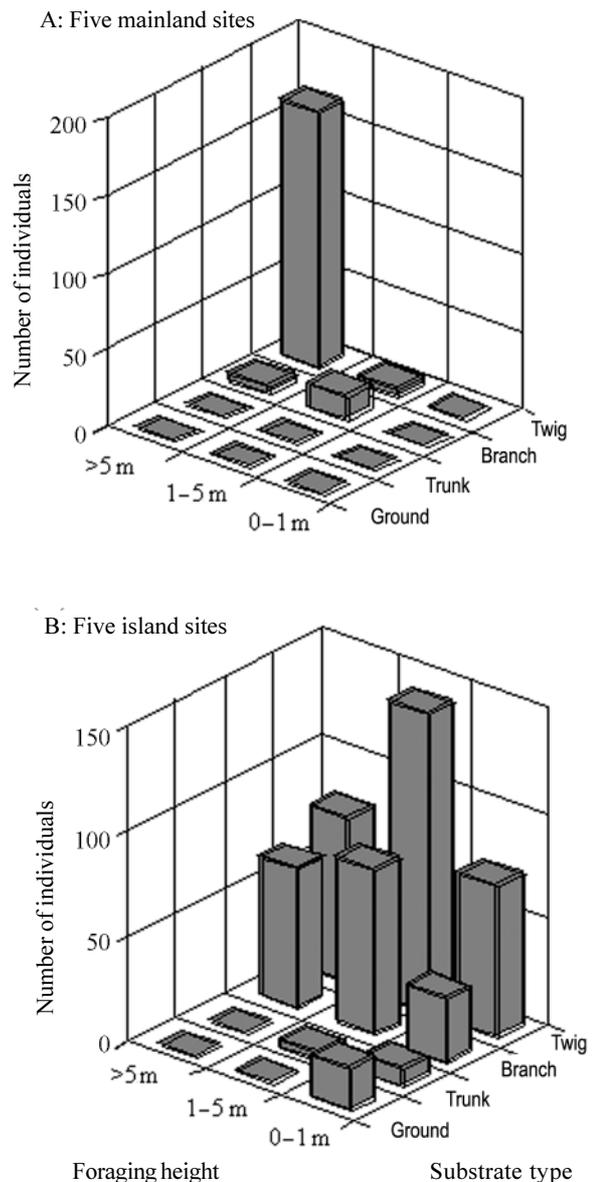


Fig. 2 Foraging behavior of silvereeyes at (A) five mainland sites and (B) five island sites

Foraging position is categorized on a 3-point scale with respect to height, and a 4-point scale with respect to substrate. See Scott et al. (2003) for further details.

by using the Shannon-Wiener Index to quantify the extent of foraging specialization within each population. From there we compared the extent of specialization among mainland populations with that among island populations.

The results supported the traditional, niche expansion explanation for the island rule. In general, island populations showed a greater range of foraging behaviors than mainland populations (Fig. 2).

6 Are individuals generalists?

We then investigated whether the degree of foraging specialization shown by Heron Island silvereyes was consistent with that expected by chance alone. Data on foraging behavior were collected from two sources: from ‘natural’ observations of foraging behavior under normal field conditions, and from “experimental” observations of foraging on an experimental tree, to control for effects of variation in habitat structure (for methodology, see Scott et al., 2003).

We again recorded behavior with respect to foraging height and foraging substrate, and quantified the degree of individual foraging specialization using a Shannon-Wiener Index. In this case, however, an index known as an ‘equally common behavior’ or ECB (Werner and Sherry, 1987) was calculated. ECB values are based on the degree of utilization of available heights and substrates and range between 0 (extreme specialist) and infinity (extreme generalist). It was used as an index of the degree of foraging specialization shown by an individual in any one foraging period. We then used Kolmogorov-Smirnov one-sample tests to compare the shape of the observed ECB frequency distribution (across individuals) with expected distribution resulting from the Monte Carlo bootstrap procedure.

The observed and expected distributions of ECB values are shown separately in Fig. 3 for natural and experimental observations and for height and substrate. Kolmogorov-Smirnov tests revealed that in all cases there was a significant difference ($P < 0.05$) between observed and expected distributions, the observed distributions consistently containing more specialists than expected by chance (Fig. 3). These results, therefore, do not support the predictions of the traditional explanation of the island rule.

Such findings are in broad agreement with a detailed study of the apparently generalist Cocos finches, which were also revealed to comprise a diversity of extreme specialists. However, no detectable association between foraging behavior and morphology was found at the individual level (Werner and Sherry, 1987). Interestingly, similar overall patterns are found in the true Darwin’s finches of the Galapagos, a group well known for their staggering range of foraging behaviors at the species and population levels but which also often show specialization at the level of individuals (Grant and Grant, 1989). When combined with our own results, these findings suggest that niche expansion and the adoption of generalist foraging behavior do play an important role in insular evolution in passerines,

though perhaps not exactly in the way traditionally envisaged.

7 Conclusions

We have demonstrated that, contrary to existing dogma, birds do follow the ‘island rule’ already established for other vertebrate groups, namely, that small-bodied forms tend to become larger on islands while large-bodied forms become smaller. This is true for size of both body and bill. Our results, however, provide only qualified support for its traditional explanation. It is true that insular populations show a greater diversity of foraging behaviors than do their mainland counterparts overall; but significantly more individual foraging specialists were found in a generalist island population than expected by chance alone. This indicates that the concept of generalist niches is not the full explanation for the island rule in birds. Our ongoing work on insular white-eyes aims to test the relative importance of other factors known to be associated with morphological shifts, such as physiologically optimum body size (Damuth, 1993), reduced risk of predation (Lomolino, 1985), reduced need for dispersal (Alder and Levins, 1994), and increased intraspecific competition in high-density insular populations

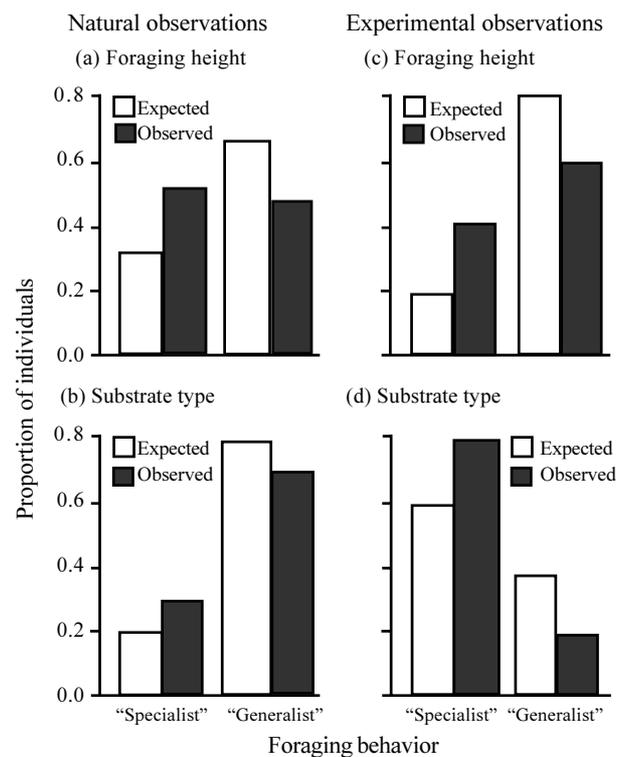


Fig. 3 Comparisons between the observed and expected frequency distributions of feeding specialization for island-dwelling silvereyes foraging under both “natural” and “experimental” conditions

Graphs show specialization with respect to (a) foraging height under natural conditions, (b) foraging substrate under natural conditions, (c) foraging height under experimental conditions, (d) foraging substrate under experimental conditions. See Fig. 2 for height and substrate types, and Scott et al. (2003) for further details.

(Kikkawa, 1980; Robinson and Owens, 2003).

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S15-5 Population differentiation on islands: a case study using blue tits in habitat mosaics

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Abstract We hypothesized that changes in life history traits of populations on islands, especially the components of niche enlargement, habitat tenacity and reduced dispersal of the “insular syndrome”, would result in greater rather than smaller phenotypic variation in populations on islands as compared to mainland counterparts. We tested these predictions with long term studies of blue tits (*Parus caeruleus*) on Mediterranean mainland and insular habitats. These habitats are particularly suitable for investigating the causes and consequences of phenotypic variation affected by spatially variable selection regimes because they are mosaics of patches in which strongly divergent selection pressures result from major habitat-specific differences in the timing and abundance of food. Considerable inter-habitat phenotypic variation was found in a series of life history traits (demographic, morphometric, behavioral) in the tits, variation that was much higher on the island of Corsica, in particular, than the adjacent mainland. Birds there synchronized their breeding more tightly to local seasonal variations in food than on the mainland as a result of low dispersal and strong site tenacity. Two populations only 25 km apart and subject to strongly divergent resource-based selection regimes became so differentiated that they reached reproductive isolation. Local differentiation in blue tits on Corsica supports the divergence-with-gene-flow model of speciation, which is central to the evolution of reproductive isolation.

Key words Blue tit, Corsica, Deciduous oak, Evergreen oak, Mediterranean, Phenotypic variation

1 Introduction

Islands and archipelagos are often claimed to present more ecological opportunities for differentiation and speciation than mainland source areas, a claim supported by the spectacular radiation of many groups of plants and animals in such remote archipelagos as Hawaii and the Galapagos. In addition to greater ecological opportunities, birds on islands may also recognize more habitats as a result of behavioral and demographic shifts, leading to phenotypic differentiation within species. Few studies have demonstrated the causal relationships between phenotypic variation and variation in selection pressures at a micro-geographic scale (Schluter, 1996; cf. Grant and Grant, 1995). And, as far as we know, no studies have compared such relationships among birds of insular and mainland environments.

Depending on territorial behavior and species-specific dispersal distance between birth and first reproduction, variation in biological traits is determined by their response to environmental heterogeneity. The ratio of scales of dispersal to the scales of selective pressures is crucial. If the range of dispersal is small relative to the scale of environmental heterogeneity, considerable variation can occur over very short distances, especially if the landscape includes habitat types that differ in selection regimes. In that case, local specialization, that is, the evolution of traits that have been selected in a given environment and which do not

change if the organism migrates to another environment, is likely to occur.

Island landscapes should provide more opportunities than mainland counterparts for local specialization in response to environmental heterogeneity because niche enlargement, reduced dispersal, strong philopatry and site tenacity, all components of the so-called “insular syndrome” (Diamond, 1983; Grant, 1998; Blondel, 2000), should enhance the micro-evolutionary consequences of natural selection. The many advantages of sedentariness, which eventually lead to flightlessness on islands, include energy saving (McNab, 1994) which is beneficial when food is locally abundant and predictable year-round. Such advantages increase as those of dispersal decrease, with the result that a single large population may become split into several locally-adapted populations that, in turn, differentiate in demographic and morphologic traits (Grant, 1998).

We tested the prediction of greater phenotypic variation on islands as a consequence of higher site tenacity from long-term studies of blue tits (*Parus caeruleus*) in Mediterranean mainland and insular habitats. Mediterranean landscapes are particularly suitable for investigating the causes and consequences of phenotypic variation because they are mosaics of habitats dominated by either deciduous (e.g., *Quercus humilis*) or evergreen (e.g., *Q. ilex*) oaks. A key feature of these habitats is the difference in timing of spring development of leaves and their associated leaf-eating ar-

thropod fauna (caterpillars), the main prey for tits then: it is one month earlier in the former than in the latter (Blondel et al., 1993), generating quite different selection pressures for the tits. Moreover, the abundance of leaf-eating caterpillars is much higher in deciduous than evergreen oaks, which renew only 30% of their foliage yearly. The differences in the timing and abundance of caterpillars are crucial because this food supply has consistently been shown to determine, both proximately and ultimately, such fitness-related breeding traits as laying date and clutch size (Perrins, 1965; van Balen, 1973; Lambrechts et al., 1997).

2 Methods

Blue tit populations were studied in two landscape mosaics of similar geographic configuration, one in southern France, near Montpellier, and the other on the island of Corsica. Each landscape includes habitat patches of either deciduous or evergreen trees. Within each landscape, five study areas, dominated either by deciduous (*Quercus humilis*) or by evergreen (*Quercus ilex*) oaks, were chosen within 40 km of one another on the mainland and 60 km on Corsica. This scale is much narrower than the usual scale for interpopulation variation in passerine birds (Avisé, 1994).

Breeding and morphometric parameters were collected from birds breeding in nest-boxes, which were erected at a density of *ca* 2 nest-boxes ha⁻¹ in each study area. Thus a total of 600 nest-boxes were available across the ten study sites. Nest-boxes were routinely checked at least once a week, and laying date (first egg), clutch size (first clutches), hatching date, number of hatchlings and fledglings were recorded. Adults were caught when nestlings were close to fledging, identified from their ring number if ringed, sexed, and aged. All adult birds were measured (body mass, wing length, tarsus length, bill length), as well as young birds just prior to fledging (see Blondel et al., 1993; Lambrechts et al., 1997 for details).

3 Results

Considerable inter-landscape (mainland vs. island) and inter-habitat (deciduous vs evergreen oakwoods) varia-

tion was found in all the traits examined, including breeding traits (Blondel et al., 1993; Lambrechts et al., 1997), behavior (e.g., social tolerance and territorial behavior: Perret and Blondel, 1993), song structure (Doutrelant et al., 1999), and morphology (Blondel et al., 1999, 2001). In this paper we only consider laying date which is crucial for breeding success because birds which best synchronize the nestling stage with the short period of maximal caterpillar abundance raise more and better quality young which, in turn, have a better chance of recruitment. Corsican populations, on average, started laying later than mainland populations (Table 1), though, crucially, with much greater interpopulation variation than on the mainland. A comparative analysis of within-landscape variation in laying date between the mainland and Corsica using Bartlett's test of equality of variance (Snedecor and Cochran, 1980) revealed remarkably higher differentiation in laying date on Corsica than on the mainland ($\chi^2=165.24, P<0.0001$): the five mainland populations started laying within 12 days of one another compared to 36 days on Corsica (Table 1).

Since the timing of food availability was coincident in the two regions, with caterpillars becoming available one month later on evergreen oaks in both (Blondel et al., 1993), the smaller inter-habitat variation in laying date on the mainland necessarily resulted in a greater mismatching of resource supply and demand across populations than on Corsica. Mismatched populations were found to be those breeding in evergreen oaks which are prevented from adapting to the local peak in food availability by gene swamping from deciduous oakwood populations where birds are rightly timed (Dias and Blondel, 1996). These differences in degree of adaptation to the timing of food availability result in a source-sink system (Dias et al., 1996).

Breeding pattern differed strikingly on Corsica where phenotypic variation was higher. In two populations in habitats only 25 km apart, one dominated by evergreen oaks ("evergreen 1" in Table 1) and the other by deciduous oaks ("deciduous 2" in Table 1), both were rightly timed to the peak of caterpillar abundance, effected by a difference of one month in their laying dates (Table 1). In contrast to the pattern on the mainland, both populations had adapted their

Table 1 Mean laying dates, with standard deviation in parenthesis, of blue tits in ten deciduous and evergreen Mediterranean mainland and insular habitats, taken from "March-date" (e.g., 32 = 1st of April)

	Mainland	<i>N</i>	Island	<i>N</i>
Deciduous 1	37.8 (8.6)	380	61.9 (7.4)	45
Deciduous 2	42.0 (6.0)	43	38.0 (9.7)	183
Evergreen 1	50.5 (11.9)	54	73.8 (6.6)	256
Evergreen 2	50.0 (4.3)	28	53.6 (7.0)	15
Evergreen 3	47.4 (5.1)	25	72.5 (5.1)	28
Mean	39.8 (9.9)		59.6 (18.3)	
Range	38 – 50		38 – 74	

Record series range between 3 and 15 years, depending on habitats. *N* = sample size.

breeding phenology to local variation in food supply (Lambrechts et al., 1997; Blondel et al., 1999). Furthermore, they differed significantly in all measured demographic and morphometric traits as well, e.g. wing length, body mass, tarsus length and bill length (Blondel et al., 1999). Yet a genetic analysis of population structure using microsatellite loci (Charmantier, 2000) showed that genetic differentiation between the two populations was small, albeit significant ($F_{st} = 0.0072$ to 0.0108 depending on years, $P < 0.01$).

4 Discussion

This case study provides a striking, and as far as we know the first, example in birds of an adaptive response of suites of life history traits to habitat-specific selection regimes that operate on a scale much smaller than the scale of potential gene flow. A strong interpopulation variation in laying date is particularly meaningful because suites of other traits, including morphometric traits, are likely to co-vary with laying date.

Because mainland and Corsican landscapes are well matched in geographic configuration and proportion of habitat types, something other than landscape structure must be involved to explain the patterns. The most likely is that dispersal distances are lower and habitat fidelity, as well as habitat-specific assortative mating, higher on the island, supporting our prediction about the role of dispersal and habitat selection in population differentiation on islands.

In vertebrates, population differentiation on a micro-geographic scale has rarely been proven to be adaptive (Schluter, 1996), even though local variation in fitness-related traits resulting from divergent resource-based selection expresses the process of adaptation (Reznick et al., 1990; Endler, 1995; McKinnon and Rundle, 2002). Examples of genetically-based micro-geographic variation that relates suites of covarying traits to environmental factors within species have been found in fishes (Endler, 1995), mammals (Nevo, 1986; Daly and Patton, 1990), and lizards (Losos et al., 1997). Yet in such mobile organisms as birds, local population differentiation in response to divergent selection pressures is supposed to be rare on a scale smaller than the dispersal range of individuals because of the homogenizing effects of gene flow.

Theory predicts, nevertheless, that if the environment is relatively constant in space, maximizing mean fitness results in adaptive differentiation of specialized phenotypes because environmental constancy favors the evolution of specialization (Futuyma and Moreno, 1988), even if gene flow is in excess of a few migrants per generation (Barton and Whitlock, 1997). Corsican blue tits support these predictions because their specialization to local habitats results from divergent selection pressures which are presumably sufficiently strong to outweigh the effects of gene flow, if any (Slatkin, 1994; Endler, 1995). This is an illustration of the 'divergence-with-gene-flow' model of speciation (Maynard Smith, 1966) whereby reproductive isolation can evolve between populations connected by gene flow when-

ever divergent selection stemming from environmental differences is strong relative to it (Rice and Hostert, 1993; Schluter, 2001). Moreover, the overall pattern of differentiation between the two Corsican populations is consistent with Rice and Hostert's (1993) claim that speciation proceeds most rapidly when several traits covary under divergent selection, as is the case here (Blondel et al., 1999). Whatever the extent of dispersal between the two populations, gene flow between them must be low because of premating isolating mechanisms, whether physiological or behavioral, which depend on traits that diverge in association with the exploitation of different habitats and resources.

Given their large phenotypic variation, the small degree of genetic differentiation between the two Corsican populations is surprising and suggests substantial gene swamping. Genetic differentiation across conspecific populations, nevertheless, does not necessarily parallel patterns of morphological variation (Lovette et al., 1998). Neutral markers may have not yet tracked the evolution of diverging suites of traits because it has been too recent and/or too rapid. Although microsatellites are among the most rapidly evolving repetitive markers, and hence sensitive detectors of intra-specific differentiation, adaptive evolution of gene combinations determining fitness-related traits may presumably occur still more rapidly, ahead of change in neutral regions of the genome.

Such an explanation has been proposed to explain the low genetic differentiation among well-differentiated populations of cuckoos (egg color of cuckoo genges) (Gibbs et al., 1996) and among sympatric morphs of the Arctic charr (*Salvinus alpinus*) in Iceland (Danzmann et al., 1991). The relatively recent structure of Corsican landscapes, which results from long-lasting human impact on the vegetation (Reille, 1992), supports the interpretation of low genomic differentiation in spite of the evolution of distinct ecological morphs. Comparing the responses of less dispersive island birds and more dispersive mainland birds to similar spatial diversity of habitats provides a practical demonstration of the relationships between dispersal, spatially variable selection and local adaptation which may be conducive to speciation (Via, 2001). One consequence of the 'insular syndrome' favoring local differentiation is compensation for the lower inter-specific diversity in impoverished insular communities by greater intra-specific diversity.

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Symposium 16 Chemical ecology and the study of bird reproduction

Introduction

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Chemical ecology investigates the chemical interactions between organisms and their environment. Chemicals play a key role in the functioning of organisms, either as resource such as vitamins which influence phenotype development, or as stimulus such as odor which regulates interactions between partners (attraction), enemies or competitors (defence). It is therefore surprising that chemical approaches are rarely applied to problems related to avian biology. This is illustrated by the dearth of reports of avian chemical defences, by the near-absence of controversy surrounding olfaction in ornithology, and by the of research on avian chemical ecology at international meetings.

This symposium aimed to redress these circumstances by promoting a chemical approach to the study of avian

reproductive biology. Invited participants presented studies that show how chemicals can contribute to the better understanding of proximate and ultimate aspects in avian reproduction. Key questions addressed were the chemicals involved, how they are perceived and exploited proximately, and how they influence fitness. Chemical components discussed for different avian model systems (e.g., birds of prey, shorebirds, and passerines) include preen wax chemicals, vitamins, plant volatile compounds, and carotenoids. These were investigated in the proximate contexts of egg formation, chick development, immune function development, and in the functional contexts of pair formation, parental care, resource exploitation, predator-prey interactions, and bird-parasite interactions.

S16-1 Discerning adaptive value of seasonal variation in preen waxes: comparative and experimental approaches

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Abstract Birds possess a preen (or uropygial) gland on their rump that secretes substances which are preened into the plumage, and which are probably essential for plumage maintenance. Secretions of the uropygial gland consist predominantly of wax-esters: fatty acids esterified to alcohols. These wax components vary in chain length and in degree and location of branching of the carbon skeletons, resulting in complex mixtures of many different wax esters in preen gland secretions. We have found that shorebirds show pronounced seasonal changes in the composition of their preen waxes. Between arrival on and departure from breeding grounds, their usual monoester wax at winter quarters changes dramatically to a more complex diester-based wax, which is maintained throughout the breeding season. The diesters have higher molecular weights and probably different physical properties than monoesters, and the secretion and use of diesters rather than monoesters may entail specific costs and benefits. We discuss how natural and sexual selection could explain the evolution of compositional shifts in preen waxes and outline possible approaches for future research.

Key words Preen wax, Uropygial gland, Chemical signaling, Annual cycle, Sandpipers

1 Introduction

Almost all birds possess a uropygial or preen gland from which complex mixtures of waxes are secreted and smeared into plumage. The chemical composition of preen waxes have been the subject of many studies, resulting in detailed chemical characterization of the preen wax mixtures in a number of bird species — for review, see Jacob and Ziswiler (1982). The preen waxes in most species consist predominantly of wax esters (esterified alcohols and fatty acid moieties) in which the location and length of branching of the carbon skeleton varies. This results in complex mixtures of waxes (Dekker et al., 1999).

There has been much speculation about the function of uropygial gland secretions (e.g., Jacob, 1976, 1978a and references therein), but they are evidently essential for plumage maintenance. Waxes are hydrophobic and probably contribute to the waterproofing of feathers (Jacob and Ziswiler, 1982). Preen waxes may also protect plumage by delaying abrasion and keeping feathers flexible (Jacob and Ziswiler, 1982), and they can have antiparasitic effects (Jacob et al., 1997).

Recent research on a long distance-migrating, high arctic-breeding shorebird, the red knot (*Calidris canutus*), shows that the chemical composition of preen waxes shifts dramatically from the usual monoester mixture to a mixture consisting solely of diesters just before the breeding season (Piersma et al., 1999; Sinninghe Damsté et al., 2000). Piersma

et al. (1999) proposed that the diester waxes could function as a sexually-selected quality signal. A recent comparison of the occurrence and timing of shifts in preen wax composition among 19 different but closely-related sandpiper species (Scolopacidae) showed that, in addition to the period of mate choice, sandpipers also secreted diester preen waxes throughout incubation (Reneerkens et al., 2002). Thus, there is more to the function of diesters than providing a quality signal during mate choice. Here we extend our dataset by providing information for six plover species (Charadriidae) and an oystercatcher (Haematopodidae) for the first time. We also discuss comparative and experimental tests of costs and benefits of mono- and diester- preen waxes that may help to unravel the functional aspects of such qualitative shifts.

2 Materials and methods

Preen wax was sampled from 25 shorebird species of plovers (Charadriidae), sandpipers (Scolopacidae) and oystercatchers (Haematopodidae) on spring and autumn migration, as well as during courtship, incubation and chick rearing. Preen gland secretions were collected on a cotton bud used to massage the preen gland “nipple”. Preen waxes were dissolved in ethyl acetate to a standard concentration of 1 mg/ml and analyzed by gas chromatography as described in Dekker et al. (2000). From visual examination of the gas chromatograms, their composition was then classified into mixtures of (1) monoesters, (2) diesters, and (3)

mixtures of both mono- and di- esters (after Reneerkens et al., 2002).

3 Results

Gas chromatography of intact preen waxes revealed substantial changes in chemical composition over the annual cycle of the shorebirds. Shifts from mono- to di- ester preen waxes occurred in all species investigated at the start of courtship and mate choice; it was thus not limited to sandpipers (Fig. 1; Reneerkens et al., 2002). The secretion of diesters was maintained during the whole period of incubation and chick-rearing (Fig 1; Reneerkens et al., 2002).

Diester preen waxes have been described before in several bird species (e.g., Jacob, 1976, and references therein; Jacob 1982); but to our knowledge, comparable annual variation in preen wax composition has been described only for ducks (Jacob et al., 1979; Kolattukudy et al., 1987) and sand-

pipers (Reneerkens et al., 2002). Livezey et al. (1986) and Levy and Strain (1982) nevertheless noted that use of preen wax composition for phylogenetic reconstruction may be problematic because of intra-specific variation in preen wax composition due to differences between sexes and dietary factors. In red knots, however, there is no evidence for dietary effects on preen wax composition (our unpublished data). Sex differences in preen wax composition during the breeding period have been found in ruffs (*Philomachus pugnax*) and curlew sandpipers (*Calidris ferruginea*) (Reneerkens et al., 2002), and in mallards (*Anas platyrhynchos*).

4 Discussion

4.1 Costs and benefits of different preen wax mixtures

To understand the evolution of variation in preen wax

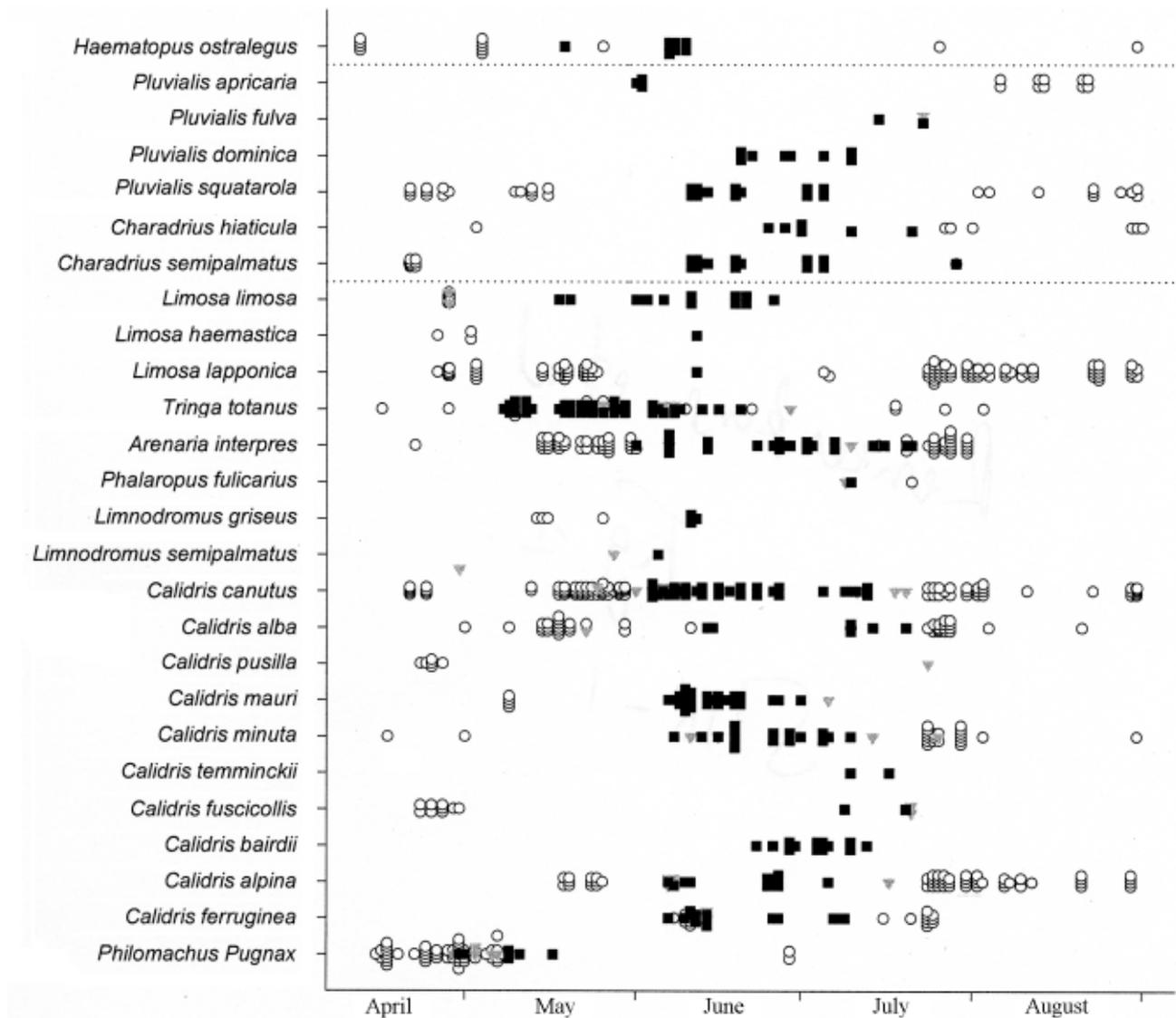


Fig. 1 Seasonal shifts from mono- (open circle) to di- ester (black square) preen waxes in adult shorebirds. Each symbol represents a single individual. Horizontal dotted lines divide from top to bottom: oystercatcher (Haematopodidae), plovers (Charadriidae) and sandpipers (Scolopaciidae). Mixtures of mono- and di- esters are depicted as gray triangles. Diester secretion is maintained throughout the breeding period (mid May–early July) in all species investigated.

compounds, their functions need to be established, i.e. the costs and benefits of different mixtures of preen waxes. Costs and benefits can be expressed in terms of energy, nutrition and time, or as reproductive currency. Natural selection is expected to select against costly traits if there are no benefits that outweigh their costs. For example, diester waxes could be functional in attracting mates but perform less well than monoesters in protecting plumage against ecto-parasites.

We performed an experiment with captive red knots in which, in addition to annual cycles in body mass and molt (Piersma and Ramenofsky, 1998), annual changes in preen wax composition followed the pattern in free-living conspecifics. The birds were provided with daily food just sufficient to maintain stable body mass. This allowed us to compare the presence and annual timing of shifts in preen wax composition in them with controls offered *ad libitum* food. Significantly, fewer food-restricted birds switched to diester waxes during the breeding period, indicating that there are energetic or nutritional costs involved in the shift to diester preen waxes (J. Reneerkens, unpubl. data).

4.2 Do preen waxes provide a quality signal?

Piersma et al. (1999) postulated that diester preen waxes could alter the appearance of plumage and act as a sexually selected quality signal during mate choice. The honesty of the signal would be guaranteed by the energetic and/or time costs associated with the shift to more viscous diester waxes that would be more difficult to apply under the low temperatures that prevail in the High Arctic. By assessing the time that captive birds spent preening before and after a switch from mono- to di- ester waxes under different ambient temperatures, one could evaluate such time costs. Birds would be expected to spend more time preening diester waxes on to their plumage than monoester waxes at similar ambient temperatures.

A prerequisite for a function such as quality signal is that different preen wax cocktails can be distinguished visibly by conspecifics. The eyes of birds are designed differently from those of humans (Hart et al., 2000), and can detect wavelengths of light invisible to the human eye (e.g., Maier, 1994; Cuthill et al., 2000). We used photospectrometry to obtain objective measures of light reflection (i.e., color) of breeding plumage in red knots. The reflectance of feathers of the same individual, both with a coat of mono- and diester waxes and after removal of the waxes with a solvent, were measured. The results showed that: (1) the removal of preen waxes did not change the intensity of reflection of the light spectrum presumed to be visible for birds (300–750 nm), and (2) a coat of diester waxes did not alter the reflectance of plumage from that with a coat of monoester waxes (Reneerkens and Korsten, unpubl. data). As diesters could alter plumage shine or gloss, rather than color, the quality signal hypothesis cannot be rejected as yet. Mate choice experiments with preen wax-manipulated birds would provide the best tests of the hypothesis.

Jacob (1978b) suggested that the preen wax products

of female mallards showed pheromonal activity. However, preen wax compounds are not particularly volatile, a property that would not be enhanced under prevailing ambient temperatures on the arctic tundra where many shorebirds reproduce. Rather, because temperatures there are substantially lower than on wintering grounds, a shift to a lower rather than a higher molecular weight of wax mixture would be expected. Jacob et al. (1979) then suggested that products resulting from hydrolysis of preen waxes (alcohols and fatty acids) were more likely to function as pheromones. Yet we have never detected alcohols, diols or fatty acids, the hydrolysed products of wax esters, in the plumage of red knots.

As diester preen waxes continue to be secreted during incubation, they are likely to fulfill functions other than signaling individual quality. In sandpiper species in which only one sex incubates, diesters were only secreted by the incubating sex (Reneerkens et al., 2002), suggesting that diester preen waxes are more likely to play a role during incubation.

4.3 Naturally selected functions

Shorebirds typically nest on open ground and hence are vulnerable to mammalian predation. A shift to less volatile diester preen waxes could reduce the smell of an incubating bird and diminish the chance of being detected by predators that use the sense of smell to detect prey. Such “olfactory crypticism” would have a large selective advantage. Comparisons of the chemical composition of preen waxes in closely related species that have or have not been exposed to predators (e.g., island populations that always have been free of mammalian predators) could test this hypothesis. The hypothesis could also be tested experimentally with dogs or rats that are trained to smell out hidden objects coated with either mono- or di- esters.

If feather abrasion is more serious during incubation than at other stages of the annual cycle, e.g., because of repeated contact with the ground, then wear and tear could selectively favor preen waxes that protect feathers better against abrasion. Abrasion of feathers impregnated with different preen wax mixtures can be studied in laboratory experiments.

Preen waxes may also be important in regulating the growth and ecology of bacteria, fungi and feather mites hosted by birds. Both inhibition and stimulation of growth of bacteria and fungi, which occur naturally on skin and feathers (Burt and Ichida, 1999), have been reported (Bandyopadhyay and Bhattacharyya, 1996, 1999; Jacob et al., 1997; Law-Brown, 2001). Alcohols and fatty acids, which are hydrolysed products of preen waxes, have been shown to affect the growth of dermatophytes (Jacob et al., 1997; Bandyopadhyay and Bhattacharyya, 1996, 1999). Fatty acids may inhibit growth of ectosymbionts by lowering pH, but it needs to be questioned how common the hydrolysis of wax esters is under natural conditions. Diester preen waxes in chickens were found to inhibit the growth of five species of fungal dermatophytes yet promote the growth of another (Bandyopadhyay and

Bhattacharyya, 1999). The bacterial flora of chicken skin also depends largely on the presence of (diester) preen waxes (Bandyopadhyay and Bhattacharyya, 1996). Seven of the 17 wax compounds in red-billed wood hoopoes (*Phoeniculus purpureus*) showed inhibitory action against 13 species of pathogenic bacteria and one parasitic bacterium (Law-Brown, 2001). Preen waxes possibly also play a role in protecting eggs against fungal infection if they are smeared onto the eggs, either directly or via plumage. As birds have been suggested to ingest preen waxes (Elder, 1954), the secretions could also offer protection against ingested (pathogenic) bacteria.

Feather mites appear not to be affected by the preen wax secretions of wood hoopoes (Law-Brown, 2001). Indeed, feather mites may feed on preen waxes and material trapped in them (Blanco et al., 2001). Removal of preen waxes by mites probably entails only small costs for birds and could even be beneficial, as microorganisms, including pathogens, may proliferate if preen waxes are not replaced regularly (Blanco et al., 2001). Seasonal variation in ectosymbionts may lead to the evolution of qualitative variation in preen waxes if different preen wax mixtures have different effects on them. We need to find out whether mono- or di- ester secretions of shorebirds have different effects on ectosymbionts if their role in the evolution of shifts in preen wax composition is to be understood. Microbiological tests with different ectosymbionts grown on culture media with both mono- and di- ester wax supplements (cf., Jacob et al., 1997; Law-Brown, 2001) could show whether ectosymbionts selectively favor different preen wax secretions.

Interesting patterns in intra-individual variation of preen waxes have been discovered only recently. Descriptive and experimental research is needed to gain insight into the exciting adaptive interaction in their variation.

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S16-2 The abundance of essential vitamins in food chains and its impact on avian reproduction

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Abstract Birds produce fewer or less viable eggs if the micro-nutrient requirements for reproduction cannot be met. For example, embryos from failed eggs of European sparrowhawks *Accipiter nisus* often show anomalies that indicate vitamin B2 deficiency. B2 is only produced by plants and is propagated through the food chain. Here, egg B2 concentrations were compared between habitats (great tit, *Parus major*), food chain levels (great tit and sparrowhawk), and within clutches (great tit). Invertebrates were sampled to detect food chain differences between habitats. The range of B2 concentrations was narrow and three times lower in sparrowhawks than in great tits. Repeatability of vitamin concentration within great tit clutches was low. In poor habitat, there was a skew towards low vitamin levels. Because there were differences between habitats in invertebrate density and composition, the question remains whether habitat differences in vitamin concentrations occur due to differences in food abundance or its vitamin load.

Key words Vitamin B2, Avian reproduction, Food chains, Sparrowhawk, Great tit

1 Introduction

Avian reproduction requires micro-nutrients such as minerals, vitamins and amino acids. Few examples, however, show this in wild birds, for example where essential amino acids limit clutch size (Ramsay and Houston, 1998; Selman and Houston, 1996) and calcium deficiency results in poor quality egg shell (Graveland et al., 1994). Others provide indirect evidence of lowered reproductive success due to micro-nutrient deficiencies (Bolton et al., 1992; Van den Burg, 2000). Embryos from failed eggs of birds of prey often show symptoms (Romanoff and Bauernfeind, 1942; Romanoff, 1972), including those of vitamin B2 deficiency (Van den Burg, 2000).

Avian embryos have a high demand for the vitamin riboflavin, hereafter B2 (White, 1991). B2 is a precursor of two coenzymes, flavin mononucleotide and flavin adenine dinucleotide, on which many catabolic enzymes depend (White, 1991). The β -oxidation of fats pathway, which is the most significant metabolic pathway by which the embryo generates energy from yolk lipids, is particularly sensitive to shortage of B2. Its first step involves three enzymes that all depend on flavin coenzymes: acyl CoA dehydrogenase, electron transferring flavoprotein (ETF), and ETF dehydrogenase. Under a low and narrow range of B2 concentrations, embryonic mortality occurs (Romanoff, 1972; Squires and Naber, 1993). B2 deficiency in the adult, furthermore, will normally prevent production of any eggs at all (Fabri and Kühne, 1988; Squires and Naber, 1993; White, 1991).

Because of its important role in metabolism, B2 can-

not be invested in reproduction at the expense of adult requirements (Romanoff and Romanoff, 1949; White, 1991). Moreover, birds cannot store or produce B2 (Engbersen and De Groot, 1992; Romanoff and Romanoff, 1949). As a result, B2 investment in eggs depends on daily intake (Squires and Naber, 1993). Birds of prey, such as the bird-eating European sparrowhawk (*Accipiter nisus*), may be especially vulnerable to shortages because B2 cannot accumulate in their prey. Vegetation characteristics and invertebrate fauna composition may both contribute to the B2 budget of sparrowhawks, because B2 is only produced by plants and has to be relayed through the food chain by insects and songbirds to become available to them.

Thus the aims of this study were to compare B2 concentrations among habitats via the great tit (*Parus major*), at food chain levels via the great tit and sparrowhawk, and within clutches via the great tit. Invertebrates were sampled to detect food chain differences between habitats.

2 Materials and methods

2.1 Field study procedures

This study was performed in 2002. Great tits were studied in nest boxes in three different habitats on Southwest-Veluwe, a forested area in the central Netherlands. One habitat site, "Bennekom", is in mixed forest typical of the western and southern section of Southwest-Veluwe. Another, "Ginkel A", is situated in the northern and eastern part, which is dominated by pine plantations on former moors and sand drifts. Old forest relicts persist there as well among the pine plantations, dominated by oaks (*Quercus robur*). These relicts form the third habitat site, "Ginkel B". Bennekom,

representing good tit habitat, was used as reference for the tit populations of Ginkel where, due to poorer soil (Ginkel A and B) and poorer vegetation (Ginkel A), B2 shortages were more likely to occur. Sparrowhawk nests were mostly localized in the western and southern part of Southwest-Veluwe.

Orders of egg laying were determined by daily nest visits during which eggs were marked and measured. Collection of third and last eggs from great tit nests was undertaken shortly after clutch completion. Six clutches from Bennekom were sampled entirely after their nests were abandoned upon trapping of the female (clutch size: 1×12, 3×9, 1×8, 1×7). In total, 24 sparrowhawk eggs of known position in the clutch were collected from 16 nests; and 2 eggs were collected from 8 nests. Eggs were weighed before opening and the contents were mixed. Samples were stored at -20 °C until further analysis.

In April, invertebrate density in Bennekom and Ginkel A was measured from branches about 70 cm long cut from pine and birch trees. Samples were taken from 20 trees per tree species per study site. Branches were carefully inspected and shaken above a cloth, and the invertebrates counted and identified to major groups. To compare invertebrate species composition between areas and tree species, spiders were collected as well from the lower branches of birch and pine trees by shaking. The similarity in spider faunas between every two samples was expressed as shared proportion. Cluster analysis was undertaken using average linking.

2.2 Measurement of B2

Reference samples were prepared using commercially available B2 (SIGMA) and sparrowhawk egg extract (see below). Absorption measurements were performed by a λ -25 spectrophotometer (Perkin Elmer), using extract without additional B2 as control. Between 0 and 118 $\mu\text{g/ml}$, concentration and absorption (at 456 nm) showed a straight-line relation given by the equation: concentration ($\mu\text{g/ml}$) =

absorption / 0.0142. To obtain egg extract, egg samples were mixed 1:1 with chloroform and spun for three minutes at 10000 g. Then 75 μl of the aqueous phase was used to measure the absorption spectrum between 550 and 350 nm against 75 μl B2 free albumen. Peak heights were corrected for the 550 nm absorption because of differences in protein concentration between the sample and control albumen. Samples that contained excess protein were first diluted. Correction for evaporative water loss from the eggs was estimated by multiplying the calculated B2 concentrations by egg density.

2.3 Statistics

Two standard statistical tests (Mann-Whitney, χ^2) were used, as indicated in each test result. χ^2 tests were performed in Excel. Statistical significance was accepted at $P < 0.05$.

3 Results

Within great tit clutches, there was no clear pattern of B2 allocation, and B2 concentrations were largely independent of one another (Fig. 1). B2 levels of third and last eggs from 30 nests did not differ significantly (third egg $30.3 \mu\text{g/ml} \pm 4.36$ (SD), last egg $29.0 \mu\text{g/ml} \pm 4.12$ (SD); Mann-Whitney, $P < 0.1$).

Because Ginkel A was selected as a poor food site, a low nest box occupancy could be expected; and the difference in nest box occupancy between Ginkel A and B was nearly significant (Table 1; χ^2 , $P = 0.05$). Clutch completion in Ginkel A and B was over 10% lower than in Bennekom, due to predation and calcium shortage. There were no significant differences between sites in clutch size or laying dates.

The variation in B2 concentrations ranged between 20 and 40 $\mu\text{g/ml}$, and was similar for all three sites (Table 2). In Bennekom, the median value for all eggs was $29.7 \mu\text{g/ml}$. Of the poor forest habitats, only Ginkel A differed signifi-

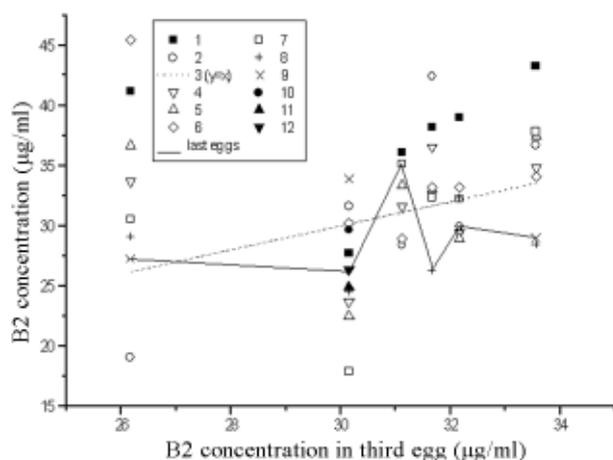


Fig. 1 Vitamin allocation in three representative great tit clutches from Bennekom

Vitamin concentrations varied irregularly and with low repeatability among eggs within clutches.

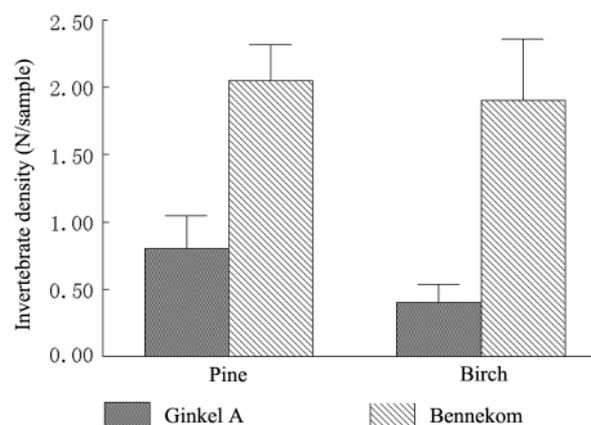


Fig. 2 Invertebrate density per study area and tree species in April

Invertebrate densities were lower in Ginkel A than in Bennekom (Mann-Whitney; $P < 0.001$).

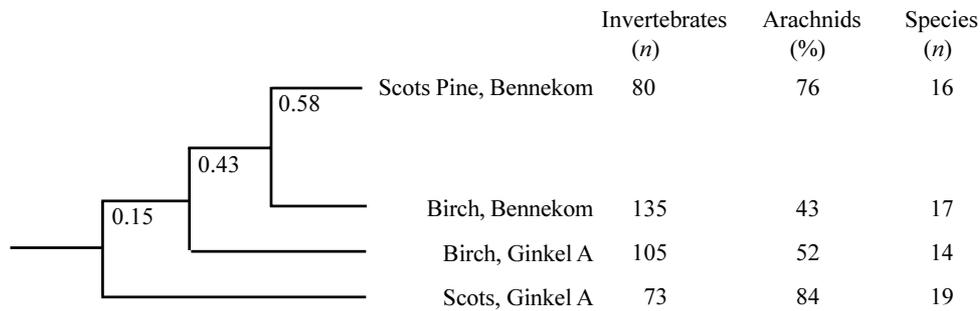


Fig. 3 Species composition of spiders per study area and tree species in April

Spiders were the dominant group among invertebrates overall. Their species composition showed specificity for both area and tree species. Similarities depict shared proportions. The comparative tree was constructed by average linkage.

cantly from Bennekom. There only 28% of the eggs exceeded the median value for Bennekom (χ_1^2 ; $P=0.035$; Table 2). Both third and last eggs showed a trend towards lower values, but it was significant for last eggs only ($n=26$ for Bennekom; $n=12$ and 11 for third and last eggs, respectively, for Ginkel A; χ_1^2 third eggs, $P=0.25$; χ_1^2 last eggs, $P=0.035$). Egg failure rates, at between 4.0% and 9.2%, did not differ between study sites ($n=93$ eggs). Five embryos were obtained from failed eggs; these did not show anomalies indicating B2 deficiency.

Prey densities on Scots pine and birch were significantly higher in Bennekom than Ginkel A (Mann-Whitney, $P<0.001$; Fig. 2). Spiders were the most common group among the invertebrates (Fig. 3). Spiders from the same tree species did not group together, indicating a site-area effect on the spider fauna. A further effect from tree species was also involved because the spider fauna on Ginkel A birch trees resembled that from Bennekom more than on adjacent Scots pines.

B2 concentrations in sparrowhawk eggs (10.84 $\mu\text{g}/$

ml, ± 1.14 (SD), range: 4.41 $\mu\text{g}/\text{ml}$, $n=24$) were about three times lower than in great tit eggs. The clutch with the lowest B2 values (8.68 and 9.25 $\mu\text{g}/\text{ml}$) was deserted during laying; the clutch containing the second lowest values (9.28 and 9.39 $\mu\text{g}/\text{ml}$) did not yield any offspring, and one of its two incubated eggs contained an embryo showing signs of B2 deficiency.

4 Discussion

Because B2 cannot be stored in the vertebrate body (Engbersen and De Groot, 1992; Romanoff and Romanoff, 1949) and not invested in eggs at the cost of female requirements (Romanoff and Romanoff, 1949; White, 1991), females can hardly make strategic decisions about B2 investment in eggs. Typically, B2 levels in eggs reflect daily intake in poultry (White, 1991). Complete saturation of riboflavin-carrier protein can be limiting; but this would result in high constant B2 levels within clutches (White, 1991), which is contrary to results from great tit nests. Therefore, it seems reasonable to assume that intra-clutch variation in B2 levels is

Table 1 Nest box occupancy (first clutches) and the proportion of clutches that were completed

Study area	Nestboxes (n)	%	Occupied (n)	Completed clutches %
Bennekom	58		55 (32)	88
Ginkel A	105		19 (20)	70
Ginkel B	87		31 (27)	74

Ginkel A had lower nest box occupancy than Ginkel B (χ_1^2 ; $P=0.05$). Nest box occupancy was highest in Bennekom, but there the nest boxes were further apart.

Table 2 Vitamin concentrations in great tit eggs from nests in which third and last eggs were analyzed

Study area	n	Median B2 concentration ($\mu\text{g}/\text{ml}$)	25% quartile ($\mu\text{g}/\text{ml}$)	75% quartile ($\mu\text{g}/\text{ml}$)	Below median	Above median	% above median
Bennekom	28	29.7	27.2	33.0	12	12	50.0
Ginkel A	18	27.4	26.6	30.8	13	5	27.8
Ginkel B	18	30.5	25.9	33.2	8	10	55.6

In Ginkel A, the distribution of vitamin concentration was skewed to the lower end of the range and few eggs contained more vitamin than the median of all eggs from Bennekom (χ_1^2 ; $P=0.035$). The skewed distribution for Ginkel A suggests a threshold for egg production between 20 and 25 $\mu\text{g}/\text{ml}$.

determined by variation in daily intake. If so, the B2 concentrations at the high end of the range are around the maximum achievable. And because these are little different from the apparent minimal levels for egg production, there may be a narrow window for egg production indeed, especially in sparrowhawks. Regrettably, birds that were unable to lay due to nutritional deficiencies remained unobserved in this study.

Romanoff and Romanoff (1949) reported substantial individual variation in B2 transfer efficiency in poultry. In the field, temporal and spatial variation in B2 availability, possibly enhanced by nonrandom habitat choice, may well obscure such differences between individuals.

Low B2 levels in great tit eggs coincided with poor habitat, in terms of soil and vegetation, low invertebrate numbers, and low nest box occupation. Because Ginkel A and B differ in B2 investments and vegetation, but not soil substrate, vegetation is the influencing factor. Differences in insect densities and species composition between the different vegetations could be correlated as well. The effect of invertebrate species composition is larger if differences in B2 load exist between species which is not unlikely.

At the other end of the food chain, sparrowhawks were expected to have difficulties obtaining sufficient amounts of B2, as their prey have no storage capacity for this vitamin. Indeed, B2 concentrations were lower and within a narrower range in sparrowhawk than great tit eggs. Because B2 uptake by the embryo depends first of all on the rate of diffusion, and thus concentration, of B2 in the yolk, B2 concentration is the biologically relevant measure of B2 availability to the embryo, notwithstanding that a sparrowhawk egg may, because of its size, hold more B2 than a great tit egg.

As B2 investments in eggs depend on habitat characteristics, B2 availability may be enhanced by habitat, especially type of vegetation and management. The question remains whether, in this case, B2 investments in the great tits of Ginkel A could be improved by an increase in food abundance as well as an increase of B2 load in their

prey.

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S16-3 Parasite defence in birds: the role of volatiles

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Abstract European starlings (*Sturnus vulgaris*) mix fresh herbs, preferably species rich in volatile compounds, into their dry nest material. By investigating air samples from starling nest boxes, we found that nestlings and their parasites encounter volatile compounds such as sabinene, myrcene, limonene, phelandrene and ocimene, some of them with medicinal properties. We compared mite load and nestling condition in experimental nests with and without herbs. Herbs had no effect on the quantity of nest-dwelling ectoparasites, but a significantly inhibiting effect on bacterial growth in late nests. There was also a tendency for mosquitoes to visit nests containing herbs less often than nests without herbs. Chicks that fledged from herb nests with higher body mass had more red blood cells and differed in some immunological parameters from controls. Herb chicks also had more basophil leucocytes, but fewer lymphocytes than nestlings from nests without herbs. More yearlings from herb nests were identified and showed interest in nest boxes in their first year as adults. The better condition of herb chicks may have been due to plant compounds that stimulate elements of the immune system to help nestlings cope better with harmful impacts from parasites and other stressors. Apart from their effects on parasites and nestlings, volatile compounds in herbs that are carried into the nests by males may also play a role in mate attraction.

Key words *Sturnus vulgaris*, Green nest material, Parasite defence

1 Introduction

In the evolutionary arms race between host and parasite, plants have developed a defence system based on secondary plant compounds comparable to the immune system of animals. One category of such compounds are volatiles, substances that dissipate in air and can act from a distance. In plants, volatiles play several roles. They fight diseases by impairing viruses, bacteria or fungi; they prevent plants from being eaten by herbivorous animals; and they are essential for reproduction because they attract insects and vertebrates for pollination and seed dispersal.

Many bird species, especially those that reuse the same nesting sites year after year (a circumstance that may result in heavy parasite loads), incorporate fresh plants into their nests. In a survey of 137 passerine species, Clark and Mason (1985) estimated that those occupying nests repeatedly were about 6 times as likely to employ green nest material as those which used nests only once. American wood storks (*Mycteria americana*), for example, provide their nests with aromatic plants like cypress, wax myrtle or pine (Rodgers et al., 1988). European starlings (*Sturnus vulgaris*) in America prefer wild carrots, yarrow, agrimony and fleabane (Clark and Mason, 1985, 1987). Corsican blue tits (*Parus caeruleus*) use milfoil, lavender, mint and other aromatic plants (Lambrechts and Hossaert-McKey, this symposium), and South African mossies (*Passer melanurus*) also use odorous plants as nest material (Milton and Dean, 1998). Starlings in South Germany carry about 70 different plant spe-

cies into their nest boxes, but preferentially select those rich in volatile compounds like milfoil (*Achillea millefolia*), hogweed (*Heracleum sphondylium*), cow weed (*Anthriscus sylvestris*) or elder (*Sambucus niger*), not just immediately available plants such as clover (*Trifolium pratense*) or dandelion (*Taraxacum officinale*). In an aviary choice experiment, males preferred volatile to nonvolatile plants as green nest material (Gwinner, 1997; Lampert, 1999).

Various hypotheses have been proposed to explain the use of green nest material, but only two make sense for the European starling (Clark, 1991). One is the courtship hypothesis which maintains that fresh, odorous plants serve as a tool to attract females in species where only males bring aromatic nest material, preferably in the presence of females; in such cases, no more plants are incorporated after egg laying (Kessel, 1957; Fauth et al., 1991; Gwinner, 1997). The other is the nest protection hypothesis, according to which aromatic nest material is used as an adaptation against parasites: birds, like herbalists, may use the intrinsic properties of plants against harmful parasites and pathogens (Widmann, 1922; Wimberger, 1984; Clark, 1991).

Apart from nest reuse, which is common in hole-nesting birds, colonial breeding and communal roosting are also conducive to infestation by parasites and pathogens because of the higher probability of transfer due to social contact (Rothschild and Clay, 1957). European starlings are thus a suitable model for investigating the significance of volatiles in parasite defence.

2 Methods

2.1 Estimation of parasite load

The main ectoparasite of starlings in a South German nest box colony is the red fowl mite (*Dermanyssus gallinae*). We scored mites from the nest boxes and the scabs on the bellies of nestlings, which are remains of the mite blood meals (Feare, 1984; Gwinner et al., 2000); we also sampled bacteria on nestling bellies with agar paddles. The paddles were incubated in the laboratory, and the attached bacteria colonies counted. Mosquitos were caught in the nest boxes as well, with sticky paper.

2.2 Nest investigation and manipulation

For one season we collected, weighed and identified the herbs that males had carried into their nests from the onset of nest building to egg deposition. To investigate the effect of green nest material on ectoparasites and nestlings, we collected data over five reproductive seasons from more than 150 nests. Natural starling nests were exchanged for artificial ones. In half of them — the “herb nests” — we mimicked the nest condition of an average starling nest in our colony. It comprised a mixture of the six most frequent green nest plants. The control nests, so called “grass nests”, consisted of the same amount of dry material supplemented only with fresh grass, a material almost never used as nest greenery (Gwinner, 1997; Gwinner et al., 2000). To identify the volatile plant compounds, the air in the nest boxes was sampled and analyzed by gas chromatography and mass spectrography. For the statistical analyses (ANOVA, *T*-test and Mann Whitney *U*-test), means per nest were used.

3 Results

3.1 Are nestlings exposed to volatile compounds in their nests?

Because no plants are carried into nests after egg laying, we investigated whether volatile compounds were still present in the nest boxes during the nestling period. We sampled head-space air from nest boxes with both experimental and natural nests inhabited by 7- to 10-day-old nestlings. In the samples from herb nests and natural nests, but not or hardly at all in grass nests, we detected and identified such volatile substances as sabinene, myrcene, limonene, phelandrene or ocimene, which are used in human medicine or parasite defence (Gwinner and Krock, unpubl.).

3.2 Herbs and parasites

Parasite load of nests can be expected to increase through the reproductive season. The main parasite of our starlings, the fowl mite, produces about one generation per week (Sikes and Chamberlain, 1954). Nestlings of one or two broods are found in nests from early May through June. If the incorporation of green nest material serves for parasite defence, starlings should enhance their efforts progressively through the season to provide later nests with more

herbs. This we found, the mass and the numbers of plant species carried to the nests by males increasing in parallel with the seasonal development of mites ($P=0.0001$, $n=53$). In spite of this, no effects reducing nest-dwelling mites and other ectoparasites could be detected (Gwinner et al., 2000).

Bacteria load in the nest boxes also increased through the season. It was higher, however, in nests containing no herbs. More bacterial colonies were counted on samples from grass nests than from herb nests late in the season ($P=0.025$, $n=26/27$; Gwinner and Berger, unpubl.).

Fewer mosquitoes were caught in herb than grass nests ($P=0.055$, $n=26/25$). Due to weather conditions in the year of this experiment, mosquitoes were in low numbers. Hence mosquitoes then probably played no role as blood suckers, although as vectors for diseases they may still have been effective.

3.3 Herbs and nestlings

Apart from insecticidal or bactericidal effects, volatile compounds may influence the condition of nestlings as well. They could, for example, reinforce the appetite of nestlings, as spices do in seasoning. They might also soothe the itching caused by mites, fleas or other ectoparasites. Chicks may “feel” better, eat more, and gain more weight. We compared the body mass of fledglings that grew up in herb and grass nests over years. In some years, there were significant differences between them, but not in others. Overall, however, it was highly significant ($P=0.005$, $n=77/77$). The effect of herbs was particularly marked when environmental conditions were unfavorable, for example when mite load in nests was high, temperature low, and nutrition of the nestlings reduced due to persistent rain or high clutch size (Fig. 1). In all these contexts, herbs in nests had a significantly beneficial overall on fledgling mass, whereas for other environmental conditions, only the feeding mode of the parents had a significant additional effect” (Fig. 1c). Herb chicks also had significantly more red blood cells (hematocrit: $P=0.003$, $n=50/44$) during three of five years of the investigation.

We ringed more than 300 nestlings individually to determine recruits for the following year. Out of 23 returned yearlings, 15 had grown up in herb nests and only 8 in grass nests. Ten birds from herb nests but only one from a grass nest showed interest in nest boxes. Four of the 10 herb birds bred and reared young.

Herb effects were more clearly expressed in adverse environmental conditions. Malnutrition, cold weather, and parasites can cause stress; and stress affects the immune system. Some plants, *Echinacea* for example, are known to boost the immune system, especially phagocytosis (Wagner and Jurcic, 1991; Steinegger and Haensel, 1988). We therefore hypothesized that nest herbs may act like a drug stimulating the defence system. We investigated young of 25 nests for leucocyte expression and found that nestlings from grass nests had more lymphocytes than herb chicks ($P=0.01$). This may be related to a higher bacterial load in grass nests.

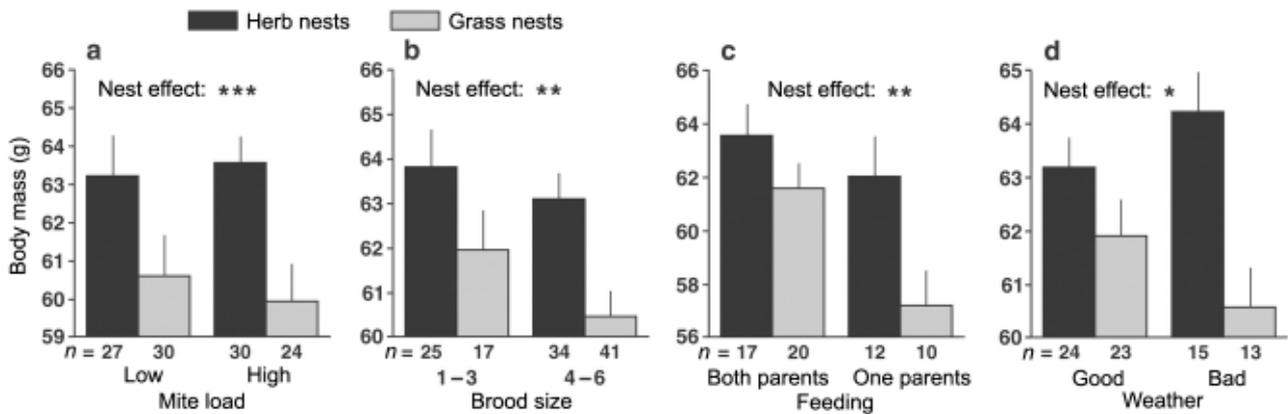


Fig. 1 Body mass of wild starling nestlings in experimental nests at day 18, close to fledging

Black columns = with herbs, pale columns = without herbs. Left two columns in each graph = favorable conditions: (a) low mite load, (b) small brood size, (c) both parents feeding, (d) good weather during first week of nestling life (mean max T 19°C and 2 days with 2 l rain/m). Right two columns in each graph = unfavorable conditions: (a) high mite load, (b) high brood size, (c) little or no feeding by males, (d) bad weather (mean maximal T °C and 7 days with 6 l rain/m).

Another white blood cell, the basophil, was seen more often on blood smears of herb chicks than of grass chicks ($P=0.01$, $n=12/13$; Gwinner et al., 2000). Basophils are reported to play a role in parasite defence, wound healing processes, and in coping with extreme temperatures and malnutrition, all situations to which nestlings can be exposed (Roitt et al., 1996; Maxwell and Robertson, 1995). We therefore consider it likely that volatile compounds of herbs strengthen elements of the immune system, allowing the nestlings to cope better with detrimental conditions so that their growth can proceed undisturbed.

3.4 Do volatiles play a role in the sexual life of starlings?

It is the male that provides the nests with herbs. Males often display green plants in an obvious manner to surrounding females. Plant incorporation peaks 4–5 days before the first egg is laid, when females decide on a male, and it stops almost completely with laying. Starlings can discriminate odors, and do so especially well during the reproductive season (Clark and Mason, 1987; Clark and Smeraski, 1990). In an aviary experiment, we tested whether hand-raised yearling males without courtship experience prefer plants scented with milfoil (the most preferred plant under natural conditions) or vanilla (unknown in the natural environment of starlings) over non-scented plants of the same species. Males significantly preferred milfoil-scented plants to non-scented or vanilla-scented plants for presentation to females. Hence we consider that male starlings discriminate herbs by olfactory cues, with preference for an odor associated with the most preferred nest plant in nature (Gwinner and Berger, unpubl.).

4 Conclusions

Volatile plant compounds seem to play much the same roles in starling nests as in plants, where they evolved to counteract the injurious activities of parasites and pathogens and for reproductive purposes. Nevertheless, studies

of the role of nest greenery have produced controversial results. A study of European starlings in north America found that some plants, such as wild carrots, depressed the population growth of northern fowl mites in nests (Clark and Mason, 1985, 1988; Clark, 1991). Another American study by Fauth et al. (1991) could not confirm such effects. Moreover, the use of aromatic nest material did not impair the main parasite (dermestid larvae) of wood storks (Rodgers et al., 1988). The fowl mite, which can affect nestlings of European starlings adversely, was not inhibited by herb treatment in our starling population. It is thus conceivable that plant compounds have effects other than that of simply suppressing parasites. Volatiles could, for example, reduce hunger for blood in the parasites, for the benefit of the host. The higher hematocrit levels in herb chicks could reflect this; but it could also just express good health. Under laboratory conditions (Clark and Mason, 1988) and in our field study, nest herbs suppressed the development of bacteria.

Odors of herbal nest material may disorient mosquitoes by masking the cues they need to find their host (Lambrechts and Dos Santos, 2000; our study). Nestlings from herb nests were fitter than nestlings in nests without herbs. This could reflect immunostimulating properties or other direct effects of the herbs on the nestlings (Gwinner et al., 2000).

For more than 4000 years, the Chinese have used certain plants to strengthen the “shield”, as they called it, which protects against disease. We interpret volatiles evaporating from nest greenery as such a shield, protecting nestlings from pathogens, the harmful actions of parasites, and other stress-inducing environmental factors. Volatile compounds may also play a role in mate attraction in which males prefer volatile herbs as “show objects” during courtship display. Whether females, however, can assess male quality from his perfume remains to be investigated.

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S16-4 Olfaction, volatile compounds and reproduction in birds

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Abstract Despite research in several biologically-relevant contexts, including orientation and resource acquisition, olfaction studies in free-ranging reproducing bird populations are rare. This, inter alia, hampers the quantitative study of fitness-consequences of olfaction. Here we provide a brief review of the use of avian smell in the context of reproduction, focusing on a model system, the blue tit. Corsican blue tits (*Parus caeruleus ogliastreae*) incorporate into their nests small fragments of aromatic plants that deliver high levels of volatile compounds easily perceived by a human observer. Blue tits use olfactory cues to anticipate the changes of the aromatic environment in their nests by repeatedly delivering fresh plant material with high concentrations of volatile compounds. A chemical approach will enable measurement of volatile compound concentrations, the identification of the volatile compounds involved, and ultimately the study of the functional meaning and fitness consequences of olfaction in free-living populations of birds.

Key words Olfaction, Volatile compounds, Nest maintenance

1 Introduction

Olfaction or smell is defined as the capacity to detect airborne chemical compounds at a distance from their source. Anatomical, neurophysiological and behavioral studies carried out during the last four decades show that the use of olfaction in birds is more common than originally thought. Estimates of absolute olfactory sensitivity thresholds exist for at least 15 domestic and non-domestic bird species (Roper, 1999).

In contrast to extensive work on avian smell in the laboratory, the use of olfaction in the everyday life of birds remains an understudied subject. Recent investigations indicate that avian smell may be used in a wide range of biologically-relevant contexts, including orientation and resource identification. However, its importance in reproduction remains a contentious issue, mainly because its study in free-ranging reproducing bird populations is rare.

Here we focus on the role of avian olfaction in perceiving plant volatile compounds used for nest maintenance, as illustrated by a model system, the blue tit. To introduce it, we briefly review available studies of olfaction in other reproductive contexts.

2 Olfaction in different reproductive contexts

Whether free-living birds smell, or not, can be demonstrated with experimental alterations of the odorous environment, or techniques that manipulate the olfaction system, such as transection of olfactory nerves, sealing nostrils, or chemically manipulating olfactory mucosa

(Roper, 1999). Expected outcomes are modification of behavior in response to the treatment that has been carried out. All these approaches have revealed use of olfaction in different biologically important contexts, including those related to reproductive activities.

2.1 Food location

The ability to find food by smell can be placed in a reproductive framework if food located by smell contributes to forming eggs, feeding partners during courtship or incubation, or raising chicks. For instance, procellariiform seabirds (e.g. Wilson's storm-petrels, *Oceanites oceanicus*; great shearwaters, *Puffinus gravis*) have a well-developed olfactory apparatus used for detecting food on the sea in the absence of visual food cues (e.g., Grubb, 1972; Verheyden and Jouventin, 1994). Procellariiforms can distinguish between cod-liver oil and control samples (e.g., sea water), and even a single chemical compound (dimethyl sulphide), indicating that optimal prey may be identified by smell (Nevitt et al., 1995). Some studies, nevertheless, failed to find olfactory effects, perhaps because of differences among the biological needs of different species or experimentally induced artifacts (e.g., Grubb, 1972; Nevitt, 1999; Bonadonna and Bretagnolle, 2002). None of these studies demonstrated experimentally that smell increases reproductive output because it enhances foraging efficiency.

2.2 Courtship and mate recognition

The avian uropygial gland may be a potential chemical source exploited for olfactory communication. The size of the uropygial gland peaks around the reproductive period in some species of birds, and the chemical compounds

produced by that gland seem to vary between species, between the sexes, and over time (e.g., Jacob et al., 1979 and references therein). Body odors thus may contain cues that help in mate or species recognition (e.g., Thibault and Holyoak, 1978; Jacob et al., 1979). The odors might also be used to select a high-quality partner, if the odors reflect health or body condition (e.g., Neerkens, this symposium; Douglas et al., 2001).

Certain aspects of sexual behavior are inhibited in ducks from which olfaction capacity has been removed, suggesting that olfaction may play a key role in courtship (Balthazart and Schoffeniels, 1979). Otherwise, experimental evidence for the use of olfaction in partner recognition or choice is rare.

2.3 Nest building

Many bird species incorporate fresh plant material into the nest to ameliorate the living conditions of parents and chicks (e.g., Gwinner, this symposium). More than a decade ago, Clark and Mason (1987) and Clark and Smeraski (1990) provided evidence that captive European starlings (*Sturnus vulgaris*) are especially sensitive to specific volatile compounds of plants and use them in defence against enemies in the nest, including disease and blood-sucking ectoparasites. However, these investigations, which provide one of the best available examples of the use of olfaction in a reproductive context, do not reveal how olfaction is used in field conditions.

2.4 Nest relocation and discrimination

Olfactory navigation can be placed in the context of reproduction if returning quickly to the nest enhances efficiency in caring for mate or chicks. Birds may also use odor cues to relocate breeding grounds after migration, which could affect the probability of acquiring a mate or optimal breeding site. Studies on homing pigeons (*Columba livia*) and starlings showed that anosmic individuals returned to the colony or nest site at a significantly lower rate than controls when individuals were displaced over increasingly long distances. The results suggest that, independent of artifacts (e.g., stress), olfaction may help in orientation, especially in unfamiliar areas (e.g., Wallraff et al., 1995; Walraff, 2001).

Selection may favor olfaction in avian species that cannot use visual or acoustic cues for finding the nest. This implies that burrows or nests possess individual odor signatures, such as produced by chemical compounds in stomach oil or preen waxes (e.g., Jouventin 1977; Thibault and Holyoak, 1978; Jacob et al., 1979). In nocturnal Leach's petrels, breeding captives discriminate between own nest material and plain dirt after controlling for visual and acoustic cues (Grubb, 1974). However, captives of the same species did not seem to discriminate between stomach oil, preen gland oil and control odors during choice experiments.

Comparative analyses of nine species of petrels suggest the existence of a relationship between the development of smell and circadian activity patterns, i.e. nocturnal

vs. diurnal activity (Bonadonna and Bretagnolle, 2002). Some anosmic, nocturnally-active petrels and shearwaters had difficulties in relocating their burrows at night (e.g., Grubb, 1974; Benvenuti et al., 1993; Bonadonna et al., 2001; Bonadonna and Bretagnolle, 2002; but see Shallenberger, 1975), whereas diurnally active species can relocate burrows without smell (Bonadonna and Bretagnolle, 2002). Surprisingly, some nocturnal species, such as Manx shearwaters (*Puffinus puffinus*) seem to use visual rather than odor cues to find their burrows at night, as indicated by results of field experiments manipulating odor, visual and acoustic features in and around the burrow (Brooke, 1978; James, 1986). Furthermore, some species with well-developed olfactory bulbs, such as the snow petrel (*Pagodroma nivea*), may also use visual signs to relocate the nest site (e.g., Hafthorn et al., 1988).

Chicks of British storm petrels (*Hydrobates pelagicus*) use smell to recognize the nest. Nest recognition by chicks may be useful in species where parent-offspring recognition is not well developed and adults limit care to chicks that stay in the nest (Minguez, 1997). In domestic chicks (*Gallus domesticus*), an attractive response to odor is developed around the time of egg hatching (Porter and Picard, 1998).

2.5 Offspring recognition

Olfaction may be used in offspring recognition, and therefore may influence parental care. This has been experimentally demonstrated in ring doves (*Streptopelia risoria*). Experimental body odor change in squabs (young) resulted in higher squab mortality and lower body weight (Cohen, 1981). Potential side-effects of experimental design, such as systemic toxicology induced by the odor treatment, were excluded. Manipulation of the olfactory nerves of the parents restored, to some extent, parental care for odor-manipulated squabs. Changes in parental care in response to such changes of the odor environment have not been reported in natural populations.

3 Nest maintenance, volatile compounds and olfaction: blue tits as a model system

Cavity-nesting female blue tits on Corsica add fragments of fresh plant material to the nest cup from the time of egg laying to fledging (Lambrechts and Dos Santos, 2000; Petit et al., 2002). Of over 200 plant species available in blue tit habitat, only 10 (< 5%) were recorded in the nest. Five plant species were found in at least 40% of the more than 100 nests sampled: *Achillea ligustica* 79%, *Lavendula stoechas* 52%, *Mentha suaveolens* 45%, *Pulicaria odora* 43%, *Helichrysum italicum* 39%. Some of the selected plants were not observed in blue tit breeding territories, indicating that it can be costly to acquire them. The number of plant species per nest differed between 1 and 5, perhaps due to variability in herb availability or parental experience in finding herbs.

The plants added to the nests are all highly aromatic, delivering strong-smelling aromatic odors easily perceptible by humans. Chemical analyses of the volatile compounds emitted by the five more important species were performed on three potted plants of each. Petit et al. (2002) used the headspace technique to do this. Volatile compounds were then identified using a gas chromatograph (GC) and GC/MS. These analyses revealed numerous volatile compounds, mainly monoterpenes and sesquiterpenes. The mean number of volatile compounds emitted varied between 12 (*Pulicaria odora*) and 30 (*Lavandula stoechas*) per plant species.

A Principal Component Analysis was performed on the relative proportions of the volatile compounds in the five species using a covariance matrix. The first axis of the PCA explained 35 % of total variance and the second component 30% (Fig. 1). The first component clearly separates odors from *Mentha suaveolens* (Mint) and *Achillea ligusta* (Ac). The second component clearly separates odors from *Lavandula stoechas* (Lav). Higher loading on the two components are mainly for monoterpenes found in one or other of the studied species, such as fenchone and camphor (P36 and P48) in *Lavandula stoechas* or piperitone and piperitenone (P60 and P66) in *Mentha suaveolens*. Because the chemical profiles clearly differ across the five plant species, blue tits most probably maintain a “cocktail” of odors in the cavity nest (also Lambrechts and Dos Santos, 2000).

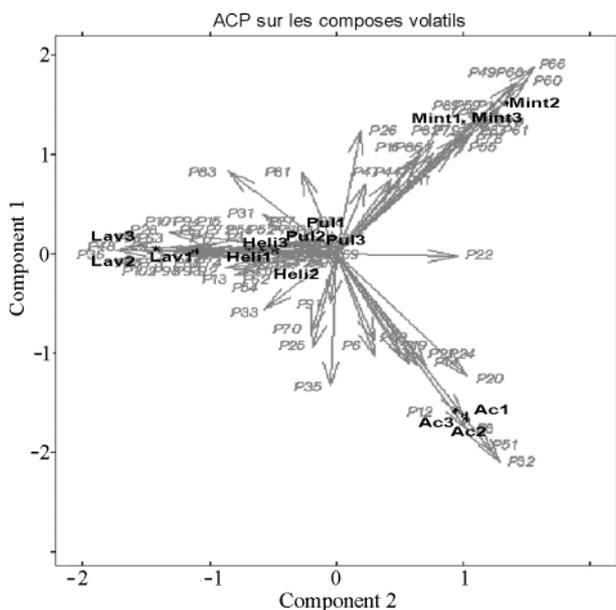


Fig. 1 Results of Principal Components Analysis on covariance performed on the percentage of volatile compounds identified by GC analyses in the bouquet of five primary herb species in nests of Corsican blue tits

The first (35% of the variance) and second (30%) principal components clearly separate all five species. Volatile compounds are indicated by arrows (multiplied by 100 to fit the scale of the graph), showing that each species has a different bouquet of volatile compounds.

The high selectivity for plants brought to the nest, their aromatic properties, and their regular replacement, suggests that olfaction plays a key role in nest maintenance in blue tits. To test whether the tits respond directly to nest odor, all aromatic plant fragments were first removed from all nests, and then hidden caches of fresh aromatic plants were replaced in half of the nests (“Herb+” treatment) while the rest were left devoid of aromatics, as controls (“Herb-” treatment). Nests were checked at intervals of 24 hours ($n = 16$) and 48 hours ($n = 64$) after the treatments to monitor for newly-added aromatic plant fragments and score the presence or absence of the five primary plant species.

Blue tits added fragments in significantly lower proportion in “H+” nests than “H-” nests over both time periods (24 hours: H+: 0% vs. H-: 87.5%; 48 hours: H+: 56% vs. H-: 94%). In other words, the tits brought more new fragments to nests without any aromatics than to those in which such fragments could be smelled but not seen. The simplest interpretation of these findings is that the blue tits are sensitive to changes in the olfactory environment of the nest. In the nests devoid of fragments, odor concentrations probably decreased quickly to levels low enough to stimulate the tits to look for fresh material, whereas in nests with hidden fragments, a sufficiently high level of odor concentration was maintained to inhibit “herb reload” behavior (Petit et al., 2002).

The nest protection hypothesis is the most probable functional explanation for herb loading by blue tits (Petit et al., 2002). The majority of the aromatic plant species used widely employed in human house cleaning or soft-medicine, possessing chemical substances known for their antibacterial, antiviral, fungicidal, insecticidal and/or insect repellent action: camphor, eucalyptol, limonene, linalool, myrcene, piperitenone, pulegone, and terpin-4-ol (unpubl. data). This suggests that blue tit olfaction helps to maintain a strongly smelling disinfected living environment. Further experiments should determine whether the tits are especially responsive to those chemical compounds that defend the birds against parasites and disease, and whether they prefer odor cocktails from different plants rather than odors of single plant species.

4 Conclusions

A fundamental, yet rarely tested, assumption in evolutionary ecology is that avian olfaction has been selected to respond to those chemical cues that maximize fitness. Some studies indicate, for instance, that birds are sensitive to plant volatiles that kill or repel nest parasites, or respond to odor cues that indicate the presence of resources essential for survival. We therefore suggest that future studies of avian olfaction should focus even more on the identification of the chemical cues that are exploited by free-living populations of birds, and at the same time on the consequences of odor cue recognition for survival and reproduction. Comparative and experimental studies will also be required to reveal genetically based adaptive differences

in odor cue recognition across populations and species. It is clear that the techniques developed in chemical ecology are essential for the development of successful multi-disciplinary approaches that aim to understand better the adaptive significance of avian olfaction.

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S16-5 Carotenoid biochemistry, transformation and function

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Abstract Antioxidants (carotenoids, vitamin A and vitamin E) play important roles by eliminating free radicals. These biochemicals are often rare and their availability is limited because of their rate of turnover. Signals such as bright gape color in nestling birds may provide reliable information about the quality of offspring because bright color derives from carotenoids that are used in competition. Hosts defend themselves against parasites by raising immune responses that often depend on rapid cell proliferation, or excessive production of biochemicals, which in turn generate free radicals. Supplementation with carotenoids can increase the strength of immune responses, suggesting that availability of carotenoids can affect host response to parasite attack. Maternal effects are common in birds because of substances deposited in the eggs by females; several studies have shown that quality of coloration in female plumage and integumentary structures directly reflects the quality of carotenoid content in their eggs.

Key words Antioxidants, Immunity, Life history, Maternal effects, Migration, Yolk

1 Introduction

Energy is traditionally considered to be the single-most important currency in the activities of living organisms. This view in biology has predominated in recent decades, favoring optimality solutions to biological problems as the research approach. Although biological processes, by definition, are fuelled by energy, this does not necessarily mean that energy is the limiting resource. We suggest that many biological phenomena involving biochemical processes may be better understood if the production of free radicals, and the role of carotenoids and other antioxidants in eliminating such free radicals, are considered.

All physical activity gives rise to production of free radicals that can cause damage to molecules (Leffler, 1993). Free radicals are atoms or molecules with unpaired electrons, and they arise as by-products of normal metabolism and rapid cell proliferation during immune function. DNA, proteins and lipids, including molecules used in immune defence, can be damaged by free radicals. If not eliminated, changes in membrane properties (fluidity, flexibility) and functions (intracellular signaling, enzymatic activities) caused by oxidative stress can result in reduced immunocompetence (Chew, 1996). The negative effects of free radicals can be neutralized by antioxidants, such as carotenoids and vitamins A and E (Surai, 1999; Møller et al., 2000).

Production of free radicals and antioxidant defences are usually balanced under normal physiological conditions, but this balance can be disrupted by stress in favor of free radical production, thereby creating oxidative stress (Sies, 1997). Oxidative stress arises from insufficiency of anti-

oxidants in diet, inadequate dietary proteins and synthesis of metal-binding proteins, excess production of free radicals from metabolism of toxic compounds, and excessive activation of radical-producing natural systems such as phagocytosis during inflammation (Halliwell, 1996).

Here we propose that antioxidants may play an important role affecting the evolution of many phenomena in avian biology, even impacting on phenotypic variation within populations. In this overview, we first describe carotenoids and their biochemistry. Then we review examples of the importance of carotenoids in determining the expression of signals, modulating immune responses, mediating maternal effects, and affecting optimal bird migration.

2 Carotenoid biochemistry and function

More than 600 different carotenoids are grouped into xanthophylls and carotenes based on their molecular structure, whether oxygenated or aliphatic chains. Carotenoids can only be synthesized by algae, bacteria, fungi and plants (Fox, 1979; Latscha, 1990; Stradi, 1998), and, therefore, animals must ingest carotenoids for use in physiological processes or display. Animals differ in their rate of carotenoid absorption (Scheidt, 1989; Blount et al., 2002a), in their ability to convert ingested carotenoids (Fox, 1979; Stradi, 1998), and in their rate of carotenoid deposition in signal colors (Brush and Power, 1976). Birds preferentially accumulate xanthophylls, particularly lutein, zeaxanthin and canthaxanthin, and carotenes less readily, e.g., β -carotene (Brush, 1981; Stradi, 1998; Blount et al., 2002a).

Many carotenoids have been found in the feathers of

birds, some ingested and others derived from oxidative transformation. β -carotene, for example, may be converted into echinenone, and sometimes canthaxanthin or 3-hydroxy-echinenone, adonirubin and astaxanthin (Stradi, 1998). Furthermore, β -carotene can be converted into vitamin A (Damron et al., 1984; Schaffer et al., 1988), and vitamin A also has antioxidant activity. Xanthophylls are more widely distributed, plentiful and diverse than carotenes (Latscha, 1990). Thus, xanthophylls in circulation and storage seem more likely to be of direct dietary origin than sourced from transformation of carotenes. Occurrence of xanthophyll in a signal color might indicate availability of donor xanthophyll or transformed carotene, and hence reflect allocation to signals.

Carotenoids play important roles in immuno-regulation and immuno-stimulation in vertebrates (Bendich, 1989). β -carotene and other carotenoids enhance T- and B-lymphocyte proliferation, stimulate effector T-cell function, enhance macrophage and cytotoxic T-cell capacities, increase the populations of specific types of lymphocyte, and stimulate the production of cytokines and interleukins (Bendich, 1989). Cockerels fed β -carotene and canthaxanthin produce significantly higher antibody titres against Newcastle disease virus than controls (McWhinney et al., 1989); and experimentally increased dietary intake of β -carotene and vitamin E increase immunity against *Escherichia coli* (Tengerdy et al., 1990). Laying hens fed supplemental carotenoids transfer these to chicks via egg yolk, and produce chicks with enhanced spleen and bursal lymphocyte function *in vitro* (Haq et al., 1996). Thus, carotenoids affect different immune functions directly.

Carotenoids also have detoxification effects that are related to their effects on immune function. With other antioxidants, they act as free radical scavengers and protectors of biologically important molecules, serving as free radical traps and efficient quenchers of singlet oxygen (Ames, 1983). They effect a decrease in immuno-suppressive peroxides, and maintain membrane receptors that are essential for immune function. Immune cells use free radicals to kill bacteria and other infections by stimulating free radical production by macrophages (Chapple, 1997). Therefore, enhanced immune cell activity can overproduce free radicals and here antioxidant protection is vital (Gille and Sigler, 1995).

3 Specific examples of carotenoid function

3.1 Signaling

Communication is based on signals. Reliability of signals is generally ensured by an absence of conflict of interest between sender and receiver, or, more frequently, by the cost of the signals. More expensive and effective signals can be produced only by signalers of high quality because of costs, ensuring that cheating only occurs rarely. Many visual sexual signals are based on carotenoids, reli-

ably reflecting the amounts of carotenoids ingested (e.g., Hill, 1992). Such signals provide accurate information about the condition of individuals because use of carotenoids for signals competes with use for immune function or free radical scavenging (reviews in von Schantz et al., 1999; Møller et al., 2000).

Begging signals provide reliable information about the condition of offspring, and parents may use such information to allocate limited resources to those most viable (Saino and Møller, 2002). Nestling barn swallows (*Hirundo rustica*) with more brightly colored gapes receive more food than their siblings (Saino et al., 2000). Experimental challenge to their immune system with an antigen reduces gape coloration (Saino et al., 2000). Such a reduction in the level of signaling can be reversed by lutein supplements, causing the nestlings to regain bright gape color (Saino et al., 2000). A subsequent study revealed that nestlings with bright gape colors indeed had superior condition and stronger immune responses than their siblings (Saino et al., 2003). Thus, nestling signals are mediated by carotenoids and reflect offspring condition reliably.

3.2 Host-parasite interactions

Carotenoids have immuno-stimulating and immuno-modulating effects. These effects act through stimulation of immune responses, elimination of free radicals produced during immune responses, and elimination of free radicals after they have been used to combat pathogens susceptible to free radicals. There are, however, relatively few examples of host immune function being affected by carotenoids in free living birds. One example for nestling barn swallows has been described in the previous section. Adult barn swallows have red plumage color on the head, partly dependent on lutein. Males with brightly colored plumage are more healthy than pale males which have lower leukocyte counts and circulating levels of immunoglobulins (Saino et al., 1999). Chicks of moorhens (*Gallinula chloropus*) have brightly colored feathers and skin on the head, and parent moorhens use intensity in chick coloration to allocate parental effort. Moorhen chicks provisioned with extra lutein had a stronger T-cell dependent immune response than controls (Fenoglio et al., 2002). Thus, carotenoids can boost immune responses in free-living birds.

3.3 Maternal effects

Female birds invest in progeny by transferring antioxidants to their eggs. Since the hatching process causes oxidative stress (Surai, 1999), antioxidant protection is vital. Carotenoid and vitamin E concentrations in embryonic tissues reach maximal levels at hatching (Surai et al., 1996), providing maximal antioxidant protection to tissues with high levels of polyunsaturated fatty acids (Speake et al., 1998); such tissues are vulnerable to free radical attack (Surai, 1999). Since carotenoids are not accumulated in the body to any extent (Surai and Speake, 1998), there must be a premium on the capacity of a female to transfer carotenoids to egg yolk. Maternally-derived carotenoids in yolk reduce

susceptibility to oxidative stress (Surai and Speake, 1998), and probably preserve passively-acquired maternal antibody from oxidation in embryos and chicks (Blount et al., 2000).

Oxidative stress arising from the production of free radicals is likely to be greatest in rapidly growing embryos because of their high levels of oxidative metabolism (Vleck and Bucher, 1998). Antioxidants transferred to eggs or synthesized by the developing embryo (ascorbic acid, reduced glutathione or antioxidant enzymes) build an effective antioxidant system responsible for maintaining protection against the damaging effects of free radicals (Surai, 1999). Thus carotenoids play a role in the control and destruction of free radicals towards limiting oxidative stress in growing chicks.

A comparative study of eggs from more than 50 different species of birds has shown that concentration of antioxidants varies by more than an order of magnitude among species, and that species-specific differences in yolk carotenoids are statistically highly significant (J.D. Blount et al., unpublished data). Lesser black-backed gulls provided with extra carotenoids before egg formation increased the intensity of yellow coloration of legs, beak and eye ring (Blount et al., 2002b). This increase in female coloration was directly reflected in the quality of eggs in terms of carotenoid concentration and growth performance of young (Blount et al., 2002b; J.D. Blount unpublished results). In great tits (*Parus major*) breeding in two different habitats of differing quality, females were more brightly yellow in the rich habitat (Hörak et al., 2002). More brightly yellow females also laid eggs with higher concentrations of antioxidants independent of habitat, and nestlings hatched from such eggs grew better than the nestlings of paler females. Thus, female color in these two very different species reflects the amount of carotenoids put into eggs.

Carotenoid deposition in yolk by female barn swallows is affected by the trade-off between self-maintenance and allocation to offspring (Saino et al., 2002). A challenge to the immune system of females before start of laying reduced yolk carotenoids. This result demonstrates that females trade their own use of carotenoids against allocation to eggs. Moreover, female allocation of carotenoids to eggs was found to be related, through experimental manipulation, to the size of a secondary sexual character in their mates. Male barn swallows with longer tails are more attractive to females, and males with such tails have few parasites and strong immune responses (Møller, 1994).

Offspring also resemble parental males with respect to parasite load, suggesting that levels of parasitism have a genetic basis (Møller, 1994). Thus, the young of short-tailed males may have more activated immune systems than those of long-tailed males. Tail length manipulation of males significantly affected the concentration of carotenoids in yolk, since females allocated more carotenoids to eggs when their mates had their tails shortened (Saino et al., 2003). This is in accord with predictions because offspring derived from such eggs are likely to suffer more from parasitism than

other offspring; and therefore they have a highly activated immune system that is dependent on egg carotenoids for balance.

4 Future prospects

Carotenoids and other antioxidants have important consequences for birds, as has been illustrated by studies of signaling, host-parasite interactions, and maternal effects. Two particular areas need more research effort. First, there needs to be much more integration of research in energetics, free radicals and antioxidants. Only when we know how levels of activity translate into production of free radicals and use of antioxidants will we begin to understand the magnitude of stores required, from the rate of acquisition of antioxidants compared with their rate of use. Secondly, a broad understanding of carotenoid availability, use and function in relation to ecology of different species is needed. Such comparative analyses could explain the determinants of levels of circulating and stored carotenoids, and potentially their impacts on reproductive strategies and life-history.

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Symposium 17 Evolutionary history of selected bird taxa from the Sino-Himalayan region

Introduction

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Within the palearctic realm, the Sino-Himalayan fauna is of central significance. Because of their climatic and orographic complexity, China and the Himalayas harbor an extremely rich bird fauna — more than 1 250 species in China and more than 850 species, including about 600 breeding species, in the tiny country of Nepal. Moreover, the fauna of present-day China and adjacent areas is considered to be the center of origin of large and speciose genera of passerine birds. Leaf-warblers (*Phylloscopus*), redstarts (*Phoenicurus*), rosefinches (*Carpodacus*), laughing-thrushes (*Garrulax*), parrot-bills (*Paradoxornis*) and snow sparrows (*Pyrgilauda*, *Montifringilla*) are among the most diverse. From presumed central and east Asian centers, some species groups even reach the west palearctic, although in low numbers. Within China and the Himalayas, local species richness is often high: up to ten species of leaf-warblers may be scattered over a mountain slope less than 2000 m in height. Within the passerines, speciation processes

led to considerable extension of niches; and a multitude of habitats, including subtropical environments as well as Tibetan mountain steppe, are occupied by closely related species. At the same time, China harbors many narrow-range species which are considered relics. Some of their close relatives live in the northern palearctic, and others in the south in subtropical environments.

This symposium addresses the evolutionary history of these assemblages, both the radiation of speciose genera and the localization of narrow-range relics. Aspects of biology, ecology, distribution, vocalization and molecular phylogeny in the genera *Seicercus*, *Montifringilla*, *Pyrgilauda* and *Phoenicurus* are used to shed light on the evolutionary history of species-rich genera. For narrow-range Chinese endemics, such as the almost unknown Chinese grouse (*Bonasa sewerzowi*) and Sichuan jay (*Perisoreus internigrans*), other historical explanants are put forward to account for present distributions.

S17-1 Ethological and acoustical characters of the Chinese grouse (*Bonasa sewerzowi*), compared with sibling hazel grouse (*B. bonasia*) and ruffed grouse (*B. umbellus*)

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Abstract Woodland grouse of the genus *Bonasa* occur allopatrically in circum-polar temperate and boreal forests. An inter-specific comparison of the size and pattern of eggs, the downy feathers of pulli and other morphological characters in the three species suggests convergence in character sets. Yet species-specific differentiation is evident in the color and number of tail feathers, in signals of territorial advertisement, and in investment for nest-site preparation, mate guarding and caring for the brood. When ranking specific characters of *Bonasa* species, the hazel grouse (*B. bonasia*) shows the richest diversity of vocalization, while the range-restricted Chinese grouse (*B. sewerzowi*) appears to be the least varied. Reconstruction of the speciation of woodland grouse based on morphology, ethology and mitochondrial DNA analysis indicates that the Chinese grouse seems to represent an archetypal form, not only in the genus *Bonasa* but for all tetraonids worldwide.

Key words *Bonasa*, Morphology, Behavior, Acoustical characters, Evolution

1 Introduction

The subfamily Tetraoninae is a well-defined group of Galliformes, which, restricted to the northern hemisphere, dwells mostly in forests and tundra and also, in the Nearctic, on open steppes. In this subfamily, the circumpolar genus *Bonasa* comprises three allopatric species: (1) the hazel grouse (*Bonasa bonasia*) which ranges widely across north Eurasia, (2) the ruffed grouse (*Bonasa umbellus*) which occurs over vast areas of northern North America, and (3) the Chinese grouse (*Bonasa sewerzowi*) which is anomalously confined to small pockets in east Asia, well isolated in the small forest belt adjacent to the Tibetan plateau. The great conformity of their ecological niches — clearings with young successional stands of forest of characteristic pioneer species — has resulted in a number of convergent adaptations in body size, cryptic plumage and locomotor specializations. Our intra-specific comparisons also reveal divergent species-specific differences which, in their variation, indicate pathways of radiation within the genus *Bonasa* and perhaps even tetraonids in general.

2 Materials and methods

Extensive field studies were carried out on the three species as follows:

Hazel grouse: alpine areas, Austria 1968–1980 and 1990–2002; Bavarian Forest National Park, Germany 1972–2000; Białowieża National Park, Poland 1974–1975; Bohemian

Forest, Czech Republic 1980–2002; Slovakian Paradise National Park, Slovakia 1984–1985; St. Petersburg, Russia 1982; Magadan, East-Siberia 1998; Changbai Mts, China 1992–1993.

Ruffed grouse: Duluth, Minnesota, USA 1986; Smithers, British Columbia, Canada 1986; Northern Cascades, Washington, USA 2001.

Chinese grouse: Lianhua Shan, Gansu Province, China 1994–2002; Jiuzhaigou, Sichuan Province, China 1997.

Detailed information about geographical and ecological conditions of the study areas is published in Bergmann et al. (1996), Klaus et al. (1996) and Sun et al. (2003). From the field program we compiled a database of observations and characters of the three species using the same protocols for observing, sound-recording and filming aspects of behavior, voice, and site features for interpreting the context, meaning and function of visual and acoustical signals. In addition, 2–3 pairs of hazel and ruffed grouse were kept in captivity over several years for more detailed observations of courtship, reproduction and chick-caring, as well as for tracking circadian rhythms.

3 Results

Acoustic signals for territorial advertisement are conspicuous, carry over great distances and are strikingly different between species. The hazel grouse utters a unique, extremely high-pitched “spearing” cantus (Fig. 1a); and the

Chinese grouse gives a whirring, bi-syllabic flutter-jump (Fig. 1b). Such signals reach their highest level of complexity in the ruffed grouse, which also gives an extraordinary wing-drumming that produces a series of low-pitched, thumping blows, accelerating to a quick whirr (Fig. 1c; also Bump et al., 1947; Gullion and Martinson, 1984; Hjorth, 1970). Furthermore, the ruffed grouse utters a broadly differentiated range of instrumental sounds that resemble rasping, slapping, flapping, clapping with wings against body or feet, stamping with feet or pecking the ground, all audible only within a short distance (Table 1; Scherzinger in Bergmann et al., 1996).

Signals used in short-distance communication in courtship or agonistic context are, in contrast, broadly similar among all species. During “offensive-run” display behavior, hazel males utter a specific “offensive-whistle” whereas male Chinese grouse sing a crumpling “offensive-cantus” with a constant and distinct rhythm. In “imposing” behavior against both rivals and females, males of all species fan the tail feathers conspicuously, spread the lowered wings moderately, and enlarge the body, fluffing ruffled plumage particularly on the neck.

Neck ruffling is extraordinarily specialized in the Ruffed Grouse, its prolonged, contrastingly colored neck feathers forming striking ruff around the head when erected. The effect of this signal is not only visually intensified by demonstrative head-twisting, but also acoustically stressed by a strange “wheezing-cantus”, which resembles a starting locomotive. The twisting and wheezing then accelerates rhythmically to culminate in the “rush”, a powerful jump with grinding wing-tips and a long hissing note (Hjorth, 1970; Scherzinger in Bergmann et al., 1996). In all species, the “imposing” display is expressed maximally in pre-copulatory behavior, when the male struts in a “circular walk” around the female, dragging its wings on the ground. In

both palearctic species, an “imposing warble” accompanies this excitement-generating behavior.

As environmental pressure may markedly affect selection in long-distance signals, vocalizations used in short-distance communication, in a non-agonistic context, are more appropriate for inter-specific comparisons of genetic relationship. The “whining” of abandoned chicks, for example, sounds similar in all three species, whereas their “moaning” notes become intensified by lining in a scale-like row. In this situation, chicks of Chinese grouse climb a bush up to 1.5 m high, as their “crying” from this elevated position may carry further. Because of high predator pressure on all small species of grouse, alarm calls are of high importance, especially at times of mating when pairs are in constant contact. Common to all three species is a rattling “twitter”, a warbling “brurr”, a shrill “craiy” or “crrir”, and a soft groaning “serial warning”. The staccato “cackle” was observed in only two species.

Although *Bonasa* species have only weakly differentiated syrinxes (Potapov, 1985), their vocal inventory is high in diversity. The hazel grouse is surprisingly endowed with 26 calls, and the Chinese grouse comparatively poor and simple; only 14 calls have been recorded, although a number of low-pitched sounds have still to be elucidated (Table 2).

4 Discussion

Among the three species of *Bonasa*, the Chinese grouse is the least complex in its vocalizations and behavior. It is usually supposed, when analyzing phylogenetic trees, that simpler specific characters are “older”, or rather “primitive”, and more complex characters “younger”. The question then is: does the Chinese grouse resemble the ancestral form more closely, having conserved archaic characters during longtime isolation, or has its behavioral reper-

Table 1 Comparison of instrumental signals within the genus *Bonasa*

Characters	Chinese grouse <i>B. sewerzowi</i>	Hazel grouse <i>B. bonasia</i>	Ruffed grouse <i>B. umbellus</i>	Remarks
Flutter jump				
Wing dragging (in circular walk)				
Territorial display flight				
Wing grinding (in rush)	?			
Wing slapping				
Wing clapping				
Foot stamping				
Ground pecking (aggressive)		?		
Wing rasping (in strutting walk)				species specific
Wing drumming				species specific
Total = 10 signals	3	6(7)	9(10)	

Dark blocs = present and obligatory, pale blocs = present and facultative, and white blocs = absent. In all three species, advertising behavior is accompanied by non-vocal sounds, with greatest diversity in the ruffed grouse for short-distance communication.

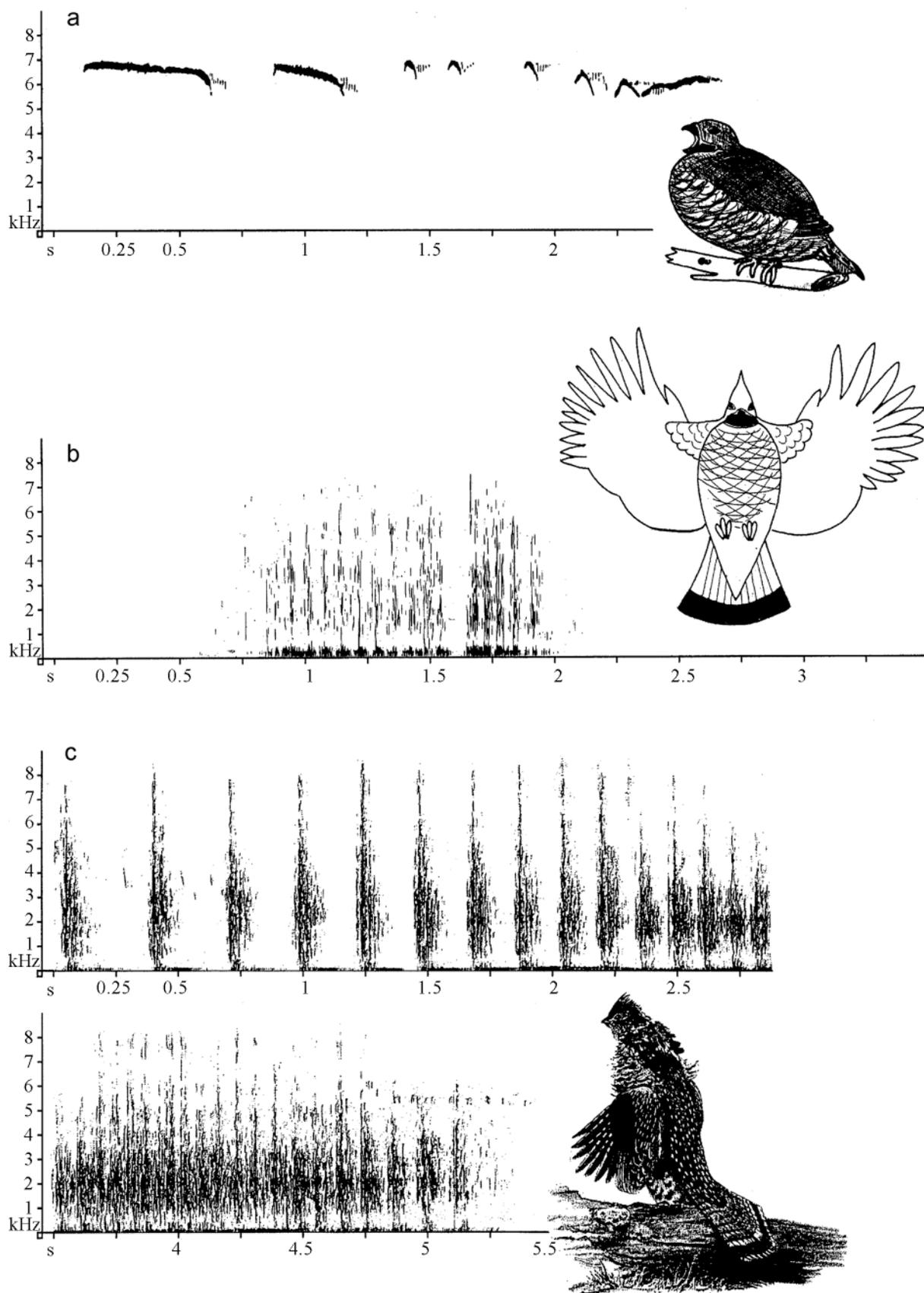


Fig. 1 Different territorial signals in male *Bonasa* grouse

(a) territory-marking “song” of the hazel grouse, a high-pitched whistle (tape recording of captive male, Germany); (b) primary advertising “flutter jump” signal of the Chinese grouse, typically disyllabic because of separate starting and landing phases (tape recording, from Gansu Province, China); (c) specialized territorial “wing-drumming” in the ruffed grouse, with thumping blows in a typical accelerating rhythm (tape recording of captive male, Germany).

Table 2 Inventory of vocalizations within the genus *Bonasa*

Characters	Chinese grouse <i>B. sewerzowi</i>	Hazel grouse <i>B. bonasia</i>	Ruffed grouse <i>B. umbellus</i>	Remarks
Adult grouse				
Simple contact call				
Intense contact call				
Scale				
Brooding note				
Serial warning				
Rattling twitter-alarm				
"Brurr"-alarm				
"Crraiy"-alarm / "crrir"-alarm				
Imposing warble				
Advertisement call (cock)				
Squeal (nest-site demonstration)				
Nesting note (egg laying)	?			
Chicken guiding note				
Cackle (warning)				
Hiss	?			
Offensive cantus ("crumpling")				species specific
Offensive whistle			?	spec. specific ?
"Peeyu" drawling alarm				spec. specific ?
Hen specific call				species specific
Territorial cantus ("spearing")				species specific
Cheeping (nest-site demonstration)				species specific
Serial "tsipp"-note (nest-demonstr.)				species specific
Fear twitter				spec. specific ?
Buzzing (in "follow up")				species specific
Wheezing cantus ("locomotive")				species specific
Whizzing sound (warning)				species specific
Groaning (warning ?)	?			spec. specific ?
Grouse chick				
Simple contact-call				
Intense contact-call				
Moaning / scale				
Fear-call				
Whining / whisper				spec. specific ?
Total = 32 calls	14	26	21	

Dark blocs= present, white blocs = absent. Basic utterances and chick calls are strikingly alike in all species, as are the repertoires of vocalization in hazel and ruffed grouse. The hazel grouse is the most diverse in vocal signals, and the Chinese grouse least.

toire become impoverished secondarily due to environmental pressures?

Recent reconstruction of *Bonasa* phylogeny by cytochrome-*b* sequences from the mitochondrial genome (Lucchini et al., 2001; Baba et al., 2002) confirm that *Bonasa* is monophyletic, that the ruffed grouse branched off very early, and that hazel and Chinese grouse diverged later, probably within the Pleistocene. This sequence and its timing seems paradoxical in the historical context of grouse evolution.

The fossil record of tetraonid grouse dates back to the middle Miocene, 9–6 MYA. Ancestral species evolved in temperate forests of the west Nearctic (Short, 1967), and should have embodied the ancestral form. After ancestral ruffed grouse evolved, a part of the American grouse population emigrated to Eurasia, its founding form represented by ancestral hazel grouse, “*prae-bonasia*”. This species must have conserved relatively primitive characters for millions of years. Repeated invasions of American grouse to Asia across the Bering bridge gave rise to the *Falcipecten*, *Tetrao* and *Lagopus* complexes, while the group of prairie-dwelling grouse evolved in the Nearctic.

The oldest fossil evidence for primeval hazel grouse in Europe dates back to 600 000–500 000 years ago, but distributional range changed continuously with the expansion and retreat of the ice cover during glacial-interglacial cycles. We conclude that, during a phase of extreme retreat to far east Eurasia, an isolate of these populations was trapped in woodlands close to the east rim of the Tibetan plateau. The Chinese grouse arose from this event.

If these assessments of phenotypic characters (Short, 1967; Potapov, 1985), behavior and vocalization (Scherzinger in Bergmann et al., 1996), and mtDNA sequences hold, the Chinese grouse should not only be closest to the ancestral form of its genus, but for all tetraonid grouse as well. This species, thus, is not only a faunistic treasure of remote mountain woodlands in inner Asia but also a key reference point in grouse phylogeny.

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S17-2 The social unit and habitat of the Sichuan jay (*Perisoreus internigrans*) in Zhuoni, Gansu, China

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Abstract The Sichuan jay (*Perisoreus internigrans*) is a rare Chinese endemic found in coniferous forests on the Qinghai-Xizang (Tibet) plateau. In 2000–2001, we undertook a preliminary investigation on its ecology and behavior at Zhuoni, Gansu, China. Eighteen birds were banded and most were measured; mean body mass was 103.4 g for 16 birds. Home range size in the spring breeding period was estimated at 0.53 km² ($n=4$). In the pre-breeding season, the birds were observed in groups 3 to 5 (mean = 3.8). Vegetation analysis of breeding habitat estimated an average tree density of 4.86 ± 4.09 conifers/ha and 1.72 ± 3.99 deciduous trees/ha, indicative of open wooded habitat where the cut rate of conifer trees was 28.1%.

Key words Sichuan Jay (*Perisoreus internigrans*), Habitat, Social unit

1 Introduction

The Sichuan jay (*Perisoreus internigrans*) is a reclusive Chinese endemic of the Qinghai-Xizang (Tibet) plateau. The few available reports indicate that this rarely seen bird occurs in montane coniferous forest in south Gansu, west Sichuan, east Tibet and southeast Qinghai provinces (Sun et al., 2001). Since its discovery in Sichuan by Thayer and Bangs in 1912, its status and ecology have received no attention at all. Nothing was known of its nesting, and all that Madge and Burn (1994) could add in their monograph of the Corvidae was that it is “skulking and unobtrusive”. Its listing as a “globally threatened species” (Collar et al., 1994) subsequently led, in 2000–2001, to a preliminary investigation of its status at Zhuoni, Gansu Province, one of the 14 locations where it is known to occur. This study site lies at the northernmost limit of its known range.

2 Materials and methods

2.1 Study area

Our main study area is Zhuoni county, Gansu, central China (34°27'35", 103°25'94"), at an altitude of 3 000–3 600 m. Local meteorological data shows yearly mean air temperature ranging between –25°C to 28°C. Patchy coniferous forest, with dominant trees of fir (*Abies fargesii*) and spruce (*Picea asperata*) mixed with rhododendron (*Rhododendron* spp.), occurs on northward slopes. Rhododendrons constitute over 90% of broad-leaved trees in the forest patches. Shrub and grassland occurs on insolated southern slopes. From 1958 to 1995, this area had been selective logged and the overall timber production was reported as 39 m³/ha (Bailongjiang Forestry Administration, 1995).

2.2 Field methods

Field techniques used successfully for assessing the status of the related gray (*Prisoreus canadensis*) and Siberian (*P. infaustus*) jays were employed. Lard was nailed on branches or stems to attract the birds, and the sites video-cameraed to provide preliminary information of group size. Potter traps baited with lard were then used to capture birds. After basic measurements were taken, trapped birds were radio-tagged with 3.8 g mounts on the base of central rectrices, and tracked by radio telemetry integrated with a GPS receiver. Group home ranges were calculated by the Minimum Convex Polygon method using location data from more than 25 workdays.

10 m × 10 m vegetation samples were taken from the breeding habitat of one nesting pair; and 35 sample plots were scattered randomly through foraging home ranges. The number of coniferous and deciduous trees present, canopy cover, grass cover, shrub cover and moss cover were all recorded; very small trees with a DBH (diameter-at-breast-height) of less than 3 cm were counted as shrubs. To evaluate the effects of deforestation, the cut rate of the forest was calculated by the equation:

$$\text{Cut rate} = \frac{\text{Base Area of Cut Stems}}{\text{Base Area of (Spring + Fir + Cypress + Cut Stems)}}$$

Sample plots outside or at the edge of the forest patches were manually abandoned in computation of the cut rate.

3 Results

3.1 Measurements

Over the duration of the study, 18 birds were banded, and 8 radio-tracked for more than 50 workdays. Table 1 gives measurements of selected birds. As sex and age could not be distinguished, these classes are combined.

3.2 Group size and home range

In March and April at the beginning of breeding, group size varied from 3 to 5 birds, with a mean of 3.8 ($n = 5$). In October 2000, one group of 7 individuals was recorded. Estimated home range in April–May was 0.53 km² ($n = 4$).

3.3 Breeding habitat

Jays spent much of their time in dense forest patches, especially in April–May during breeding. More than 95% of daylight hours were spent there then. The one nest found in Zhuoni was in a forest patch which had been logged only once. Principal vegetation characteristics are given in Table 2. Table 3 details the base areas of the conifers and the cut rates for conifer forest.

4 Discussion

Our results show that group size in the Sichuan jay during the breeding season averages 3.8 individuals, with extra-pair birds present. Groups of such size are found also in its congeners, the gray and Siberian jays. As delayed dispersal and offspring retention, associated with cooperative breeding, are well known in these last two species

(Strickland et al., 1993; Ekman et al., 1994), it seems likely that the Sichuan jay is a cooperative breeder too. Even so, the social role of extra-pair birds in the groups is still unclear and may vary within the genus. The body mass of the Sichuan jay (mean 103.4 g) is considerably greater than in the gray jay (62–82 g) and Siberian jay (68–90 g) (Madge and Burn, 1994).

Our data indicate that the breeding habitat of the Sichuan jay is restricted to montane coniferous forest, as had already been suggested by earlier records (Cheng, 1987; Cheng et al., 1965, 1998; Madge and Burn, 1994). The denser parts of the forest are favored in breeding season, suggesting that concealment might be important at that stage. At our study site, we recorded birds in forest with a maximal cut rate of 28.1%, much lower than the 62.6% reported by Sun et al. (2001) for the area generally. This suggests that a culling rate of any more than a quarter of primary, old growth forest is likely to affect breeding. Further work is needed to determine the “threshold” of habitat disturbance to breeding habitat that the jay can withstand.

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Table 1 Measurements of the Sichuan jay at Zhuoni, Gansu, 2000–2001

	Body mass (g)	Length (mm)	Wing (mm)	Tail (mm)	Tarsus (mm)	Alula (mm)	Culmen (mm)
<i>n</i>	16	12	10	9	11	10	13
Range	92–110	280–295	160–165	150–165	40–43	17–22	22–25
Mean	103.4	288.8	162.4	153.7	41.4	19.4	23.3

Table 2 10 × 10 m vegetation sampling of the breeding habitat of the Sichuan Jay ($n = 35$)

	Factors					
	Coniferous forest	Deciduous forest	Canopy cover	Shrub cover	Grass cover	Moss cover
	trees (<i>n</i>)	trees (<i>n</i>)	(0–1)	(0–1)	(0–1)	(0–1)
Range	0–15	0–16	0–0.9	0–0.85	0.1–0.95	0.1–0.96
Mean ± <i>SD</i>	4.86 ± 4.09	1.72 ± 3.99	0.39 ± 0.30	0.24 ± 0.25	0.30 ± 0.30	0.49 ± 0.40

Table 3 Mean base area of coniferous forest, conifer components and the estimated forest cut rate
From 10 × 10 m vegetation sampling of breeding habitat ($n = 22$ plots)

	Coniferous components				
	Spruce	Fir	Cypress	Total living conifers	Cut stems
Base area (cm ² /100 m ²)	111.9	2432.4	2.4	2546.4	993.1
Number of trees in 100 m ²	0.20	7.33	0.20	7.73	2.4
Component percentage (%)	2.6	94.8	2.6	100	
Forest cut rate (%)			28.1		

Prof. H.B. Willam, Dr. T.A. Waite, and Prof. J. Ekman.

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S17-3 The golden-spectacled warbler (*Seicercus burkii* auct.) — a Sino-Himalayan species swarm

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Abstract The Golden-spectacled warbler (*Seicercus burkii* auct.), a widespread “species” in southeastern Asia, consists of a swarm of cryptic species. Recently unmasked independently by a Swedish and a German team, it comprises *S. burkii* s. str. (Himalayas), *S. whistleri* with two subspecies *S. w. whistleri* (Himalayas) and *S. w. nemoralis* (northeast India, north Myanmar), *S. valentini* with two subspecies *S. v. valentini* (central and south China) and *S. v. latouchei* (southeast China), *S. omeiensis* (Sichuan, Myanmar), *S. soror* (central and southeast China), *S. tephrocephalus* (central, south and southeast China, northwest Myanmar, north Vietnam), and *S. affinis* (east Himalayas, central and southeast China, Vietnam). Molecular-genetics confirm a close relationship among those species of the complex with backs colored a glowing green, clearly defined black crown stripes and particular song-syntax characters. In the Chinese mountains up to four species, and in the Himalayas two or possibly three, coexist on a mountain slope in well-defined vertical parapatry. Up to three species also assemble in local sympatry in high population density in Sichuan, China. The species of the *S. burkii* complex live at altitudes ranging from subtropical foothills at 550 m a.s.l. in China to the cold-temperate zone of subalpine coniferous forest in Nepal at 3 800 m (*S. whistleri*) and on the Omei Shan in China at 4 000 m (*S. valentini*).

Key words Cryptic species, Species swarm, *Seicercus burkii* complex, Himalayas, China

1 Introduction

“Swarms” of closely related species often escape detection because their component members are so extremely similar in their suites of external characters. Therefore, the members of such complexes are often recognized as elements of a single polymorphic species. The case of *Seicercus* is typical of such cryptic complexes in that extreme outward similarity among all members hides internal species limits. Their species-specific morphological characters only appear when seen in the light of acoustic and molecular data, because of which data collection must be extremely careful and precise. Here we report on the *Seicercus burkii* complex in the Himalayas, China and countries close-by. By an array of methods, this complex has been shown to be highly diverse with at least seven biospecies, each of which can be identified by several characters.

2 Material and methods

Field studies were carried out in Nepal between 1969 and 2001 (6 trips during the breeding season summing to over 2 years), and in China between 1997 and 2002 (4 trips during the breeding season summing to 20 weeks in three provinces where *Seicercus* is present) (Martens, 1987; Martens and Eck, 1995: 52–64). Skins, song recordings including song specimens, and tissue samples were collected,

with emphasis on combining the documentation of song and tissue sampling with skins.

For molecular-genetic analysis, we sequenced 706 bp of the cytochrome-*b* gene of the mitochondrial genome for 74 samples comprising seven taxa in the complex: *S. burkii* s. str. — 2 specimens, E Nepal; *S. w. whistleri* — 13, west and east Nepal; *S. v. valentini* — 14, Sichuan, Gansu, Shaanxi; *S. omeiensis* — 17, Sichuan, Shaanxi, Cambodia; *S. soror* — 14, Sichuan, Shaanxi, Cambodia; *S. tephrocephalus* — 12, Sichuan, Shaanxi, north Thailand; and *S. affinis intermedius* — 2, Sichuan. Protocols are given in Martens et al. (1999).

In bioacoustical analysis, all recordings were checked, sonographed and measured by means of a Kay Elemetrics Sona-Graph, model 5500.

For external morphological characters we examined some 260 skins from various collections, as well as those taken by us.

3 Results

3.1 Morphology

The *S. burkii* complex comprises medium-sized leaf warblers, all of which are remarkably uniform in coloration and patterning: greenish back, glowing yellow underside

with fine differences in tone, and head with a green or gray median crown stripe and two blackish lateral crown stripes of definition varying between species (color plates and photos in Martens et al., 1999, 2000, 2003; Alström and Olsson, 1999). The eyes are surrounded by yellow feathers that form a delicate ring which varies in width between species. In all species, the inner vanes of the outer tail feathers T6 and T5 always bear white markings, larger in *S. whistleri* and present on T4 in all species except *S. soror*. Relative dimensions, such as length of wing and tail, and their proportions, also differ significantly among members, wing/tip index and tail/wing index providing particular insights into feather proportions and relative length of tail and wing (Martens et al., 1999, 2003).

3.2 Bioacoustics

Songs within the *burkii* complex, in most cases easily recognized by the human ear, have a simple syntactic structure; each male employs many conspicuously different verse types but all follow species-specific patterns. The species fall into two groups on verse structure: *S. whistleri*, *S. valentini* and *S. soror* in one, and *S. burkii* s. str., *S. omeiensis*, *S. tephrocephalus* and *S. affinis intermedius* in the other. In the verses of the first group, a temporally offset introductory element with descending frequency is followed by a group of two (rarely three) elements. This element group is repeated once or rarely twice, which completes the verse. Within this group, *S. whistleri* and *S. valentini* are especially similar in their songs, which are also noteworthy for the small frequency bandwidth of the verses ($\xi = 2.4$ kHz in both species, $n = 12$ and $n = 30$, respectively). Slight differences between *whistleri* and *valentini* songs show up in the slightly lower frequency of the latter. *S. soror* stands apart in its much broader frequency band ($\xi = 4.4$ kHz; $n = 25$).

Verse syntax is more irregular in the second group. A common feature is a trilled ending to many verses. This applies to 80% of verses in *S. affinis intermedius*, 51% in *S. tephrocephalus*, 48% in *S. omeiensis* and 39% in *S. burkii* s. str. The songs of *S. omeiensis*, *S. tephrocephalus* and *S. burkii* also have a broad bandwidth ($\xi = 4.0$ – 4.7 kHz), but that of *S. affinis intermedius* is very narrow ($\xi = 2.3$ kHz). In both sonagram and auditory impression, the songs of *S. omeiensis* and *S. tephrocephalus* resemble one another closely. That of *S. tephrocephalus* always begins with one or two broadband modulated introductory elements (for sonagrams, see Alström and Olsson, 1999, 2000; Martens et al., 1999, 2000, 2003).

All seven species give quite different and clearly distinguishable calls (Martens et al., 1999; Alström and Olsson, 1999). These may be brief, steeply rising (*S. burkii* s. str.) or softer, descending (*S. valentini*) individual calls, or groups of two sharp calls each descending in frequency (*S. tephrocephalus*, *S. omeiensis*, *S. whistleri*). Complicated “calling songs” are produced by *S. soror* and *S. affinis intermedius*, and in the latter species each individual has a call repertoire.

3.3 Molecular genetics

The deep incision in the cladogram (cf. Martens et al., 1999) separates two species groups: (i) one with *S. affinis intermedius*, *S. burkii* and *S. tephrocephalus*, and (ii) the other with *S. whistleri*, *S. valentini*, *S. omeiensis* and *S. soror*. The species in the first group are colored a glowing green on their upper surfaces, and their crown stripes stand out clearly in black. Their distribution is predominantly southern, either in subtropical regions or limited to lower altitudes in the Himalayas (*burkii* s. str.).

The species of the second group are dull green on the upper surface, and their dark lateral crown stripes tend to be ill-defined and faded, often with a scattering of lighter gray or greenish feathers. They are centered in the northern parts of central China and the Himalayas, at relatively high altitudes in the mountains where *S. whistleri* and *S. valentini* always occupy the uppermost belt in species altitudinal sequences, up to temperate coniferous forests. The genetic distance values between individual species range from 5% to 9% (uncorrected; Martens et al., 1999) and are highest between species of the two main clades; the lowest values lie within each of the two species groups.

3.4 Distribution

The *S. burkii* complex, as currently understood, ranges along the entire Himalayan chain, from an area to the west of northern Pakistan as far as southeast Tibet, then from the forested regions on the eastern flank of the Tibetan plateau northwards to south Gansu (Lianhua Shan, *S. v. valentini*), and along the southern and northern flanks of the Qinling Mountains (*S. v. valentini*, *S. omeiensis*, *S. soror*, *S. tephrocephalus*) to Guandong and the Wuyi Shan in Fujian (*S. valentini latouchei*, *S. tephrocephalus*, *S. affinis intermedius*). In the south, its distribution is bounded by Mt. Victoria in Myanmar in the west (*S. omeiensis*, *S. tephrocephalus*, *S. whistleri nemoralis*) and by the northern and perhaps parts of southern Vietnam in the east. It is likely that the complex is widespread throughout central and southern China in forested mountains above ca. 500–600 m a.s.l., occasionally in dense populations and even in secondary growth (Cheng 1987, 2000). The ranges of individual species are much more poorly documented. *S. burkii* s. str. and *S. whistleri* are almost exclusively Himalayan, *S. affinis* is Himalayan and Chinese, *S. omeiensis* Chinese and Burmese, *S. soror* and *S. valentini* only Chinese, and *S. tephrocephalus* is widespread within China, Myanmar and northern Vietnam.

3.5 Ecology

All members of the complex are forest birds. They inhabit open and secondary stands as well as closed primary forests. The forest communities occupied, however, differ much between individual species, and range from tropical forests (*S. tephrocephalus*) to temperate coniferous forests up to 3 800 m in the Himalayas (*S. whistleri*). There are exceptions where up to four species may live in sympatry, but usually local species are separated in altitu-

dinal zones of often differing vegetation in mostly narrow bands of up to 650 m in China (*S. omeiensis*) and 1 500 m in Nepal (*S. whistleri*); most zones are considerably narrower and often sharply delimited. Such parapatric zoning has been documented most accurately in the Omei Shan (Alström and Olsson, 1999; Martens et al., 1999).

This altitudinal “layering” of species may appear different on different mountain complexes, but the sequence of species is always maintained, from (sub)tropical ones to those of cool-temperate affinity. In the case of China, the species sequence from the foot of the mountains into the tops of peaks seems to be as follows: *S. tephrocephalus*, *S. soror*, *S. affinis*, *S. omeiensis*, *S. valentini*. Where altitudinal range is limiting, either *S. tephrocephalus* or *S. soror* lives at the foot of the mountain, not both. Closer to the peak lies *S. omeiensis*, and above that a belt of *S. valentini* that regularly extends to the upper limits of habitat. In the Himalayas, *S. burkii* s. str. occupies the lower belt, and *S. whistleri* the upper.

Early data indicated that ecological exclusion between the species was incomplete, but could not distinguish whether observed overlap was due to occasional vagrants of out-of-zone species (e.g., occasional *burkii* in the zone of *whistleri* in Nepal, *soror* in the range of *valentini* and *affinis* in the range of *soror* on the Omei Shan), or whether local syntopy was frequent, even routine. We have since been able to document, with tape recordings, skins and tissue samples, that three species in the Qincheng Shan live sympatrically together in high density at 1 200 m a.s.l.: *S. soror*, *S. tephrocephalus* and *S. omeiensis*.

4 Discussion

The *Seicercus burkii* complex is a species swarm that was discovered from analyses using modern methods (Alström and Olsson, 1999; Martens et al., 1999). Earlier reviews (Bangs, 1929; Stresemann, 1940) failed to sort out the complexity of the group due to lack of basic field data. Most intriguing is the lack of morphological variation among the species. Because of this, previous revisers saw the complex as a continuous morphological “series”, were not in a position to take account of other characters, and so overlooked species boundaries. The individual species are distinguished by a delicate mosaic of characters involving coloration, head and tail patterning, length of wings and tail and feather proportions.

Careful calibration of these characters was all the more necessary because as many as four species in the complex may live in vertically adjacent zones on a mountain slope, and up to three species can occur side by side in one area. Only in rare cases can species can be determined from allopatric breeding grounds. Vocalizations helped significantly in separating the “morphological continuum” into species units. Yet this approach, too, was not without its snags, because several widely disjunct populations were found to have convergently similar songs and calls even though relatively well separated morphologically (*S. burkii* s. str./*S.*

omeiensis; *S. whistleri*/*S. valentini*). Even within narrowly circumscribed habitats, we found different species with voices that were very difficult to distinguish by sonagram as well as listener (*S. omeiensis*/*S. tephrocephalus*). To function as pre-mating isolating mechanisms, vocalization differences would have been expected to be especially distinctive here, to prevent interspecific mating; and, indeed, we did not find any signs of hybridization.

Molecular-genetic characters provided the ultimate confirmation that *S. burkii* auct. was a complex of at least seven well-differentiated species. The molecular phylogeny also showed that great similarity in song did not necessarily imply close kinship of the singers, as was found for *S. burkii* s. str. and *S. omeiensis*. Each of the clearly distinguishable “molecular species” was distinctly structured genetically within itself, as evidenced by up to nine haplotypes of the *cyt-b* gene. The high distance values indicate that the species are not very young. Following the 2% differentiation per million years rule (Zink and Klicka, 2000), the species range from 2.5 to 4.5 million years old, taking their origin back to the late Pliocene.

Little is still known about the distributional ranges of the individual species. In addition to one widely distributed subtropical species (*S. tephrocephalus*), there are several narrowly localized endemics, such as *S. omeiensis* with two disjunct populations in Sichuan and Myanmar and, at the subspecies level, *S. valentini latouchei* in Fujian Province. Even less is understood about how these distributional patterns have been formed. How did niche partitioning and altitudinal zonation develop in the parapatric taxa? We can only conclude from the rich structure of the *cyt b* haplotypes within individual species that none of the species passed through a strict population “bottleneck”, perhaps during the Pleistocene ice ages, which would have sifted out haplotypes in refugia. Speciation in the *Seicercus burkii* complex thus provides new and impressive evidence that in the transitional zone between China and the Himalayas, where the Palearctic and Indomalayan fauna mingle, evolutionary processes may have long remained little or even undisturbed.

The following species and subspecies are now distinguished in the *S. burkii* complex (Alström and Olsson, 1999, 2000; Martens et al., 1999, 2000, 2003), as follows:

Group 1:

Seicercus affinis, with two subspecies: *S. a. affinis* (Hodgson, 1854) and *S. a. intermedius* (La Touche, 1898);

Seicercus burkii (Burton, 1836);

Seicercus tephrocephalus (Anderson, 1871) = *S. tephrocephalus* “group 4” sensu Alström and Olsson, 1999, syn. *Cryptolopha burkii distincta* La Touche, 1922 = *S. distinctus* sensu Martens et al., 1999.

Group 2:

Seicercus whistleri, with two subspecies: *S. w. whistleri* Ticehurst, 1925 and *S. w. nemoralis* Koelz, 1954;

Seicercus valentini, with two subspecies: *S. v. valentini* (Hartert, 1907) and *S. v. latouchei* Bangs, 1929;

Seicercus omeiensis Martens, Eck, Päckert and Sun, 1999 = *S. tephrocephalus* “group 6” sensu Alström and Olsson, 1999;

Seicercus soror Alström and Olsson, 1999 = “*S. latouchei*” sensu Martens et al., 1999, nec *latouchei* Bangs, 1929.

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S17-4 The Qinghai-Tibet Plateau: center of evolution for snow sparrows (*Montifringilla* s. str.) and mountain-steppe sparrows (*Onychostruthus*, *Pyrgilauda*)

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Abstract Conventionally, the snow sparrows comprise 7 species in the sole genus, *Montifringilla* Brehm, 1828. Our studies on their morphology, ecology and behavior, as well as cytochrome-*b* sequencing carried out independently, separate the group into 8 species in 3 genera: *Onychostruthus*, *Pyrgilauda* and *Montifringilla* s. str.; the Tibet snow sparrow (*M. henrici*) is shown to be a valid species. *Montifringilla nivalis* (western area) and *M. adamsi* (eastern area) form a superspecies. Unexpectedly, Blanford's mountain-steppe sparrow (*Pyrgilauda blanfordi*) and Père David's mountain-steppe sparrow (*P. davidiana*) are differentiated only in nuclear LDH but not mtDNA cytochrome *b* of the genes sequenced. To assess the evolutionary history and zoogeography of extant species, we calculated divergence times and compared them with updated data on distribution patterns in Central Asia. We found a high degree of sympatry in *Montifringilla*, suggesting that the Qinghai-Tibet plateau is a center of evolution for the group and that their adaptive radiation peaked during the Pliocene 1.9 to 4.8 myr ago. Ancestors of *M. nivalis* reached the European alps along chains of mountains raised through western Asia in the Tertiary.

Key words Tibet plateau, Snow sparrows, Mountain-steppe sparrows, Systematics, *Montifringilla*, Evolution, Ecology, Central Asia

1 Introduction

Because of the inaccessibility of the Qinghai-Tibet plateau, its endemic bird fauna is poorly studied and understood systematically. Following studies on several snow finches, *Montifringilla* sensu lato, in the 1930s and 1990s (Schäfer, 1938; Ivanitsky, 1991; Gebauer and Kaiser, 1994), we carried out further research into the biology and systematics of Asian representatives of the group.

The snow finches have been grouped by convention in one genus, *Montifringilla* Brehm, 1828 (Sibley and Monroe, 1990; Clement et al., 1993; Fu et al., 1998; Mlikowski, 1998). Our results dispute this. Snow sparrows are members of an array of Central Asian bird genera with a high concentration of sympatry, with many “congeners” living together in shared habitats. Six of the eight species of snow finches are centered on our study area, the Qinghai-Tibet plateau, their putative evolutionary source. This raises the question: when and how did the component species arise and how did their present distributions develop?

2 Materials and methods

Field studies were carried out on high altitude steppes

and mountains of the Qinghai-Tibet plateau (Qinghai Province, China) on several trips between 1990 and 2002. Locations visited were near Qinghai Hu (36°45'N, 99°30'E to 36°50'N, 99°38'E), Madoi (34°55'N, 98°09'E) and Huashixia/Donggi Cona (35°06'N, 98°53'E).

Detailed morphological examination was undertaken on about 250 specimens from various museum collections.

For molecular analysis, the 1 041 base pairs of the entire cytochrome-*b* mtDNA gene was sequenced. Protocols are those given in Helbig and Seibold (1999), including the sequences of primers used. The phylogenetic tree was calculated with MEGA 2.0 (Kumar et al., 1993), using Neighbor-Joining and Kimura 2-parameter distance. Divergence times were calculated from nucleotide differences at the rate of 2% per million years (Zink and Klicka, 2000).

3 Results

3.1 Ecology

We found two major species groups with distinct and different ecological requirements. One was confined to high-altitude steppes. These are the “mountain-steppe” sparrows, the four species of which live in close associa-

tion with small burrowing mammals (pikas, *Ochotona* sp.), depending on the burrows for their nest holes. The sparrows involved are *ruficollis*, *blanfordi*, *davidiana*, and *taczanoswskii*, for which the generic names *Pyrgilauda* and *Onychostruthus* are available. The other group was confined to high-altitude mountains; it comprises the true “snow sparrows”. When breeding, their members settle on steep slopes and cliffs and build their nests in fissures and crevices in and beneath rocks and boulders; none have any affinity with small mammal activity. The species taxa involved are *adamsi*, *nivalis* and *henrici*, for which the generic name *Montifringilla* is available.

3.2 Morphology

Mountain-steppe sparrows have body proportions that are different from those of snow sparrows, as well as differences in the distribution of white patterning on primaries and secondaries and on the tail. Moreover, we found that *henrici* differs from the two other snow sparrows (*nivalis* and *adamsi*) in body proportions and coloration. Body mass (40 g) and the maximum wing (126 mm) and tail (78 mm) lengths of *henrici* are higher than in *adamsi*. The bill/tail ratio of *henrici* is 14.3 % (*sd* 0.65, *n* = 13) and that of *adamsi* and *nivalis kwenlunensis* 11.7 % (*sd* 0.54 and *sd* 0.69, *n* = 33, 12 respectively). Thus *henrici* has a propor-

tionally longer bill than the other two species.

3.3 Vocalizations

To further evaluate difference among the taxa, we analyzed calls given by the birds when flushed or flying off. There are two types of such calls, A and B. Snow sparrows give both types, but mountain-steppe sparrows only type B. Type B is characterized by a modulated main frequency with a narrow span (max. 0.9 kHz), which is centered near 2 kHz in all snow sparrows and near 3 kHz in all mountain-steppe sparrows. Only *Onychostruthus taczanoswskii* clearly modulates the call, but without any ascent or descent in pitch. Type B calls, moreover, are alike in *Montifringilla nivalis* and *M. adamsi* but different in *M. henrici*. In the last, there is only a slight overall fall in frequency, but in the first two it first descends rapidly from 4.5 kHz to 2.5 kHz within 0.03–0.05 s, then more gently to the end of the call.

3.4 Distribution

We found up to five species in close sympatry: *Pyrgilauda blanfordi*, *P. ruficollis*, *Onychostruthus taczanoswskii*, *Montifringilla adamsi* and *M. henrici* near Huashixia at 4 250 m a.s.l., the three last in syntopy. We also discovered sympatry between *adamsi* and *henrici* at a sec-

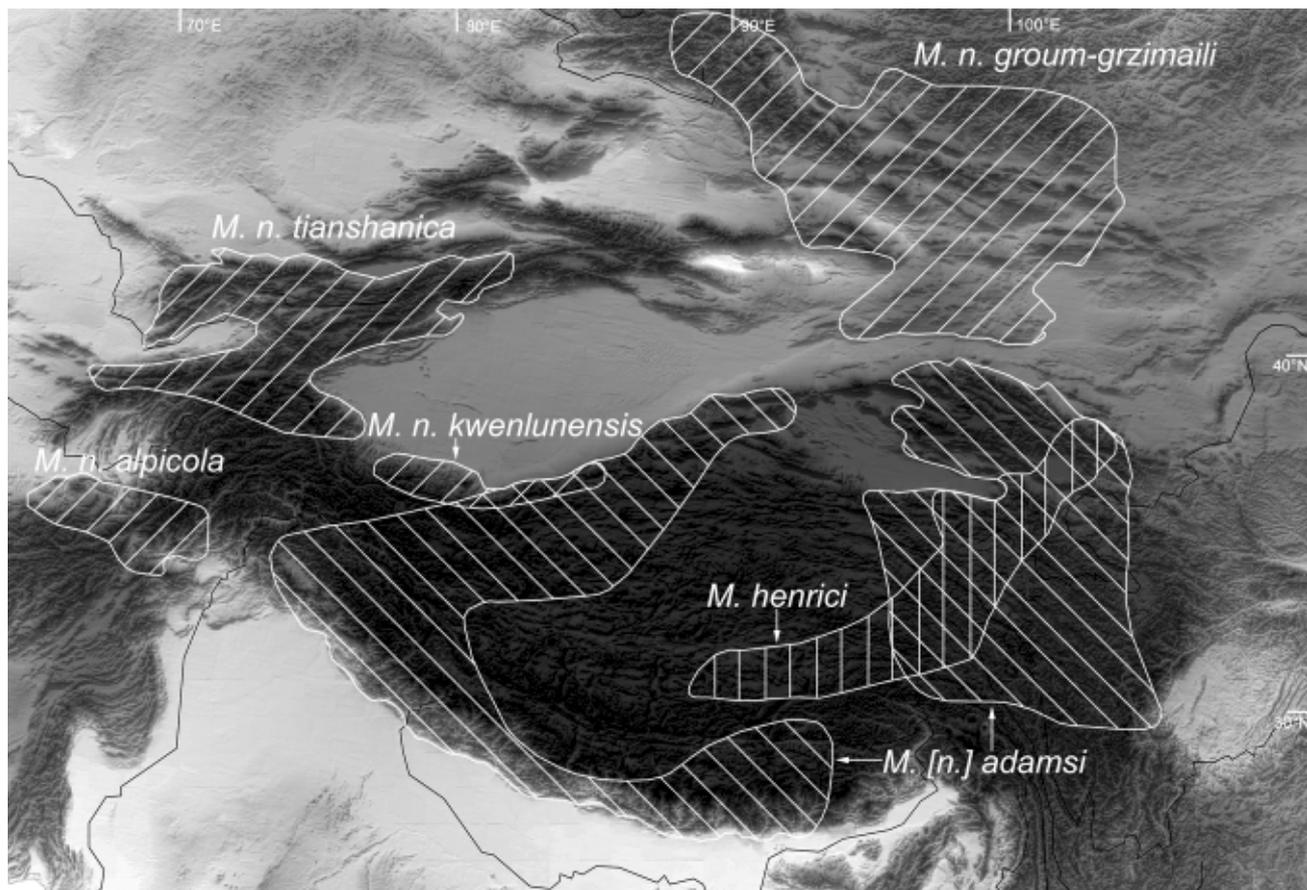


Fig. 1 Current distribution of the species of the genus *Montifringilla* in central Asia, as defined here

The pale area at the foot of the geogram is the northern lowland of India and Pakistan, and the mid grey depression in the center is the Xinjiang Desert.

ond site, near Heimahe, southwest of Qinghai Hu at 3 935 m a.s.l., including nests of both taxa within 50 m of one another. Our results thus update the current distribution of all central Asian snow and mountain-steppe sparrows recorded in Loskot et al. (1978, 1980, 1981) and Mauersberger et al. (1974); see Fig. 1 for *Montifringilla*.

3.5 Molecular genetics

Analysis of the cytochrome-*b* gene (Fig. 2) clearly corroborates a deep split between mountain-steppe sparrows (*Pyrgilauda*) and snow sparrows (*Montifringilla*), but with weak bootstrap support (51%). Basic to *Pyrgilauda* stands *taczanaowskii*. The monophyly of the snow sparrows is well supported but not the position of the relevant species. The neighbor-joining tree shows deep splits between the three terminal taxa of *Montifringilla*, indicative of long divergence (4.4%–8.5%). The distance of 4.8 % between nominate *nivalis* (European Alps) and *M. n. alpicola* (Caucasus) hints to a complex evolutionary situation within west palearctic *M. nivalis*, and may indicate a still unrecognized species. Unexpectedly, *Pyrgilauda blanfordi* and *P.*

davidiana are differentiated by their nuclear LDH gene, not by mtDNA cytochrome *b*. *P. ruficollis* differs from *P. davidiana* and *P. blanfordi* by 6.9% and 7.6%, respectively.

4 Discussion

4.1 Classification

The following generic- and species-level taxa are distinguished by the present study:

1. White-rumped mountain-steppe sparrow (*Onychostruthus taczanowskii*)
2. Theresa's mountain-steppe sparrow (*Pyrgilauda theresae*)
3. Rufous-necked mountain-steppe Sparrow (*Pyrgilauda ruficollis*)
4. Blanford's mountain-steppe sparrow (*Pyrgilauda blanfordi*)
5. Père David's mountain-steppe sparrow (*Pyrgilauda davidiana*)

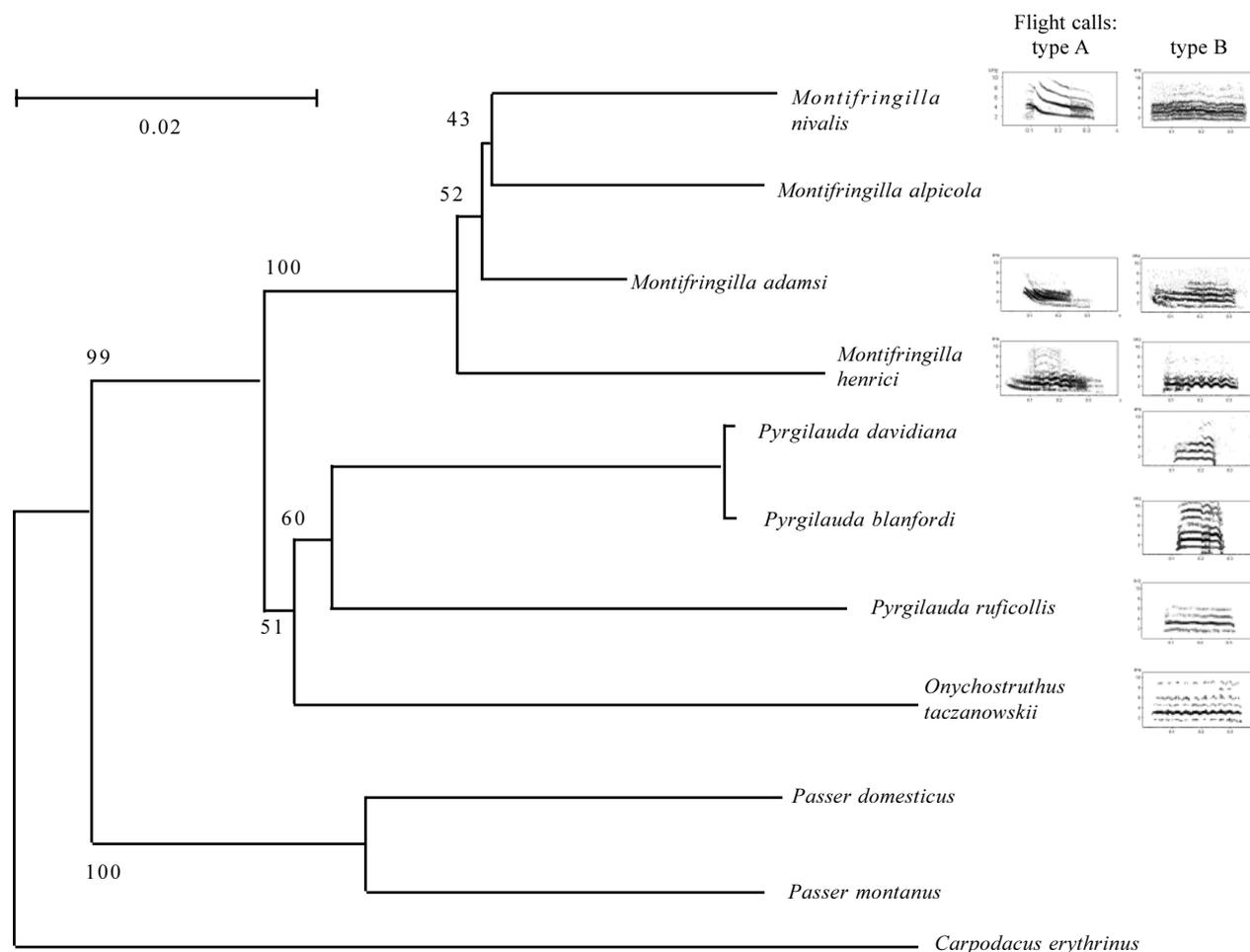


Fig. 2 Neighbor-joining tree for eight snow and mountain-steppe sparrow taxa based on 1 049 bp from the mtDNA cytochrome-*b* gene

Sonograms of departure calls A and B of relevant taxa are superimposed. Outgroups: *Passer domesticus*, *P. montanus*, *Carpodacus erythrinus*.

6. Tibet snow sparrow (*Montifringilla henrici*)

7. Adam's snow sparrow (*Montifringilla [nivalis] adamsi*)

8. White-winged snow sparrow (*Montifringilla [nivalis] nivalis*)

Specific separation of *Montifringilla henrici* was first suggested by Martens and Eck (1995) and Eck (1996), based on skin studies and on sympatric distribution among the taxa.

4.2 Phylogeny and geography of evolution

Allopatric speciation is widely accepted as the sole mode of speciation in birds. It postulates that populations only differentiate and develop functional isolating mechanisms in isolation from one another. Accordingly, we examined whether annidations are recognizable in sympatric species in behavior and habitat preferences. This is indeed the case with respect to *Montifringilla henrici* and *M. adamsi*. In Tibet, Stegmann (1932) and Schäfer (1938, 1942) found widespread sympatry in both, but their interpretations were inappropriate. Local syntopy and strong morphological, behavioral and genetic "gaps" between these taxa confirm species status for both under the biological species concept (Fig. 1), contrary to Stegmann (1932), Clement et al. (1993) and Glutz von Blotzheim and Bauer (1997) for *M. henrici*.

The diversity and density of snow sparrows and mountain-steppe sparrows in central Asia suggests that the region has been a historic center of their evolution (Weigold, 1949; Diesselhorst, 1968; Vaurie, 1972). Indeed, several workers have used *Montifringilla* sensu lato as an example of the central Asian origin of alpine passerines in the palearctic (Stresemann, 1920; Schäfer, 1942). According to the timetable suggested by cytochrome-*b* data, their ancestors probably arose in the middle Tertiary (Oligocene, Miocene) with the beginning of the uplifting of the Qinghai-Tibet plateau. By the Pliocene (6–1.8 MYA) — prior to the Pleistocene glaciations — it is likely that most modern species-level taxa had evolved. Divergence times among extant taxa estimated from genetic distance data range between 1.9 and 4.8 million years across all taxonomic levels from subspecies to genus.

Thus adaptive radiation among the snow and mountain-steppe sparrows probably peaked in the Pliocene. This coincides with pronounced Pliocene mountain building which led to separation of populations on mountain "islands". Within the snow sparrows themselves, comparable evolution took place among the widely scattered populations of *Montifringilla nivalis*, leading to extensive subspeciation (Fig. 1). These populations are isolated today on separate high blocs of mountain ranges, without interconnection and gene exchange; several of the subspecies are undoubtedly well on the way to divergence as species.

The identical cytochrome-*b* pattern in *Pyrgilauda*

blanfordi and *P. davidiana* may be explained by limited hybridization and gene exchange between them, followed by its fixation. Hybridization may have occurred when *P. davidiana* was forced into sympatry with *P. blanfordi*, or vice versa, at some time in the past. Similar patterns of cytochrome-*b* commonality occur in *Stercorarius* skuas (Cohen et al., 1997) and in *Zonotrichia* sparrows (Weckstein et al., 2001). That differentiation between *Pyrgilauda blanfordi* and *P. davidiana* is recent is indicated by their extensively allopatric distribution with a sole contact zone in the Qinghai Hu area.

Obviously, *Onychostruthus taczanowskii* is the oldest form among the mountain-steppe sparrows because of its long divergence time of more than 4 million years (genetic distance from other taxa, 8.2%–9.4%). Kozlova (1950) drew the same conclusion from her morphological studies, as did Weigold (1949) from zoogeographical insights. According to the latter, *O. taczanowskii* and *Pyrgilauda ruficollis* developed in the dry region uplands from so-called Angara elements, which reached the plateau in the late Pliocene, the penultimate stage of uplifting. These extremely steppe-adapted birds did not reach Europe either. Europe never became linked to central Asia by steppe habitat, which also accounts for the absence of burrowing pikas there. Only *P. theresae*, a species living in Afghanistan on the plateaux of the Hindu Kush, moved further to the west. Mountain building itself formed barriers between high plateau steppe in the late Tertiary, dividing the populations of mountain-steppe sparrows and driving their speciation. When and how the species came back into contact has still to be resolved.

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S17-5 The evolutionary history of Eurasian redstarts, *Phoenicurus*

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Abstract The bird genus *Phoenicurus* comprises 10 to 11 species that occur from Europe through Asia. To resolve their phylogenetic relationships, their phylogeography and the tempo of their evolution, the mitochondrial cytochrome-*b* gene was sequenced for 16 taxa. The Bayesian maximum likelihood tree and neighbor-joining dendrogram computed from the resulting data are nearly identical. The genus seems to have diverged from turdine stock approximately 5.25 ± 0.25 MYA in central Asia, and then underwent a rapid radiation during the recent orogenesis of the Himalayas. This radiation took place in two waves, at 4.9 ± 0.4 and 3.05 ± 0.35 MYA, producing a core-group represented by *P. aureus*, *P. erythrogaster*, *P. hodgsoni*, *P. ochruros*, *P. phoenicurus* and *P. schisticeps*, and three more distantly related species: *P. caeruleocephalus*, *P. erythronotus* and *P. frontalis*. The latter species are about equally divergent from one another as well as from the core group.

Key words Cytochrome *b*, Molecular clock, *Phoenicurus*, Phylogeny, Central Asia

1 Introduction

The passerine genus *Phoenicurus* consists of 10 to 11 small to medium-sized species ranging throughout Europe and Asia, with foci in the Caucasus and the Himalayas/China where up to 6 species are sympatric. The phylogenetic relationships of this highly diverse, predominantly Sino-himalayan genus have not yet been worked out. This seems to be particularly important for the systematics of the group as hybridization in *Phoenicurus* seems to be a regular event and was observed quite often in *P. phoenicurus* and *P. ochruros*.

The traditional view that hybrids are a rare and irrelevant phenomenon in nature has changed in recent decades; and it is estimated today that approximately 10% of all bird species hybridize regularly (Grant and Grant, 1992). Within *Phoenicurus*, moreover, it does not seem to be a trivially infrequent event. Similarities in natural hybrids between the Redstart (*P. phoenicurus*) and Black Redstart (*P. ochruros*) in Europe to several subspecies of the Black Redstart in the Middle East and east Asia (Kleinschmidt, 1908; Landmann, 1987) suggest that historic hybridization may be involved in the origin of those forms. These morphological similarities have been reflected in breeding experiments (Berthold et al., 1996), where hybrids and backcrosses have been studied for several years.

Additional breeding experiments (Görl, unpublished) and results from the following microsatellite-analysis further indicate that hybridization is also found occasionally between *P. hodgsoni*/*P. aureus* and *P. hodgsoni*/*P. ochruros phoenicuroides* or *P. o. rufiventris*. Because of many intermediate forms, especially in the subspecies of *P. ochruros* in Turkey, the Middle East and Asia, it is often

difficult to identify single individuals from morphology alone. The sequence data presented here now permit estimation of phylogenetic relationships among the taxa and determination of whether those that hybridize are distinct species.

2 Materials and methods

2.1 Sampling

Blood samples were collected from across Europe and on two expeditions to Asia in 1996 and 1997. Asian locations were east Turkey where populations of the Common Redstart (*P. phoenicurus*) and Black Redstart (*P. ochruros*) were the focus of sampling, and Sichuan and Gansu Provinces in China, where many other members of the genus were collected. Birds were caught with mist nets, scored for morphological characters and sampled for blood by extraction from the ulnar (wing) vein. Additionally, diverse tissue samples (feathers, skin, sole-pads, tarsus, tongue) were taken from specimens in museum collections in Berlin, Bonn, Frankfurt, Munich and Vienna.

2.2 Laboratory procedures

PCR was used on 75 blood samples to amplify the cytochrome *b* gene in mitochondrial DNA (mtDNA). Depending on the nature of the sample, total cellular mtDNA was extracted from over 500 samples with either QIAGEN-extraction-kits or with phenol/chloroform-, ethanol/isopropanol (with and without guanidine)-, or chelex- extraction-protocols. Seventy five samples were then chosen for sequencing reactions, representing all available taxa and populations. To minimize the risk of sequencing fragmented chromosomal-copies of the mitochondrial genome (Quinn,

1992; Smith et al., 1992; Kornegay et al., 1993), the whole gene was amplified first with the amplification-primers A and F (Helbig et al., 1995), yielding a PCR product of approximately 1 000 bp for the cytochrome *b* gene. After isolation and purification of the PCR-product, sequencing followed using an ABI 377 cycle-sequencer with internal primers B, D and G, which guarantee further control because of overlapping regions.

2.3 Phylogenetic analysis

To identify pseudogene PCR products, the sequences were edited and inspected for stop-codons or unusual transition/transversion ratios. Phylogenetic analysis was performed using the programs MEGA 2.0 for the neighbor-joining dendrogram (Kimura-2-Parameter and pairwise distance method; Kumar et al., 2001) and MrBayes 2.01 (Huelsenbeck et al., 2001) for the maximum likelihood tree (Monte-Carlo-Markov-Chain algorithm; MCMC). Outgroups were *Acrocephalus scirpaceus* and *Sylvia atricapilla*.

3 Results

3.1 Variability in cytochrome *b* gene sequences

280 out of 398 variable nucleotide positions were phylogenetically informative and usable for tree construction.

The analysis yielded distance values of up to 4.0% at subspecies level, with *rufiventris* in *P. ochruros* the most divergent subspecies at 2.3%–4.0%. *P. phoenicurus samamisticus* from East Turkey differed by 2.3% from European nominate *phoenicurus*; and central Asian *P. erythrogaster grandis* also differed from nominate *erythrogaster* in the Caucasus by the same value. Interspecific distance values ranged from 4.9% to 11.3%, and generally matched expectations from morphological studies. Most surprising was the unexpectedly high divergence value of 10.5% between the two populations of *P. frontalis* in Gansu (China) and Nepal.

3.2 Variability in amino acid sequences

In contrast to synonymous substitutions, the distribution of non-synonymous substitutions shows a bias, revealing highly variable areas in the transmembrane domains, the inner regions of the cytochrome *b* protein, and more conservative redox-centers of the molecule (Howell, 1989). Within the genus *Phoenicurus*, the total number of non-synonymous substitutions ranges from 0–3 at subspecies level and 0–14 at species level. *P. schisticeps* (4–11), *P. caeruleocephalus* (5–14), and the two *P. frontalis* populations (7–14) show particularly high numbers of amino-acid replacements. The distantly related outgroup taxa, *Acrocephalus scirpaceus* and *Sylvia atricapilla*, showed

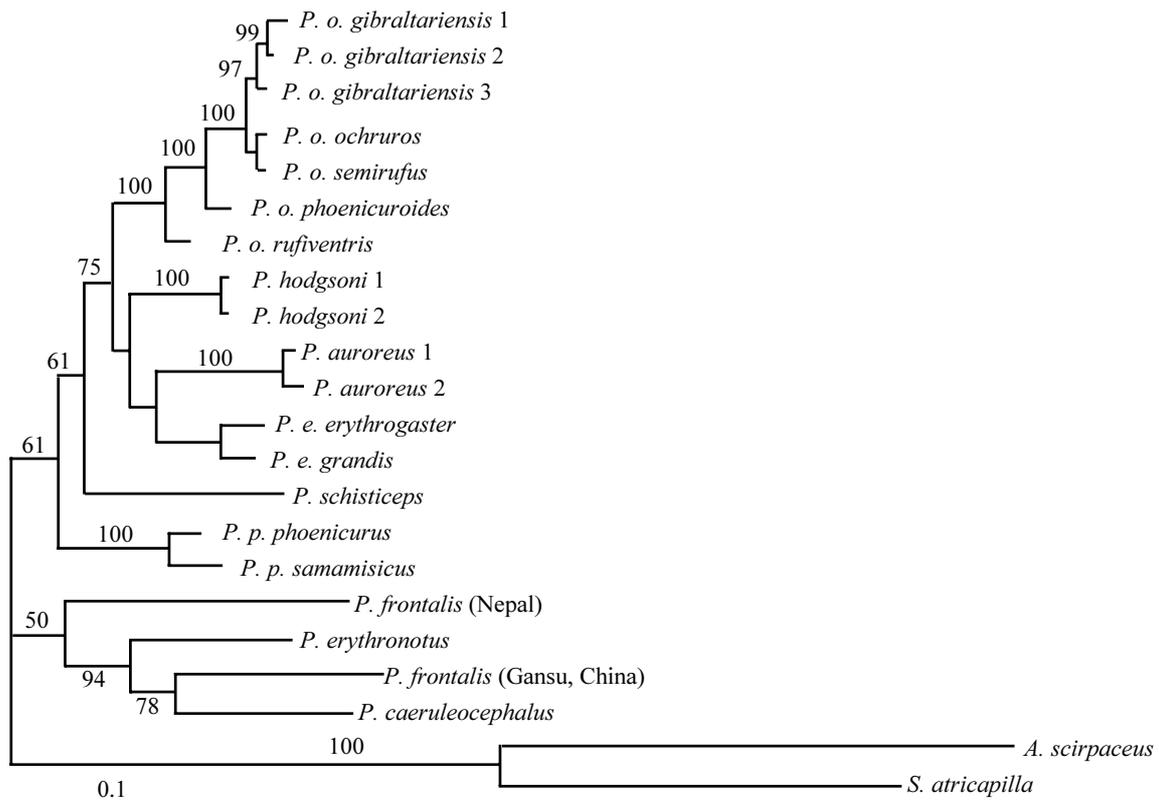


Fig. 1 Bayesian maximum likelihood tree of phylogenetic relationships of taxa in the genus *Phoenicurus* (P.), based on mtDNA sequence data from the cytochrome-*b* gene

Program MrBayes 2.01 here uses the Monte-Carlo-Markov-Chain algorithm (MCMC) to calculate the statistical support (indicated in numerals against branches). o = *P. ochruros*, e = *P. erythrogaster*, p = *P. phoenicurus*. For identity of outgroups *A. scirpaceus* and *S. atricapilla*, see text.

the highest number of substitutions (24–37), as expected.

4 Discussion

The topology of the resulting Bayesian maximum likelihood tree and neighbor-joining dendrogram (Figs. 1, 2) are nearly identical, with most branches supported by high statistical values. In the dendrogram, branches with bootstrap values under 60 were collapsed, which resulted in improved concordance with the Bayesian tree. Each species represented by 2 or more unique sequences was resolved as a monophyletic group, except *P. frontalis*. The cytochrome-*b* sequences also confirmed that the hybridizing taxa (Ertan, 2000) are distinct species. *P. ochruros*, *P. phoenicurus*, *P. hodgsoni*, *P. aureus*, *P. erythrogaster* and *P. schisticeps* form a core group in the genus, with uncorrected distance values of 4.9% to 7.9%. *P. caeruleocephalus*, *P. erythronotus* and the two populations of *P. frontalis* are about equally divergent from both one another and the core group (7.3%–11.1%). This result is concordant with morphological studies, which also separate these three (four) species from the rest of the genus (Alí and Ripley, 1987; Glutz von Blotzheim and Bauer, 1988). The significance of the unexpectedly high divergence (10.5%) between the two populations of *P. frontalis* from Gansu and Nepal, which are not monophyletic on either the Bayesian tree or neighbor-joining dendrogram, still needs elucidation.

Early research on a number of mammalian lineages revealed corrected mitochondrial third-position divergence rates of approximately 10% per million years (Irwin et al., 1991; Thomas and Martin, 1993). Other studies, however, have shown lower rates, as in whales (Martin and Palumbi, 1993), consistent with considerable evidence suggesting that molecular evolutionary rates vary among taxonomic lineages (Britten, 1986; Li et al., 1987) and are much lower in birds (Martin and Palumbi, 1993). Therefore it is not surprising that studies calibrating molecular clocks for mitochondrial DNA have resulted in different evolutionary rates (of 0.4%–2%, uncorrected and 1.6%–2.9%, corrected per million years) for several bird orders (Arnaiz-Villena et al., 1999; Helm-Bychowski and Wilson, 1986; Klicka and Zink, 1997; Krajewski and King, 1996; Nunn et al., 1996; Tarr and Fleischer, 1993). Most convincing and applicable here are those studies that calibrated long fragments of the cytochrome-*b* gene against the fossil record. These record average evolutionary rates of 0.4% to 1.7% per million years for the Galliformes (chicken and pheasants), Gruiformes (cranes) and Procellariiformes (albatrosses and petrels).

According to such rates, the genus *Phoenicurus* would have diverged from other turdine stock 6–25 million years ago (MYA). Because most redstarts are centered in the high mountain regions of central Asia, it is more likely that their radiation occurred more recently, driven by isola-

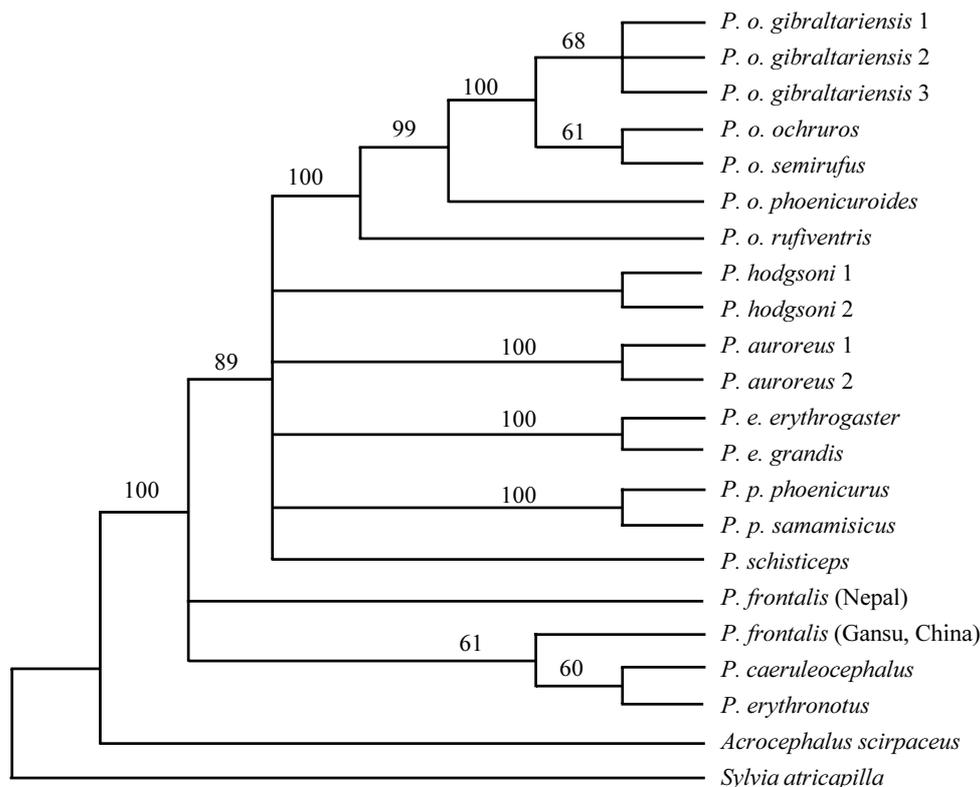


Fig. 2 Neighbour-joining dendrogram of taxa in the genus *Phoenicurus* (*P.*), based on mtDNA sequence data of the cytochrome-*b* gene

Tree generated with MEGA 2.0 (Kimura-2-parameter and pairwise distance method). Branches with bootstrap values lower than 60 are collapsed.

tion resulting from the rapid Himalayan orogenesis around 5 MYA. Calibrating their highest mtDNA distance values with this geological event would result in average evolutionary rates of approximately 2% per million years, a value was also recorded in passerines using restriction enzymes (Tarr and Fleischer, 1993). This would shift the second wave of radiation within the genus, that of the core group, into a time frame of 3.05 ± 0.35 MYA.

Judged from mtDNA distance values, proto western subspecies of the Black Redstart (proto *semirufus*, *ochruros*, *gibraltariensis* and *aterrimus*) were separated from central Asian stock (proto *phoenicuroides* and *rufiventris*) 1.5 ± 0.25 MYA, and began to expand westwards in distribution. In the course of this expansion, subsequent populations were cut off in the Middle East (proto *semirufus*) and East Turkey (proto *ochruros* and *semirufus*) around 1.15 ± 0.58 and 0.53 ± 0.16 MYA respectively, until finally central Europe was reached (Ertan, 2002). The central European population (*gibraltariensis*) and morphologically quite different Iberian population (*aterrimus*) probably diverged from one another when separated during the last ice age. The central European stock probably withdrew to ice-free parts of south and southeast Europe then, until the onset of warmer post-glacial periods allowed expansion once more. Reports of historical shifts in the European avifauna support this reconstruction. Indeed, general northwards expansion is still in progress, the Black Redstart itself gradually occupying northwest Europe as a breeding bird over the last 180 years (Glutz von Blotzheim and Bauer, 1988).

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Symposium 18 Sexual signaling and speciation

Introduction

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Connections between sexual selection and speciation were first discussed by Darwin (1872) and Gulick (1890). More recent contributions come from the theory of Lande (1981) and the review by West-Eberhard (1983) who noted two features of sexual selection that are the subject of this symposium. First, sexually selected traits may diverge rapidly, and secondly, recognition of such traits may diverge at the same time. Thus different populations may diverge so far that members of each fail to recognize suitable mates in the other; the populations are then essentially good species. Whether complete speciation occurs in this way is a major issue in evolutionary biology. It is being addressed through a diversity of approaches, as summarized in the four contributions to this symposium. The fifth paper, an oral from Ben Sheldon concerning the role of sexual selection in hybridizing of *Ficedula* flycatchers, is published in abstract form in the Abstract Volume for the Congress.

The great infusion of molecular data has enabled us to assess just how rapidly sexually selected traits may evolve; and the answer is sometimes quickly, at least on evolutionary timescales. This is exemplified by the work of Omland and Kondo on species of orioles. Two species are extremely similar in their DNA sequences but differ strikingly in plumage patterns. One problem with the scenario of rapid evolution is that if traits are closely linked genetically, then evolution of one trait may lead to deleterious changes in others. Badyaev and Snell-Rood suggest ways by which

rapidly evolving traits may sometimes become less integrated (i.e., share lower correlations with other traits).

A second question concerns how and whether pre-mating isolation evolves along with the trait. In birds, sexual imprinting provides the crucial means by which individuals recognize conspecifics as mates. This learning process seems to create a conflict between directional (sexual) selection and selection against novelty. We are beginning to understand how this conflict is resolved; ten Cate discusses the ideas. Because it appears that pre-mating isolation is often incomplete, other sources of reproductive isolation are likely to contribute to species barriers. Selection against hybrids may lead to increased levels of pre-mating isolation (reinforcement). Price addresses the relatively unexplored question of the extent to which sexual selection against hybrids imposes both post- and pre-mating isolation. It appears likely that post-mating isolation is important in bird speciation, and that sexual selection plays a major role.

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S18-1 Rapid evolutionary divergence of environment-dependent sexual traits in speciation: a paradox?

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Abstract Expression of sexual displays is often closely linked to individual performance in a particular environment, i.e., male condition. Female preference for environment- and condition- dependent sexual displays in males evolves because of benefits of male condition to female fitness. Variation in these benefits can lead to divergence in female preferences that eventuate in speciation. To indicate condition reliably, sexual displays should have a significant environmental component in their development. Furthermore, mate preference favors a greater dependence on organismal functions in the development of ornaments (i.e., greater condition-dependence). Both environment- and condition-dependence might constrain evolutionary elaboration of the sexual trait as well as its effectiveness in achieving post-mating genetic isolation among divergent populations. Here we discuss an apparent paradox between the prevalent role of environment- and condition- dependent sexual displays in producing population divergence, and their expected slow rate of evolution.

Key words Integration, Modularity, Ontogeny, Sexual ornaments, Speciation

1 Introduction

Sexual ornaments and displays play an important role in establishing and maintaining reproductive isolation between divergent populations (Mayr, 1939; Dobzhansky, 1940; Schluter, 2000). There are several reasons for this. First, sexual traits are often highly sensitive to local environment and thus can reflect an organism's performance and local adaptation in a particular environment (reviewed in Andersson, 1994). For example, the expression of diet-dependent carotenoid ornamentation in male birds can express ability in finding sources of dietary carotenoids and so enable evolution of female preference that is locally adaptive (Endler, 1983). Secondly, selection for higher detectability in a particular environment favors greater dependency of sexual trait expression on environmental variation (Endler, 1992; Schluter and Price, 1993). For example, components of bird song differ in susceptibility to habitat structure, and female preference for the most detectable song features will enable locally adaptive female choice (reviewed in Slabbekoorn and Smith, 2002). Thirdly, sexual ornaments and displays can facilitate mate recognition and prevent interbreeding by imprinting or cultural inheritance of the local expression of sexual ornaments (Grant and Grant, 1996a; Irwin and Price, 1999). Ultimately, population divergence in the coevolution of trait expression and female preference will lead pre-mating isolation to eventuate in the genetic isolation of divergent populations (Grant and Grant, 1996b, 1997a).

Implicit in these explanations is the assumption of rapid evolutionary change, especially compared to non-

sexual traits. Moreover, rapid gain and loss of sexual ornaments is especially important for reproductive isolation when there is a spatial or temporal lag between female preference and ornament expression (Payne and Krakauer, 1997; Price, 1998; Brooks and Coullidge, 1999; Day, 2001), as is often the case with environment- and condition- dependent ornaments (Hill, 1994; Irwin and Price, 1999). The prediction of rapid evolution in sexual displays is well supported — it is commonly observed that sexual traits have high evolutionary lability, and closely related species differ more in sexual ornaments than nonsexual traits (e.g., Civetta and Singh, 1998). However, the mechanisms underlying rapid evolutionary change of sexual ornaments are not well understood.

Moreover, what is known about sexual ornaments is that their evolution — especially in those determined environmentally — is likely to be slow (Badyaev, 2003). First, the expression of sexual traits, such as elongated tail feathers or carotenoid-based pigmentation, is a complex summary of many organismal processes (Andersson, 1994). Because of this, sexual traits are probably involved in many organismal functions (Wedekind, 1992, 1994), and such involvement should constrain evolutionary change (Cheverud, 1996). Secondly, to indicate individual performance reliably in a local environment, the expression of sexual ornaments must incorporate a substantial amount of environmental variation during development (Andersson, 1994). If environmentally-dependent sexual traits are likely to respond rapidly to environmental change, they are less likely to facilitate genetic isolation between divergent

populations, especially in the absence of post-mating reproductive barriers. Thirdly, the expression of sexual displays and the preference for them are often specific to the social and ecological environment of breeding (Tregenza and Wedell, 2000; Qvarnström, 2001; Badyaev and Qvarnström, 2002). Although context-dependency in ornament expression or sexual imprinting on the phenotype of relatives or locally born individuals may enable locally adaptive female choice, it might also prevent the directional change in both trait expression and trait preference necessary for speciation.

Here we discuss the apparent paradox between the expectations of low evolutionary lability of environment-dependent sexual ornaments and their widespread role in speciation, and offer possible explanations.

2 Speciation by sexual selection: models and evidence

Correlated evolution of ornament expression and mate preference can strongly facilitate speciation (Lande, 1982). In allopatry, different environments or gene pool compositions can lead to elaboration of different sexual ornaments and thus population divergence (Lande, 1980; West-Eberhard, 1983; Lande and Arnold, 1985; Price, 1998). Unstable equilibria in ornament expression and preference is expected to result in repeated cycles of ornament elaboration and exaggeration of different sexual traits (Pomiankowski and Iwasa, 1998; Iwasa and Pomiankowski, 1999). Sympatric speciation by sexual selection may occur through similar mechanisms (Wu, 1985; Payne and Krakauer, 1997; Day, 2000) or the splitting of an existing trait or preference into two extremes (Turner and Burrows, 1995; Higashi et al., 1999; Takimoto et al., 2000); but see Turelli et al. (2001) for a discussion of assumptions.

Three lines of evidence suggest that sexual selection strongly facilitates speciation (Price, 1998). First, in many avian taxa, intensity of sexual selection, often measured as the degree of sexual dimorphism, is correlated with species diversity (Barraclough et al., 1995; Mitra et al., 1996; Prum, 1997; Moller and Cuervo, 1998; Owens et al., 1999). Secondly, sexually-selected traits within species are often those used in species recognition, suggesting that a mate-recognition system evolved as a by-product of divergent sexual selection (Wiernasz and Kingsolver, 1992; Ryan and Rand, 1993; Gray and Cade, 2000; McKinnon and Rundle, 2002). Moreover, in taxa where speciation is incomplete, an evolutionary lag between the extent of trait expression and preference for it often leads to preference for traits of heterospecific males, resulting in hybridization (e.g., Collins and Luddem, 2002; Price, 2002). Thirdly, speciation can occur rapidly through divergence in sexually-selected traits prior to divergence in ecology or onset of genetic incompatibility (Deutsch, 1997; Masta and Maddison, 2002; Price, 2002). Thus, sexual selection can facilitate pre-zygotic isolation through genetic change in ornament expression and female preference (Hollocher et al., 1997; Ting et al., 2001).

3 Mechanisms of sexual selection and the development of sexual traits

That sexual displays differ in genetic and environmental determination has important consequences for both the mechanism of mate choice and the effectiveness of speciation by sexual selection. Theory suggests that sexual displays which reflect indirect benefits should have a high genetic component, whereas those that reflect direct phenotypic benefits should have a high environmental component (Andersson, 1994), and, potentially, higher genetic integration with many of the organismal functions that produce them. Because speciation is more effective when it involves sexual traits with a greater genetic component, the rate of genetic divergence should depend on the mechanism of sexual selection.

4 The paradox: environment- and condition- dependent sexual traits play an important role in speciation

Sexual selection may facilitate speciation in birds (Barraclough et al., 1995; Mitra et al., 1996; Grant and Grant, 1997b; Moller and Cuervo, 1998; Badyaev and Hill, 1999; Uy and Borgia, 2000). Given that sexual ornaments with a considerable genetic component are expected to diverge more rapidly and thus facilitate speciation, their displays should be the most common. Yet, empirical studies suggest that most sexual displays are condition- or environment-dependent (Veiga and Puetra, 1996; Badyaev and Hill, 1999; Qvarnström, 1999; Hill, 2000; Kotiaho et al., 2001). Furthermore, phenotypic effects of male condition that affect female survival and fecundity directly generate much stronger selection in female preference than do indirect effects (Kirkpatrick, 1985; Kirkpatrick and Barton, 1997; Møller and Jennions 2001), and thus should be more effective in speciation. How do can the importance of sexual traits of greater genetic component be reconciled with the apparent prevalence of condition- and environment-dependent sexual displays in the speciation process?

5 Resolution of the paradox

5.1 Environmental component of condition is genetically determined

Whereas the development of a sexual trait that indicates direct benefits may be determined largely by the environment, an individual's ability to acquire resources (e.g., behavior) can have a genotypic basis (Moore et al., 1997; Wolf et al., 1997, 1998). For example, ability to take and hold high quality territory or food may be determined genetically by aggression. Although the probability of inheriting a complete developmental program for expressing these complex behavioral traits may be low, its inheritance and modification might strongly facilitate genetic isolation (Badyaev, 2003).

5.2 Allocation of resources between an organism and

sexual ornaments has a significant genetic component

Individual differences in acquisition and allocation of resources between nonsexual traits and a sexual display may have a genetic basis (Brooks, 2000; David et al., 2000; Kotiaho et al., 2001), and be subject to mate choice. Thus, whereas the proximate target of sexual selection might be the elaboration of sexual ornaments, the ultimate target is the underlying relationship between the expression of the ornament and condition of the organism, i.e., the developmental program of the ornament.

5.3 Allocation of resources among components of sexual ornaments has a significant genetic component

Mate preference for different condition-dependent benefits of ornament expression may favor the evolution of composite sexual ornaments, the components of which are linked to different organismal processes and thus reliably reflect condition across a wide range of environments (Badyaev, 2003). Although selection by female choice is expected to be stronger for components of sexual ornamentation that are more relevant locally, developmental cohesiveness and functional integration may still be needed to maintain stability in ornaments that are composite (Wedekind, 1994; Johnstone, 1995; reviewed in Badyaev, 2003).

For example, carotenoid-based ornamentation in house finches (*Carpodacus mexicanus*) requires a coordination of multiple processes associated with the consumption, digestion, transportation, and deposition of carotenoids (Badyaev et al., 2001). However, despite population variation in environment- and condition- dependence in each of these processes, and corresponding variation in female choice of different components in different environments, production of carotenoid-based sexual ornaments requires some degree of integration along these pathways, so maintaining developmental interdependency among ornament components (Badyaev et al., 2001). Mate preference for a particular component of a composite sexual ornament will result in acquisition of a complex developmental program that produces expression of this component in relation to the other parts, ultimately leading to genetic isolation (also Wu, 2002).

5.4 Greater environment- and condition- dependence in ornaments evolves after divergence

Over time, sexual display may be influenced by different mechanisms capitalizing on different aspects of the developmental program of the ornaments involved (Price et al., 1993; Kokko et al., 2002; Badyaev, 2003). Sexual ornaments may thus have different environmental and genetic determinants at different stages of population divergence. Divergent sexual selection on a sexual ornament of initially high genetic determination could, for example, facilitate speciation. As elaboration of the ornament progresses, the cost of ornament development and maintenance increases (Price et al., 1993), leading to an increase in condition-dependence (Nur and Hasson, 1984; Grafen, 1990).

Accordingly, speciation by sexual selection could follow divergence in sexual ornaments with a high genetic component, bearing in mind that these ornaments, in the course of their elaboration, may subsequently develop greater condition- and environment- dependence.

The paradox between the role of sexual traits in speciation and prevalence of condition- and environment-dependent ornaments turns on several crucial assumptions. First, it is assumed that the developmental program of sexual ornaments, in particular its genotypic and phenotypic components, remains constant over evolutionary time. This assumption is untested for sexual ornaments, but recent studies suggest that the lack of evolution in sexual ornaments under progressively stronger directional selection may be explained by an increasing environmental component in their developmental program (e.g., Merilä et al., 2001; Kruuk et al., 2002).

Secondly, it is not known whether an increase in the environmental component in the development of most sexual traits is associated with a reduction in their genetic component (Merila and Sheldon, 2001). Theoretical and empirical studies suggest that condition-dependent traits may have a significant genetic component (van Tienderen and de Jong, 1994; Rowe and Houle, 1996; Glazier, 2002), consistent with the results of recent empirical studies (David et al., 2000; Kotiaho et al., 2001). Investigating the assumptions underlying the paradox between prevailing condition-dependent sexual traits and their slow rate of evolution could provide crucial insights into speciation by sexual selection.

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S18-2 Phylogenetic studies of plumage evolution and speciation in New World orioles (*Icterus*)

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Abstract Detailed molecular phylogenies of closely related species provide an unprecedented opportunity to study the relationship between plumage evolution and speciation. Through reconstruction of ancestral character states, phylogenies enable us to separate convergence from similarity due to shared ancestry, and gains of plumage ornaments from losses. Molecular phylogenies also provide information for inferring the details of speciation: which species split, when the splits occurred, and even whether one species is nested genetically within another. We have used these approaches in a series of studies on plumage evolution and speciation in New World orioles (*Icterus*). A genus-wide study of 44 individual plumage ornaments revealed evidence of repeated convergence and reversal. Two overall plumage types, moreover, have evolved independently in the three clades of orioles. We then conducted a detailed study focused on the “northern oriole” group. Multiple samples from throughout the ranges of the Baltimore oriole (*Icterus galbula*; eastern North America) and the black-backed oriole (*Icterus abeillei*; central Mexico) confirm that these two species are each other’s closest relatives, and that they probably split very recently. They differ from each other in many plumage traits, providing a dramatic example of rapid divergence in signal characters. In orioles, it seems likely that much of this plumage divergence occurred in allopatry. Nevertheless, lineages that have evolved plumage differences in allopatry may be less likely to remerge upon secondary contact. Such a process could account for published correlations between signal divergence and species richness.

Key words Ancestral state reconstruction, *Icterus*, Phylogeny, Plumage evolution, Speciation

1 Introduction

In recent years, molecular phylogenies based on mitochondrial DNA sequences have provided an unprecedented source of information for studying plumage evolution and speciation. Prior to this technology, phylogenies for closely related bird species were often not even attempted. For example, before our studies of the New World orioles, only one study examined the entire genus of 25+ species, and then without attempting a comprehensive phylogeny (Beecher, 1950). Although closely related species of birds often have well-marked morphological differences, these differences may involve only one or two plumage characters. Thus there are generally too few informative characters to allow construction of well-resolved phylogenies for close relatives (Omland and Lanyon, 2000). Similarly, earlier molecular methods such as DNA-DNA hybridization, allozyme electrophoresis, and nuclear coding sequences are generally not sensitive enough to position closely related species. Early phylogenies based on mitochondrial DNA restriction sites and sequences (e.g., Kessler and Avise, 1984; Zink and Avise, 1990) opened up new possibilities for studying species limits, speciation, and rapidly evolving characters such as plumage and song.

Mitochondrial DNA (mtDNA) sequences continue to provide the best estimates of phylogenies for closely re-

lated species because nuclear DNA sequences have several serious limitations. First, nuclear autosomal DNA has a larger effective population size than mtDNA, and is therefore more likely to share ancestral polymorphisms between species (Palumbi et al., 2001). Secondly, nuclear DNA does not accumulate mutations as rapidly as mtDNA, and is harder to work with than mtDNA, both in the laboratory and in the analysis stage (Avise, 2000).

Having well-resolved species-level phylogenies from mtDNA studies provides two main advantages for our understanding of plumage evolution and speciation. First, we can use phylogenies to reconstruct ancestral character states. By scoring the characteristics of present day species, we can infer the likely evolutionary changes that have taken place in the past through the principle of parsimony or maximum likelihood (e.g., Cunningham et al., 1998). For example, Fig. 1 shows a hypothetical phylogeny of two sister clades of four species each. The presence or absence of an elaborate plumage ornament is reconstructed on the phylogeny using simple parsimony (see Omland, 1997).

This reconstruction enables us to infer two key aspects of signal evolution. First of all, it provides evidence of convergent evolution of the ornament: it evolved once in species B in the left clade, and it also evolved early in the history of the right clade. Secondly, the phylogeny enables us to distinguish gains from losses. For example, if A and B

are sister species, either species A lost the ornament or species B gained it. Knowing that species C and D are unornamented sister lineages enables us to infer that there was a recent gain in species B. Similarly, parsimony reconstructs a recent loss of the feather ornament in species Y, which is nested within a group of three species that all have it.

This example highlights another advantage of phylogenetic information: phylogenies can be used to pinpoint the best species for behavioral studies. For example, species B is much better than species W, X or Z in the right clade for investigating why species gain ornamentation. The right clade may well have evolved elaborate ornamentation in the common ancestor of that clade but a long time ago. A behavioral ecologist with no knowledge of the phylogeny would have a 75% chance of noticing and studying the ornament in species W, X or Z, holding him/her back from inferring the selective forces that led to its origin. Much, moreover, can be learned by studying species Y, which has recently lost the ornament. Admittedly, many explicit and implicit assumptions need to be acknowledged in such ancestral state reconstructions (Omland, 1997; Cunningham et al., 1998; Omland, 1999); yet when applied across many characters (Omland and Lanyon, 2000) or across multiple groups, ancestral reconstructions can provide a sound basis for evolutionary inference.

The other advantage of molecular phylogenies in studies of speciation and signal evolution is their provision of sound data on speciation itself. A phylogeny can tell us which taxa have speciated most recently. For example, without a phylogeny, we might assume that two parapatric taxa are each other's closest relatives, and make assumptions about how the two taxa split. This problem surfaced in the "northern oriole" group (Omland et al., 1999), as detailed below. Genetic distances among taxa can also be used to infer when two species split. Using molecular clocks to date evolutionary events may be controversial, and indeed many assumptions go into such calculations which gives rise to

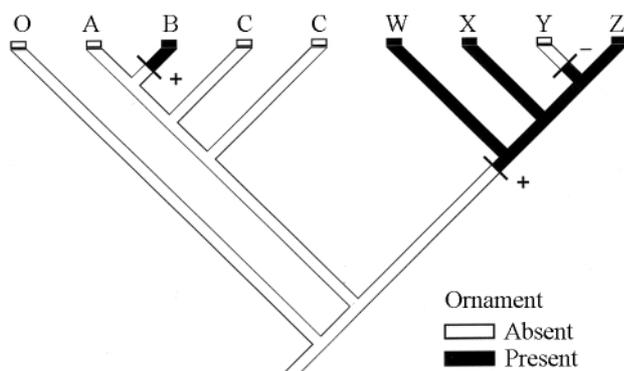


Fig. 1 Model phylogeny of nine species showing the most parsimonious reconstruction of changes in a hypothetical plumage ornament (e.g., colored wing patch or head crest) The ancestral state reconstruction suggests two convergent gains of the elaborate ornament, and one subsequent loss.

skepticism (Hillis et al., 1996; Fleischer et al., 1998). Even so, much can be learned about speciation by comparing relative levels of divergence. A well-known example of how molecular clocks have been applied to studies of bird speciation is the work of Klicka and Zink (1997), who showed that levels of divergence between putative sister species in the eastern and western US were much deeper than would be expected if speciation was caused by the most recent cycles of late-Pleistocene glaciation (cf. Avise and Walker, 1998; Arbogast and Slowinski, 1998).

Molecular data can also provide evidence of the genetic nesting of one species within another (e.g., paraphyletic species). Such findings provide a unique opportunity to study speciation and character evolution, especially because it enables reconstruction of character changes and the timing of speciation with more precision than allowed by other means. In birds, there are several cases of likely paraphyly resulting from recent speciation, involving, among others, mallards (*Anas platyrhynchos*) and the American black ducks (*Anas rubripes*) (Avise et al., 1990; Omland, 1997), though this example could also reflect hybridization (Broadsky et al., 1988).

Phylogenies are, in addition, particularly useful in research that employs the comparative method (sensu Harvey and Pagel, 1991). This paper will not present results based on the comparative method, but the discussion will address several studies that have used it to evaluate correlations between rates of speciation and plumage coloration. Rather, we simply review results of our research into speciation and plumage evolution in *Icterus*.

2 Oriole plumage reconstruction and speciation

2.1 Phylogenetic reconstruction of plumage patterns

Sexually selected characters such as plumage coloration have long been assumed to evolve rapidly and be subject to high levels of convergence (Omland and Lanyon, 2000). However, no empirical studies of all plumage traits had been conducted using a well-resolved independent phylogeny. mtDNA sequences were obtained for 45 taxa of New World orioles: all 25 recognized species and 20 additional subspecies from the genus *Icterus* (Omland et al., 1999). We obtained over 2000 base pairs of sequence from the cytochrome *b* and ND2 genes. All methods of analysis and data combinations identified three main clades, designated A, B and C (Fig. 2). Over half of the nodes on the tree received 95% bootstrap support or more. This well-resolved tree provided the phylogenetic framework for reconstructing plumage evolution (sensu Lanyon, 1993). We studied two aspects of male plumage coloration: 1) individual feather areas, and 2) overall plumage patterns.

Using museum skins, we scored all the individual feather areas that varied among oriole species (Omland and Lanyon, 2000). We found 44 plumage areas that varied, and scored whether these areas were white, black or pigmented

with carotenoid (yellow, orange, chestnut, etc). The 44 plumage patches were then mapped on to the molecular phylogeny to reconstruct ancestral plumage changes. Forty two of the 44 plumage characters showed at least some convergence or reversal (homoplasy) (Omland and Lanyon, 2000); the two characters that did not show any homoplasy involved character states that simply united different subspecies of the same species. Most plumage characters appeared independently many times on the phylogenetic reconstruction (i.e., high levels of homoplasy). For example, Fig. 2 incorporates reconstruction of crown coloration, suggesting independent gains of colored crown feathers (e.g., orange or yellow) at least six times, and at least one subsequent reversal to black. Other less parsimonious reconstructions are possible, but clearly individual feather areas in orioles are evolving rapidly, and with high levels of convergence and reversal.

Reconstruction of overall patterns also revealed much evidence of convergence and reversal (Omland and Lanyon, 2000). We identified two main plumage types that had evolved multiple times within the genus *Icterus*. Species with the “Baltimore” plumage type have completely black heads, and consistent white edging in the secondary coverts and flight feathers. Species with the “Altamira” plum-

age type have colored heads and crowns, but black foreheads and necks, and a distinct white spot on the outer primaries. These two plumage types represent extremes in a continuum of plumage convergence values (Omland and Lanyon, 2000: Fig. 8), involving species that show greater than 8% sequence divergence and range from only 3 to as many as 37 differences in plumage. Three species that show the “Baltimore” type are found in different parts of two clades: Baltimore oriole (*I. galbula*) and Scott’s oriole (*I. parisorum*) in clade C, and orchard oriole (*I. spurius*) in clade A. Species with the “Altamira” type are found in all three clades: clade A, hooded oriole (*I. cucullatus*), clade B, spot-breasted oriole (*I. pectoralis*), and clade C, Altamira oriole (*I. gularis*) (Fig. 2).

The occurrence of both plumage types throughout the oriole tree strongly suggests convergence, but this pattern could also occur if the mtDNA phylogeny is misleading. Sequences from a nuclear intron (ODC; Friesen et al., 1999) from 10 oriole species confirm the basic structure of the mitochondrial tree, and reveal the same three main clades (E. S. Allen and K. E. Omland, unpublished data). They also verify that species within each of the two plumage types are not each others’ closest relatives, thus providing strong support for convergence and reversal in producing the two

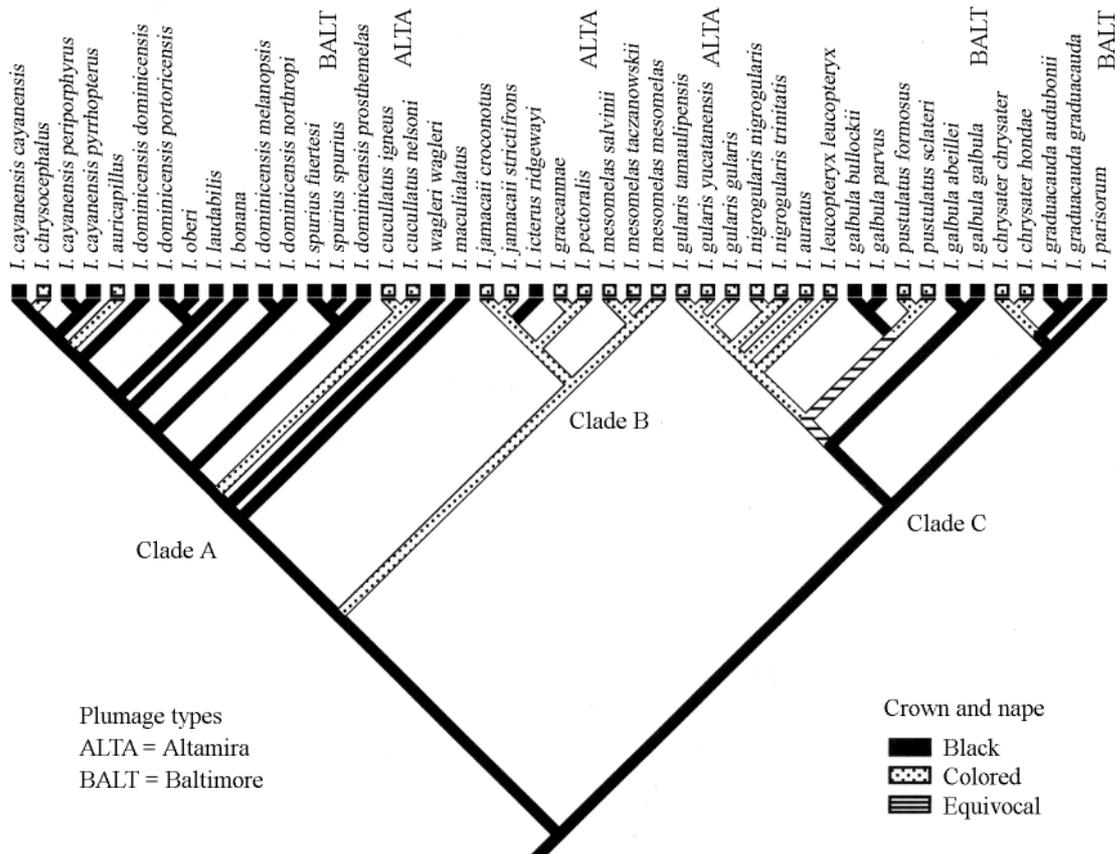


Fig. 2 Ancestral state reconstruction of crown and nape pigmentation on to the oriole mtDNA phylogeny (from Omland et al., 1999: Fig. 6)

“Colored” refers to orange or yellow coloration likely to come from carotenoid pigments. Species that exemplify the two overall plumage types are indicated above the taxon names.

main plumage types.

Our phylogenetic studies of both individual areas and overall patterns of plumage provide a much clearer picture of plumage evolution. Plumage characters are indeed changing very rapidly, probably due to sexual selection. However, the repeated convergence, reversal, and high levels of homoplasy that we found are generally not predicted by models of sexual selection (Andersson, 1994; cf. Ryan et al., 1990). Similarly, convergence would not be predicted if plumage divergence was strongly correlated with speciation. If plumage plays a major role in species recognition, then there is no reason why unrelated species of *Icterus* should be expected to evolve similar plumage areas or overall patterns. Rather, it seems much more likely that genetic or developmental processes have constrained the numbers of colors and patterns in New World orioles (Omland and Lanyon, 2000). Individual plumage patches may be changing rapidly but only according to a restricted set of character states. Convergence in overall pattern, moreover, may result from a few genes turning modular plumage elements on and off.

Price and Pavelka (1996) studied plumage patterns in Old World warblers, and also suggested the importance of developmental constraints. Such constraints may operate within many other genera that seem to have an overall plumage template with variations on that theme (e.g., Old World orioles, cardueline finches, Australasian sericornithine warblers). In contrast, other groups of birds seem much more free to vary (e.g., *Anas* ducks, birds of paradise), with nearly every species evolving novel patterns and autapomorphic ornaments. Eventually we will need genomics and other approaches to understand the genetic and developmental control of plumage coloration in birds (e.g., Theron et al., 2001). As a first step, we are using spectrophotometry and other methods to reconstruct changes in pigment types and better understand the mechanistic basis of plumage color and pattern in orioles. Some oriole species, for example, have colored patches that may not be carotenoid (C. Hofmann and K. E. Omland, unpublished data).

2.2 Speciation in the northern oriole group

The “northern oriole” group has served as the focus for more detailed studies of speciation and plumage evolution. Three taxa with distinct plumage patterns had previously been combined in one species, “northern oriole”, because of hybridization (reviewed in Rising and Flood, 1998). The eastern Baltimore oriole (*I. galbula*) has an extensive hybrid zone with the western Bullock’s oriole (*I. bullockii*) in the midwestern US. The black-backed oriole (*I. abeillei*) from Mexico was also lumped into this group because it also hybridized with Bullock’s in northern Mexico. No previous studies had suggested, however, that other Mexican species such as the streak-backed oriole (*I. pustulatus*) might be included in this species group as well.

Our mtDNA phylogeny of the whole genus revealed some surprising relationships among these species (Fig. 2). Bullock’s oriole is not at all close to the Baltimore oriole —

the two are over 4% divergent in mtDNA coding sequence. The only monophyletic group that unites these two species also includes six other species from Mexico, South America and the Caribbean (Omland et al., 1999). The most surprising outcome was the sister relationship between black-backed oriole and Baltimore orioles. The two individuals sequenced were extremely closely related — approximately 0.5% for the combined cytochrome *b* and ND2 sequence.

Because Baltimore and black-backed orioles are so closely related, they provide an unusual opportunity to investigate when, where and how speciation may have occurred. We obtained samples of both taxa from throughout their respective breeding ranges in North America and Mexico, and sequenced cytochrome *b* and the control region. This extensive sampling revealed extremely small levels of divergence between the two taxa: there is only a single base pair substitution in cytochrome *b* (from over 900 bp sequenced) that separates the most closely related individuals of the two species (B. Kondo and K. E. Omland, unpublished). These two species provide the most dramatic example of rapid plumage divergence in *Icterus*. Baltimore and black-backed males differ in 17 individual plumage areas, and have quite different overall patterns (Omland and Lanyon, 2000), yet are about as closely related as any two oriole species can be.

2.3 Reconstructing dichromatism and delayed plumage maturation in *Icterus*

We are also using the phylogeny to reconstruct the history of sexual dichromatism and delayed plumage maturation in the genus. Rigorous scoring of female and immature plumages requires more subtle methods, including spectrophotometry. Some general trends are already emerging. Most tropical oriole species are sexually monochromatic, both males and females having contrasting and elaborate black, white and carotenoid colored patterns. It seems likely that many lineages have colonized temperate habitats through long-distance migration, and that these species have lost bright female coloration independently (K. E. Omland, unpublished data). It also seems likely that delayed plumage maturation is ancestral for the genus *Icterus*, and that a few lineages may have lost it. Studying the loss of delayed plumage maturation in these species may provide unique insights into the evolution of this paradoxical life history characteristic.

3 Discussion

New World orioles have proven to be an excellent model group for phylogenetic studies of plumage evolution and speciation. Our mtDNA phylogeny has provided a firm framework for these studies, showing that individual feather areas and overall plumage patterns are evolving rapidly and convergently. Mitochondrial data are also informing us about speciation in *Icterus*, especially in the “northern oriole” group. Baltimore and black-backed orioles have speciated very recently, and provide a well-documented

example of just how rapidly bird plumage coloration can evolve. But what role has speciation played in plumage divergence; and conversely, how has plumage divergence helped drive speciation?

During the early years of the biological species concept, many papers addressed the possible role of bird plumage coloration in species recognition (e.g., Sibley, 1957; Mayr, 1963). However, during the 1980s and 1990s this issue was largely neglected, as studies focused on the role of elaborate plumage in intra-specific mate choice (reviewed in Andersson, 1994). More recently several comparative studies have documented a correlation between various indices of plumage coloration and species richness (Barraclough et al., 1995; Owens et al., 1999; Panhuis et al., 2001). Many of these studies used dichromatism as an index of plumage coloration (e.g., Barraclough et al., 1995; Owens et al., 1999).

Yet such an index needs to be used with caution. Dichromatism may work well in groups in which many species are cryptic and monomorphic, and the most elaborately ornamented species strongly dichromatic, such as the species of *Anas* (Omland, 1997). In others, however, it may work poorly, particularly those such as the New World orioles with bright monomorphic species (e.g., Trail, 1990). Many oriole species with dramatically contrasting plumage colors are sexually monochromatic, such as the Altamira oriole (*I. gularis*). As a result, orioles would probably have a fairly low index score despite the fact that they are the most speciose genus in the Icteridae. Therefore, there is a conservative bias in the methodology of the index, which would not account for the significant correlations sometimes documented.

Early studies that pointed out a correspondence between plumage ornamentation and species richness often suggested that this relationship was driven by the need for species recognition, and invoked reproductive character displacement (e.g., Sibley, 1957). Slight differences that had arisen in allopatry would be exaggerated through reinforcement of isolating mechanisms in sympatry, thus contributing to the tremendous plumage diversity, for example, in prairie regions where many *Anas* duck species breed sympatrically (Sibley, 1957; Mayr, 1963). Under this scenario, reinforcement drives the evolution of plumage diversity. However, cases of reproductive character displacement in birds are not well established (cf. Saetre et al., 1997).

Rather than character displacement, it seems likely that plumage differences could evolve entirely by sexual selection in allopatric populations. The extent of these differences could then play a prominent role in determining whether such forms would remerge or not upon secondary contact. Here plumage diversity helps drive speciation, rather than the reverse. New World orioles provide several case studies for considering the options involved. As discussed above, Baltimore and Bullock's orioles are over 4% different in mtDNA sequences, and differ by sixteen discrete plumage differences. Although the two species form

an extensive hybrid zone, recent research indicates that the zone is stable and quite ancient (Allen, 2002). Thus the two species show no evidence of merging, and plumage preferences may play a role in keeping the species distinct (reviewed in Allen, 2002).

In contrast, we have documented two mitochondrial clades in the Common Raven (*Corvus corax*) that also differ by about 4% in mtDNA sequence (Omland et al., 2000). Unlike orioles, however, these birds have no plumage differences, nor any other phenotypic characters that we know of, which would enable them to distinguish these two cryptic clades. In this case, we have evidence that the "California Clade" and "Holarctic Clade" exchange genes frequently throughout the west and may be reemerging (unpublished data). The contrast between orioles and ravens illustrates how it is still possible to find correlations between speciation and plumage coloration (e.g., Barraclough et al., 1995; Owens et al., 1999) even in the absence of reproductive character displacement (also see Price, 1998; Price, this symposium).

It seems likely that sexual selection in allopatry may indeed drive plumage divergence in *Icterus*, and that speciation is driven largely by geographic isolation. For example, the Jamaican oriole (*I. leucopteryx*) is largely confined to the island of Jamaica, where no other orioles are found. Nevertheless, this species has a highly distinctive appearance, and differs from other oriole species in at least seven plumage areas (Omland and Lanyon, 2000). In this and other island orioles, there is no evidence that isolated species lose their plumage differences, nor that continental species sympatric with other oriole species are more divergent in appearance, cf. *Anas* ducks (cf., Sibley, 1957; Omland, 1997). In fact, several similar-looking species with the Altamira-type pattern are sympatric throughout much of their ranges in Mexico and Central America (e.g., Altamira oriole and hooded oriole).

Nevertheless, much more work is needed to clarify the role of plumage in species recognition and reproductive isolation. Furthermore, research needs to focus on whether and how speciation drives plumage divergence, especially when considered in combination with other selective forces. There are several mechanisms that effect evolution of elaborate plumage ornamentation in birds, and there are studies that support each of them: 1) sexual selection by female choice, which has been documented in a large number of bird species (Andersson, 1982; reviewed in Andersson, 1994), including orchard orioles (Enstrom, 1993); 2) sexual selection for status signaling through male-male aggressive competition, which has never seriously been doubted, although the number of careful studies that document it is surprisingly small (e.g., Peek, 1972; Roskraft and Rohwer, 1987; Sorenson and Derrickson, 1994); and 3) the speciation process itself, which has also been supported by a few studies (Sibley, 1957), although there is really only one well-documented case of reproductive character displacement (Saetre et al., 1997). Predator avoidance and other processes

may also play a role (Dumbacher et al., 1992; Götmark, 1992).

Studies are needed that consider the continuum of mate choice decisions, from relative choices between otherwise acceptable conspecifics to threshold choices against unacceptable conspecifics, and choices that include individuals of other populations, races, or species (see Ryan, 1990). All such studies should be careful to emphasize individual fitness; there are cases when choosing to mate with heterospecifics may make the best of a bad situation (e.g., Nuechterlein and Buitron, 1998; Veen et al., 2001), or may actually lead to increased offspring fitness (Grant and Grant, 1996). Ultimately it will be valuable to know for at least some individual species, what roles female choice, male-male aggression, species recognition, and other processes have had in driving and maintaining the evolution of plumage and other signals. Similarly, it will be helpful to know the percentage of birds in which female choice, male-male aggression or species recognition has played the dominant role, and whether different mechanisms prevail over one another and in what circumstances. These are ambitious and long range goals, but now that there is good evidence for each of the mechanisms, more knowledge of their relative importance is needed, and of the interactions between them.

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S18-3 Causes of post-mating reproductive isolation in birds

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Abstract Speciation involves the establishment of both pre-mating and post-mating reproductive isolation between divergent populations. Post-mating barriers have been particularly difficult to study in birds. I review what is known about three main forms of post-mating isolation. The first, intrinsic genetic incompatibility, reflects hybrid infertility and inviability independent of the environment in which the hybrids are found. They can be studied using data from captive breeding experiments. Results suggest that incompatibilities imposing complete reproductive isolation often arise after the speciation process has been completed. The second, ecological selection against hybrids, results from environmental conditions and/or competition from parental types and has been demonstrated on a few occasions. The third, sexual selection against hybrids, which arises from mate preferences for one or other parental species, may be an important, relatively neglected post-mating isolation process. Hybrid males often show characteristics intermediate to the parental species, and have unusual displays. Some experiments have demonstrated that females show weaker sexual responses to courting hybrid males. Several field studies have implicated both female choice and competition among males for territories in causing hybrid unfitness. Ecological and behavioral causes of post-mating isolation may play a major role in speciation but present evidence is too limited to evaluate their importance.

Key words Hybrids, Natural selection, Pre-mating isolation, Reproductive isolation, Sexual selection, Speciation

1 Introduction

Species remain distinct ultimately because of a lack of genetic exchange between them. Genetic interchange can be cut off both through barriers at the pre-mating (e.g., mate choice) stage or at the post-mating stage. Post-mating barriers include the failure of the sperm to fertilize the egg, the failure of eggs to develop, and the inviability and infertility of hybrids. Most individuals of a species mate with conspecifics (Kirkpatrick and Ravigné, 2002), which implies that complete speciation may result from divergence in traits used in pre-mating reproductive isolation. For example, models of sexual selection have shown how correlated evolution of sexually selected traits and preferences for those traits can result in individuals from one population failing to recognize individuals from another as suitable mates (reviewed in Price, 1998).

While speciation may arise from pre-mating isolation alone, three lines of evidence suggest that post-mating isolation is usually involved as well, and may be critical to it. First, hybridization among species does occur (Panov, 1989). There are several examples of hybrid zones where hybridization is common, yet species each side of the hybrid zone remain distinct (Moore and Price, 1993). Almost 10% of all bird species have been recorded hybridizing in nature (Grant and Grant, 1992). Although many of these hybridization events are based on one or a few records they imply that rates of hybridization are at least comparable with mutation rates, and suggest that a gradual merging of species would happen unless prevented by lowered fitness in hybrids.

Secondly, post-mating isolation is integral to the model of speciation based on reinforcement of mating preferences (Dobzhansky, 1940; Noor, 1999). In this model, increased levels of pre-mating isolation result from selection to avoid mating with heterospecifics, specifically because hybrids are unfit. There is some evidence for reinforcement in nature (Howard, 1993; Sætre et al., 1997), and theoretical models show reinforcement to be a likely outcome whenever hybrid fitness is very low (Liou and Price, 1994). Reinforcement may often result from the refinement of mate recognition rather than divergence in traits used for recognition (Ratcliffe and Grant, 1983; Irwin and Price, 1999). Although not quantified, it does appear that very small differences between species occasionally form the basis of strong mate recognition. It seems unlikely that these differences would be sufficient for pre-mating isolation to have evolved entirely as a correlated response of the mate recognition system to the traits that distinguish the species, without some reinforcement of the recognition process. For example, two species of chiffchaffs *Phylloscopus collybita* and *P. sindianus* singing similar songs and with similar plumages coexist in sympatry in the Caucasus, apparently without hybridizing (Martens, 1996).

The third line of evidence implicating post-mating isolation in speciation comes from examples of hybridizing species where hybrid fitness has been measured and found to be low (e.g., Lanyon, 1979; Veen et al., 2001). Pre- and post-mating barriers seem to have accumulated between these species at a comparable rate.

In this paper I review causes of post-mating isolation in birds. These fall broadly into three categories (Coyne and Orr, 1998; Table 1), although there is overlap between them. The first is that of intrinsic genetic incompatibility: hybridization events result in no offspring or offspring with reduced fertility, defects that are independent of the environment. The second is that of hybrids with reduced fitness because they fall between the ecological niches of the parental types, and the third is that of hybrids which are unable to attract mates. Not very much is known about the latter two forms of unfitness, and they are a major gap in our understanding of speciation. It is maintained here that sexual selection against hybrids is an important form of post-mating reproductive isolation.

2 Intrinsic incompatibilities

Sexual conflict, i.e. the different interests of males and females, can result in the rapid evolution of genes affecting fertility, leading to the development of reproductive isolation between populations (Rice, 1998). First, sperm may fail to fertilize. While this may be important (Price et al., 2001), it has not been explicitly demonstrated as a cause of infertility in bird crosses. A second prediction of the sexual conflict model is that fertility problems in hybrids should arise much more frequently than viability problems (Rice, 1998). This expectation is born out (Price and Bouvier, 2002). Comparisons among species crossed in captivity indicate that hybrids are regularly produced but often show reduced fertility (Price and Bouvier, l.c.). Hybrid infertility may arise from problems of chromosome pairing at meiosis (Smith and Thomas, 1913; Mott et al., 1968), as well as genetic interactions.

The relatively rapid development of infertility implies that if intrinsic incompatibility contributes to post-mating isolation, it will be due to hybrid infertility rather than inviability. In fact, complete loss of hybrid fertility seems to take a long time (Price and Bouvier, 2002). A classic example is the mallard (*Anas platyrhynchos*) and pintail (*Anas acuta*), which may have diverged > 4 MYA (Price and Bouvier, 2002) yet still produce fully fertile hybrid offspring (Sharpe and

Johnsgard, 1966). More than half of all studied crosses between congeneric species produce fully fertile offspring (Price and Bouvier, 2002). This number is biased but it does suggest that the contribution of intrinsic incompatibility to speciation is often small.

There are several caveats. First, the timescale for at least partial loss of fertility is of the same order as that for speciation in some pairs of species. In particular, hybrid females may have reduced fertility, or even be infertile, even though males are not (Price and Bouvier, 2002). For example, female hybrids of two flycatchers (*Ficedula* spp.), which may have been separated by about 2 million years (Price and Bouvier, 2002), are infertile (Veen et al., 2001). A second caveat is to be found in the appearance of intrinsic incompatibilities in the F2 or backcross generations rather than the F1 because many of the deleterious effects of gene combinations appear to be recessive (Turelli and Orr, 2000). There are few records in ornithology where fertile F1s have been taken through either the F2 or backcross generations. Thus in the European and Japanese quail, *Coturnix* spp. (Deregnaucourt et al., 2002) and the mallard and pintail (Sharpe and Johnsgard, 1966), both F1s and F2s appear to be fully fertile. But in crosses between the gray and red junglefowl (*Gallus* spp.), the F1s show some reduced fertility with respect to parental species; and in the F2s fertility is much lower still (Morejohn, 1968).

3 Ecological selection

Hybrids may be unfit because they fall between the ecological niches of parental species. Moore (1977) and Moore and Price (1993) argued that many hybrid zones were areas of “bounded hybrid superiority”, where hybrid fitness was equal to or higher than parental fitness within the zone but lower outside it, as a consequence of spatially varying environmental conditions. Moore and Price (1977) demonstrated correlations of the spatial distributions of the hybridizing forms with several climatic and biotic variables to bolster the case.

So-called migratory divides provide more direct examples of situations where hybrids are likely to be unfit

Table 1 Types of post-mating isolation in birds, citing the most recent reviews

Category	Sub-category	Most recent review
Intrinsic genetic incompatibility	*Post mating, pre zygotic	—
Intrinsic genetic incompatibility	Hybrid inviability	Price and Bouvier, 2002
	Hybrid infertility	Price and Bouvier, 2002
	F2 and backcross breakdown	This paper
Ecological selection	Feeding	Grant and Grant, 1996
	Migratory direction divides	Irwin and Irwin, 2003
	Migratory distance divides	Rohwer and Manning, 1990
Reproductive selection	Nest building	Buckley, 1969
	Sexual selection	Price, 2002; this paper

*Although this sub-category may be important, it has not been studied in birds; a brief review of the phenomenon is given in Price et al. (2001).

(Helbig, 1991; Irwin and Irwin, 2004). If two species migrate along different routes, the hybrids may migrate along an intermediate course and have lower fitness as a consequence. Helbig (1991) conducted a captive breeding experiment on the blackcap, *Sylvia atricapilla*, which has SW and SE migrating populations, and showed that hybrids take up an intermediate orientation. Irwin and Irwin (2004) review comparative studies. They show that different subspecies of a number of Siberian species migrate to southern Asia around west or east sides of the Tibetan plateau, which infers that hybrids between two such subspecies might migrate due south across the plateau, with correspondingly reduced fitness. Migratory divides in Siberia are a good illustration of how low hybrid fitness can arise out of gradual divergence among populations: migration orientation is likely to have changed gradually as populations spread from ancestral areas (Irwin and Irwin, 2004).

In a somewhat parallel situation are the many examples of closely related taxa that include both resident and migratory members. Cross-breeding experiments among resident and migratory populations of the blackcap have shown migratory propensity to be genetic and hybrids to be intermediate (Berthold and Querner, 1981). Harris et al. (1978) showed that hybrids of herring (*Larus argentatus*) and lesser black backed (*L. fuscus*) gulls in Britain did not survive well. Although the causes are unknown, the herring gull is generally resident and the lesser black backed migratory, traits that seem to be at least partly genetic. Cross-fostered lesser black backed migrated normally, but cross-fostered herrings showed some tendency to migrate, although not as far as black backed (Harris, 1970). Rohwer and Manning (1990) and Rohwer and Johnson (1992) argued that unusual migration and associated molt patterns could lower fitness in hybrid Baltimore and Bullock's orioles (*Icterus galbula galbula* and *I. g. bullocki* respectively). Molt differences may affect hybrids of resident populations too. Gwinner and Neusser (1985) showed that differences among subspecies of African and European stonechats (*Saxicola torquata*) in timing and duration of molt were genetic and intermediate in hybrids.

Measurements comparing hybrid and parental fitness in migration and molt have yet to be taken, but some are available for foraging. Hybrids in Darwin's finches, *Geospiza* spp. (Grant and Grant, 1996) are intermediate in morphology and have diets intermediate between those of parental species, with demonstrable consequences for hybrid fitness (Grant and Grant, 1996). Good et al. (2000) found that hybrid gulls (*Larus* spp.) exhibited the habitat preferences of one species in one area, and the diet of the other in another area, both of which influenced fitness. The flipside of differences in fitness between hybrids and parental taxa in foraging is an association of similar fitnesses with similar foraging among hybrids and parentals, as appears to be the case in a gull hybrid zone (Ingolfsson, 1970).

It is common to find hybridizing species associated with distinct habitats and to hybridize only where those

habitats meet (e.g., Yang and Selander, 1968; Saino, 1992; Saino and Villa, 1992). Hybrid wagtails *Motacilla flava* (Sammalisto, 1968) and crows *Corvus corone* (Saino, 1992) have more catholic habitat preferences than parental taxa, although whether these preferences affect fitness is unknown. In the wagtails, however, Sammalisto (1968) found a strong correlation across years between the proportion of hybrids and temperature during the nestling period of the previous year.

4 Sexual selection

In birds, species recognition is attributable largely to imprinting, whereby offspring learn the characteristics of their parents and use these characteristics in mating decisions (ten Cate and Vos, 1999; ten Cate, this symposium). Imprinting on habitat may also happen (reviewed in Teuschl et al., 1998). If hybrids look or sound different from either parent, or occur in a different habitat, they may obtain mates less readily, because parental types ignore them. In addition, hybrid females may retain preferences for the parental species that raised them, rather than for hybrid males. Female zebra finches (*Taeniopygia guttata*) learn characteristics of their father's song and respond sexually to similar songs (Clayton, 1990). Male hybrids between the two subspecies of zebra finch sing songs different from either parental species and females of both parental types respond weakly to them (Fig. 1). Hybrid females do respond to songs produced by hybrid males, but they respond even more strongly to songs resembling the male that reared them (Fig. 1). In other species, hybrids may sing songs closely resembling the paternal type but differ instead in other sexually selected traits, including courtship and plumage pattern (Price, 2002). Conversely, in natural situations where hybridization is frequent, the parental taxa and hybrids are alike in at least some of these features, including voice and display (Yang and Selander, 1968), and coloration and display (Grant and Grant, 1997).

In many hybrid zones there is strong assortative mating (Jiggins and Mallet, 2000), parental types pairing with each other (Saino and Villa, 1992; Sætre et al., 1999; Grant and Grant, 1997). Hybrids also obtain mates, but it is not known how often assortative mating translates into sexual selection against them; in Darwin's finches it is thought not to (Grant and Grant, 1997). In other hybrid zones, moreover, mating is random (Ingolfsson, 1970; Moore, 1987; Good et al., 2000). Observations of random mating do not necessarily imply an absence of sexual selection against hybrids. Based on experimental manipulations of color patterns by Nobel (1936), Moore (1987) argues that an important component of selection against hybrid flickers is male competition for territories: male hybrids outside the hybrid zone are less able to establish themselves because their unusual color patterns give a less effective signal.

Quantitative measurements of sexual selection against hybrids are as rare as measurements of ecological selection. In *Vermivora* warblers, hybrid males had only 60% of the

pairing success of parental males (Ficken and Ficken, 1968); and in two sister grebe species (*Aechmophorus* spp.), early season pairing success among hybrids was 30% of that of the common parental type (Neuchterlein and Buitron, 1998). Pearson (2000) studied territory maintenance and pairing success in two *Dendroica* warblers; hybrid males had success much as in one parental species and about 75% of the success in the other. Moore and Koenig (1986) also found that hybrid flicker males had smaller broods than the parental species. They raised the interesting possibility that females paired with hybrids were less stimulated and hence put less effort into reproduction.

5 Discussion

Results from captive breeding experiments suggest that intrinsic barriers imposing post-mating isolation may be weak among closely related species. Directly assessing ecological and behavioral causes of hybrid unfitness in the field, moreover, is very difficult and there are few thorough studies (Jiggins and Mallet, 2000). The difficulties are that hybrids are often rare and that measurements of selection in general are not easy, because individuals may need to be followed through their lifetime.

Hybrids may suffer reduction in fitness from multiple causes. Thus in the crow hybrid zone studied by Saino (1992), behavioral observations suggest the possibility of forms of both sexual and ecological selection against hybrids. Moreover, egg volume, chick survival and number

of chicks fledged per nest were all lower in hybrid females than the parental types (Saino and Bolzern, 1992; Saino and Villa, 1992); and some hybrid females laid abnormal, thin-shelled eggs (Saino and Villa, 1992). Hybrid females between collared and pied flycatchers are infertile (Veen et al., 2001). Assortative mating within the hybrid zone (Sætre et al., 1999) raises the possibility of sexual selection against hybrids; and there may also be ecological selection imposed by habitat choice and migratory differences (Veen et al., 2001).

Because natural selection can generate rapid evolution, ecological causes of post-mating isolation may precede the development of intrinsic genetic incompatibilities. This is especially likely in the early stages of an adaptive radiation, characterized by rampant divergent natural selection (Schluter, 2000). But the very long time that it takes to produce genetic incompatibilities implies that the ecological conditions that promoted both divergence and associated post-mating barriers must persist for a very long time if species are to become a permanently reproductively isolated through the build up of such incompatibilities. Thus Grant and Grant (1992, 1996) showed that even if foraging differences between hybrid and parental species of Darwin's finches impose a post-mating barrier, the barrier disappears following years of abnormally high rainfall and associated changes in resource distribution. In such years, hybrids had higher survival than at least one of the parental species. Such inconsistency with the ecological barrier hypothesis may be explained by divergence along multiple ecological dimensions (prey, habitat, feeding method, nest site etc.): all dimensions are unlikely to collapse at the same time. Rice and Hostert (1993) noted the importance of multiple dimensions in their review of selection experiments promoting reproductive isolation.

The possibility that sexual selection against hybrids contributes to post-mating isolation has been relatively neglected, even though hybrid males have often been recorded as having difficulties in courtship (Sharpe and Johnsgard, 1966; Price, 2002). It is possible that an unusual hybrid will sometimes be favored more under sexual selection than either parental species, leading to a new 'hybrid' species. There is little evidence that this has ever happened in birds (Price, 2002). Sexual selection against hybrids is expected to act predominantly against males and therefore is unlikely to impose complete post-mating isolation. However, intrinsic hybrid unfitness arises first in female hybrids (Haldane's rule), and should complement any loss of fitness in males due to sexual selection (Price and Bouvier, 2002, for birds).

Sexual selection against hybrids may be less affected by altered conditions than ecological causes of hybrid unfitness. In addition, related species usually differ in multiple sexually selected traits, and may continue to accumulate more differences with time, so hybrids grow increasingly different from both parent species (Price, 2002). Thus Baker and Baker (1990) showed that both song and plumage pattern were involved in mate choice in hybridizing

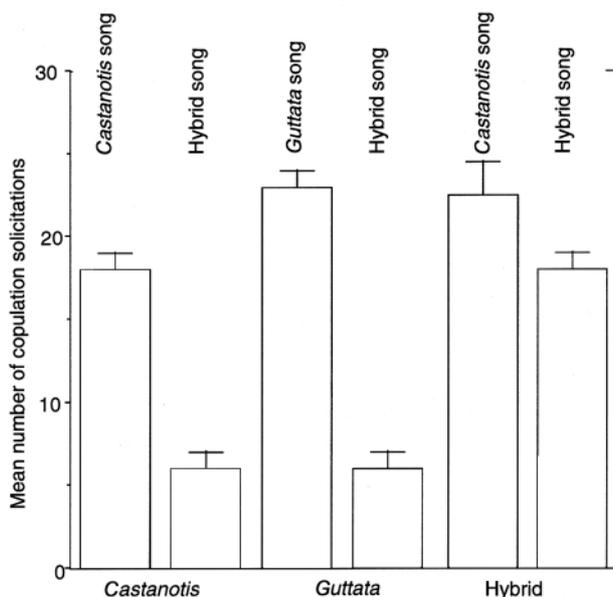


Fig. 1 Number of copulation-solicitation displays (+ SD) of estradiol-implanted female zebra finches (*Taeniopygia guttata*) to playback of songs of males of two subspecies and their hybrids

Twelve females from each subspecies (*T. g. castanotis* and *T. g. guttata*) were tested, as were 12 hybrid females that had been raised by *castanotis* females and *guttata* males. Responses were measured to 1) songs of own subspecies, and 2) songs of hybrids between the two subspecies (data from Clayton, 1990).

buntings and that these two traits contributed more or less equally to female response. The implication here is that hybrids mismatched in plumage and song would be disadvantaged.

Sexual selection against hybrids has important consequences for the ease with which reinforcement of pre-mating isolation can work. In the reinforcement model, hybrid unfitness leads to selection favoring divergence in traits used in pre-mating isolation (Howard, 1993; Liou and Price, 1994). The chief theoretical difficulty here is that the traits used in pre-mating isolation may become dissociated from those used in post-mating isolation, as a result of recombination in hybrids (Rice and Hostert, 1993). Sexual selection against hybrids is likely to be based on the same traits that are used in species recognition during mate choice, so that the traits effecting pre-mating isolation also impose some post-mating isolation, at least in males. Kirkpatrick and Servedio (1999) show theoretically how sexual selection against hybrids can lead to a strengthening of mate preferences in an island population, even when other kinds of hybrid unfitness were absent.

The two main conclusions to be drawn from this review are (1) a critical step in speciation is likely to include the generation of post-mating isolation, and (2) sexual selection against hybrids may contribute to this isolation. Even if intrinsically viable and fertile offspring are produced, post-mating isolation is often difficult to study in the field because hybridization events are usually rare. More field studies of hybrid fitness are needed, but much would also be gained from experimental studies of mate choice in the laboratory of the kind foreshadowed by Clayton (1990) and Baker and Baker (1990), both of whom showed weaker female responses to hybrid male courtship traits (Fig. 1).

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S18-5 Sexual signals, learning processes and evolution

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Abstract Examples are given of how the widespread learning processes of sexual imprinting, song learning and song preference learning may affect the evolutionary processes of sexual selection and speciation in birds. They show that sexual imprinting may occur together with perceptual biases, giving rise to preferences for mates with exaggerated traits. Sexual imprinting may also give rise to exaggeration of sexual dimorphism through “peak shift”, a by-product of discrimination learning. Imprinting and song (preference) learning seem responsible for enabling or driving the rapid speciation of some avian brood parasites. The examples highlight the point that learning processes can have a profound impact on evolutionary processes and deserve prominent attention in evolutionary theory.

Key words Imprinting, Mate choice, Evolution, Speciation, Sexual selection, Song learning

1 Introduction

Birds are frequently used as model species to examine such evolutionary processes as sexual selection or speciation. A central element in theories about these processes concerns variation in the signals involved in mate choice (sexual signals) and in the preferences for these signals. In birds, sexual signals are predominantly visual (plumage color or pattern) or acoustic (voice). But how do birds “know” to which signals they should respond in order to get the right mates? Many models of evolutionary processes assume that genetic disposition underlies trait recognition and preference. Yet learning processes too are very important in the development of such preferences in birds, and even in the development of some signals used in mate choice. Although increasing attention is now being paid to understanding how learning may affect evolutionary processes, relatively few studies as yet address this issue. In this paper I review a number of such studies, concentrating on the role of sexual imprinting and song learning.

2 Is learning important?

It has long been known that many bird species use parents as models for future mate preference: they learn from them and later prefer similar-looking mates. Such “sexual imprinting” was initially thought to be limited to special cases, notably rapidly evolving species (Immelmann, 1975). However, ten Cate and Vos (1999) have demonstrated that the phenomenon is widespread, revealing its presence in over hundred species, including members of most bird orders. Acquiring mate preference through learning thus seems the rule, not the exception, in birds.

With respect to vocal signals (songs), a distinction needs to be made between learning involved in the production of signals and learning that leads to specific preferences.

Sound production learning has been demonstrated for songbirds (oscines), hummingbirds and parrots. It may be present in some other groups, but it is also clear that several taxa can only produce the voice of their own species after cross-fostering or rearing in isolation. Less clear is the situation with respect to vocal recognition learning. Females of several species, particularly in songbirds, are known to prefer songs heard early in life. Learning may not be limited to songbirds, but for most other groups it is largely unknown whether females have to be exposed to conspecific calls if they are to respond to them later on. It is clear that both imprinting and song learning are important in birds, raising the question of their impact on evolutionary processes. Three examples of this impact follow.

3 Imprinting and sexual selection

The traditional view of sexual imprinting is one of a mechanism that enables species recognition. Both theoretical and empirical studies have concentrated on the impact of imprinting on choosing conspecifics over heterospecific mates, or choosing conspecifics of one particular color morph over another. It has even been said that imprinting results in mate preference for “those objects bearing the closest similarity to the original stimulus” (Immelmann, 1975). No wonder then that imprinting was not seen as a mechanism important in sexual selection, which implies the presence of biased preferences. This view has now changed, largely as a result of imprinting studies on Japanese quail. When raised with siblings, male and female quail both preferred to mate with birds of the same wild-type morph as their siblings; but among these individuals they preferred mates slightly different from siblings: first cousins were preferred, both over siblings and over more distantly related birds (Bateson, 1982). Other experiments have shown that males and females prefer mates with traits missing from

their parents. Thus in the zebra finch — a model species for studying imprinting — both males and females preferred mates with artificial additions such as colored leg bands or a white feather in the head (Burley and Symanksi, 1998).

So how do imprinting processes and perceptual preferences interact? This has been examined systematically in further experiments on the Japanese quail. The experiments were designed to address the question: do quail that are free to choose novel birds which differ from imprints in a specific, experimentally controlled way have a bias in choice? In the experiment, young quail were exposed only to white adults during parenting. For one group, the white adults had six black dots dyed on the breast, for another group three, and for the third none. When mature, the young quail were given choice tests. When given the choice between a bird similar to the imprinting stimulus and a wild type, the imprinted bird was preferred. However, among three white types, those with the highest number of dots were preferred significantly over the lowest, irrespective of the number of breast dots in original stimulus imprinting adults (ten Cate and Bateson, 1989). This experiment suggests that imprinting may set a standard for the mate preference, which is combined with an additional perceptual bias, leading to asymmetric preference for novel mates.

Such a mechanism might drive sexual selection (ten Cate and Bateson, 1988), leading individuals to mate with those birds showing parental traits that had diverged slightly in an exaggerated way. Offspring of such a pair would not only be likely to inherit the exaggerated trait (if based on genetic variation), but would also use it as a standard for their own preference later, thus linking trait and preference. Subsequent studies on Javanese mannikins (Witte et al., 2000) and zebra finches (Witte and Sawka, 2003) have confirmed that imprinting on novel or artificial traits can occur, although the effects may differ between sexes and also in relation to the trait itself. Recent theoretical modeling, moreover, suggests that sexual imprinting in combination with an asymmetric bias in preference alters the dynamics of the sexual selection process and may speed up the evolution of conspicuous traits (Laland, 1994; Aoki et al., 2001).

It can be concluded that sexual imprinting is not only present in species that select sexually, but may even contribute to the dynamics of the process. More experimental work is required, in particular, to elucidate the proximate and ultimate factors that give rise to variation in outcome between sexes and species.

4 Sexual imprinting and sexual dimorphism

In many species, sexual selection is supposed to be the driving force behind sexual dimorphism in appearance, e.g. in plumage pattern or coloration. If imprinting can generate plumage evolution under sexual selection, how is it implicated in the origin and maintenance of sexual dimorphism? Sexual dimorphism can arise if males and fe-

males of a species have different sexual preferences. This may be brought about in different ways. For example, males and females may differ in their balancing of sexual imprinting with respect to other mechanisms that guide visual preferences, such as perceptual biases (see above). A proper interpretation of studies purporting to show a sex difference in the outcome of the mating process in cross-fostered individuals is complicated, however, due to behavioral interactions between males and females that may obscure initial preferences for certain plumage types (ten Cate and Vos, 1999).

It is clear, nevertheless, that perceptual biases which interact with learned preferences may differ between the sexes. Also, although learning may influence both sexes, the sexes may differ in what they learn and from whom (ten Cate and Vos, 1999). For example, in the sexually dimorphic zebra finch, males develop a preference for females of similar appearance to their mother (Vos et al., 1993). And for female zebra finches, recent evidence indicates that they are more likely to imprint on their father than on their mother (Witte and Sawka, 2003). Such differential learning may facilitate the maintenance, even exaggeration, of sexual dimorphism in appearance. It shows that sexual imprinting as a mechanism is compatible with the existence of such dimorphism.

There is one further particularly interesting question: does the imprinting process itself induce its own bias towards more extreme traits, independently of perceptual biases. Several authors (e.g., Weary et al., 1993; ten Cate and Vos, 1999) suggested that sexual imprinting might lead to the enhancement of sexual dimorphism through a phenomenon known as “peak shift”. Peak shift occurs in circumstances of discrimination between two stimuli that differ slightly on one dimension. Thus an animal can learn that response to a light of one wavelength results in reward and to another in punishment. When subsequently tested with signals spanning a wider range of wave lengths, the peak response may shift to signals that exaggerate the difference between the training stimuli. A starting point for examining whether sexual imprinting may induce peak shift was the finding that male zebra finches raised by foster parents of a wild type male and a white female or vice versa, not only preferred females of their mother’s morph, but actively avoided females of the father’s morph (Vos et al., 1993). A subsequent experiment showed that zebra finch males raised by white parents differing only in beak color (red in fathers, orange in mothers) preferred females with orange beaks over those with red (Vos, 1995; ten Cate and Vos, 1999). Taken together, these experiments provide evidence for discriminatory learning during imprinting, at least among males.

The experiments also provide a model for testing whether such discriminatory learning results in peak shift: what does the preference look like when males are tested with females varying in beak color along the red/orange scale? In a preliminary experiment, males were exposed to white parents with bills painted red or orange with nail polish.

This treatment enabled experimental control for color variation, and also made it possible to generate one group in which the fathers had orange beaks and the mothers red, and a second group in which the beak colors were reversed. Later on, males were tested with females differing in beak color. Only in the father-orange, mother-red group was there a shift towards a more extreme preference (ten Cate and Vos, 1999). The experiment, however, was not conclusive, and a more extensive and rigid test is in progress. Preliminary data seem to confirm the presence of a peak shift. If present, this mechanism should drive modest sexual dimorphism towards more extreme differences as an ‘artifact’ of the imprinting process itself.

5 Sexual imprinting as a mechanism inducing speciation

Various researchers have concluded that imprinting does generate assortative mating and by doing so can contribute to speciation (e.g., Laland, 1994; Grant and Grant, 1997; Irwin and Price, 1999; ten Cate and Vos, 1999). Here follows an unusual and special example of a speciation process in which imprinting has an active role, in this case combined with song learning. It concerns the speciation process in a group of avian brood parasites, the viduid finches (indigobirds and whydahs), which parasitize estrildid finches. Most viduid finches are specialized parasites, laying their eggs in the nests of specific host species and developing clear adaptations to that host, e.g., young resemble nestlings of the host species in mouth markings and plumage (e.g., Nicolai, 1964). Male viduids, moreover, sing species-specific songs that strongly resemble those of the host species (Nicolai, 1964; Payne, 1973). Female viduids are attracted to that particular song type over others (Payne, 1973; Payne et al., 2000). The song of the host species stimulates ovarian development in parasitic females, and attracts them to its nests. The morphological similarities between parasite and host offspring, and the host-oriented behavior of the parasitic viduids, suggest a long history of co-evolution between host species and their specific parasites. Indeed, Nicolai (1964) suggested that viduid species had evolved jointly with their hosts.

Yet recent DNA-studies make this scenario unlikely. They show not only that the most likely phylogenetic branching patterns of hosts and parasites do not match, but also suggest that speciation in the parasites has occurred substantially more recently than in the hosts. These observations support an alternative model for evolution, that of ‘colonization, in which a parasitic lineage switches from one host species to another, leading to subsequent adaptation to the new host (Payne et al., 1998, 2000). But although one can imagine a female parasite laying her egg in the nest of a new host species, this still seems to be a long way from founding a new branch on the species tree.

The key to understanding how a parasitic species can colonize a new host with apparent ease and become reproductively isolated from its ancestor at the same time

lies in the mechanisms that guide host selection, mate preferences and mate attraction signals. Viduid finches are songbirds and, as in other songbirds, learning is important in developing songs as well as song preferences. Payne et al. (1998, 2000) demonstrated that when village indigobirds (*Vidua chalybeata*), which normally parasitize firefinches (*Lagnostica senegala*), were cross-fostered to Bengalese finches (*Lonchura striata*), they developed a distinctly different song. Instead of singing the usual repertoire of firefinch-like songs, they sang Bengalese finch-like songs. Moreover, cross-fostered females, which normally prefer village indigobirds singing firefinch songs, now preferred mates singing Bengalese finch-like songs. When these females were later introduced to aviaries of several potential host species, including firefinches and Bengalese finches, they preferentially laid their eggs in the nests of Bengalese finches, i.e. nests belonging to the species which raised them.

Thus, a parasitic female that lays her eggs in the nest of a novel host will produce offspring that differ substantially from their biological parents in behavior, producing parasitic individuals that have taken important steps towards colonizing the new host. Coincidentally, the same changes produce a reproductive break with conspecifics raised by the traditional host. If successful with the new host, the traditional Darwinian mechanisms of genetic mutation and selection might later lead to morphological adaptations (e.g., in nestling mimicry of mouth markings), eventually budding off a new parasitic species. So, the rapid speciation in viduid finches seems to be the outcome of an evolutionary process in which behavioral changes that result from early learning are the catalyst.

To conclude, the presence of learning processes in signal making and signal reception in mate choice affects evolutionary processes in several, and sometimes surprising, ways. It is clear that much is still to be discovered.

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Symposium 19 The evolution of avian migration

Introduction

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Since the very beginning of research into avian migration, the questions of why birds migrate and how migration originated have been at the center of interest. But only since the development of the theory of natural selection has it been possible to formulate testable hypotheses to answer these issues. Alfred Russell Wallace (1874) was probably the first to put forward ideas about how avian migration may have originated by natural selection. Today, it is generally accepted that current migration patterns are maintained and altered by selection (Lack, 1968; Berthold, 1999), yet we are only just beginning to understand the details of this process of adaptive evolution.

Investigation of the evolution of migration encompasses a wide field, including the question of the origin of migration in diverse phylogenetic lineages, mechanisms of adaptive change, and ecological conditions favoring the evolution of migration and its maintenance. Moreover, when we speak of migration, we are not dealing with one trait but with a complex, co-adapted suite of traits characteristic of migratory birds (Dingle, 1996). These traits, such as circannual rhythms, orientation mechanisms, energy storage and utilization, are not exclusive to migrants but are expressed in most birds (Berthold, 1999; Wiltschko and Wiltschko, 1999). One property that runs like a thread through recent studies, including all contributions to this symposium, is that bird migration is highly flexible and variable. Complex interactions between environments and genotypes, between historical factors and extant conditions, are the cause for a great diversity of evolutionary trajectories and of “adaptive solutions” (cf. Pulido, this symposium).

In recent years, some general but hitherto unexpected patterns have become apparent, such as the southern ancestry of most Holarctic migrants (Safriel, 1995; Rappole 1995), the ingrained universality of migratory traits in birds (Berthold, 1999; Rappole, this symposium), the inter-correlation of migratory traits and their evolution (Pulido et al., 1996; Pulido and Berthold, 2003), the flexibility and evolutionary lability of migratory traits and migratory status (Helbig, 2003; Pulido, this symposium), and the variety of ecological conditions pressuring the evolution of migra-

tion or residency (Rappole, 1995). The generality of most of these patterns, however, needs verification. Moreover, we need to investigate how specific character states and ecological conditions facilitate migration, and what evolutionary changes are necessary and adequate to enable bird populations to perform regular seasonal migration or to change migration patterns.

Over the last several years, significant progress has been made in a number of fields, such as phylogeny, biogeography, and population biology, to have had a major impact on the study of the evolution of avian migration. As a consequence, this field has flourished and ripened. We are now able to investigate the evolution of migration at different levels and on different time-frames, and to test discriminating predictions. So the time is ripe for a synthesis of the field. The contributions to this symposium will surely guide future research, because they show that insights into the evolution of migration hinge upon the integration of different fields and diverse approaches.

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S19-1 Origins and timing of avian migrant evolution in the New World

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Abstract A variety of data, including taxonomic and ecological information, confirm that the majority of long-distance land bird migrants in the New World originated from populations of tropical species. Phylogenetic distances from tropical relatives indicate that, for some species, migration had its roots in the distant past while in others it evolved very quickly and recently, judged by movement data for species introduced into the New World within the past 200 years. Long distance migrants constitute a fairly small portion of the avifauna of the Western Hemisphere. However, populations of species that undergo regular seasonal movements between intra-continental sites, areas, or regions make up a much larger percentage. In fact, data are only now being gathered that will allow determination of the extent to which the majority of tropical birds are migratory. Preliminary data indicate that two factors facilitate the evolution of migration: 1) two separate environments where fitness differs seasonally for the members of a species, and 2) the ability to move between the two environments. When these conditions are met, migration is likely to evolve because birds possess a number of appropriate adaptations, such as homing ability and energy storage capacity which allow them to capitalize on the conditions. Evolution of these adaptations is probably as old as the Class Aves itself, because these adaptations are favored in any dispersing animal. Thus, migration is probably as old as movement and seasonality, and long-distance migration is probably as old as seasonal variation in habitat quality and flight.

Key words Birds, Origin, Avian migration, Evolution, New World

1 Introduction

Nearctic avian land bird migrants are Western Hemisphere species that breed in the north temperate and boreal regions of the Western Hemisphere, and winter, all or in part, in the neotropics (Rappole et al., 1995). The purpose of this paper is to present an analysis of information relevant to three critical questions regarding these species: (1) in which geographical region did the majority of these species originate? (2) when did this process occur? and (3) what circumstances favored evolution of migratory behavior?

2 Geographical origin of Nearctic migrants

A range of data, including taxonomic and ecological information, confirm that the majority of Nearctic avian land bird migrants originated from populations of tropical species (Mayr, 1946). Thus, 48% of Nearctic migrants have conspecific populations that are resident breeders in the tropics, e.g. the red-eyed vireo (*Vireo olivaceus*), yellow warbler (*Dendroica petechia*), and peregrine falcon (*Falco peregrinus*), while 78% have congeners that are resident breeders in the tropics (Rappole, 1995). Several Nearctic migrants are members of families composed almost entirely of resident tropical species, such as the tanagers, Thraupidae, with four Nearctic migrants and 250 tropical residents.

Ecological information provides additional evidence for the neotropical origins of many Nearctic migrants. Migrants winter in all major neotropical habitats, where they integrate

as members of the avian communities there; and many have demonstrated fidelity to specific winter sites in a wide variety of habitats from one year to the next (Rappole et al., 1995). As an example of such fidelity, a Kentucky warbler (*Oporornis formosus*) was captured in rain forest understory by mist net on 28 December 1973, banded and released 1.5 km south of Tuxtla Biological Station in southern Veracruz, Mexico. This bird was recaptured within 50 m of its original capture point on 5 December 1980, still carrying its leg bands, presumably having completed seven round-trips from its Mexican, tropical wintering site and a breeding site somewhere in the eastern United States (Rappole, unpubl. data).

Members of many species, such as the northern waterthrush (*Seiurus noveboracensis*) establish and defend individual territories throughout the wintering period (Schwartz, 1964; Rappole and Warner, 1980), a phenomenon that has been documented for at least 75 species of Nearctic avian migrants (Rappole, 1995). Other Nearctic migrants, such as the chestnut-sided warbler (*Dendroica pensylvanica*) and golden-cheeked warbler (*Dendroica chrysoparia*), join mixed-species flocks during the wintering period in neotropical habitats, remaining with them throughout the winter period (Greenberg, 1984; Hutto, 1987; King and Rappole, 2000).

3 Timing of the origin of Nearctic migration

Most long-distance Nearctic land bird migrants are derived from tropical ancestors. Some clearly split from their

tropical relatives in the distant past. The migratory wood thrush, *Hylocichla mustelina*, for example, is the sole member of its genus, although clearly related to members of the turdid genus *Catharus*, which has seven tropical members and five Nearctic migrants (Winker and Rappole, 1988). Thus it seems likely that migration in this species evolved hundreds of thousands of years ago. Similarly, the closest apparent relative of the American redstart (*Setophaga ruticilla*) is the whistling warbler, *Catharopeza bishopi* (Lovette and Bermingham, 2002), a tropical resident of the West Indian island of St. Vincent, and not other Nearctic migrants of the family Parulidae. This suggests distant — and so, ancient — derivation from a tropical relative.

Such taxonomic information indicates that migration evolved long ago for many Nearctic migrants, particularly in the parulid warblers. The recent distributional history of other species, such as the cattle egret (*Bubulcus ibis*), shows nevertheless that migration can evolve rapidly. This species first arrived in South America in the late 1800s. The first individuals were recorded in the United States in the early 1950s, yet long-distance migrant populations now breed as far north in the Nearctic region as southern Canada (Telfair, 1994).

Long distance migrants, that is, species moving more than 1 000 km between breeding and wintering areas, constitute only a small portion of the avifauna of the Western Hemisphere (Rappole, 1995). However, short-distance migrants with populations that undergo regular, seasonal movements between intra-continental sites, areas or regions make up a much larger percentage. In hummingbirds, for example, as many as 40% of the 328 species undertake some seasonal movement — whether altitudinal, latitudinal, or long-distance (Rappole and Schuchmann, 2003). Only 13 of these species are Nearctic migrants, while an additional 15 are long-distance austral migrants to the temperate zone of southern South America.

The remaining 102 seasonal shifters undertake migratory movements within the tropics themselves. Such intra-tropical migration is difficult to document, requiring long-term data that shows consistent seasonal disappearance of populations from one area and coincident appearance at another. Assessment is further complicated by the fact that some of the population may not even move at all (Vega and Rappole, 1994; Rappole et al., 1997; Winker et al., 1997). Nevertheless, intra-tropical migration is probably a very common phenomenon, which future research may demonstrate is a rapidly-evolving response to seasonal change in critical resource distribution (Levey and Stiles, 1992; Rappole and Tipton, 1992).

4 Factors favoring evolution of migratory behavior

Two factors appear to favor evolution of migratory behavior. In the first, two separate environments are needed where fitness differs seasonally for members of a species; the second requires species to have the ability to move

efficiently between the two environments (Rappole, 1995). When these conditions are met, migration is likely to evolve because birds possess adaptations that allow them to capitalize on these factors: hyperphagia, which enables birds to take in food in excess of their immediate needs, storage of readily released energy reserves in the form of deposited fat, flight, and homing ability. Evolution of these adaptations are probably as old as the Class Aves, because they are adaptations that are advantageous to any dispersing animal.

So migration is probably as old as bird movement and phenological shifts; and long-distance migration is probably as old as seasonal variation in habitat quality and flight. Seasonality depends on the tilt of the earth's axis, and thus seasonal habitats are probably as old as terrestrial vegetation. Fernandez (2002) reports at least five major Ice Ages based on percent of the earth's surface covered by ice: the Late Cenozoic (1 mybp), Gondwanan (280 mybp), Ordovician (450 mybp), Varangian (680 mybp) and Sturtian (750 mybp), with smaller fluctuations throughout the Tertiary (1.6–66.4 mybp). Seasonal habitats, such as deciduous phanerogam forest, go back at least to the Eocene epoch of the early Tertiary nearly 60 million years ago, prior to the appearance of many modern avian families in the fossil record (Fig. 1; Udvardy, 1969).

That Holarctic climates were much warmer, on average, during the Tertiary is well known, with subtropical conditions prevailing as far north as 50 degrees latitude. Groups considered tropical in terms of habitat requirements, e.g., potoos (Nyctibiidae, Caprimulgiformes) and trogons (Trogoniformes), occur in the fossil record of Holarctic habitats from the Eocene and Oligocene epochs of northern Europe (Mayr, 1999, 2001; Kristoffersen, 2002), along with apparently ancestral forms of other tropical-centered groups, e.g., the colies (Coliiformes) and parrots (Psittaciformes) (Mayr and Daniels, 1998; Dyke and Waterhouse, 2001). In fact, it seems possible that, even though some modern avian families had not yet arisen, significant numbers of migrants were present, especially among frugivores for reasons elucidated by Levey and Stiles (1992). Some habitats at northern latitudes were seasonal, and were not separated from the tropics by vast stretches of disconnecting desert or sea as they are now, circumstances presumably facilitating evolution of migratory habits.

5 Conclusions

Most Nearctic land bird migrants appear to have originated from tropical resident populations, with origins dating back as much as several million years. Nevertheless, recent evolution of a migratory or nomadic habit in some species demonstrates that migratory propensity is extremely responsive to selection. The principal conditions favoring the evolution of migration appear to be seasonal environments and a facility for movement which allows individuals to increase fitness relative to sedentary individuals. Climatic, seasonal, and consequent habitat change are ancient phenomena, dating back to the beginning of life; and dur-

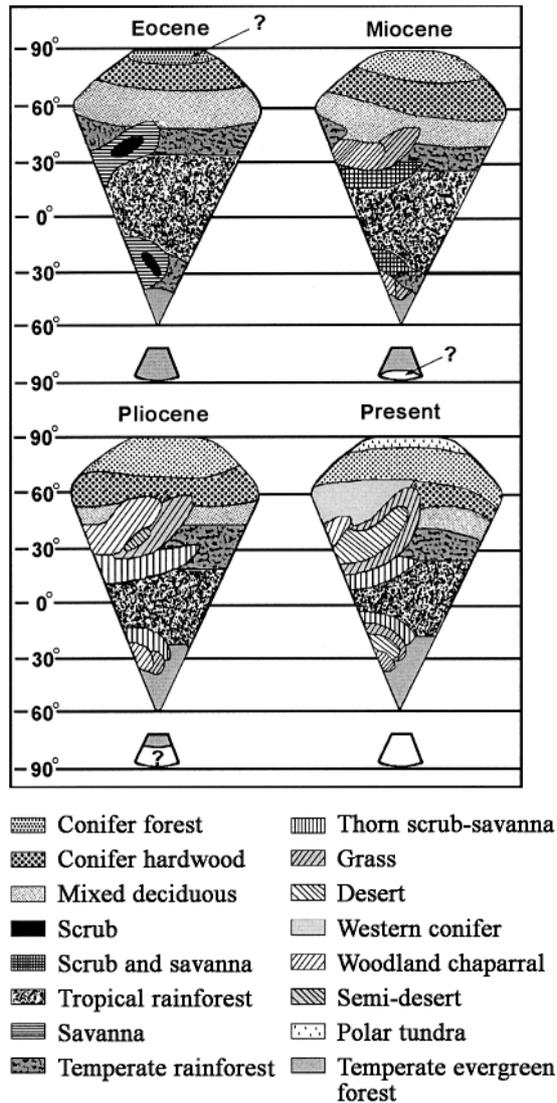


Fig. 1 Principal habitats of the Eocene (37–58 MYA), Miocene (5–24 MYA), Pliocene (2–5 MYA) and Holocene (present). Temperate, seasonal environments were extensive in these epochs. Based on material in Udvardy (1969) and Axelrod (1952).

ing the period of evolution of modern birds, there is evidence that paleohabitats in the Tertiary included such seasonal environments as temperate deciduous and coniferous forest. These Tertiary environments in the Nearctic were probably inhabited seasonally by migrant birds, perhaps even including such species as trogons and potoos which are resident in the tropics today.

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S19-2 Phylogenetic approaches to the evolution of migration

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Abstract The evolution of migration has long been the domain of evolutionary ecology. Work has focused on how natural selection drives the gain and loss of migration. We review applications of phylogenetic approaches to the question. By examining the deeper evolutionary history of migratory species and their populations rather than just their present-day ecology, such approaches, which can include historical biogeography and phylogeography, complement ecology. For example, breeding distributions appear to have been commonly displaced during the evolution of migration; component species of a migration system need not have evolved migration at the same time nor by the same processes nor in response to the same environmental pressures. The tools of historical biogeography, phylogeny and population genetics allow one to tease apart such spatiotemporal heterogeneity that may underlie the evolution of any migration system.

Key words Biogeography, *Charadrius*, *Myiarchus swainsoni*, mtDNA, Phylogeography

1 Introduction

The evolution of bird migration across and between continents has long been a major focus of study (Pulido et al., 1996; Alerstam and Hedenström, 1998). Excluding mechanisms of navigation, we note that central concerns have been how and why natural selection drives the evolution of migratory populations from non-migratory ones and vice versa (e.g., Cox, 1985; Gauthreaux, 1982; Pulido et al., 1996). The evolution of migration has thus fallen squarely within evolutionary ecology, the guiding paradigm of which is natural selection (e.g., Cockburn, 1991). How might we address questions such as whether unrelated species in a migration system, which obviously evolved migration independently, did so at the same or different times or in response to one or more environmental stimuli?

Another set of questions that evolutionary ecology has addressed but which we argue may be seen from other, complimentary, standpoints concern the so-called “ancestral home” of migrants. Seeing the problem of the ancestral home as a problem in historical biogeography, one can try to determine where long-distance migrants originally evolved and how their present-day disjunct breeding and non-breeding distributions developed. That is, did they evolve in their present-day breeding grounds with displacement of their non-breeding range or vice versa?

This paper reviews some cases in which these and other issues have been addressed with the methodologies of phylogeny and historical biogeography. Also illustrated are uses of phylogeography, i.e., the bridge between sys-

tematics and population genetics (Avice, 2000) in studying the evolution of migration. Our aims are twofold. First, we will show that these essentially historical approaches compliment and expand on the shorter term ecological approaches that have dominated the study of evolution of migration until now. In particular, we show that reconstruction of distributional shifts that have occurred during the evolution of migration is a strength of using phylogenetic, biogeographic and phylogeographic approaches. Secondly, we will show that phylogenetic approaches can bring a temporal dimension to understanding the evolution of migration. The ecology of why migration evolves is excluded from our scope although we submit that the results of phylogenetic approaches can inform ecological questions.

We stress several caveats, however. First, migration can evolve rapidly (Berthold et al., 1992) and mapping migratory status on the branches of a phylogeny should be done with caution, if at all (Klein and Brown, 1994; Joseph et al., 1999). Secondly, migratory status is likely not a single character with two character states, present or absent (Pulido et al., 1996; Zink, 2002). As Zink (2002) notes, the term “migration” is shorthand for the genetic machinery underlying migratory physiology and orientation and so comprises several different adaptive systems. We further suggest that where migration has evolved once within a clade (e.g., tanagers *Piranga* spp. — Burns, 1998; eye-ringed vireos *Vireo* spp. — Cicero and Johnson, 1998), there has also been one evolutionary shift due to homologous genetic, navigational and physiological character state changes in the ancestor of the migratory species. Where migration gains

and losses are more complex (e.g., pipits *Anthus* spp — Voelker, 1999), with possibly multiple origins, non-homologous shifts in one or more of these characters may lead to evolution of different migratory species. It is thus important to carefully set the scope of questions asked when using phylogenetic approaches to the evolution of migration.

2 Evolution of migration in *Charadrius* plovers and their relatives

A test case for use of phylogeny in exploring the evolution of migration is provided by *Charadrius* plovers and their relatives, e.g., *Oreopholus*, *Vanellus* (Joseph et al., 1999). The procedure followed in this study was to treat breeding and non-breeding ranges of the study species as separate characters to be mapped on to their phylogeny, which was itself derived independently from mitochondrial DNA (mtDNA). The character states for breeding and non-breeding ranges were the different continental regions, e.g., South and North America, as non-breeding and breeding distributions, respectively. These characters were mapped on to a phylogeny derived independently from mitochondrial DNA (mtDNA). Shifts in character states for breeding and non-breeding ranges were first reconstructed using parsimony and then mapped on to the branches of the mtDNA phylogeny. Origins in non-breeding grounds, for example, are expected to be manifest as a change in character state when breeding grounds were mapped on the phylogeny but not non-breeding grounds, and vice versa. Further analytical details of the method are given in Joseph et al. (1999).

Here it is important to stress that in using parsimony to reconstruct a range shift on the branches of a phylogeny, it is arguably more important to determine whether a shift is indicated as having occurred rather than to interpret literally the precise node(s) on the tree where it is reconstructed. This caveat derives from the fact that the behavioral attribute of migration (Zink, 2002) can be gained and lost rapidly (Berthold, 1994).

Limited taxon sampling notwithstanding, analyses suggested that *Charadrius* plovers and their relatives first evolved in the southern hemisphere, arguably in South America. A southern, Gondwanan origin concurs with distributions of genera of obscure intra-family affinity scattered across the Southern Hemisphere (e.g., *Phegornis*, *Oreopholus*, *Anarhynchus*, *Erthrogonyx*). At deeper temporal levels of history, we see evidence for past shifts in breeding range. Later, in the evolution of present-day species, shifts in breeding range are again implied. For example, in *C. vociferus* and *C. semipalmatus*, which currently breed in North America, shifts in breeding range from South to North America appeared on the branches of the phylogeny when the character of breeding distribution was mapped. In *C. alexandrinus*, shifts in both non-breeding and breeding distributions were indicated when the entire range of the species was used in the analysis. This seem-

ingly exceptional case was argued to be informative with respect to the potential of the method.

In sum, phylogenetic and biogeographic approaches to the evolution of migration in plovers and their relatives support and expand on what began to emerge from evolutionary ecology in the 1980s (e.g., papers in Keast and Morton, 1980): that migratory birds generally evolve from ancestors in the present-day non-breeding range through shifts of the breeding range. A corollary is that migratory birds are not “avoiding” winter on their breeding grounds, as much as they have evolved displaced breeding distributions under the influence of natural selection.

3 In which birds is migration most likely to evolve?

Have the same processes driven the evolution of migration in one group of birds in one region as in another? Chesser and Levey (1998) used comparative phylogenetic methodology to address this question. Specifically, Chesser and Levey (1998) tested Levey and Stiles’s (1992) hypothesis that migration will most likely evolve in lineages with at least partially frugivorous or nectarivorous species in “non-buffered” edge, canopy, and open habitats areas rather than those of “buffered” forest interiors. They found that although temperate-tropical migration in all New World passerines does tend to be associated with frugivorous lineages, especially those preferring “non-buffered” edge, canopy and open habitats, this relationship is significant only for habitat. They concluded that although the evolution of migration appears constrained in insectivorous species of forest interiors, release from those constraints has not necessarily led to its evolution. Chesser and Levey (1998) recognized that more detailed phylogenies of Neotropical birds at lower taxonomic levels would be necessary to fully explore their approach. Equally relevant here is that in exploring one more phylogenetic approach to defining the pool of species from which migrants are most likely to evolve, Chesser and Levey (1998) opened up new ways of thinking about the ecological patterns and processes underlying the evolution of migration.

4 Phylogeography and population genetics in the evolution of migration

Several recent studies have employed population genetics and phylogeography to examine the history of migration within species (Bermingham et al., 1992; Buerkle, 1999; Milá et al., 2000; Ruegg and Smith, 2001). An excellent model for exploring the use of these approaches is Swainson’s flycatcher, *Myiarchus swainsoni* (Joseph et al., 2003). *M. swainsoni* is the only extensively migratory member of the 11 South American species of *Myiarchus* tyrant-flycatchers (Lanyon, 1978).

Four subspecies are currently recognized under Mayr’s (1942) biological species concept (Lanyon, 1978; Mees, 1985; Haverschmidt and Mees, 1994), two of which

(*M. s. swainsoni*, *M. s. ferocior*) are temperate-tropical migrants within South America and two of which (*M. s. phaeonotus*, *M. s. pelzelni*) are non-migratory, resident taxa in northern and central South America. *M. s. swainsoni* X *M. s. ferocior* morphological intergrades occur in a narrow zone and also are migratory. Lanyon (1978) also recognized zones of morphological intergradation between *M. s. pelzelni* and both *M. s. swainsoni* and *M. s. phaeonotus* to its south and north, respectively. The *M. s. swainsoni* X *M. s. pelzelni* intergrades are migratory.

If the various migratory populations in the *M. swainsoni* complex are each other's closest relatives, then the assumption of a single origin of migration is necessary and adequate. More complicated histories of gains and losses of migration must be explored if they are not. A related issue is the history of shifts in breeding and non-breeding ranges that have accompanied the evolution of temperate-tropical migration in the migratory populations of the *M. swainsoni*. Tools of systematics and mtDNA-analysis have been used to address these issues (Joseph et al., submitted). Forty-nine samples from the *M. swainsoni* complex were obtained over a range of about 4 000 km from Guyana in the north to the border between Uruguay and Argentina in the south. They were part of a larger data set of 120 sequences from almost all other species of *Myiarchus* that were sequenced for the overlapping mtDNA genes, *ATPase 8* and *6* (*ATPase 8/6*). The position of *M. swainsoni* in the *Myiarchus* phylogeny reveals deep history; its population genetics and intraspecific phylogeography inform us of more recent history.

mtDNA of migratory nominate *M. s. swainsoni* is not closely related to any other *Myiarchus* sampled, species and subspecies. Residual phylogenetic uncertainty in the broader analysis does not obscure the key point that no single analysis placed all of the migrants as each other's closest relatives. mtDNAs from all other migratory and non-migratory members sampled in the *M. swainsoni* complex were extremely closely related. Thus 44 migratory and non-migratory individuals sampled across some 4 000 km of South America and from populations showing substantial morphological divergence from one another showed zero net mtDNA divergence across South America. As a group, furthermore, they are more closely related to the dusky-capped flycatcher (*M. tuberculifer*) complex than to nominate *swainsoni*. Thus at least two independent origins of migration are implied in the whole *M. swainsoni* complex, one in *M. s. swainsoni* and at least one in *M. s. ferocior* and the *M. s. swainsoni* X *M. s. ferocior* and *M. s. swainsoni* X *M. s. pelzelni* intergrades.

Thirty-one of the 44 migratory and non-migratory individuals had identical *ATPase 8/6* sequences. The other 13, which are equally widely distributed, differed by just one or two base pairs. This finding and the star-shaped statistical parsimony network for the 44 individuals are signatures of a population that has very recently expanded across its geographical range. Support for a recent range

expansion came from highly significant population-genetic statistics (Fu, 1997) and from mismatch analysis (Rogers, 1995), which showed a close fit between observed and expected patterns under a range expansion. A parameter estimated in this latter analysis, τ is the time since the expansion occurred. The range of its estimates (Joseph et al., 2003) places the expansion as having occurred within the last few hundred thousand years at most.

MtDNA of migratory *M. s. swainsoni* is substantially divergent from that of all other migrants and non-migrants in the complex (3.1% net divergence). In birds, this level of divergence is typical of that between well-marked species (e.g., Avise and Walker, 1998). It indicates a deep divergence between nominate *M. s. swainsoni* and other migratory populations in the complex. Conventional calibrations of the rate of sequence evolution in coding regions of mtDNA (Fleischer et al., 1998 and references therein) suggest that migratory *M. s. swainsoni* diverged from sister ancestral populations probably at the beginning of the Pleistocene.

When breeding distributions are mapped on to the phylogeny (*sensu* Joseph et al., 1999), independent shifts to southern South America are seen in the history of migratory *M. s. swainsoni* on one hand and in the migratory populations of the clade of migrants and non-migrants on the other. These shifts almost certainly would have occurred at very different times given the substantial divergence between the two groups of migratory populations and the shallow divergence among the 44 migratory and non-migratory individuals. A more complete analysis (Joseph et al., 2003) finds that paleo-environmental data offer support for these inferences.

5 Conclusions

The tools of historical biogeography, phylogeny and population genetics allow one to tease apart the spatiotemporal diversity in the evolution of migratory systems. A single migration system today need not have evolved in response to one set of environmental factors operating at one time or in one place. At the avian family level in such a system, the conclusion of independent origins of migration may at first seem trivial. If, however, a case can be made that migration evolved among them at different times and places, then the challenging question arises of what and how many ecological processes were involved. The *Myiarchus* example above highlights this challenge for closely related species or populations. Clearly, there is extensive scope for extending the historical approach to the evolution of migrants generally.

The example of *M. swainsoni* also shows how time frames for the evolution of migration in different migratory populations can be set. That finding in turn directs research into the palaeo-environmental processes that may have initially driven different scenarios in the evolution of migration and the range shifts that accompanied them. These scenarios can then be compared with the processes main-

taining present-day migration. Spatiotemporal heterogeneity may underlie the evolution of any migration system, and this finding could serve as a basis for study of the evolution of migration generally.

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S19-3 Bird ringing as a means for studying the evolution of avian migration — potentials, limits and prospects

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Abstract Bird ringing is the most widespread and longest established approach for studying avian migration patterns. It has been pivotal to the investigation of the evolution of migration by providing information on migration routes and their variation in space and time. Most hypotheses on the evolutionary history of migratory behavior, and constraints on evolutionary change, hinge upon precise descriptions of population-specific migration patterns. Long-term data sets collected in trapping and ringing programs have helped us to identify recent changes in avian migration in response to environmental changes. While trapping programs have limitations in identifying the causes of these changes, population studies with individually marked birds are essential for understanding selection processes and for identifying the ecological interactions underlying the changes. Future research into the evolution of avian migration will greatly benefit from combining ringing results with those from other techniques (e.g., stable isotope marking, genetic marking and satellite tracking).

Key words Climate change, Genetic markers, Migration flyway, Population studies, Stable isotopes

1 Introduction

Bird ringing has been unquestionably the most important method for those disciplines that require the identification of individuals in the field, as in population biology and behavioral ecology, or which study bird movements, as in migration and dispersal. The management of recovery data by national ringing centers facilitates the collection of large, long-term data sets that may encompass large geographic areas, complementing data obtained by local population studies. This information, across different scales, is essential for understanding the dynamics of populations at different levels and for developing and testing new ecological and evolutionary concepts, such as metapopulation theory.

Although a number of new telemetric and molecular techniques have recently been introduced to track individual birds and the movements of populations (e.g., Webster et al., 2002), bird ringing is still the simplest and most cost-effective approach for collect large samples over extensive geographic areas. Moreover, banding and capturing techniques can easily be learned and are non-invasive, which renders them suitable for studying individuals over a longer period of time. Its most important shortcomings, however, are low recovery probabilities, particularly in small passerines, and the lack of randomization of recoveries in space and time. The high dependence of recovery rates on capture and re-sighting probabilities limits the inferences that can be derived in population studies.

Accordingly, we discuss the potentials and limits of bird ringing for studying the evolution of migration and

evaluate its importance for future research.

2 Identification of migration patterns

The central contributions of bird ringing to the study of migration have come from the identification of migration routes and location of wintering areas. Yet, although many national and international atlases summarize detailed information on species-specific migration routes and winter distributions, much of the data is based on a very low number of recoveries, and the spatial and temporal resolution of recovery analyses are few, if attempted at all. A precise spatiotemporal picture of bird movements, however, is a prerequisite for identifying population-specific migration patterns and migratory connectivity (cf. Webster et al., 2002). Atlases with finer resolution are now being published or are under way (e.g., Wernham et al., 2002).

In addition to providing basic information on migration routes and wintering areas, ringing studies with a large number of recoveries, such as those for the European white stork (Fiedler, 2001), can help to detect changes in time and intra-specific variation in migration patterns. Detailed analyses of large-scale recovery data may identify distinct population-specific flyways or wintering areas. This may be the basis for drawing inferences on historical and current environmental factors, such as geographic or climatic “barriers”, that favor or constrain the evolution of migration patterns and cause the isolation of populations. Analyses of ringing recoveries of European robins (*Erithacus rubecula*), for instance, reveal that populations apparently wintering in different regions of southern Europe use different migra-

tion flyways and differ in migration phenology. Remisiewicz (2001) hypothesized that this migration system “probably reflects the pattern of re-colonization of Europe after the glacial period from the primary refuges”. Even so, the inferred migration pattern may not reflect actual migration differences but inter-site variation in ringing and recovery effort instead.

The question of whether different populations use different wintering areas and reach them by different flyways has concerned migration researchers ever since the very beginning (e.g., Palmén, 1876). The study of migration connectivity is now receiving increased attention as new techniques for its study become available and its importance for the conservation of migratory species becomes recognized (Webster et al., 2002). Genetic markers, in particular, help to identify the breeding populations of birds captured on migration or wintering grounds. This approach is particularly valuable because a knowledge of genetic population structure is essential for understanding the processes leading to inter-population differences in migration. Wennerberg (2001), for example, located the origin of migrating and wintering dunlins (*Calidris alpina*) by tracing geographic variation in the distribution of mtDNA haplotypes. She showed that different dunlin populations migrate in parallel, western populations to wintering areas in the west and eastern populations to those further east, where migration distances increase from west to east. Ringing recoveries and morphometric data supported her results.

However, the utility of genetic markers for identifying the origin of individuals is often limited because of the meager and overlapping genetic variation usually found within and among avian populations. The advent of recently developed highly polymorphic genetic markers (e.g. microsatellites, AFLPs) has improved resolution. Yet the “genetic homogeneity” of avian species is a consequence of the high mobility of most birds, resulting in strong gene flow among populations or of their recent origin. Consequently, genetic differences in neutral genetic markers are normally only found among populations that have been isolated for significant periods.

Thus, genetic studies can often assign birds only to large, well-separated breeding populations and areas (Clegg et al., 2002). Bensch et al. (1999), for example, studied genetic differentiation in a hybrid zone between two subspecies of the willow warbler (*Phylloscopus trochilus*) in central Sweden. This hybrid zone coincides with a migratory divide previously identified by ringing-recovery analyses. They found clear morphological and behavioral differences among populations on both sides of the divide, but no genetic differentiation at neutral loci (mtDNA and microsatellites, cf. Bensch et al. 2002), suggesting either recent evolution of the extrinsic differences and/or strong selection on these characters in the presence of gene flow. Stable isotope ratios in primary feathers, moreover, differ between the populations on either side of the divide, indicating in turn that each willow warbler subspecies winters

in different areas in Africa, a result reflected in the distribution of ringing recoveries (Chamberlain et al., 2000).

As do genetic markers, stable isotopes can thus help to delineate the breeding and wintering areas of unmarked birds, and unravel previously unknown migration patterns (cf. Hobson, 2002). However, the validity of data obtained by this technique has still to be assessed against other methods, such as ringing, because a number of variables (e.g., age-composition, among-year variation, altitudinal variation) can confound results (Graves et al., 2002).

3 Constraints on evolutionary change

Migration routes are commonly considered to be adaptive, to represent optimal solutions to prevailing environmental conditions (Pulido, this symposium). Yet analyses of ringing recoveries suggest that some migration routes may not be optimal. Some populations do not migrate to the closest suitable wintering area; and other populations migrate on unexpectedly long routes that resemble detours. So it is assumed that these populations use historical migration routes and destinations because they have not evolved optimal flyways. Sutherland (1998) found 43 examples of bird populations that had recently changed migration routes; and 14 currently migrate on apparently suboptimal routes. Potentially constrained evolution of migration was found exclusively in species in which parental care is short, i.e. small passerines for which we know that migration patterns are genetically controlled (Berthold, 2001). In species in which parental care is extended, i.e. those with culturally transmitted migratory behavior, changes were frequent and no evidence of suboptimal migration routes was found. This result seems to indicate that changes in migration direction are more frequent and faster in species with culturally transmitted migration patterns. However, we cannot yet exclude the possibility that this result is an artifact of biased representation of taxa.

Although some migration routes seem to be maladaptive, and constraints to evolutionary change appear to be the best explanation for them, ringing studies alone cannot exclude adaptive explanations for these patterns. Here, again, other methods can help to corroborate hypotheses founded on the results of ringing studies. Swainson's thrush (*Catharus ustulatus*), for example, is separated in coastal and continental populations which differ in migration route and wintering area. Birds breeding in Alaska undertake a long westward flight before turning south, whereas those of the coastal population on the other side of a migratory divide fly immediately southwards.

Using differences in mtDNA haplotypes, Rugg and Smith (2001) showed that the Alaskan population is closer genetically to the continental group and was established after a recent range expansion. Its apparent detour on migration most probably reflects its colonization route, constraining evolution of a more direct migration route. Nevertheless, although genetic studies can help to reconstruct colonization histories, they cannot show if or by what

factors evolutionary change has been constrained. There may be different explanations for evolutionary stasis, for which the lack of genetic variation is just one possibility (Merilä et al., 2001). The study of such causes requires long-term population monitoring to assess selection regimes, genetic variation, and the interaction of genotype and environment (Pulido and Berthold, 2003; Pulido, this symposium).

4 Recent changes in migration patterns

Many recent studies have demonstrated that migratory behavior is highly flexible, and may respond rapidly to environmental change, natural and man-made (Burton, 1995; Moss, 1998; Sutherland, 1998; Berthold, 1998; Fiedler, 2003). Migratory responses can be grouped into four main categories: (1) change in migration distance, (2) change in route, (3) change in migrant frequency, and (4) change in timing (Fiedler, 2003). The first evidence for such changes came from field observations: winter counts, visual observations of migration, first arrival counts. To address questions on evolutionary mechanisms, however, it is necessary to investigate changes within discrete populations which, in most cases, requires individual marking.

Trapping data from willow warblers on autumn migration in southwestern Germany show a recent trend towards an increase in the number of birds migrating late in the season, while the population mean has remained unaltered (Fiedler, 2003). In this study, standardized trapping and individual marking have revealed a complex change in pattern over time. Though this change may be interpreted as evidence for relaxed selection during late passage, alternative explanations cannot be excluded. It could, for example, result from an increase of individuals from late-migrating populations, in which case it would mirror changes in the admixture of populations on passage rather than timing shifts within the populations themselves. Other techniques, as for instance stable isotope analyses, could help to identify the origin of late birds and resolve the competing explanations.

In partially migratory populations, local and regional changes in the frequency of migrants may be difficult to detect because of the year-round presence of residents. Here individual marking is a prerequisite for elucidating patterns of change. In his analysis of greenfinch (*Carduelis chloris*) ringing recoveries in two areas in England, Main (1996) found an increase in mean winter recoveries from 33% to 53% and from 17% to 29% for distances over 20 km, respectively. This trend was correlated with an increase in population density and may have resulted either from an increase in the frequency of migrants or from an increase in migration distance, or both. Although both traits are tightly correlated and so difficult to separate (Pulido et al., 1996), it is important for evolutionary biology to be able to tease out and distinguish between these alternative demographic scenarios. This, in principle, is possible from analysis of large, representative, long-term data sets of ringing

recoveries. Hitherto, few such studies have attempted to investigate the mechanisms leading to changes in the numbers of overwintering birds (Dhondt, 1983; Adriaensen et al., 1993; Able and Belthoff, 1998).

As it is, examples for all four types of change in migratory behavior have been found in the wild (Fiedler, 2003); and the question now arises whether some migratory traits may change more easily than others. Ringing studies can only provide circumstantial evidence for intra-trait variation in evolutionary rates. Any hypotheses arising from it need to be verified by quantitative genetic studies (Pulido and Berthold, 2003).

5 Population studies on natural selection in the wild

In his study on stonechats (*Saxicola rubetra*) wintering in Belgium, Dhondt (1983) was probably the first to use fluctuations of numbers observed in winter to obtain circumstantial evidence for the genetic basis of migratoriness and residency. He showed that the number of wintering birds varied among years, and that wintering stonechats were recruited from the local breeding population. He tested three potential explanations for this: (1) stonechat numbers could be determined directly by the environmental conditions at the time of departure from the breeding grounds, (2) the population could be polyphenetic for migratory status, and (3) the number of wintering stonechats could vary as a consequence of fluctuations in numbers of breeding birds and of breeding success. Dhondt (1983) found no correlation between the number of wintering stonechats and the number of breeders or autumn temperatures of the area and year, rejecting hypotheses 3 and 1, respectively. He did, however, find a correlation between the number of resident birds and mean temperature in the previous winter, indicating that “differential survival of overwintering and migratory individuals took place and that individuals differ in their tendency to migrate”.

Although Dhondt could not test whether the consistency of individual behavior resulted from inheritance, cultural transmission, imprinting or other mechanisms, he concluded, that, considering the rapidity of changes in the program of migrants, a genetic basis for migratory behavior was “plausible”. One shortcoming in this work arises out of the categorization of “overwintering” birds. Alleged winter recoveries of local birds were made in October; but a recent analysis of stonechat ringing recoveries found that in all stonechat populations, even those exclusively migratory, some migrants remain in the breeding area until October (B. Helm and W. Fiedler, unpubl.). Nevertheless, Dhont’s study is exemplary in showing how individual ringing can help to test competing hypotheses for the causes of change in migratory behavior and in identifying selection processes.

Another study using ringing data to test competing hypotheses involved in the evolution of bird migration was conducted on a recently established and exploding popula-

tion of the house finch (*Carpodacus mexicanus*) in eastern USA (Able and Belthoff, 1998). It investigated whether the increase in migration distance and the proportion of migratory individuals in that population reflected evolutionary change, namely changes in genetic composition or phenotypic plasticity. That actual evolutionary change was the cause is supported by two findings. First, migration distances in newly colonizing populations were consistently larger than those in the overall population at the same time. This result is to be expected if there is heritable genetic variation in the migratory trait, because newly colonizing populations should consist of descendants of colonizers with inherently larger-than-average migratory activity. Were migration distance environmentally induced, migration distances would have been correlated with latitude — which they were not. Secondly, a higher frequency of residents in the most recently-established populations was not found, as would otherwise have been expected if migration status had been facultative and determined by environmental conditions. This study has been the first to reconstruct the evolution of migratory behavior, a result made possible only because of the large number of ringing recoveries available.

In this field, population studies may not only help to identify adaptive changes in migratory behavior and their presumptive causes but also to assess adaptability by reconstructing micro-evolutionary change (cf., Pulido, this symposium) and by providing estimates of phenotypic and genetic variation in migratory traits in the wild (Pulido and Berthold, 2003).

6 Conclusions

Bird ringing has been and still is the prevailing approach to the study of avian migration patterns and their changes in time. Ringing studies have revealed large inter- and intra- population variation in migration routes and phenology. Furthermore, they have demonstrated that migration is a very flexible, complex trait that responds sensitively to environmental change. Many bird populations are currently undergoing active shifts in migration distance, direction, timing and migratory composition. The study of these changes in long- and short-distance migrants may provide evidence for inter-trait and inter-species variation in the rate of change, and for constraints on adaptive evolution. Moreover, studies of ringed populations hold great promise for elucidating the mechanisms underlying these changes.

We believe that the combination of ringing-recovery analyses with recently developed molecular technologies will become the most powerful approach for investigating migration patterns and elucidating the evolutionary mechanisms that maintain and change them. The use of these new technologies, in complement with ringing data, will be especially important in studies of species with low recovery probability, in which ring reading is difficult, and for which recovery probabilities, including recovery notification, are highly variable in space and time. Studies on such species

will benefit as well from the application of methods that allow the delineation of the breeding areas of individuals without previous marking. Advanced tracking methods (attached data loggers, satellite tracking) will help too to unravel individual migration journeys and to refine knowledge of actual migration patterns and their dynamics.

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S19-4 Adaptation and adaptability of migratory behavior

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Abstract Environmental conditions under which extant migration patterns have evolved are diverse and have been changing repeatedly. As a consequence, avian migration is expected to be highly adaptable. Adaptation of migratory behavior in response to changing environments may be accomplished by different mechanisms and at different levels. Adaptive phenotypic plasticity facilitates immediate, fine-tuned response to environmental change at the individual level. At the population level, genetic change in response to natural selection is the mechanism underlying adaptive evolution. Traditionally, these mechanisms have been regarded as mutually exclusive. Current views of evolution, however, consider the plastic response to the environment as a major target of selection. Recent studies have shown that adaptation of migratory behavior may involve both individual adjustment and changes in the genetic composition of populations. Moderate to high levels of genetic variation in migratory traits will facilitate rapid evolutionary change. Extant genetic correlations will accelerate adaptive evolution along an axis of increasing or decreasing migratoriness. However, antagonistic genetic correlations between migratory behavior and other life-history traits may slow down adaptive evolution. Phenotypic plasticity in response to changes in day-length are an important factor in the adaptation of migration to new environments. The response to selection for shorter migration distance, for instance, will be reinforced by phenotypic responses to the photoperiod in the novel wintering area. Photoperiodic responses, however, may become maladaptive if environmental conditions change very rapidly, and birds become desynchronized with food availability.

Key words Genetic correlation, Genetic variation, Phenotypic plasticity, Selection

1 Introduction

Bird migration has evolved as a consequence of seasonal availability of food (Dingle, 1996; Rappole, this symposium). Differences in migration patterns among populations reflect differences in the environments encountered by these populations. Thus it is generally assumed that current migration patterns are adaptations to extant environmental conditions, such as food availability. But environments have forever been changing, and, therefore, migratory behavior has had to readjust repeatedly to new conditions. As a consequence, migratory birds are expected to have evolved specific mechanisms to cope with environmental fluctuations at different spatial and temporal scales (cf. Meyers and Bull, 2002).

Basically, there are two levels at which adaptations can take place: in individuals and in populations. Adaptations in populations, i.e. adaptations in the strict sense, are genetic changes sifted by natural selection. Adaptations at the level of the individual are plastic responses to the environment that do not involve genetic changes. Environmentally-induced changes at the level of the individual, however, are often adaptive and have a genetic basis. If, in a population, there is genetic variation in individual response, this adaptive phenotypic plasticity will become subjected to adaptive evolution, i.e. genetic changes at the population level. Thus phenotypic plasticity may evolve, just as

any other trait, and may be one of the prime targets in adaptive evolution (cf. Pigliucci, 2001). The mechanisms by which adaptive changes in migratory traits are achieved, and their consequences for the evolution of migratory behavior, are the subject of this contribution.

2 Adaptive evolutionary change

Adaptive evolution is the result of natural selection. Natural selection is a process that will work if there is phenotypic variation in a population, if this variation is correlated with fitness differences, and if it is heritable (Endler, 1986). Natural selection in the wild has been demonstrated repeatedly (Kingsolver et al., 2001), but there are a number of factors that may prevent evolutionary change or its detection, such as inherent plasticity, fluctuating selection, genetic correlation (cf., Merilä et al., 2001). Numerous approaches can potentially be used to detect natural selection (Reznick and Travis, 1996). It may, however, be difficult to test for all prerequisites and to obtain reliable models of micro-evolutionary change. In principle, this requires long-term, comprehensive population studies that investigate the ecology and evolution of a population (e.g., Grant and Grant, 2002). Although long-term population studies in birds have probably yielded the best cases for natural selection in the wild, migratory behavior — the incidence, timing, distance and direction of migration — has rarely been the

focus of investigation, partly because it is difficult and labor-intensive to reliably measure migratory traits in individual birds in the wild (cf., Brown and Brown, 2000).

In the last two decades, a number of studies have demonstrated the presence of moderate to high amounts of additive genetic variation in migratory traits in both the laboratory and the wild (Pulido and Berthold, 2003). Genetic variation is one prerequisite for rapid evolutionary change. In the blackcap (*Sylvia atricapilla*), for example, the onset of autumn migratory activity was delayed by almost two weeks after two generations of directional artificial selection (Pulido et al., 2001a). Three to six generations of directional selection on migratoriness transformed a partially migratory blackcap population into becoming wholly sedentary or completely migratory (Berthold et al., 1990). These high selection responses are in accord with responses predicted from the amount of genetic variation found in these populations (Pulido et al., 1996; Pulido et al., 2001a).

There are to date only two studies that identify potential genetic constraints on adaptive evolution of migratory behavior. In a field study on Spanish pied flycatchers (*Ficedula hypoleuca*), no evidence for genetic variation in the timing of spring arrival was found (Potti, 1998). In a common-garden experiment on European blackbirds (*Turdus merula*), a corresponding result was obtained for migratory activity, which is equivalent to migration distance in the wild (Partecke, 2002). It is unclear why no significant heritabilities of migratory traits were found by these studies. One possible explanation is that the traits under scrutiny were difficult to measure and that measurement error may have inflated phenotypic variation (cf. Pulido and Berthold, 2003). Alternatively, low heritabilities could result from increased sensitivity to environmental variation, and could be adaptive. This has been discussed for the termination of migration in the blackcap and other species (Pulido, 2000). Other possible explanations, such as the erosion of genetic variation by natural selection or bottlenecks, need to be explored.

As migratory traits are part of a syndrome, i.e. a suite of coadapted traits, we expect genetic correlations to be major determinants of evolutionary trajectories and of the rate of adaptive evolution (Dingle, 1996). Presently, genetic correlations have only been estimated for migratory behavior in the blackcap (Pulido et al., 1996; Pulido and Berthold, 1998; Pulido, 2000), but corresponding phenotypic correlations among migratory traits in other species suggest that these results may apply generally (Pulido and Berthold, 2003). In view of moderate to high genetic correlations among migratory traits in the blackcap, we expect that the response to selection for any migratory trait will be influenced strongly by selection on other traits. Extant genetic correlations may facilitate rapid adaptation to changes in latitude (e.g., as a result of range expansion) or to climatic changes involving shifts in global temperature. The correspondence between the direction of selection vectors and genetic correlations is most probably the result of recurrent

and persistent environmental changes in the evolutionary history of migratory bird populations (Pulido and Berthold, 1998).

3 Natural selection in the wild

At present, there are only two studies that have investigated adaptive micro-evolution of avian migratory behavior in detail (also Fiedler and Pulido, this symposium). These studies, which are exceptional in elucidating the bases of adaptive change (fitness differences and genetic change), are reviewed here.

3.1 Selection for later spring arrival in the cliff swallow (*Petrochelidon pyrrhonota*)

In a large cliff swallow population in central North America, an exceptionally long cold period caused a high mortality in the spring of 1996. In following years, cliff swallows arrived at their colonies significantly later, as the birds that had survived this cold spell were among the latest that had arrived that year (Brown and Brown, 2000). Thus, there is strong evidence for directional viability selection for later arrival time caused by a cold spell in spring. Brown and Brown (2000) hypothesized that such mortality in years with longer periods of cold weather in spring could mitigate the effects of selection on “normal” years. Birds arriving early in spring usually have the highest breeding success and produce offspring with the highest rate of survival. However, because of these rare yet regularly recurring years with high spring mortality, the arrival date in the cliff swallow population did not change over time. This example shows how fluctuating selection causes evolutionary stasis, without incurring balancing selection.

3.2 Evolution of a novel overwintering area in the blackcap (*Sylvia atricapilla*)

In the early 1960s, a blackcap ringed in Austria and recovered in Ireland puzzled ornithologists, because blackcaps were not known to winter on the British Isles. The traditional wintering areas for central European blackcaps are in the western Mediterranean region and in East Africa. Over subsequent decades, the numbers of blackcaps wintering in Britain, Ireland or northern France increased considerably (cf., Berthold and Terrill, 1988). Several proximate explanations for the increase in blackcaps wintering in these areas were proposed: (1) central European blackcaps could have genetically changed their migration route, (2) birds breeding in Scandinavia — which regularly migrate through Britain — could have started to winter closer to their breeding grounds, and (3) British breeding birds could have become resident. To test these alternatives, Berthold and his colleagues caught blackcaps wintering in Britain, took them to Radolfzell (Germany) and measured their preferred migratory direction in a controlled environment (Berthold et al., 1992).

Their direction of NNW differed significantly from that in south German birds. Subsequently, the English test birds were bred in aviaries; and their offspring too showed

the same mean migratory direction as their parents. Thus, blackcaps breeding in Britain are descendants of birds breeding in central Europe with “genes” for migrating in a new direction. This micro-evolutionary change in wintering area was probably driven by improved survival of blackcaps on the British Isles in winter and higher reproductive success as a consequence of earlier breeding (Berthold and Terrill, 1988).

Evolutionary change in this population not only involved migration direction but also migratory distance and timing. Migration distance for “British winter visitors” is shorter by about one third than for birds migrating to traditional wintering areas around the southwestern Mediterranean. Furthermore, birds wintering in Britain arrive significantly earlier back on the breeding grounds. Although the presence of large amounts of additive genetic variation in migration timing and distance (Berthold and Pulido, 1994; Pulido et al., 2001a) would have allowed this rapid change, phenotypic plasticity responding to photoperiodic conditions in the novel wintering area could alone have advanced spring arrival by more than two weeks (Terrill and Berthold, 1990), shortening migration distance in the process. Thus, it is likely that phenotypic plasticity reinforced selection for this novel wintering area and accelerated the evolutionary changes involved (see below).

4 Adaptive phenotypic plasticity

“Phenotypic plasticity is the property of a given genotype to produce different phenotypes in response to distinct environmental conditions” (Pigliucci, 2001). In principle, phenotypic plasticity may accelerate or slow down adaptive responses. Populations with high levels of adaptive phenotypic plasticity may show fast, immediate responses to environmental change. Such changes, however, will mainly reflect plastic modification of individual phenotypes and not involve genetic change. Yet, evolutionary change is to be expected once directional selection shifts the optimal phenotype beyond the range of environmentally-inducible phenotypes. Although plasticity may enable organisms to survive and reproduce under a wide range of environmental conditions, it is not universal because of the limits and costs to it (cf., DeWitt et al., 1998). Whether adaptive plasticity rather than genetic differentiation is to be expected as the response to changing environmental conditions depends on the spatial and temporal scales at which the changes take place, as well as the frequency and predictability of the changes (cf. Pigliucci, 2001; Meyers and Bull, 2002).

The most important, and probably the best studied, environmental variable influencing migratory behavior is the photoperiod. In seasonal environments, day-length is used by most birds to synchronize the timing of annual life-cycle events with food availability (Gwinner, 1996). In the northern hemisphere, for example, birds experiencing long day-lengths in winter accelerate pre-nuptial molt, spring migration and breeding. Exposure to short days in summer

and autumn accelerates autumn processes: post-nuptial and post-juvinal molt and autumn migration. It has been shown that the strength and direction of these responses have a genetic basis and that there is within- and among-population genetic variation to this response (cf., Widmer, 1999; Pulido, 2000; Pulido et al., 2001b; Helm, 2002; Partecke, 2002).

Inter-population differences in the timing of molt and migration may be largely a consequence of differences in population reaction norms (Helm and Gwinner, 1999; Widmer, 1999; Helm, 2002; Partecke, 2002). Generally, we expect these responses to be adaptive and to reflect inter-population variation in environmental conditions, as in the predictability of food availability (Widmer and Pulido, in prep.). If, however, conditions change rapidly and in directions not previously “experienced” in the evolutionary history of the population, reaction norms may become maladaptive (Schlaepfer et al., 2002), leading to desynchronization of life-cycle events with optimal food availability (Visser et al., 1998), and to an attenuation of selection responses (Coppack et al., 2001). Phenotypic plasticity may also facilitate adaptive evolution if the selection response and environmentally induced change is in the same direction (cogradient variation). The evolutionary response to selection for shorter migration distance, for instance, may be reinforced by the plastic response to the photoperiodic conditions in the new wintering area (Coppack et al., 2003).

In the process of adaptation to current climatic change, a number of rapid changes in avian life-cycle stages, and in migratory behavior in particular (Fiedler 2003), have been observed. Most of the changes in avian breeding have been attributed to phenotypic plasticity (Przybylo et al., 2000; Both and Visser, 2001; Sheldon et al., 2003). Avian migratory behavior may also respond plastically to climatic change. In two recent studies investigating the timing of spring migration, it was found that variation between years in arrival or passage in a number of species was attributable to variation in climatic conditions in the previous winter (Forchhammer et al., 2002; Hüppop and Hüppop, 2003). Although this correlation between phenotypic and environmental variation is indicative of phenotypic flexibility, phenotypic plasticity can only be identified in latitudinal studies (Przybylo et al., 2000). Moreover, if related individuals in a population can be studied, changes in breeding values can be used to estimate the relative contribution of phenotypic and genetic change to adaptive phenotypic change (Sheldon, 2003; Réale et al., 2003).

5 Conclusions

Adaptation to changing environmental conditions may be very complex, as changes can occur at different levels and time scales. Recent breeding experiments and quantitative genetic studies in the wild suggest that different components of migratory behavior may change rapidly in response to directional selection. Moreover, genetic correlations among migratory traits may accelerate the response to selection imposed by global warming. However, unfavourable

vorable genetic correlations between migratory traits and other life-history traits, such as molt, may constrain adaptive evolution. Thus, for predicting adaptive evolution in migration, we need to take into account not only the suite of traits constituting the migratory syndrome, but also those traits to which they are genetically and functionally linked. Moreover, the interaction between selection response and phenotypic plasticity, and the fact that individual birds may modify their migratory behavior by learning from previous experiences, may be important factors determining the direction and rate of evolutionary change. The question how genetic and non-genetic variation interact to facilitate adaptation, and if and why different populations have evolved different adaptive strategies, will be central to future research on the micro-evolution of migratory behavior.

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S19-5 Annual routine models and the evolution of migration

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Abstract Annual routine models are state-dependent dynamic models which enable the computation of optimal behavioral schedules in seasonal environments. We provide an outline of the computational scheme, and illustrate the method with results on the optimal timing of breeding and migration in the annual cycle. The results demonstrate that the dynamics of a state variable denoted as condition, which is compromised by demanding activities such as breeding and migration and recovers slowly, can explain the observation that autumn migration is more spread out in time than spring migration. Annual routine models promise to be a useful method for analyzing how physiological processes shape life-histories and are in turn shaped by ecological and behavioral demands.

Key words Annual routines, Dynamic models, State dependence, Avian migration

1 Introduction

Evolution is in its essence a historical process, but optimality models are usually ahistorical. They can play, nevertheless, an important role in the study of evolution, especially the study of *adaptive* evolution. Given a particular background defined by constraints of all sorts, including phylogenetic constraints, it is possible by optimization methods to identify potential selective regimes that have shaped and currently maintain the trait or traits under consideration. It is also possible to make predictions about the outcome of manipulations — if they are possible — and to identify the possible causes of supposedly adaptive intra- and inter-specific variation.

A widespread criticism of optimality models is that such approaches are usually only concerned with one behavioral trait and not with the interactions among several traits. This is sometimes justified. The advent of dynamic state-variable models has, however, weakened that objection significantly (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000). Only limited by computing power and, far more seriously, by our ability to interpret results, this technique allows us to examine any number of traits, their interactions and trade-offs. The method starts from the insight that decisions should be state-dependent. As decisions are affected by state and decisions change state, optimal strategies will often turn out to be time-dependent. The effects of actions are evaluated in the future; thus it is natural to start computations in the future and to calculate backwards (for technical details, see Houston and McNamara, 1999; Clark and Mangel, 2000).

Weber et al. (1998), Farmer and Wiens (1998, 1999) and Clark and Butler (1999) used this method to study migration strategies. The method, however, presupposes that the reproductive value — the universal currency in dynamic

models and evolution — of all possible states is known at some time point in the future. Dynamic models are therefore an excellent technique for modeling behavior over well-defined time intervals in the life-history of an organism, such as overwintering of birds. But this technique can be taken further to address entire life-histories. There are, however, some problems that need to be addressed.

Attempts to model the optimal scheduling of state-dependent behaviors in seasonal environments pose special problems. For example, some periods of the annual cycle may offer good conditions for several, sometimes mutually exclusive activities: which activity should be performed? When should a second brood be attempted or preparations for migration be started? Should molt occur before or after autumn migration? The chosen schedule of actions may also have long-term effects: reproductive effort in one season may determine the condition at which a bird enters the winter, and the bird's condition at the end of winter will affect its ability to breed in the following spring and the quality of its offspring. The consequence of these complications is that there is no obvious point in the annual cycle where a backward calculation should start — the linkages between the seasons, mediated by the state-variables, can be quite complex. Houston and McNamara (1999) present a model that overcomes these problems and allows the calculation of fully consistent optimal annual routines.

2 The model

The basic outline of this model was developed by Welham et al. (1998) and the results reported here are based on a more recent version of it. General technical details of the computational procedure can be found in Houston and McNamara (1999). The environment consists of two locations: a “northern” location with a seasonally chang-

ing food supply and a “tropical” location with a stable supply (Fig. 1). Decisions are calculated on a weekly basis. Birds are characterized by five state variables: reserves, condition, foraging experience, brood age and location. The experience variable describes the foraging proficiency of individuals. It is low after birth and increases slowly with time. This variable is introduced so that juveniles do not start reproducing immediately after independence. Sources of mortality are predation, starvation and disease. Predation and metabolism are mass-dependent, starvation occurs if reserves drop to zero, and the probability of dying from a disease increases with decreasing condition. At each point in time, birds have to decide which activity to perform: to forage, to start breeding, to continue breeding if they have a brood or to abandon, or to start migration. For each activity, a foraging intensity must be chosen as well. Condition is compromised by high foraging intensity.

The computations maximize the number of descendants left far into the future. Calculations start by “breaking” the annual cycle at some convenient point — in the current in midwinter at week 51 — and by defining a terminal reward function at this point in time. As in standard dynamic programming, backward iterations are used to calculate reproductive value and the best action and foraging intensity for each combination of state and time. Reproductive values one year back are obtained and these serve as the starting point for a new round of iterations. This procedure is repeated until convergence occurs, that is until the reproductive values do not change any longer if iterations are repeated. The results are independent of the terminal reward chosen at the beginning of the computations.

3 Results

We illustrate the possibilities offered by annual routine models with two examples based on the above model and a version including molt instead of migration.

Fig. 2 shows the timing of migration and breeding in the annual cycle. There is one breeding attempt, peaking at around week 20, i.e. before the peak in food supply. The

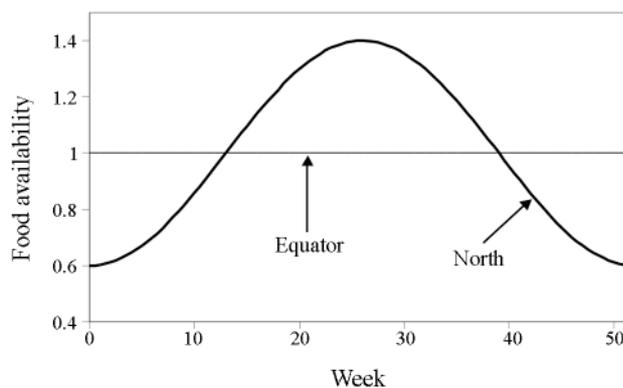


Fig. 1 Food availability as a function of time of year for the two locations in the model

Mean food availability in both environments is 2.

peak in food supply coincides with the raising of the brood. The output reproduces the well-known observation that autumn migration is far more spread out in time than spring migration. With the help of the model we can try to formulate causal hypotheses for why this is the case. Spring migration is concentrated because there are penalties for arriving too early and too late. Individuals that arrive too early encounter a poor food supply, have to work hard to build up reserves, and thus are unable to increase their condition sufficiently fast to breed at all, or to produce offspring that are born early enough to gain their own condition before migration. Late arriving birds are penalized for two reasons: they may arrive too late for successful breeding, or if they are successful, they and their offspring may be low in condition such that their future expectations are bleak.

If the effects of body mass and the condition variables on mortality risk are removed from the model, both autumn migration and spring migration are very concentrated in time. Furthermore, the mean departure time in autumn is delayed by one week: the increased spread and mean of departure times in autumn thus depend on the effects of state. Why migrate early in autumn if condition matters? Early departing birds have high reserves and are in good condition. They arrive early on the wintering ground with decreased condition and have plenty of time to recover before spring migration and breeding. By leaving early they also avoid the need to build up energy reserves for migration at a time when food availability in the breeding area is decreasing. Why migrate late in autumn? Some birds are in such a bad condition after breeding that they need time to recover before they can depart. Without the condition variable there is neither the need to migrate early nor late. With the help of the model we can formulate a causal hypothesis: the slow dynamics of the state variable condition is responsible for the observed departure schedules in spring and autumn.

The following example demonstrates how annual routine models can deal with other questions. One important step is the redescription of the condition variable. Fig. 3 shows the scheduling of molt for a non-migratory species

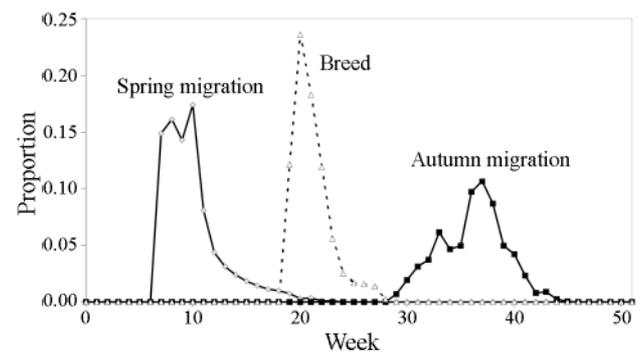


Fig. 2 Proportion of animals migrating and breeding throughout the annual cycle

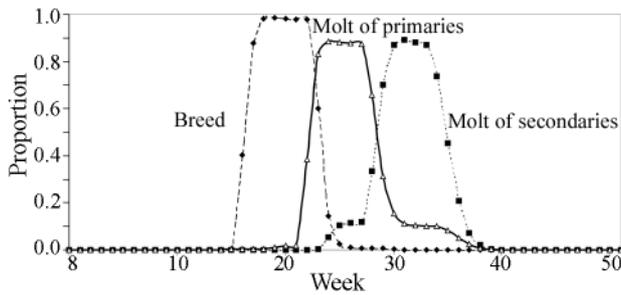


Fig. 3 The optimal scheduling of molt of primaries and secondaries in a resident species

The figure shows the proportion of animals engaged in each activity.

living in the temperate zone. In this model, the above condition variable is replaced by two variables describing the quality of primaries and secondaries respectively. Birds may molt both feather tracts simultaneously or with a variable degree of overlap. Molt can also overlap with breeding. During molt, flight performance is compromised and thus foraging is more costly in terms of predation and metabolic expenditure. The decrease in feather quality depends on foraging intensity. The graph shows that after breeding birds first replace the primaries, which have a substantial effect on flight importance, and then the secondaries.

4 Discussion

What can migration research expect from optimality models now and in the future? Modelers are used to experience two kinds of extreme attitudes towards their efforts: either hope that all problems will at last be solved, or complete disdain. These are two endpoints in a continuum, even though not that rare. Models, however, are just one item in the toolbox of evolutionary biology — and hardly any complex problem can be solved satisfactorily with just one tool.

Annual routine models offer opportunities and, of course, have limitations. The above model can be extended to investigate more locations and problems, such as stop-over choices, choice of wintering latitude and migration routes. Annual routine models seem to offer an especially promising avenue for the linkage of behavioral and physiological processes, and thus may provide insights into the physiological foundations of life-history evolution. A slowly changing state-variable defined as “condition” is responsible for many of the often subtle but complex patterns that arise. This state-variable is responsible for the links between seasons. But what exactly is meant by “condition”? The physiological processes envisaged will depend on the problem studied. In the above model, condition could potentially be identified with immunocompetence (Apanius, 1998).

It still has to be worked out in reasonable detail how immunocompetence enables and constrains life-cycle stages — breeding, migration, molt — and how these events affect immunocompetence. When studying the scheduling of molt

in the annual cycle of migrants and non-migrants, one appropriate condition variable should be feather quality. How do migration and breeding affect feather quality and flight performance? We still do not know the answers to most of such questions about condition variables. They will, however, hopefully spark new research programs, making it possible to ask not only how physiology constrains evolutionary responses but also how physiological processes are shaped by ecological and behavioral demands. Long-distance migration is one of the most demanding of activities, and should offer considerable scope for studying the link between physiological and behavioral adaptations, both experimentally and theoretically.

Annual routine models as they are today have limitations. For example, they do not deal with fluctuating environments. In such environments, all individual without exception are affected by the fluctuations (Lewontin and Cohen, 1969) and the usual fitness measures do not apply. Such models are especially pertinent for annual or short-lived organisms. It remains to be seen how relevant they are for long-lived organisms. More seriously, current annual routine models do not consider frequency-dependence, which most likely is pervasive in nature. This is not an impossible hurdle, but a logical extension to be considered in the future. The models are already complex in their simplest form. An understanding of the current models is needed first before contemplating the addition of further complications.

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Symposium 20 Evolutionary genetics of the Phasianidae

Introduction

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This symposium updates results of ongoing research projects on evolutionary and conservation genetics of species of Phasianidae. The use of molecular methods is producing growing datasets of DNA sequences and allelic frequencies for pheasant species and their populations. As the papers presented show, these data are being used to infer interspecific phylogenetic relationships, to estimate the extent of intraspecific differentiation and to trace phylogeographic population structuring. Thus the symposium contributes to reconstructing phylogenies and evolutionary processes in pheasants. Moreover, pheasants include a number of highly endangered taxa, particularly in Southeast Asia. Although most of them are kept in captivity,

many are bred without appropriate demographic and genetic management. Accordingly, papers in this symposium evaluate recent results produced by conservation genetics programs. These programs assess levels of gene diversity and inbreeding, and detect cases of interspecific hybridization in captive stocks, all needed for implementing effective conservation strategies and reintroduction programs.

All papers presented are published here, except the fourth by Koon Wah Fok and David Parkin. That presentation covered genetic differentiation and evolution in the eared pheasants, *Crossoptilon*; and its abstract is published in the Abstract Volume for the Congress.

S20-1 Supra-generic cladistics of landfowl (Order Galliformes)

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Abstract Molecular and organismal evidence bearing on the evolutionary relationships of gamebirds within the order Galliformes is reviewed. The monophyly of most traditionally recognized supra-generic taxa is supported, but the Phasianini (pheasants) and Perdicipini (partridges and quails) are shown to be polyphyletic. Contrary to DNA-DNA hybridization data, New World quails (Odontophoridae) did not branch off the galliform evolutionary tree before the guineafowl (Numididae), but rather immediately after; and the cracids (Cracidae) and megapodes (Megapodiidae) are not sister groups of one another. Evidence is presented to support the notion of very early divergence among species currently confined to the New World, Africa and southeast Asia. Evidence from mtDNA sequences (cytochrome *b* and D-loop), proteins (ovomucoids), life history, behavior, and bones and feathers is analyzed phylogenetically in three ways: separately, combined and combined but differentially weighted. Separate analysis always produces less well-resolved trees than those suggested by combined data; and downweighting putatively less informative evidence undermines rather than enhances phylogenetic signal. Furthermore, analysis of combined data produces a tree with a novel, but biogeographically meaningful, topology, with organismal and molecular information more useful at respective more basal and more terminal branches of the tree.

Key words Galliformes, Phylogeny, Combined vs separate vs downweighted evidence

1 Introduction

The phylogeny of the pheasant, quail and turkey order Galliformes is reconstructed for 102 in-group taxa listed in Crowe et al. (1992, Appendix 3) and rooted on two representatives of the Anseriformes, a duck (*Cairina moschata*) and a screamer (*Chauna torquata*). Exemplars represent all putative supra-generic taxa and 55 traditionally recognized genera (after del Hoyo et al., 1994). Character data include a combination of 949 phylogenetical informants, from morphology and behavior ($n = 47$), ovomucoid amino acids ($n = 47$), and gene sequences in mitochondrial cytochrome *b* and D-loop ($n = 522, 333$ respectively). Raw data matrices for these three sources of character variation are available from the senior author or from the web site of the Percy FitzPatrick Institute.

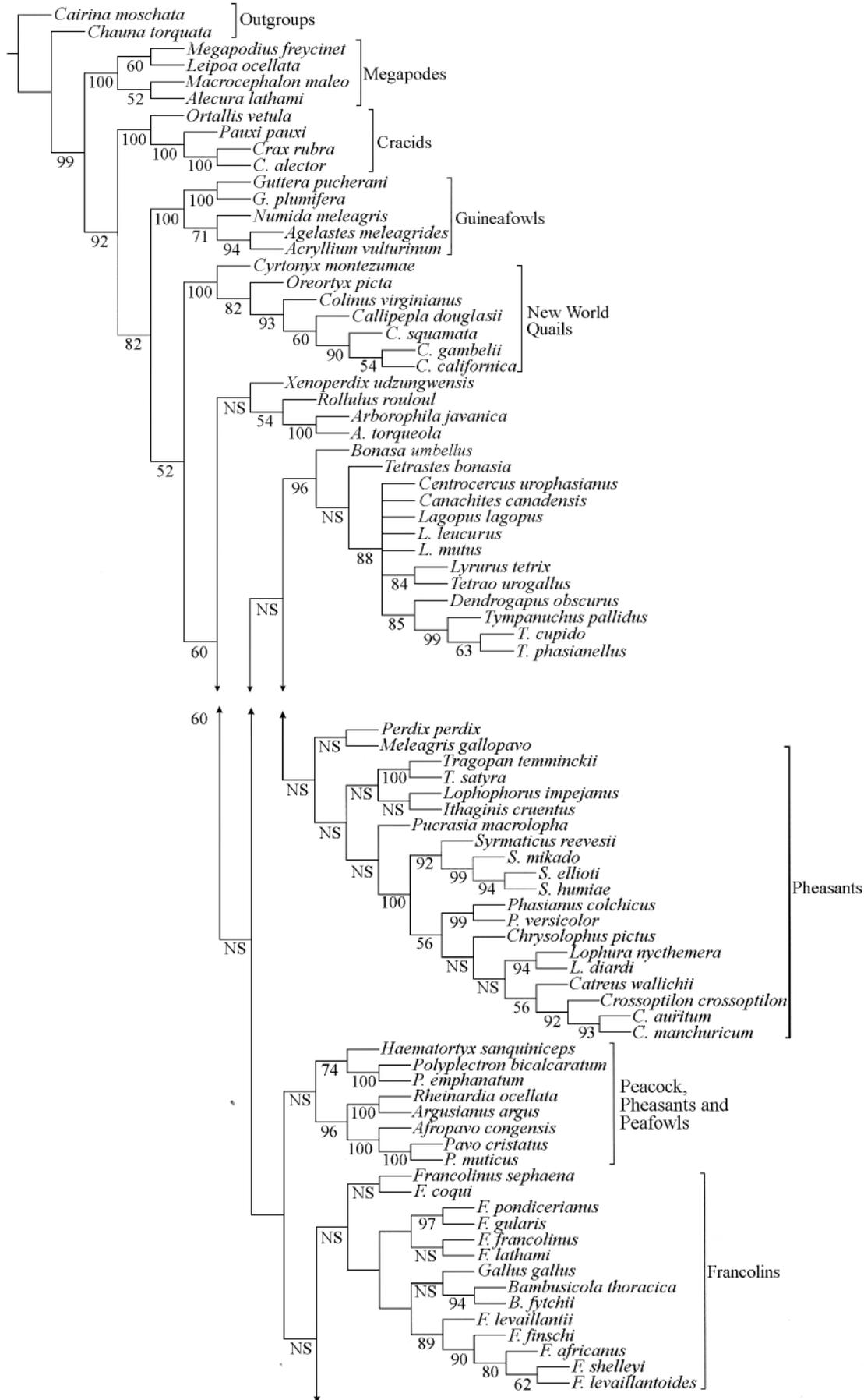
2 Methods

Phylogenetic analyses were conducted using WinClada ver. 0.9.99m8.1 BETA (Nixon, 2000). The searching strategy employed was the Ratchet Island Hopper (1 000 iterations; 2 trees to hold; $\pm 10\%$ characters to sample; and amb. poly. = option), with organismal characters as additive and all molecular characters nonadditive. Bootstrap

analyses were conducted with 1 000 replicates.

3 Results and discussion

Analysis of the combined dataset of characters yielded two equally parsimonious trees (CI = 0.21, 7 296 steps), of which a strict consensus application required the collapsing of five nodes, all within the tetraonine grouse (Fig. 1). Traditionally recognized supra-generic taxa supported by this consensus tree with $\geq 50\%$ bootstrap support are: (1) the Superfamily Phasianioidea, including all galliforms except the megapodes and cracids; (2) the megapodes (Megapodiidae); (3) the cracids (Cracidae); (4) the guineafowls (Numididae); and (4) the New World quails (Odontophoridae). Resolution within the Phasianidae is not well supported. Within the phasianids, the grouse (Tetraoninae), the gallo-pheasant subset of the pheasants (Phasianinae, including *Syrnaticus*, *Phasianus*, *Chrysolophus*, *Lophura*, *Catreus* and *Crossoptilon*), and the pavonine peafowl (Pavonini, including *Rheinardia*, *Argusianus*, *Afropavo* and *Pavo*) are supported. However, although grouping with the gallo-pheasants, the basal pheasant assemblage of Johnsgard (1986), excluding the junglefowls (*Gallus* spp.) and peacock-pheasants (*Polyplectron* spp.), does not have “significant” ($\geq 50\%$)



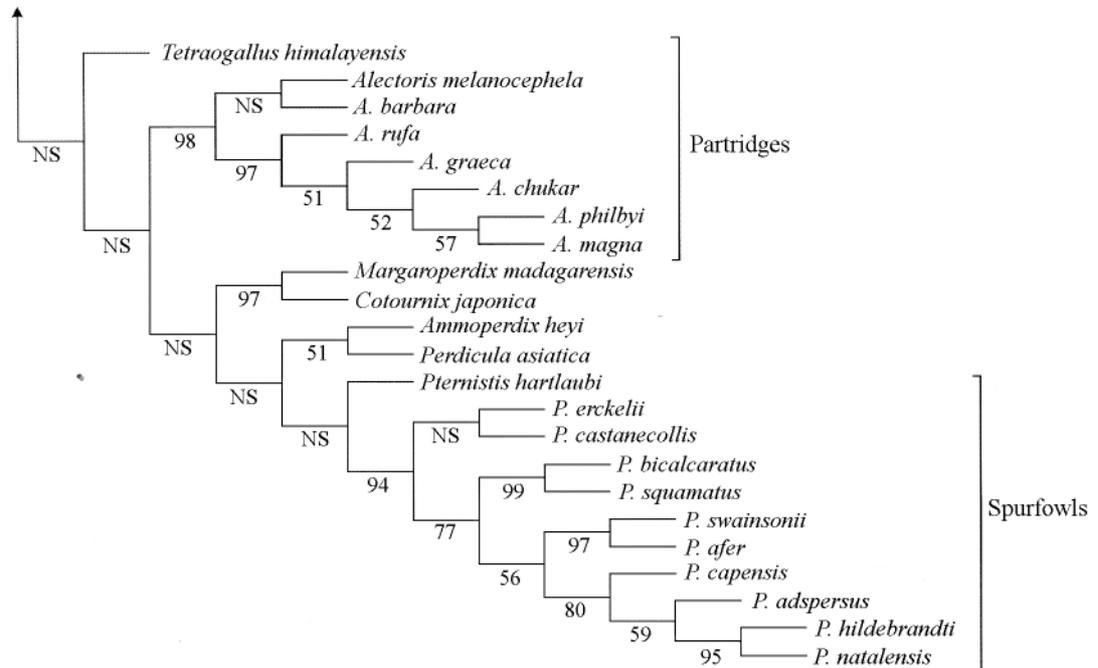


Fig. 1 (page 355 and above) Phylogenetic relationships of galliform birds

Tree based on maximum parsimony analysis of a combination of 949 phylogenetically informative morphological-behavioral, ovomucoid amino acid, and mitochondrial cytochrome *b* and D-loop characters. Numbers at nodes are bootstrap values (NS = not supported by bootstrap values of ≥ 50).

bootstrap support.

The monophyly of several traditionally recognized groupings is not supported. The megapodes and cracids which comprise the order Craciformes or superfamily Cracoidea are paraphyletic with respect to one another. Partridges (tribe *Perdicini*) are highly polyphyletic. The grey partridge (*Perdix perdix*) groups with the wild turkey (*Meleagris gallopavo*) or with the pheasants when the turkey is excluded. The sister taxon of the Madagascan partridge (*Margaroperdix madagarensis*) is the common quail (*Coturnix coturnix*), and that of the sand partridge (*Ammoperdix heyi*) is the bush quail (*Perdix argoondah*). The francolins (*Francolinus* spp., *sensu* Hall, 1963) comprise at least two distantly related clades: (1) true francolins, including *Dendroperdix*, *Peliperdix*, *Francolinus* and *Scleroptila*, and (2) spurfowls, including *Pternistis* (also Crowe et al., 1992; Bloomer and Crowe, 1998).

Contrary to DNA-DNA hybridization results (Sibley and Ahlquist, 1985, 1990; Sibley, 1994) and those of 'culled' DNA sequences of mitochondrial cytochrome *b* from a small set of exemplar taxa (Kornegay et al., 1993), the New World quails, although basal within the Phasianoidae, are not basal relative to the guinea-fowls. Noteworthy among the other novelties is the placement of the red junglefowl (*Gallus gallus*) with bamboo partridges (*Bambusicola* spp.), within a clade dominated by "francolins" and "partridges" and outside of clades including pheasants (cf., Fumihito et al., 1995; Kimball et al., 1999). Other novel groupings include the association of the recently discovered African "partridge" *Xenoperdix udzungwensis* (Dinesen et al., 1994) with

Asiatic "partridges" (*Rollulus rouloul* and *Arborophila* spp.), and the crimson-headed wood partridge (*Haematortyx sanquineus*) with the peacock-pheasants (*Polyplectron*).

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S20-2 Using molecular phylogenetics to interpret evolutionary changes in morphology and behavior in the Phasianidae

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Abstract We used molecular phylogenies derived from mitochondrial and nuclear DNA sequence data to interpret changes in morphological and behavioral characters among several genera of phasianids. This approach has been difficult to develop because relationships among the Phasianidae are poorly resolved. Bayesian analyses of cytochrome *b* with more complex, codon-based models improved resolution relative to previous maximum parsimony analyses. We mapped several characters (presence of fleshy traits, ability to rapidly enlarge fleshy traits, and frontal displays) on to our molecular phylogeny to explore trait evolution. We also reconstructed traits incorporating uncertainty (unresolved nodes) in the phylogeny by reconstructing gains and losses of traits using a set of trees obtained through Markov chain Monte Carlo sampling. Assuming equal weights for gains and losses, we conclude that fleshy traits have been gained and lost multiple times in the course of trait evolution, with wide 95% confidence intervals. In contrast, the ability to rapidly enlarge those fleshy traits is restricted to a single, well-supported clade in which it appears to have been gained only once. Like the presence of fleshy traits, the presence of a frontally-oriented display appears to have evolved many times, perhaps in correlation with the evolution of specific ornamental traits.

Key words Galliformes, Cytochrome *b*, Homology, Ornaments, Sexual selection

1 Introduction

In the past decade, molecular sequencing technologies have led to a renaissance in the field of systematics. One of its most exciting aspects is its potential to construct molecular phylogenies for examining other evolutionary questions. This approach can establish whether specific morphological and behavioral traits of living species have been gained or lost during evolution, provide information on trends and directions in evolutionary changes, and test hypotheses regarding speciation. Examining these questions effectively, nevertheless, requires that the molecular phylogeny is well supported.

Many members of the Phasianidae (pheasants, partridges, grouse and turkeys) exhibit extreme ornamental traits and elaborate displays. For example, many species have plumage that is brightly colored, exhibits striking patterns or is highly modified. Many phasianids also have bare patches of colored flesh in a variety of shapes and locations on head and neck. These fleshy traits vary in color, though red is the most common. In some species, their color and shape may remain relatively constant over time while varying in others. The patches are often involved in displays and appear to be important in female mate choice in some species (Ligon, 1999).

We have now examined the evolution of specific ornamental traits in two phasianid genera using well-supported molecular phylogenies. The patterns of speciation and trait evolution in *Tragopan*, a genus of five Indo-Himalayan species, were examined using sequences of the mitochondrial cytochrome *b* gene (CYB) and its control region (CR) (Randi et al., 2000). Evolutionary relationships within *Polyplectron*, a genus of six southeast Asian and Sunda species, were also examined using CYB, CR and intron G of the nuclear ovomucoid gene (OVOG; Kimball et al., 2001).

Males of the strikingly sexually dimorphic species of *Tragopan* wear fleshy throat lappets and horns that can be enlarged rapidly. The horns project and vibrate during display, while the lappet expands to cover the breast; lappets are brightly colored in blue, red, yellow and/or orange. The mtDNA phylogeny for tragopans is better supported than alternative topologies inferred from morphological and behavioral traits, and is consistent with the geographic distribution of *Tragopan* species (Randi et al., 2000). Evolutionary diversification in tragopans is compatible with allopatric speciation in two different episodes about 4 and 2 million years ago, possibly driven by uplift of the Himalayas. Lappets of similar coloration or patterns occur in different clades, suggesting that lappet coloration and pattern has evolved independently more than once. Thus, differences

in ornamental traits in different species probably reflect differences in selection on an ancestral lappet template. Randi et al. (2000) concluded that as each population became isolated by vicariant events, female preference could have selected for unique color patterns that ultimately resulted in independent evolutionary trajectories for the lappets in each species.

Peacock-pheasants of the genus *Polyplectron* are characterized by ocelli (ornamental eyespots) in the plumage of all but one species (*P. chalcurom*). The ocelli appear in many parts of the plumage (tail, tail coverts, wing, wing coverts and mantle), their size and distribution varying among species. All species perform lateral displays, but those with ocelli are more frontal in orientation towards females. The two least ornamented species have long been considered primitive (e.g., Johnsgard, 1999), and were originally placed in another genus. This evolutionary scenario implies that ocelli in *Polyplectron* are derived. Our phylogenetic analyses indicated the opposite, that the ocellated species are basal and the two least ornamented derived (Kimball et al., 2001). Thus, the absence and reduction of ocelli and related display behaviors reflect relatively recent losses of a trait thought to be under sexual selection. Examination of other morphological and behavioral traits suggested that the less ornamented species have not shifted to a different target in sexual selection. Analyses of CYB also provided weak evidence that the closest relatives of *Polyplectron* are the true peafowl (*Pavo*), the Congo peafowl (*Afropavo*), and the argus pheasants (*Argusianus* and *Rheinartia*), although alternative hypotheses could not be eliminated. Thus, it remains unclear whether the ocelli of *Polyplectron*, *Pavo*, and *Argusianus* have a common evolutionary origin.

The difficulty in establishing relationships among phasianid genera that have ocelli underlines the difficulties of developing analyses applicable at a larger evolutionary scale, despite the clear potential of this approach to provide testable hypotheses for behavioral evolution. Analyses of CYB, CR, and OVOG sequences indicate that phasianids have undergone a relatively rapid radiation, making relationships among phasianid lineages extremely difficult to establish (Kimball et al., 1999; Armstrong et al., 2001). Such lack of resolution has limited the unravelling of evolutionary pathways within the family. Here we focus on three questions concerning phylogenetic relationships among the phasianids. First, can more realistic models of molecular evolution improve resolution of phasianid relationships? Secondly, can new insights into trait evolution be gained with improved phylogenetic resolution? Thirdly, can phylogenetic uncertainty be incorporated in the examining of patterns of evolutionary change?

2 Materials and methods

We used CYB sequences from a variety of sources (e.g., Kimball et al., 1999; Randi et al., 2000, 2001). Maximum parsimony (MP) bootstrap analyses were conducted using

PAUP* 4.0b10 (Swofford et al., 2002), and Bayesian analyses were conducted in MrBayes 2.01 (Huelsenbeck and Ronquist, 2001), both following the methods of Braun and Kimball (2002). Model selection used Akaike weights calculated as described in Burnham and Anderson (1998), with likelihood values corresponding to maximum values from the Bayesian analyses. Information about traits and behaviors was taken from Johnsgard (1999) and references therein. Numbers of gains and losses for specific morphological and behavioral characters were reconstructed using MacClade 4.0 (Maddison and Maddison, 2000) from 5 000 trees sampled by MrBayes. The average number of changes under multiple equally parsimonious reconstructions is reported when gains and losses are weighted equally and the 95% confidence interval (95% CI) is given.

3 Results and discussion

3.1 Resolution of phasianid radiation

Additional MP analyses of CYB using a larger number of taxa still failed to produce many well-supported clades at the base of the phasianids (Fig. 1). No better results were obtained from larger CR and OVOG alignments (unpubl. obs.). However, analyses of CYB in which parameters were added to describe differences in rates at different codon positions resulted in substantial improvements in model fit. Some of the well-supported clades that appear in these new analyses are also supported by analyses of other mitochondrial and nuclear markers (e.g., Dimcheff et al., 2002; unpubl. obs.). Although the model used in these analyses is relatively parameter-rich, we feel there is still substantial room

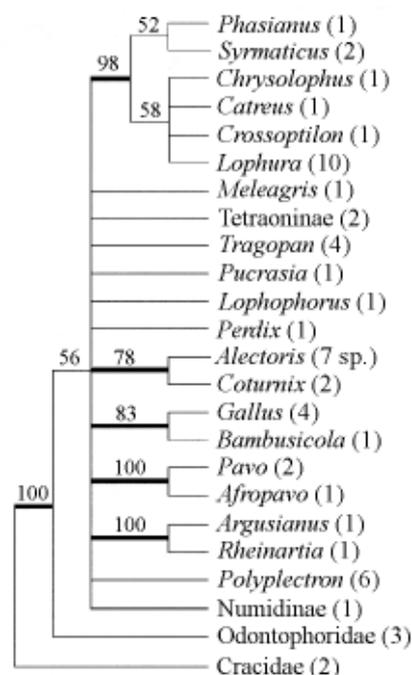


Fig. 1 MP bootstrap analysis

Numbers in parentheses indicate the number of species included in that branch. Branches were collapsed when bootstrap support was <50%, and are presented as thick lines when bootstrap support was >70%.

for improvement and additional resolution may be obtained using novel models.

3.2 Reconstruction of ancestral states in phasianids

Examining the evolution of many traits is difficult, because traits may be diverse and data on character states hard to obtain. Therefore, we only examined several traits of particular interest. Fleishy wattles are not only prevalent in many lineages, but have also been shown to be the targets of sexual selection in some species (Ligon, 1999). Mapping their presence and absence on to our phylogeny reveals that they have probably been gained and lost multiple times (gains: mean = 5.5, 95% CI = 1.5–7.7; losses: mean = 3.9, 95% CI = 1.5–8.0). In the species of *Tragopan*, the fleshy parts can be enlarged rapidly during display. It is an ability that appears in only one well-supported clade (Fig. 2), an ability that thus appears to have evolved only once (95% CI = 1.0–1.0).

Although lateral displays are common in most phasianids, those in several species (e.g., *Polyplectron* spp.) are more frontal in orientation. The evolution of frontally oriented display appears labile, with multiple gains (mean = 4.5, 95% CI = 2.0–6.2) and losses (mean = 2.9, 95% CI = 1.0–6.0), suggesting that such displays are not homologous among all species. Evolution of frontal displays may be driven by changes in ornamentation and sexual selection, as in *Polyplectron*. While additional sequence data may

allow us to further refine our estimates of gains and losses, it is clear that insights about trait evolution can be obtained even without complete resolution of all lineages.

3.3 Using phylogeny to examine homology

The types and differences in position of fleshy traits among phasianids might suggest that such traits are not homologous. However, the ability to rapidly enlarge fleshy traits in one clade of phasianids (Fig. 2) suggests the existence of physiological mechanisms likely to be homologous in the fleshy traits in this particular lineage. Thus, it is possible that superficially different fleshy traits develop in response to common regulatory gene(s) that arose once (Mindell and Meyer, 2001), and therefore that the fleshy traits in this lineage have a homologous genetic base.

4 Conclusions

We have demonstrated that combining more complex models with Bayesian methods can improve phylogenetic reconstruction, providing improved resolution in existing data sets. The addition of further sequence data may ultimately produce a well-resolved phasianid phylogeny. Even available CYB data, nevertheless, can track character evolution, particularly for single traits appearing in single lineages. Incorporating phylogenetic uncertainty into ancestral state reconstruction can also provide useful information when some nodes are poorly supported.

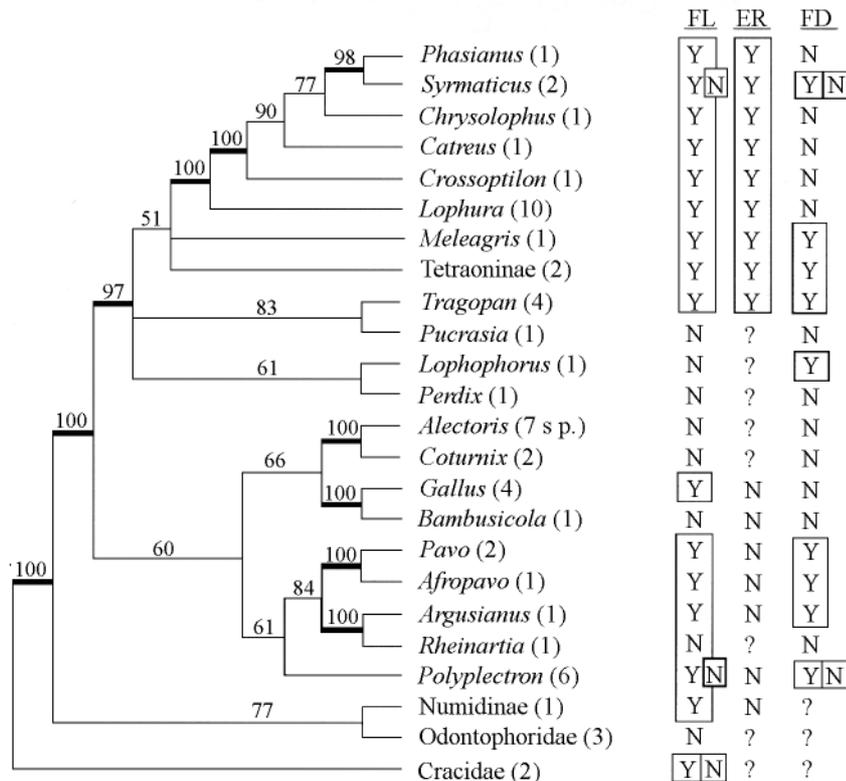


Fig. 2 Bayesian analysis and character state distribution

Numbers in parentheses indicate the number of species included in that branch. Branches were collapsed when the posterior probability of the clade was <50%, and presented as thick lines when posterior probability was >95%. FL = fleshy traits, ER = rapidly enlarging wattles, FD = frontal display, Y = present, N = absent, ? = unknown.

Acknowledgements We thank all colleagues who have assisted us in this project.

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S20-3 The α^A -globin gene as a new nuclear marker for galliform birds

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Abstract Nuclear DNA sequences are used increasingly in phylogenetic and population genetic analyses to complement mitochondrial DNA-based data. I describe primers for the amplification of a major part of the α^A -globin, a nuclear single copy gene, for a broad range of galliform taxa. The variability of this gene is useful for phylogenetic analysis at different scales. At the ordinal level, exon sequences and/or deduced amino acid sequences are applicable. As intron sequences can be aligned unambiguously within the Phasianidae, and exons exhibit rather high variability for a nuclear gene, both yield useful information up to the family level. At taxonomic ranks comparable to those normally assessed with mitochondrial DNA (e.g. the cytochrome *b* gene), the globin gene suffers less from saturation effects due to a higher transition/transversion ratio, while its introns exhibit the same variability. Two intron sequences are suitable for studies of population genetic structure, and may also be used for poultry typing, potentially leading to a better understanding of the history of domestication in the chicken.

Key words Galliformes, Alpha-hemoglobin nuclear gene, Cytochrome *b*, Homology, Ornaments, Sexual selection

1 Introduction

Many phylogenetic and population genetic studies in birds are based on mitochondrial DNA sequence differentiation (Avisé and Ball, 1991; Mindell et al., 1998). For many reasons, however, it is desirable to use additional and independent nuclear encoded markers to supplement and cross-check these data. Because nuclear genes are much less variable than mitochondrial genes (Brown et al., 1979), usually only intron sequences are able to provide comparable resolution at lower taxonomic levels. On the other hand, the use of introns at higher taxonomic levels is limited by alignment problems and saturation of substitutions. Thus, a combination of nuclear introns and sufficiently variable exons can potentially cover a broad range of taxonomic levels with the same marker system and thus enable taxonomic comparisons at different scales. Moreover, those nuclear introns that are variable enough for population genetic studies also enable comparison of population genetic data across a whole family, something that cannot be done, for example, with microsatellite markers.

Hemoglobin is one of the most-studied proteins with respect to structure-function relationships (Jukes, 1991), and has proved useful in bridging the functional links between amino acid sequence, physiological adaptation and ecological value (Hiebl and Braunitzer, 1988). The variability of hemoglobin α -chains in birds is rather high compared to that in β -chains (Braunitzer and Oberthür, 1979; Scherer, 1993), in contrast to mammals, where the opposite is true. The α -genes form a gene family the members of which are tandemly arranged on a single chromosome (Lewis et al., 1991), and exhibit the canonical three exons / two introns pattern of vertebrate globin genes. The introns of α^A , one

of the globins that is expressed in the adult organism, have a length of usually less than 150 bp each in birds and are the shortest known introns of globin genes in general.

Therefore, by application of EPIC (exon-priming, intron-crossing)-PCR (Palumbi, 1994), primers anchored in the first and third exon enable amplification of a major part of the gene, namely that section comprising the central exon coding for the main heme-binding domain of the protein. The chance of amplifying another globin gene accidentally is negligible because differences among globin genes of the same organism are much greater than, for example, between α^A -globin genes among species of birds and mammals. Moreover, the α^A of birds is a single copy gene (Dodgson et al., 1981), in contrast to mammals in which it is duplicated and subject to concerted evolution (Bailey et al., 1992). I designed gene-amplifying primers for a broad range of galliform species to investigate its utility for phylogenetic and population genetic comparisons at different taxonomic scales.

2 Methods

Genomic DNA from whole blood was isolated by standard methods and primers were developed based on the published chicken sequence (GenBank accession number X59989). 100 μ l-PCR reactions contained 1.5 mmol/L $MgCl_2$, 200 μ mol/L of each dNTP, 0.5 μ mol/L of primers 5'-TCCGCTGCTGACAAGAACAACG-3' (sense) and 5'-TCAGGGCAGCAGGGTGGTGG-3' (antisense), a few nanograms of genomic DNA and 1–2.5 U of *Taq* DNA polymerase in Mg-free reaction buffer (Promega). 35 PCR cycles (1 min 94°C, 45 sec 55–63°C, 1 min 72°C) were performed with an initial denaturation step of 4 min at 94°C and a final extension step of 10 min at 72°C. Identity of the fragments was

verified by single read sequencing of the PCR products (GATC-Biotech, Konstanz, Germany). A pheasant and a further chicken sequence were fully determined by cycle sequencing or subcloning as previously described (Fehrer, 1996) and deposited in GenBank (AF125311 and AF125312). Due to the high G/C content of this gene (about 60 % on average; parts of introns can reach up to 70 %), subcloning of PCR products is recommended.

3 Results and discussion

Most species tested (Table 1) yielded a single PCR product of about 600 bp \pm 30 bp due to intron length variation. Annealing temperature ranged from 63°C (chicken) to 55°C (*Talegalla cuvieri*), while 60°C was suitable for most species. *Crax rubra* (Cracidae) samples failed to yield a specific PCR-product, concerning which analyses of the cytochrome *b* gene have shown that cracids stand apart from all other galliform birds (Kornegay et al., 1993). Amplification of samples from other bird orders gave no product even when degenerate primers were used.

The introns of chickens differed by six substitutions and four indels within the one form (white leghorn), indicating individual variability (Fig. 1). Thus, the intron sequences of the α^A -globin gene should yield sufficient information for tracing the history of domestication of chickens, as well as for analyzing the population genetics of galliform birds and poultry races in addition to the RAPD and microsatellite markers that have already been applied (Giesel et al., 1997; Wei et al., 1997; Vanhala et al., 1998). Moreover, whereas those microsatellite markers are only applicable in particular species (Liu et al., 1996), the α^A -globin gene provides a marker system that crosses species at population levels, permitting comparisons among different phasianid species and genera.

Pheasant (*Phasianus colchicus*) and chicken se-

quences differ by 11 substitutions (4%) in the coding regions and 26 substitutions (13%) plus several indels in the non-coding sectors (Fig. 1). Most substitutions are transitions or — in the case of the coding regions — also transversions at synonymous sites. The variability of the introns corresponds to that of mitochondrial cytochrome *b* gene in galliform birds (Kornegay et al., 1993). However, the transition/transversion ratio of the α^A -globin gene of chicken and pheasant is higher than that of cytochrome *b* (3.17 compared to 2.1), indicating that the globin gene may be less subject to saturation effects at low taxonomic levels. Within the Phasianidae, intertaxic introns can be aligned unambiguously. Preliminary phylogenetic analysis of the partial sequences (Table 1) suggest that chicken and pheasant are among the most distant species in the family phylogenetically, and so not representative of its core characteristics.

Comparison with the only other α^A -globin gene sequences known for birds — in the duck, *Cairina moschata* (Erbil and Niessing, 1982) and the pigeon, *Columba livia* (Ikehara et al., 1997) — reveals that intron variability is too great for alignment. The same is probably true for the megapode sequence, of which only a small section was obtained — enough to demonstrate its identity, but too small for more detailed analysis. For relationships above family level, a restriction on exons or the deduced amino acids might be appropriate.

Thus, the alpha-globin gene provides a new marker system for phylogenetic analysis, studies of population genetic structure and poultry research in galliform birds. By comparing coding and noncoding sequences of the same gene across a variety of closely related taxa, the influence of selection in relation to function, development and ecology can now be addressed at the DNA level, access to which is much easier than to the amino acid sequences

Table 1 Species tested for amplification of the globin gene

Family	Subfamily	Species	Amplified/Sequenced	
Megapodiidae		<i>Talegalla cuvieri</i>	+ / +	
Cracidae		<i>Crax rubra</i>	- / -	
Phasianidae	Tetraoninae	<i>Bonasa umbellus</i>	+ / +	
		<i>Alectoris chukar</i>	+ / -	
	Perdicinae	<i>Alectoris melanocephala</i>	+ / +	
		<i>Ithaginis cruentus</i>	+ / -	
		<i>Tragopan satyra</i>	+ / -	
	Tragopaninae	<i>Tragopan blythii</i>	+ / +	
		<i>Meleagris ocellata</i>	+ / +	
	Meleagridinae		<i>Meleagris ocellata</i>	+ / +
	Argusianinae		<i>Polyplectron inopinatum</i>	+ / +
	Pavoninae		<i>Pavo cristatus</i>	+ / +
	Numidinae		<i>Numida meleagris</i>	+ / +
	Phasianinae		<i>Lophophorus impejanus</i>	+ / -
			<i>Phasianus colchicus</i>	+ / +
		<i>Gallus gallus</i>	+ / +	

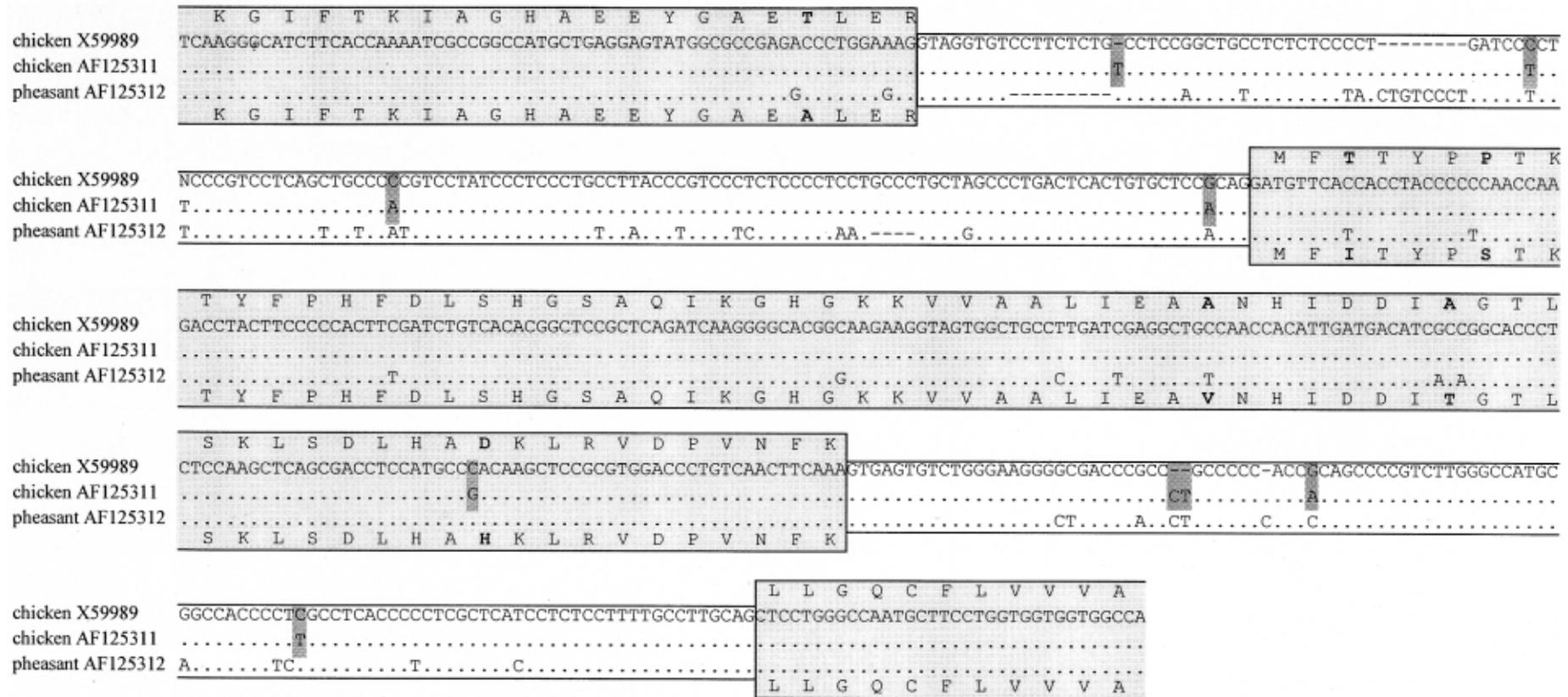


Fig. 1 Alignment of chicken and pheasant sequences: suitability of the globin gene at different taxonomic scales

Exons are shown as light grey boxes with the deduced amino acid sequences given in the one-letter code above and below the nucleotide sequences. Substitutions within the chicken “white leghorn” form are highlighted in dark grey. Dots indicate identity with the first sequence. Substitutions between chicken and pheasant are more frequent in the introns, but also occur in exons; those leading to amino acid replacements are highlighted in boldface. GenBank accession numbers are appended.

used previously.

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S20-5 Evolutionary and conservation genetics of the rock partridge, *Alectoris graeca*

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Abstract Rock partridge (*Alectoris graeca*) populations are declining throughout their range due to habitat changes and overhunting. Massive restocking with captive-reared hybrid birds may lead to risk of genetic pollution. We sequenced 450 nucleotides from the mitochondrial DNA control-region, and genotyped eight microsatellite loci with the aim of investigating phylogeography and population genetic structure in five geographic regions. Both mtDNA and microsatellites indicate that rock partridge populations are significantly differentiated (mtDNA $\phi_{ST} = 0.86$, microsatellite $F_{ST} = 0.35$, $P < 0.001$). The mtDNA haplotypes cluster in two phylogroups (bootstrap values $\geq 93\%$), splitting partridges from Sicily from all the other sampled populations. Divergence times suggest that rock partridges have been isolated in Sicily for more than 200 000 years. This deep genetic subdivision is confirmed by multivariate analyses, Bayesian clustering and population assignment tests of microsatellite genotypes. Genetic data indicate differentiation between partridges in the Alps and populations in the Apennines, Albania and Greece, enabling delimitation of distinct conservation units. Rock partridges in Sicily (*Alectoris graeca whitakeri*) meet the criteria of an evolutionary significant unit, and should be managed accordingly.

Key words Rock partridge, *Alectoris graeca*, mtDNA control-region, Microsatellites, Population structure, Phylogeography, Population genetics, Conservation genetics

1 Introduction

The rock partridge, *Alectoris graeca*, is a polytypic Mediterranean, Balkanic and Alpine species with four described subspecies: *A. g. graeca* (Greece, Albania and south-western Balkans), *A. g. saxatilis* (northwestern Balkans, Dinaric Alps and Alps), *A. g. orlandoi* (central-south Italian Apennines), and *A. g. whitakeri* (Sicily). It occurs patchily in dry rocky subalpine zones on mountains, mainly between 900 and 1 500 m a.s.l., but exceptionally down to 100 m in Greece and up to 3 000 m in the Alps (Johnsgard, 1988).

Rock partridges are declining in most of their range. They use open woodlands, deforested habitats, pastures and vineyards that were created over the last few thousand years by agriculture and livestock grazing. The abandonment of traditional agriculture in mountains, reforestation in the Alps and Apennines, and widespread overhunting, have led to the eradication of many local partridge populations, particularly in the Apennines and Greece. In hunting areas, population decline contrasts with massive releases of captive-bred rock partridges, often of hybrid stock from interbreeding with the closely related chukar partridge (*A. chukar*). The concomitant decline of natural populations, overhunting and the risk of genetic pollution from released captive-bred stock has raised concern for the future of the rock partridge to critical levels.

A fundamental prerequisite for effective conservation and management is knowledge of the taxonomic iden-

tity of target animals and the genetic relations and geographic distribution of component populations (Avise, 2000). The historical biogeography of the west Mediterranean region provides a priori estimates of the phylogeographic structure of *A. graeca*. Rock partridges would not have occurred over much of the Alps and northern Apennines during the last glaciation. Those on Sicily were probably isolated from mainland populations repeatedly due to cyclical separation of the island from the western tip of peninsular Italy through the Holocene. And populations on eastern and western sides of the Adriatic may have been connected via the late Pleistocene landbridge (Lucchini and Randi, 1998).

To clarify population structure and phylogeography in the rock partridge towards identifying evolutionary units for conservation and management, we accordingly sequenced the left half of the mtDNA control-region (CR) and genotyped a panel of eight microsatellites.

2 Materials and methods

DNA was extracted from 332 tissue and feather samples of rock partridges from various locations in Italy, Albania and Greece (Table 1). The entire mitochondrial DNA control-region (mtDNA CR) was PCR-amplified using the external primers PHDL (tRNA^{Glu}; 5'-AGGACTACGGCTTAAAAAGC-3') and PHDH (tRNA^{Phe}; 5'-CATCTTGGCATCTTCAGTGCC-3'). 450 nucleotides were se-

Table 1 Rock partridge (*Alectoris graeca*) collection sites and sample sizes (*n*)

Country	Population	<i>n</i>
Italy	Alps	59
	Apennines	39
	Sicily	35
Albania	Albania	13
Greece	Greece	186

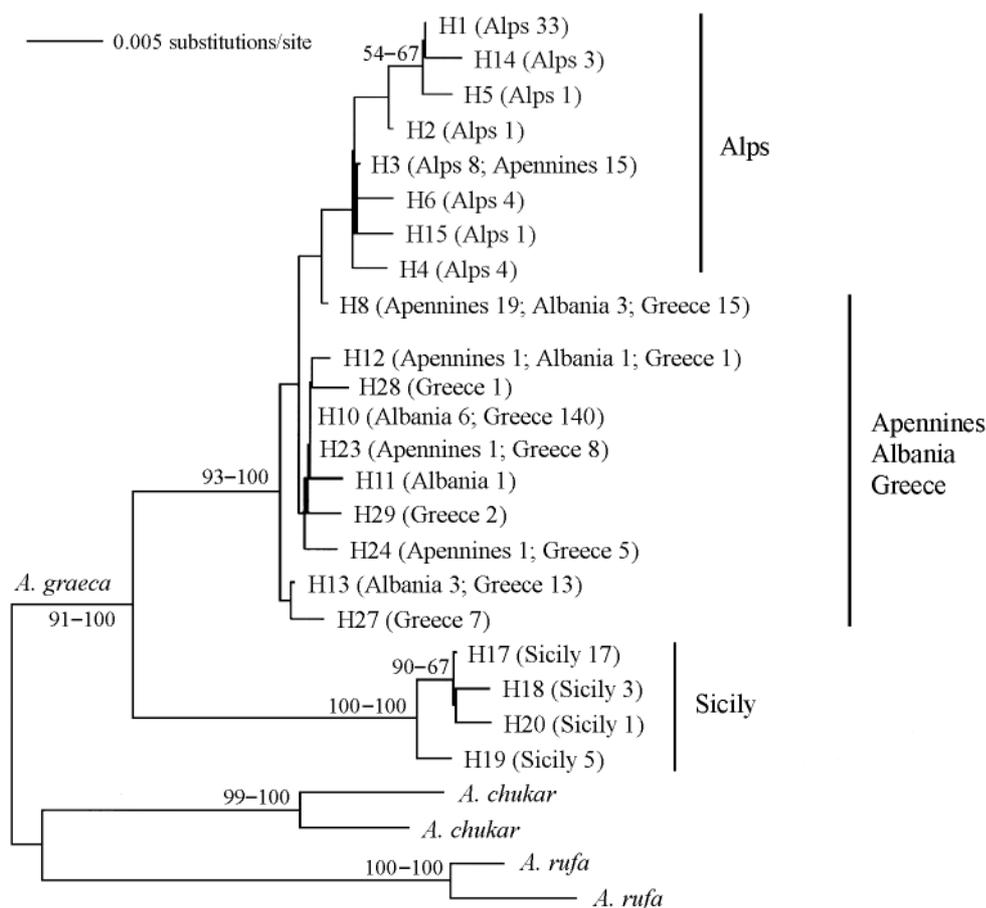
quenced from the left side of the mtDNA CR, mapping positions 1–450 and including the hypervariable domain CR-IA (Randi and Lucchini, 1998). All samples were genotyped as well using eight microsatellites originally isolated from a chicken (*Gallus gallus*) in the genomic DNA library of the Wageningen University Animal Sciences web site: <http://www.zod.wau.nl/abg/index.html>.

Phylogenetic trees were reconstructed using PAUP* 4.0b2a (Swofford, 2002) and the neighbor-joining procedure (NJ) with pairwise genetic distances estimated with Tamura-Nei's model (TN93). Support for the internodes in NJ trees was assessed by 1 000 bootstrap resamplings (BP). Phylogenetic trees were rooted using homologous mtDNA CR

sequences from red legged (*A. rufa*) and chukar (*A. chukar*) partridges as out-groups.

The partitioning of genetic diversity within and among populations was analyzed using the AMOVA procedure (Excoffier et al., 1992). The significance of F_{ST} values was determined by permutations. Patterns of individual and population differentiation were visualized by Factorial Correspondence Analysis (FCA; Benzécri, 1973) of individual multilocus scores, computed with GENETIX (Belkir et al., 1996–2001; <http://www.University-montp2.fr/~genetix/genetix.htm>). Presence of population structure was also inferred from a Bayesian clustering procedure implementing the program STRUCTURE (Pritchard et al., 2000; <http://pritch.bsd.uchicago.edu>). This program is designed to identify regional populations from the individuals sampled and to simultaneously assign the individuals to those populations.

The mutation rate and coalescence time of mtDNA CR haplotypes were computed following Rooney et al. (2001). The number of transversions (*tv*) between the rock partridge and the chukar outgroup haplotypes were counted, and the number of substitutions per site were estimated using the formula $d = (tv + tvR)/m$, where *R* = transition/transversion ratio in rock partridges and *m* = length of the sequence. The rate of nucleotide substitution per site per

**Fig. 1** Neighbor-joining tree clustering mtDNA CR haplotypes in rock partridges

The tree is rooted with homologous mtDNA sequences from red-legged and chukar partridges as outgroups. Values at internodes indicate bootstrap support at $\geq 50\%$. Haplotypes, sampling locations and sample sizes are also indicated, the latter two in parentheses.

lineage per year is $\lambda = d/2T$, where T is the divergence time between ingroup and outgroup species ($T = 2.0$ million years; Lucchini and Randi, 1998). The mutation rate per site per generation is $\mu = \lambda g$, where g is the generation time ($g = 2.05$ years in rock partridges; Bernard-Laurent and Leonard, 2000). The mutation rate per haplotypes is $\nu = m\mu$, and the coalescence time in generations is $t = \tau/2\nu$ (Rogers and Harpending, 1992).

3 Results and discussion

The NJ tree split rock partridge haplotypes into two deeply divergent haplogroups (Fig. 1). The first included all haplotypes sampled from Sicily (BP = 100%), and the second all haplotypes from all remaining populations (BP = 93%). All the haplotypes sampled from the Alps formed a second sub-cluster among mainland European populations (BP = 50%). The average TN93 genetic distance between Sicilian and mainland haplotypes was $d = 3.5\%$, corresponding to 65% of the average inter-specific distance between *A. graeca*, *A. rufa* and *A. chukar* ($d = 5.4\%$). The average TN93 distance between partridges from the Alps and the Apennines-Albania-Greece was $d = 0.9\%$, that is, six times lower than the average inter-specific distance. The phylogenetic tree and genetic distances indicate that the rock partridges of Sicily constitute a separate monophyletic group deeply divergent from all other populations.

The eight microsatellites were polymorphic, comprising 63 alleles in total, with an average of 7.9 alleles per locus. Allelic diversity ranged from 3.2 to 5.5 in populations from Sicily and Greece, respectively. Heterozygosity was in the range of 0.20 (H_o in Sicily) to 0.48 (H_e in Albania). Partridges from Sicily showed the lowest values of H_e and H_o , suggesting that they evolved in isolation at small effective population size for many generations.

An AMOVA performed on the five local populations together (Table 1) showed that 13.5% of total mtDNA genetic variability was distributed within, and 86.5% among populations ($\phi_{ST} = 0.86$, $P < 0.001$). Microsatellite diversity was also significantly partitioned among the five partridge populations ($F_{ST} = 0.35$, $P < 0.001$). All pairwise F_{ST} values among populations were significant ($P < 0.001$), except in comparisons between partridges from Albania and Greece.

The FCA plotting of individual microsatellite genotypes (Fig. 2) supported the sharp distinction of partridges from Sicily, which were grouped apart on the first factorial component (FC-I). Partridges from the Alps, Apennines and Greece were also almost completely distinct on FC-II and FC-III. Samples from Albania were admixed mainly within partridges from Greece and the Apennines.

Bayesian structure analysis indicated that partridges can be split into five distinct genetic clusters. The propor-

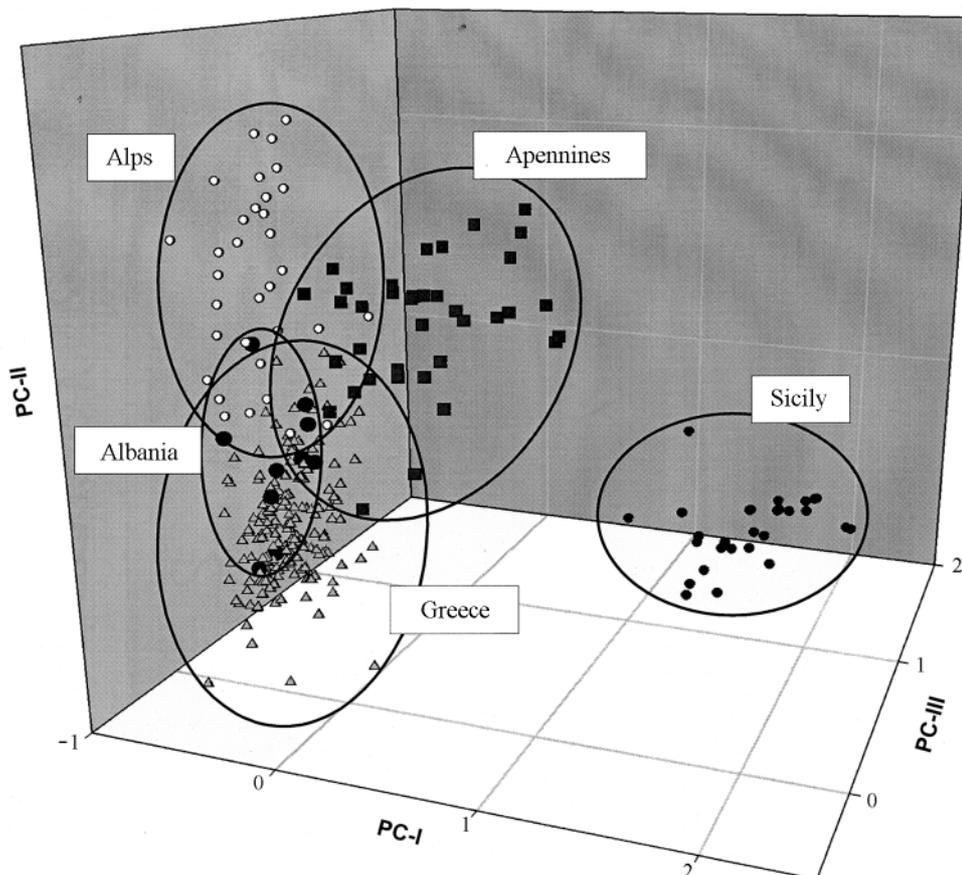


Fig. 2 Three-dimensional Factorial Correspondence plotting of individual microsatellite genotypes. Ellipses were drawn to delimit the dispersion clouds around individual scores; they have no statistical meaning.

Table 2 Proportions of membership of each rock partridge population sampled in five inferred clusters

Cluster Population	I	II	III	IV	V
Italy Alps	0.032	0.030	0.005	0.028	0.905
Italy Apennines	0.815	0.078	0.023	0.025	0.059
Italy Sicily	0.004	0.004	0.983	0.004	0.004
Albania	0.248	0.454	0.018	0.133	0.147
Greece	0.040	0.444	0.007	0.465	0.044

tions of membership of each sampled population in the five inferred clusters are reported in Table 2. Partridges from the Alps were assigned to cluster V ($q_V = 905$); partridges from Sicily were assigned to cluster III ($q_{III} = 0.983$); and partridges sampled from the Apennines were assigned to cluster I ($q_I = 0.815$). Partridges from Albania and Greece were not assigned to any single cluster with $q \geq 0.800$, but split instead into two (Greece) or more (Albania) clusters. Consequently, all the individuals from Sicily and 95.1% of the individuals from the Alps were correctly assigned to their own geographic clusters on genetic information alone; unassigned individuals in the other populations ranged from 54% to 72%.

There were 11 observed transversions between rock partridge and outgroup chukar partridge haplotypes. In the rock partridge, the ts/tv ratio was $R = 8.7$. The average number of nucleotide substitutions per site on the 431 nucleotide-long mtDNA CR alignment was $d = 0.25$. The rate of nucleotide substitutions per site per lineage per year was $\lambda = 0.25/(2 \times 2\,000\,000) = 6.25 \times 10^{-8}$, assuming an inter-specific divergence time T of 2.0 million years; and the rate of substitution per generation was $\mu = 2 \times 6.25 \times 10^{-8} = 1.25 \times 10^{-7}$, assuming a generation time of 2.0 years. The mutation rate for the entire haplotype was $u = 1.25 \times 10^{-7} \times 431 = 5.39 \times 10^{-5}$. The coalescence time $t = \tau/2u$, which corresponds to time since divergence from the most recent common ancestor (TMRCA), was estimated from $\tau = 2ut = 12.84$. The divergence time for the split between Sicily and the other partridges yielded $t_g = 12.84/2 \times 5.39 \times 10^{-5} = 118\,889$ generations, corresponding to $t = 237\,778$ years. The divergence time for the split between Alpine and Albania-Greece populations was $\tau = 1.85$, corresponding to $t = 17\,130$ years. The divergence time between Apennine and Albania-Greece populations was $\tau = 0.41$, corresponding to $t = 3.796$ years. Obviously, these estimates are only as good as the assumed rate of divergence.

4 Conclusions

Mitochondrial DNA and microsatellite data reveal significant genetic structuring in rock partridges. The mtDNA phylogenetic tree grouped all the Sicilian haplotypes into a fully supported monophyletic clade, and further indicated that populations in the Alps formed a discrete subgroup. Patterns of population divergence, visualized by multivariate analyses, showed that Sicilian partridges were sharply

divergent from all the other populations. Partridges from the Alps, Apennines and Greece were also partially distinct from one another in the factorial plotting, while genotypes from Albania were admixed with those from Greece and the Apennines. Distinct population clusters, congruent with sampling locations, could be reconstructed using only genetic information and a Bayesian clustering procedure.

Genetic differentiation strongly supports the long isolation of rock partridges in Sicily, estimated coalescence time of mtDNA CR haplotypes suggesting beyond the last glaciation. In contrast, weak distinction suggests that partridges in the Apennines and southeastern Adriatic regions have been interconnected until recently, perhaps via a late Pleistocene north Adriatic landbridge, and only became separated at the beginning of the Holocene, when the Mediterranean rose to flood the land bridge. The rock partridges in the Alps, genetically homogeneous and distinct from those in the Apennines, Albania and Greece, could have originated either from the south east (northern Dinaric Alps), south west (northern Apennines), or from both sources after the last glaciation. Partridges from Greece could have contributed to postglacial colonization of the northern Balkans and, perhaps, of the Apennines. In contrast, the deep genetic distinction of Sicilian partridges suggests that this population did not contribute to the recolonization of the Apennines and Alps.

Nowadays, partridge populations in the Apennines are isolated and demographically independent from all the other populations. Therefore, I recommend management of the Apennine partridges as a distinct Management Unit (MU: Moritz, 1995), pending additional genetic analyses. Phylogeographic and genetic data are concordant in indicating that the Sicilian partridge (*A. g. whitakeri*) meets the criteria for an Evolutionary Significant Unit (ESU: Moritz, 1995), namely monophyly of mtDNA haplotypes and significant divergence in allelic frequencies at nuclear marker loci.

The risk of genetic pollution continues for the rock partridge population in Sicily and elsewhere. In this study, only 11 interspecific hybrids were identified in 343 rock partridges sampled, indicating, fortunately, that hybridization and gene introgression is not yet widespread in natural populations. However, the mass-release of captive-bred birds that has been going on still has potential to disrupt prey-predator equilibria, consume habitat resources and spread parasitic and infectious diseases. Conservation planning should aim to control and limit the use of captive-reared birds for population restocking on the European mainland, should prevent the release and mixing of rock partridges from different biogeographical areas (Apennines, Alps, south eastern European countries), and should stop captive-breeding and release programs on Sicily altogether.

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M. Pandolfi, and I. Artuso. My deep gratitude goes to A. Bernard-Laurent and A. Meriggi for their contributions to the conservation biology of the *Alectoris* partridges. V. Lucchini, C. Tabarroni and S. Rimondi performed all laboratory and computing analyses at INFS. This project was supported by INFS, Italian Consiglio Nazionale delle Ricerche (CNR) and the Ministero dell'Ambiente e della Tutela del Territorio, Direzione Conservazione della Natura.

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Symposium 21 Visual behavior in birds: linking brain and behavior

Introduction

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Many aspects of avian behavior essential for adaptation and survival — foraging, selection of mates, territorial defense and detection of predators — depend on a well-developed visual system. No other class of animals, in fact, depends as much on vision as do birds. This symposium explores visual function in birds in the framework of the neuroanatomy and neurophysiology of visual systems and visual behavior. A number of recent findings make this topic timely. One of the most important advances in understanding visual processing and development in birds is the recognition that the avian visual system is lateralized at both midbrain and forebrain levels. The papers presented in this symposium address this characteristic, each from a different perspective.

The tectofugal visual pathway in birds is particularly complex; it transforms retinotopic place coding to a functionotopic coding system. Onur Güntürkün discusses complementary functional specializations of the forebrain hemispheres for processing visual information, and how they are affected by light stimulation of the embryo. As we have no detailed knowledge of the organizing principles of the equivalent visual pathway in humans, studies on birds are providing us with unique information. This paper also presents new information on neurochemical asymmetries that develop in the optic tecta as a consequence exposure of the embryo to light.

Contrary to earlier assumptions, there are many vi-

sual projections that cross the midline of the avian brain, as Chao Deng has shown and discussed here. This has consequences for processing visual information. In particular, it has significance for the ways in which the two forebrain-linked visual pathways are differentially involved in controlling pecking at food and social approach behavior.

The development of visual behavior in birds is discussed by Lesley Rogers. In particular, exposure of the egg to light over a particular range of intensities leads to the development of asymmetry in the visual pathways and lateralized feeding and agonistic behavior. Hormonal condition of the embryo interacts with the influence of light, and the ecological significance of both factors are discussed.

Shifts in hemispheric dominance and eye preferences to view stimuli take place during development in birds. Richard Andrew discusses his research on the domestic chicken showing how these shifts ensure that behavior is appropriate at each phase of development. The role of the shifts in hemispheric dominance in constraining and guiding learning is also considered.

In a fourth paper given orally, Shu-Rong Wang discussed the function of subtectal and centrifugal visual structures in the pigeon, concluding that the centrifugal system alerts ground-foraging birds to predators seen in the upper field. A full abstract of this paper is published in the Abstract Volume for the Congress.

S21-1 Structure-function relations of lateralized visual behavior in the pigeon

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Abstract Visual asymmetry in birds is induced by an embryonic right-eye light stimulation that establishes a left hemispheric superiority in object discrimination. It is possible that the prehatch asymmetry of light stimulation only alters visual circuits in the light-stimulated hemisphere, making that side dominant for some visual tasks. However several experiments clearly show that transient lateralized stimulation changes left- and right-hemispheric functions. One examines visuo-perceptual discrimination accuracy as well as visuomotor speed in dark- and light-incubated pigeon embryos. Whereas birds hatched from eggs incubated in the dark are not asymmetrically organized at all, those from eggs incubated in light displayed increased visuo-perceptual discrimination accuracy in the left hemisphere, and a decrease of visuomotor speed in the right. Thus, both measures result in superiority in the right eye (left hemisphere) but by different mechanisms. A similar result is obtained in the second study, by analyzing the effect of light- and dark-incubation on tectal GABA- and Parvalbumin- neurons. Both GABA- and Parvalbumin- cells comprise non-overlapping interneuronal populations which modulate intratectal processes. This study reveals that both cell types develop asymmetrical soma sizes after embryonic light stimulation while dark incubation prevents the establishment of left-right differences. However, light engendered a significant size decrease in GABA-cells in the right tectal hemisphere while inducing a significant shrinkage of Parvalbumin-cells in the left. Since these neurons probably participate in different neuronal circuits, visual asymmetry seems to be established by differentially altering divergent intratectal circuits on the left and right sides of the brain.

Key words Left and right vision, Visuo-perceptual discrimination, Visuomotor speed, Tectofugal neurons, Retinal pathway

1 Introduction

The following review brings together information towards substantiating a hypothesis first formulated by Jerre Levy in 1972 (Levy et al., 1972). According to her view, neither of the hemispheres in the brain dominates a sensory, cognitive or motor process, but makes different and complementary contributions to its achievement. The notion that left and right brains of humans and other animals divide tasks into complementary subprocesses to be executed in parallel has, since then, gained widespread acceptance. This is especially because the hypothesis provides a ready explanation for why asymmetries may have evolved: because complementarity inevitably involves a reduction of redundancy and therefore an increase of processing capacity, lateralized brains will have a selection advantage.

Indeed, human neuropsychological literature shows that language, face and spatial orientation systems are organized such that each hemisphere makes its own and unique contribution (Davidson and Hugdahl, 1995). The same notion has also been put forward convincingly in literature dealing with asymmetry in animals (Rogers and Andrews, 2002). What is lacking, however, is a detailed neurobiological analysis of how this complementarity is created neuronally, and how it is reflected in lateralized behavior.

To this end, I review here a series of experiments with pigeons that show how a short lateralized stimulation during a critical developmental period can induce asymmetrical but complementary processes in the two hemispheres which result in divergently tuned aspects of visually guided behavior.

2 The avian visual system

Birds are the most visually dependent class of vertebrates; and the phrase of Rochon-Duvigneaud (1943) that a pigeon is nothing other than two eyes with wings is valid for most avian species. We humans see the world with about one million ganglion cells within each of our retinæ. This is only 40% of the number of retinal ganglion cell axons counted in a single optic nerve of pigeons and chickens (Binggeli and Paule, 1969; Rager and Rager, 1978). The optic nerves in birds decussate nearly completely, and less than 0.1% of the fibres proceed to the ipsilateral side (Weidner et al., 1985). Because only limited numbers of axons recross via mesencephalic and thalamic commissures, the avian visual system is remarkably crossed.

In birds, two parallel retinal pathways process information to the forebrain: the tectofugal and the thalamofugal system, which are suggested to be equivalent to the respective extrageniculo-cortical and the geniculo-cortical

visual pathways in mammals (Güntürkün, 2000). Within the thalamofugal pathway, visual input comes from within the contralateral nucleus geniculatus lateralis, pars dorsalis (GLd), which itself projects predominately ipsilaterally to the telencephalic visual Wulst (Miceli et al., 1990). In pigeons, approximately 90% of the retinal ganglion cells project topographically on to the contralateral tectum opticum (TO), the first center of the tectofugal pathway. Tectal output is instituted by neurons of the deep tectal layer 13 that project bilaterally on to the nucleus rotundus (Rt), which is connected to the ipsilateral ectostriatum of the forebrain (Hellmann and Güntürkün, 2001).

3 The asymmetry of vision

The avian visual system is asymmetrically organized. Studies in various avian species reveal a superiority of the right eye in experiments which require the birds to distinguish visual objects (Mench and Andrew, 1986; Güntürkün and Kischkel, 1992; Vallortigara et al., 1996), to memorize hundreds of abstract patterns (Fersen and Güntürkün, 1990), or to infer a higher-order rule from serial visual color reversals (Diekamp et al., 1999). Due to the virtually complete crossover at the optic chiasm, these asymmetries could arise from a left hemispheric dominance in the processing of visual objects. Studies in chickens and food-storing birds also reveal a right hemispheric superiority in relational spatial processes (Mench and Andrew, 1986; Clayton and Krebs, 1994; Tommasi and Vallortigara, 2001). These and other experiments reveal that the left hemisphere is not dominant for vision as such, but that each side makes its own and unique contribution to visually guided behavior.

Left hemispheric superiority for object discrimination correlates closely with neuroanatomical asymmetries of the tectofugal pathway. In pigeons, structural asymmetries in the tectofugal pathway have been found in morphological differences between left and right tectofugal structures (Güntürkün, 1997; Manns and Güntürkün, 1999a,b), excessive bilateral afferents on the left side of the tectofugal pathway (Güntürkün et al., 1998), and a prominent left-right difference in transcommissural interactions over midbrain commissures (Keyser et al., 2000).

Visual lateralization is triggered by exposure of the embryo in the egg to light shortly before hatching. Avian embryos adopt an asymmetrical posture with the head turned to the right such that the right eye receives proportionately more light through the translucent shell, leaving the left eye covered by the body. Such asymmetrical stimulation by light modulates synaptic patterns of the ascending pathways in a brief period shortly before to shortly after hatching. If birds are incubated and hatched in the dark, lateralization does not develop (Rogers, 1982; Güntürkün, 1993). The direction of lateralization can even be reversed experimentally by shutting off light to the right eye shortly before hatching in chickens (Rogers, 1990) or thereafter in pigeons (Manns and Güntürkün, 1999b). Together with behavioral asymmetries, anatomical left-right differences can also be

reversed or altered according to experimental manipulation of light stimulation. These experimental interventions have to be performed before hatching in chickens and shortly after in pigeons (Rogers, 1996; Manns and Güntürkün, 1999a,b).

At the first glance, it would seem that only light stimulation early in ontogeny induces changes in the left hemisphere to give it an advantage in object discrimination. However, it is also possible that both hemispheres are altered, albeit in different ways. Skiba et al. (2002) investigated this possibility by testing dark- and light- incubated pigeons in two visual experiments which both yield a right eye advantage but probably tap different kinds of visual processes. One tested grain-grit discrimination, in which the birds had to peck grain from a trough mixed with grain and grain-resembling grit for 30 seconds. Because the number of grains eaten depends on left and right monocular conditions, not the number of pecks, visual asymmetry is tested by accuracy in discrimination, not visuomotor speed.

This is different from the other successive pattern discrimination test using lean variable ratio schedules like VR (visual receptor) 32. Here, the birds had to distinguish the correct pattern right at the beginning of the trial; success then should be reinforced by speed of pecking. Consequently, right eye superiority should be reflected in the number of pecks, while the two monocular conditions generally should not differ with respect to discrimination scores (Güntürkün and Kischkel, 1992). Pattern discrimination here should thus reflect mainly asymmetry in visuomotor speed.

The results of the Skiba et al. (2002) experiments showed that all birds incubated under light revealed a pronounced right eye / left hemisphere dominance in both behavioral testing paradigms. A closer inspection of the results, however, revealed that, in the grit-grain task, the marked right eye dominance in light incubated birds resulted from a selective enhancement of left hemispheric performance. In contrast, right eye superiority in the pattern discrimination test followed from a decrease in right hemisphere performance. Because the grain-grit and successive discrimination tasks teased apart perceptual and visuomotor processes, respectively, these functions are obviously altered differently in both hemispheres. Taken together, incubation under light seems to induce a visual left hemispheric superiority in object discriminations by modulating two different processes: a) an increase in left hemisphere capacity for visuperceptual processes, and b) a decrease in right hemispheric capacity for visuomotor speed.

4 Complementary morphological changes in both hemispheres

The results of Skiba et al. (2002) imply that the effects of embryonic light stimulation are not restricted to simple unihemispheric enhancement of visual processing, but involve mechanisms selectively supporting some neural circuits in one hemisphere and inhibiting other circuits

in the other. Indeed, several recent experiments show that asymmetrical light stimulation results in cellular alterations in both hemispheres. Manns and Güntürkün (submitted) studied soma sizes of tectal GABA- and Parvalbumin- neurons (PV) in adult pigeons which had been light- and dark-incubated during embryogenesis. Both GABA- and PV- cells comprise mostly non-overlapping tectal interneurons which modulate intratectal processes. For example, GABAergic neurons in layer 5 tune the glutamatergic visual input to projection neurons of layer 13 and thus directly influence the tectofugal system (Tömböl, 1998; Tömböl and Németh, 1999).

Manns and Güntürkün (submitted) found that both cellular populations develop asymmetrical soma sizes after embryonic light stimulation whereas dark incubation prevents the establishment of left-right differences. Thus, without asymmetrical light stimulation during embryogenesis, no morphological left-right-differences develop. Light stimulation, however, induced a significant decrease in the size of GABA-cells in the right tectum and a significant shrinkage of PV-cells in the left tectal hemisphere. Since these neurons probably participate in different neuronal circuits, visual asymmetry seems to be established by differential altering of different intratectal circuits. To my knowledge, this is the first demonstration of complementary and lateralized alterations of morphological factors. It strongly underscores the notion that visual asymmetry in birds does not imply a simple enhancement of left hemisphere efficiency but results from differential adjustments of left- and right- hemisphere circuits.

These complementary and hemisphere-specific adjustments of cellular populations and behavioral constituents are probably parts of a general system in which left- and right- brain mechanisms diverge along a small set of principal variables. Studies in humans suggest that the difference between a left-hemispheric “feature”-based and a right-hemispheric “gestalt”-based mode could be among the main driving forces inducing behavioral asymmetries. Studies using discriminations of visual geometrical and object cue-based spatial locations may reveal a similar dichotomy in birds (Tommasi and Vallortigara, 2001). If so, the complementary behavioral and morphological asymmetries outlined above could be constituents of this dichotomy.

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S21-2 Relative contributions of the two visual pathways to avian behavior

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Abstract Birds have two main visual pathways to the telencephalon: the thalamofugal and tectofugal pathways. In the thalamofugal pathway in the chicken (*Gallus gallus*), neurons on each side of the thalamus receive visual afferents from the contralateral retina and project to either the ipsilateral or contralateral Wulst of the telencephalon. These projections are organized asymmetrically: there are more contralateral projections from the left thalamus to the right Wulst than vice versa. This organization is consistent with lateralized visual processing in the Wulst. Since the visual Wulst has reciprocal connections with many telencephalic regions, we suggest that the Wulst is not simply a primary visual area, but also an integration area of the telencephalon. In the tectofugal pathway, each optic tectum (TeO) receives contralateral retinal afferents and then projects to the n. rotundus (Rt) of the thalamus, and, in turn, Rt projects to the ectostriatum in the telencephalon. Contrary to earlier assumptions that TeO projects to only the ipsilateral Rt (via large, myelinated axons), it has now been found that many TeO neurons project bilaterally via small, unmyelinated axon collaterals to the Rt on both sides of the thalamus. Thus, there are two stages of visual transmission in the tectofugal pathway: the first involves rapid transmission to the ipsilateral Rt only and the second involves delayed transmission to both the ipsilateral and contralateral Rt. The significance of these two stages of visual transmission in controlling behaviors is discussed, as well as the differential roles of the two visual pathways in reversal learning and other behavioral controls.

Key words Thalamofugal pathway, Tectofugal pathway, Visual behavior, Lateralization

1 Introduction

Birds have two main visual pathways, the thalamofugal and tectofugal, which send visual information to the forebrain (Fig. 1). The telencephalic area of the thalamofugal pathway is the visual Wulst, which receives visual input via the nucleus geniculatus lateralis pars dorsalis (GLd) of the thalamus (Deng and Rogers, 1998a). The telencephalic area of the tectofugal pathway, the ectostriatum (E), receives afferents from the nucleus rotundus (Rt) on each side of the thalamus; Rt receives visual inputs via the optic tecta (TeO) (Deng and Rogers, 1998b). Over the past three decades, a great deal of effort has been put into working out how the two pathways are organized and what roles they play in controlling various visually guided behaviors.

Although it is now clear that the tectofugal pathway plays a fundamental role in visual information processing, particularly in birds with pareally-positioned eyes, the function of the thalamofugal pathway and its role in visually guided behavior are still obscure. Here it should also be kept in mind that, until recently, knowledge of the function of the avian visual pathways has been based largely on investigations of one species, the pigeon, and that that knowledge has been used to explain the visual behavior of other species. Our recent studies have found, however, some clear differences in the organization of visual pathways between the chicken and pigeon (Deng and Rogers, 1998a,

b; Rogers and Deng, 1999). In this paper, I examine the functional organization of visual pathways in the chicken and their role in visual behavior, and then compare them to those in other species of birds.

2 Visual transmission in thalamofugal and tectofugal pathways in the chicken

One important feature of the avian visual system is the complete decussation of optic nerves in the optic chiasm. Therefore, the optic nerves from one eye project completely to the TeO of the tectofugal pathway and the GLd of the thalamofugal pathway on the other side of brain. Although it has long been known that the GLd sends its efferents to both the ipsilateral and contralateral visual Wulst, the TeO has only recently been found to project substantially to the contralateral as well as ipsilateral Rt in the thalamus (Deng and Rogers, 1998a,b). Thus there are bilateral projections in both pathways: the bilateral GLd-Wulst and TeO-Rt projections. Because information from left and right eyes can only be superimposed on the same neural structure by bilateral projections, such an arrangement is essential for binocular processing and intraocular interaction of information. I have now examined the organization of the bilateral projections in the two pathways of the chicken using double labelling methods.

I injected the fluorescent tracer fluorogold into the

visual Wulst or Rt on the one side of brain and rhodamine B isothiocyanate into the other and then examined the labeled neurons by fluorescent microscopy. This showed that the organization of the projections in the thalamofugal pathway is different from that of the tectofugal pathway (Deng and Rogers, 1998b). In the thalamofugal pathway, there are very few bilaterally projecting neurons, which means that GLd neurons project solely to either the ipsilateral or the contralateral visual Wulst and suggests that different kinds of visual information are transmitted by each projection to the Wulst (i.e., transmitted through separate channels). The GLd-Wulst projections are also organized asymmetrically: there are more contralateral projections from the left thalamus to the right Wulst than vice versa (Rogers and Deng, 1999). Given the presence of these asymmetries, the organization of the thalamofugal pathway should enable the left and right Wulst to process different visual information simultaneously. In fact, functional lateralization has been found in the Wulst of chickens (Deng and Rogers, 1997).

It is also possible that, even though the visual Wulst of the chicken receives visual inputs from the frontal visual field, it is not involved in binocular vision because different visual information is transmitted to each Wulst. Even so, it should be noted that in owls and other birds with frontally-oriented eyes, the thalamofugal pathway is involved

in binocular vision, including stereoscopic depth perception (Nieder and Wagner, 2000).

In contrast to the GLd-Wulst projections, there are many bilaterally projecting neurons (up to 45%) in the TeO which, via their collateral branches of axons, project simultaneously to both the ipsilateral and contralateral Rt. Therefore, after receiving inputs from the contralateral eye, the tectal neurons could send the same information to both the ipsilateral and contralateral Rt via these bilaterally projecting neurons and then to the ectostriatum (E) in each hemisphere. It has been shown that the TeO neurons projecting to the ipsilateral Rt have large, myelinated axons, whereas those projecting bilaterally to both the left and right Rt, and neurons projecting only to the contralateral Rt, have small, unmyelinated axons (Saleh and Ehrlich, 1984). Based on this organization, it has been proposed that visual transmission in the tectofugal pathway of chickens is two-staged. In the first, visual information is transmitted rapidly from each eye to the contralateral hemisphere, and the second transmission is delayed, the information being transmitted slowly to both hemispheres.

It is possible that rapid neural transmission may be used for detecting the stimulus and priming the neuronal activities of the relevant forebrain areas. Then the delayed neural transmission that follows may be used for further

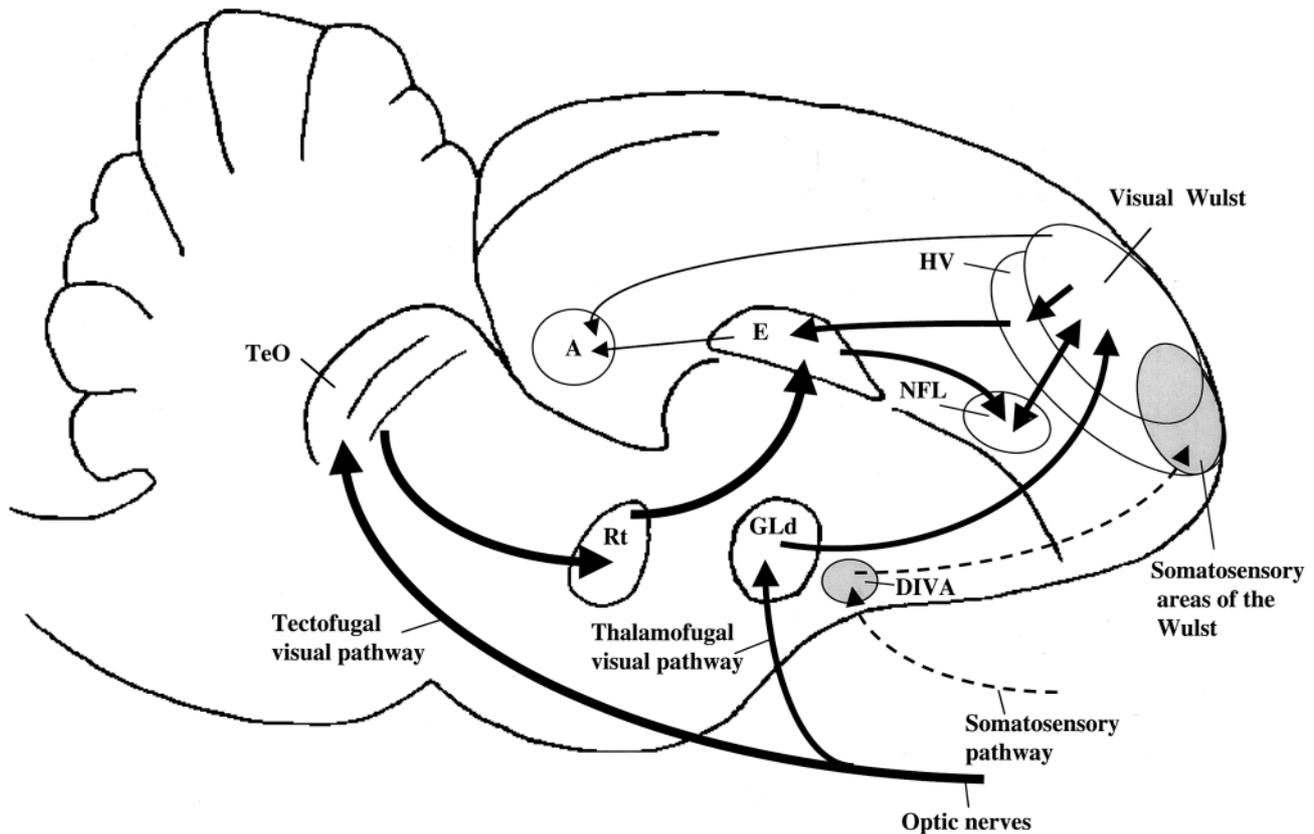


Fig. 1 Schematic view of the two visual pathways and the intratelencephalic connections between them

Note: in the Wulst, the visual area is overlapped with the somatosensory area. Abbreviations: A, archistriatum; E, ectostriatum; DIVA, n. dorsalis intermedialis ventralis anterior; HV, hyperstriatum ventrale; NFL, neostriatum frontale, pars lateralis; GLd, n. geniculatus lateralis pars dorsalis; N, neostriatum; Rt, n. rotundus; TeO, tectum opticum.

binocular information processing, including information used for perceiving depth and analyzing details of visual targets. Consistent with this interpretation, binocular neurons have been found in both the Rt and E of the zebra finch, and information from both eyes interacts in these binocular cells (Schmidt and Bischof, 2001).

3 Telencephalic connections of the telencephalic visual areas

The visual Wulst receives inputs not only from GLd, but also from a large number of connections with other telencephalic areas (Deng and Rogers, 2000). The visual Wulst has dispersed reciprocal connections with the ipsilateral neostriatum frontale, pars lateralis (NFL), the ipsilateral neostriatum intermedium, the ipsilateral dorso-lateral neostriatum (including neostriatum caudale, pars lateralis), and also the bilateral archistriatum (A) (Deng and Rogers, 2000). The visual Wulst, moreover, occupies only a part of the Wulst. The Wulst, as a heterogeneous structure, also receives inputs from other modalities, such as somatosensory and auditory signals (Deng and Wang, 1992, 1993); in fact, the rostral somatosensory area of the Wulst overlaps with the visual area in the pigeon (Fig. 1; Deng and Wang, 1992). It is particularly interesting that the somatosensory inputs interact with visual information on single neurons located in the overlapping areas (Deng and Wang, 1993). All of the evidence supports our hypothesis that the Wulst is not simply a primary visual area but also a telencephalic integration area (Deng and Wang, 1993; Deng and Rogers, 1997), which could explain why the Wulst is particularly important for some cognitive functions and complex behaviors, such as reversal learning.

In contrast to the Wulst, the ectostriatum (E) is specialized for processing visual information only. The core region of E, which receives inputs from Rt, projects to its belt/surrounding neostriatum area; and this region, in turn, projects mainly to NFL, the dorsolateral portion of the tempero-parieto-occipital area (TPO), the lateral portion of the neostriatum intermediale (NIL) and, in a few efferents, to the NCL and A (Husband and Shimizu, 1999; Alpár and Tömböl, 2000). Through these connections, the visual information may be processed in the target areas. For example, Delius et al. (1984) have found that lesions of a lateral telencephalon region, including the NFL and TPO, impair pattern discrimination in the pigeon. Apart from the reciprocal connections with the surrounding neostriatum found in the chicken, however, no other direct reciprocal connections with any telencephalic areas have been found in birds (Husband and Shimizu, 1999; Alpár and Tömböl, 2000).

Some telencephalic areas, such as the NFL and A, receive projections from both the Wulst and E (Fig. 1). It is possible that visual information from both the tectofugal and thalamofugal pathways interacts in the NFL and A, an interaction that may play a role in some cognitive functions. Moreover, although the Wulst does not project directly to the E, it does project to the HV (Hyperstriatum ventrale;

Alpár and Tömböl, 1998). Since the HV projects to E, the Wulst could modulate visual processing in the E via indirect Wulst-HV-ectostriatum connections (Fig. 1). In fact, the visual Wulst has an excitatory influence on flash-evoked responses in the E of the zebra finch (Engelage and Bischof, 1994). Such indirect connections are the neural basis for coordinating the two pathways in controlling visually guided behavior.

4 Roles of two visual pathways in visually guided behavior

The thalamofugal and tectofugal pathways not only have different organization but also differential roles in visual processing and in controlling visually guided behavior. Lesions of the Rt and E cause severe deficits of simple color, visual intensity and pattern discrimination, but similar lesions of the GLd and Wulst have no or little effect on the performance of these tasks (Bessette and Hodos, 1989). However, lesions of the Wulst impair some cognitive functions, such as food versus non-food categorization (Deng and Rogers, 1997), sun-compass associative learning (Budzynski et al., 2002) and reversal learning (Benowitz and Lee-Teng, 1973).

Recently, I have collaborated with L.J. Rogers in an investigation of the roles played by the two pathways in pattern reversal learning by *c-fos* (an early immediate gene) expression. Chickens were trained to search for food in paper cones (length 25 mm, diameter 10 mm) that were printed with black and white checked patterns or toned simply grey without a pattern. During the training period of 5 trials a day for 4–5 days, the patterned-cones contained grains for reward (positive stimuli) and the grey cones none (negative stimuli). Once the chicken had learned this discrimination, it was exposed to reversal, in which the grey cones were filled with grains (now positive) and the patterned cones empty (negative). After only 15 trials (3 re-training sessions, each of 5 trials), the chickens learned the reversed association of the visual stimuli. After completing this relearning task, the *c-fos* expression in the brain was examined by immunohistochemistry.

Preliminary results revealed no *c-fos* immunoreactive neurons in the GLd or Wulst of control chickens. There was, however, a strong *c-fos* expression in the TeO, and also weak expression in the E and Rt. In contrast to the controls, many *c-fos* immunoreactive neurons were found in the GLd and Wulst in the chickens subjected to reverse learning, and also many in the Rt and E. There was, however, no clear difference between control and reverse learning birds in *c-fos* expression in the TeO.

This outcome suggests that the TeO may be activated by general visual stimuli. It is possible that this non-specific activation of the TeO is suitable for monitoring environmental changes; but the Rt and E may be involved in this function also, at a lower level. Since an obvious increase of *c-fos* expression was found in Rt and E after re-

Table 1 Comparison of functions of the telencephalic visual areas of the thalamofugal and tectofugal pathways (based on lesion studies)

Visually guided behaviors	Lesions in the Wulst	Lesions in the Ectoatrium
Simple visual tasks: Brightness discrimination Pattern discrimination Color discrimination	No or little impairment (pigeon, Pritz et al., 1970; Reley et al., 1988)	Severe impairment (pigeon, Hodos and Karten, 1970; Bessette and Hodos, 1989)
Visual acuity	Reduction in the lateral visual field (pigeon, Güntürkün and Hahmann, 1999)	Reduced in the frontal visual field (pigeon, Güntürkün and Hahmann, 1999)
Psychophysical tasks: Intensity-difference threshold Size threshold Line orientation threshold	Minor but stable impairment (pigeon, Hodos et al., 1986; Pasternak and Hodos, 1977)	Elevation of threshold (pigeon, Hodos et al., 1988; Mulvaney, 1979)
Complex and cognitive function: Pattern-reverse learning	Marked deficits (Bobwhite quail, Stettner and Schultz, 1967; chicken, Benowitz and Lee-Teng, 1973; pigeon, Macphail 1976)	(Ectoatrium may also be involved in pattern-reverse learning based on the recent c-fos repression study in chickens)
Color-reverse learning	Marked deficits (pigeon, Shimizu and Hodos, 1989)	Impaired (pigeon, Chaves and Hodos, 1998)
Matching-to-sample performance	Marked deficits (pigeon, Pasternak, 1977)	
Sun-compass associative learning	Deficits (pigeon, Budzynski et al., 2002)	No deficits (pigeon, Budzynski et al., 2002)
Food vs non-food categorization	Deficits (chicken, Deng and Rogers, 1997)	No deficits (chicken, Deng and Rogers, 1997; pigeon, Watanabe, 1992)
Recognition of individual conspecifics	No deficits (pigeon, Watanabe, 1992)	Deficits (pigeon, Watanabe, 1992)

verse learning, the tectofugal pathway is involved in its visual processing. This is consistent with lesioning studies in pigeons, which have shown that lesions of both the Rt and E impair color-reverse learning (Chaves et al., 1993; Chaves and Hodos, 1998). Chaves et al. (1993) also found that lesioning in the GLd of the thalamofugal pathway has no effect on color-reverse responses in the pigeon, even though the Wulst is crucial for both color- and pattern-reverse learning in all avian species studied. They suggested that the Wulst receives visual inputs required for color-reverse learning through the tectofugal pathway, but not thalamofugal afferents (Chaves et al., 1993; Chaves and Hodos, 1998). Our present experiment provides clear evidence that the GLd is involved in reverse learning, at least in pattern-reverse learning.

Based on evidence for the organization of the visual pathways and the behavioral studies described above, I suggest that the tectofugal pathway is responsible for detail analysis of the visual stimulus. Without doubt, visual processing in this pathway is also important in higher cognitive function. The thalamofugal pathway, in particular the Wulst, may be otherwise important for some cognitive func-

tions and controlling other complex behaviors. For example, lesions of the E but not the Wulst impair discrimination of color, visual intensity and pattern. Lesions of the Wulst also impair some cognitive functions. The tectofugal pathway may well be responsible for monitoring changes in environment; further activation in that pathway and the turning-on of the thalamofugal pathway may be followed up for further analysis of visual targets and controlling relevant behaviors. Thus, interaction between the two pathways seems necessary for controlling visually guided behavior, particularly for those visual functions involved in higher cognition.

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S21-4 Development of the two visual pathways and lateralized visual function in the chicken

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Abstract As lateralization of visual function has been shown in seven avian species, as well as in a broad range of both lower and higher vertebrates (Rogers and Andrew, 2002), it can be assumed to be a general characteristic of vertebrates even though it may be expressed in different ways in different species. Some evidence, mentioned here, indicates that a lateralized brain enhances cognitive performance; and this may be a reason why it evolved and has been retained across species. This paper discusses the asymmetrical organization of the visual pathways in birds and the role that exposure of the avian embryo to light plays in the development of lateralization of some visual functions. It considers species differences in transmission of light through the egg shell, and the intensity of light required to generate the asymmetry. The development of asymmetry in visual projections to the forebrain in the chicken is prevented not only by incubating eggs in the dark but also by exposing them to light of high intensity. The extent of light exposure received by the embryo depends on the color and construction of the egg shell, as well as on the location of the nest and the incubating behavior of the parent(s). Steroid hormones also affect light-dependent development of lateralization, mediating the influence of maternal stress on the strength of lateralization in offspring.

Key words Visual behavior, Lateralization, Light stimulation, Steroid hormones

1 Introduction

Visual lateralization was discovered in the domestic chicken (*Gallus gallus*) over two decades ago, as specialization of the left hemisphere for learning to discriminate grains of food from small pebbles and specialization of the right hemisphere to control attack and copulation responses (Rogers and Anson, 1979). Subsequent research confirmed this finding and extended it to demonstrating lateral biases in motor responses guided by left and right eyes (Andrew et al., 2000; Rogers and Andrew, 2002) and to the display of eye preferences to view different stimuli (McKenzie et al., 1998). A large body of empirical evidence now allows us to formulate a general model for lateralization of visual function in the chicken, namely that the right eye and its associated left hemisphere are used preferentially when responses have to be considered against alternatives, as in the case of learning, while the left eye and right hemisphere are used when the response must be given without hesitation (Andrew and Rogers, 2002; Rogers, 2002a). The latter system is demonstrated clearly by a recent study showing that chickens respond with shorter latency to a model predator when it is introduced into their left, not right monocular visual field (Rogers, 2000).

The pigeon (*Columba livia*) shows visual lateralization in terms of faster pecking to feed and superior memory of visual images when using the right eye (Güntürkün, 1985, 2000). This is consistent with findings in the chicken; and the same right eye preference for controlling feeding re-

sponses has been found in the zebra finch, *Taeniopygia guttata* (Alonso, 1998). Other studies of visual lateralization in avian species have measured eye preferences in wild birds monitoring their surrounds for predators or prey. The dark-eyed junco (*Junco hiemalis*) exhibits a right-eye preference for this, whereas the American tree sparrow (*Spizella arborea*), tends towards a left-eye preference (Franklin and Lima, 2001), the latter consistent with the chicken. The kookaburra (*Dacelo novaeguineae*), also shows a strong preference for using the left eye to scan the ground for prey several meters beneath its perch (Rogers, 2002b). Most impressive of all is the New Caledonian crow (*Corvus moneduloides*), which uses of its right eye preferentially when cutting its tools from pandanus leaves with its bill (Hunt, 2000).

All of these studies demonstrate lateralization at the species level; but the eye preferred varies, probably according to the specific processing being used by the bird in each context. Use of the left eye, for example, may indicate vigilance and readiness for a rapid response (either fight or flight) with processing of spatial information, since the right hemisphere is specialized for assessing spatial cues (Rashid and Andrew, 1998; Tommasi et al., 2000). Further research will be needed to clarify the differences among species in eye preferences.

2 Response of the embryo to light exposure

At least some features of visual lateralization in birds develop as a consequence of monocular stimulation of the visual system in the embryo, as shown first in the chicken (Rogers, 1982) and later in the pigeon (Güntürkün, 1993). During the final stages of incubation, the embryo in these species, and probably in most birds, is oriented in the egg so that the left eye is covered and the right positioned near the air sac where it can be stimulated by light passing through the shell and membranes (Rogers, 1990). As a consequence, the left side of the thalamus and its projections to the left hemisphere receive visual stimulation ahead of the right side of the thalamus and its projections. This establishes lateralization of feeding responses (right eye) and attack responses (left eye) since chickens hatched from eggs incubated in the dark during the final 3 days of incubation are not lateralized for such functions, at least during the first 3 weeks of life post-hatching (Rogers, 1997).

Likewise, pigeons not receiving monocular exposure to light lack asymmetry of their feeding responses (Güntürkün, 1993). In the chicken, in fact, it is possible to achieve a complete reversal of lateralization of feeding and attack responses by occluding the embryonic right eye and exposing the left eye to light instead (Rogers, 1990). Other expressions of lateralization (e.g., of social recognition) are not dependent on embryonic visual experience even though light experience after hatching is important (e.g., Deng and Rogers, 2002a).

3 Lateralization of the visual pathways

The lateralization of feeding and attack responses in the chicken has been traced to asymmetry in the thalamofugal visual system (see below). This system projects from the region of the thalamus known as the nucleus geniculatus lateralis pars dorsalis (GLd) to the visual Wulst of the forebrain (Deng and Rogers, 1997, 2002b). The other visual system, the tectofugal, which projects from the optic tectum via the nucleus rotundus to the ectostriatal region of the forebrain is not asymmetrical in the chicken (Rogers and Deng, 1999), unlike the pigeon (Güntürkün, 1997).

Rogers and Sink (1988) discovered asymmetry in the projections of the rostral thalamus to the visual Wulst of the chicken by injecting a retrograde tracer into the left or right Wulst regions of the hemispheres and counting the labelled cells on either side of the thalamus. The ratio of the number of labelled cells contralateral to the injection site to the number ipsilateral to the same site (*c/i* ratio) was higher for right-side than for left-side injections. A later study by Rogers and Deng (1999), using other tracers, confirmed that this asymmetry was located in the projections that cross the midline of the brain, from one side of the thalamus to the contralateral Wulst; there are more projections from the left thalamus to the right Wulst than vice versa (Fig. 1). This is the arrangement in chickens hatched from eggs exposed to light. Chickens hatched in the dark lack asymmetry in these projections, while in those stimulated by light to the left eye pre-hatching have the direction of lateraliza-

tion reversed (Rogers and Sink, 1988). This result was confirmed recently by Koshiba et al. (2002).

Koshiba et al. (2002) also discovered asymmetry in a region located in a rostral part of the pars dorsolateralis pars anterioris (DLA), which also develops after the embryo is exposed to light. This region sends primarily ipsilateral projections to the Wulst. The DLA contralateral to the light-exposed eye has more projections to its ipsilateral Wulst than does its equivalent on the other side of the thalamus. Hence, depending on the region of the GLd, there is asymmetry in the contralateral or ipsilateral projections to the visual Wulst (Fig. 1).

4 Egg shell transmission of light and lateralization

Most experiments investigating the effects of light exposure on the development of lateralization in embryos have used ambient, white light at intensities of 100 to 800 lux for 24 hours on day 19/20 of incubation in chickens (Fig. 2). I have found that asymmetry of the thalamofugal visual projections does not develop following exposure of eggs to only 1 300 to 1 500 lux, probably because sufficient light penetrates the egg to stimulate both eyes of the embryo. This result was obtained using white shelled eggs, which transmit approximately 8% of ambient light (Fig. 3). Brown egg shells transmit only 1% to 2% of ambient, white light. Hence, color and construction of the egg shell is a major factor determining whether embryos receive too little or too much exposure to light for lateralization to develop. In the natural environment, the position of the nest, the hours and intensity of sunlight, and the periods during which the in-

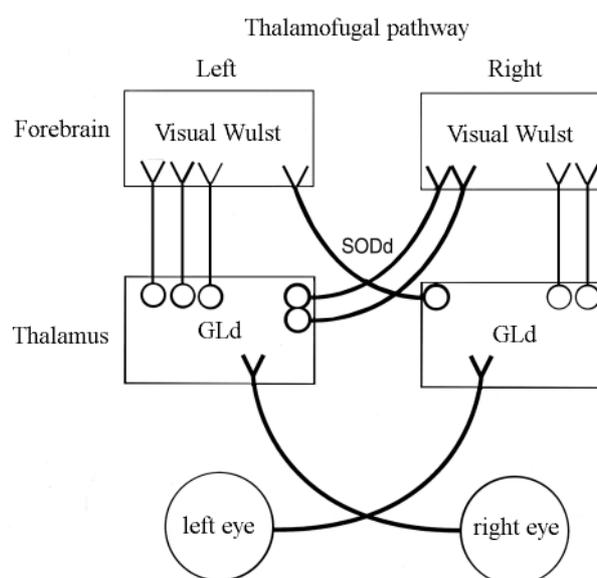


Fig. 1 The thalamofugal visual system showing the location of asymmetry in the projections from the GLd region of the thalamus to the visual Wulst region of the forebrain

There are more contralateral projections from the left GLd to the right Wulst than vice versa, and more ipsilateral projections from the left GLd to the left Wulst than vice versa.

cubating parent leaves the nest to forage, thereby exposing the eggs to light, will all have influences.

These data raise the possibility that species which nest in the open in full sunlight have eggs shells that minimize light transmission, such that it helps embryos to develop lateralization. As a first step in testing this idea, light transmission by the egg shell of the emu (*Dromaius novaehollandiae*) was determined; the results are presented in Fig. 3. It can be seen that the amount of light entering the emu egg is much less than that entering the egg of a domestic chicken: ambient intensities above 1 500 lux would not prevent the development of visual lateralization in emu chicks. It is not yet known whether emu chicks are lateralized but, given the ubiquity of lateralization, this is to be expected.

As to the advantages conferred by lateralization on visual behavior, some evidence shows that strongly lateralized chickens have superior ability in detecting an overhead predator as they feed (Rogers, 2000), and that strongly lateralized pigeons perform the pebble-grain discrimination task more successfully (Güntürkün, 2000). Thus there may be survival advantage in maintaining lateralization. If so, egg shell color and construction should affect the developmental process. Egg shell color, in particular, may serve this function in addition to its role in camouflage and for species and individual recognition.

5 Hormonal effects on lateralization

The level of steroid hormones also affects the development of lateralization, as shown in the chicken for testosterone (Schwarz and Rogers, 1992) and oestrogen (Rogers and Rajendra, 1993). Abnormally elevated levels of these hormones during the final stages of incubation prevent the

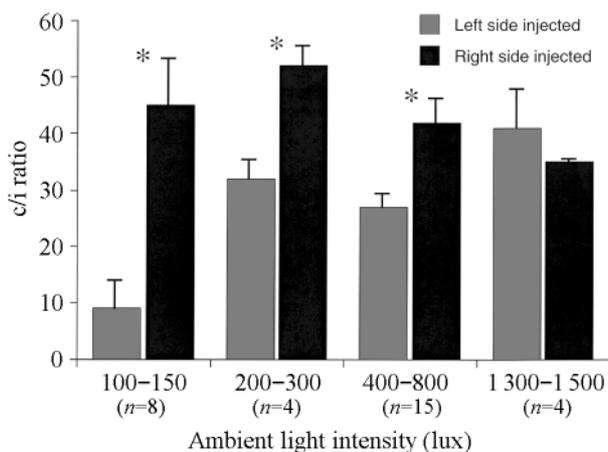


Fig. 2 The effect of variation in ambient light intensity on lateralization of the thalamofugal visual projections

The ratio of contralateral to ipsilateral projections (c/i ratio) is presented following injection of tracer dyes into the left or right Wulst. Note significant asymmetry (indicated by asterisks) for all intensities apart from the highest (1 300–1 500 lux), and a trend for the c/i ratio into the left Wulst to increase as light intensity increases.

light-sensitive development of asymmetry in the thalamofugal visual projections. Recent work has shown that corticosterone too has a similar effect (Deng and Rogers, 2002c).

The effect of steroid hormones on the embryonic development of asymmetry is of significance because of the influence that environment has on the level of testosterone that the maternal bird deposits in her eggs. Whittingham and Schwabl (2002) have shown that the concentration of testosterone in egg yolk either increases or decreases with laying order of the eggs in the clutch, the direction of change depending on the species. The level of testosterone deposited also depends on the number of aggressive interactions that the maternal bird experiences before or during egg laying, as shown in tree swallows (*Tachycineta bicolor*). This effect might well apply to other species and it suggests a means by which social conditions experienced by the female might influence the degree of lateralization of visual pathways and associated behavior patterns in her offspring.

Hence, light exposure and maternal hormonal contribution in the egg both influence the development of certain forms of visual lateralization. These influences, in response to social and ecological demands, must modulate the development of lateralization to cause individual differences.

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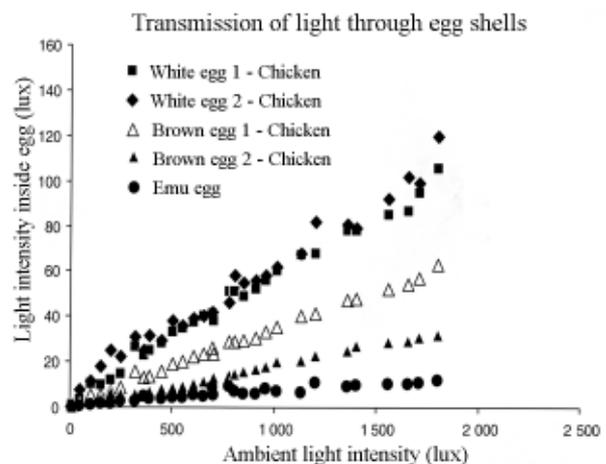


Fig. 3 Transmission of sunlight through egg shells

Light intensity inside the eggs is plotted against ambient light intensity. The white-shelled chicken eggs transmit a higher percentage of ambient light than brown chicken eggs and especially more than emu eggs.

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S21-5 Use of head position by birds to determine mode of analysis of what is seen

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Abstract Task properties determine which eye birds use in viewing. Thus the right eye system (RES) is used during visual control of manipulation and response, and the left eye system (LES) for wide search and other tasks requiring diffuse attention. As well, biases are imposed at different ages that are probably not generated by the current task. These biases determine what kinds of stimuli are found interesting. The changes in behavior that result are appropriate to the stage of development reached. Thus, in domestic chickens, shifts in bias are associated with such phases as close following of the mother, exploration of the environment, and learning about strange conspecifics. In addition, the assumption of specific head postures, coupled with standard eye positions, allow the bird to control the extent to which the RES and LES are responsible for visual analysis. This can be simple: for example, viewing by the right eye alone when planning a manipulation, or by the left eye alone when approaching a site at which the target of response cannot yet be seen. Or it can be complex, and involve both systems though with one still leading. The implications of these varying strategies of eye use, so different from our own experience, are discussed.

Key words Visual analysis, Right eye system, Left eye system, Head positioning

1 Introduction

Birds, and probably most vertebrates other than higher mammals, must see the world in a way quite different from ourselves. For most of the time their eyes are diverged in the “primary position of gaze” (Wallman and Pettigrew, 1985). The two eyes then see different areas of the world, right and left. The main lateral fixation points, which involve specialized foveae in some but not all birds (Walls, 1942), lie at around 60° to the longitudinal axis. In the domestic chicken, on which much of the work considered here has been carried out, the fixation point is about 63° (Dharmaretnam and Andrew, 1994), and it is not specialized beyond a slightly enhanced density (Ehrlich, 1981) and regularity of placement of receptors (Morris, 1982). This arrangement is important because there is evidence in the chicken (below) that the use of the main lateral fixation point has more to do with positioning the object of interest in a standard way on the retina than with making use of higher acuity of resolution.

One consequence of the far lateral placement of the lateral fixation points is that the two eyes can never be brought into register, as our foveae always are, so that both see the same object. While the eyes are in the primary position of gaze, the frontal fixation areas are also diverged, so that binocular vision does not occur. The independent functioning of the two eyes is enhanced by the fact that accommodation is entirely independent (Schaeffel and Howland, 1987), and eye movements, although often synchronized, move in different and independent directions (Wallman and

Letelier, 1993). Not only do the visual systems fed by right and left eyes (RES and LES) process different information, since they see different things, but they do so in different ways. As a result, RES and LES can elaborate different records of the same visual experience.

When both eye systems are attending to the same stimulus, two different strategies can be used. In one, the head may turn so that the two lateral fixation points are used alternately. Although this strategy has not been studied experimentally, it would allow the specialized abilities of the two sides of the brain to be brought to bear in turn on the single target of current interest. In the second strategy, the eyes may converge so that the frontal fields become binocular. Binocular fixation then allows both eye systems to see the stimulus simultaneously. Again there is clearly a single object of interest. However, it will be argued below that during such fixation it is more likely that a single visual strategy is applied, such as how to respond under visual guidance.

2 The role of head position

Head position is used by birds to ensure that the eye system, RES or LES with abilities appropriate to the task in hand, will analyze the object of interest. Two different strategies are available. As already noted, the head may be turned so that only one eye can see the object. Alternatively, the head may point more nearly at the object but turned so that it is clearly averted to the right or the left visual hemifield. In the second case, part of the retina of the other eye may or

may not see the stimulus. The key point is that it lies in one hemifield. Mechanisms of this sort have been described for vertebrates as widely separated as zebrafish (Miklósi et al., 1998) and rhesus monkeys (Hauser et al., 1998). In humans there is direct evidence that perceived position of a stimulus determines which side of the brain undertakes its analysis (Pierson et al., 1983).

A by-product of this ability is that the side on which a bird unexpectedly detects a stimulus will affect the kind of response that may be evoked. No doubt there are costs as a result, but these are evidently outweighed by the ability to choose and sustain processing by the appropriate eye system, using head posture.

3 Specializations of RES

RES is concerned with the visual control of response. In vertebrates that do not, like ourselves, manipulate the world with paired forelimbs, a crucial property is visual control of the mouth. In birds, this not only includes accurate guidance of the bill to its target, but also the matching of gape size to target size (Zeigler et al., 1993). It is remarkable here that visual control of a medial effector is lateralized in a way reminiscent of human handedness. The most sophisticated example of such control so far described is the use by *Corvus moneduloides* (New Caledonian crow) of the right eye when positioning the series of bites that detach a hooked strip of pandanus leaf to serve as a tool (Hunt, 2000). Eye use in nest construction would clearly repay study in the avian world.

In the chicken, it has been shown that the head is positioned during approach to bring the right eye to bear only when the object to be grasped or manipulated can be seen (Andrew et al., 2000; Tommasi and Andrew, 2002). In such circumstances, the head is turned 25° to the left to bring the right eye to bear. This position is assumed at a considerable distance, and is presumably associated with the establishment and maintenance of the requisite motor plan. When nothing to be pecked or grasped is seen during approach, the head is then turned to bring the left eye to bear. This is best understood functionally as a default condition. Use of the LES improves detection of novelty and analysis of the topographical layout of the environment. Direct approach to visible food hardly requires advanced topographical skills; yet change is always possible in the most familiar of environments, and is predictive of danger. Left eye use may help detection of such unexpected change.

4 Head saccades

When domestic chickens fix on an interesting object at a distance of about 55 cm they use two standard head positions. These center on 35–36° and 62–63°. The latter coincides with the angle of the pupillary axis of the eye, measured in a relaxed chicken (Wallman and Velez, 1985). It is thus associated with viewing at the main lateral fixation point, with eyes in the primary position of gaze. The other head position (35°) appears to be the first of a series

of head positions used during approach to a target. These run from 25° through 15° to 5° (Tommasi and Andrew, 2002). The distribution of preferred head positions suggests that 10° head saccades are usual under such circumstances.

Such peaks of preferred head position when fixating a large object reveal that a standard alignment with the object must be assumed. That the center of the object is aligned initially with the main lateral fixation point is the most likely possibility, but there is no direct evidence for this yet. Were there no such alignment, any peaks of usage would be smeared out by varying choices of points on the object.

The full sequence is likely to follow initial establishment of alignment using the lateral fixation point, succeeded by transfer of this point first to 35°, and then by a series of standard 10° saccades to a point close to but not yet identical with frontal fixation. The most probable function of standardized saccades is to ensure that features of the object transfer in a coherent way across the retina. If a feature picked out by region A transfers predictably first to B and then to C, this will facilitate rapid identification of the feature after each shift, allowing simultaneous analysis of information relating to the object of interest over a wide area of the retina. The breadth of high acuity along the streak connecting central and temporal retinas (Martin, 1993) allows this.

That a further mechanism is involved is suggested by two actual series of head positions, separated by 10°. The second series is 20°, 10° and 0°. When this series comes into use, the point of alignment is on the way to being transferred to the frontal fixation position at 0°, which presumably involves binocular convergence. The data are thus consistent with the use of a slight divergence of the optical axes in the 25°, 15° and 5° series to prevent binocular supply to visual units that would receive such input after full convergence. The head positions that would be associated with such slight divergences are used in search. This is clear for the food dish without a lid experiment, where the saccades are initiated at the point at which food becomes visible and a particular grain must be selected. The same is true for lids where a decision has to be taken exactly where to place the bill around the edge.

In free search over a floor on which food grains are scattered, it is clearly advantageous to involve both eyes. This requires some degree of independence of eye control, in that each eye should be able to move independently to fix on a target. In the next step, the eye system, left or right, that has the more promising target takes control of head position as well (Rogers and Andrew, 1989). The target is captured by the lateral point of fixation, and then the head is turned for frontal fixation during approach and peck. What is here suggested is that independence of analysis continues until binocularity is assumed, and that the critical change probably comes with the establishment of binocular inputs to appropriate visual units. This marks the transition to the kind of single vision that we use.

5 Specializations of LES

In the domestic chicken, the forced use of one or other eye shows that the use of more distant topographical features to locate a site at which food is known to be hidden is enhanced when the left eye is employed (Rashid and Andrew, 1989). When the right eye is used, chickens tended instead to rely on landmarks close to the site. Use of the left eye also increases responsiveness to small changes in the properties of a model social partner (Vallortigara and Andrew, 1991).

Preferential LES use of topographical information is also exhibited by marsh tits when hoarding (see below). The greater importance of the right cerebral hemisphere in rats for orientation by topographical features (Adelstein and Crowne, 1991; Cowell et al., 1997) confirms that this condition is general amongst tetrapod vertebrates, and not just confined to humans. Note that the LES links to the right hemisphere in birds.

6 Different memories in RES and LES

It seems certain that the two eye systems must collaborate in many tasks. Direct evidence for this is provided by cases in which each has learned different things about single incidents. Once again, the fact that the two eyes see different aspects provides a simple but powerful control mechanism, according to the hypothesis that each eye system records what it sees and therefore analyses.

The most striking case is provided by hoarding in marsh tits (Clayton and Krebs, 1994), in which both eyes are used differentially. In the experiment, the tit first placed the storage item in a hole surrounded by a specific local specific pattern. There were many such hoarding sites in different areas of the room, each with a different identifying pattern. Immediately after hoarding, the patterns were shifted to different holes. Five minutes later, the bird was reintroduced to recover the item, but now with one eye covered. When the left eye was in use, the bird visited the correct place in the room, but when the right eye was in use it chose the correct pattern in a new position. Given that the original placement was done under visual control by the RES (as expected), then the right eye would see the identifying pattern, whereas the left eye was free to scan the environment.

Cues used to identify the center of an area are another example. Tommasi et al. (1997) trained chickens to find food hidden in the center of an arena. The chickens were then tested in enlarged and distorted versions of the arena. When the left eye was in use, search was concentrated in the geometric center, cued by the point furthest from all walls and averaging estimates in all directions. When the right eye was in use, the chickens searched on a different pattern. They now moved around the full perimeter, always keeping to distances from the nearest wall that had separated the center from the closest point to a wall during control feeding. Exactly such a pattern would be generated

if the RES recorded what it saw during feeding, including the lateral view of a wall. The LES, in contrast, would have had to record and integrate a series of views all around the general site of feeding, whether from search during a single or series of sessions.

The visual control of response, once initiated, goes beyond control of a motor plan. It is also necessary to choose an appropriate target, on the basis of past experience of response outcomes. It is likely that the RES is the more important here. In a standard test of acquisition of feeding discriminations, chickens perform better when using the right eye. Familiar food grains are scattered amongst small pebbles of roughly the same size but the grains are stuck down so that they cannot be taken up in the bill. Inhibition of pecks at pebbles develops faster with right eye use (Rogers and Anson, 1979; Deng and Rogers, 1997). The specific involvement of the RES in recording the consequences of response is suggested by the finding (Cozzutti and Vallortigara, 2001) that “devaluation” of a food affects choice of food site only when the right eye is in use. Devaluation is the temporary reduction in preference for an acceptable type of food after a hearty meal of such food.

The hypothesis can thus be extended. The RES may be supposed to use records of past response that include the appearance of the target that was chosen, the nature of the response itself and its outcome. As more and more comparable experiences occur, the cues defining the target will inevitably vary between successive targets, so that the RES is likely to be faced with the need to select key cue dimensions and to establish criteria of match. This would explain its superiority in acquiring discrimination between pebbles and food grains, for example.

Feeding is not the only type of response that is preferentially controlled by the RES. Male zebra finches approach females in a copulatory display in which the right side is directed towards her (Workman and Andrew, 1986). The same is true when testosterone-treated chickens approach a model to copulate (Workman and Andrew, 1986). When a conspecific is perceived on the left, in contrast, chickens are more likely to exhibit aggressive and sexual behavior than when it is seen on the right (Rogers et al., 1985). The same is true of a range of other vertebrates (Andrew and Rogers, 2002). Here motivational changes that result from seeing conspecifics are resisted when the RES is controlling. Such resistance may be part of a necessary ability of the RES to inhibit other responses during ongoing behavior (Andrew, 2002). It will be interesting to see whether this left/right difference is also used to control behavior by choice of eye. Evocation of behavior that is unwise in a particular social situation might be avoided by right eye use.

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Symposium 22 Torpor in birds: regulation of energy metabolism and body temperature

Introduction

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Energy-saving mechanisms in birds such as torpor have been documented with increasing frequency, especially since Jaeger's (1948, 1949) classic work on the dormancy of the common poorwill, *Phalaenoptilus nuttallii*. However, ultimate as well as proximate factors determining the significance of these mechanisms for birds — body mass and condition, availability of food, weather conditions, phase of circadian/annual cycle, geographic range — are still being evaluated.

The symposium addressed a wide range of the factors affecting torpor. Recent advances have come from new methods of study, including remote temperature sensing by miniature long-range transmitters, resulting in new insights into the physiology of unrestrained birds, especially with regard to the phenology and patterns of torpor. Data on the use of torpor was presented for a great variety of birds of different phylogenetic groups, body masses, and ecological backgrounds. The results of these studies also raise new questions with regard to the significance of torpor in the life histories of birds. Thus to regard torpor and related phenomena merely as physiological responses to energetic challenges is now generally agreed to be an over simplification. Rather, it is coming to be understood as being of central importance for the survival of birds in habitats with an unpredictable or low-quality food supply and for the colonization of new habitats. There is, for example, evidence that birds are able to undergo energy saving states prior to energy demanding phases such as migration or preparation for hibernation or migration. Moreover, the symposium demonstrated that torpor is probably common in a much wider array of endotherms with a wider range of body mass than previously thought (Körtner et al., 2000; Schleucher, 2001; McKechnie and Lovegrove, 2002).

Two theoretical papers address the problems of correct terminology in thermal biology (Elke Schleucher and Roland Prinzinger) and the potential ecological and evolutionary determinants of torpor (Andrew McKechnie). The remaining three papers (Claus Bech, Mark Brigham et al., and Fritz Geiser et al.) concentrate on manifestations of torpor in specialists such as aerial feeders (nightjars), occupants of narrow food niches (e.g. frugivores), and birds with highly specialized modes of flight (hummingbirds). A key difficulty for assessing hypometabolic states in birds is the fact that many birds do not readily enter them under laboratory conditions. Indeed, recent studies show that there are distinct differences between torpor in field and laboratory conditions, raising the possibility that many more birds enter this state in nature (Geiser et al., 2000).

Via description of regulatory patterns of metabolism and body temperature in both laboratory and field, and models predicting the occurrence of torpor in birds, the symposium laid some of the foundations towards quantifying the significance of avian hypometabolic states.

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S22-1 Heterothermia and torpor in birds: highly specialized physiological ability or just deep “nocturnal hypothermia”? — The limitations of terminology

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Abstract Advances in thermal physiology, especially of torpor and related phenomena, are complicated by wide inconsistencies in the use of terms for describing thermoregulatory states. We compare definitions given by the IUPS Thermal Commission (2001) and Swan (1974), which epitomize the variety in terminology. “Hypothermia” is the most widely disputed of the terms because in human physiology and clinical applications it describes a pathological state associated with thermoregulatory breakdown. We maintain that a term employed primarily for a pathological state should not be used; or if so, it should be qualified by adjectives such as “regulated” or “controlled” to account for the fact that torpor is not a functionally primitive mode of thermoregulation. The terminology for the physiology of hypometabolic states such as torpor and hibernation should be directed towards one which clearly distinguishes between terms that are descriptive and those that are mechanistic. It also seems desirable to separate the terminology used for the physiology of wild animals from that commonly applied to human physiology and clinical attributes. We further stress the lack of common standards for describing even basal metabolic rate and corresponding body temperatures, especially with regard to the phase (activity, α ; or rest, ρ) of the daily cycle within which measurements are taken. Here rest (ρ) phase values are recommended as the standard of reference.

Key words Terminology, Hypothermia, Heterothermia, Body temperature, Torpor

1 Introduction

We review current information on the terminology of the phenology of avian body temperatures (T_b), with emphasis on the definitions of T_b involving euthermic and heterothermic birds. The questions addressed are: what is the euthermic T_b of birds? How should deviations from this “normal” level be defined? What mechanisms underlie the patterns of heterothermia, and does terminology define them adequately? Mean euthermic T_b for birds in the rest phase (ρ phase; Aschoff and Pohl, 1970) is 38.5 ± 0.96 C (\pm SD; $n = 202$ species, 26 orders), irrespective of phylogenetic relationships and body mass (Prinzinger et al., 1991). Values below the mean resting T_b are commonly regarded as representing “hypothermia”. Use of this term, nevertheless, is confusing because in the context of human physiology, as well as in some research on the physiology of wild animals, it is used to for *pathologically* depressed T_b . Torpor in birds, however, is a process clearly under permanent control of the hypothalamic regulatory systems, and does not reflect a failure of thermoregulation. So use of such terms and definitions as hypothermia is ambiguous, both descriptively and mechanistically.

Recent advances in technology, especially the development of miniature temperature transmitters and loggers, have allowed more detailed monitoring of phenology and patterns of T_b regulation in the field as well as the laboratory.

Those advances raise new issues concerning the biological value of states of low T_b and metabolic rates (MR). It is now widely accepted that these states, far from simple reactions to energy shortages, are used by many species to manage energy utilization even before acute challenges occur. There is evidence, for example, that they facilitate accumulation of fat prior to migration or hibernation (McKechnie and Lovegrove, 2002). So we consider it crucial to re-evaluate currently available definitions towards developing a “common language” in thermal physiology that is unambiguous.

2 Discussion

The terminological issues in thermal physiology are summarized in the following questions:

1. Can and should terms used to describe torpor and related processes in animals be divorced from terms used to describe pathological states in humans?
2. Should the hypometabolic state in animal physiology be regarded as under constant thermoregulatory control within particular species?
3. From which phase of the daily cycle, α or ρ (Aschoff and Pohl, 1970), should values for basal metabolic rate (BMR) and corresponding body temperatures (T_b) be drawn? If the IUPS Thermal Commission definition is used as standard, normal T_b oscillations within the daily cycle

need to be taken into account and distinguished from “heterothermic” states. Against this background, is it possible to define a certain T_b boundary or threshold below which the term torpor applies?

4. Do present data permit a clear terminological differentiation between phenomena, as between torpor, “nocturnal hypothermia”, etc.? Should they be regarded as steps in a physiological continuum or do they involve different physiological mechanisms requiring definition?

5. Is it possible to develop a terminology that clearly distinguishes between descriptive terms and terms implying mechanism?

2.1 Hypothermia

The IUPS Thermal Commission definition is too generalized and allows use of the term for pathological as well as “regulated” conditions. If it has to be used in avian physiology, we recommend qualifying it with a suitable adjective to emphasize the controlled nature of torpor and related phenomena.

Swan’s definition reflects the point of view of medical doctors, where hypothermia is clearly defines the state of a pathological, non-regulated decrease in body temperature below the mean rest T_b . T_b in birds is significantly dependent on the phase of the daily cycle (Aschoff and Pohl, 1970; Prinzinger et al., 1991). In the rest (ρ) phase of the daily cycle, values fall to between 38 and 40°C, irrespective of taxon or body mass. It is also quite clear that T_b values at or above 40°C are no longer resting values (Prinzinger et al., 1991). Hence, we suggest use of the ρ phase values for reference, and also for basal metabolic rate (BMR). There is still considerable inconsistency in the definition of standards for the BMR, as, for example, in whether it should be measured in waking or sleeping animals (Reinertsen, 1996; Norberg, 1996; Dawson and O’Connor, 1996; Dawson and Whittow, 2000).

2.2 Heterothermia

This term might be considered as a useful alternative to hypothermia if that term is eliminated from definitions of non-pathological phenomena.

2.3 Torpor

The IUPS definition does not consider physiological boundaries or limits, only taking account of behavioral aspects. This implies that while an animal remains capable of responding quickly to stimuli, the state cannot be defined as torpor. Examples are larger birds such as vultures, or passerines in which T_b may hold only slightly below mean T_b range (Heath, 1968; Haftorn, 1972).

Swan’s (1974) definition not only considers behavioral aspects but also takes account of the regulatory phenomena behind torpor. It separates torpor from non-regulated, pathological states as well.

2.4 Adjectival use of “regulated” and “controlled” for qualifying hypothermia

In torpor and related phenomena, both T_b and MR are obviously regulated closely. Even on entry into torpor, when decrease of T_b follows physical conditions passively and $(T_b - T_a)$ is negligible, the torpid organism is capable of defending a lower critical T_b even if $T_a \ll T_b$, where T_a = ambient/environmental temperature. Hence, in the classical conception of torpor, can there be, by definition, such a thing as “non-regulated torpor” (Reinertsen, 1996)? There is no evidence to date that normal healthy torpidators do not defend a minimal T_b set-point or limit. Rather, hypothermia and torpor have been shown to be under constant thermoregulatory control in species investigated so far (Walker et al., 1983; Graf et al., 1989; Krüger et al., 1982; Prinzinger et al., 1991; Merola-Zwartjes and Ligon, 2000; Schleucher, 2001). We thus recommend the use of the adjectives “regulated” and “controlled” if the term “hypothermia” cannot be avoided.

2.5 Adjectival use of “facultative” for qualifying hypothermia or torpor

Use of this term is problematic because its antonym is “obligatory”. These terms do not clearly differentiate regulated from pathological decrease in T_b . In fact, evidence exists that torpor can be an *obligate* feature needed to maintain energetic balance (e.g., Bucher and Chappell, 1992). The experimental need to impose food restriction (starvation) on birds to induce torpor is — at least in cases of hummingbirds and mousebirds — probably an artifact of captivity (Prinzinger et al., 1981; Prinzinger, 1982). The reason for this is that captive animals are often overweight and require a certain degree of starvation to regain normal body mass; under natural conditions, such birds are “forced” to undergo torpor every night without prior acute energy depletion. In such circumstances, it would be misleading to define this form of hypothermia as “facultative”; much more information about the frequency of torpor and related phenomena is needed before its use should be considered.

2.6 Anapyrexia

Like hypothermia, this term has unfortunately been applied in general use to a pathological state (IUPS definitions; Bicego et al., 2002; Steiner and Branco, 2002). However, if accompanied by a qualifier such as “regulated” or “controlled” and by a clear definition, it does describe a condition precisely and the circumstances under which it occurs.

3 Outlook and recommendations

1. It is necessary to agree on common standards in animal physiology, especially to reach precise definitions for such basic concepts as BMR and mean T_b . Here we recommend consistent use of (ρ) phase values as the standard of reference.

2. Reconsideration of definitions for terms in thermal physiology needs to take account of the following factors:

Behavior: Is the animal in question still capable of reacting to external stimuli; or is it lethargic, and how deep

Table 1 List of commonly used terms in thermal physiology from two sources

	IUPS Thermal Commission, 2001	Swan, 1974
Eu- (Ceno)- thermia, from eu [Gk] = well or good, and koinos [Gk] = common, shared	The condition of a temperature regulator when its core temperature is within $\pm 1 SD$ of the range associated with the normal post-absorptive resting condition of the species in the thermoneutral zone. Synonym: euthermy, normothermy.	A range of body temperature that is suitable, i.e., chronically viable; the zone of body temperature between the maximum ... and minimal critical body temperature in non-torpidating homeotherms (in this instance synonymous with normothermia); ... The range of body temperature in which torpidation may occur.
Normothermia, from normalis [L] = average, usual	see Cenothermy-ia.	The range of body temperature of non-torpidating homeotherms between the minimal and maximal critical body temperatures; the zone of thermoneutrality in non-torpidators. Not applicable to torpidators... (see euthermy).
Hypothermia, from hypo [Gk] = less than usual, beneath	The condition of a temperature regulator when core temperature is below its range specified for the normal active state of the species. Hypothermia may be regulated (e.g. Torpor, Hibernation)...	A range of body temperature in a homeotherm which is below the minimal critical (body) temperature of a non-torpidator or below the minimal viable temperature of a torpidator or a poikilotherm; a body temperature below euthermy or normothermia, which if sufficiently prolonged, is lethal.
Heterothermia, from hetero [Gk] = other than usual, different	The pattern of temperature regulation ... in which the variation in core temperature ... exceeds that which defines homeothermy.	A vertebrate animal without a narrow range of usual temperature; an animal with a broad range of viable temperature... (.. torpidants).
Torpor, from torpere [L] = stiff, numb	A state of inactivity and reduced responsiveness to stimuli (e.g. during hibernation, hypothermia, or estivation).	... the biological state of vertebrate animals involving the onset, progression and maintenance of a diminished metabolic rate associated with a profound state of central nervous system depression resembling coma, including suppression and readjustment of thermostatic control but without complete loss of CNS monitor and control functions.
Anapyrexia*, from ana [Gk] = reverse, and pyretos [Gk] = fever	A pathological condition in which there is a regulated decrease in core temperature. Anapyrexia is distinct from hypothermia in that thermoregulatory responses indicate a defence of the anapyretic level of core temperature.	
Basal metabolic rate	Metabolic energy transformation calculated ... in an organism in a rested, awake, ... post-absorptive state, and thermoneutral zone.	

The two sources reflect divergent backgrounds and approaches among animal and human physiologists, and show that new advances in thermal physiology have only in part been considered and accommodated.

is the lethargy?

Physiology: Are the thermoregulatory systems under consideration constantly active, even during processes of passive cooling? Is there any biological evidence requiring a clear discrimination between shallow depressions of nocturnal T_b ("nocturnal hypothermia", 2–5°C below euthermy), and "true" torpor (e.g., in the range $T_b < 30^\circ\text{C}$)? And is the definition of thresholds justified? For detailed discussion, see Prinzing et al. (1991), Barclay et al. (2001),

and McKechnie and Lovegrove (2002).

Ecology: Recent studies show that captivity has a major impact on the occurrence and patterns of torpor in birds (Geiser et al., 2000; Geiser and Ferguson, 2001). The importance of hypometabolic states for birds therefore needs to be re-assessed under natural conditions.

The terminology for the physiology of hypometabolic states, such as torpor and hibernation, should be directed towards a scheme that clearly distinguishes between de-

scriptive terms and those with a mechanistic basis, as already realized in the terms poikilotherm/homeotherm, ectotherm/endotherm, thermoconformer/thermoregulator. To avoid further confusion, it is also desirable to separate the terminology used in animal physiology from that commonly applied to human physiology, particularly in clinical circumstances.

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S22-2 Metabolic aspects of torpor in hummingbirds

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Abstract Tropical species of hummingbirds generally use nightly torpor during which they defend body temperatures (T_b) of between 12 and 20°C. We review metabolic aspects in several Brazilian species covering the three phases of the torpor cycle: entrance, basic state and arousal. The entrance phase is characterized by initial rapid decline in metabolic rate (MR), apparently related to abandonment of cold-induced shivering. This drop is then followed by a much slower decrease in MR, possibly due to a Q10-effect of the lowered body temperature. Hence, active metabolic depression does not seem to be involved. During the basic state phase of torpor, hummingbirds will respond to low ambient temperatures by an increased MR, often to values which exceed their basal metabolic rates. At the circulatory level, changes in blood oxygen transport are accommodated mainly by an increase in stroke volume rather than in heart rate. During the arousal phase, the metabolic rate increases noticeably, reaching peak rates of oxygen consumption nearly indistinguishable from those values measured during hovering flight. The achievement of such high levels of MR during arousal is even more remarkable considering that the peak rates of MR occur at T_b of about 32–35°C, considerably below T_b during active flight (>40°C). These results clearly demonstrate the very high degree of expansibility in the rate of oxygen consumption in hummingbirds.

Key words Energy expenditure, Flight, Hummingbirds, Temperature regulation, Torpor

1 Introduction

The majority of hummingbirds (Trochilidae) are very small, some weighing just two grams and over 90% of species with body masses less than 8 grams (Dunning, 1993). Hummingbirds thus include some of the smallest homeotherms known. Small body size is generally associated with high metabolic costs, and so also with the potential danger of negative energy balance. As a consequence, hummingbirds are renowned for their use of nightly torpor, during which they regulate their body temperature at levels just a few degrees above ambient temperature (Bicudo, 1996; Bech et al., 1997). This in turn greatly reduces nightly energy expenditure. When one considers the high costs of energy expenditure during flight, thermoregulatory needs in the cold and low metabolism during torpor, it is clear that hummingbirds must be able to adjust their energy expenditure across a very large range of values (Bicudo and Chau-Berlinck, 1998). Hence, both the respiratory and the circulatory systems must show considerable flexibility.

Here we review several aspects of the use of torpor in hummingbirds, focusing on those metabolic characteristics concerned with changes in oxygen consumption during nightly torpor.

2 Materials and methods

The study was carried out at the Museu de Biologia, at Santa Teresa in Espirito Santo, Brazil (19°55'S, 40°36'W), at about 700 m a.s.l., on the following species: frilled coquette *Lophornis magnifica* (~ 2.7 g), amethyst woodstar *Calliphlox amethystina* (~ 2.7 g), versicolored emerald *Amazilia versicolor* (~ 4.1 g), Planalto hermit *Phaethornis pretrei* (~ 5.2 g), white-throated hummingbird *Leucochloris albicollis* (~ 5.4 g), black jacobin *Melanotrochilus fuscus* (~ 7.5 g), Brazilian ruby *Clytolaema rubricauda* (~ 7.7 g), and swallow-tailed hummingbird *Eupetomena macroura* (~ 8.7 g). All species were common breeding birds in the study area (Ruschi, 1982), where they were accustomed to feed at artificial feeders. Individuals of all species studied were easily caught at these feeders.

Rates of oxygen consumption (VO_2) were measured by flow-through respirometry: an individual hummingbird was placed in the respirometry chamber during the evening and was taken out again the next morning. The volume of the metabolic chamber was 650 ml for the smaller species or 1 880 ml for the larger. Airflow rate was kept at approximately 70 ml min⁻¹. Because of low rates of oxygen consumption during torpor, we were obliged to use a low flow-to-volume ratio. When calculating values of oxygen

consumption, however, we corrected for the washout-characteristics of the system with the method described by Niimi (1978). Hence we obtained the instantaneous rate of oxygen consumption at any time. Changes in ambient temperature were created by circulating water from a thermostatically-controlled water-bath around the chamber.

VO_2 during hovering flight was measured by the method described by Berger and Hart (1972). Air was sucked continuously through a small tube attached to the top of an artificial flower connected to a small glass container of liquid sugar solution. When the hummingbirds were feeding, we were able to collect all expired air, and VO_2 during hovering flight was calculated by integrating the output signal. Total time feeding was recorded by an infrared detector placed above the artificial flower. All measurements of hovering VO_2 were recorded at "room" temperature (22–25 °C).

Body temperature (T_b) was measured with a copper-constantan thermocouple (California fine wire, type 00) placed subcutaneously and laterally on the pectoral muscle. The thermocouple was fixed in place with small pieces of adhesive tape. During measurement, the wing covered the subcutaneously placed tip of the thermocouple. Control experiments showed that such measurements of pectoral temperature did not differ by more than 0.2–0.3 °C from simultaneously measured rectal temperature (Bech et al., 1997). Ambient temperature (T_a) was measured using a similar thermocouple. All thermocouples were connected to a Data Translation (DT 2805) A/D converter, via a DT-757 Terminal board, and processed by a computer using a Labtech Notebook data acquisition program.

Heart rates were measured with thin electrodes made from 0.4 mm insect needles that were inserted subcutaneously at the neck and the caudal part of the sternum. The signals were amplified using a Grass amplifier and the electrocardiograms recorded on a Brush pen recorder.

3 Results and discussion

3.1 The entrance phase of torpor

A central topic, which has been widely debated, is whether homeotherms enter torpor by active metabolic down-regulation. Is the drop in metabolic rate caused by active metabolic depression or is it caused only by a passive Q_{10} -effect of a lowered body temperature? Several studies, both empirical and theoretical, have addressed this question, and there have been arguments both for and against an active component (Geiser, 1988; Snyder and Nestler, 1990; Malan, 1993; Song et al., 1996).

We obtained simultaneous measurements of T_b and VO_2 during complete torpor bouts from six of the studied species. For these species we also obtained measurements of basal metabolic rate (BMR) at thermoneutral conditions. All entries into torpor were qualitatively alike and showed a two-step pattern (Fig. 1: Brazilian Ruby). First there is a sharp drop in oxygen consumption until it reaches the pre-

dicted BMR-level; this is probably related to an abandonment of cold-induced thermogenesis (i.e., shivering). Through the second step, VO_2 changes at a much slower rate, generally following the predicted changes in the BMR. The predicted change in BMR was calculated using the actual measured changes in T_b , the measured values of BMR and assuming a Q_{10} -effect of 2.5. It is obvious from the results (Fig. 1), that the overall change in metabolic rate from normothermia to torpor, need not involve active depression of metabolism, for VO_2 is not at any time substantially below the BMR-level.

The same general two-step entry is also manifested when individual hummingbirds are exposed to such low ambient temperatures that a regulated torpor is induced. In such cases, metabolic rate will first fall quickly to a low level and, as the defended body temperature is approached, then secondarily increase once more to the level required for maintaining T_b during torpor. Overall results thus indicate that no active metabolic depression is necessary for hummingbirds to enter torpor, at least in the species studied. A similar conclusion was reached by Song et al. (1996) for

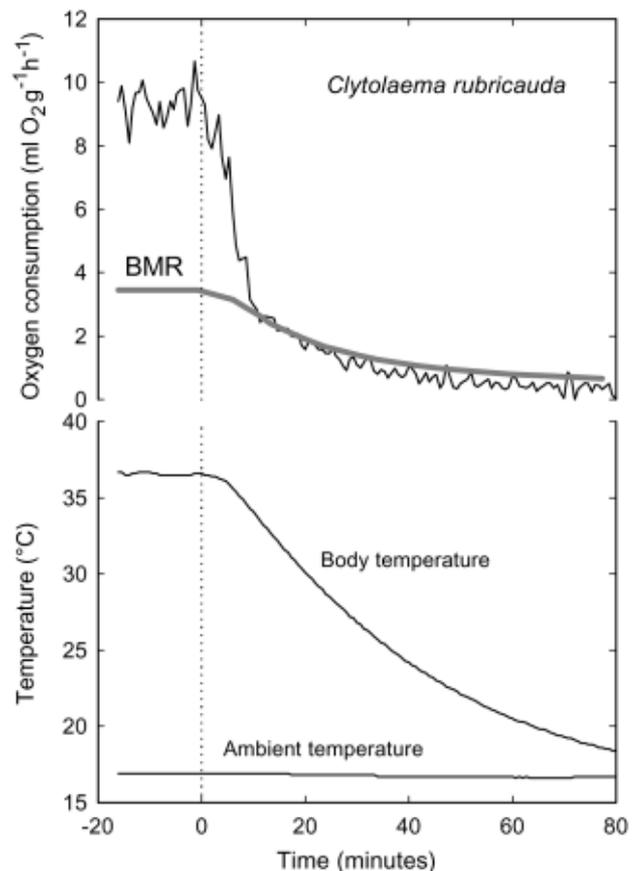


Fig. 1 Changes in oxygen consumption, and body and ambient temperature during entry into torpor in *Clytolaema rubricauda*

The thick line denotes the level of BMR during both normothermia (measured value) and during the entrance phase (based on the measured body temperature and assuming a Q_{10} of 2.5). The vertical stippled line indicates the initiation of body temperature decrease.

small mammals entering torpor, also with a two-step entry.

3.2 The basic state of torpor

In the tropics, species of hummingbirds employ nightly torpor to conserve energy, during which they defend body temperatures between 12 and 20°C (Bech et al., 1997). This implies that exposure to lower ambient temperatures will induce regulatory thermogenesis: torpid hummingbirds must necessarily increase their metabolic heat production during exposure to low T_a s. The corresponding high values of VO_2 may actually reach values that exceed its thermoneutral value. An important question then arises: does the low body temperature constrain oxygen transport mechanisms?

The regulation of T_b during torpor is brought about by a several-fold increase in heat production to compensate for the increased body-to-ambient temperature gradient and hence increased heat loss. During this regulation, heart rate changes only slightly (Fig. 2). As a consequence, however, the stroke volume, and hence the oxygen pulse (the amount of oxygen transported per heart beat), must increase considerably. In such situations, the oxygen pulse may reach values of up to $0.7 \mu\text{l g}^{-1} \text{beat}^{-1}$, which otherwise only occurs during flight (Fig. 2).

Our data indicate that use of an increased oxygen pulse for altering oxygen uptake is especially important in two situations: during hovering flight and during regulated torpor. During flight, the very high levels of oxygen consumption (more than 10-times the resting thermoneutral rate) apparently cannot be met solely by an increased heart rate (only 3-fold increase). With the heart beating at its maximum, the birds need to increase the oxygen pulse as well. During regulated torpor, constant low body temperature apparently limits increases in heart beat; and so the birds are forced to increase the oxygen pulse instead. In this context, it is note-

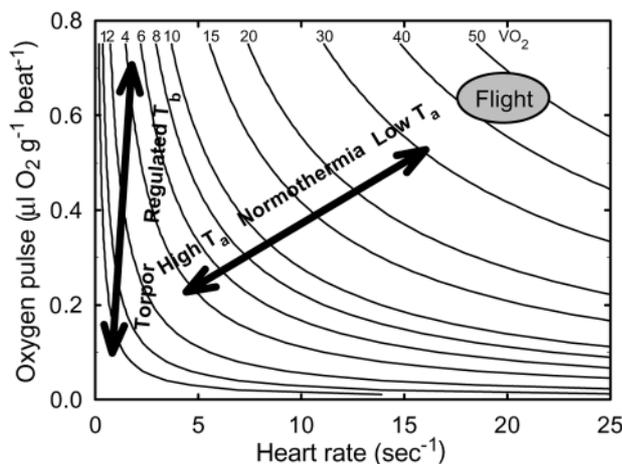


Fig. 2 Normogram showing the combinations of heart rate (HR) and oxygen pulse (OP) for the two smallest species studied. The amount of oxygen taken up per heart beat is calculated as VO_2/HR . Isopleths show the resulting values of VO_2 expressed in $\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}$. The two arrows indicate the combinations of HR and OP during torpor (left) and during normothermia (right).

worthy that hummingbirds have much larger relative heart masses than other birds (Bishop and Butler, 1995). A larger heart mass would presumably provide a relatively much larger stroke volume, and in turn confer advantages in terms of enlarged cardiac output and aerobic capacity. This may be especially important during regulated torpor, when low body temperature may constrain the use of heart rate in oxygen transport.

3.3 The arousal phase of torpor

During arousal, metabolic rate increases sharply to a peak value which may be much higher than that during daytime homeothermy. Earlier reported magnitudes of these peaks have varied a great deal, probably because different methods have been used for calculating rates of oxygen consumption; some early studies made no attempt to account for the rapid changes when calculating it by the flow-through method. We accounted for washout characteristics when calculating the instantaneous level of oxygen consumption and found peak rates to vary between 17 and $41 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1}$ (species-specific mean values; Fig. 3). In some of our species, peak rates reached actually correspond to an increase in oxygen consumption of about 100 times the lowest level recorded during the torpid state.

To compare these values to values of VO_2 during flight, we measured VO_2 during hovering flight as well, finding little difference in peak rates during either activity (Fig. 3). The achievement of such high rates of oxygen consumption during arousal is even more remarkable considering that the peak values of VO_2 occur at a time when body temperature is still increasing and, at between 32 to 34°C, well below body temperature during active flight.

4 Conclusions

These results demonstrate a very high degree of expansibility in the rate of oxygen consumption in hummingbirds. Hummingbirds can operate at levels equal to basal metabolic rate, whether they are at thermoneutral

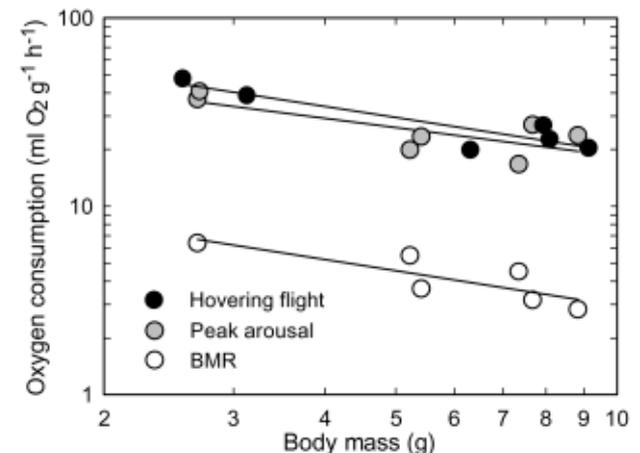


Fig. 3 BMR, peak VO_2 during arousal from torpor, and VO_2 during hovering flight, as a function of body mass in some Brazilian hummingbirds

condition and maintaining a high T_b , or are exposed to very cold ambient conditions and defending torpid T_b by regulated thermogenesis. Additionally, they may generate equally high VO_2 values whether hovering for food or just sitting quietly at low T_b and warming up. There also appears to be a possible temperature constraint on the circulatory system, which torpid hummingbirds overcome by increasing their VO_2 to defend body temperature. In such circumstances, low body temperature may constrain the heart rate, making an increase in oxygen transport necessary.

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S22-3 Ecological correlates of torpor use among five caprimulgiform birds

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Abstract We review recent studies of torpor use by free-ranging caprimulgiform birds in North America and Australia: common poorwill (45 g), whip-poor-will (55 g), common nighthawk (80 g), Australian owlet-nightjar (50 g), and Tawny Frogmouth (500 g). Reproductive activity, ambient temperature, body size, and prey abundance influence the energy status of endotherms and may be correlated with torpor use under natural conditions; our review suggests that no one factor is most important. To date, most studies have been correlational in the wild, and experimental studies at multiple locales are now needed to resolve uncertainties concerning the evolutionary and ecological significance of torpor.

Key words Torpor, Caprimulgiformes, Ecology, Energetics, Temperature, Foraging

1 Introduction

Endothermy is a process of thermoregulation characterized by a high, controlled rate of heat production which helps mammals and birds maintain an elevated body temperature (T_b ; IUPS Thermal Commission, 2001). While a constant elevated T_b provides a thermally stable internal environment for optimizing physiological functions, it requires a metabolic rate (MR) 10–30 times (Nagy et al., 1999) greater than the standard MR of ectothermic reptiles. The cost is especially pronounced in small endotherms, which lose most endogenously produced heat to the environment (Song et al., 1998). To conserve energy or other resources, many mammals and a growing list of birds abandon normal elevated T_b . Such facultative heterothermy or torpor is a physiological state characterized by reduced MR and T_b . To date, the vast majority of studies have focused on the ability of mammals to reduce energy expenditure through daily or seasonal bouts of torpor (hibernation; Geiser and Ruf, 1995). Prolonged torpor of 1–3 weeks by hibernators typically occurs during winter at low ambient temperatures (T_a ; Geiser, 1998). In contrast to hibernation, daily torpor is employed at a variety of T_a s and throughout the year (Geiser, 1998).

Until recently, birds were thought to be less prone to use torpor than mammals (McKechnie and Lovegrove, 2002). Daily torpor has now been recorded from seven orders of birds, most commonly in hummingbirds (Trochilidae; Calder and Booser, 1973; Calder, 1994; Bech et al., 1997) and nightjars (Caprimulgiformes; Bartholomew et al., 1957; Peiponen, 1966; Reinertsen, 1983). In both orders, daily

torpor bouts typically last several hours, T_b dropping by 4–35°C and metabolic rate by 5%–90%. “Hibernation” has been anecdotally reported for only one species, the common poorwill (Jaeger, 1948; 1949). The factors that prompt birds to use torpor or hibernation, however, remain unclear.

Daily torpor and hibernation appear to be outwardly similar among birds and mammals, except for greater reported frequency in mammals (McKechnie and Lovegrove, 2002). Reinertsen (1983) postulated that the apparent rarity of torpor in birds might be related in part to migration, which allows them to avoid adverse weather conditions and prolonged food shortages. Geiser (1998) recently addressed the evolution of torpor and concluded that in birds, unlike mammals, it occurs in modern rather than ancestral orders, suggesting that it is not an ancestral avian condition. However, there are qualitative similarities in ecology, and morphology and physiology between heterothermic birds and mammals. For example, torpor in both groups appears most commonly in small, temperate-zone species that exploit a fluctuating food supply (e.g., nectar and insects; Reinertsen, 1983). This suggests that predictable ecological constraints, resulting in periodic energy shortfalls, represent important selection pressures for both groups.

Thus the purpose of our paper is to review hypotheses, drawn from the mammalian literature, concerning ecological, behavioral and morphological determinants that may account for patterns of torpor use by birds. We also review recent data for five species of free-ranging nocturnal caprimulgiforms and specifically address the influence of body size, T_a , prey availability, foraging strategy, and reproductive activity on torpor use (Table 1).

2 Torpor occurrence in five caprimulgiform birds

2.1 Common poorwill (*Phalaenoptilus nuttallii*)

Outside of the breeding season, bouts of daily torpor are routinely used by common poorwills (45 g) throughout their range in western North America (Brigham, 1992; Csada and Brigham, 1994; Woods, 2002). Both sexes typically forage for 30–240 minutes after dusk before entering torpor and remain in torpor throughout the night, foregoing a foraging bout at dawn. Torpor bouts typically last 8–12 h, with arousals triggered by increasing T_a the following morning. In Arizona, most birds use torpor when minimum T_a falls below 10°C; and there is a clear relationship between T_a and the abundance of flying insects (Woods, 2002). On a given night, however, some individuals remain euthermic whereas others fall into torpor (Brigham, 1992; Woods, 2002). Individuals of both sexes rarely enter torpor when incubating and brooding (Brigham, 1992; Kissner and Brigham, 1993; Csada and Brigham, 1994; Woods, 2002).

Jaeger (1948, 1949) reported that some poorwills in the southern California desert remain in the same location for weeks during winter, and was the first to suggest that they hibernate. French (1993) characterized such hibernation as “seasonal dormancy” based on individuals remaining inactive for prolonged periods without foraging. Woods (2002) followed radio-tagged birds near Tucson, Arizona, and found a range of thermoregulatory and behavioral responses to low T_a . Some individuals remained inactive for weeks without interruption. Inactive birds used deep torpor every day but invariably warmed to near euthermic levels on sunny days, principally due to exposure to solar radiation. However, when inactive birds were shaded to prevent solar exposure, birds aroused about every five days using endogenous heat, resembling the periodic arousal pattern of classic mammalian hibernators. This suggests that periodic arousals may be common to both birds and mammals, but that birds rely more on an exogenous heat source to facilitate re-warming and reduce arousal costs.

2.2 Common nighthawk (*Chordeiles minor*)

High mortality in captive birds forced into torpor (3 of 4; Lasiewski and Dawson, 1964), and a lack of evidence for it in free-ranging common nighthawks (80 g) in British Columbia, Canada (Firman et al., 1993), suggests that torpor is not used regularly by this species. Brigham et al. (1995) anecdotally reported torpor in two nighthawks, and

Fletcher et al. (in review) found two free-ranging birds in southwest Saskatchewan, Canada, using shallow torpor at night during late August prior to migration. Taken together, these observations suggest that while nighthawks can enter shallow torpor if stressed, they probably do not normally use heterothermy for conserving energy.

2.3 Whip-poor-will (*Caprimulgus vociferus*)

Whip-poor-wills (55 g) are marginally larger than poorwills and are found throughout deciduous woodlands in eastern North America. A short-term study in Ontario failed to record torpor (Hickey, 1993), but Lane (2002), working in southeast South Dakota, recorded occasional torpor use in spring (May) and fall (September) by both sexes, beginning at dawn. The lowest body temperature recorded was about 18°C. Passive re-warming by the sun appeared to be important but not essential for re-warming.

2.4 Australian owlet-nightjar (*Aegotheles cristatus*)

The Australian owlet-nightjar (50 g) is ubiquitous in Australian woodlands where it roosts in cavities that may offer protection from predators and greater thermal stability than exposed roosts (Brigham et al., 1998). Free-ranging birds regularly use shallow bouts of torpor during winter (May–September) near Armidale NSW (Brigham et al., 2000) but not during the breeding season (October to January). Like whip-poor-wills, owlet-nightjars rarely use torpor during normal activity at night; most (95%) torpor bouts begin at dawn (Geiser et al., this symposium).

No T_a threshold delineates days on which owlet-nightjars do or do not enter daytime torpor. The individual monitored over the winter of 1998 used torpor every morning for 64 consecutive days from June–August, despite variable minimum T_a s from –7 to 11°C (Brigham et al., 2001). The regularity of torpor implies that it is used for more than energetic emergencies (*sensu* Carpenter and Hixon, 1988). Night torpor was uncommon and then only on very cold nights ($T_a < 5^\circ\text{C}$). This, when combined with data on activity, suggests that foraging is profitable on most nights (Brigham et al., 1999).

2.5 Tawny frogmouth (*Podargus strigoides*)

Despite avoiding torpor in the laboratory (Bech and Nicol, 1999), free-ranging tawny frogmouths (500 g) regularly use shallow torpor in bouts about 7 hours after foraging at dusk (Körtner et al., 2000, 2001). At dawn, frogmouths re-warmed and resumed foraging or moved to new roosts and re-entered torpor (Körtner and Geiser, 1999). The mini-

Table 1 Summary of data on life history and thermoregulatory parameters for five free-ranging caprimulgiform birds

	Mass (g)	Roost	Foraging	Torpor use	Depth	Duration	Timing
Common poorwill	45	Ground	Sally	Common	Deep	> One day	Night
Whip-poor-will	55	Ground	Sally	Rare	Shallow	Hours	Morning
Common nighthawk	80	Ground/branch	Hawk	Very rare	Very shallow	Hours	Night
Aust. owlet-nightjar	50	Cavity	Sally/walk	Common	Shallow	Hours	Morning
Tawny frogmouth	500	Branch	Sally/pounce	Common	Shallow	Hours	Night

imum T_b of frogmouths was about 29°C. Its timing was markedly different from that in owlet-nightjars, although the studies were done at the same time of year at the same site.

3 Ecological determinants

3.1 Body size

It is generally thought that small animals are more likely to use deep torpor than large ones because of their large surface area to volume ratio (Geiser, 1998). This assumption is not supported by the data for tawny frogmouths (Körtner et al., 2000, 2001). Recent work on geese and pigeons corroborates the finding that large birds do use torpor (Butler and Woakes, 2001; Schleucher, 2001). These discoveries demonstrate that body size does not account for patterns of torpor in birds alone. Future studies of other large caprimulgid birds are imperative. Clearly, the energetic savings of torpor need to be treated as an integrative function because depth, duration and frequency of bouts all influence the energy savings. Thus, while deep torpor appears restricted to small endotherms, shallow bouts appear important for the energy budgets of larger species.

3.2 Breeding

The five caprimulgiforms studied in the field to date rarely use torpor when nesting. It is not clear whether this reflects active avoidance of torpor by reproducing birds, or a consequential result of usually greater abundance of prey and more favorable weather during the nesting period. High concentrations of particular hormones (e.g., testosterone) were thought to be incompatible with the regular use of seasonal or daily torpor in mammals (Lee et al., 1990), although this does not appear true for bats, ecologically perhaps most similar to caprimulgids (Willis, 2006). In birds, prolonged bouts of torpor may compromise the development of embryos and chicks (Webb, 1987; Csada and Brigham, 1994), in connection with which the non-incubating member of a breeding pair will occasionally use torpor during the nesting period (Woods, 2002). Laboratory and field studies addressing torpor use by animals living in relatively non-seasonal climates will help to separate the effect of reproduction from T_a as proximate determinants of torpor use.

3.3 Foraging strategy

Of the five caprimulgiforms so far known to use torpor naturally, four are strictly nocturnal; nighthawks are mostly crepuscular. Whip-poor-wills, poorwills and owlet-nightjars sally after prey, owlet-nightjars also searching for it while walking on the ground. Frogmouths commonly pounce on terrestrial arthropods while nighthawks catch flying insects on the wing. Apart from an insectivorous lifestyle, there is no obvious connection between torpor use and foraging strategy in these birds. Furthermore, foraging style does not explain the differences in timing of torpor bouts (Table 1). In this context, studies that address the importance of T_a and roost selection to facilitate passive re-warming are needed.

3.4 Ambient temperature and prey abundance

Among endotherms generally and in caprimulgiforms specifically, torpor is assumed to represent an energy saving strategy to cope with low T_a . However, most studies have been conducted in temperate areas where it is difficult to separate T_a and prey abundance as proximate factors. Furthermore, most studies make no attempt to measure prey abundance. In a tantalizing experiment, Woods (2002) erected lights to create prey concentrations within the territories of poorwills. Despite a small sample size, he found that poorwills occupying territories with prey concentrations entered torpor less often than controls. Experimental studies like this, especially at sites that remain warm year-round, hold promise for teasing apart the ecological basis for torpor use.

In conclusion, this review suggests that no single ecological, behavioral or morphological factor single-handedly explains patterns of torpor observed in free-ranging birds. Rather, it seems that the interactive effects of a number of environmental and evolutionary constraints combine to shape avian heterothermy. We suggest that three approaches will be useful for future studies. First, experimental manipulations such as hormone treatment and shading of roosts, secondly, comparative studies of sympatric species to address the importance of phylogeny, and thirdly, data from tropical species and wide-ranging conspecifics.

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S22-4 Torpor in Australian birds

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Abstract Energy-conserving torpor is characterized by pronounced reductions in body temperature and metabolic rate and, in Australian birds, is known to occur in the Caprimulgiformes (spotted nightjar, Australian owl-nightjar, tawny frogmouth), Apodiformes (white-throated needletail) and the Passeriformes (dusky woodswallow). Anecdotal evidence suggests that it also may occur in the white-fronted honeyeater, crimson chat, banded whiteface, red-capped robin, white-backed swallow, mistletoebird, and perhaps welcome swallow. Daily torpor (bouts lasting for several hours) appears to be the most common pattern, although anecdotal evidence indicates that white-backed swallows can undergo prolonged torpor. Diurnal birds enter torpor only during the night but nocturnal birds may use it by the day and/or night, and often in more than one bout/day. Body temperatures fall from ~38–41°C during activity to ~29°C during torpor in spotted nightjars, tawny frogmouths, dusky woodswallows and white-throated needletails, and to ~22°C in Australian owl-nightjars. In the spotted nightjar, a reduction in T_b by ~10°C resulted in a 75% reduction in metabolic rate, emphasizing energy conservation potential. Since torpor is likely to be more crucial for the survival of small birds, a detailed understanding of its use is important, not only for physiologists but also ecologists and wildlife managers. It is thus disappointing that so much information on torpidity in Australian birds is anecdotal, and that so little effort has been made to characterize its patterns and quantify the resulting energy savings and survival benefits for birds in the wild.

Key words Australia, Energy expenditure, Thermoregulation, Torpor

1 Introduction

Endothermic birds and mammals differ from ectotherms primarily in their ability to regulate body temperature (T_b) using internal heat produced from combustion of food fuels. Because the surface area/volume ratio of animals increases with decreasing size, many small endotherms must produce an enormous amount of heat to compensate for heat loss during exposure to cold. Obviously, prolonged periods of high metabolic heat production can only be sustained by high food intake; and, during adverse environmental conditions and/or shortage of food, the cost of thermoregulation may be prohibitively high. Therefore, not all mammals and birds maintain permanent homeothermy, but during certain times of the day or year enter a state of torpor (Lyman et al., 1982; Geiser and Ruf, 1995).

Torpor in these “heterothermic endotherms” is characterized by a controlled reduction of T_b , metabolic rate (MR), and other physiological processes with the main apparent function of reducing energy expenditure substantially. Torpor conserves energy because (i) over a wide range of ambient temperatures (T_a), no thermoregulatory heat production is required, and (ii) the substantial fall of T_b , and in some species inhibition of MR, can substantially lower energy expenditure to well below the basal metabolic rate (BMR). Torpor is commonly used to cope with acute environmental challenges or food shortages, but can also be employed to balance daily energy expenditure without ob-

vious stress or even to enhance fuel storage to cope with future energy bottlenecks (Carpenter and Hixon, 1988; Geiser and Masters, 1994).

Although both birds and mammals can use torpor (MacMillen and Trost, 1967; Dawson and Hudson, 1970; Reinertsen, 1983; Prinzinger and Siedle, 1988; Geiser and Ruf, 1995; Schleucher, 2001; Downs and Brown, 2002; McKechnie and Lovegrove, 2002), it is widely believed that torpor in small birds is far less common than in small mammals because birds can migrate to avoid adverse conditions. This argument is based on the assumption that birds in general use long distance migration, which is, of course, not the case. Many Australian birds are sedentary or nomadic instead and, because the Australian continent is characterized by low rainfall, high evaporation rates, prolonged droughts and low primary productivity, food will be limiting periodically, in addition to the usual seasonal challenges experienced elsewhere. Sedentary insectivores and frugivores, in particular, should suffer energetic bottlenecks under such conditions; and since they do not migrate far, they are likely to use physiological adaptations that help them to survive.

Australian birds are an interesting group from an evolutionary point of view. Many species are endemic, and the majority of passerines appear to be the result of a massive Australian radiation (Sibley and Ahlquist, 1985; Schodde and Mason, 1999), and therefore are especially likely to be

physiologically adapted to the idiosyncrasies of the continent.

In this paper we review published information on torpor in Australian birds, and also present some unpublished data. Worldwide, heterothermic species, judged by capacity to reduce $T_b > 6^\circ\text{C}$ (McKechnie and Lovegrove, 2002), are known from seven bird orders, but so far from only three include them in Australia (Table 1).

2 Caprimulgiformes (nightjars and allies)

Anecdotal reports of torpor in Australian birds have been around since the 1920s, but the first quantitative data were provided by Dawson and Fisher (1969) for captive spotted nightjars (*Eurostopodus argus*). The T_b of one individual fell from $\sim 39^\circ\text{C}$ during normothermia (regulating a high T_b) to 29.6°C during torpor, and MR was reduced to only $\sim 25\%$ of resting MR in normothermic individuals. More data on torpor in Australian caprimulgiforms have become available recently. Free-ranging Australian owl-nightjars (*Aegotheles cristatus*) frequently entered torpor in the early morning in winter, with T_b falling to a minimum of 22°C (Brigham et al., 2000). Torpor lasted for ~ 4 hours through the morning and birds re-warmed near midday, perhaps using radiant heat from the sun which substantially reduces the energetic costs of re-warming (Geiser and Drury, 2003). Only one third of monitored birds re-entered a second bout in the afternoon, before arousing for nocturnal activity. Captive owl-nightjars entered torpor as well, but it was shallower and shorter than in the field (Geiser et al., 2000).

Although laboratory investigations suggested that tawny frogmouths (*Podargus strigoides*) are homeothermic (McNab and Bonaccorso, 1995; Bech and Nicol, 1999), and the species is ~ 10 -fold larger than any caprimulgid recorded with torpor, they do enter torpor in the wild (Körtner et al., 2000, 2001). Its pattern, however, differs substantially from that in owl-nightjars: frogmouths entered torpor at night, typically after a brief period of activity. Moreover, the minimum T_b of frogmouths (29°C) was well above that in owl-nightjars. After a bout of night torpor lasting ~ 7 hours, frogmouths always re-warmed actively before sunrise before flying to a day roost, and there often re-entered a second, dawn torpor that terminated in the late morning.

Torpor in tawny frogmouths occurred exclusively during winter, and was correlated with average night T_a . During cold dry winters, when night T_a frequently dropped $< 5^\circ\text{C}$, night torpor frequency reached up to 60% of observations; but during warmer, wetter winters, it fell to $\sim 30\%$. In all winters, morning torpor was less common than night torpor (Körtner and Geiser, 2000).

Although both owl-nightjars and tawny frogmouths enter torpor in the same habitats in the wild, pattern and timing differ substantially. These differences appear to be related to differences in size, mode of foraging and roosting.

Frogmouths at 500 g mass carry fat reserves and seem to be able to survive over several nights without foraging; they are sit-and-wait predators of active arthropods and are unlikely to be very successful when cold T_a limits insect activity. Owllet-nightjars at 50 g mass, in contrast, have a much lower capacity to store fat; they also forage actively on the ground, and may be able to find food on most nights.

A possible reason for differences in the timing of their torpor may also be related to roosting. Owllet-nightjars roost in tree cavities potentially protected from diurnal predators, whereas Frogmouths, although well camouflaged, roost on branches in the open (Brigham et al., 2000). Differences in the minimum T_b between the two species (frogmouths 29°C , owllet-nightjars 22°C) are probably related to body mass. Small birds have lower minimum T_b than large birds (Geiser and Ruf, 1995), which maximizes the reduction of MR, and thus energy-savings during torpor.

Thus it appears that Australian caprimulgids use torpor extensively, as on other continents (Jaeger, 1948; Bartholomew et al., 1957; Peiponen, 1965; Withers, 1977; Brigham, 1992; French, 1993). Ecological factors influencing torpor use by caprimulgids are discussed elsewhere in this symposium (Brigham et al., 2006).

3 Apodiformes (swifts and hummingbirds)

The only observations of torpor in Australian swifts are those by Pettigrew and Wilson (1985) for a white-throated needletail (*Hirundapus caudacutus*). A captive bird went into torpor every night over several nights, and body mass declined during that time. On one night when cloacal T_b was continually monitored, T_b fell from 38.5°C to 28°C and the bird remained torpid for 10 hours. The bird aroused actively the following morning after human disturbance. In view of the large size of *Hirundapus* swifts (85 g), we think it likely that other Australian swifts, all of which are smaller, are also heterothermic.

4 Passeriformes

The oldest report on a torpor-like state in passerines claims that welcome swallows (*Hirundo neoxena*) show "semi hibernation", huddling in rock crevices in winter and foraging only on warm days (Dove, 1923). This report implies that the birds remained in the crevices for several days, but it was not quantified systematically and it is not clear whether birds simply huddled or were torpid.

Heumann (1926) reported a torpor-like state in mistletoebirds (*Dicaeum hirundinaceum*). He recorded that six birds froze close to death while in transit to America and were resuscitated four times. He also observed that captive mistletoebirds became cold regularly in winter in an aviary, but no quantitative measurements were taken.

Reports on torpor in white-backed swallows (*Cheramoeca leucosternum*) are based on observations made near Perth, Western Australia (Serventy, 1970). A group

Table 1 Torpor in Australian birds

	Body mass (g)	Minimum T_b (°C)	Torpor duration (h)	Notes	Source
Caprimulgiformes					
Spotted nightjar <i>Eurostopodus argus</i>	75	29.6		Torpor in captive bird in summer	Dawson and Fisher, 1969
Australian owl-nightjar <i>Aegotheles cristatus</i>	50	22.4	4–6	Dawn torpor in winter, arousal near midday, and 2nd bout in afternoon; nocturnal torpor only on cold winter nights	Brigham et al., 2000
Tawny frogmouth <i>Podargus strigoides</i>	500	29	7	Nocturnal torpor on cold winter nights, arousal near sunrise, 2nd dawn bout common	Körtner et al., 2000, 2001
Apodiformes					
White-throated needletail <i>Hirundapus caudacutus</i>	85	28	~10	Nocturnal torpor in captive bird in summer	Pettigrew and Wilson, 1985
Passeriformes					
White-fronted honeyeater <i>Phylidonyris albifrons</i>	~20			Nocturnal torpor	Ives, 1973
Noisy miner <i>Manorina melanocephala</i>	70	33	~10	Nocturnal shallow torpor	Geiser, unpublished
Crimson chat <i>Epthianura tricolor</i>	~10			Nocturnal torpor in juveniles lasting till late morning	Ives, 1973
Banded whiteface <i>Aphelocephala nigricincta</i>	~10			Regular nocturnal torpor in winter	Ives, 1973
Red-capped robin <i>Petroica goodenovii</i>	~9			Nocturnal torpor	Ives, 1973
Dusky woodswallow <i>Artamus cyanopterus</i>	35	29	~12	Regular spontaneous nocturnal torpor in outdoors aviary in autumn/winter	Maddocks and Geiser 1999
White-backed swallow <i>Cheramoeca leucosternum</i>	13			Diurnal torpor in group of birds in burrow on cold winter day	Serventy, 1970; Congreve, 1972
Welcome swallow <i>Hirundo neoxena</i>	12			Torpor in groups of birds huddling in tree cavities or rock crevices in winter?	Dove, 1923
Mistletoe bird <i>Dicaeum hirundinaceum</i>	9			Birds in intercontinental transit appeared dead, resuscitated after rewarming	Heumann, 1926

of ~20 torpid swallows were found in a burrow; they did not move and were cold to touch when removed for examination. The birds had disappeared a week later. As this observation was made during the daytime on a cold winter's day, it is not an example of the nocturnal torpor common in diurnal birds but may instead represent prolonged torpor. This interpretation is supported by further observations on four individuals (Congreve, 1972) that were found at the end of a tunnel during the collection of sand. When first discovered at 13:15 h the birds were cold to touch, by 13:35 h they were shivering and at 14:00 h they could fly. Congreve suggests that the swallows may spend some of the winter in a state of torpor, again implying that this species may enter prolonged bouts of torpor.

Ives (1973) reported behavioral observations of tor-

por in several Australian arid-zone birds. Young crimson chats (*Epthianura tricolor*) disperse from the nest early in development, and spend the night on the ground. During the night they appear to enter a torpid state and when handled on the following morning remain inert, reviving only after passive re-warming. Captive banded whitefaces (*Aphelocephala nigricincta*) enter torpor each night and re-warm when T_a rises in the morning. Nocturnal torpor was also reported in red-capped robins (*Petroica goodenovii*) and white-fronted honeyeaters (*Phylidonyris albifrons*), but no details were provided.

Honeyeaters are a successful endemic Australian bird family. They are relevant to the context of this paper as they mainly eat insects and nectar, the availability of which fluctuates with weather or season. Free-ranging noisy miners

(*Manorina melanocephala*), a medium sized honeyeater (70g), showed substantial and predictable reductions of T_b on every night in winter (T_b measured $\pm 0.5^\circ\text{C}$ with implanted iButtons). The most extreme fluctuation of T_b occurred during mid-winter (July), with daily shifts of up to 9°C . Although minimum T_b of 33°C was relatively high, it would still be classified as torpor under many definitions. Daily T_b fluctuations followed the dark- and light- phases very closely, with a steep decline of T_b at the beginning of the night, a further reduction of T_b until $\sim 2\text{--}3$ am, which was followed by slow rise of T_b before sunrise and finally a steep rise back to normothermic T_b of $\sim 41^\circ\text{C}$ after sunrise. When food was withheld, captive noisy miners showed a similar nightly reduction of T_b and reduced MR to $\sim 50\%$ of that during the day (Maddocks, 2001).

Dusky woodswallows (*Artamus cyanopterus*) at 35 g also enter nocturnal torpor in captivity. They feed mainly on the wing on flying insects, and roost in tightly packed communal swarms in the wild. They also exhibit predictable daily changes in T_b , which are even more pronounced than in noisy miners. T_b fell at dusk, even when food was available throughout the day, and birds remained torpid throughout the night, re-warming at dawn. Especially in May/June, T_b fell regularly from $\sim 41^\circ\text{C}$ to $\sim 30^\circ\text{C}$ and on some occasions to 29°C (Maddocks and Geiser, 1999).

Torpor thus appears to be commonly used by Australian birds for energy conservation. However, more quantitative work is required to establish its impact on avian survival in general.

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S22-5 Evolutionary and ecological determinants of avian torpor: a conceptual model

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Abstract We constructed a generalized, conceptual model that attempts to predict the occurrence of avian torpor. A recent hypothesis suggests that endotherm heterothermy is monophyletic, and predicts that torpor should be more widespread in phylogenetically older taxa. Once phylogeny is accounted for, the most important determinant of avian torpor is body mass (M_b). We used an existing model of endotherm torpor to predict the relationship between M_b and minimum body temperature (T_b) during torpor. The available data show that the lower limit of torpor T_b is determined by the M_b -dependent costs of re-warming following a torpor bout. In addition to phylogeny and M_b , the relationship between the relative energetic benefits and potential ecological costs of torpor is likely to be an important determinant of torpor. We constructed a model which predicts that torpor should be more prevalent in species near the extremes of the avian metabolic continuum. Available data provide tentative support for this prediction. In addition to such generalized factors as phylogeny and M_b , specific aspects of the ecology of individual species need to be considered when predicting the occurrence of avian torpor.

Key words Body size, Ecology, Evolution, Metabolic rate, Torpor, Phylogeny

1 Introduction

Recent evidence suggests that avian torpor is more common, and occurs in a wider variety of ecological contexts, than previously thought. For example, torpor occurs routinely under natural conditions in several members of the Caprimulgidae and their relatives (Brigham, 1992; Brigham et al., 2000; Körtner et al., 2000). Evidence also exists that torpor is not necessarily confined to periods of energy shortage. In hummingbirds, its use is determined by a suite of proximate factors, including seasonal variation in the propensity for torpor, the perceived availability of food, and temporal variation in assimilation efficiency (Hiebert, 1991). Collectively, these observations suggest that the contribution of the capacity for torpor to avian fitness has been underestimated.

Facultative hypothermic responses have been investigated in 95 avian species, and approximately 30% apparently involve torpor (McKechnie and Lovegrove, 2002). The limited data set available makes it difficult to identify generalized evolutionary and ecological determinants of avian torpor. Here, we present a conceptual model for generating hypotheses concerning the occurrence or absence of torpor in particular species. Specifically, we argue that the occurrence of avian torpor can be predicted by (1) phylogeny, (2) body mass (M_b) constraints, (3) trade-offs between energetic benefits and potential ecological costs, and (4) specific ecological factors. We test these predictions where available data permit.

2 Phylogeny

The evolutionary origins of torpor remain controversial (Geiser, 1998). Malan (1996) has argued that hibernation and torpor in endotherms represent a release of an inhibition of the primitive tendency towards wide-amplitude T_b (body temperature) cycling, which comprised a hypothesized intermediate step in the transition from ectothermy to endothermy. His hypothesis concerning the ancestral nature of heterothermy provides a potential starting point for a model of the evolutionary determinants of avian torpor. If this hypothesis is correct, then torpor should be more prevalent in phylogenetically older taxa, once other factors are controlled for. Although insufficient data are currently available to test this prediction, torpor does appear to be more common in phylogenetically older taxa. In particular, it is more common in the Coliiformes, Trochiliformes and Strigiformes than in the Passeriformes, the most derived avian order (McKechnie and Lovegrove, 2002). Malan's (1996) view of torpor as a plesiomorphic, monophyletic trait may well explain its absence in many of the passerines investigated, even those permanently resident in Arctic and sub-Arctic regions. *A priori*, the absence of torpor in these species is surprising, as they routinely face low ambient temperatures combined with low food availability and short photoperiod (Reinertsen, 1996).

3 Body size

The potential energetic benefits of torpor are con-

strained by the mass-dependent relative cost of re-warming following a hypothermic bout. Prothero and Jürgens (1986) showed that the relationship between M_b (body temperature) and the time in torpor for which total energy savings during the entry and maintenance phases are equal to the costs of re-warming during the arousal phase is given by the equation:

$$W^{1-b} = \frac{1}{\left(\frac{24s}{1-\alpha}\right)\left(\frac{1}{a}\right) - \left(\frac{1}{2C_0}\right)} \left(\frac{t_{fc}}{T_b - T_a}\right)$$

(A24 in Prothero and Jürgens, 1986) where $W = M_b$ = body mass in kg; s = specific heat in kcal/(kg.°C); C_0 = coefficient relating cooling rate during the entry phase to M_b (°C. h⁻¹.kg^{1-b}); t_{fc} = time spent fully cooled in hours, i.e. duration of maintenance phase; T_b = body temperature (°C); T_a = ambient temperature (°C); $\alpha = 10/[(T_b - T_a) \cdot Q_{10}]$ in °C⁻¹; a and b are the intercept and coefficient respectively of the equation relating resting metabolic rate (RMR) to W (M_b), i.e. $RMR = aW^b$ in kcal.day⁻¹. This equation can then be used to calculate the critical M_b (i.e., the M_b at which the net energy savings equal zero) by setting the right-hand side of equation A24 to Q , such that:

$$W_c^{1-b} = Q \quad (\text{A22 in Prothero and Jürgens, 1986})$$

or

$$W_c = 10^{(\log Q)^{1-b}} \quad (\text{A23 in Prothero and Jürgens, 1986}).$$

These authors assumed that during torpor, $T_b = T_a$. The assumption is not critical since Q_{10} values, rather than temperature gradients ($T_b - T_a$), were used to calculate reductions in metabolic rate, and the model still operates if T_b is maintained above T_a during torpor. A second assumption was that the decrease in T_b during the entry phase occurred linearly. Although this is not the case, the authors showed, using empirical data for a hummingbird, that the model is adequate. Prothero and Jürgens (1986) used the model to calculate critical M_b s for varying bout lengths, but it can also be used to calculate critical M_b s for various torpor T_b s for a specific bout length. We assumed $s = 0.932$ kcal/(kg.°C) (specific heat of tissues; Withers, 1992), $C_0 = -0.519$ (scaling exponent for avian rest-phase thermal conductance; Schleucher and Withers, 2001), $Q_{10} = 2.5$, and normothermic $T_b = 38.5^\circ\text{C}$ (mean avian rest-phase T_b ; Prinzinger et al., 1991). For a and b , we used values from a conventional least-squares linear regression of field metabolic rate (FMR) on M_b for 81 bird species (Tieleman and Williams, 2000). We then calculated critical M_b s for a range of T_b s during torpor (Fig. 1).

A comparison of the plots generated by the Prothero and Jürgens (1986) model with the observed relationship between avian M_b and minimum hypothermic T_b (torpor and

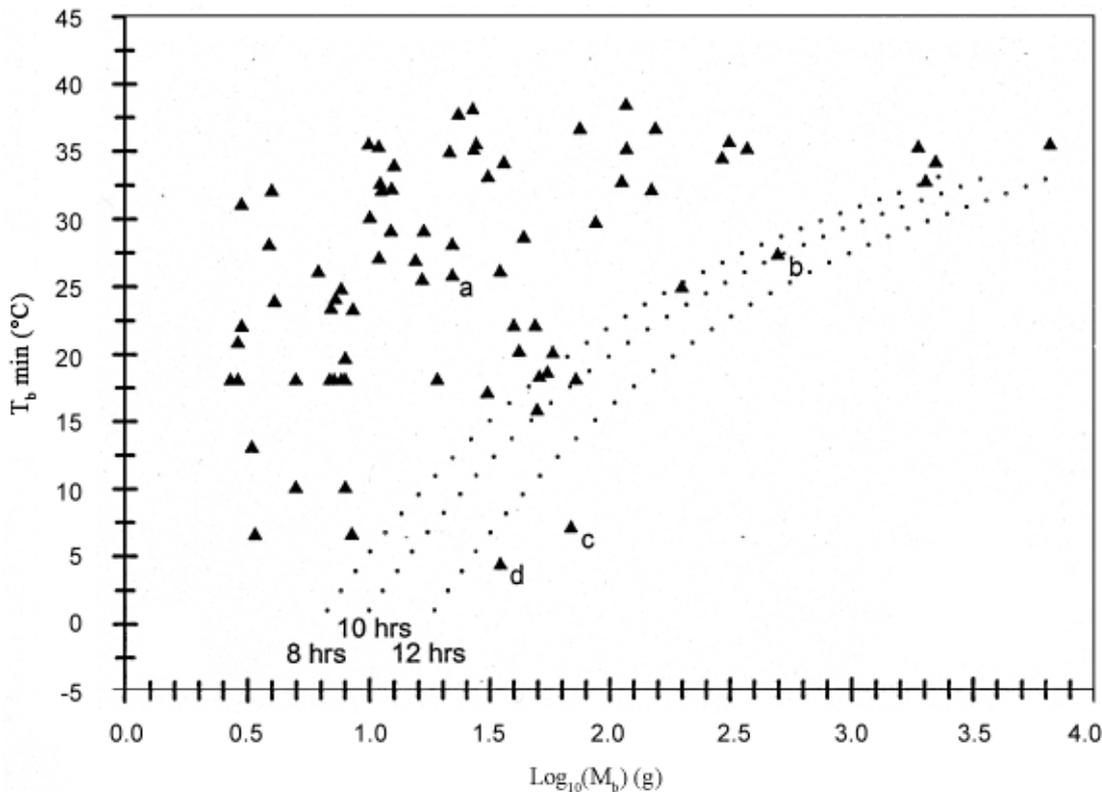


Fig. 1 Relationship between minimum body temperature during avian facultative hypothermia (T_b hypo) and \log_{10} body mass (M_b) The dotted lines indicate the minimum T_b at which a facultative hypothermic response will result in a net energy saving for a given bout length (indicated), and were calculated using Prothero and Jürgens' (1986) energetic model for daily torpor. Data for (a) *Delichon urbica* (Prinzinger and Siedle, 1988), (b) *Podargus strigoides* (Körtner et al., 2000), (c) *Caprimulgus europaeus* (Peiponen, 1966) and (d) *Phalaenoptilus nuttallii* (Brigham, 1992) are indicated by respective lower case letters.

rest-phase hypothermia) in 74 bird species (Fig. 1) suggests that the lower boundary of this relationship is determined by M_b -dependent constraints on re-warming. The only data that lie outside the theoretical boundaries plotted in Fig. 1 are those for *Phalaenoptilus nuttallii* and *Caprimulgus europaeus*. In *C. europaeus*, a minimum T_b of ca. 7°C was recorded during a bout lasting approximately 16 hours (Fig. 6 in Peiponen, 1966). In *P. nuttallii*, a minimum T_b of 4.3°C occurred during a bout of 8–10 hours (R.M. Brigham, pers. comm.).

Fig. 1 also reveals that a large component of variation in observed torpor T_b cannot be attributed to body size alone. Much of this variation may reflect phylogenetic variation in the capacity for torpor. The Prothero and Jürgens (1986) model allows the observed minimum torpor T_b to be compared with the critical value expected on the basis of M_b and bout length. By predicting critical T_b , and thus the maximum depression of T_b that will result in a net energy saving, the model provides a scale on which the hypothermic responses of a particular species can be assessed. For instance, a minimum T_b of 27°C in a 500 g tawny frogmouth (Körtner et al., 2000; symbol b in Fig. 1) is close to the critical T_b for a species of such size. In contrast, a minimum T_b of 25.7°C in a 22 g house martin (Prinzinger and Siedle, 1988; symbol a in Fig. 1) is considerably higher than critical T_b . The extent of T_b reduction as a percentage of the predicted maximum will be useful when comparing the extent to which facultative hypothermia has evolved as an energy-saving mechanism in closely related species. It should be noted that the Prothero and Jürgens (1986) model assumes that all of the energy required for arousal is derived from endogenous sources, such as shivering and non-shivering thermogenesis. The potential importance of solar radiation in reducing the costs of re-warming following avian torpor bouts deserves closer attention (see Brigham et al., this symposium).

4 Trade-off between energetic benefits and ecological costs

Species that possess the capacity for torpor by virtue of their phylogenetic position and M_b are likely to use torpor only if it confers direct fitness benefits. Presumably, the use of torpor is adaptive when the energetic benefits exceed the potential ecological costs. An understanding of the factors that determine these costs and benefits will facilitate the identification of species likely to use torpor.

The major energetic benefit of torpor is a reduction in rest-phase energy expenditure (Reinertsen, 1996). The relative benefits of torpor are hence likely to be correlated with other energetic traits that determine energy requirements in birds. Adaptive variation in such traits may be useful in identifying species in which the energetic benefits of torpor are relatively high. One such energetic trait exhibiting adaptive variation is basal metabolic rate (BMR). For instance, birds inhabiting desert habitats characterized by erratic rainfall and low primary production typically pos-

sess lower BMRs than species living in more predictable environments (Tieleman and Williams, 2000).

The adaptive variation in avian BMR implies that species near the lower end of the metabolic continuum, those with low relative BMR, have undergone strong selection for reduced energy requirements. Hence, the capacity for reducing energy requirements by means of torpor is likely to be similarly adaptive for these species. Data for both mammalian and avian heterotherms supports the hypothesized association between low BMR and torpor (Lovegrove, 1996; McNab, 1988). In contrast, species at the upper end of the metabolic continuum possess high relative BMRs and elevated energy requirements. In these species, the capacity for torpor is likely to be adaptive when the ability to meet metabolic requirements is limited by intake rates. For instance, McWhorter and Martinez del Rio (2000) found that intake rates of broad-tailed hummingbirds (*Selasphorus platycercus*) were limited by their digestive physiology.

The energetic benefits of torpor are presumably greatest at the extremes of the avian metabolic continuum. On the other hand, the potential ecological costs of torpor are presumably related to an increased risk of predation (Reinertsen, 1996; McKechnie and Lovegrove, 2002). Hence, potential ecological costs are independent of relative metabolic rate and constant across the metabolic continuum. A model of the relative energetic benefits and potential ecological costs of torpor (Fig. 2a) predicts that torpor should be more prevalent at the extremes of the metabolic continuum. In species at the extremes, the likelihood that the energetic benefits of torpor exceed the potential ecological costs is highest (Fig. 2a). The model also predicts that this effect should be more pronounced in species for which the potential ecological costs of torpor are high.

To test the prediction that torpor should be more prevalent at the extremes of the avian metabolic continuum, we obtained measures of BMR for 420 avian species from the literature. We calculated a conventional least-squares linear regression of \log_{10} BMR on $\log_{10} M_b$ (\log_{10} BMR = $0.667 \log_{10} M_b + 0.838$), and then calculated a \log_{10} BMR residual for each species. These residuals were approximately normally distributed. Of the 420 species, 35 are known to exhibit torpor (*sensu* Reinertsen, 1996; $T_b < 30^\circ\text{C}$). BMR and torpor T_b data are available on request from the corresponding author. The frequency distribution of the \log_{10} BMR residuals of these 35 species differed significantly ($\chi^2 = 68.934$; $df = 24$; $P \ll 0.05$) from the overall distribution. A frequency distribution of the proportion of species known to exhibit torpor (Fig. 2b) reveals that torpor is indeed more prevalent in species near the extremes of the avian metabolic continuum.

5 Ecological factors

We have argued that generalized factors, namely phylogeny, body size, and energetic traits such as BMR, can be used to generate hypotheses concerning the occur-

rence of avian torpor. However, both the relative energetic benefits that a bird derives and the potential ecological costs that it incurs by using torpor are determined by a suite of ecological factors. Any attempt to predict the occurrence of torpor in a particular species needs to take into account specific aspects of its ecology and behavior. Here we assess a specific example in attempting to identify the ecological determinants affecting the relative costs and benefits of torpor.

Schleucher (1994, 2001) investigated hypothermic responses in two small (ca. 40 g) doves, *Oena capensis* and *Geopelia cuneata*, and the relatively large (200 g) fruit-dove *Drepanoptila holosericea*. Both *O. capensis* and *G. cuneata* exhibited shallow hypothermia in response to food deprivation, with minimum T_b s of 35.3°C and 34.4°C respectively (Schleucher, 1994, 2001). In contrast, *D. holosericea* exhibited torpor (minimum T_b = 24.8°C) during *ad libitum* feeding at T_a s between 12°C and 27°C (Schleucher, 2001). *A priori*, the two smaller, desert

granivores might seem more likely candidates for torpor than a larger, rainforest frugivore. However, *O. capensis* and *G. cuneata* are nomadic, continental species (Baptista et al., 1997), and are presumably able to avoid areas of low food availability. Moreover, both these species have several potential nocturnal mammalian predators (Nowak and Paradiso, 1983). In contrast, *D. holosericea* is a non-migratory species restricted to New Caledonia (Baptista et al., 1997). In the Australasian zoogeographical region, the El Niño Southern Oscillation (ENSO) causes unpredictable, severe droughts (Stone et al., 1996; Philander, 1983). A sedentary, frugivorous species such as *D. holosericea* is likely to encounter large fluctuations in fruit availability associated with ENSO events (Van Schaik, 1986). We argue that *D. holosericea* experiences stronger selection for reduced energy requirements than *O. capensis* or *G. cuneata*. Moreover, there are no mammalian predators on New Caledonia (Nowak and Paradiso, 1983), and *D. holosericea* presumably has virtually zero risk of nocturnal predation.

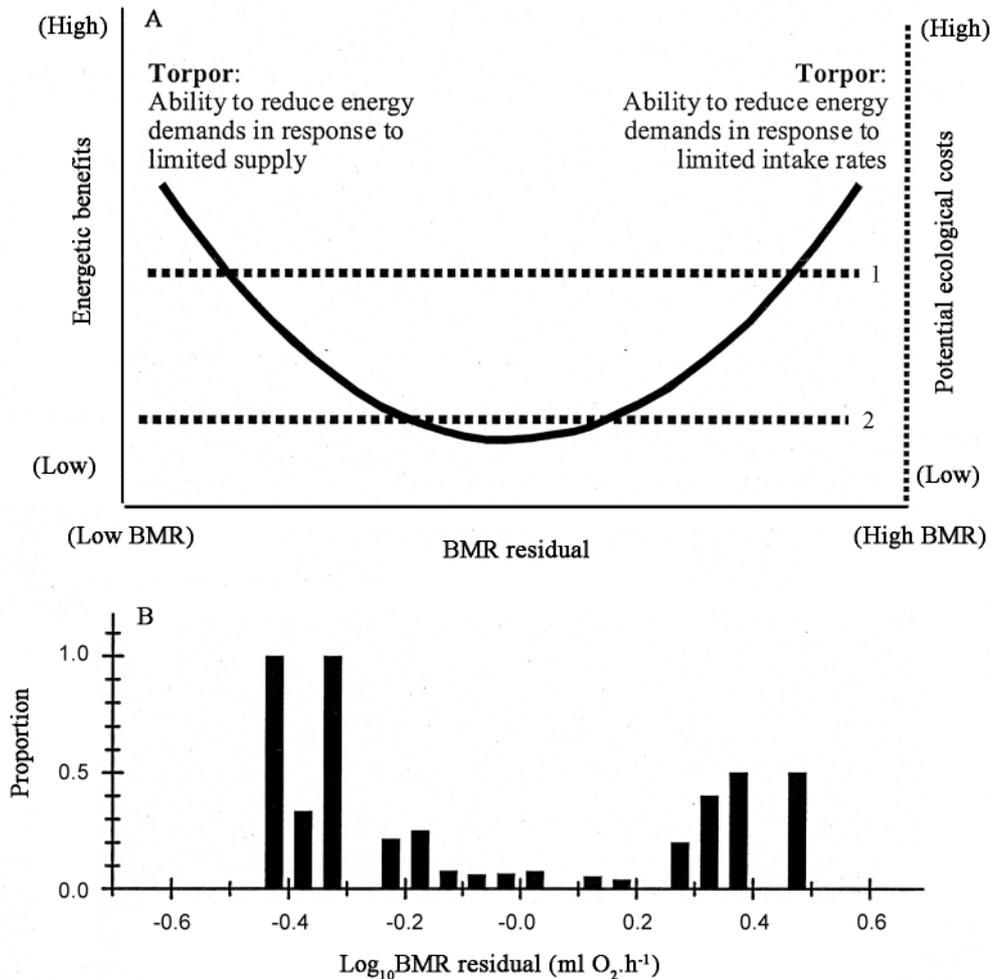


Fig. 2 A model of the relative energetic benefits and potential ecological costs of avian torpor

(A) The energetic benefits of torpor (solid line) are greatest at the extremes of the metabolic continuum. Dotted line 1 indicates a taxon in which the potential ecological costs of torpor are high (e.g., a large, non-cryptic species easily located by predators). Dotted line 2 indicates a taxon in which the potential ecological costs of torpor are low (e.g., small, cryptic species). The capacity for torpor should be adaptive when the energetic benefits are greater than the potential ecological costs, i.e. when the solid line is above the dotted line. (B) A frequency distribution of the proportion of species known to use torpor which supports this prediction.

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Symposium 23 The biological species concept: application in pure and applied ornithology

Introduction

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Central to all biological endeavour, and especially to all comparative work whatever the field, is knowledge of the species taxa under study. Unfortunately, confusion continues to affect our understanding of what is meant by “species concept”, “species category”, species as phyletic lineages and species as real ecological units in nature, all of which are commonly embraced within a simple, non-discriminatory perception of the “species”. This symposium addresses these issues; and it does so from the viewpoint that difficulties in applying the conventional biological spe-

cies concept (BSC) are best resolved by resetting and augmenting that concept, not by discarding it in favor of novel alternatives with practical inadequacies of their own. One particular shortcoming of the BSC in conservation is its frequent down-grading of operational biodiversity units to subspecies or races. Towards resolving this problem, the symposium considers neutral ideas, such as the newly proposed “ultrataxon” concept, that can identify all conservation units necessary while remaining compatible with whatever species concept is used

S23-1 The history of the biological species concept

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Abstract Populations of the same species are potentially capable of interbreeding and do not normally interbreed with populations of other species. The biological species concept (BSC) implies population thinking and models of speciation; it is process-driven, not pattern-driven. Several naturalists developed these views empirically during the course of the 19th century. The roots of these interpretations go back to the typological ideas of 18th and 17th century naturalists who stated that the constant succession of similar individuals constitutes the species, and cross-sterility preserves the distinctness of species, thus guaranteeing their permanence and fixity. A causal analysis of the BSC became possible only after the rise of population genetics during the 1930s. Several alternative species “concepts” proposed in recent years are basically guidelines for the delimitation of species taxa rather than different theoretical species concepts. The term “species” refers to the theoretical species concept, to the species category in taxonomy and to individual species taxa.

Key words Species, Biological species concept, Species taxa, Population genetics, Typology, Hybridization

1 Introduction

Ernst Mayr (1942: 120) defined biological species as “groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups”. The Biological Species Concept (BSC) is based on populations sharing a common gene pool, and reproductive isolation means genetic isolation from other species. Isolating mechanisms preserve the adaptive gene combinations of species. However, minor gene-flow between them from low-level interspecific hybridization does not affect the integrity of biological species. The BSC implies population thinking and models of speciation; it is a process driven concept. Although Ernst Mayr was not the originator of the BSC, as he himself emphasized repeatedly, his simple, concise definition and arguments led to its widespread acceptance from the mid 20th century on.

The previously applied species concept had been the typological species concept of most 18th and 19th century naturalists (Fig. 1). As Buffon (1749) had stated, “A species is a constant succession of similar individuals that can reproduce together” (Mayr, 1982). The type or essence of each species supposedly maintains their permanence and fixity. Under the typological species concept, variation is no more than the imperfect manifestation of the type and so-called “essential” characters distinguish the constant species.

2 Germ and growth of the biological species concept

The event which generated the paradigm shift from typological species based on the notion of essentialism to biological species based on the notion of evolution was the

appearance of Charles Darwin’s *Origin of Species* in 1859. The change-over was rapid and smooth in North America, but more hesitant and argumentative in Europe. Perceptions of the BSC developed slowly there over a long transitional period in the late 19th century (Mayr, 1957; Grant, 1994). “A solution to the problem of species diversification required an entirely new approach, and only the naturalists were in the position to find it. Leopold von Buch in the Canary Islands, Darwin in the Galapagos, Moritz Wagner in North Africa, and A. R. Wallace in Amazonia and the Malay Archipelago were the pioneers in this endeavor” (Mayr, 1991:19).

The first author to discuss briefly but accurately the nature and origin of biological species was Leopold von Buch (1819, 1825), one of the great naturalists of the first half of the 19th century. After Darwin returned from his expedition in 1836, he searched the literature on island biotas and read Von Buch’s “admirable discussion,” as he mentioned in one of his Transmutation Notebooks. He pointed out that speciation is achieved as soon as geographically separated populations reach reproductive isolation from their geographical representatives. During the late 1830s and 1840s Darwin came very close to the modern BSC, but from the 1850s he conceived species mostly by “degree of difference” rather than reproductive isolation. Even so, certain passages in the *Origin* (1859) indicate that he still appreciated the importance of biological criteria, including reproductive isolation (Kottler, 1978: 292–293).

The thread of genetic isolation reappeared elsewhere too. The Swiss malacologist Albert Mousson observed in 1849 that “If a peripheral variety does not interbreed with the basal form of the species ... then this constant variety would have to be elevated to the status of a separate

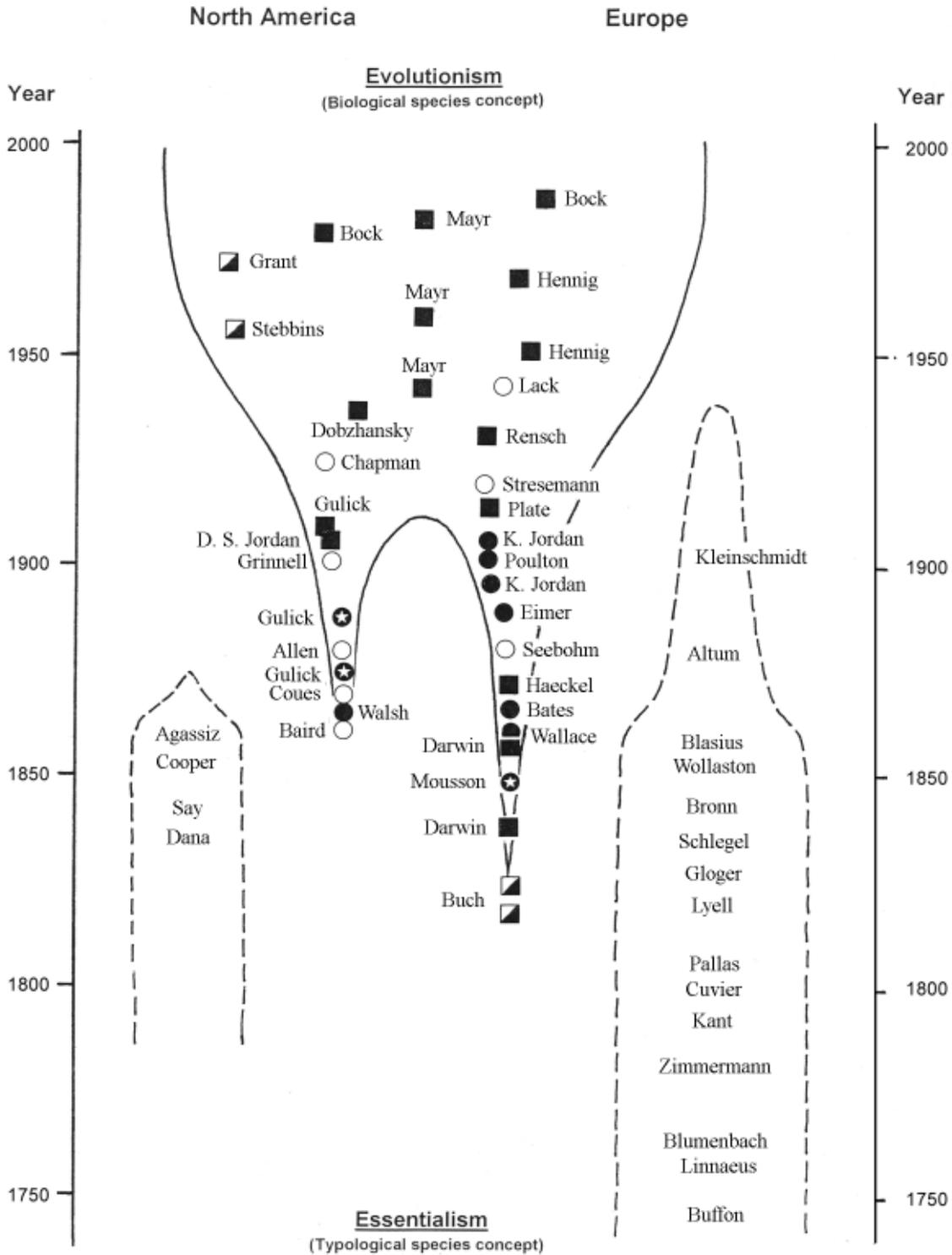


Fig. 1 Interpretations of species in biology under the notions of essentialism (below) and evolutionism (above)
 The names of selected authors are indicated at their respective time levels. Solid squares refer to publications on animals in general, half-filled squares to those on plants, solid circles to insects, circled stars to mollusks and open circles to birds.

species". During the 1860s H. W. Bates and A. R. Wallace (1864: 158–159) were of the opinion that a new species would be produced "if a slight variety had become fixed as a local form, and afterwards been brought into contact with the parent species, with little or no intermixture of the two." The naturalist traveler Moriz Wagner (1868) became a vigorous advocate of the role of geographic isolation in taxonomic differentiation when he published his separation theory of evolution. He maintained that geographical isolation was necessary not only for speciation but also evolutionary change (Mayr, 1963: 485).

The theoretical views of most North American ornithologists of the late 19th century were fully in accord with the theory of evolution and they called geographical subspecies somewhat simplistically as "nascent species." Henry Seebohm (1881: X) in Britain was the first ornithologist to emphasize geographical isolation as a precondition for speciation in birds. He observed that two forms "become so far separated, that should their areas of distribution again overlap they will nevertheless not interbreed and the two species may be considered to be completely segregated." Then came Karl Jordan (1905) with the next conceptual step, the coexistence of distinct natural populations at a single locality at the same time: "The living inhabitants of a region are not a chaotic mass of intergrading groups of individuals, but ... are composed of a finite number of distinct units which are sharply delimited against each other and each of which forms a closed unit ... The units, of which the fauna of an area is composed, are separated from each other by gaps which at this point are not bridged by anything. This is a fact which can be tested by any observer."

The main ideas embodied in the biological species and of speciation had been established empirically by naturalists during the course of the 19th century (Haffer, 1992). Their causal analysis became possible, however, only after the rise of population genetics during the 1930s. Dobzhansky's endorsement of the BSC (1935, 1937) contributed to its increasing popularity; and then through Ernst Mayr's publications of 1942 and 1963, as well as those of Stebbins (1950) and Grant (1971), the BSC became one of the central tenets of the modern synthetic theory of evolution. David Lack (1944, 1949) added important ecological explanants of species and the speciation process.

3 Theoretical considerations

The "horizontal" perception of biological species, as shown in Fig. 2, refers to genetically isolated reproductive communities at a particular time, whether present or past. The "vertical" life or the "duration" of a species is a matter of convention and, in most cases, determined by the incompleteness of the fossil record. Phyletic lineages through time are not involved in the processes of evolution and should not be designated as species. Phyletic evolution and speciation take place in living species populations (Bock, 1986; Szalay and Bock, 1991).

The theoretical BSC is nondimensional and can be

applied directly only to sympatric or parapatric populations of bisexual organisms. It is the multidimensional species notion in taxonomy, with its extensions over space and time, that applies to the real units observed in nature (Fig. 3) and which is subject to all the difficulties of any pragmatic application of a theoretical concept (Mayr, 1963, 1982; Bock, 1986). The distinctiveness of species becomes increasingly vague as one progresses geographically and/or chronologically farther and farther away from an area where two species occur in sympatry or parapatry. Within continents, intergradation of contiguous populations or their geographical exclusion along their contact zone (without or with restricted hybridization) determines their rank as subspecies and paraspecies, respectively. Allopatric populations are assigned subspecies or species status by inference (Mayr, 1969: 197; Mayr and Ashlock, 1991: 104–105; Helbig et al., 2002). Several alternative species concepts proposed in recent years are merely guidelines for the delimitation of species taxa rather than different theoretical species concepts.

Irrespective of their theoretical views of species, field naturalists of the 19th and 20th centuries in practice delimited species taxa narrowly, intermediately or widely according to the particular species category which they applied (Table 1). The narrow Linnaean species taxon of many 19th century ornithologists comprised only one morphologically-defined taxon, such as a subspecies of a polytypic species or a monotypic species in modern terminology. Often their reference points were only one or two specimens which supposedly represented the Platonic type of the species. Intermediates were dismissed as accidental variants or hy-

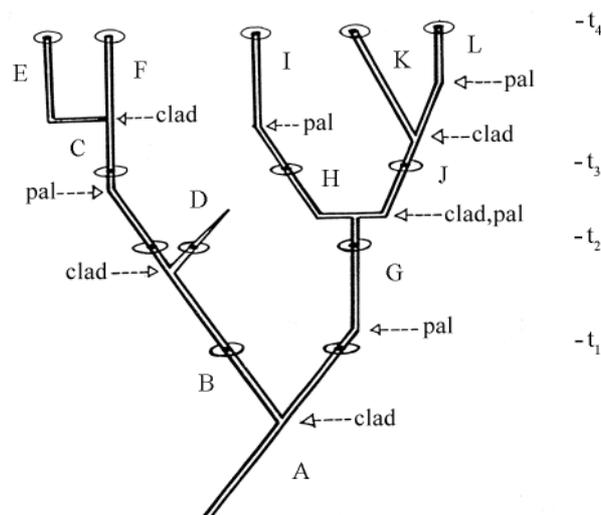


Fig. 2 "Species" limits under the cladistic concept (clad) and the paleontological concept (pal) applied schematically to several imaginary phyletic lineages

Groups of populations representing the various lineages at particular time levels (e.g., $t_1 - t_4$) are different biological species (oval circles). Present time is level t_4 . Vertical scale = geological time; horizontal scale = morphological and other biological change. A – L represent paleontological "species", except "species" C and F, which together form two cladistic "species" in one paleontological "species".

birds with no more significance than any abnormality. Such were the species of many museum workers, e.g. C. J. Temminck, L. P. Vieillot, R. P. Lesson, N. A. Vigors, C. L. Bonaparte, G. R. Gray, J. Gould, J. Verreaux, G. Hartlaub, P. L. Sclater, R. B. Sharpe, E. Dresser, H. E. Oustalet, J. Cabanis, T. Salvadori, and A. Reichenow.

Geographical population differences within a variable species, however, had been mentioned in the literature since the time of Linnaeus, Esper (the coiner of “subspecies” in 1781), G. L. Buffon, I. Kant, E. A. W. Zimmermann and P. S. Pallas (Mayr, 1963, 1982). Thus many early naturalists delimited species taxa rather widely, but without making clear whether geographical forms of species should be merely described or named formally with trinomina. As Table 1 illustrates, systematists adhering to the same theoretical species concept may delimit species taxa quite differently and systematists adhering to different theoretical species

concepts may delimit species taxa similarly.

The narrowly-defined species category in taxonomy resulted in high numbers of species taxa, mainly through the influence of the authoritative *Catalogue of the Birds in the Collection of the British Museum* (27 volumes, 1874 – 1898). Within the next 20 years, the situation changed entirely. Numerous Linnaean morphospecies were reinterpreted as subspecies and combined in more widely conceived biological species taxa. The result was a precipitous decline in the number of species recognized (Fig. 4). Several authors went too far in “lumping” geographically allopatric forms into species units. This trend was eventually halted, especially by Rensch’s (1928, 1929) emphasis on the existence of closely related allopatric or parapatric species that together form a superspecies.

A period of moderate stability for species numbers followed during the late 1930s and early 1940s, when Mayr

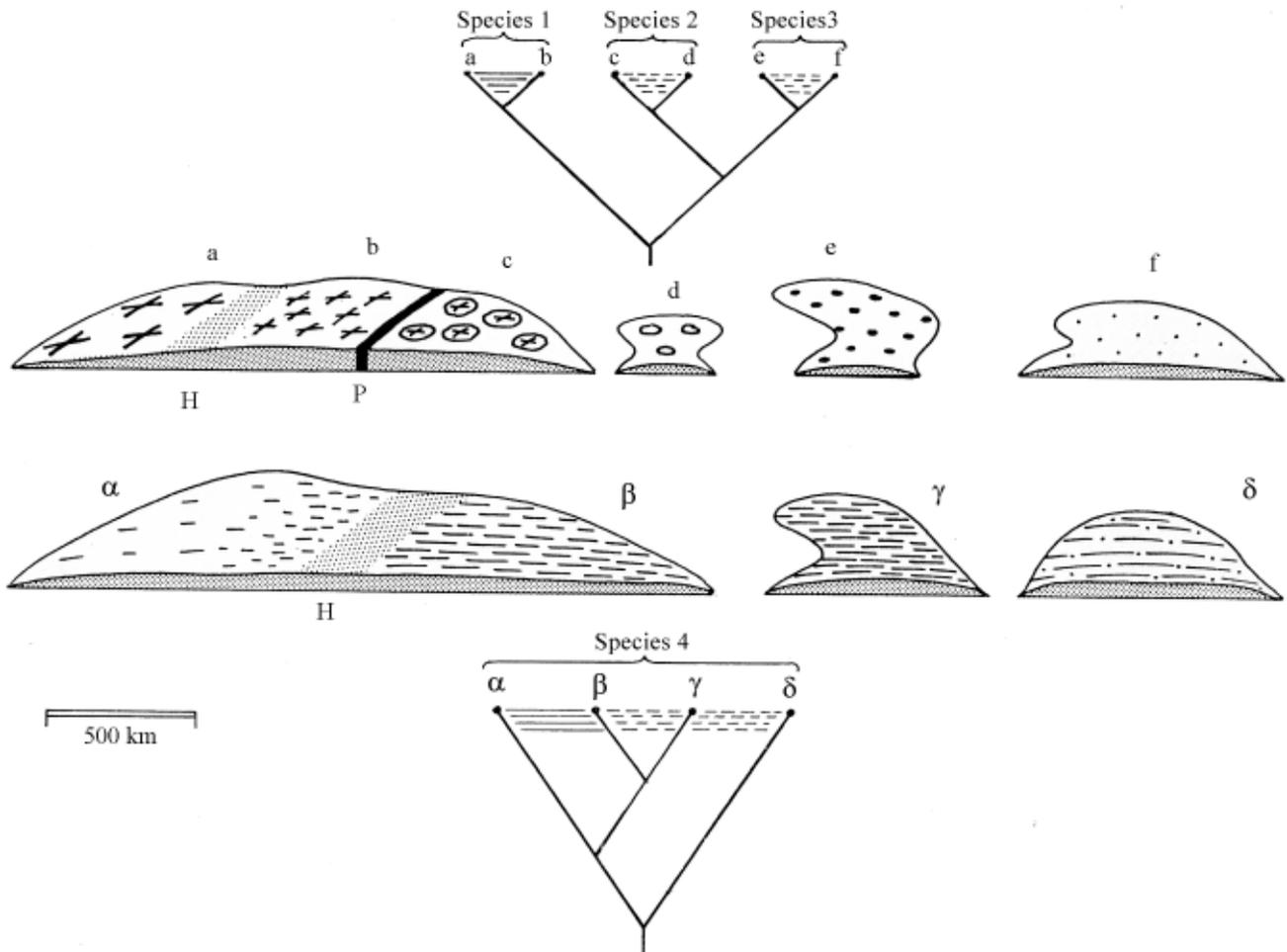


Fig. 3 Schema of two sets of species and subspecies taxa forming one large continental unit (left) and several geographically isolated populations (right), with respective hypothetical cladogram

H = hybrid zone between subspecies, P = parapatric contact zone between species. In the cladograms, hatching indicates known intergradation (hybridization) and dashes indicate presumed hybridization. In all areas, the respective sympatric populations of these two entities are specifically distinct with respect to each other (biological species). In the upper unit, forms a and b hybridize and together represent species 1 which does not hybridize with species 2 (subspecies c and d). The taxonomic status of island populations d – f is judged by inference. Because, in the lower unit, forms α and β hybridize freely where they meet, forms γ and δ are also assumed to hybridize were they to establish contact; so all four taxa are considered subspecies of one polytypic species. Species 1 to 4 are all monophyletic.

Table 1 Theoretical species concepts (horizontal) and species limits under different taxonomic species categories (vertical), as applied during the 19th and 20th centuries (Simplified from Haffer, 1992)

Species category	Species concept	
	Typological	Biological
Wide	Gloger Middendorff Kleinschmidt	Hellmayr 1920s Stresemann 1919–1927
Intermediate	Brehm Schlegel Blasius	Hartert Stresemann Chapman Mayr
Narrow	Temminck Vieillot Sclater Sharpe	Stepanyan

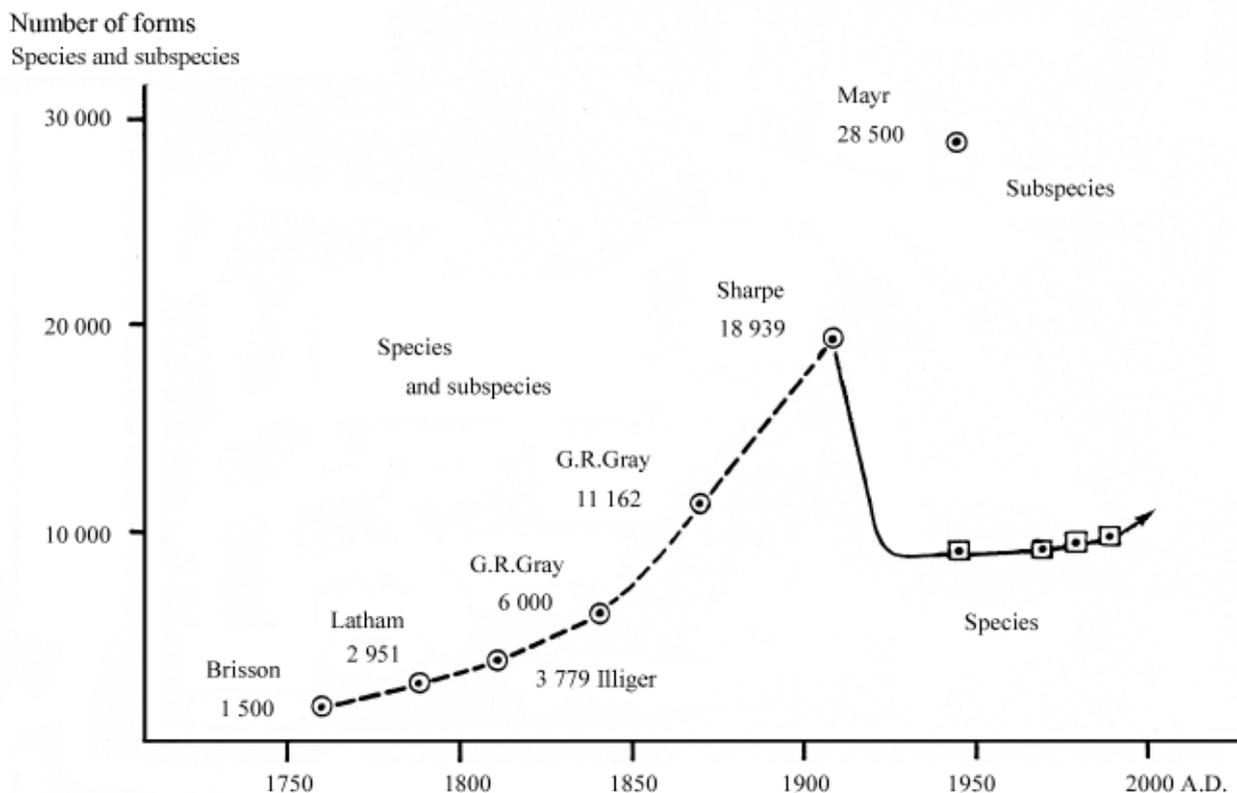


Fig. 4 Increases in the number of species and subspecies of birds recognized during the last 250 years
 Delimitation of polytypic species taxa (under the BSC) shortly after the end of the 19th century resulted in a precipitous fall, a trend halted during the late 1920s when geographically representative biospecies were recognized. From Haffer (1992).

(1946: 68) estimated the total number of known bird species to be 8 616. From the late 1940s on, many geographically isolated forms were reinterpreted as species and combined in superspecies. This “quiet revolution” (Mayr, 1980) at the microtaxonomic level led to a continuous increase in the number of bird species, only slightly boosted by the discovery of genuine new biospecies. Bock and Farrand (1980) recognized a world total of 9 021, and Sibley and Monroe (1990) 9 672. In the latter, superspecies are indicated to add an estimate of global ecological units of geographical replacement forms.

The world total of species would rise dramatically to about 20 000 bird species were species taxa to be delimited narrowly, ranking thousands of subspecies as taxonomic species. Almost all recent ornithological textbooks and all regional handbooks, however, have preferred the now traditional BSC and an intermediate delimitation of species taxa to reflect the global diversity of birds (Sibley and Monroe, 1990; del Hoyo et al., 1992; Dickinson, 2003) or of single continents (Cramp and Simmons, 1977; Brown et al., 1982; Ridgely and Tudor, 1989; Marchant and Higgins, 1990).

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S23-2 Species concepts versus species categories versus species taxa

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Abstract A clear distinction must be made between concept, category and taxon when discussing ideas of species, and it is best to always use the term “species concept” rather than “species” alone in that context. The species concept is part of basic biological theory, and evolutionary theory in particular, and bound up with the evolution of sexual reproduction in living organisms. The biological species concept, that a “species is a group of actually or potentially interbreeding populations of organisms which are actually or potentially genetically isolated in nature from other such species”, fits neatly within currently accepted evolutionary theory. Species concepts which define the phyletic lineage instead should be rejected. A species taxon possesses genetic, reproductive and ecological properties that separate it from other species taxa and which are commonly expressed in phenotypic features that evolve during speciation. Recognition of narrowly delimited species taxa in sexually reproducing organisms such that geographical replacing populations are treated as species is often inappropriate and should be rejected as a rule. To do otherwise would raise several or more populations of humans to species level. No particular species concept or approach to recognizing species taxa is intrinsically better than another in conservation because the term “species” in conservation law and regulation is defined legally, and is not commensurate with species definitions or species taxa within biology.

Key words Species concept, Species category, BSC, Phyletic lineage, Species properties, Conservation

1 Introduction

The species concept has always been part of basic biological theory, not just systematics, and used to the present day as the theoretical base for delimiting groups of organisms living at the same time. Over the last 200 years, moreover, it has evolved to apply only to sexually reproducing organisms. Yet today one commonly reads such statements in taxonomic papers, both theoretical and practical, as: “I am unable to apply the biological species concept to the organisms under study”. True, but it is equally impossible to apply any species concept directly to such biological organisms. A series of steps stands between the theoretical concept and the empirical recognition of actual species taxa.

A major source of misunderstanding concerning the ‘definition’ of species stems from the confusion among a series of related terms, including the term “species” itself which is commonly used indistinguishably for four different ideas and phenomena. These ideas are the species concept, the species category, the species taxon (the actual unit of biodiversity in nature), and the phyletic lineage. Species taxa are based on the species category which in turn stems from the species concept; each is sharply distinct from the others. It must be emphasized here that the recognition of species taxa requires considerable inference. Additional difficulties arise because of failure to distinguish between horizontal and vertical comparisons in space and time, because it is commonly assumed that the two are ef-

fectively one and the same. Herein I examine these different ideas and explain the relationships between them. For further discussion, see Bock (1967, 1979, 1986, 1995, 2000) and Mayr (1942, 1963, 1969, 1995, 1996).

2 The species concept

Under the currently accepted Biological Species Concept (BSC), species exist only in sexually reproducing organisms as a consequence of the mechanisms of genetic shuffling and recombination during meiosis and in zygote formation. Species do not exist in asexually reproducing organisms except as an artificial classificatory convenience. The BSC is usually defined as: *groups of actually or potentially interbreeding populations in nature which are reproductively isolated from other such groups* (Mayr, 1942, 1963:19, 1969:26). As such it is a core idea in the Synthetic Theory of Evolution, and altogether different from morphological, phylogenetic, and evolutionary species concepts which either take no account of gene flow within species (and barriers to it without) or confuse the species in space with the phyletic lineage in time.

By reproductive isolation, evolutionists mean that no gene flow exists between different species, not necessarily that members of different species cannot interbreed and produce hybrids. It is unfortunate that the adverb “reproductively” has been used in definitions of the BSC because it does not explicitly state the property of no gene flow between species as the defining criterion for species. Evolu-

tionists actually use the criterion of lack of gene flow between different species, rather than lack of reproduction, as the theoretical base for practical taxonomic work on them. Thus I advocated (Bock, 1986:33) a modified definition of the BSC, namely: *a species is a group of actually or potentially interbreeding populations of organisms which are genetically isolated in nature from other such groups*. This definition conveys the same intention as the conventional definition, but is more precise and appropriate in its wording.

The distinction between these two definitions is clarified in the classification of intrinsic isolating mechanisms (Mayr, 1963:92), as follows:

1. Mechanisms that prevent interspecific crosses (prematuring mechanisms)

(a) Potential mates do not meet (seasonal and habitat isolation)

(b) Potential mates meet but do not mate (ethological isolation)

(c) Copulation attempted but no transfer of sperm takes place (mechanical isolation)

2. * Mechanisms that reduce full success of interspecific crosses (postmaturing mechanisms)

(a)* Sperm transfer takes place but egg is not fertilized (gametic mortality)

(b)* Egg is fertilized but zygote dies (zygote mortality)

(c)* Zygote produces an F_1 hybrid of reduced viability (hybrid inviability)

(d)* F_1 hybrid zygote is fully viable but partially or completely sterile, or produces deficient F_2 (hybrid sterility)

All of these intrinsic isolating mechanisms serve to prevent exchange of genetic material between members of different species taxa and achieve genetic isolation. However, mechanisms marked with an asterisk do not reflect reproductive isolation between species, indicating shortcomings with that criterion in the definition of the BSC.

Species possess three individual sets of properties that separate them from one another:

1. Genetic coherence: the members of a species form a genetic community which is genetically isolated from other species. Genetic material from reproduction thus will flow between members of a single species, but not from one species to another under natural conditions. Genetic isolation is maintained by the possession of intrinsic genetic isolating mechanisms (see asterisked mechanisms above).

2. Reproductive coherence: the members of a species form a breeding community which is reproductively isolated from other species. Members of one species do not interbreed or attempt to interbreed with members of another species under natural conditions, regardless of the barriers to gene flow between them. Interbreeding between members of different species would be prevented by particular intrinsic reproductive isolating mechanisms. It must be stressed that reproductive isolation between species is

not the same as genetic isolation, and that it is possible for two species to be genetically isolated without being reproductively isolated.

3. Ecological coherence: the members of a species have similar ecological requirements that differ from those of other species. Competition between sympatric members of different species is thus greatly reduced. Ecological properties common to the members of a species are enabled by shared phenotypic features which differ from those of other species. The phenotypic features must be integrated co-adaptively into whole organisms. Mechanisms of meiosis and of zygote formation during reproduction have the potential to disrupt the genetic basis underlying phenotypic co-adaptation. Such disruption is prevented by maintenance of individual variation in the interbreeding population (and hence the species) within acceptable bounds, as advocated by a number of evolutionists (Mayr, 1963).

In fully evolved species, all three sets of properties are developed such that the species are completely genetically isolated, completely reproductively isolated and largely ecologically separated from other sympatric species. Although species taxa must be genetically isolated to maintain themselves sympatrically, not all species taxa have these properties fully or equally well developed; indeed in some species taxa, reproductive isolation or ecological separation may not be developed at all. These three properties of species rarely evolve at the same rate and the same time, and not as a result of the same evolutionary causes during the speciation process. Moreover, the evolution of all three basic properties are not absolutely irreversible; species taxa are not necessarily immortal, and can merge as a consequence of future evolutionary events. Depending on the nature of the features underlying each of these properties, functionally sympatric species taxa can again become a single genetic unit, reproductive unit and/or ecological unit, as shown by two former species of towhees (*Pipilo erythrophthalmus*, *P. ocaei*). Living sympatrically in the Mexican highlands, these species started to hybridize introgressively some hundreds of years ago to become a single genetic-reproductive-ecological unit over most of their range today (Sibley, 1950).

3 The species category

Categories are the different levels of the Linnaean hierarchy used in biological classification. The species category is the basic level in this hierarchy, in that all other categories are defined at levels relative to it, either directly or secondarily. Most workers have assumed that the species category is the same as the species concept, and hence that the BSC is the species category. This assumption is invalid because the species category must apply to all organisms, including asexual ones, and the biological species concept applies only to sexually reproducing organisms. A broader definition of the species category is needed, concordant with the BSC.

Defining the species category for all organisms is

awkward, but can be summarized as: *the fundamental level in the Linnaean hierarchy for describing the diversity of biological organisms that is based on the biological species concept for sexually reproducing organisms or on the equivalent of the ecological unit of biological species for groups of asexual organisms*. This definition omits all mention of monophyly because valid taxa at the level of the species category need not be monophyletic under the general sense of that concept. Species taxa include polyploid, aneuploid and apomictic taxa of plants, often evolved from hybridization between two species and which can potentially arise more than once.

4 The species taxon

Species taxa — the taxonomic groups at the level of the species category — are never defined, but are recognized and delimited descriptively to permit identification of individual organisms as members of their species taxon. Given the definition of the species category, the problem facing taxonomists is how to recognize species taxa when describing the total diversity observed in nature. Clearly authors accepting the same species concept (or species category) can differ greatly in recognizing rather broadly or more narrowly delimited species taxa. The criteria used to recognize species taxa, be they for sexually or asexually reproducing organisms, need not be the defining criterion used in the species concept, but may include morphological, behavioral and other phenotypical attributes as well. Starting with the species category, taxonomists proceed to ascertain how to recognize species taxa in nature for both sympatric and allopatric organisms, on the understanding that the limits of the taxa should be approximately equivalent in any one group of organisms, such as birds. Inference about genetic isolation is an important tool in reaching decisions about the specific status of allopatric forms (Mayr, 1996). What must also be kept in mind is that species taxa, just as they do for all other taxa in biological classification, serve as the taxonomic foundation for all other biological disciplines: hence species taxa should be as equivalent as possible.

The argument that the BSC is wrong because it does not apply to all species taxa in all groups of organisms simply has no merit. Contrary to the beliefs of many systematists, the value of the BSC or any other species concept can be decided only by its role within evolutionary theory, not by its role in systematic practice. Recognition of species taxa must, however, be as concordant as possible with the theoretical species concept (Mayr, 1996).

5 The phyletic lineage

The phyletic lineage may be defined as: *the temporal continuum formed by a species taxon reproducing itself generation after generation through time*. It can remain single for long periods of time or it can split into two or more lineages (speciate) from time to time. The characteristics of the members of a phyletic lineage can remain the

same over periods of time or can change over time (phyletic evolution). Recognition of actual phyletic lineages is of no concern to neontologists because of the insignificance of the time period that their samples of Recent organisms represent. Yet recognition of phyletic lineages can be of real concern to paleontologists, especially when dealing with excellent fossil records over significant lengths of time. A cross-section of a phyletic lineage at any point in time is a species taxon. Cross-sections of the same phyletic lineage at different points in time are species taxa. But it is a non-question to ask whether these cross-sections are the same or different species taxa because no species boundaries can be established between the different cross-sections. They are simply different cross-sections of the same phyletic lineage, the earlier being ancestral to the later.

Species evolve, but phyletic lineages do not; change takes place in the members of a lineage through time, but the lineage remains the same. Species and phyletic lineages are closely related concepts, but they are not the same and must be clearly distinguished from one another. Several species concepts, notably the evolutionary and phylogenetic, fail to distinguish between these two ideas. Phylogenetic, evolutionary, and internodal species concepts actually define a phyletic lineage or segments thereof. Many philosophers of science confuse the species and the phyletic lineage. The species concept, with the idea of species boundaries and differences between species, has meaning only in horizontal comparisons between different phyletic lineages at the same point of time, and not through it (Bock, 1967, 1989). Within evolutionary theory, the species concept and hence species boundaries have absolutely no meaning in vertical comparisons — that is between organisms at different times along the same phyletic lineage. Hence all ideas such as the time of origin of a species, species age, trans-specific evolution, and evolution beyond the bounds of a species are equally without meaning within evolutionary theory.

6 Discussion

Over the last two decades, some workers have advocated particularly narrow limits to species taxa, many of them still introgressing with neighboring taxa, under the advocacy of the phylogenetic species concept (PSC). It is argued that such species taxa are more useful because they are strictly monophyletic and are more effective for conservation. These claims ignore the real issue: the nature of the resulting species taxa. It must be noted, first, that the phylogenetic species concept does not necessarily require recognition of narrowly delimited species taxa. Moreover, the consequences of applying narrow recognition criteria to delineate species taxa must be considered carefully.

One consequence is that biologists would have to deal with two quite different types of species taxa, one at or close to the final stages of speciation and the other at the very first stages. Combining of these two types of species taxa in general faunal inventories, inevitable in practice for the fore-

seable future, would render further analyses difficult at best. The second consequence is that biologists would suddenly find themselves members of several different species taxa of humans, that is, if the narrow limits of species taxa advocated by PSC workers are to be applied consistently across organisms. I, for one, firmly reject this approach, and hence also the narrow criteria for avian species taxa argued under the PSC.

The difficulties in recognizing species taxa, especially among populations that replace one another geographically, is well shown by the North American fox sparrow, *Zonotrichia iliaca* (Zink, 1994). The many subspecies of this polytypic taxon can be combined into four major groups: reddish *iliaca*, grey-headed and slate-colored *schistacea*, grey-headed, browner and thick-billed *megarhyncha*, and sooty *unalaschensis*. These taxa are more similar to one another morphologically than are the other species taxa of *Zonotrichia*, and even more similar to one another than some of the accepted geographic races of the song sparrow (*Zonotrichia melodia*). Zink (1994:106) accepts a phylogenetic species concept which he defines as “*minimally diagnosable clusters of individuals, or basal evolutionary groups, which may or may not be reproductively isolated.*” On the basis of this species definition, and in spite of hybridization between members of these major subspecies groups of the fox sparrow, Zink concludes that the four major geographic forms of the fox sparrow should be treated as different species. The result is that the allopatric species taxa of the Fox Sparrow recognized by Zink represent very different evolutionary units from other species taxa of *Zonotrichia* and other genera within the Emberizinae.

The disparity created among recognized species taxa by introduction of the PSC to formulate the species category and hence infer species taxa, whatever its value in conservation, would have disastrous consequences for all subsequent biological studies based on surveys of these species taxa, without any significant advantage over taxa based on the BSC.

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S23-3 The ultrataxon and its use in pure and applied biology

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Abstract The basic units of avian biodiversity are arguably panmictic regional taxa that are genetically distinct from sister taxa in the same or different regions. Historically, the “species” has been used as their taxonomic surrogate. The role of the species as such a standard, however, is confounded by its use under the biological species concept, and by the introduction of other species concepts to replace it, e.g. phylogenetic species concept. In practice, the first commonly lumps sister allopatric units under a single species; and the second, which does single out regional units, nevertheless employs the term “species” for taxa with quite different properties, thereby creating confusion in the meaning of the term for the rest of the biological and administrative world outside systematics. To keep the “species” in its traditional biological context, to avoid confusion over its meaning and to provide a simple, neutral reference point for identifying biodiversity units, new terms such as “ultrataxon” are needed. Meaning far end taxon, “ultrataxon” may be used for any terminal taxon at any taxonomic rank on the phylogenetic tree; and it has already been applied at the level of “biological subspecies” (= regional biodiversity units) for Australian passerines. Such a term overcomes the stigma attached to subspecies in conservation biology, and averts reclassifying the world’s bird fauna under alternative species concepts.

Key words Biological species, Phylogenetic species, Concept applications, Ultrataxon

1 Introduction

In birds, as in all bisexually reproducing organisms, the basic units of biodiversity are panmictic regional populations that are genetically separated from sister populations in the same or different regions. They are, in the context of evolution, at once the products of the past and the potential building blocks of the future. Knowledge of them is the first step in piecing together knowledge of the whole of biodiversity, information that is essential for using, managing and conserving the earth’s bio-resources sustainably. Only after the units have been quantified in the first place is it logical to go about qualifying them, in terms of genetic distinctness, for prioritizing resource management.

By tradition, it is the taxonomic (or classificatory) arm of systematics that has had the job of identifying the units of biodiversity for biology and the community at large. This places an enormous responsibility on that discipline to “get it right”, and highlights a core functional question: what is the taxonomic category appropriate for the purpose? Traditionally, the “species” category has been used as the surrogate for the units. How well does it serve this role? Judged by its use today in conservation biology, in other biological disciplines outside systematics, in sciences outside biology, and in industry and public sectors outside science, it is generally considered satisfactory. Thus for ecologists working on the birds of a small region, the geographic frame for most ecological studies, that region will normally possess a suite of clearly differentiated populations of birds that equate with species in any current taxo-

mic classification. Species in such situations have tangible reality, each occupying its own niche separate from others.

2 Species concepts and problems in their application

Yet populations of any one of these “species” in widely separated regions, such as the east and west coast forests of temperate north America, or the eucalypt woodlands in different corners of Australia, are often quite different from one another in appearance or behavior or ecology, or all three (Fig. 1). Even though not necessarily as differentiated as sympatric species, they have, over time, diverged genetically from one another through isolation past and present to become units of biodiversity. Despite this, they are still commonly treated as forms of one and the same species because they fulfil, or are presumed to fulfil, the criteria of the species concept with greatest currency in biology at present. That concept is the biological species concept (BSC) of Dobzhansky (1935, 1937), Mayr (1942, 1963), Bock (1986, 1995), and Johnson et al. (2000); and the criteria that such populations are presumed to fulfil are those of genetic miscibility were they to come naturally into contact.

Such a taxonomy may well contribute to the understanding of adaptive and evolutionary processes, and serve other ecological and biological ends as well. But for the basic inventoring of biodiversity units, it commonly lumps — sweeps “under the carpet” — genetically-differentiated

sister populations that replace one another geographically or which hybridize introgressively where they meet. The BSC does distinguish them as subspecies, but, perhaps because they are perceived as less than species and because of conflicting and often trivialising definition (Ford, 1974; cf. Mayr, 1942, 1969), subspecies are viewed pejoratively and widely ignored outside systematics. Over the last 50 years or more, species-level taxonomy in birds, and resulting handbooks and most checklists apart from Peters', have focused far more on assessing whether allopatric or parapatric populations qualify as species than in inventing subspecies. So biologists, administrators and others outside systematics who rely on such sources for their information on biodiversity are denied access to the fundamental units that they need. The biological species is simply too coarse a measure of biodiversity for taxa that are polytypic and differentiated allopatrically.

As the essential unit of biodiversity, the "species" has problems on another front as well. They are encapsulated in the question: "What is a species?" Through much of the 20th century, that question meant finding out whether the characteristics of a population or group of populations met the criteria for a species under the BSC. Today it means instead: "What is the species concept used". Since the time of Darwin, numerous species concepts have been advanced for circumscribing "species" in nature (Claridge et al., 1997), many of them put forward in the later 20th century as understanding of genetic and evolutionary processes has grown. Haffer (1992) groups them into three categories:

(i) first, the pre-Dobzansky-Mayr morphological concepts of the 19th and early 20th centuries, then underpinning what is now understood as alpha-taxonomy;

(ii) secondly, the biological species concepts, based on the panmictic or inter-fertile breeding population and its genetic isolation from others; and



Fig. 1 Three regional taxa (biodiversity units) of the Australian magpie (*Gymnorhina tibicen*) in situ
In each pair, the bird on the right is male.

(iii) thirdly, the historic time concepts, based on unique phylogenetic lineages termed clades in cladistic theory (after Hennig, 1966).

The historical time concepts are the newcomers, embedded within which are the Evolutionary Species Concept of Simpson (1961) and Wiley (1978), and the Phylogenetic Species Concept (PSC) of Cracraft (1983, 1989, 1992), McKittrick and Zink (1988), Zink (1996a) and others. However healthy this is for evolutionary and taxonomic debate, it can be confusing for biology outside systematics, especially as the properties of species circumscribed under the different concepts are quite different (see Bock, this symposium). Under the BSC, genetic isolation from sister populations, from whatever cause, is the defining point of speciation, the point where speciated populations travel separate evolutionary paths into the future. Retracing its steps leads to a top-down approach to mapping biology's evolutionary tree, beginning with population interaction. The outer nodes of that tree are real populations of organisms in space at one time, the present; and the criterion of species-level nodes is, as stressed above, one of genetic miscibility.

Under historical time concepts such as the PSC, species taxa are essentially the ultimate tips on the evolutionary tree, the present result of past evolution along a lineage or clade. Such concepts conceive the evolutionary tree from the bottom up. The outer as well as inner nodes of the tree are divergence events rather than populations or taxa themselves; and the criterion of species is, quite simply, diagnosability at the terminal level. In this scheme, the issues of genetic miscibility and reproductive isolation are irrelevant. It should be immediately obvious that the application of historical time concepts will consistently identify, as species, the units of biodiversity so often hidden within polytypic biological species. So too do the old morpho-species concepts, upon which much of invertebrate and plant taxonomy is still based in practice. This is perhaps the cardinal reason why the "species", whatever its conceptual base, has served so long and so well as the basic taxonomic unit for biology.

Is this sufficient reason to discard the biological species in systematics? Of course not. The BSC, encompassed in its wider sense by the Comprehensive Biological Species Concept of Johnson et al. (2000), is far too deeply embedded in biological theory and thinking outside systematics, far more so than the historic time concepts. Born of biological processes in space as well as time, it places animal species in *both* those dimensional frames, and is involved integrally in the ideas of niche partitioning, character displacement, ecological interaction, adaptation, founder populations, genetic bottlenecks and exchange, selection pressure and rates of genetic change. Wedded to Linnaean binominal nomenclature, it provides a ready reference to sister and geographical replacement taxa, vital for a range of applied disciplines such as bioprospecting.

Overtuning the BSC would bring considerable prac-

tical problems to applied as well as pure biology, precipitating wholesale change in species-level taxonomy and nomenclature in birds. If, for example, it was replaced by terminal taxa under the PSC, the principles for circumscribing species, and so the species taxa themselves, would shift, the latter roughly doubling in number (Zink, 1996b). Not only would an enormous amount of biological information and theory, the outcome of the last 100 years of developmental thinking in ornithology, become confounded because the concepts and identities of species had changed, but all existing field guides, manuals, monographs and handbooks would become largely redundant. Prescriptions for bio-resource conservation would have to be extensively redrafted and relevant law rewritten. Extending this situation to the rest of the better-known groups in the living world brings the magnitude of the problem into even clearer focus.

3 Towards resolution — the ultrataxon concept

If the biological species is kept, what then are the options for bringing the real units of biodiversity into public knowledge? One approach, given that the units represent differentiated gene pools, is to introduce genetic concepts such as the Evolutionary Significant Unit of Moritz (1994a,b). Such units can nest within biological species, like subspecies. Moritz's (*ll.cc.*) criteria for such units are reciprocal monophyly for DNA alleles and significant frequency differences at nuclear loci; thus they introduce exclusively molecular yardsticks. Ultimately it may be the course to follow, but at this stage it raises once more the question of practicality. Whatever the units of biodiversity are called, they must be identifiable by the biologists who study them, by the managers and administrators who deal with them, and by the general community that is concerned with them. It may be that in the 25th century, a Buck Rogers civilization will find a way to beam on to animals with portable ray DNA decoders to read out their identities in the field; but that technology is still far off. This does not mean that we should dismiss the approach or stop building DNA libraries. It does mean, however, that we cannot yet discard the external signal traits — color, shape, structure, behavior, voice and even smell — that have served systematics well for two and a half centuries, and are accessible and familiar to almost everyone.

This throws the problem back into the lap of taxonomy for an answer. The most obvious solution is to find a naming concept that will single out biodiversity units within the context of the biological species, without the stigma attached to subspecies. One such offering is the term *ultrataxon*. It is defined as any terminal taxon on a lineage of organisms, an idea readily understood in biology (Schodde and Mason 1999: 2). Why the term *terminal taxon* itself was not used was because the reaction to it that was tapped in Australia suggested that its reception would have been terminal. The advantages of the term *ultrataxon* are that it is a single

word encapsulating a simple concept that can be readily assimilated and applied not just within systematics but, importantly, in biology, and bioresource management and conservation as well. Unlike the phylogenetic species, moreover, it is a neutral term that does not compete conflictingly with the biological species in biology. Its principal disadvantage is that it is yet another new term in a discipline already overloaded with terminology.

In practice, terminal taxa at all ranks, such as monotypic species, genera and families, are *ultrataxa*, as are terminal biodiversity units within species. For purposes of bioresource management and conservation, Schodde and Mason (1999) used the term to replace subspecies, employing the familiar Linnaean trinomial nomenclature for them. Only perceived genetically discrete populations, whether isolated geographically or secondarily intergradient, were treated as *ultrataxa* however. The end points of what were considered to be primary clines, also often recognized as subspecies, were not distinguished.

In the end, the idea of the “species” itself may be too ingrained in the human psyche to be completely replaced as the taxonomic unit for bioresource management and conservation. If that is so, and the biological species remains the standard, its conceptual modification by such genetic and cultural variants as have been put forward by Paterson (1985), Templeton (1989), Avise and Ball (1990), Bock (1995) and Grant and Grant (1997) may be needed to shift the criteria of speciation to earlier stages in the process if the catch of biodiversity units is to improve. Even so, this will never, in practice, catch all the *ultrataxa*; indeed, as much as 70% or more may fall through. Concepts such as *ultrataxa* — and subspecies — need to be kept if all biodiversity units in the Aves are to be found, identified and rated.

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S23-4 Species concepts and their application: insights from the genera *Seicercus* and *Phylloscopus*

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Abstract Using several examples from the Old World warbler genera *Seicercus* and *Phylloscopus*, I highlight difficulties in ranking allopatric taxa whatever the conceptual base for species delimitation. Given that related sympatric taxa are separate species whatever their conceptual base, the complexity of morphological, vocal and genetic characters makes ranking of allopatric taxa problematic. Under the Phylogenetic Species Concept, judgement of diagnosability becomes a core problem. If the Biological Species Concept is applied, the issue shifts to evaluation of the degree of reproductive isolation. And under the Monophyletic Species Concept, phylogenetic hypotheses are required.

Key words Species concepts, Sympatry, Allopatry, Morphology, Vocalizations, DNA

1 Introduction

The concept of species has been debated for decades, and a plethora of different species concepts have been formulated (reviews in Haffer, 1992; Zink and McKittrick, 1995; Mayden, 1997). Nearly all classifications of birds in the past 50 years are based on the Biological Species Concept (BSC) of Mayr (1942) and others, while the Phylogenetic Species Concept (PSC) of Cracraft (1989), Nixon and Wheeler (1990) and others forms the basis for some recent classifications, as in Hazevoet (1995) and Sangster et al. (1999). The Monophyletic Species Concept (MSC) of Mishler and Donoghue (1982) and Lidén and Oxelman (1989) is another that has been adopted in one recent taxonomic review (Alström et al., 2003).

Here I use examples from five well studied groups in the Old World warbler genera *Seicercus* and *Phylloscopus* (Table 1) to highlight difficulties in ranking allopatric (geographically disjunct) and parapatric (geographically abutting) taxa whatever the conceptual base for species delimitation.

2 The *Seicercus burkii* complex

This species complex, which comprises eight taxa (Table 1), has recently been revised by Alström and Olsson (1999, 2000) and Martens et al. (1999). Up to four taxa are syntopic (Fig. 1), although almost entirely segregated altitudinally. All taxa are diagnosably different in both morphology and vocalizations, except the parapatric *valentini-latouchei* and the disjunct *whistleri-nemoralis* groups, which only differ from each other in plumage, not in song. The disjunct *tephrocephalus-burkii* and, especially, *valentini/latouchei-whistleri/nemoralis* groups resemble

each other to a high degree in morphology and, particularly, song. According to mitochondrial DNA (mtDNA) sequence data, *S. burkii sensu lato* is non-monophyletic (Fig. 2; Olsson et al., 2004). mtDNA further reveals that *valentini-latouchei* and *whistleri-nemoralis* separated considerably later than other taxa (Fig. 2), yet are diagnosable by molecular markers (U. Olsson and P. Alström, unpublished).

The syntopic taxa are separate species whatever the conceptual base for species delimitation (Table 2), since they are diagnosably different and apparently reproductively isolated from each other. In contrast, the classification of recently diverged allopatric sister taxa only diagnosable by genetic markers (*valentini-latouchei*, *whistleri-nemoralis*) varies with the species concept adopted (Table 2). All of the disjunct taxa are treated as species under the PSC, while

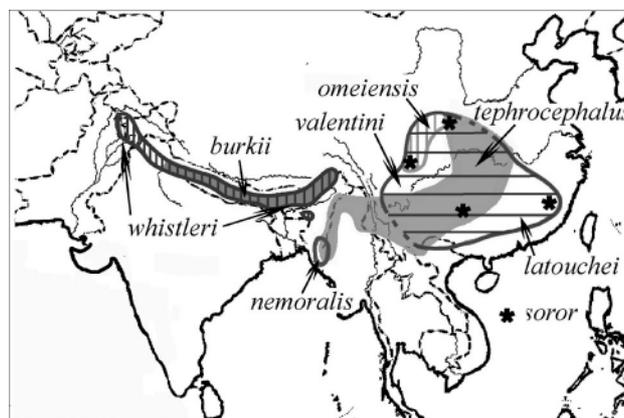


Fig. 1 Distribution of taxa in the *Seicercus burkii* complex Based on Alström and Olsson (1999, 2000), Martens et al. (1999) and Olsson et al. (2004). The border between *valentini* and *latouchei* is uncertain and indicated by a dashed line.

such ranking is arbitrary for some under the BSC (Table 2). The close similarity in vocalizations within *burkii- tephrocephalus* and, especially, *valentini/latouchei - whistleri/nemoralis* groups suggests, *a priori*, that they would interbreed if in contact. That, however, is contradicted by playback tests, even though only a few males have been tested (Alström and Olsson, 1999). Moreover, it is possible that non-vocal cues would act as reproductive isolating barriers between these taxa were they to meet. Under the MSC, there are alternative options for ranking the allopatric taxa (Table 2).

3 The *Seicercus affinis-poliogenys* complex

The four taxa in this complex (Table 1) have more southerly distributions than the *S. burkii* complex. The

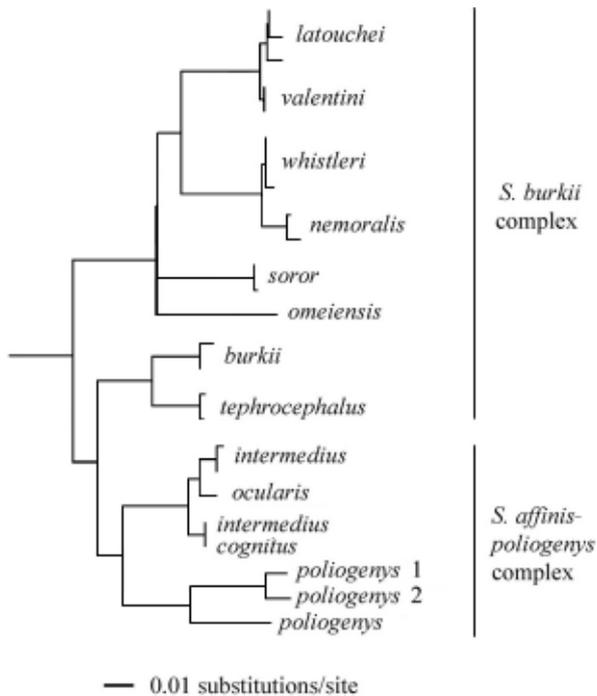


Fig. 2 mtDNA tree of the *Seicercus burkii* and *S. affinis-poliogenys* complexes

taxon *poliogenys* is sympatric with *affinis* and *ocularis*, while the distributions of the latter two, as well as *intermedius*, are disjunct; and all except *ocularis* are sympatric with two to five taxa in the “*S. burkii*” complex. Except for *ocularis*, which is usually synonymized with *affinis*, the taxa are diagnosable morphologically. Vocally, *poliogenys* differs from the others, which all have similar songs. According to mtDNA (Olsson et al., 2004: Fig. 2), *intermedius* is non-monophyletic, and different populations of *poliogenys* differ markedly from each other.

The sympatric taxa are species under any species con-

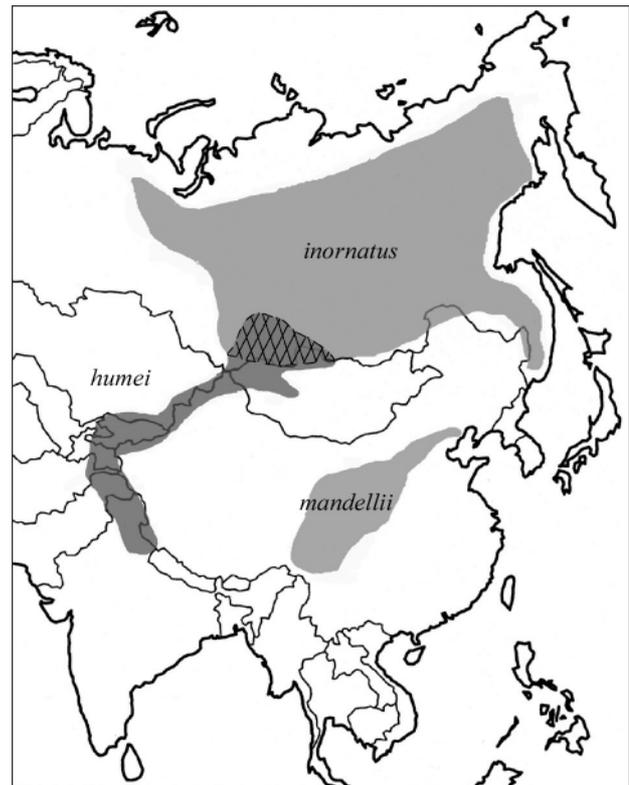


Fig. 3 Distribution of taxa in the *Phylloscopus inornatus* complex

Based on Irwin et al. (2001a). The cross-barred area represents sympatry between *inornatus* and *humei*.

Table 1 Species complexes discussed in this paper

<i>Seicercus burkii</i> complex	<i>Seicercus affinis - poliogenys</i> complex	<i>Phylloscopus inornatus</i> complex	<i>Phylloscopus proregulus</i> complex	<i>Phylloscopus trochiloides</i> complex
<i>burkii</i>	<i>affinis</i>	<i>inornatus</i>	<i>proregulus</i>	<i>trochiloides</i>
<i>tephrocephalus</i>	<i>ocularis</i> ¹	<i>humei</i>	<i>kansuensis</i>	<i>obscuratus</i>
<i>omeiensis</i>	<i>intermedius</i> ²	<i>mandellii</i>	<i>chloronotus</i>	<i>plumbeitarsus</i>
<i>soror</i>	<i>poliogenys</i>		<i>simlaensis</i>	<i>viridanus</i> ³
<i>valentini</i>				<i>nitidus</i>
<i>latouchei</i>				
<i>whistleri</i>				
<i>nemoralis</i>				

¹Usually synonymized with *affinis*. ²*cognitus* treated as a color morph. ³*ludlowi* synonymized with *viridanus*.

cept (Table 3), because they are diagnosably different and reproductively isolated from each other. The disjunct *ocularis*, *intermedius* and different populations of *S. poliogenys* are all separate species under the PSC (Table 3), because they are diagnosable genetically (*affinis* not studied). In contrast, they are treated as subspecies or are unrecognized under the BSC (Table 3) since, owing to their morphological and vocal similarities, they can be assumed to interbreed freely should they meet. Under the MSC, there are alternative options for ranking these taxa (Table 3).

4 The *Phylloscopus inornatus* complex

This complex comprises the partly sympatric *inornatus* and *humei* and the disjunct *mandellii* (Table 1, Fig. 3). Although there are morphological differences between all three taxa, it is doubtful that they are diagnosable by morphology because of much overlap. Vocally, *inornatus* differs markedly from the other two, while *humei* and *mandellii* differ only in call, not in song (Irwin et al., 2001a). mtDNA suggests that *humei* and *mandellii* are sister taxa, which have been separated a long time (Irwin et al., 2001a; Fig. 4).

The sympatric taxa are treated as separate species

under all species concepts (Table 4), since they are diagnosably different and reproductively isolated. The ranking of the geographically isolated *mandellii* differs between the BSC and the PSC, while any of the alternatives canvassed is possible under the MSC (Table 4).

5 The *Phylloscopus proregulus* complex

The four taxa in this complex (Table 1) have disjunct or parapatric distributions (Fig. 5). The taxa *proregulus*, *chloronotus* and *simlaensis* differ in plumage, but at least the two latter, at least, are doubtfully diagnosable; *kansuensis* is indistinguishable morphologically from *chloronotus* (Alström and Olsson, 1990; Alström et al., 1997). Vocally, the parapatric *simlaensis* and *chloronotus* are similar, while the other two are very distinct (Alström and Olsson, 1990; Alström et al., 1997). Hence, there is no correspondence between morphological and vocal differentiation. Based on mtDNA, all taxa are diagnosably different (U. Olsson and P. Alström, unpublished).

Under the PSC, all four taxa are separate species, since they are at least diagnosable genetically (Table 5). In

Table 2 Three alternative classifications of the *Seicercus burkii* complex

1. BSC 1/MS C 1	2. BSC 2/MS C 2	3. PSC/MS C 3
<i>S. burkii</i>	<i>S. burkii</i>	<i>S. burkii</i>
<i>S. tephrocephalus</i>	<i>S. b. burkii</i>	<i>S. tephrocephalus</i>
<i>S. omeiensis</i>	<i>S. b. tephrocephalus</i>	<i>S. omeiensis</i>
<i>S. soror</i>	<i>S. omeiensis</i>	<i>S. soror</i>
<i>S. valentini</i>	<i>S. soror</i>	<i>S. valentini</i>
<i>S. v. valentini</i>	<i>S. valentini</i>	<i>S. latouchei</i> ¹
<i>S. v. latouchei</i>	<i>S. v. valentini</i>	<i>S. whistleri</i>
<i>S. whistleri</i>	<i>S. v. latouchei</i>	<i>S. nemoralis</i> ²
<i>S. w. whistleri</i>	<i>S. v. whistleri</i>	
<i>S. w. nemoralis</i>	<i>S. v. nemoralis</i>	

BSC = Biological Species Concept; MSC = Monophyletic Species Concept; PSC = Phylogenetic Species concept. ¹Only diagnosably different from *valentini* by mtDNA. ²Only diagnosably different from *whistleri* by mtDNA.

Table 3 Three alternative classifications of the *Seicercus affinis-poliogenys* complex

1. BSC 1 ¹	2. PSC/MS C 1	3. MS C 2
<i>S. affinis</i>	<i>S. affinis</i>	<i>S. affinis</i>
<i>S. a. affinis</i> ²	(<i>S. ocularis</i> ³)	<i>S. a. affinis</i>
<i>S. a. intermedius</i>	<i>S. intermedius</i>	<i>S. a. ocularis</i>
<i>S. poliogenys</i>	<i>S. sp. 1</i> ⁴ (“ <i>intermedius</i> ”)	<i>S. a. intermedius</i>
	<i>S. poliogenys</i>	<i>S. a. ssp. 4</i> (“ <i>intermedius</i> ”)
	<i>S. sp. 2</i> ⁴ (“ <i>poliogenys 1</i> ”)	<i>S. poliogenys</i>
	<i>S. sp. 3</i> ⁴ (“ <i>poliogenys 2</i> ”)	<i>S. sp. 4</i>
		<i>S. sp. ssp. 1</i> ⁴ (“ <i>poliogenys 1</i> ”)
		<i>S. sp. ssp. 2</i> ⁴ (“ <i>poliogenys 2</i> ”)

BSC = Biological Species Complex; PSC = Phylogenetic Species Concept; MSC = Monophyletic Species Concept.

¹It is not common practice under the BSC to recognize taxa based only on molecular characters, hence the small number of taxa. ²*ocularis* is usually synonymized with *affinis*. ³It is not known whether *ocularis* is diagnosably different from *affinis*. ⁴Unnamed: only diagnosable genetically.

contrast, *chloronotus* and *simlaensis* are best considered conspecific under the BSC, because they intergrade where they meet, suggesting gene flow. Ranking of the others is arbitrary under the BSC (Table 5), since their ranges do not overlap, although it seems likely that the striking differences in songs would act as reproductive isolating barriers were they to meet. Under the MSC, options are open for ranking taxa (Table 5).

6 The *Phylloscopus trochiloides* complex

This complex comprises five taxa (Table 1), four of which occur in a parapatric chain around the Tibetan plateau; one additional taxon is geographically isolated from the others (Fig. 6). There is somewhat continuous variation in morphology and song around the “chain”, except for a sharp transition in central Siberia where the ranges of *viridanus* and *plumbeitarsus* overlap (Irwin, 2000; Irwin et al., 2001b). The taxa comprise two main clades (Fig. 7; Irwin et al., 2001b).

Under the PSC, at least four of the taxa would be treated as separate species, since they are diagnosable, at least genetically (Table 6). Ranking is very problematic under the BSC. The taxa *viridanus* and *plumbeitarsus*, which are marginally sympatric and apparently reproductively isolated (Irwin, 2000; Irwin et al., 2001b), should be treated as separate species. These two taxa, however, are connected to *trochiloides* through intermediate populations, and there is evidence of past or present gene flow between *viridanus* and *trochiloides* (Irwin, 2000; Irwin et al., 2001b). The classification in Table 6 might be the most sensible outcome

Table 4 Two alternative classifications of the *Phylloscopus inornatus* complex

1. BSC/MS C 1	2. PSC/MS C 2
<i>P. inornatus</i>	<i>P. inornatus</i>
<i>P. humei</i>	<i>P. humei</i>
<i>P. h. humei</i>	<i>P. mandellii</i>
<i>P. h. mandellii</i>	

BSC = Biological Species Concept; MSC = Monophyletic Species Concept; PSC = Phylogenetic Species Concept.

under the BSC, although it should be noted that it conflicts with the phylogeny. Polytypic species that are paraphyletic are not acceptable under the MSC (Table 6).

7 Discussion

Because speciation is a gradual process in time, different populations are in different stages of divergence. Some lineages have split recently and only just started to differentiate, whereas others have evolved multitudinous differences and are reproductively isolated from their nearest relatives. Furthermore, divergence rates vary considerably, both among lineages and in the traits affected, whether morphological, vocal, behavioral or genetic. As is evident in examples above, plumage differentiation can be very slow compared to vocal or mtDNA differentiation. Such phenomena seriously hamper attempts to sort observed variation in nature.

Least-inclusive nominal taxa are usually delimited using morphological characters. The PSC is unique among the species concepts addressed here in explicitly stating how least-inclusive taxa should be delimited: “smallest diagnosable clusters” (Cracraft, 1989; Nixon and Wheeler, 1990). Such principles could equally well be adopted by proponents of the BSC and MSC, in which case the same taxa would, theoretically, be recognized unanimously. As is evident from disagreements among taxonomists, the delimitation of allopatric taxa — especially those recently diverged — is highly subjective. Molecular markers are unlikely to solve the problem, and few ornithologists would endorse taxa that are only identifiable genetically. Even so, use of

Table 5 Two alternative classifications of the *Phylloscopus proregulus* complex

1. BSC	2. PSC/MS C
<i>P. proregulus</i>	<i>P. proregulus</i>
<i>P. kansuensis</i>	<i>P. kansuensis</i>
<i>P. chloronotus</i>	<i>P. chloronotus</i>
<i>P. c. chloronotus</i>	<i>P. simlaensis</i> ¹
<i>P. c. simlaensis</i>	

BSC = Biological Species Concept; PSC = Phylogenetic Species Concept; MSC = Monophyletic Species Concept. ¹ Only diagnosably different from *chloronotus* by mtDNA.

Table 6 Three alternative classifications of the *Phylloscopus trochiloides* complex

1. BSC	2. PSC/MS C 1	3. MS C 2
<i>P. trochiloides</i>	<i>P. trochiloides</i>	<i>P. trochiloides</i>
<i>P. t. trochiloides</i>	<i>P. obscuratus</i>	<i>P. t. trochiloides</i>
<i>P. t. obscuratus</i>	<i>P. viridanus</i>	<i>P. t. obscuratus</i>
<i>P. t. viridanus</i>	<i>P. nitidus</i>	<i>P. t. plumbeitarsus</i>
<i>P. t. nitidus</i>	<i>P. plumbeitarsus</i>	<i>P. viridanus</i>
<i>P. plumbeitarsus</i>		<i>P. v. viridanus</i>
		<i>P. v. nitidus</i>

BSC = Biological Species Complex; PSC = Phylogenetic Species Complex; MSC = Monophyletic Species Complex. Ranking is problematic under the BSC.

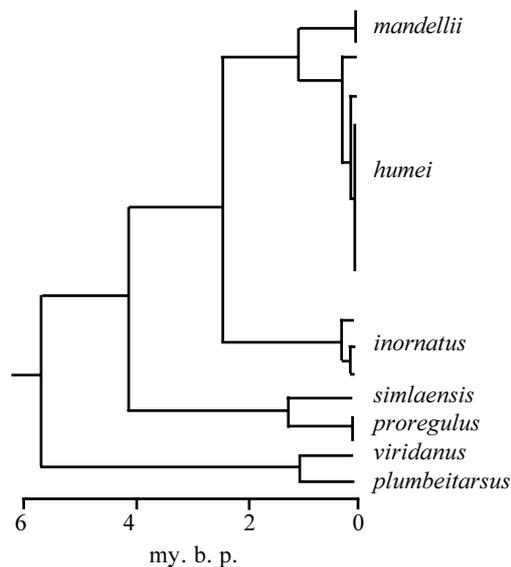


Fig. 4 mtDNA tree of the *Phylloscopus inornatus* complex. Based on Irwin et al. (2001a).

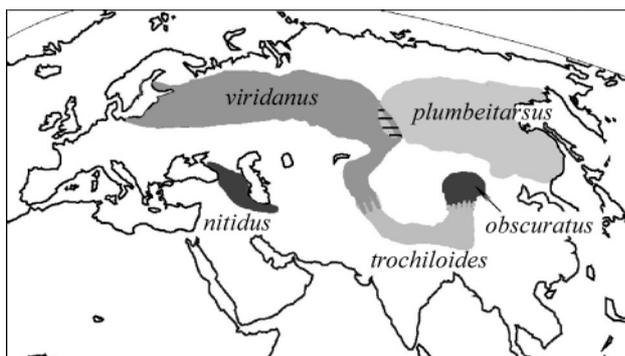


Fig. 6 Distribution of taxa in the *Phylloscopus trochiloides* complex. Based on Irwin et al. (2000, 2001b). The hatched area represents sympatry between *viridanus* and *plumbeitarsus*.

DNA sequencing may uncover previously overlooked “cryptic” taxa, opening their existence to confirmation by fine but genetically significant differences in morphology and voice, as in the *Seicercus affinis* - *S. poliogenys* complex.

The main operational discrepancy between different species concepts involves the principles by which least-inclusive taxa are ranked. Under the BSC and MSC, they are ranked either as monotypic species or as subspecies of polytypic species, while all valid taxa are species under the PSC *sensu* Cracraft (1989). Under the BSC, inferring the degree of reproductive isolation between taxa poses the main problem; under the PSC, the issue is one of simple diagnosability; and under the MSC, resolution turns on whether replacement taxa are monophyletic. As is evident from Tables 2–6, classifications based on different species concepts disagree in the treatment of allopatric (disjunct) or parapatric taxa.

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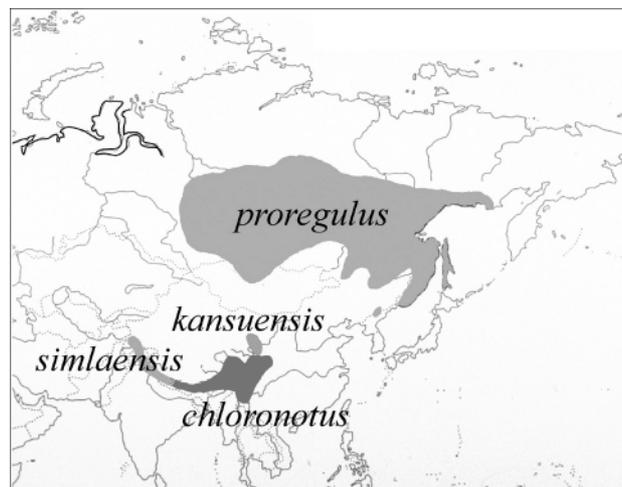


Fig. 5 Distribution of taxa in the *Phylloscopus proregulus* complex. Based on Alström and Olsson (1990) and Alström et al. (1997).

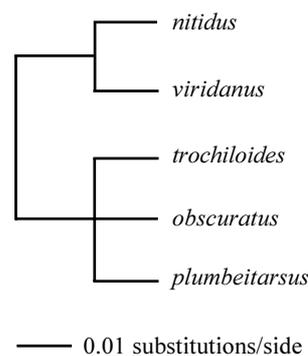


Fig. 7 mtDNA tree of the *Phylloscopus trochiloides* complex. Based on Irwin et al. (2001b).

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S23-5 Developing guidelines to assist in defining species limits

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Abstract This review describes the reasoning behind the “Guidelines for assessing species rank” developed by the Taxonomic Subcommittee of the British Ornithologists’ Union, and recently published in the *Ibis*. It sets out criteria for delimiting species taxa based primarily on the Evolutionary Species Concept and General Lineage Concept of Species (Mayden, 1997; de Queiroz, 1999), and secondarily on the Biological Species Concept, Recognition Species Concept and Phylogenetic Species Concept. Procedures and scenarios are canvassed for defining diagnosability and for determining species limits in situations of sympatry, parapatry, allopatry and hybrid zones. The role and significance of DNA sequence data is also addressed.

Key words Species criteria, Species concepts, Diagnosability, Sympatry, Parapatry, Allopatry, Hybrid zones, DNA sequence data

1 Introduction

The period since the publication of the “Voous” list of Holarctic birds (Voous, 1977) has been one of comparative stability for Europe’s avian taxonomy. Changes in species limits have occurred, but these have been relatively modest. Recently, however, there have been rapid, even accelerating, developments in biology with profound impacts upon our ability to define species limits. Enhanced data sets and improved statistical methodology have allowed more refined analysis of morphology. The opening-up of hitherto little known parts of Asia has resulted in increased knowledge of the region’s zoogeography, and the relationships of taxa previously known from only a few specimens, such as the herring gull (*Larus argentatus*) complex. Research into bioacoustics has revealed the importance of song and call in promoting reproductive isolation (Slabbekoorn and Smith, 2002). But, especially, the application of molecular genetics has allowed more detailed investigations of taxon divergence (Helbig et al., 1995) and monophyly (Friesen et al., 1996).

These have combined with a more critical view of the nature of species (Mayden, 1997) to improve our appreciation of avian biodiversity. With a growing awareness of the need to quantify biodiversity, and the consequences of anthropogenic effects such as global warming, habitat destruction, population fragmentation and over-exploitation, conservationists have increasingly sought a standardized inventory of avian species and their inter-relationships.

The British Ornithologists’ Union (BOU) has been

mindful of its responsibility for this, especially within Great Britain and Northern Ireland, and the taxonomic list maintained by the BOU (the “British List”) has now become the “official” list adopted by statutory and conservation agencies in the United Kingdom. With this responsibility came a need for a consistent treatment of taxonomic problems, and three years ago the BOU formalized a Taxonomic Subcommittee (TSC) to advise on changes to the taxonomy of the British List for all end-users.

The TSC quickly recognized the need for a set of guidelines to improve consistency in taxonomic decision-making, and to assist non-specialists to understand the rationale behind any changes to the British List. It was well aware that such guidelines could prove a “hostage to fortune”, since any departure — however well intentioned — could open them to criticism. The guidelines were finally published in 2002 (Helbig et al., 2002), the result of extensive debate among members of the TSC and 24 significant revisions; their conclusions are summarized below.

2 Species concepts

The species concept to adopt presented immediate problems. Committee views ranged from the Biological Species Concept to the Phylogenetic Species Concept, but it was finally agreed to adopt criteria close to the General Lineage Concept of Species (GLCS) of de Queiroz (1999). Thus, the TSC regards a species as an extant segment of a lineage of populations, similar to the Evolutionary Species Concept (ESC; Mayden, 1997), but the TSC preferred the

name General Lineage Concept because essentially all species concepts are evolutionary.

There are many alternative species concepts (see Mayden, 1997), and the TSC concluded that those most relevant to avian systems are the Biological (BSC), Recognition (RSC) and Phylogenetic (PSC). The TSC agreed to apply the concepts that were most appropriate to the data under investigation. When population genetic data were available, such as fitness of individuals and their hybrids, the arguments of the BSC would be applied. If behavioral or acoustic data were presented, the RSC would be implemented. When phylogenetic reconstructions had been undertaken, with analyses of monophyly and diagnosability, the data would be interpreted according to the tenets of the PSC. Effectively then, the TSC followed Mayden (1997) and de Queiroz (1999) in recognizing the ESC/GLSC as the primary species *concept* to tell it what a species is, and the BSC, RSC, PSC as secondary species concepts or *species criteria* to tell it how to recognize their limits. This approach was adopted as a compromise. The TSC also agreed that, in general, only material published in peer-reviewed journals would be considered.

3 Species limits

When considering species limits, the TSC addressed two key questions:

Are the taxa diagnosable? Are they likely to maintain their genetic and phenotypic integrity in the future?

3.1 Diagnosability

The TSC deemed it necessary to define its view of diagnosability. In birds, there are generally two kinds of characters: qualitative and quantitative. Qualitative characters are presence-or-absence features, such as wing bars in *Phylloscopus* warblers, as opposed to discontinuities in a continuously varying trait. The TSC accepted diagnosability if members of at least one age/sex class could be distinguished from those of all other taxa in at least one qualitative difference.

Quantitative diagnosability is more problematic, since if large enough samples are available, it is theoretically possible for an individual of almost any size to emerge in a population. However, the TSC recognizes the practicalities of finite populations, and accepted quantitative diagnosability when at least one age/sex class is separated by a complete discontinuity in at least one continuously varying character from the same age/sex class in an otherwise similar taxon. Judgement and statistical interpretation are necessary here, but an example is to be found in the extent of yellow on the bill of the two forms, *columbianus* and *bewickii*, of the tundra swan, *Cygnus columbianus* (Evans and Sladen, 1980). The TSC agreed not to rely on characters that are evolutionarily labile, such as wing lengths of migrant and non-migrant populations. It also agreed to multivariate diagnosability, when overlap occurs in a single character. Thus, if a major component in a Principal Com-

ponents Analysis showed a complete discontinuity in the same age/sex class, then the taxa would be regarded as diagnosably distinct.

3.2 Genetic integrity

The TSC then turned to the more vexed problem of whether two diagnosable taxa would retain their differences into the future. This reduced to a question of the level of gene flow, actual or potential, between them. Four scenarios requiring different approaches were recognized here: sympatry, parapatry, hybrid zones and allopatry.

3.3 Sympatry

Taxa that coexist at pair formation will remain distinct if they are reproductively isolated. The TSC did not know of any examples where absolute reproductive isolation had broken down. Thus, it decided to rank as species diagnosable taxa that are broadly sympatric without hybridization, e.g. marsh and willow tits, *Parus montanus* and *P. palustris*. Most sympatric species fall into this category. However, diagnosable taxa were also ranked as species if they were broadly sympatric and hybridized only rarely, so that gene flow is so limited that gene pools are unlikely to merge, e.g. *Larus argentatus* and *L. fuscus*. Here can be inferred a strong barrier to gene flow that may be pre- or post-zygotic (or both), since hybrid young produced from cross-fostering experiments apparently survive less well than pure bred progeny (Harris et al., 1978).

3.4 Parapatry

Strictly parapatric taxa — those that exclude each other geographically — are considered species because their parapatry implies reproductive isolation. Icterine and melodious warblers (*Hippolais icterina*, *H. polyglotta*) are largely parapatric, and hybridize only rarely (Cramp, 1992). They are essentially reproductively isolated. Although hybridization in the contact zone is slightly more frequent, a similar situation holds for pied and collared flycatchers (*Ficedula hypoleuca*, *F. albicollis*), although here the reduced fitness of the hybrids has been demonstrated experimentally (e.g., Saetre et al., 1999). Secondary contact is involved here. Diagnosable taxa are ranked as species if their contact is relatively recent, through whatever cause, and if their overall divergence suggests that they will remain distinct. An example of recent contact is the spread of ruddy duck (*Oxyura jamaicensis*) into the Iberian range of the globally endangered white-headed duck (*O. leucocephala*). Although there is currently hybridization (Green and Hughes, 2001), increases in the abundance of the ruddy ducks may lead to a resumption of positive assortative mating.

3.5 Hybrid zones

The TSC distinguishes between hybrid zones and clines. The first occurs when populations within the zone contain one or both parental forms in addition to the hybrids. In a cline, the phenotype changes progressively through

space. In both scenarios, the population mean will change across the zone, but variance is higher in populations through a hybrid zone because of the wider range of phenotypes present. An example of a hybrid zone is the region of contact between carrion and hooded crows, *Corvus cornix* and *C. corone*, in various regions of the Palearctic (Parkin et al., 2003). A cline is typified by the progressive increase in wing-length with latitude in the Western Palearctic, or the transition from olive brown to grey in common chiffchaffs (*Phylloscopus collybita*) across Europe.

Hybrid zones probably always indicate some intrinsic barrier to gene flow between the two taxa, as has been demonstrated in the crows (Parkin et al., 2003). The TSC will rank as species diagnosable taxa that hybridize following secondary contact, if a stable and distinct hybrid zone connects them. It will regard the area of contact as a hybrid zone if local populations contain one or both parental phenotypes, plus F1 and backcross individuals. Stability implies that the zone has changed little in breadth through historical time, although it may have moved in position. Such taxa are regarded by some as semispecies (see below).

3.6 Allopatry

Here lie the real problems, for reproductive isolation cannot be tested in nature. Captive breeding is generally of little use (cf. Lanyon, 1979), since genetic incompatibility may be preceded by a variety of behavioral and ecological barriers to reproduction. Acoustic (playback) experiments may help, but are not conclusive. The taxonomic status of diagnosable taxa can only be assessed through the extent of their divergence, so comparison with species pairs that are taxonomically close, but occur in sympatry, is important. Even so, the assignment of species rank will always be hypothetical rather than proven. Here the TSC recognizes three more or less distinct scenarios that require different treatment with procedures slightly more rigorous than for sympatric or parapatric taxa.

First, allopatric taxa are regarded as species if they are fully diagnosable in each of several discrete or continuous characters that relate to different functional contexts, the sum of which corresponds with those distinguishing related sympatric species. Different functional contexts implies independently varying characters such as morphology, vocalizations and DNA sequences. Excluded are covarying characters such as leg and bill length in wading birds, or wing and tail length in small passerines. Bonelli's warbler complex (*Phylloscopus bonelli* / *P. orientalis*) is an example (Helbig et al., 1995). Its members are allopatric, with differences in vocalizations (marked), morphology (slight) and DNA sequences that are as great in magnitude as those between these taxa and the wood warbler (*P. sibilatrix*). If the latter is regarded as specifically distinct from *bonelli* / *orientalis*, then logically *bonelli* and *orientalis* must themselves be treated as separate species.

Secondly, allopatric taxa that do not fulfill the previous criteria are still regarded as species if at least one char-

acter is fully diagnostic and overall divergence in other characters is equivalent to that in closely related sympatric species. For example, male *Anas crecca* and *A. carolinensis* are fully diagnosable on the basis of the white line along the sides (vertical or horizontal), and are as divergent from one another at molecular levels as they are from the northern pintail, *Anas acuta* (Johnson and Sorenson, 1999).

Thirdly, allopatric taxa are regarded as species if they are statistically diagnosable by a combination of two or three functionally independent characters, and overall divergence in other characters is equivalent to that in closely related sympatric species. Covarying characters relating to body size or wing/tail length are not independent, although size and color are. DNA sequence data can be used as a character here, but the TSC considers it unwise to use a single base (or amino acid) difference as diagnostic, even though this may imply a substantial period of isolation. It seems unwise to invoke a character that might be reversed by a single mutational event. An example of statistically diagnosable taxa is the Armenian and herring gull complex (*Larus armenicus*, *L. argentatus*), the two members of which can be differentiated by Principal Components Analysis (Liebers and Helbig, 1999).

4 Superspecies

Taxa that meet in a hybrid zone are sometimes referred to as "semispecies" (Short, 1969), and those that are allopatric as "allospecies". While these are useful terms, a majority of the TSC did not wish to use them formally, preferring instead to apply them adjectivally in describing species that are very closely related and which come together to form a hybrid zone or are allopatric.

5 DNA sequences

There is no doubt that DNA sequence data are a powerful tool for elucidating evolutionary relationships, and their application continues to grow, especially in phylogenetics. However, although they can be used as an objective measure of genetic divergence in comparative studies, and applied in phylogenetic reconstructions to develop hypotheses of evolutionary relationships, molecular difference is not a taxonomic character. Hypotheses of relationship based upon a single sequence are greatly strengthened when supported by a second independent analysis, whether based upon comparative morphology or a functionally independent DNA sequence. A phylogeny based upon the mitochondrial gene cytochrome-*b* cannot be regarded as supported by a second mitochondrial sequence, however, since these are effectively inherited as a single unit or haplotype. On the other hand, a concordant phylogeny based upon one or more independent nuclear sequences will greatly strengthen confidence in the overall result.

The TSC also recognizes that paraphyly is to be avoided in classification, and that molecular phylogenetic evidence is a powerful technique for testing monophyly and revealing paraphyly. In the case of *Anas crecca* and *A.*

carolinensis (Sangster et al., 2001), a molecular phylogeny indicates that the sister group of *carolinensis* is not the Eurasian *crecca*, but the South American Speckled Teal, *A. flavirostris* (Johnson and Sorenson, 1999). This species shows no sexual dimorphism, its sexes share in parental care, and it differs in behavior and ecology from *carolinensis* (Madge and Burn, 1988). No one has suggested that *flavirostris* is conspecific with *carolinensis*. Using the criterion of monophyly, if *flavirostris* and *carolinensis* are sister taxa and distinct species, then logically *crecca* should be separated as well.

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Symposium 24 New directions in avian molt ecology

Introduction

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Comprehension of feather molt and plumage sequences is of fundamental importance in avian biology. Constraints between physiological and ecological requirements have given rise to diverse molt strategies and eco-physiological adaptations that appear in regular patterns in phylogenetically distant but ecologically closely related groups. Earlier studies of molt pattern suffered from the lack of a general model for determining molt parameters (timing and duration) unambiguously, and had to rely on such temporally imprecise categories as post-breeding, complete, pre-breeding and partial molt for their comparisons. New concepts and statistical methods introduced over the last two decades have now led to a sound theoretical base for the

use of molt parameters in comparative and evolutionary studies.

Ecological and physiological adaptations of feather replacement and evolution of molt strategies in different taxonomic groups were principal themes in this symposium. Conservation issues linked to molt requirements, such as habitat quality, food availability, and identification and protection of molt sites, were also implicated. One of the main papers addressing these last matters, by A.D. Fox on adaptations to balance nutrient budgets during the critical period of wing molt in waterfowl (Anatidae), was given only as an oral address. Its abstract is published in the Abstract volume for the Congress.

S24-1 Progress with the statistical analysis of primary molt

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Abstract This paper considers two extensions to the statistical analysis of primary molt. The first extension relates to the development of statistical models that allow the simultaneous estimation of molt parameters for diverse groups of birds. Parameter estimation uses the method of maximum likelihood and the EM algorithm. The likelihood ratio criterion is applied in statistical hypothesis-testing for equality of sets of parameters, and the Akaike Information Criterion is used to guide model selection. This extension is illustrated using primary molt data for willow warblers (*Phylloscopus trochilus*) over 11 years. The second extension is the realization that important insights into the way that primary molt is incorporated into the annual cycle of birds can be obtained by investigating the parameters of molt of individual primary feathers. This extension is illustrated using six data sets from four species of waders, Charadriiformes.

Key words Primary molt, Statistical models, Waders, *Phylloscopus trochilus*

1 Introduction

The basic model developed by Underhill and Zucchini (1988) to estimate the parameters of primary molt adopted a particular approach. First, it assumed that all birds sampled were subject to the same basic trio of parameters describing primary molt, i.e. that birds molting at a given site have a single mean starting date, duration of molt, and standard deviation from starting date. The latter measures the spread of starting dates for individual birds, i.e. the extent to which molt is synchronized. Secondly, it interpreted primary feathers as arising from a single feather tract. This paper extends both assumptions. The first assumption, or extension, requires the development of statistical models, with associated likelihood equations and the mathematical tools to solve them. The second extension takes up the original model and applies it in a novel way.

2 Extension 1: molt models to enable comparisons between groups of birds

The basic model did not facilitate comparisons between groups of birds, between sexes, sites and years. The extended model allows these comparisons and enables sensible model fitting, with significance tests for parameters. Brandao (1997) produced the mathematical statistics to accomplish this for her as yet unpublished PhD thesis. She developed the likelihood equations, and used the method of maximum likelihood and the EM algorithm to estimate molt parameters. She then applied the likelihood ratio criterion to test for equality of parameters, and made use of the Akaike Information Criterion to guide model selection (Akaike, 1973; Linhart and Zucchini, 1986).

The value of the extended model is illustrated by a

dataset for the willow warbler (*Phylloscopus trochilus*), for which we have primary molt protocols for 678 birds over 11 years at Lake Ladoga near St. Petersburg, Russia. Under the original version of the Underhill-Zucchini molt model, the only way to examine inter-year differences would have been to estimate the three molt parameters for each year, for a total estimate of 33 parameters. Theory developed by Brandao (1997) enables us to examine first whether the standard deviation parameters were the same for each year, immediately reducing the parameters to 23. Then followed a test of whether moult durations were the same for each year, such that only mean starting dates differed. It yielding just 13 parameters: 11 starting dates, a common duration, and a common standard deviation.

The next step tested which years had the same mean starting dates, few of which were unique due to exceptional conditions. At the end, the statistically most parsimonious model combining data for males and females suggested one mean starting date (12 July) for all except four years, a common duration of 45 days for all years, and a common standard deviation of 11 days for all years. The four exceptions to mean starting date were: 1979 (3 days early), 1980 (7 days late), 1985 (9 days late), and 1989 (6 days early). We have no auxiliary data to help explain the biological meaningfulness of this model.

The extensions developed by Brandao (1997) effectively enable analyses to be performed with a single “grouping” variable, analogous to one-way analysis of variance. The next step is to develop extensions that would simultaneously model more than one variable, such as year and sex, and the interactions between them. There is also a need for models which incorporate continuously explanatory variables. In the example above, it would be useful to be

able to test whether the starting date of molt depends on factors such as mean temperature in June, and to be able to fit models of the form:

$$\text{starting date in year } i = a + b (\text{temperature in year } i)$$

where a and b would be two parameters to be estimated by the model, along with duration and standard deviation.

3 Extension 2: the parameters of molt of individual primary feathers

3.1 Duration data

Prior to Serra (2000), studies of primary molt focused on primary feathers as a single unit, considered as a tract of nine or ten feathers (e.g., Prater, 1981). Serra (2000) initiated the investigation of the parameters of molt of individual primary feathers. His analysis for the grey plover (*Pluvialis squatarola*) showed interesting differences between the

Table 1 Estimates of the key molt parameters of individual primaries in grey plovers (*Pluvialis squatarola*) in Britain Overall estimates are also shown (from Serra, 2000).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	SD	M	SD	S	SD
P1	28.4	1.2	37.9	1.0	24.3	0.9
P2	28.9	1.1	41.1	0.9	22.2	0.8
P3	31.2	0.9	46.3	0.6	18.0	0.5
P4	30.6	0.8	51.1	0.5	16.0	0.4
P5	29.7	0.8	58.1	0.4	15.0	0.4
P6	26.8	0.7	68.3	0.4	13.6	0.3
P7	25.6	0.8	79.8	0.4	11.8	0.3
P8	22.6	0.9	92.1	0.6	12.4	0.3
P9	18.4	1.0	105.3	0.8	14.0	0.5
P10	16.7	1.1	117.4	0.9	16.5	0.8
P1–10	89.5	1.0	49.9	0.4	13.8	0.2

Table 2 Estimates of the key molt parameters of individual primaries in grey plover (*Pluvialis squatarola*) populations in warm southern latitudes Overall estimates are also shown (from Serra, 2000).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	SD	M	SD	S	SD
P1	30.6	3.6	15.7	4.0	29.7	2.8
P2	28.5	3.4	20.0	3.4	25.1	2.4
P3	25.2	2.9	29.7	2.8	24.9	2.2
P4	26.3	2.6	40.5	2.3	24.5	1.8
P5	25.1	2.5	51.5	2.1	24.1	1.6
P6	26.6	2.4	61.2	1.9	21.6	1.3
P7	23.9	2.3	77.9	2.0	21.5	1.2
P8	30.3	2.5	92.3	2.2	24.4	1.3
P9	27.1	2.5	111.8	2.3	27.8	1.5
P10	33.4	2.7	129.0	2.4	30.2	1.5
P1–10	136.4	3.0	26.2	2.0	25.6	0.9

strategies used by populations molting under differing climatic conditions. These differences hinted that further such research on other species might yield significant results. The first step was taken by Underhill (2002).

Serra (1998) showed that grey plovers molting in Britain completed molt in about 90 days (Table 1), whereas those molting in the south (southern India, Kenya, southern Africa and Australia) completed molt in about 130 days (Table 2), regardless of the time available. By estimating the parameters of molt for each of the 10 primaries, abbreviated here to P1 (innermost) to P10 (outermost), Serra (2000) examined the strategy employed by grey plovers to speed up molt in the north (Tables 1 and 2). Essentially, the innermost primary feathers (P1 and P2) were shed at the same pace in both environments. However, the outermost primary feathers (P8 to P10) were shed at short intervals and grown rapidly with the impending approach of freezing winter weather.

Underhill (2002) repeated this approach on four data sets: ruddy turnstones (*Arenaria interpres*) in southern Africa and Scotland (data from Summers et al., 1989, in which primaries were considered as a tract), reported in Tables 3 and 4; sanderlings (*Calidris alba*) in southern Africa (from Summers et al., 1987, in which primary molt data were not analyzed), reported in Table 5; and red knots (*Calidris canutus*) in southern Africa, from a previously unanalyzed dataset reported in Table 6.

The durations of primary molt in ruddy turnstones in southern Africa and Scotland were estimated to be 119 days and 94 days, respectively (Tables 3 and 4). Primary molt commenced early in August and ended early in November in western Europe; in southern Africa, it started in the second week of October and ended near the start of February. The durations of molt from P1 to P6 in southern Africa increased steadily from 10 days to a maximum of 27 days; and durations for P7 to P10 were fairly constant, varying between 24 and 27 days (Table 3). In contrast, the durations of molt of P1 to P5 in Scotland were fairly constant, varying

Table 3 Estimates of the parameters of molt of individual primaries in the ruddy turnstone (*Arenaria interpres*) in southern Africa Overall estimates are also shown (from Underhill, 2002).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	SD	M	SD	S	SD
P1	10.0	4.2	103.3	6.2	23.3	3.7
P2	13.4	4.6	103.8	5.9	22.4	3.4
P3	18.5	4.9	105.0	5.9	23.5	3.0
P4	16.9	4.3	113.2	5.9	25.9	3.0
P5	22.3	4.2	119.4	5.9	27.9	3.0
P6	27.2	4.0	128.4	5.2	29.1	2.9
P7	26.9	3.6	141.9	4.6	36.3	3.4
P8	25.6	3.1	162.6	3.3	35.2	2.8
P9	24.1	2.7	179.9	2.7	34.7	2.4
P10	26.2	2.7	191.7	2.5	34.6	2.1
P1–10	118.9	5.7	101.0	4.6	31.4	1.6

from 15 to 17 days; molt of P6 to P9 varied from 19 to 28 days, while P10 took 39 days to molt (Table 4).

The duration of primary molt in sanderlings in southern Africa was 98 days (Table 5). It commenced in early November and was complete by the middle of February. Molt from P1 to P6 increased in steady progression; P6 had the longest estimated molt duration of the ten primaries, and the molt durations of P7 to P10 were similar but slightly shorter (Table 5). The duration of primary molt for the knots in southern Africa was 95 days (Table 6). It commenced in late October, and was completed towards the end of January. Durations for individual primaries varied between 14 and 20 days, apart from P10 which took an estimated 24 days (Table 6).

3.2 Implications of molt duration data

What is remarkable about these results is their variability, not just the overall timing and duration of primary molt but particularly the patterns within the 10 prima-

Table 4 Estimates of the parameters of molt of individual primaries in the ruddy turnstone (*Arenaria interpres*) in Scotland Overall estimates are also shown (from Underhill, 2002).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	SD	M	SD	S	SD
P1	15.3	3.1	35.3	4.5	16.0	2.2
P2	15.7	3.1	35.3	4.5	16.0	2.2
P3	16.2	3.2	34.5	4.7	17.0	2.3
P4	16.7	3.2	34.6	4.7	17.8	2.3
P5	16.3	2.7	39.0	4.0	18.5	2.1
P6	19.4	2.3	48.5	2.6	16.5	1.4
P7	28.2	2.0	54.7	1.9	15.9	0.9
P8	23.2	1.7	70.2	1.5	17.6	1.0
P9	28.0	1.8	82.7	1.3	18.0	1.1
P10	38.8	2.2	89.0	1.3	19.1	1.0
P1-10	93.6	1.6	27.3	2.3	15.6	0.7

Table 5 Estimates of the parameters of molt of individual primaries in the sanderling (*Calidris alba*) in southern Africa Overall estimates are also shown (from Underhill, 2002).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	SD	M	SD	S	SD
P1	12.5	1.3	129.9	1.3	19.6	1.1
P2	12.7	1.3	132.1	1.3	19.3	1.1
P3	15.6	1.5	134.4	1.3	19.5	1.0
P4	19.0	1.6	139.1	1.4	20.6	1.0
P5	19.5	1.6	147.4	1.5	22.5	0.9
P6	22.8	1.7	156.4	1.5	23.3	0.9
P7	21.3	1.6	171.5	1.5	22.0	0.9
P8	19.7	1.4	186.5	1.4	20.8	0.8
P9	18.6	1.3	199.1	1.3	20.0	0.8
P10	21.3	1.3	208.5	1.2	19.0	0.7
P1-10	97.6	1.6	132.7	1.1	20.5	0.5

ries themselves. A striking example of the latter is the difference in molt strategies in ruddy turnstones and grey plovers in Britain. Both species completed primary molt in about 90 days (Tables 1 and 3), beginning in early August and finishing in early November prior to the advent of freezing conditions in late autumn and winter. Ruddy turnstones, however, molted P1 to P4 almost simultaneously and P5 four days later to complete molt of the first five primaries within about 20 days (Table 3). In contrast, molt of the same primaries took 50 days to complete in the grey plover (Table 1). Molt of the last five primaries (P6 to P10) in the ruddy turnstone took 79 days, and in the grey plover 66 days.

At northern sites, 20%–30% of grey plovers fail to complete molt prior to the onset of winter, and suspend molt until improved conditions occur in spring (Serra, 1998). Similar suspension does not occur in the ruddy turnstone which makes a rapid start to molt in August, when conditions are still favorable, and completes molt at a leisurely pace adapted to the increasing harsh conditions faced through autumn. In particular, P9 and P10 are estimated to take 28 days and 39 days ($SD = 2$ days in both) to grow, respectively (Table 3). Growth duration for these feathers is, with the exception of P1 and P2 in northern grey plovers, the longest of any in the six populations examined here (Tables 1–6). We conclude that molt strategy in the ruddy turnstone is better adapted to northern conditions than in the grey plover. This might reflect the recent colonization of northern latitudes by grey plovers, their numbers reaching Britain having increased six fold over the past three decades.

The duration of molt in the four species in southern Africa was remarkably variable: red knots took 92 days, sanderlings 100, ruddy turnstones 119 and grey plovers 131 (Tables 2, 4–6). The duration of primary molt in red knots there is similar to that in northern populations of ruddy turnstones and grey plovers, and to estimates of the duration of molt in red knots in Britain and the Netherlands (Boere, 1976; Ginn and Melville, 1983). This might indicate

Table 6 Estimates of the parameters of molt of individual primaries in the red knot (*Calidris canutus*) in southern Africa Overall estimates are also shown (from Underhill, 2002).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	SD	M	SD	S	SD
P1	13.7	2.5	119.8	3.2	23.8	2.2
P2	14.1	2.4	120.3	3.2	23.4	2.1
P3	15.7	2.4	122.5	3.0	23.4	2.0
P4	18.6	2.5	128.2	2.8	23.9	1.9
P5	20.1	2.4	135.0	2.8	26.4	1.9
P6	16.8	2.2	146.4	2.6	27.7	2.0
P7	15.7	2.0	157.5	2.3	28.1	1.9
P8	16.5	2.0	168.2	2.3	29.9	1.9
P9	18.6	2.0	178.4	2.2	30.4	1.7
P10	23.5	2.1	188.5	2.2	32.4	1.6
P1-10	94.8	3.5	118.5	2.9	30.8	1.2

that red knots have not migrated to hot environments in the non-breeding season for long enough to adapt to the opportunity to extend molt through the period available for it.

On the other hand, populations of grey plovers that migrate sufficiently far south, so that harsh weather does not constrain the duration of primary molt, extend the molt period to about 130 days, regardless of the time available (Serra, 1998). Only P1 and P2 are molted in quick succession, four days apart, and grow slowly; the remaining feathers grow at a fairly constant rate. The average intervals between shedding of the smaller primaries P2 to P6 is 10 days; for the larger primaries P6 to P10, the average interval lengths to 17 days (Table 2).

Although the overall durations of primary molt differed among red knots, sanderlings and ruddy turnstones, the sequences within the 10 primary feathers were similar. The three species molted P1 to P3 in quick succession, and then the remainder at a fairly constant rate.

Primary molt of grey plovers commences shortly after the completion of southwards migration, and extends over about 130 days (Serra, 1998); populations of grey plovers in the northern tropics therefore have long “slack” periods between the end of primary molt and preparation for migration, such as accumulation of fat reserves and acquisition of breeding plumage. This species appears to be adapted to molting in the tropics and subtropics, these environments probably providing the best conditions for it out of breeding.

In contrast to grey plovers, northern ruddy turnstones molt their inner five primaries extremely rapidly, a strategy which seems adapted to reducing stress in northern regions. The only trace of this “northern strategy” in southern Africa is the rapid molt of the first three primaries; the overall duration of primary molt in the ruddy turnstone in warm climates approaches that of the grey plover (Tables 2 and 3). We conclude that the ruddy turnstone is a species which is primarily adapted to molting in northern latitudes, but has modified this strategy to capitalizing better on the opportunity to extend molt in tropical and subtropical areas.

Waders are well known for the diversity of strategies used in their life cycles. We have demonstrated that this is also true for their patterns of primary molt. We now need to extend analyses of the kind used here to a broader range of

species, beyond waders and migrants.

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S24-2 Molt of the African penguin, *Spheniscus demersus*, in relation to its breeding season and food availability

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Abstract In South Africa, most adult African penguins molt between September and January; at Namibia's Mercury Island, most molt in April and May. Throughout their range most immature birds molt between November and January. The season of breeding varies between colonies but at each takes place when food is likely to be most abundant nearby. The main molt of adults occurs when food is least available near colonies. Birds that stop breeding earlier than usual may undertake an early molt.

Key words Molt timing, Breeding timing, Food availability, African penguin

1 Introduction

African penguins (*Spheniscus demersus*) molt annually. Molt takes ca. 21 days from arrival at a breeding locality, after a pre-molt fattening-up period, to departure after replacing plumage. Birds undertake periods of fattening of ca. 34 days before and ca. 41 days after molt (Randall and Randall, 1981), so that the overall time allotted to molt, including pre- and post-molt gains in condition, is about 96 days per annum. The annual cycle of African penguins has been described for St. Croix Island at Eastern Cape, and Robben Island at Western Cape, South Africa (Randall and Randall, 1981; Crawford et al., 1995a). The cycle at Robben Island lags behind that at St. Croix by about one month. Breeding and molt at Mercury Island, Namibia, occur several months later than at Robben Island (Crawford et al., 1995b). In this paper we collate published and unpublished information on the period of molt of African Penguins at seven localities and assess how molt and breeding are related to the availability of food.

At Robben Island in 1994/1995, it was noted that the molt of adults was less synchronized than normal. This was attributed to the stopping of breeding and early commencement of molt in birds oiled by the foundering of the *Apollo Sea* in 1994 (Underhill and Crawford, 1999). In 2000, large numbers of penguins were again oiled at Robben Island, following the foundering of the *Treasure*. The date of molt in banded birds known to have been both oiled and unaffected was monitored to investigate further the likelihood that oiled birds molted earlier than normal. Results are

reported.

2 Materials and methods

Counts of African penguins in the feather-shedding phase of molt were made at Mercury Island (25°43'S, 14°50'E) from July 1996–July 2001 (Kemper et al., 2001, 2002), at Lambert's Bay (32°05'S, 18°18'E) from September 1997–June 2002, at Dassen Island (33°25'S, 18°05'E) from November 1994–June 2002, at Robben Island (33°48'S, 18°22'E) from October 1988–June 2002 (Underhill and Crawford, 1999), at Dyer Island (34°41'S, 19°25'E) from September 1999–June 2002, at St. Croix Island (33°48'S, 25°46'E) from July 1979–June 1981 (Randall, 1983; Randall et al., 1986) and at Bird Island (33°50'S, 26°17'E) from June 1992–May 1997. At Bird Island, counts were of adult birds only; at all other localities birds in both immature and adult plumage were counted. Methods of counting were as described by Underhill and Crawford (1999).

Counts were made at weekly intervals at Dassen Island and bi-weekly at other localities. Gaps in data were filled by interpolation. In African penguins, the feather-shedding phase of molt lasts on average 12.7 days, so that counts at intervals of two weeks would be of different birds. The sum of such counts over a year thus provide an estimate of population size per colony (Randall et al., 1986). Counts at intervals of one week provide two such estimates. A procedure similar to that described by Underhill and Crawford (1999) was used to calculate numbers of birds molting in each month for which observations were made.

At Robben Island, band numbers were recorded weekly for penguins in the feather-shedding phase between October 2000 and January 2001 (Hemming, 2001). For each week, the ratio of oiled to unoiled birds was calculated. Information on the phenology of breeding of African Penguins, and on the availability of prey near colonies, was obtained from literature. The average monthly catch of the sardine (*Sardinops sagax*) off South Africa's Eastern Cape during 1989–2001 was calculated from records maintained at Marine and Coastal Management.

3 Results

At Mercury Island, the proportion of adults molting was greatest in April and May. At South African colonies, it was greatest from September to January, with a tendency to start earliest at Bird Island and latest at Dassen and Robben islands (Fig. 1a, b). At all six localities monitored, most immature birds molted between October and January, molt being about one month earlier at Lambert's Bay and Dyer Island than at the other localities (Fig. 1c,d).

From October until the first week of December 2000, the number of oiled and cleaned birds molting at Robben Island was more than twice, and up to nine times, the num-

ber unaffected. In the second and fifth weeks of December 2000, numbers of oiled and unaffected birds in molt were approximately equal. In other weeks in that month and throughout January 2001, most banded birds that were molting had not been oiled (Fig. 2).

On Eastern Cape, the average annual catch of sardines is low in January, increases to a peak in May, remains high in June, and then falls into a trough in September. Reasonable catches are made in November and December (Fig. 1b).

4 Discussion

Off Namibia, sardine and anchovy (*Engraulis capensis*), two of the main prey species of African penguins (Shelton et al., 1984), usually occur north of penguin breeding localities. However, both may spawn off central Namibia, sometimes as far south as Mercury Island, the first mainly from October to December and the latter from November to April. Spawning occurs inshore (King, 1977). Another prey species, the pelagic goby (*Sufflogobius bibarbatus*), is also present in high densities near Mercury Island, where it spawns inshore from July to February, peaking in November and December. In February 1980, pelagic

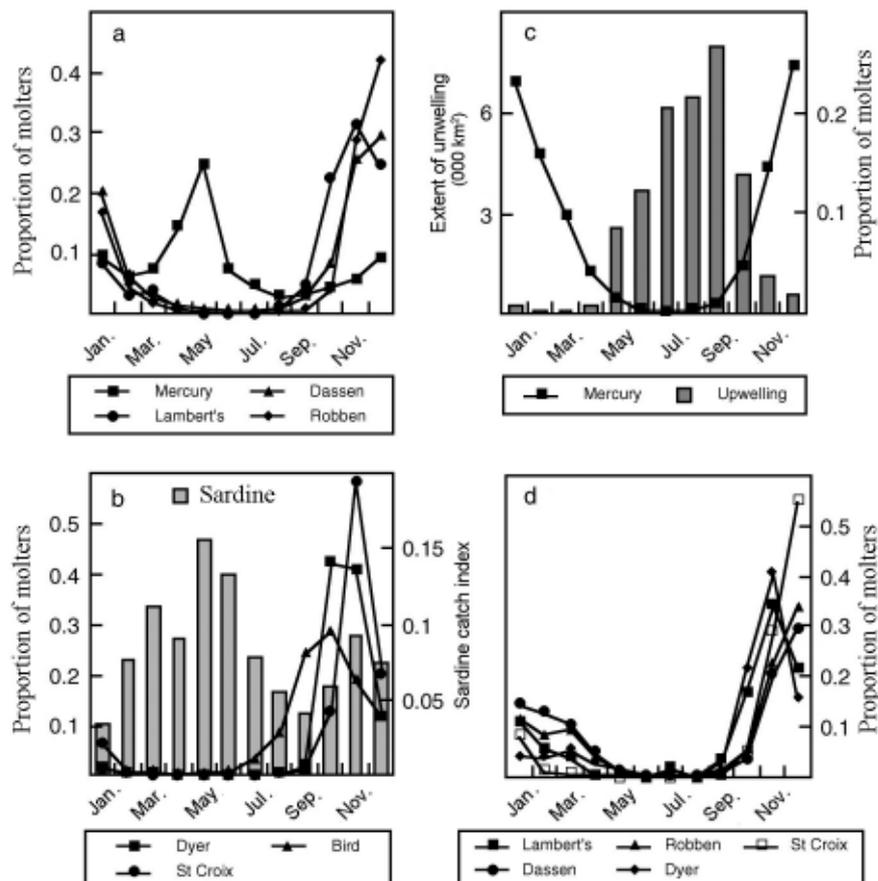


Fig. 1 Proportions of African penguins molting each month: a, adults at Mercury, Dassen and Robben islands and Lambert's Bay, west South African coast; b, adults at Dyer, St Croix and Bird islands, south South African coast; c, immature birds at Mercury Island; and d, immature birds at five South African colonies

The average monthly catch of sardine off Eastern Cape during 1989–2001 is shown in b, and the seasonal extent of intense Benguela upwelling in the vicinity of Mercury Island in c, estimated by Hagen et al. (2001).

gobies comprised 73% of food eaten by African penguins at Mercury Island (Crawford et al., 1985).

Most penguin breeding at Mercury Island takes place between August and March, peaking between October and January (Crawford et al., 1995b; Kemper, unpublished information). At adjacent Ichaboe Island, most chicks have hatched by November (Shelton et al., 1984), so that chick rearing and fledging periods coincide with spawning anchovy, sardine and pelagic goby nearby. The main molt in adults then takes place in April and May when anchovy and sardine are locally scarce.

In South Africa, young sardine and anchovy congregate inshore along the west coast from March until September. They then migrate south to their spawning grounds over the Agulhas Bank, where they arrive from August onwards. Old sardine also are available along the west coast from March to September. Sardine of intermediate age are abundant on the western Agulhas Bank from January to April, after which some migrate past the Eastern Cape to KwaZulu-Natal for winter (Crawford, 1980). Unlike the situation in Namibia, most spawning over the Agulhas Bank takes place between 30 to 130 km offshore, and mainly from September to February in both fish (Armstrong and Thomas, 1989).

At South Africa's Western Cape, African penguins breed mainly from February to September (Crawford et al., 1995a) when young anchovy and sardine and older Sardine are most abundant in the area. At St Croix Island off Eastern Cape, the main breeding season is from January to July (Randall and Randall, 1981). Sardine is abundant off Eastern Cape from March to June (Fig. 1), the period when chicks from first-laid clutches are being reared and departing to sea (Randall and Randall, 1981). Most penguins in South Africa molt during the spawning period for sardine and anchovy, when these fish are generally farther offshore and beyond the usual foraging range of breeding penguins. Off western South Africa, the foraging range of penguins feeding chicks is estimated to be 11–15 km; off Eastern Cape, however, breeding birds may forage up to 40 km from their colonies (Heath and Randall, 1989; Wilson et al., 1989).

Molting in adults at Lambert's Bay peaks earlier than at Dassen and Robben islands, matching the southward

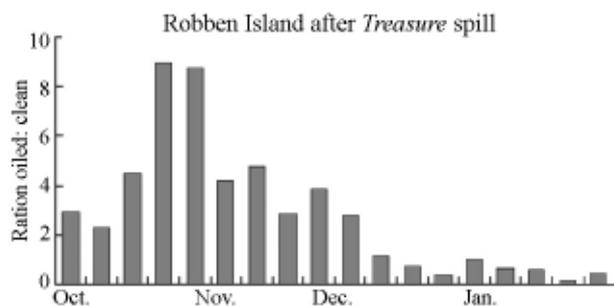


Fig. 2 The ratio of oil-affected banded penguins in molt at Robben Island to those unaffected for each week during October 2000–January 2001 (Data from Hemming, 2001).

movement of young anchovy and sardine to spawning grounds on the Agulhas Bank through winter and spring. Adults molting at Dyer and St Croix islands also peak ahead of those at Dassen and Robben islands. In spring, maturing anchovy join spawning shoals over the Agulhas Bank, and on the south coast may not be available regularly in waters near penguin breeding colonies inshore. At Bird Island, the easternmost breeding colony of African penguins, numbers of adults molting increase markedly from September, after sardine on the south coast have moved to KwaZulu-Natal or commenced spawning.

As observed by Randall and Randall (1981), it appears that availability of fish in the vicinity of breeding colonies determines the main breeding season of African penguins and that this, in turn, determines when adults molt. Birds are able to forage farther afield on feeding trips undertaken before and after molt than when breeding. After terminating breeding in 2000, two African penguins from Dassen and Robben islands spent lengthy periods at feeding grounds well beyond the normal foraging ranges of penguins when breeding at these islands (<http://www.uct.ac.za/depts/stats/adu/oilspill/sapmap.htm>).

In South Africa, immature and adult African penguins molt at more or less the same time. At Mercury Island in Namibia, immature penguins do not molt at the same time as adults. Rather, they and immature birds at Ichaboe (26°17'S, 15°46'E), Halifax (26°38'S, 15°05'E) and Possession (27°01'S, 15°12'E) islands (Kemper et al., 2002), molt at much the same time as immatures in South African colonies. It is the exception to the rule that African penguins molt when food is least abundant near breeding colonies. Immature penguins at Mercury Island molt when the seasonal surface waters there reach minimum temperatures of <13°C (Fig. 1c). Hagen et al. (2001) assume that this water provides an index of intense Benguela upwelling. However, in a review of other information, Shannon (1985) suggests that upwelling around Mercury Island peaks between October and December. From May to September, when the extent of cold surface water near Mercury Island is greatest, immature penguins may move north to feed on sardine and anchovy, which are then abundant at about 23°S.

The generally earlier molt in oil-affected adults at Robben Island in 2000/2001 (Fig. 2) suggests that rehabilitated birds stop breeding and enter molt before unaffected birds. Ability to alter the onset of molt will enable penguins shifting to other colonies with different breeding times to adjust their annual cycle to that of the new colony (Underhill and Crawford, 1999). Established breeders invariably return to former breeding localities to locate their mates (Randall, 1983), but those breeding for the first time may move elsewhere (Whittington, 2002). This provides a mechanism for African penguins to respond to long-term changes in the distribution of their prey (Crawford, 1998).

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S24-4 Identification and occurrence of a biannual complete molt

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Abstract A complete molt twice a year is rare in birds. I used the following criteria to identify double molt from museum collections: (1) seasonal pattern of occurrence of primary molt, (2) seasonality of fresh and worn breeding and non-breeding plumages, and (3) percent active primary molt in the total sample. In species with well-synchronized seasonal cycles, all three criteria reveal a clear simple annual molt pattern. In tropical taxa, however, they indicated pattern in only a fraction of molting birds: >25% of species showed a possible double molt and <15% a single molt. Out of 21 *Prinia* species, 11 appear to have a double molt.

Key words Double molt, Cisticolidae, *Prinia*, Africa, Specimen sampling

1 Introduction

Two complete molts per year are generally called a “biannual molt”, a term that is nevertheless ambiguous because it also means “every second year”. “Semi-annual” is an alternative, but suggests six-monthly intervals which is also inaccurate. Accordingly, “double molt” will be used in this paper to categorize this phenomenon; and, except when otherwise stated, molt refers to complete replacement of plumage.

Replacement of all feathers twice a year is rare in birds. In a review, Prys-Jones (1991) found sufficient evidence for it in only seven passerines in six families. Subsequently, Herremans (1999) identified it in the black-chested prinia *Prinia flavicans*, the first record for a resident African species. There are several other reports of a complete double molt (e.g., Verheyen, 1953; Ali and Ripley, 1983; Baker, 1997). Some are of individual cases (Prys-Jones, 1991); others are misinterpretations (Prys-Jones, 1991; Hobson et al., 2000); and some are inadequately documented. Proving double molt is difficult and laborious, because it requires information at both population and individual level.

This paper presents simple methods for screening museum collections for candidate species, and illustrates them with examples from the Cisticolidae.

2 Materials and methods

I studied primary molt in museum specimens by scoring the primary bases and classifying them into the following stages: (1) no molt, (2) start of primary molt, i.e. replacement of inner three primaries, (3) mid stage of molt, i.e. molt focus between primaries 4 and 6, and (4) end of molt, i.e. molt of primaries 7–10. For birds not in active molt, plumage condition at the time of collection was further classified as: (1) fresh, i.e. recently molted, (2) intermediate, and (3) worn,

i.e. close to being replaced again. Based on these classifications, the following parameters were used to assess molt: (1) seasonal occurrence of primary molt, (2) seasonality of fresh and worn breeding and non-breeding plumages, and (3) percent birds in the total sample in active primary molt. Only adult birds were used in the analyses.

Data from different subspecies or populations (e.g., north and south of the equator) were only pooled when patterns and seasonality were the same. Information on the seasonality of breeding was obtained from literature.

3 Results

3.1 Reference pattern for double molt

I re-analyzed data for the black-chested prinia (*Prinia flavicans*) from Herremans (1999) using the above plumage classifications. The resulting information presented in Fig. 1 provides a reference for species with a double molt. This subtropical African species shows a clear but complex seasonality, breeding during the moist austral summer

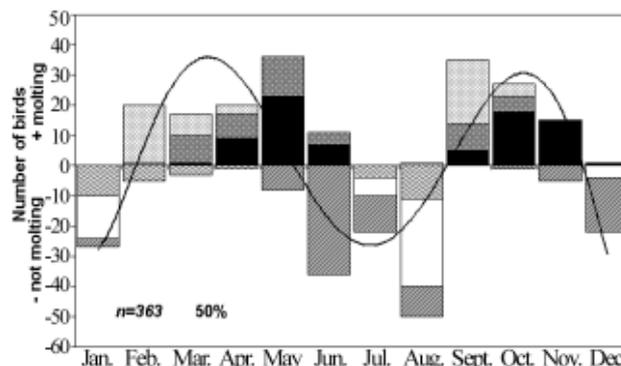


Fig. 1 Seasonality of breeding, primary molt and plumages in the black-chested prinia, *Prinia flavicans*. For legend, see Fig. 2; breeding recorded October–May.

(October–May) and recuperating during the dry winter months (June–September). It undergoes two periods of primary molt, overlapping the beginning and ending of breeding. Moderate to high proportions of museum samples are in active molt (>20%–25%).

3.2 Reference pattern for single molt

The southeast Asian hill prinia (*Prinia atrogularis*) shows a more traditional annual cycle (Fig. 2). It breeds in May–August, and undergoes a single molt in October–January. Plumage becomes increasingly worn over the boreal summer. The overall proportion of molting birds in collections is small (7%).

3.3 Equatorial populations

The tawny-flanked prinia (*Prinia subflava graueri*) from southern equatorial Africa does not show seasonality at population level (Fig. 3). Breeding and molting occur throughout the year, and birds in worn and fresh plumage are found in all months. The high overall percentage of birds in active molt suggests a double molt, at least.

3.4 Taxa with irregular annual cycles

Seasonal cycles in many arid zone birds are opportunistic, resulting in irregular breeding and molting. Small-scale random sampling over many years, as in museum collections, produces complex population patterns. The rufous-eared warbler (*Malcorus pectoralis*) of southern African deserts may breed or molt in nearly any month, with a tendency to breed more in early summer, September–December (Berruti, 1997), and to molt more in late summer and autumn, January–June (Fig. 4). Because of this and the fact that some birds molt faster than others, it is difficult to judge the overall plumage stage in many birds. An intermediate percent of the total sample was in active molt. The breeding-molt pattern in the pale prinia (*Prinia somalica*) appears to be similar (15 % molting).

3.5 Summary for Cisticolidae

I examined 5 513 adults of 21 prinia species (76 taxa), and 1 845 adults of 5 cisticola species (12 taxa), the details

of which will be presented elsewhere.

Most prinia species (11) appear to have a double molt (*Prinia flavicans*, *P. subflava*, *P. inornata*, *P. hypoxantha*, *P. bairdii*, *P. sylvatica*, *P. rufescens*, *P. hodgsonii*, *P. buchanani*, *Schistolais leucopogon* and *Heliolais erythropus*). Over >20% (mostly >25%) in the overall sample were in active molt. Six taxa (the four subspecies of *Prinia socialis*, *P. inornata extensicauda*, and *P. (inornata) insularis*) undergo an extensive pre-breeding molt of the contour plumage, which occasionally also includes the primaries: 13%–16% are in primary molt. Seven species undergo a single molt: *P. maculosa*, *P. gracilis*, *P. polychroa*, *P. atrogularis*, *P. burnesii*, *P. criniger* and *P. flaviventris*. Up to 10% in the overall sample were in active molt. When the core ranges of taxa are classified according to climate, a tendency emerges for a double molt to prevail in species from wet, tropical areas, and a single molt in temperate or arid climates.

I found molt patterns more difficult to interpret in cisticolas. Four species (*Cisticola ruficeps*, *C. natalensis*, *C. galactotes* and nominate *C. t. tinniens*) showed an extensive partial pre-breeding molt, including tail feathers, tertials and, in a minority of birds, primaries and secondaries. An intermediate percentage (15%–20%) of the overall sample in all five species was in active primary molt. Most of the birds undergoing a complete pre-breeding molt were young of the previous year.

4 Discussion

A study of museum specimens can at best provide circumstantial evidence at population level for the existence of a double molt. Data from museum skins may give a clear indication of candidate species, but confirmatory field studies with marked birds remain necessary. Proof at the individual level, however, is rarely obtained and “circumstantial evidence” still dominates the issue. Even in the willow warbler (*Phylloscopus trochilus*), one of the best studied double molters (Underhill et al., 1992), I am not aware of a single case of a bird ringed while molting at breeding grounds being recaptured while molting on nonbreeding

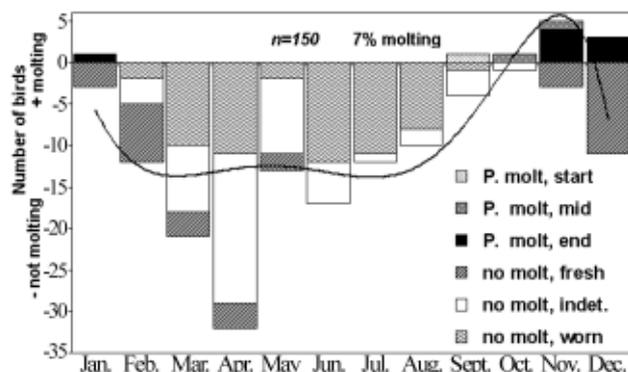


Fig. 2 Seasonality of breeding, primary molt and plumages in the hill prinia, *Prinia atrogularis* (6 ssp) Breeding recorded October–August.

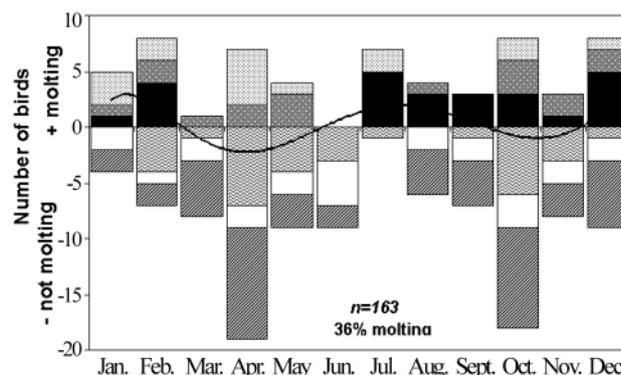


Fig. 3 Seasonality of breeding, primary molt and plumages in the equatorial tawny-flanked prinia, *Prinia subflava graueri* For legend, see Fig. 2; breeding recorded throughout the year.

grounds, and *vice versa*.

In species with clear, well-synchronized seasonal cycles, the identification of a single or double molt is straightforward (Figs. 1–2). All three criteria (molt sequence, plumage sequence and fraction in active molt) reveal the same pattern. In populations without a synchronized annual cycle, e.g. many equatorial birds (Fig. 3) or erratic breeders (Fig. 4), the information on molt and plumage sequences becomes uninformative.

The total fraction of molting birds is then the only remaining criterion, but it is nevertheless sensitive to several sampling biases. When data from living birds are used (e.g., data contributed by ringers), there may be a bias to report only molting birds. If birds hide during molt, sample sizes may become unrepresentatively small, resulting in an underestimation of the overall proportion in molt.

Molt speed is another factor that can affect the fraction of molt in samples. Opportunistic desert species may molt fast in a year with good rains, but protract or even suspend molt during drought. Such strategies cannot be described by a single parameter, and therefore, the fraction of birds in molt is most meaningful in populations with a rather similar molt speed. In any case, small passerines with >25% in active primary molt across a year may be double molters, while populations with <15% in molt are more likely

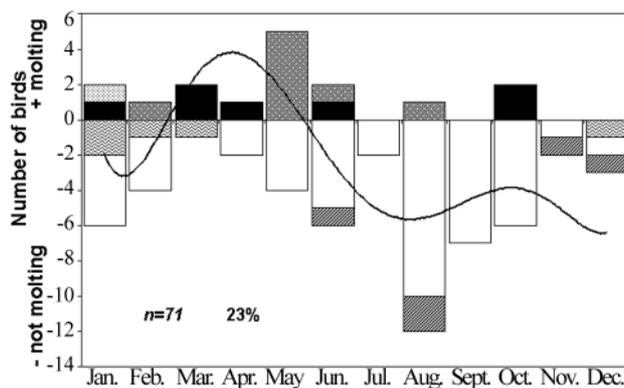


Fig. 4 Seasonality of breeding, primary molt and plumages in the rufous-eared warbler, *Malcorus pectoralis*. For legend, see Fig. 2; breeding recorded throughout the year.

to be single molters.

If juveniles undergo a complete molt at different times than adults, this may create a confusing bimodal pattern. When juvenile and adult plumages differ, this is rather easily resolved, except that young birds finishing molt are often difficult to distinguish from adults.

The present scan of museum specimens in the Cisticolidae increases to 18 the number of species suspected to have a double molt. Many more probably remain to be discovered, and these would constitute interesting comparative models for many studies. Unfortunately, because of the lack of well-marked seasonality in the wet tropics, the most promising species are also the most difficult to elucidate.

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S24-5 The regulation of primary molt speed in the grey plover, *Pluvialis squatarola*

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Abstract Grey plovers wintering at different latitudes differ in duration of molt. We investigated the role of simultaneous primary shedding and different growth rates of individual primaries on regulation of molt speed. We also explored relationships between length and mass of primaries and primary growth rates. Grey plovers adjusted molt speed by varying the number of primaries growing simultaneously and the growth rates of individual primaries. As a result, total production of primary mass was not constant during molting but regulated in relation to proximate factors, such as day-length and temperature. The outermost long primary (P10) had growth rates different from innermost primaries, possibly because of a different mass/length ratio.

Key words Feather growth rate, Feather mass, Primary molt, *Pluvialis squatarola*

1 Introduction

Primary molt is a major event in the annual cycle of birds and affects their life histories crucially. Timing and duration of molt are therefore under strong selective pressures and have relevant fitness costs (Helm and Gwinner, Symposium 40). Molt patterns and associated mechanisms of molt regulation have been poorly investigated in free-living populations, due partly to the lack of an efficient statistical method for analyzing them. As a result, a constant rate of feather molt has generally been assumed (Underhill and Zucchini, 1988). This assumption was based on the belief that whole-body protein synthesis was constant during main molt phases, and on empirical observations which showed that (1) growth rates of individual feathers were rather constant (Newton, 1967), and (2) birds compromised the quality of feathers produced rather than feather growth under food restriction (Payne, 1972).

This study reassesses that assumption by comparing regulation of duration and speed of primary molt in different populations of grey plover, *Pluvialis squatarola*. Populations wintering in areas with cold winters are known to have fast molts, with an average duration of *c.* 90 days, while those localized at milder sites have slower molts of *c.* 120–130 days (Serra, 1998). Data from individuals representing these two molt groups are used to investigate the role of simultaneous shedding and growth rates of primaries in the regulation of molt speed, and to explore the relationship between length and mass of primaries and their growth rates.

2 Methods

Primary molt data obtained from birds ringed at six

wintering sites (Britain, Kenya, South Africa, India, northwest Australia, southeast Australia) were analyzed. Molt parameters (timing and duration) for these populations were calculated using the model of Underhill and Zucchini (1988) and subsequent extensions (Underhill et al., 1990; Underhill, in prep.). Details of molt parameters are found in Serra et al. (1999), Balachandran et al. (2000), Minton and Serra (2001), Pearson and Serra (2002), and Serra et al. (submitted). Birds wintering in Kenya, South Africa, India, and northwest and southeast Australia were treated here as a single group of “slow-molting populations” because durations of primary molt among the various populations did not differ significantly at the 5% level (overall duration 136 days, *SD* 3 days; standard deviation of the model 26 days, *SD* 1 day). The slow molting populations differed, however, in the timing of molt. To unify them, dates of capture of individuals were translated to a common time origin (day 0) using the mean starting date of molt in their respective populations. The pooled group of slow-molting birds was then compared with a sample of British birds which had molted at a faster rate (90 days, *SD* 1 day; standard deviation of the model 22, *SD* 3 days).

The Underhill and Zucchini model (1988) was also applied to calculate molt parameters for individual primaries in slow- and fast-molting populations (Serra, 2000; Underhill, 2001). Here the first assumption of the model was that growth rate is constant for each primary. A trend close to linearity in the growth rate of individual primaries had already been reported in passerines (Newton, 1967) and waders (Sach, 1968). Therefore, transformations of 0 to 5 primary scores for individual feathers (Ginn and Melville, 1983) into percentage feather-mass grown or percentage feather-length

grown were considered unnecessary, and primary scores were simply re-coded on a 0 to 1 scale.

The 10 long primaries were numbered from the innermost (P1) to the outermost (P10), the latter forming the wingtip. Total primary length (tip of rachis to base of calamus) was measured to an accuracy 0.1 mm on flattened and stretched feathers. These were extracted from an adult plover in fresh plumage collected in Italy on 20 October 1998. Percentage primary masses were taken from literature (Underhill and Joubert, 1995). Daily percentage production of feather mass is the relative feather mass produced by each primary during each day of molt, assuming a constant rate of growth between days. The size of feather follicles was estimated as the maximum measured diameter of the calamus (accuracy: 0.1 mm).

3 Results

Grey plovers molting at the fast rate had on average a larger number of primaries growing simultaneously than those molting at the slow rate, especially among P4–P7 (Fig. 1). The duration of molt for each primary did not significantly differ between P1 and P10 in slow molting birds, or between P1 and P8 in fast molting birds. Molt durations of P9 and P10 in fast molting birds were significantly shorter

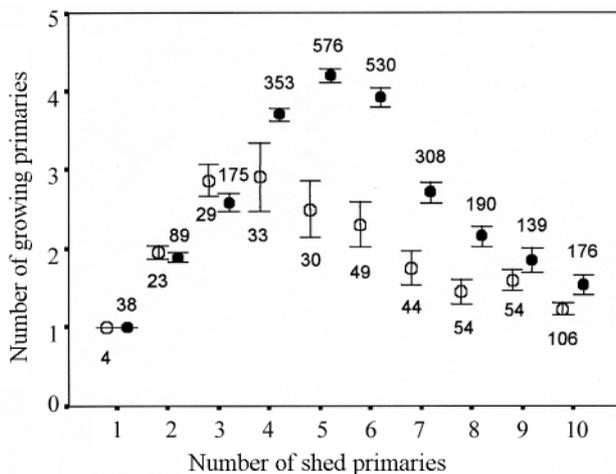


Fig. 1 Molt progression in grey plovers

Plot shows the number of primaries growing simultaneously during molt against the number of shed primaries from the innermost primary outwards. Solid symbols = fast-, and open symbols = slow- molting populations. Bars are 95% confidence limits.

than those for their innermost primaries and also those of P9 and P10 in slow molting birds (Table 1).

Primary mass and total length can be assumed to be proportional to follicle size (Rohwer, 1999), because feathers are generated by single rings or short cylinders of cells nested within each follicle. Taking the diameter of the feather calamus as an index of follicle size, both mass and total length of primaries can be related to calamus diameter by linear regressions. For both regressions, P10 lies outside the 95% confidence limits (Fig. 2). Moreover, inclusion of P10 worsens the fit of the regression models. The variance in all primaries explained by the models (mass: $r^2 = 0.94$, $F_{1,8} = 129$, $P < 0.001$; primary length: $r^2 = 0.83$, $F_{1,8} = 38$, $P < 0.001$) increases by 4% and 15% respectively if P10 is excluded (mass: $r^2 = 0.98$, $F_{1,7} = 434$, $P < 0.001$; primary length: $r^2 = 0.98$, $F_{1,7} = 307$, $P < 0.001$).

The relationship between primary mass and total primary length was assumed to be a power curve. Power equations are most often used to describe size-correlated changes in shape (Redfern, 1989; Worcester, 1996). Again, P10 falls outside the 95% confidence limits (Fig. 3). In this case, too, the variance explained by the model ($r^2 = 0.993$, $F_8 = 1141$, $P < 0.001$, $b_0 = 4.0 \times 10^{-5}$, $b_1 = 2.541$) increases if P10 is excluded but only by 0.6% ($r^2 = 0.999$, $F_7 = 13723$, $P < 0.001$, $b_0 = 5.8 \times 10^{-5}$, $b_1 = 2.461$).

Provided that environmental and physical body conditions do not change, the relationship between primary growth expressed in terms of mass (daily percentage feather-mass grown) and length (total primary length) is expected to be linear or very close to linearity because both variables are proportional to follicle size. In slow-molting birds, this relationship can be assumed to be linear between P1 and P9 ($r^2 = 0.972$, $F_{1,7} = 239$, $P < 0.001$), with P10 as outlier (Fig. 4a). In fast-molting birds, on the contrary, the best fit of the point is given by a quadratic curve between P1 and P8 ($r^2 = 0.998$, $F_5 = 1133$, $P < 0.001$), with P9 and P10 as outliers (Fig. 4b).

The average total daily percentage mass grown in primaries increased linearly during the growth phase from P1 to P5 both in both fast- and slow- molting populations (Fig. 5), although at different rates ($F_1 = 35.6$, $P < 0.001$). During the growth phase from P6 to P10, however, daily feather mass gain remained constant in slow-molting birds, but increased after the growth period of P6 and P7 in fast-

Table 1 Duration (in days) of molt of individual primaries (P1–P10) in slow- and fast- molting populations of grey plovers

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	
Duration (SD)	Slow	31 (4) 23–39	29 (3) 23–35	25 (3) 19–31	26 (3) 20–32	25 (2) 21–29	27 (2) 23–31	24 (2) 20–28	30 (3) 24–35	27 (2) 23–31	33 (3) 27–39
	Fast	28 (1) 26–30	29 (1) 27–31	31 (1) 29–33	31 (1) 28–32	30 (1) 25–29	27 (1) 24–28	26 (1) 24–28	23 (1) 21–25	18 (1) 16–20	17 (1) 15–19
95% Confidence limits	NS	NS	NS	NS	NS	NS	NS	NS	**	**	

** = difference significant at the 5% level.

molters.

4 Discussion

Speed of primary molt can be regulated by varying the number of feathers growing at the same time and/or by varying rates of feather growth. Grey plovers do both. Regulation by shedding rate is probably widely used at individual level. Among Charadriiformes, different shedding rates have been recorded in dunlins, *Calidris alpina* (Hölmgren et al., 1993; Serra et al., 1998) and black terns, *Chlidonias niger* (Zenatello et al., 2003).

It is generally accepted that rates of feather growth are little affected by feather length or mass because both the latter depend on follicle size (Rohwer, 1999). Data here, however, strongly suggest that, in grey plovers, this relationship holds true only for feather tracts P1–P9, P10 differing possibly because of greater specific mass. This is confirmed by the relationship between feather mass and total length. An intuitive explanation for the heavier and hence possibly more resistant structure of P10 is that it forms the

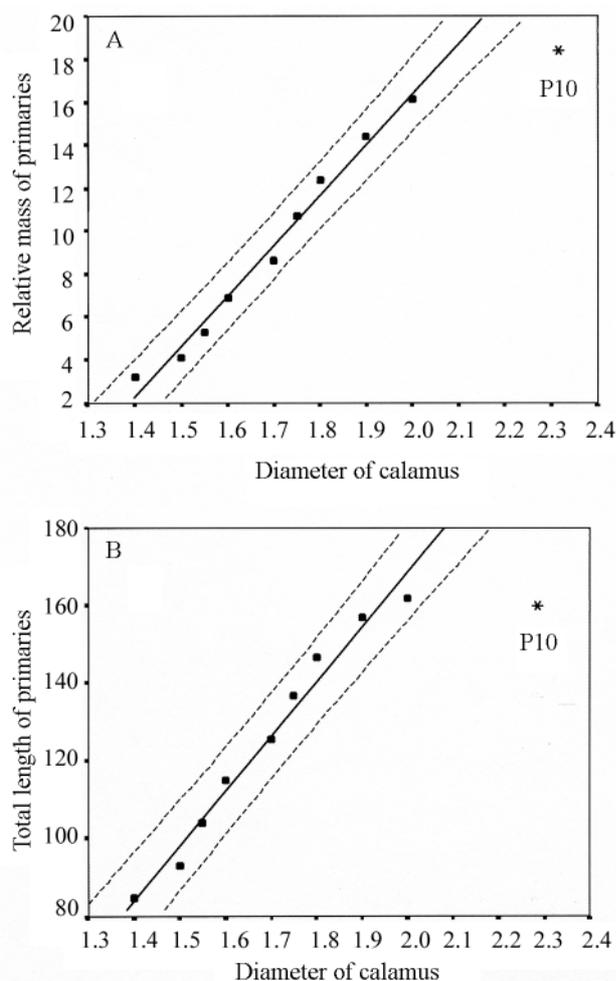


Fig. 2 Relative mass (A) and total length (B) of primaries in relation to the diameter of the calamus (mm) in grey plovers. The solid line is the least-square regression fitted to the points (primaries from P1 to P9); dashed lines are 95% confidence limits. P10 is an outlier.

leading edge of the wing and must therefore accomplish different aerodynamic functions. It has been observed that the vanes of outer primaries are more resistant to out-of-plane forces than those of the inner primaries, an observation explained by the need to sustain larger aerodynamic forces in flight (Ennos et al., 1995). The similar flexural stiffness observed among primaries in different relative positions on the wing, whether leading, central or trailing (Worcester, 1996), corroborates this idea. Redfern (1989) found that primary mass was proportional to length in a plot of nine primaries of five species. However, it seems unlikely that primaries of different species can be described effectively by a single curve. We would rather suggest the existence of species-specific relationships, linked to wing shape and flight characteristics. Comparative studies should shed light here.

With the expected exception of P10, primary growth in slow-molting birds correlates linearly with primary length, suggesting that such birds do not change primary growth rate during molt. This could reflect environmental stability at their wintering sites. In fast molting birds, the quadratic relationship indicates an acceleration of growth rates through the whole molt period, possibly linked to decreasing day-length (Dawson, 1994, 1998), and that the function of increase changes at P9 and P10, possibly in response to decreases in temperature at the time of molting these primaries (Payne, 1972). This final acceleration of feather mass production can be interpreted as a response to environmental signals of the arrival of winter. That molt can respond adaptively is supported by the fact that 35% of British grey plovers suspend primary molt just before winter when molt limit is at P9 or P10 (Branson and Minton, 1976; Serra et al., submitted).

This analysis shows that production of primary feather mass is not constant through the molt period because primaries differ in growth rate. In contrast to previous hypoth-

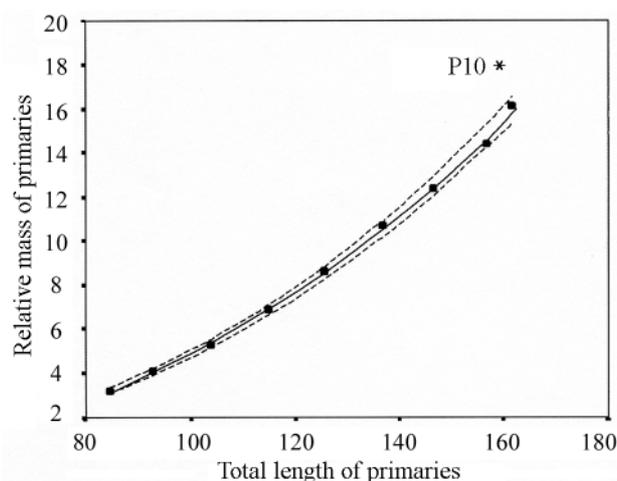


Fig. 3 The best fit of the relative mass of primaries P1 to P9 on their total length (mm) in grey plovers is a power curve (solid line). Dashed lines are 95% confidence limits. P10 is an outlier.

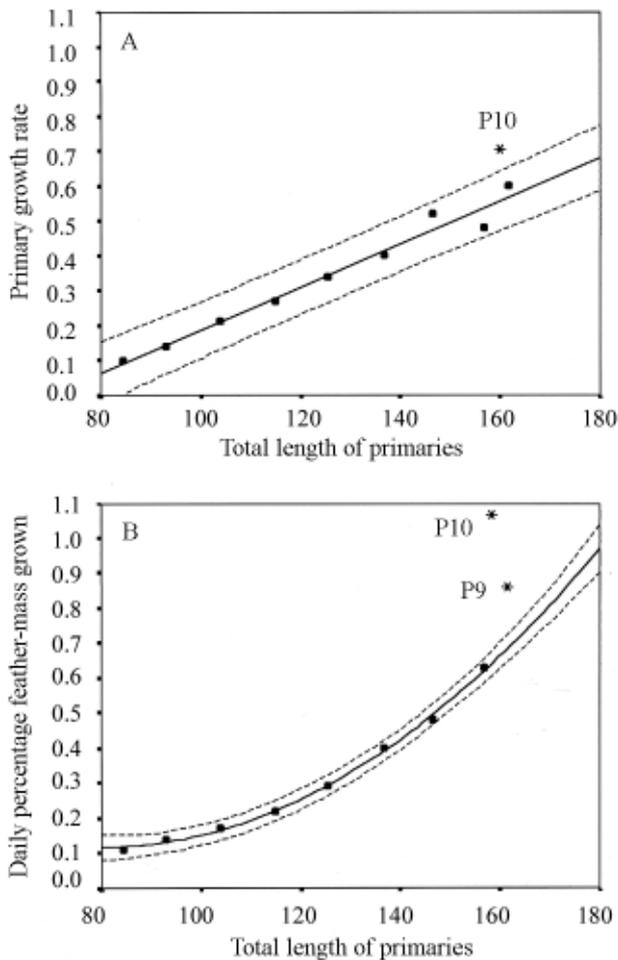


Fig. 4 Primary growth rates of slow- (A) and fast- (B) molting populations on total length of primaries (mm) in grey plovers. The relationship can be assumed to be linear in slow-molting birds (P10 outside 95% c.l.), but follows a quadratic regression in fast-molting birds (P9 and P10 outside 95% c.l.). Solid lines are regression lines, dashed lines are 95% confidence limits.

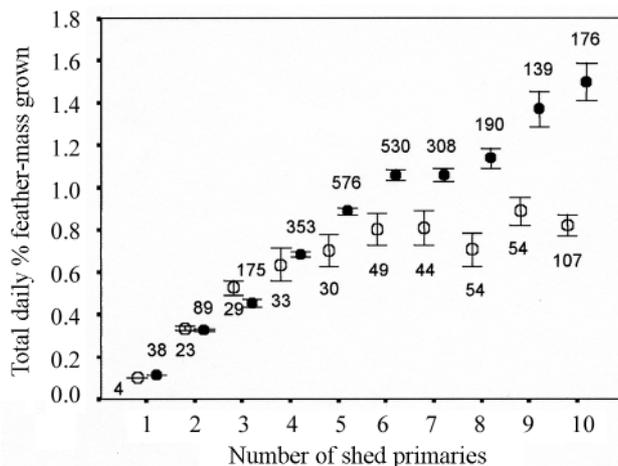


Fig. 5 Average total daily percentage feather-mass grown during molt progression in grey plovers

Mass grown was calculated on the assumption that all the primaries grew simultaneously in each bird. For explanation of symbols, see Fig. 1.

eses (Underhill and Zucchini, 1988), growth rate can be regulated in relation to proximate factors. In slow-molting birds, nevertheless, production of primary mass can be assumed to be constant between P6 and P10, i.e. when 72% of total primary mass is produced. It might explain why percentage feather-mass grown is rather effective in removing the curvature of molt score distributions (Summers et al., 1983). The assumption of linearity does appear to break down, however, near the end of molt — but this is a topic that needs further investigation by Underhill-Zucchini molt models.

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Symposium 25 Population regulation in heterogeneous landscapes: a means for predicting the consequences of environmental change

Introduction

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Habitats vary in quality as a result of variation in food abundance, nesting site quality, predation and diverse other factors. This symposium aimed to identify individual and population responses to such variables, and from them to develop a better understanding of the factors regulating the natural populations of birds. Accordingly it sought answers to a range of questions: how do birds respond to habitat heterogeneity and variation in quality? Do birds move in response to quality differences? What is the effect of competition for food or territory? What happens to those that cannot find food or territory? With such information it is then possible to create predictive models of population demography; and these then can be used to predict shifts in population size should habitat vary as a result of environmental change.

Two of the five papers offered are published here. Nicholas Rodenhouse and Richard Holmes incisively dissect out the mechanisms regulating bird populations, demonstrating the important role of site-dependence and carefully explaining procedures for its identification and why it

needs to be distinguished from 'crowding' in conservation management. Jo Ridley and colleagues outlined progress towards developing a model for predicting population sizes and regulation in cooperatively breeding groups of birds, using as their test species the endangered Seychelles warbler.

Of the remaining three papers, all reported as orals, William Sutherland and Hanna Kokko dealt with the prediction of bird population responses to novel conditions, such as could arise from environmental change. Henrik Smith and colleagues considered the effects of interference and competition in heterogeneous landscapes, developing a model to predict outcomes with implications for bird monitoring and habitat evaluation. Hanna Kokko and colleagues then carried on the theme of competitive effects in a study of a colonially breeding seabird, the Common Guillemot. Their model of costs and benefits predicts that the frequency of fighting for good nest sites should increase at higher population densities. The abstracts of all three oral papers are published in the Abstract volume for the Congress.

S25-3 Contribution of site-dependence to regulation of population size: evidence and consequences for biological monitoring of populations

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Abstract Site dependence, the pre-emptive use of sites (e.g., breeding territories) that differ in suitability for survival and reproduction, is a little-studied negative feedback mechanism that can potentially regulate population size. Because its operation depends upon heterogeneity among sites, it can operate at both local and landscape scales. Field tests on a population of a parulid warbler (*Dendroica caerulescens*) showed that sites differed greatly in suitability and were occupied pre-emptively. More poor sites were also occupied when population size was large. Because site dependence operates across a range of spatial scales it is difficult to test. The challenges it creates for sampling include the following. First, sampling designs need to include a broad range of the heterogeneity in suitability found among sites. This requires sampling across relevant environmental gradients and terrain (e.g., elevation, moisture, etc.) that are not typically found within small study plots. Secondly, direct measures of site suitability, such as both territory-based measures of food abundance and measures of bird population density and site-specific demography, are required to distinguish site-dependence from other potential regulatory mechanisms such as crowding. Given these sampling requirements, it is not surprising that site dependence, as one of the multiple mechanisms regulating bird populations, remains poorly understood. Nevertheless, knowledge of site dependence and other regulatory mechanisms is essential for understanding avian population dynamics and for the conservation of bird populations.

Key words Site dependence, Sampling design, Habitat heterogeneity, Population regulation, Site demography, Site suitability, Population dynamics, Conservation

1 Introduction

Density dependent negative feedback on demographic rates is essential for population regulation (Murdoch, 1994). Multiple kinds of density dependent mechanisms, however, can generate the feedback necessary to regulate population size or density (Sutherland, 1996; Rodenhouse et al., 1997; Newton, 1998). These mechanisms fall into three classes: (1) those emphasizing the primacy of direct or indirect interactions among individuals (e.g., crowding, territoriality), (2) those generated from environmental heterogeneity (e.g., buffer-effect, source-sink, site-dependence), and (3) those arising from intrinsic differences among individuals, i.e., population structure (see Lomnicki, 1988; Sutherland, 1996; Rodenhouse et al., 1999).

Crowding mechanisms necessarily occur at local spatial scales because they are generated by direct interactions among neighbors (e.g., fighting) or indirectly via increases in nest predation or parasitism as population density increases. In contrast, regulatory mechanisms arising from environmental heterogeneity or population structure can occur across a wide range of spatial scales, from local to landscape. To date, studies of regulatory mechanisms have focused largely upon crowding effects due to interactions among individuals (Dhondt, 1992; Rodenhouse et al.,

1997; Bonsall et al., 1998) or on source-sink processes associated with environmental heterogeneity at regional spatial scales (Robinson et al., 1995; Donovan and Thompson, 2001). The site-dependence mechanism, in particular, has only recently been described (Rodenhouse et al., 1997, 1999, 2000; McPeck et al., 2001) and tested in the field (Rodenhouse et al., 2003).

Regulatory feedback via the site-dependence mechanism does not depend upon intrinsic differences among individuals or upon local interactions among them. Rather, it occurs when individuals pre-emptively use sites that differ in suitability for reproduction and/or survival (Rodenhouse et al., 1997; McPeck et al., 2001). Sites are areas occupied exclusively by individuals or breeding pairs, and species may be considered site-dependent when their reproduction or survival depends on the characteristics or quality of a site. The suitability of sites is typically determined by multiple characteristics, including food abundance, vegetation structure, risk of nest predation, etc. Sites for most bird species would be the breeding and wintering territories that they occupy. Pre-emptive occupancy means that the best sites are occupied first and that site holders are not usually displaced by conspecifics (Pulliam and Danielson, 1991).

Regulation by site-dependence can occur because, as population size grows, the average suitability of the sites occupied declines, reducing average reproductive performance and survival as proposed by Brown (1969), Holt (1985, 1987) and Dhondt et al. (1992). This negative feedback slows and stabilizes population growth (Rodenhouse et al., 1997; McPeck et al., 2001). Conversely, when population size declines, due to catastrophe or low breeding productivity, only the best sites are occupied, which results in higher average demographic rates and leads to population growth. Site-dependence, therefore, has two essential features: (1) environmentally-caused heterogeneity among sites in suitability for reproduction and/or survival, and (2) pre-emptive site occupancy, with the tendency for individuals to select initially or move subsequently to sites of higher suitability as they become available (Rodenhouse et al., 1997). The strength of site-dependent negative feedback, therefore, depends upon the distribution of site suitability, i.e., the proportions of sites of different suitability and how steeply site quality declines from the best to the poorest sites occupied.

We stress that site-dependence is not an alternative to density dependence. Density dependence refers to the negative feedback that can be generated by a variety of mechanisms (Berryman, 1989), and site-dependence is one of those mechanisms (Rodenhouse et al., 2000). We prefer the name “site-dependence” rather than “sequential habitat occupancy” (Newton, 1998) or “habitat heterogeneity” (Both, 1998a), because site-dependence operates at the spatial scale of sites used by individuals or breeding pairs rather than habitats themselves, and because the negative feedback derives not just from heterogeneity among sites but from such heterogeneity combined with pre-emptive use of sites (Rodenhouse et al., 1997). Tests of site-dependence, therefore, need to focus on environmental heterogeneity and pre-emptive use, as well as on the relationship between population size and key demographic variables such as fecundity and survival.

In this paper, we review the evidence from tests of site-dependence, finding growing support for its operation as a regulatory mechanism. We also examine how sampling needs to be conducted to reveal the site-dependence process, as one of potentially several negative feedback processes that may be operating simultaneously to regulate population size (Rodenhouse et al., 1999). The data required to reveal the relative importance of multiple negative feedback mechanisms affecting population size will not be obtained or unravelled easily. We argue, nevertheless, that they are essential for understanding and projecting fluctuations in the size and density of bird populations, and so essential for the monitoring and conservation management of bird populations.

2 Methods

2.1 Study site

The research described here was conducted within the 3 000+ ha Hubbard Brook Experimental Forest (HBEF) in

north-central New Hampshire, USA. The Hubbard Brook valley contains an environmental gradient extending from an elevation of about 250 m to 850 m a.s.l., and is vegetated mostly by northern hardwoods, grading into boreal forests on the north facing slopes and along the ridges (Bormann and Likens, 1979). Research conducted over the past 40 years as part of the Hubbard Brook Ecosystem Study provides extensive information on the ecology of these northern hardwood forests (<http://www.hubbardbrook.org>), including their avifauna (Holmes and Sherry, 2001).

2.2 Study species

We have been investigating the demography of the black-throated blue warbler (*Dendroica caerulescens*) within the HBEF since 1982 (Rodenhouse and Holmes, 1992; Holmes, 1994; Holmes et al., 1992, 1996; Sillett and Holmes, 2002). From 1997 to 1999, we expanded this work to include multiple, spatially separated areas within the HBEF and undertook intensive study of environmental features of individual territories. The black-throated blue warbler is suitable for demographic studies because of the accessibility of its nests in the shrub stratum and because its abundance has been relatively stable in the HBEF, and regionally in New England, over at least the past 30 years (Holmes and Sherry, 2001; Peterjohn and Sauer, 1994). The black-throated blue warbler is a forest-interior species that is considered “area sensitive” (Robbins et al., 1989) and thus of conservation concern.

3 Results

3.1 Evidence for site-dependence in black-throated blue warblers

Based on Rodenhouse et al. (1997), conditions necessary for the operation of site-dependent regulation include: (1) differences among sites in suitability that affect reproduction or survival, and (2) pre-emptive use of sites, i.e., good sites are occupied more frequently or before those of lower suitability. Where these features occur, site-dependent negative feedback must be generated. In association with such feedback, an inverse relationship between population size and variance in demographic rates is also expected, because site-dependent feedback occurs without lowering the performance of individuals on the best sites (Both, 1998a).

Testing directly for site-dependent feedback — a positive relationship between population size and use of successively poorer sites — has its problems because of the difficulty in defining and measuring population size for species distributed across regionally variable landscapes and in multiple habitat types. It is possible, however, to use indices of population size such as density or abundance on plots that include wide differences in suitability to test this relationship; and we present such a measure below. Even so, whether the negative feedback generated by site-dependence is strong enough to regulate population size in the manner observed in the actual population can only be assessed by computer mod-

eling of population processes (Rodenhous et al., 1997; Bradbury et al., 2001) or by density perturbation experiments (Sutherland, 1996; Newton, 1998).

Our studies of black-throated blue warblers revealed pre-emptive use of sites, i.e., sites used only periodically were of lower suitability than those always occupied. Sites used in all three years of the study had 82% greater abundance of caterpillars and spiders clinging to leaves, 47% greater density of deciduous leaves in the shrub layer, and 28% fewer nest predators (Fig. 1). These large differences in the suitability of the sites used would suggest a potentially strong role for site-dependence in population regulation if they were reflected in annual fecundity — the number of young produced per territory per season. Indeed, territories occupied by black-throated blue warblers in all three years produced about twice the number of young per year as those occupied for less than three years (a mean of 4.1 vs. 1.9 young per territory per season; Fig. 2).

We also found evidence of site-dependent negative feedback in an inverse relationship between the total abundance of black-throated blue warblers on all of our study plots and the best predictor of site quality for black-throated blue warblers: mean density of deciduous leaves in the shrub layer (Rodenhous et al., 2003). Leaf density in the shrub layer is the best predictor of territory quality (Steele, 1992)

because it varies less within and among years than food abundance and nest predator density. In summary, we found that black-throated blue warblers pre-emptively used sites that differed in suitability for reproduction and that the suitability of the sites occupied was inversely related to population size, as is expected where site-dependent negative feedback occurs (Rodenhous et al., 1997).

3.2 Evidence for site-dependence in other bird species

Several studies indicate that heterogeneity among sites occupied by breeding pairs contributes to population regulation in other bird species (e.g., Andrén, 1990; Dhondt et al., 1992; Komdeur, 1992; Ferrer and Donazar, 1996). There is also evidence of significant differences in site suitability and pre-emptive use of sites. None of the studies, however, assessed whether the negative feedbacks were strong enough to be regulatory. Blanco et al. (1998) found density dependent clutch size in a population of red-billed choughs (*Pyrrhocorax pyrrhocorax*): mean clutch size decreased as population density increased. Because this pattern was associated with an increase in the variance of clutch size, they attributed it to “habitat heterogeneity” rather than a crowding mechanism. Pre-emptive use of territories was reported by Kruger and Lindstrom (2001a) in a study of the northern goshawk (*Accipiter gentilis*); territories that were occupied earlier and more frequently, i.e., pre-emptively, had larger

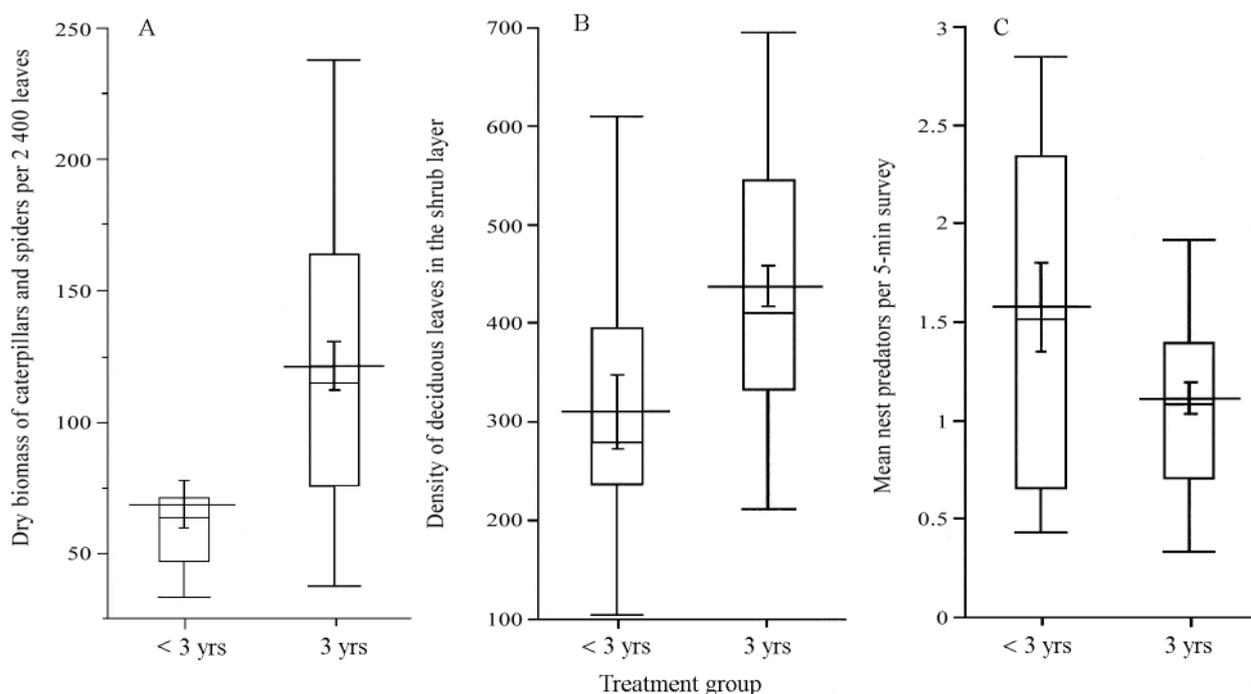


Fig. 1 Environmental characteristics of black-throated blue warbler (*Dendroica caerulescens*) territories within the Hubbard Brook Experimental Forest

These differed between “good” territories, those occupied during all three years of the study (labelled 3 yrs), and “poor” territories, those occupied in two or fewer years (< 3 yrs). Good sites were characterized by significantly (A) more food for Black-throated Blue Warblers (mg dry biomass of caterpillars and spiders/2,400 leaves; Median test, $\chi^2 = 8.37$, $n = 13$, $m = 35$, $P = 0.004$), (B) greater density of deciduous leaves in the shrub layer (t -test, $t = -3.05$, $df = 51$, $P = 0.004$), and (C) lower abundance of nest predators (median number observed per 5 min census; Median test, $\chi^2 = 3.80$, $n = 14$, $m = 37$, $P = 0.05$) (after Rodenhous et al., in review). Box plots depict the mean (horizontal line extending outside of the box), standard error of the mean (short whiskers), median (horizontal line within the box), quartiles (box), and 10 and 90% deciles (long whiskers).

brood sizes. Similarly, in a study of an expanding population of ospreys (*Pandion haliaetus*), Lohmus (2001) found that nest sites closer to foraging areas and near more lakes were occupied first as population size increased. This pattern of habitat selection resulted in greater breeding productivity on these better territories and average productivity declined as population size increased, as would be expected in a site-dependent mechanism.

Alternatively, some studies reported no strong role for site-dependence. Both (1998b) found that female great tits (*Parus major*) seemed to adjust clutch size to changes in population density rather than in accord with habitat heterogeneity. Although an excellent study in many ways, it included no direct measures of habitat heterogeneity (or suitability), and breeding sites within habitats were assumed to be of similar suitability. All differences in clutch size within habitats were therefore attributed to differences among individual females rather than partitioned among individuals and the suitability of their breeding sites. A study of the common buzzard (*Buteo buteo*), however, found that characteristics of individuals, particularly breeding experience, were more important than habitat quality in determining annual fecundity (Kruger and Lindstrom, 2001b).

From these studies, it is apparent that site-dependence

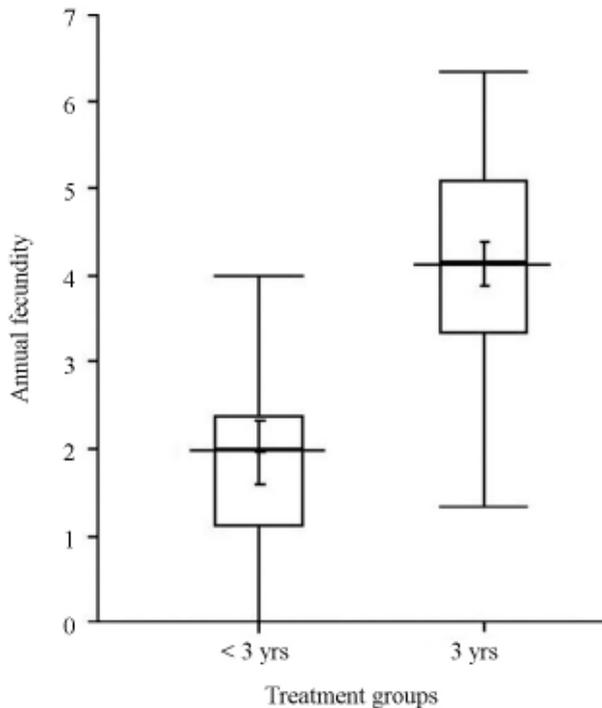


Fig. 2 Fecundity of the black-throated blue warbler (*Dendroica caerulescens*) within the Hubbard Brook Experimental Forest

More young were fledged per pair per year (annual fecundity) on good sites (occupied for 3 years) than poor sites (occupied < 3 years): t -test, $t = -4.94$, $df = 42$, $P < 0.0001$ (after Rodenhouse et al., in review). Box plots depict the mean (horizontal line extending outside of the box), standard error of the mean (short whiskers), median (horizontal line within the box), quartiles (box), and 10 and 90% deciles (long whiskers).

ence operates in some species and situations but not in others; most of the studies tested for this mechanism, nevertheless, have found evidence of it. What is not yet clear is whether any generalizations about its operation are possible. For example, is site-dependence likely to be stronger in some habitats than others (e.g., stronger in habitats with patchy resource distribution) or for some types of birds (e.g., open-cup nesting birds or species with larger territory sizes such as raptors). We suggest that there is not enough evidence yet to make such distinctions. The mechanism, however, warrants further study, in part because the nearly ubiquitous occurrence of extensive heterogeneity among sites creates a potentially strong role for this mechanism. Few studies, however, have tested the site-dependence mechanism explicitly, the primary reasons for which are probably that testing for it requires territory-specific sampling of environmental characteristics and demography at a spatial scale that encompasses a broad range in site suitability, both of which require levels of extensive and intensive sampling that are difficult to achieve in field studies.

3.3 Regulation of population size via multiple mechanisms

All of the recent studies that have tested for site-dependent processes have also assessed the relative importance of multiple negative feedback mechanisms. Except for ours, each of the studies reviewed above (Both, 1998a; Guillermo et al., 1998; Kruger and Lindstrom, 2001a, 2001b; Lohmus, 2001) concluded that one mechanism was predominant. The results for black-throated blue warblers, however, suggest that not only was site-dependence operating but crowding as well. Sillett (2000) found that when the pairs abutting focal territories were removed permanently, the mean number of young fledged annually by pairs experiencing reduced local density was nearly twice that of control pairs. These findings lead us to propose that site-dependence and crowding mechanisms can operate simultaneously because they operate at different spatial scales (Rodenhouse et al., 2003). Crowding operates at the scale of individuals and their neighbors, while site-dependence occurs on a larger (i.e., regional) spatial scale which includes a broad range in site suitability.

Furthermore, it is possible for either mechanism alone to regulate population size. Crowding reduced annual fecundity to only about 3.9 young per pair, which is replacement-level reproduction for this population (Sillett and Holmes, in review), and hence, would eventually halt population growth. Use of poor suitability sites in some years — a site-dependence mechanism — further lowered annual fecundity to 1.9 on the lowest quality sites, which is well below estimated replacement level (Rodenhouse et al., 2003).

3.4 Sampling to reveal site-dependent regulation

Ours is one of few studies reporting multiple negative feedback mechanisms operating within the same population, and this finding was perhaps due to a unique sampling protocol. Hence, we consider here the types of

sampling needed to detect and quantify the operation of site-dependence and other negative feedback mechanisms potentially contributing to regulation of population size or density. The goals of sampling in studies of demography and population regulation are to test hypotheses relevant to specific mechanisms of regulation and to obtain estimates of demographic parameters that can be used in population modeling (Johnson, 1995). The latter is essential for determining whether any negative feedback is strong enough to regulate population density or size.

What variables should be sampled? For detecting site-dependence, those features of the site that affect basic demographic parameters, such as fecundity, survivorship, immigration and emigration should be sampled, as should annual fecundity and survival as well. For our study species, long term monitoring coupled with experiments have revealed that vegetation structure, food availability, predator abundance and weather conditions are the features of sites that most influence reproductive success (Rodenhouse and Holmes, 1992; Steele, 1992; Reitsma, 1990; Sillett et al., 2000). The key environmental features affecting demography, however, are likely to differ among bird species and perhaps locations.

When sampling reproductive performance, it is essential to measure the annual fecundity of pairs (number of young produced per sites per season) and not simply the success of individual nests, for example as given by Mayfield estimates (see Powell et al., 1999; Murray, 2000; Thompson et al., 2001; Nagy, 2002). Sampling only nesting success requires the assumption that the sample of nests is randomly distributed among pairs on sites of different suitability and across the breeding season. Such an assumption is unlikely to be true and is seldom tested.

Quantifying survivorship is essential to parameterize the demographic models needed for testing whether den-

sity dependent feedbacks are strong enough to be regulatory. Estimates of survival for young in the nest, juveniles and adults are needed for population modeling. However, estimating juvenile survivorship for species with extensive natal dispersal, which includes many migrants such as the black-throated blue warbler, is notoriously difficult (Anders et al., 1997; Thompson et al., 1999; Sillett and Holmes, 2002).

Sample size Sample sizes for hypothesis-testing can be determined from preliminary data by examining the power of the test (Zschokke and Lüdin, 2001); and sample sizes should be as large as are needed to minimize the variance of parameter estimates. For example, variance in annual fecundity of black-throated blue warblers was consistently reduced by sampling additional years, even over a 14 year period (Fig. 3). Similarly, relatively large sample sizes are needed to characterize distributions of site characteristics that are often non-normal. For example, distributions of two of the three variables that we used to characterize site suitability for black-throated blue warblers were not normally distributed. The abundance of nest predators on sites (Shapiro-Wilks test, $W_{50} = 0.93$, $P = 0.004$) and the biomass of food for birds (Shapiro-Wilks test, $W_{47} = 0.90$, $P = 0.0005$, for samples of caterpillars and spiders clinging to leaves), were both strongly non-normal.

Because the likelihood of mistakenly classifying a non-normal distribution as normal increases as sample sizes become smaller, it may be necessary to take relatively large samples of sites to correctly describe the distribution of site suitability. We sampled 48 sites to determine the distribution of site suitability as measured by food biomass. When subsamples of 20 sites were selected randomly from this total, only half (5 of 10 subsamples) of the resulting distributions for food biomass could be distinguished from normal, indicating that sample sizes larger than 20 would be necessary to characterize this variable accurately. Precise characterization of the distribution of site suitability is essential because it is the distribution of site suitability that determines the regulatory strength of site-dependence (Rodenhouse et al., 1997; McPeck et al., 2001).

Spatial scale of sampling It is unlikely that the distribution of site suitability will be adequately represented by focusing on small study plots, as is usually done (also Brown, 1969; Watkinson and Sutherland, 1995; Smith et al., 1996). To reveal the full range of site suitability, the sites studied should be selected in a stratified random manner to represent a large portion of the range of environmental conditions used by a population — and this implies measuring “territory” suitability even in some locations and years when a formerly occupied territory, for example, is not occupied. Because of the few studies of site-dependence to date, it is not clear how broad an area must be sampled. Determining what spatial scale is appropriate is extremely difficult for most studies of populations, but especially for migratory bird species that disperse widely across multiple habitat types.

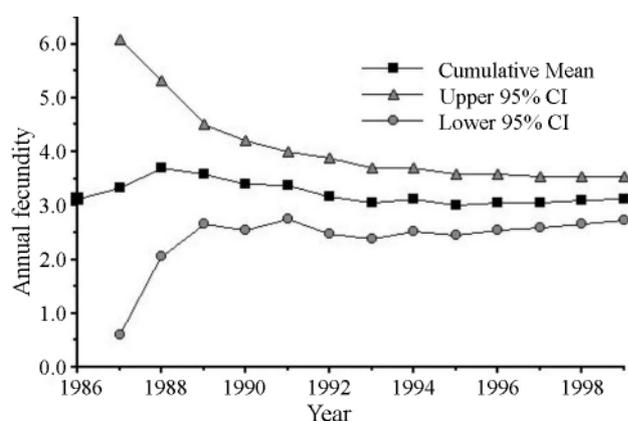


Fig. 3 Variance in mean annual fecundity of black-throated blue warblers (*Dendroica caerulescens*) on the long-term study plot within the Hubbard Brook Experimental Forest

Variance was reduced with each new sample point (year) added to the data set throughout the 14-year sampling period. The means and confidence intervals displayed are cumulative, i.e., each year with a confidence interval includes the data for all years that came before it.

It is likely, however, that the appropriate spatial scales will be influenced by natal and adult dispersal distances which can differ greatly among species. In our study of black-throated blue warblers, we sampled across a 600-m elevational range, representing about 6.5 km distance on the ground, to include as broad a range of site suitability as could be found within the HBEF. We found that this extensive range of conditions was necessary because of disparate trends in suitability as measured by different variables. Food biomass and leaf density on sites, for example, increased from low to high elevation (Fig. 4). Moreover, nest predator abundance on sites differed between low and higher elevations. It is obvious from Fig. 4 that sampling sites at only one of any of the main elevations would have represented variation in site suitability inadequately across the region.

Sampling to detect multiple mechanisms A sampling design that will detect multiple negative feedback mechanisms (e.g., crowding, site-dependence and population structure) is ideal, because some evidence suggests that more than one mechanism may operate in some systems (Rodenhouse et al., 1999, in review; den Boer and Reddingius, 1996). A sampling design allowing this would include a random sample of sites spanning the environmental conditions used by the population. Often it will be convenient to work in study areas rather than on single isolated territories, but if this is done, then the sites sampled should be randomly selected from those available in the

area to avoid the problem of pseudoreplication.

All individuals should be marked uniquely and their ages determined as accurately as possible so that population structure can be monitored and considered in statistical analyses. Crowding-related interactions among neighboring pairs or territorial pairs and floaters can easily be detected by observing the behavior and demographic performance of individuals within much smaller areas (e.g., 10 s of ha) than are needed for sampling site suitability. Hence, it might be profitable to select locations along an environmental gradient (e.g., by elevation or population density) to carry out such measures, so that site specific measures of suitability are made across the full range of sites used when population density is high and low.

Crowding effects may not easily be revealed by monitoring, particularly during short time periods and if the population is tightly regulated. Therefore, density manipulations are helpful and they have been done by enhancing (e.g., Alatalo and Lundberg, 1984; Brawn, 1987) or reducing (e.g., Dhondt et al., 1992; Both, 1998a; Sillett, 2000) density of conspecifics. Indeed, strong inferences of the occurrence and operation of any mechanism can only be achieved with manipulations of the appropriate variables; hence, this should be incorporated into study designs whenever possible. Because of the inherent variability of natural systems, particularly in areas of low suitability, long-term studies in which characteristics of site suitability for marked

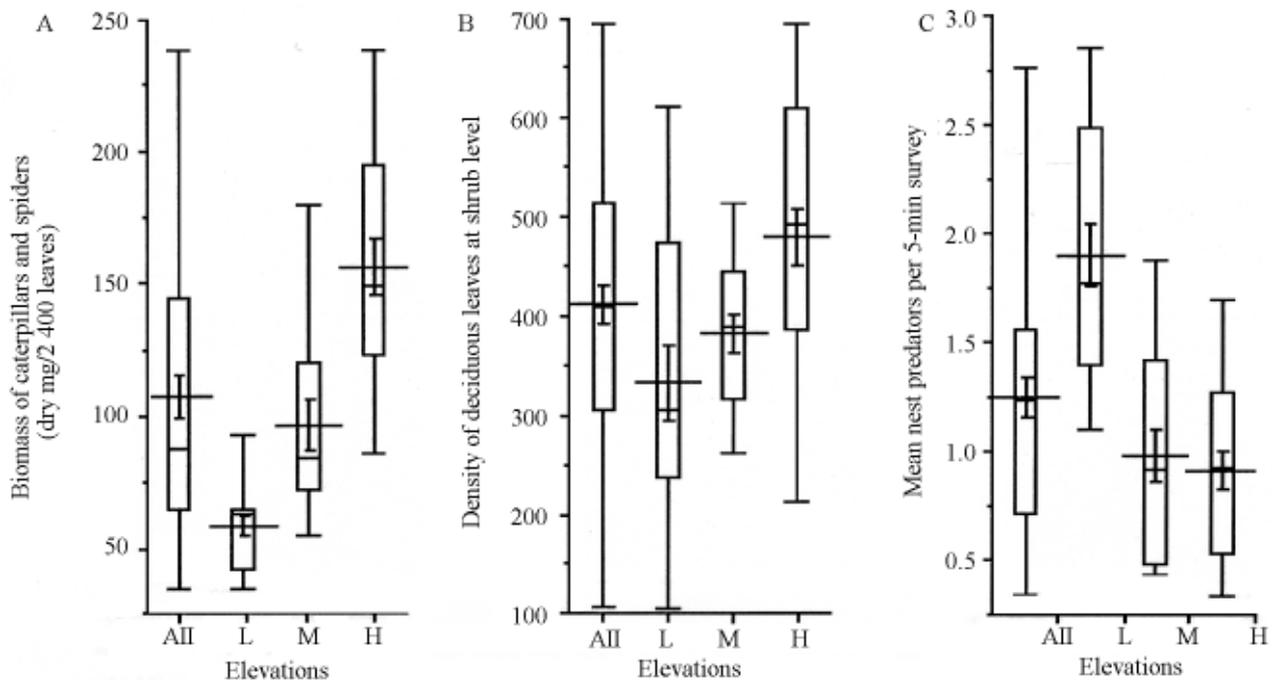


Fig. 4 Environmental characteristics of black-throated blue warbler (*Dendroica caerulescens*) territories along an altitudinal gradient within the Hubbard Brook Experimental Forest

Characteristics differed in means and variability at different elevations: low (L), middle (M) and high (H). In addition, the patterns observed across elevations differed among the variables sampled, where A = dry biomass of caterpillars and spiders per 2,400 leaves, B = density of deciduous leaves in the shrub layer, and C = mean abundance of nest predators per 5-min survey (for methods, see Rodenhouse et al., in review). Box plots depict the mean (horizontal line extending outside of the box), standard error of the mean (short whiskers), median (horizontal line within the box), quartiles (box), and 10 and 90% deciles (long whiskers).

populations and population density are measured will provide the most complete information, allowing time for both monitoring under a range of conditions and experimental manipulation of the study system. Such studies of expanding or contracting populations as those of Lohmus (2001) may be particularly informative.

4 Discussion

Despite extensive study of density dependence (Newton, 1998; Turchin, 1999), the specific mechanisms by which “density” affects demographic rates are not at all clear for most populations. Attempts to reveal these mechanisms must confront many challenges, because numerous factors affect demographic rates, making them highly variable and making multiple density dependent mechanisms possible. Furthermore, these multiple mechanisms may be operating at very different spatial scales. In our study system, we have shown that both crowding and site-dependence mechanisms are in operation, although their relative importance along with other mechanisms is yet to be determined. Moreover, whether the operation of site-dependence, in particular, is widespread is far from clear because of the dearth of tests; most studies to date have not collected the data needed to assess the operation of multiple mechanisms.

To illustrate this point, typical studies of population regulation are much like that of Wiklund (2001) studying the merlin (*Falco columbarius*). This is an excellent long-term study that includes experimental and monitoring components, and provides much insight into population processes in the study species. In particular, population density and survival were found to be food limited, population dynamics were density dependent, and the population expanded into suboptimal habitat whenever population size was large. However, these findings could result from either a crowding or site-dependent mechanism or both. Here the density dependence mechanism(s) underlying population processes in the merlin were not addressed.

In our opinion, it is important to distinguish such mechanisms because the regulatory mechanisms of the population generate its dynamics, determine its equilibrium level and are necessary for making specific conservation recommendations. In site-dependent regulation, the equilibrium population size and dynamics are determined by the distribution of site suitability, e.g., the proportion of sites of highest quality and how steeply site quality declines from best to poorest. Moreover, site-dependence can theoretically regulate population size at levels below habitat saturation (Rodenhouse et al., 1997; McPeck et al., 2001). With a crowding mechanism, in contrast, such limitation and regulation can only occur when suitable habitat is at or near saturation (Murray, 1994; Hixon et al., 2002). Equilibrium in such cases is determined by the total amount of habitat relative to population size, and dynamics are determined by the intrinsic rate of natural increase in the population and the strength of the negative feedback due to crowding.

Differences in how equilibrium in population size and

its dynamics are determined have clear conservation implications. Knowledge that site-dependence is operating focuses conservation efforts on site suitability at the local level and, particularly, on sustaining the suitability of the best sites (Rodenhouse et al., 1999; McPeck et al., 2001). Under a crowding regime, however, the local population is at or near carrying capacity and is performing as well as can be expected. One would expect any improvements in site quality to be countered by crowding-related reductions in performance. Hence conservation efforts should in this case shift toward expanding the total amount of habitat available.

In sum, determining whether one or more negative feedback mechanism is regulating population size or density is key to understanding avian population dynamics and conservation. This is because knowledge of these mechanisms and their interactions helps to clarify how demographic performance is affected by behavioral responses in specific environments (also Sutherland, 1996). Such information allows identification of the environmental variables that are key to managing and conserving species. At present, however, there are too few studies that assess the prevalence or relative importance of the multiple regulatory mechanisms that may be operating. We suggest that only by designing and conducting studies that include site-specific information on suitability and on annual fecundity and survival of marked individuals can site-dependence be adequately tested, evaluated and identified as one of the multiple mechanisms that regulate populations.

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S25-5 Population predictions for Seychelles warblers in novel environments

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Abstract A major challenge for population ecology is to be able to predict population sizes in novel conditions, as in those following habitat loss or translocation. To do this successfully, we show here that it is necessary to understand the behavioral basis of dispersal decisions as they affect fitness. The Seychelles warbler, like many socially complex species, lives in family groups. This leads to the stable usage of sink habitats through kin competition. Sink usage means that bird density is not representative of habitat quality, and consequently that simple extrapolations from current habitat occupancy mis-estimate the effects of habitat loss. Similarly, per territory reproductive success for Seychelles warblers declines with density within a habitat class, in common with many territorial species. This too undermines the use of simple extrapolations to predict the consequences of habitat loss. Retrospective predictions for two actual translocations show some success, while the extent to which they fail emphasizes the need for full understanding of the links between the environment occupied and reproductive success.

Key words Population size prediction, Sink usage, Reproductive success, Seychelles warbler; Habitat quality, Habitat loss

1 Introduction

Many species of birds breed in social groups within which reproduction is unequally shared: 3.2% breed cooperatively (Sibley and Monroe, 1990), and many more breed in groups including either non-breeders or with high levels of reproductive skew (Cockburn, 1996; Heg et al., 2000; Ekman et al., 2001). Species threatened by habitat loss or change include many with socially complex systems (Fitzpatrick et al., 1991; Virkkala, 1991; Walters et al., 2002), producing a demand for population models that can predict the consequences of such threats, and guide conservation management to mitigate them. Existing models of group-living species (e.g., Breininger et al., 1998; Root, 1998; Walters et al., 2002), are based on patterns of dispersal or correlated habitat use. Because dispersal rates are measured in contemporary environments, it is unsafe to assume that they will be the same in modified habitats. This view is reinforced by recent evidence that, for socially complex species, models based on fixed probabilities of dispersal produce far less sensible predictions than those based on optimal dispersal decisions (Stephens et al., 2002).

By 1959, the global population of the Seychelles warbler (*Acrocephalus sechellensis*) had become restricted to Cousin Island where, because the native vegetation had been replaced largely with coconut plantations, only 26–29 birds survived (Komdeur et al., 1998). Since then, the popu-

lation has rebounded from habitat restoration, reaching a plateau of around 320 birds in 1982 (Komdeur, 1992; Komdeur et al., 1998). Translocations of birds to other islands have further improved the prospects of the species. Here we compare the success of different modelling approaches for predicting population sizes for island populations of the Seychelles warbler. First we illustrate why family-based groups and territoriality compromise simple extrapolations for predicting consequences of habitat loss. Secondly, we attempt to predict retrospectively the success of the translocations to Aride and Cousine Islands, and in so doing, demonstrate the significance of interspecific interactions in population predictions.

2 The model

2.1 Seychelles warbler life history

The life history, study site and methodology for the Seychelles warbler study have been covered in detail elsewhere (Komdeur et al., 1995). In brief, the Seychelles warbler is a cooperatively breeding insectivore that is endemic to the Seychelles archipelago and which maintains year-round territories. Territory quality is estimated by the number of leaf insects present, enabling territories to be divided into three categories of quality: low, medium or high (Komdeur, 1992). On Cousin Island, high quality territories are situated in the center of the island, surrounded concen-

trically with medium, then low quality territories on the outer rim (Fig. 1). Territorial groups typically comprise a dominant pair (henceforth “breeders”), together with some retained offspring, 88% of which are female (Komdeur, 1999). Retained females (henceforth ‘helpers’) alloparent and achieve a minor share of reproductive success (Richardson et al., 2001). Retained males rarely alloparent, 78% of them queuing to acquire a breeding position on either natal or adja-

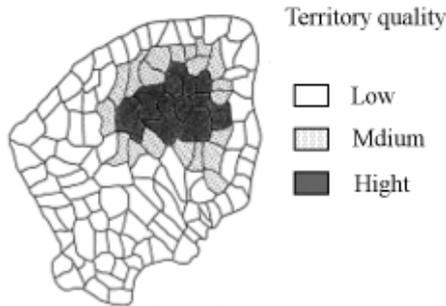


Fig. 1 Map of Cousin Island (29 ha) showing the distribution of high, medium and low quality territories of the Seychelles warbler

From Komdeur (1992).

cent territories upon the death of the male breeder (Komdeur and Edelaar, 2001a).

2.2 Model structure

The structure of the model employed is detailed elsewhere (Ridley and Sutherland, 2002; Ridley et al., 2003). Because our aim here is to analyze the potential of the model to guide conservation management, rather than validate its methodology, we include only a summary of key features useful for understanding its output. The model is individual- and fitness- based: individuals hatch, have one or more opportunities to disperse, possibly to become breeders, and finally die (Fig. 2). Survivorship and fecundity are determined directly by empirical measures (Ridley et al., 2003). Survivorship varies with habitat quality only (Komdeur, 1992), whereas fecundity varies with both habitat quality and group size, being highest at intermediate group sizes (Komdeur, 1994). Dispersal, by contrast, is determined only indirectly by empirical data: it occurs when so doing increases individual fitness.

Fitness is estimated as lifetime reproductive success, weighted firstly to account for kin competition among

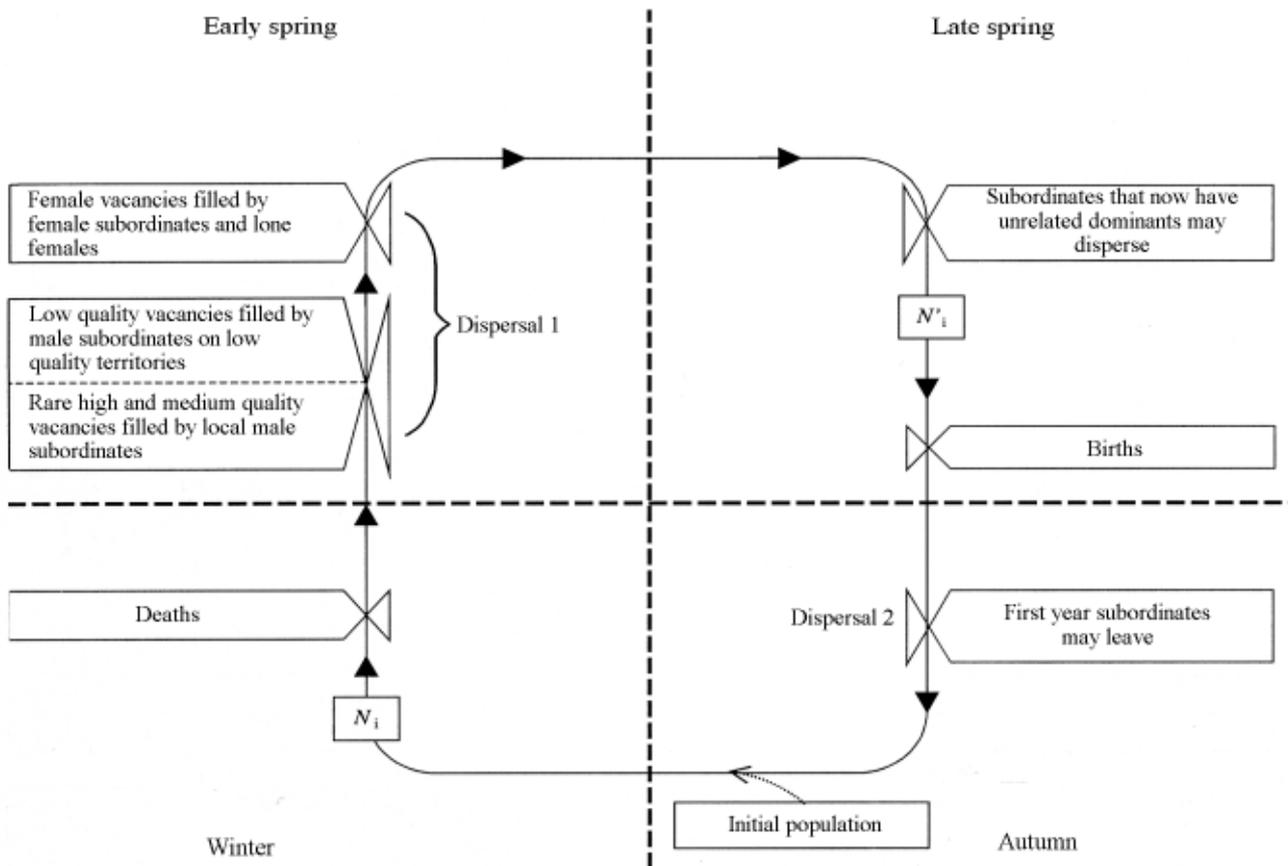


Fig. 2 Summary of key features incorporated in the model for population size prediction in the Seychelles warbler

Death: appropriate to territory specific survivorships (Komdeur, 1992). Dispersal 1: vacancies filled by randomly selected helpers, queuers or floaters from a pool of all those whose fitness would be increased by the move. Eviction: helpers and queuers leave territories following the establishment of a new male breeder, moving to either the best available breeding vacancy, or if none, to become floaters. Breeding: according to territory quality (Komdeur, 1992) and number of helpers (Komdeur, 1994; Ridley et al., in review), sex ratios (Komdeur et al., 1997), rates of cuckoldry (Richardson et al., 2001) and co-breeding (Richardson et al., 2002). Dispersal 2: yearlings dispersed, either to the best breeding vacancy, or failing this, as floaters.

queues (Ridley and Sutherland, 2002) and secondly to account for density dependent changes in per territory reproductive success. It is assumed that kin competition arises among those male subordinates that queue on better quality territories because longer queues depreciate the reproductive value of future offspring. Density dependence in territory quality occurs because territories are larger, and the cost of their defence lower, when there are fewer birds in a habitat.

3 Results

3.1 Predicting effects of habitat loss on population size

Our model is contrasted first with two simpler approaches for predicting the consequences of habitat loss on population size. The first approach assumes that current group sizes would remain unchanged by habitat loss. High quality territories on Cousin Island at present hold 3.7 birds, medium 2.9 birds, and low 2.4 birds (Komdeur, 1992). Where dispersal is based on fitness maximization, a progressive removal of high and medium quality habitat should lead to falling group sizes in low quality habitat until hatchings and deaths are in balance. In contrast, the assumption that group sizes stay constant leads to markedly high population predictions, with hatching and death rates out of balance (Fig. 3).

A second, more sophisticated approach predicts the consequences of habitat loss on the basis of current rates

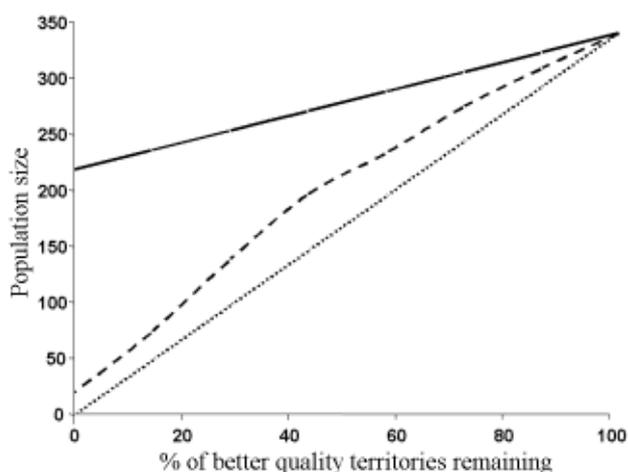


Fig. 3 Three predictions for the progressive removal of high and medium quality habitat for populations of the Seychelles warbler on Cousin Island

If habitat occupancy, or equivalently, habitat specific group-sizes are assumed to be constant and independent of habitat loss (solid line), a markedly larger population size is predicted than if dispersal, and thus habitat occupancy, is determined by attempts to maximize individual fitness (dashed line). If hatching and death rates are assumed to vary with density, consistent with observed data (Komdeur, 1996) and the rate of increase, the low quality habitat on Cousin Island is a pseudosink (Watkinson and Sutherland, 1995). Accordingly, the assumption that habitat specific hatching and death rates are density independent overestimates the consequences of removing the better quality habitat (dotted line).

of hatching and death. According to it, no population will survive once all high and medium quality habitat is lost because on Cousin Island, at present, hatching rates are lower than death rates in low quality habitat. As density falls, however, territory sizes increase and so does the per territory reproductive output (Komdeur and Edelaar, 2001b), in common with many territorial species. If this increase is incorporated, as it is in our fitness maximizing model, the effect is sufficient to lift hatching rates above death rates such that lifetime reproductive success is above one in low quality habitat. In these circumstances, the population would persist at a lower density than at present (Fig. 3), but above the zero level that a simple extrapolation from current hatching and death rates suggests (Fig. 3).

3.2 Predicting effects of translocation on population size

In 1988 and 1989, birds were translocated from Cousin Island to Aride and Cousine Islands respectively. Beforehand, habitat quality on Aride and Cousine had been measured by insect density, a procedure found successful for identifying habitat on Cousin Island (Komdeur, 1992). Territory sizes average 250 m² on Cousin Island, and this, together with the insect density data, was used to estimate the potential number of high, medium and low quality territories on Aride and Cousine Islands (Table 1). We then ran the Cousin model for Aride and Cousine by altering the number of territories appropriately. For Cousine, the model prediction was reasonably good, whereas for Aride it underestimated true population size (Fig. 4).

4 Discussion

4.1 Sink usage and despotism compromise simple predictions

In territorial systems, density dependence may arise in two ways: intraspecific competition can effect falls in total reproductive success across territories or move individuals into poorer habitats and delay breeding. Seychelles warblers show evidence of both (Komdeur, 1992; Komdeur and Edelaar, 2001b; Ridley et al., 2003). In the case of the first, some territories will offer lifetime reproductive success of more than one because they are the only territories that can sustain groups (Kokko and Sutherland, 1998). For a population to be in equilibrium, individuals that produce more than one replacement must be counterbalanced by others that produce less: either they do not breed or they

Table 1 Territory numbers by habitat quality on the Seychelles islands of Cousin, Cousine and Aride, as used in the model

	Territory quality		
	High	Medium	Low
Aride	128	72	72
Cousin	14	20	89
Cousine	15	44	45

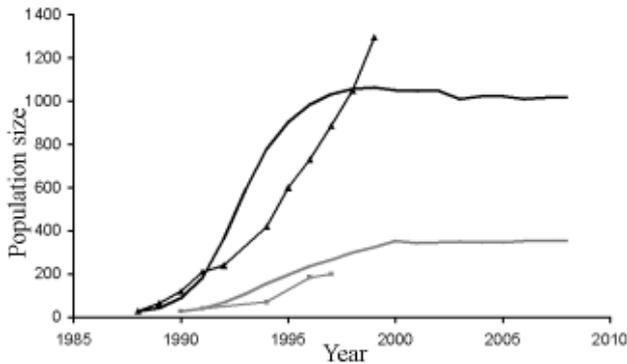


Fig. 4 Observed (lines with triangles) and model-predicted population sizes for Aride Island (black lines) and Cousine Island (grey lines)

While the prediction for Cousine is close, that for Aride is an underestimate.

breed in sinks.

The low quality territories on Cousin Island are sinks; and given that many group-systems are founded on the family (Cockburn, 1998), and that kin competition appears to be an almost inevitable consequence (Ridley and Sutherland, 2002), sink usage will probably prove to be a widespread form of regulation in communal-living species. Where sinks are used, the densities of individuals are not representative of habitat quality. This undermines the use of both habitat quality indices (e.g., Burgman et al., 2001) and the matrix-type models based on field estimates of dispersal rates (e.g., Breininger et al., 1998; Root, 1998; Walters et al., 2002) for predicting habitat occupancy in novel environments. The only systems for which these approaches are valid are (1) those where there is no kin competition, and (2) those where dispersal is 'free' (*sensu* Fretwell and Lucas, 1970) and individuals cannot restrict one another's access to resources. It is only in the absence of both despotism and kin competition that population density is directly proportional to resource abundance alone. Because Seychelles warblers are subject to both despotism and kin competition, simple extrapolations fail to predict the consequences of habitat loss on population size.

4.2 Sinks can be pseudosinks

At low population densities, space is not limiting and the costs of territorial defence are lower. As a result, per territory reproductive success is higher at low densities, and on Cousin Island implies that the low quality territories are pseudosinks (*sensu* Watkinson and Sutherland, 1995). Using a restricted definition, Hunt and Law (2000) argue that territorial populations are 'not necessarily' subject to density dependence, while White (2001) argues that they are 'not' at all. In effect, they advocate the Ideal Despotism model (Fretwell and Lucas, 1970), whereby territorial systems comprise a fixed array of territories of fixed quality. White (2001) thus argues that any changes in density are correlates, and not causes of declines in mean fitness.

The Seychelles warbler bears all the hall marks of a

highly despotic species: there is high variance in fitness both within (Richardson et al., 2001) and among habitat types (Komdeur, 1992), and subordinates typically leave their natal territories following the establishment of a new breeder (Komdeur, 1999). That territory quality is density dependent in the Seychelles warbler, under any definition of the term, and also in other systems (Stamps, 1990; Calsbeek and Sinervo, 2002), suggests that this phenomenon is widespread. Thus Ideal Despotism models of territorial systems are not sufficient to model their population dynamics. Adopting the view that territorial populations are simply limited by resources will overestimate the dangers posed by habitat loss (Fig. 3). It will also overestimate the benefits of resource supplementation because a proportion of the additional resources will be spent on intra-specific fighting.

4.3 Predicting consequences of translocations

Our results show that predicting the size of populations following such substantial change as translocation remains a challenge. With hindsight, it is possible to identify at least two reasons why our modelling approach worked for Cousine but not Aride Island.

First, the model, though complex, is still a single species model and overlooks the roles of predation and parasitism. The Seychelles fody (*Foudia sechellarum*) is a significant egg stealer (Komdeur and Kats, 1999) on Cousin Island, and its presence on Cousine (29.4% eggs lost, $n = 17$) but not Aride (0% eggs lost, $n = 23$) is a likely cause of the differential success in predicting the population sizes for these two islands.

Secondly, the model for Cousin Island classes habitat into three types: high, medium and low quality. Territories in high quality habitat have more than 3 000 insects per m^2 of leaf area, with a maximum of ca. 4 500. However, while the maximum recorded on Cousine Island is similar to that on Cousin, it is ca. 12 000 on Aride. As a consequence, reproductive success is higher on Aride than on either of the other islands, such that on Aride there is nonstop breeding in super-quality territories (Komdeur, 1996). On Aride, moreover, 2-egg fully fertile clutches are the norm compared to mostly single-egg, partly fertile clutches on Cousin and Cousine. To predict population sizes accurately after major habitat change, the relationship between fecundity and resource availability will have to be understood and incorporated.

Thirdly, habitat on Aride Island is altogether different from that on Cousin or Cousine Islands, and has a much more complex vegetational structure. As a result, insect-density profiles are unlikely to yield a true representation of territory size and quality for the Seychelles warbler.

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Symposium 26 How birds sing

Introduction

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Birds possess a highly sophisticated communication system in the form of vocal signals. In recent years, the question of how these signals are produced has gained increasing attention. Intrinsically, this question is of great interest: how do birds produce their sometimes amazingly complex and varied vocalizations? Extrinsically, the question is highly relevant to other aspects of vocal communication. Thus, if one wants to understand the neurobiology of song and song learning, insight is needed as to how neural activity is translated into vocal signal. If, moreover, one needs to understand why particular vocalizations or vocal traits are correlated with singer quality, knowledge of causal links between physiology, morphology and sound production in the singer is essential.

Until recently, theories and models concerning the way birds vocalize were based on indirect evidence from analyses of the structure of vocalizations and inferences from syrinx morphology, combined with insights from physics. A major stumbling block to testing the models lay in the impossibility of examining sound production in a vocalizing bird because experimental interference prevented birds from singing. New technologies, however, now en-

able direct measurements of the processes occurring within an actively singing bird - an important and exciting breakthrough. Combined with data from increasingly sophisticated analyses of vocal signals, the ideas about how birds sing has changed rapidly. Several traditional hypotheses on vocal production have been proven wrong, and new ones are emerging. These concern, inter alia, such issues as the contribution of left and right halves of the syrinx to song production, the role of lateral labia rather than medial tympaniform membranes as prime sound sources, the role of vocal tract resonance in modulating the sound, and the discovery of nonlinear processes involved in sound production.

This symposium updates our understanding of vocal production in birds, bringing together studies on both songbirds and non-songbirds. The contributions deal with the mechanisms involved in sound production and add insights into how birds sing, demonstrating that knowledge about sound producing mechanisms can provide new perspectives on the function and evolution of vocalizations and, at the same time, raise new questions.

S26-1 Respiratory dynamics and syllable morphology in songbirds

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Abstract Song in birds is produced as air flows past the vibratory structures of the syrinx typically during expiration. Whereas there is detailed information about bilateral syringeal contributions to sound production, little is known of the interactions of air sac pressure and airflow, and how these affect sound frequency and sound amplitude. We studied air sac pressure and airflow during song in brown-headed cowbirds, cardinals and zebra finches, three species with acoustically dissimilar songs. Results revealed no consistent relationship between air sac pressure and airflow during song syllables with different acoustic structure, suggesting that adjustments in syringeal resistance play an important role in airflow regulation. In cowbirds and zebra finches, high frequency sounds were produced with higher air sac pressure. In these same species, sound amplitude appears to be greater for high than low frequency sounds, suggesting greater efficiency in transforming fluid dynamic energy into acoustic energy.

Key words Air sac pressure, Airflow, Sound frequency, Sound amplitude, Acoustics

1 Introduction

Singing in birds is an acoustic behavior important for male-male and male-female communication in a reproductive context. In songbirds, learning plays a major role in song development, which is thought to enhance information content about the fitness of the sender and is therefore involved in sexual selection (e.g., Nowicki et al., 2002). A first step towards understanding the evolution of song is to explore physiological requirements for song production and possible physiological constraints on temporal and acoustic patterns of song.

Song is typically produced during a series of expiratory pressure pulses, which generate airflow past the vibratory structures of the vocal organ, the syrinx. The songbird syrinx consists of two independently controlled sound sources, creating the potential for greater acoustic complexity of song than is possible with only one source. The variable use of the bi-partite syrinx to enhance vocal complexity has been analyzed by recording physiological information about the contributions of both syringeal halves to song (Suthers and Goller, 1997).

Songbird species use their two independently controlled sound sources in various ways, presumably to enhance different aspects of song complexity. These uses range from simultaneous generation of different sounds (two-voice) to alternating emissions between the two halves, either to increase frequency range or to generate a pattern of alternating low and high frequency syllables. For example, song in brown-headed cowbirds consists of a sequence of 3–4 expiratory pulses separated by mini-breaths. The first 2–3 pulses generate notes that alternate between low-fre-

quency left-side generated (450–1 100 Hz) and higher frequency right-side generated (1 000–4 500 Hz) notes. Syllables of very high fundamental frequency (6–12 kHz), generated entirely on the right side of the syrinx, end the song (Allan and Suthers, 1994). In cardinals, song consists of sequences of repeated syllables, and each individual bird may have repertoires of 6–16 syllable types. Most syllables are either frequency upsweeps or downsweeps. Frequencies below approximately 3.5 kHz are generated by the left side of the syrinx and higher frequencies by the right, such that a syllable covering a wide frequency range is generated by sequential use of both sides (Suthers and Goller, 1997).

Despite this detailed information on syringeal contributions, very little is known about how air sac pressure and syringeal airflow relate to sound frequency and sound amplitude. Where syllables are repeated, the sound amplitude of a syllable typically increases as air sac pressure and airflow increase (e.g., Gaunt et al., 1973; Suthers and Goller, 1997). However, it is not known whether this relationship also applies to different syllables with different frequency components. We investigated the relationship between air sac pressure and airflow for sounds of different acoustic characteristics in three songbirds whose songs vary widely in syllabic structure. The results indicate a general relationship between the frequency and amplitude of syllables that cannot be explained simply by airflow or air sac pressure conditions.

2 Methods

Experiments were performed on three adult males of

each of the following three species: brown-headed cowbird (*Molothrus ater*), cardinal (*Cardinalis cardinalis*) and zebra finch (*Taeniopygia guttata*). Vigorously singing birds were selected from a holding aviary and isolated in a small cage. There they were fitted with an elastic belt around the thorax and tethered to a counterbalance arm, which permitted free movement within the cage and compensated for any additional mass added during the experiment. Once birds resumed singing, surgical implantation of the flow transducer and air sac cannula was performed under isoflurane anesthesia. The specific procedures are described in detail in Hartley and Suthers (1989) and Suthers et al. (1994), so only a brief summary is given, as follows.

A cannula was inserted into a thoracic air sac through a hole made into the body wall below the last rib and sutured in place. The free end of the cannula was routed to the back, where a piezoresistive pressure transducer (Fujikura FPM-02PG) was mounted on a Velcro tab on the elastic belt. Tracheal airflow was measured with a miniature thermistor bead implanted into the base of the trachea right above the syrinx. A small hole was made into connective tissue between two tracheal cartilaginous rings through which the thermistor was inserted, such that the bead was centered in the tracheal lumen. The flow probe was sutured to a tracheal ring, and the wires were routed subcutaneously to

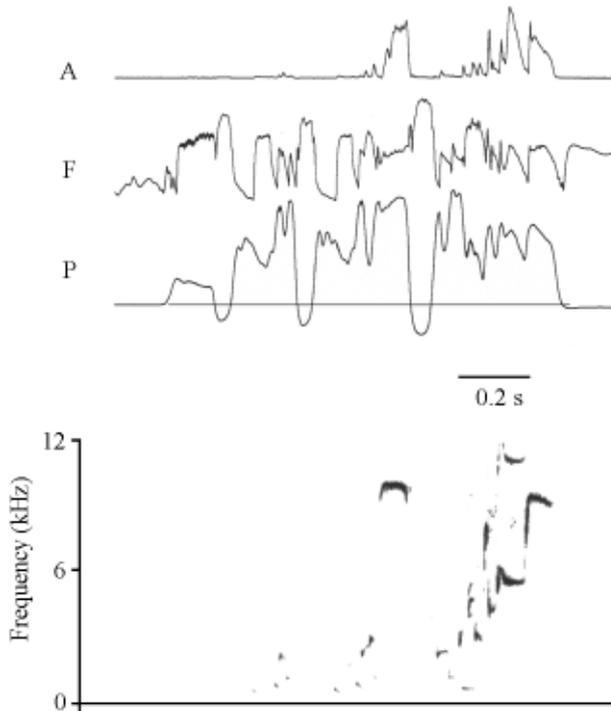


Fig. 1 Typical example of a cowbird song showing simultaneously recorded motor patterns and vocal output

Top panel: A = rectified and integrated oscillogram, F = tracheal airflow, P = subsyringeal air sac pressure pattern; bottom panel: spectrogram. The first expiratory pressure pulse results in almost inaudible sound despite the high airflow. At the beginning of expiratory pressure pulses 2 and 3, both sides of the syrinx are closed (no airflow). The significance of this silent period is not understood.

the back. Stronger wires led from the backpack to signal conditioning equipment. Airflow was determined as the voltage needed to maintain the thermistor bead at approximately 60°C (Hector Engineering). The voltage is nonlinearly proportional to airflow. Airflow data were not calibrated, so all comparisons are based on relative voltage changes.

Song was recorded with a microphone (Audiotechnica AT8356) placed approximately 30 cm from the bird. Airflow, air sac pressure and acoustic data were recorded on different channels of a multi-channel data recorder at 25 or 40 kHz sample rate (TEAC 135T or Metrum Information Storage, model RSR 512) and later played into a computer at 40 kHz per channel (Data Translation 2821G) for analysis with Signal software (version 3.1; Engineering Design). Segments of acoustic syllables with relatively constant fundamental frequency were chosen, and average air sac pressure, tracheal airflow and sound amplitude were calculated for these segments. In cardinals, short frequency sweeps were used in their entirety

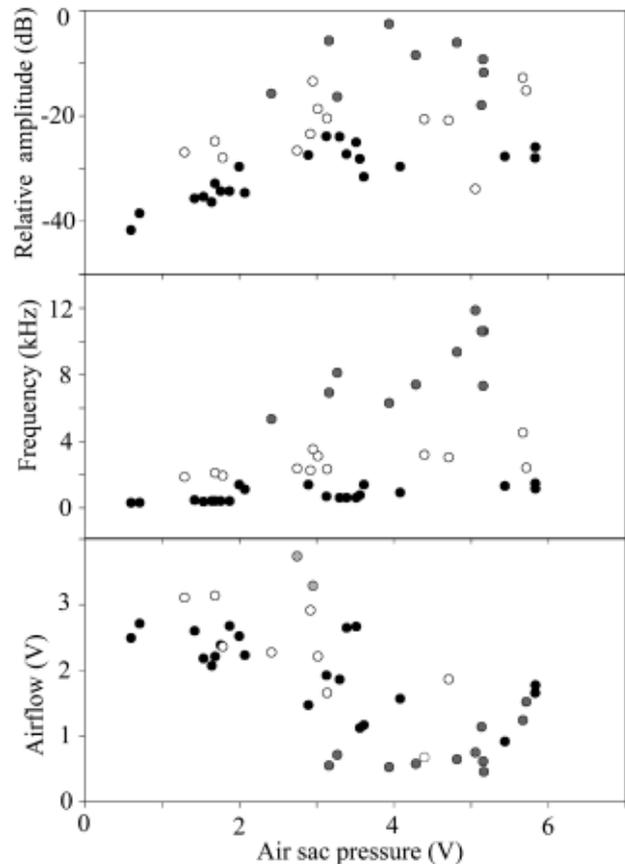


Fig. 2 Relationships between air sac pressure, airflow, and sound frequency and amplitude in cowbird song

The relationships are not simple. Mean values are plotted for individual notes in the introductory note clusters according to the side of the syrinx on which they are produced: left = black circles, right = open circles. All notes in the final whistle (gray circles) are produced on the right side. Side of production was inferred from Allan and Suthers (1994). The only two-voice segments are characterized by the highest airflow (light gray circles in the bottom panel). Data represent measurements taken from 3 songs of each of 3 song types sung by one individual.

to calculate average values for all measured parameters. The measurements were then analyzed for relationships between the various physiological and acoustic parameters.

3 Results

Patterns of airflow and air sac pressure, and corresponding acoustic parameters, are illustrated in cowbird song in Fig. 1. Airflow during inspiration is higher than during phonation, which occurs during the expiratory phase. Airflow during various parts of the song also varies and does not follow air sac pressure. This pattern is clearly illustrated by quantitative analysis in Fig. 2.

3.1 Air sac pressure and airflow

The relationship between air sac pressure and airflow varied between the three species. Whereas there was a general increase in airflow with increasing air sac pressure in cardinals and zebra finches, cowbirds showed an overall weak declining trend (Figs. 2–4). As expected, the rate of airflow during two-voice syllables, in which both sides of the syrinx are phonating, is high compared to unilaterally produced syllables, when one side of the syrinx is closed (Suthers, 1999; Suthers and Goller, 1997). In all cases,

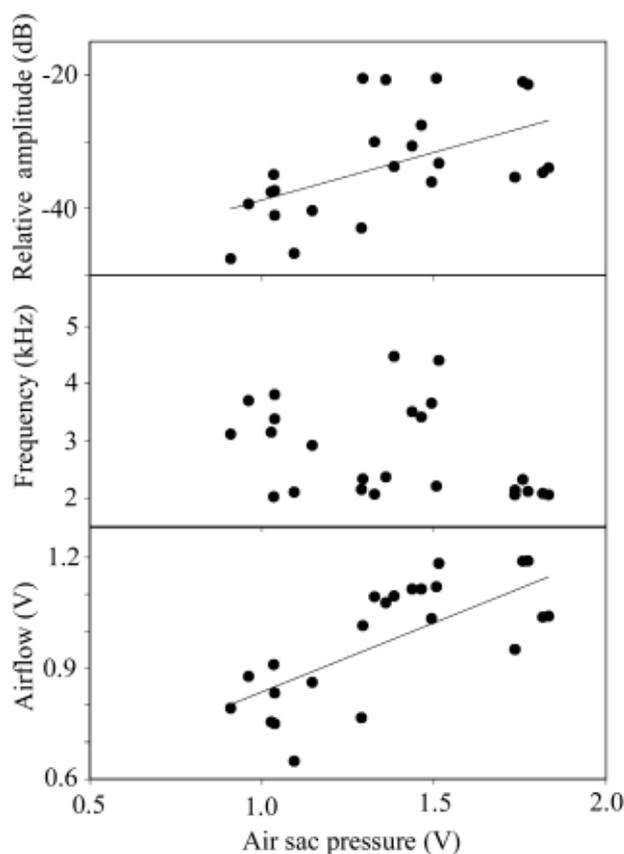


Fig. 3 Relationships between air sac pressure, airflow, and sound frequency and amplitude in cardinal song Air sac pressure and airflow show a positive relationship ($r^2=0.49$), although sound frequency is not tightly correlated with air sac pressure in this individual. Amplitude generally increases with increasing air sac pressure ($r^2=0.28$). Data points represent measurements from 7 syllable types of one individual.

however, there was substantial variation in the pressure/airflow relationship between syllables with different acoustic structure.

3.2 Air sac pressure, airflow and frequency

The air sac pressure/flow relationship varied with the fundamental frequency of the sound in all three species. High-frequency sounds in the zebra finch and the final whistle in the cowbird were produced with higher air sac pressure than low-frequency sounds. Despite higher air sac pressure, airflow during high-frequency sounds was nevertheless generally lower than during low-frequency sounds (Figs. 2, 4). In cardinals, airflow tended to increase with air sac pressure, and in one individual it also increased with increasing fundamental frequency of sonation.

3.3 Frequency and sound intensity

Sound intensity can only be estimated from our recordings because orientation of birds towards the microphone may have varied during and between songs. However, the amplitude of high frequency syllables was 15–25 dB greater than for low-frequency sounds in all three species. Such a difference in amplitude cannot be attributed to higher airflow; but high-frequency sounds are typically associated with high air sac pressure.

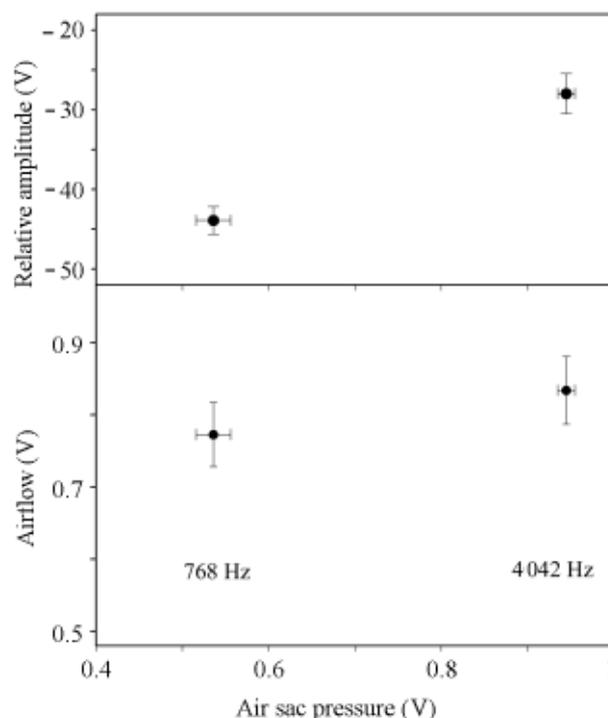


Fig. 4 Relationships between air sac pressure, airflow, and sound amplitude in zebra finch song

High-frequency syllables are generated with higher air sac pressure than low frequency syllables, but airflow is similar for both (Means $\pm 1 SE$; bottom panel numbers indicate the mean frequency of included sound segments). The amplitude of high frequency sounds is substantially greater than that of low frequency syllables. Values include data from 3 motifs of each of three individuals.

4 Discussion

The inconsistent relationship between air sac pressure and airflow indicates a complex regulation of airflow by adjustments of airway resistance. The most likely structures involved in regulating airflow are the syringeal valves. The presence of two independently controlled labial valves probably allows more elaborate regulation of airway resistance. However, because no clear relationship was apparent for most individuals, even for unilaterally generated sounds, a complex interplay of sound characteristics must be postulated to account for the absence of direct dependence between air sac pressure and airflow.

A possible explanation lies in the amplitude of labial movements during low versus high-frequency vibrations. High frequency sounds are generated with more tightly adducted labia and smaller amplitude movements of the vibrating labia than low-frequency sounds (Goller and Larsen, unpubl. results). Increased activity in the gating muscles during high-frequency sound is consistent with this interpretation (Goller and Suthers, 1996). The evidence together suggests that syringeal resistance is higher for generation of high-frequency sounds.

The frequency dependence of sound intensity is somewhat surprising. In all species, and particularly zebra finches and cowbirds, high-frequency sounds were substantially greater in amplitude. Greater amplitude occurred even though airflow was consistently lower than for low frequency syllables, despite high air sac pressure. This suggests that the small aperture associated with high syringeal resistance enables the vibrating labia to convert more of the fluid dynamic energy in the expiratory air stream into acoustic energy, increasing the efficiency of producing high frequency over low frequency vocalizations. It is also possible that the filtering properties of the upper vocal tract generally favor higher frequencies. In cardinals, for example,

low frequency sounds are sung with very little opening of the beak. When the beak is held open experimentally during song, the fundamental frequency of low-frequency sounds is drastically reduced in amplitude relative to upper harmonics (Suthers and Goller, 1997).

It appears that production of low frequency sounds at high intensity may be difficult for songbirds within the size range of the species used in this study. Although the lowest fundamental frequencies of zebra finch song are exceptional for a small bird, the harmonic content of the radiated sound is shifted upward in favor of higher harmonics.

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S26-2 Bilateral motor skills in domestic canary song

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Abstract Songbirds may exhibit varying degrees of lateral syringeal dominance during song production. In the canary (*Serinus canaria*), the contributions that each side of the syrinx make to song can vary according to strain and individual abilities. Common domesticated, border and wild strains all sing complex syllables which appear to be produced by both sides of the syrinx. Using copulation solicitation displays (CSD) as the index of female preference in domestic canaries, we demonstrate that some complex syllables sung repetitively (“A” phrases, at $\geq 16/s$) have clear behavioral significance during inter-sexual encounters. Moreover, male receivers may discriminate among conspecific song phrases; and “A” phrases are also used in intra-sexual communication. No strong syringeal lateral dominance was found when airflows, air sac pressures and sound production in the left and right bronchi were monitored in domestic males singing with both sides of the syrinx and vocal tract intact. We also confirm that “A” phrases of wide bandwidth (roughly 4 kHz) and sung at high repetition rates involve bilateral sound production. Unilateral bronchial plugs and nerve cuts reduced syllable complexity drastically, regardless of which side remained intact. Taken together, these data demonstrate that bilateral sound production is commonly used in the domestic canary, increasing phonetic and temporal complexity, two acoustic features of song that are important in inter- and intra- sexual communication.

Key words Bird song, Syrinx, Domestic canary, Neural lateralization, Vocalization

1 Introduction

In songbirds, the duplex structure of the tracheo-bronchial syrinx controls sound production independently on each side, thereby significantly increasing the flexibility of vocal production and the potential complexity of song. In some species, both sides of the syrinx contribute about equally to most of the song components. Conversely, Wasserschläger canaries exhibit a clear unilateral left dominance (Nottebohm and Nottebohm, 1976; Hartley and Suthers, 1990). Even though motor programs are sent to each side of the syrinx, the right side often remains silent in this strain (Suthers and Goller, 1997).

Other domestic, border and wild strains of canaries (*Serinus canaria*) frequently sing complex syllables that appear to be produced by both sides of the syrinx. Using the copulation solicitation display (CSD) as an index of female preference, we showed that at least some of the complex syllables, the “A” or so-called “sexy” phrases sung at high repetition rates ($\geq 16/s$), had a clear behavioral significance during social encounters, especially for attracting domestic and Wasserschläger females (Vallet and Kreutzer, 1995; Vallet et al., 1997, 1998; Leitner et al., 2001). Recent experiments demonstrate that domestic females, whether raised in the aviary or acoustic isolation, prefer supernormal computer-edited phrases that maximize both the syllable rate and the frequency bandwidth of complex syllables (Draganoiu et al., 2002). Moreover, we found that male re-

ceivers may discriminate among conspecific song phrases, and that “A” phrases are used for intra-sexual communication as well (Parisot et al., 2002). Taken together, these data are consistent with the hypothesis that special complex syllable types might be a reliable index of male quality.

To assess the contribution made by each side of the syrinx to different types of syllables, and to study the motor constraints involved in producing simple and complex syllables in domestic canaries, we (1) examined the vocal ability of birds forced to sing on one side of the syrinx, and (2) monitored physiological correlates of phonation in birds singing with an intact vocal system (Suthers et al., 2001).

2 Materials and methods

To compare the properties of song produced on each side of the syrinx, the song repertoires of 8 adult male domestic canaries (*Serinus canaria*) were recorded before and after one side of the syrinx was surgically disabled by occluding one bronchus. Birds were anesthetized with chloropent (4.0 $\mu\text{l/g}$, i.m.). The syrinx was exposed through a midline ventral incision in the interclavicular air sac and dental impression medium (Kerr, Light bodied permalastic) was injected into one primary bronchus a few rings below the syrinx and held in place by a droplet of tissue adhesive (Vet Bond). Four birds were injected in the left bronchus and the other four in the right. This bronchial plug abolished phonation in the ipsilateral side of the syrinx by pre-

venting air from flowing through it. The interclavicular air sac was then closed and the birds allowed to recover.

Birds with unilateral bronchial plugs began to sing several days after surgery. Their post-plug song was recorded for several days to obtain a post-plug repertoire. After the full repertoire was recorded, the tracheosyringeal branch of the hypoglossal nerve on the plugged side was sectioned to paralyze the ipsilateral syringeal muscles. This was accomplished by anesthetizing the birds and making an incision in the neck over the trachea, midway between the glottis and syrinx. A section of the tracheosyringeal nerve about 3 mm long was removed on the side with the bronchial plug, which was not disturbed. The incision was then closed; and the birds often began to sing within a day or two after surgery.

Song was recorded with a Marantz PMD 20 cassette recorder and condenser microphone (LEM Industries, model EMU 4535). Birds were exposed to long day periods (16L8D) in individual cages in an aviary in visual and auditory contact with other canaries. The song repertoire of each individual was recorded before the bronchial plug (intact or control), after the bronchial plug but before the ipsilateral nerve cut (post-plug), and after the ipsilateral nerve was cut (post-cut). Prior to and after both surgical treatments, song was recorded for at least two 15 min recording sessions each day for about one week. More than 80 songs, each at least 0.7 s in duration, were recorded from each individual. Recorded songs were digitized at a sample rate of 22 kHz (16 bits) using SoundEdit 16 version 2 software (Macromedia). Minimum and maximum frequencies, the duration and syllable repetition rates were measured with cursors for each syllable type from the spectrograms. Syllable types were identified by visual inspection of the spectrograms.

In three canaries, the syrinx was exposed under anesthesia and a microbead thermistor (Thermometrics, Edison NJ, BB05JA202N) was placed in the lumen of each primary bronchus. The interclavicular air sac was sealed, and the thermistor leads attached to a small connector on a backpack. A silastic cannula was inserted into the cranial thoracic air sac and connected to a piezoresistive pressure transducer (Fujikura, model FPM-02PG) on the birds' backs. When they recovered from anesthesia, the birds were returned to cages. Signals from the thermistors indicating the rate of airflow through each side of the syrinx, and signals from the pressure transducer indicating subsyringeal pressure in the cranial thoracic air sac, were routed on fine wires from the backpacks through the top of the cage to signal conditioning and recording instruments. A feedback circuit maintained the thermistors at a constant temperature of about 60°C. The current needed to maintain this temperature provided a nonlinear measure of the rate of airflow. By monitoring the rate of airflow through each side of the syrinx and the driving respiratory pressure during song, we aimed to determine the sides of the syrinx used to produce each note.

3 Results

3.1 Repertoire size

Intact birds prior to bronchial plugging had a mean repertoire of 32.4 ± 6.9 syllable types. Silencing one or other side of the syrinx with a bronchial plug caused only a slight drop in the size of the repertoire. The mean repertoire size of right-plugged birds was 28.5 ± 3.1 syllables, and left-plugged birds 25.7 ± 6.1 syllables. Most post-plug syllables were different from those in the intact, control repertoire: only 4 or 5 syllables in post right plug repertoires were present as well in the intact repertoire. Of the four birds plugged on the left side, three did not retain any syllables from the intact repertoire, and the fourth only 1.

Paralyzing one side of the syrinx by removing a section of the tracheosyringeal nerve ipsilateral to the bronchial plug had little further effect on mean repertoire size (31.8 ± 10.2 , right cut; 27.5 ± 9.8 , left cut). Repertoires increased a little in some individuals and decreased in others, regardless of which side of the syrinx was disabled. Moreover, only a minority of the post-cut repertoires included syllables present in either post-plug or intact repertoires, again irrespective of the side disabled.

3.2 Effect of surgery on frequency range

Surgical treatment reduced the range of sound frequencies according to the side of syrinx disabled. In intact birds, maximum frequencies of repertoire syllables ranged between about 2 100 and 7 800 Hz. In birds with the right syrinx disabled so that vocalizations originated only on the left side, whatever the treatment, the upper portion of frequency distribution above 5 800 Hz was lost. Distribution of minimum sound frequency, however, changed little. Silencing the left side of the syrinx had the opposite effect. Neither bronchial plug nor nerve cut altered maximum frequencies much but greatly reduced the number of syllables with minimum frequencies below about 1 700 Hz.

In the light of lateral differences in frequency range, it is not surprising that disabling one side of the syrinx reduced the fundamental bandwidth of the syllables. In intact repertoires, 27 % of the syllables had a bandwidth greater than 3 500 Hz, but after unilateral bronchial plugging, this dropped to 9% and remained at this value after ipsilateral nerve cutting as well.

3.3 Syringeal contributions to song

Analysis of the patterns of airflow through each side of bilaterally intact syringes during spontaneous song indicates that each side of the syrinx produces some of the syllables in the repertoire. Neither side of the domestic canary syrinx dominates song production consistently. In some multi-note syllables, birds switch sound production from one side to the other between notes. Both sides of the syrinx rarely if ever produce sound simultaneously. The canary controls which side of the syrinx generates sound by

using syringeal muscles to close the labial valve at the cranial end of one bronchus, thereby preventing airflow through that side of the syrinx and silencing it.

4 Discussion

We have shown that unilateral bronchial plugs and nerve cuts to the syringes of male domestic canaries has little effect on the number of song syllables, but that the composition of the repertoire is very different. We do not know if the new syllables that appear after surgical intervention are the result of disrupted or incomplete motor patterns of intact syllables. The frequency range of syllables depends on which side of the syrinx is intact. Silencing the right side causes the loss of high frequencies and silencing the left side loses low frequencies. This indicates that each side of the syrinx in canaries is specialized to cover different though overlapping ranges of frequencies.

Post-plug and post-nerve cut syllables were generally simpler in their structure. Although a few two-note syllables were produced by lesioned birds, they lacked the bandwidth characteristic of “sexy” syllables most effective in eliciting CSD’s from receptive females. Overall, syllable complexity was drastically reduced in most of the birds, regardless of which side remained intact. In post-operative birds, high frequency sounds (6.0–9.0 kHz) were produced exclusively by the right side of the syrinx. However, either side appeared to contribute to syllables within the frequency band of 0.5 to 6.0 kHz. In this frequency domain, both left and right nerve-cut canaries reorganized their syllable repertoire.

Studying airflow and air sac pressure in males singing with both sides of their syringes and vocal tract intact, we demonstrated that domestic canaries, unlike conspecific *Wasserschläger* males, show no strong syringeal lateral dominance. We also confirm that “A” phrases with a wide bandwidth (roughly 4 kHz), and sung at high repetition rates, are produced by sequential contributions from both sides of the syrinx. Once again, the vocal register of the right side was found to extend to higher frequencies than that of the left.

By using both sides of the syrinx in song production, domestic canaries can increase the phonetic and temporal complexity of their songs. Previous work shows that these two acoustic features are important in inter-sexual and in-

tra-sexual communication (Vallet and Kreutzer, 1995; Vallet et al., 1997, 1998; Leitner et al., 2001; Parisot et al., 2002). In domestic canaries, certain sequential contributions from both sides of the syrinx may be needed to produce complex syllables with a large bandwidth. This is certainly an important additional cue used by females during inter-sexual communication (Draganoiu et al., 2002). “Sexy” phrases of complex syllables sung at a high repetition rate are only common in the songs of certain individual males. Their production may demand excellent motor skills that indicate something about the fitness of the singer and/or his hormonal, reproductive state (e.g., Leitner et al., 2001).

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S26-3 Aspects of syringeal mechanics in avian phonation

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Abstract The vocal organ of birds, the syrinx, is formed by modified cartilages of the trachea and bronchi. Recently, the use of thin, flexible endoscopes has made direct observation of the syrinx possible *in situ*. The effects of direct muscle stimulation on the syringeal aperture identified adductor and abductor muscles, confirming results from electromyographic studies. Endoscopic observations also revealed the dynamics of syringeal reconfiguration during phonation. In songbirds, phonation is initiated by rostral movement and stretching of the syrinx together with simultaneous movement of the medial and lateral labia into the bronchial lumen where they form a narrow slot. The medial tympaniform membranes play a minor role in vocalization as their removal causes only small changes to song. In the tracheal syrinx of the pigeon, sound production is initiated by almost full adduction of the lateral tympaniform membranes into the tracheal lumen, where they bulge rostrally during phonation. Endoscopic observation combined with vibration detection by laser light suggests that the avian sound generating mechanism is a pulse-tone mechanism similar to that in the human larynx, with the labia (or lateral tympaniform membranes) forming a pneumatic valve. A numerical, two-dimensional model of the pigeon syrinx is proposed.

Key words Sound production, Songbird, Pigeon, Pneumatic valve, Endoscopic technology

1 Introduction

The avian vocal organ, the syrinx, is a specialized structure located rather inaccessibly where the trachea bifurcates into the two primary bronchi. This is one of the reasons why most of our knowledge about syringeal mechanics is based on such indirect evidence as electromyography, emitted sound, and anatomy. The syrinx of different avian taxa varies in position (King, 1989), and consists of a skeletal framework comprising modified cartilage (or bony) rings, flexible membranes or soft tissue masses (labia) stretched between elements of this framework, and the syringeal muscles (Fig. 1).

Early investigations showed that sound production could be induced by airflow in an excised syrinx (Rüppell, 1933) or by injecting air into subsyringeal air sacs (Miskimen, 1951). The “classical model” of songbird sound production is based on these early studies. It states that in songbirds, sound is generated by oscillations of the edge-clamped, very thin medial tympaniform membrane (MTM) while a soft tissue mass, the lateral labium (LL), provides constriction of the syringeal lumen to induce MTM vibrations (Gaunt and Gaunt, 1985). An alternative model, the pulse-tone model, in which the labia act as a pneumatic valve, has also been proposed (Klatt and Stefanski, 1974).

Arising from theoretical difficulties in explaining how a vibration-based mechanism can generate tonal sounds (Casey and Gaunt, 1985), a third model, the “whistle

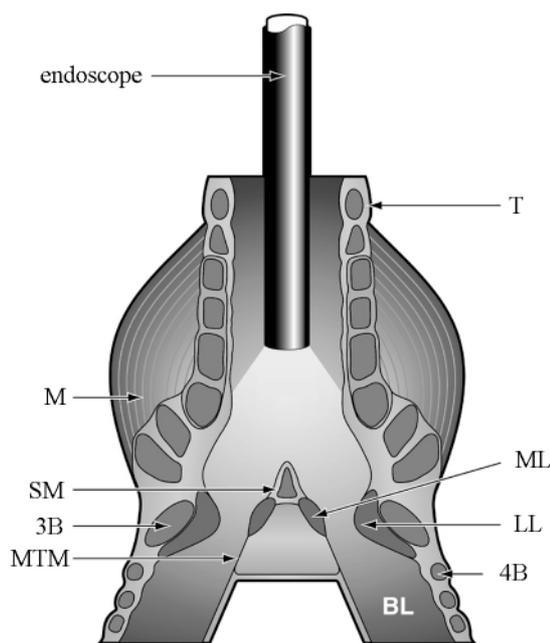


Fig.1 Vertical section through the syrinx of a typical songbird, illustrating the main morphological structures involved in sound production

Abbreviations: 3B and 4B = 3rd and 4th bronchial cartilages, BL = bronchial lumen, LL = lateral labium, M = syringeal muscles, ML = medial labium, MTM = medial tympaniform membrane, SM = semilunar membrane, T = trachea. Modified after Larsen and Goller (2002).

hypothesis”, was formulated (Nottebohm, 1976; Gaunt et al., 1982). Recent mathematical models of the songbird syrinx confirm, however, that generation of tonal sounds by vibration of one or both labia in combination with upper vocal tract filtering is theoretically possible (Gardner et al., 2001). Testing the different models experimentally is difficult. Indirect methods, such as analyses of song generated in a helium-oxygen atmosphere (Nowicki, 1987; Ballintijn and ten Cate, 1998), did not support the “whistle hypothesis” but could not distinguish between the “classical model” and the “pulse-tone model” either.

These problems generated a need to visualize the syrinx during phonation *in situ*. We therefore developed techniques that allowed direct visualization of the intact phonating syrinx by filming it during sound generation through fine endoscopes (Goller and Larsen, 1997a,b; Larsen and Goller, 1999, 2002). These experiments provide support for a pulse-tone model of sound production in which labia (songbirds) or lateral tympaniform membranes (pigeons) form an oscillating pneumatic valve. We also tested the role of the MTM in songbirds (Goller and Larsen, 1997b, 2002), and attempted a mathematical simulation of the acoustic behavior of the simple pigeon syrinx from first principles.

2 Materials and methods

We inserted a fine endoscope (Olympus angioscope AF14, 1.4 mm outer diameter) into the trachea of anesthetized birds through a small opening in the neck area and advanced it to a suitable position above the bronchial partition (Fig. 1). To visualize muscle function we inserted bipolar 0.025 mm stimulation electrodes into different syringeal muscles near their rostral insertion and stimulated them one by one.

We induced phonation in anesthetized birds by electrically stimulating a song control nucleus in the brain (HVC) in three songbird species: brown thrasher (*Toxostoma*

rufum), northern cardinal (*Cardinalis cardinalis*), and hill myna, (*Gracula religiosa*); the DM of the brain was also stimulated similarly in experimental pigeons (*Columba livia*). A tame crow (*Corvus brachyrhynchus*), with angioscope inserted, was allowed to recover from anesthesia as well, and its spontaneous calls were recorded. The endoscopic images of the syrinx together with sound recordings were stored on a videocassette recorder. For a detailed description of all endoscopic procedures and laser vibration detector equipment, see Goller and Larsen (1997a, b) and Larsen and Goller (1999, 2002).

In ablation experiments we directly tested the idea that the MTM is the principal sound generator in songbirds (Fig. 2; details of procedures and analysis in Goller and Larsen, 1997b, 2002). Song was recorded on cassette tape from each of five individual zebra finch males (*Taeniopygia guttata*) prior to manipulation. We opened the membrane of the interclavicular air sac, destroyed the MTM with fine forceps, and carefully closed the air sac membrane with tissue adhesive. Recording of song started one day after MTM removal and continued daily for 4–7 weeks. In most individuals, some MTM regeneration was noticed after a few weeks; but after removal of regenerated tissue, the MTM stayed fully ruptured to the end of recordings. Syllable similarity between song bouts was quantified with software developed by Tchernichovski et al. (2000). For pre- and post-comparisons of song recovery we normalized each similarity score.

Our two-dimensional numerical model of the pigeon syrinx consisted of an infinitely stiff air tube, with two symmetrically positioned elastic membranes enclosed in an air space to simulate the air sac enclosing the syrinx (Fig. 3). To calculate flow-induced sound, we applied Newton’s second law of motion to obtain the Navier-Stokes equation and made a numerical approximation of the latter. This was coupled with a solid mechanics model of membrane vibra-

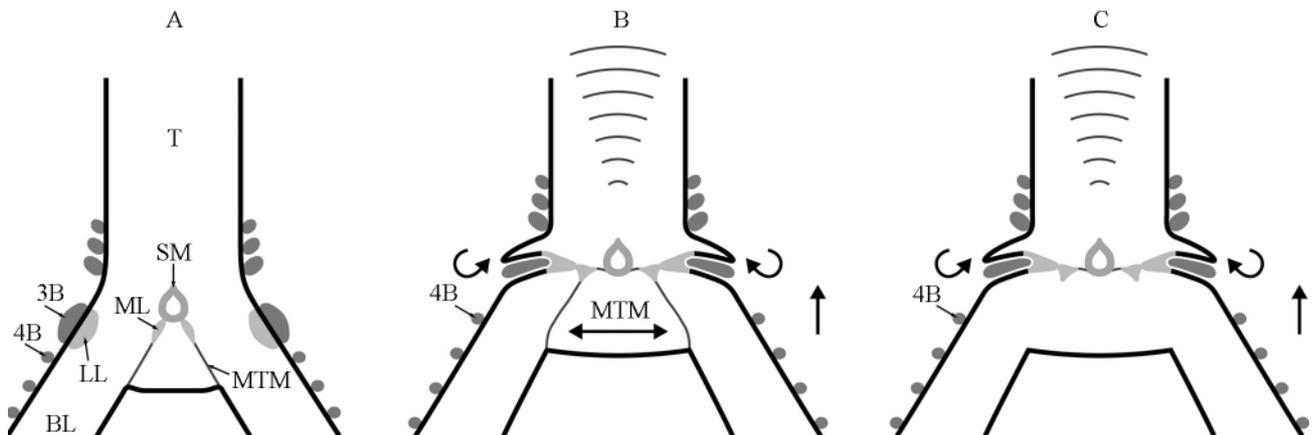


Fig. 2 Schematic interpretation of the songbird syrinx in quiet respiratory position (A), phonatory position (B), and with the medial tympanic membrane (MTM) removed (C)

The typical phonatory position, according to endoscopic evidence, involves a stretching of the bronchi and the medial tympaniform membrane as the syrinx is moved upward, accompanied by closure of the syringeal lumen by the labia to form a narrow vibrating slot that acts as a pneumatic valve. Removal of the MTM (C) does not prevent sound production; abbreviations as in Fig. 1. Redrawn from Goller and Larsen (1997b).

tion and implemented in a computer program written in MatLab.

3 Results

3.1 Syringeal muscle function in songbirds

Electrical stimulation and endoscopic observation show that contraction of the dorsal tracheobronchial muscle constricts the syringeal lumen by rotating and translating the third bronchial cartilage such that the medial edge is drawn inward, thereby pushing the lateral labia (LL) into the bronchial lumen (Figs. 1, 2a, b).

This rotation is probably facilitated by syringeal geometry, since artificial stretching of an excised syrinx causes the third bronchial cartilage to move somewhat into the lumen. The medial portion of the dorsal syringeal muscle appears to be involved in moving the medial labia (ML) into the lumen, but the mechanics of this movement are not understood. Activity in the ventral tracheobronchial muscle enlarges the syringeal lumen, as upon its contraction, the LL is rotated out of the lumen. Contraction of the prominent ventral syringeal muscle does not result in observable movement but seems to tense the ML and is correlated with the frequency of emitted sound.

3.2 Dynamics of syringeal sound production

Observations from the four songbird species, including the spontaneously vocalizing crow, indicate that phonation proceeds in three steps: a repositioning of the syrinx in preparation, tissue vibrations closely correlated with emitted sound, and a return to the syringeal resting position upon cessation of sound. External observations show that prior to phonation there is a vigorous upward movement of the whole syrinx, which leads to a stretching of the anchored bronchi, including substantial stretching of the MTM (note the position of 3B and 4B in Figs. 2a and b). Sound is produced when the syrinx is in its uppermost position, after which it drops back to its resting position.

Internal observations show that syringeal stretching coincides with movement of ML and LL into the bronchial lumen (Figs. 2a, b). The LL covers approximately two thirds of the bronchial lumen in the fully adducted state as it comes

into close contact with the ML. Here ML and LL form a narrow slot in the airway and appear to vibrate during phonation. A detailed video analysis of the vibrations is not possible because we filmed at 30 frames per second. However, measurements with a custom-built laser vibrometer in the trachea show that the vibration wave shape closely matches that of the emitted sound. A similar sequence of events is observed in the tracheal syrinx of the pigeon where the cranially bulging lateral tympaniform membranes form the narrow slot during phonation.

3.3 Role of the medial tympaniform membrane (MTM)

The “classical model” of songbird sound production predicts that ablation of the MTM will silence the bird. Male zebra finches with MTM removed, however, sang readily on their first post-operative day. Song structure had changed somewhat in all individuals, most likely because of the destruction of the MTM and not because of post-operative effects. Over time, song structure improved in all individuals and, at the end of the experiment, was either qualitatively indistinguishable from control song or at least much improved over initial post-operative song. Quantitative similarity scores gradually improved over time as well and, after approx. 25 days, pre- and post- syllable comparisons approached nearly 100%. So, the MTM is not required for song production in zebra finches, but may play a role in adjusting tension of the labia.

3.4 Numerical simulation

We calculated fluid flow through a model of the relatively simple pigeon syrinx (Fig. 3) by numerical solution of the Navier-Stokes equation. The simulation predicted two-dimensional variation in air pressure (Fig. 3), velocity, and vorticity as a function of time. The model also predicted a fundamental sound frequency of about 500 Hz, as well as sudden jumps in sound intensity and fundamental frequency, but included more high frequency components than are present in real pigeon vocalizations.

4 Discussion

Our direct endoscopic observations largely confirm conclusions based on indirect evidence (Suthers et al., 1999) that, in songbirds, the labia are moved by indirect action of intrinsic syringeal muscles. Even though the biomechanics of the songbird syrinx has been described (Klatt and Stefanski, 1974), the precise mechanism of how muscle force effects movement of the third bronchial cartilage is not sufficiently clear, even from our endoscopic observations.

From our experiments, we conclude that the principal sound generating mechanism in the songbird syrinx involves vibration of the medial and lateral labia, and that sound production is not dependent on the presence of the MTM. This “labial hypothesis” suggests that the physical mechanism of phonation in songbirds is very similar to that in the human larynx. Calculations based on models of human vocal fold vibration can also describe sound generation in songbirds (Gardner et al., 2001; Laje et al., 2002).

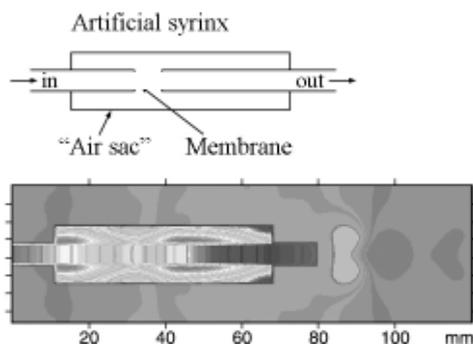


Fig. 3 The two-dimensional model of the pigeon syrinx (upper panel) and the predicted sound pressure distribution in the model after 200 ms (lower panel)

The stretching of the syrinx may facilitate repositioning of the labia. This event preceded sound production in all endoscopic observations of the phonating syrinx (Goller and Larsen, 1997a,b; Larsen and Goller, 1999, 2002). The repositioning makes generation of a pressure differential across the syrinx possible, between bronchi BL and trachea T (Fig. 2b). Such a differential causes increased velocity of airflow inducing Bernoulli forces, which act on the labial tissue forming the constriction and pull it towards the center of the lumen. The interplay between Bernoulli forces and elastic recoil forces acting on the labia is thought to constitute a self-oscillating system, a pneumatic valve, which generates and sustains the labial vibrations that modulate the airflow. Although the labial hypothesis describes the basic model of sound production in songbirds (Goller and Larsen, 1997b) and some non-songbird groups (Larsen and Goller, 1999), it is likely that multiple mechanisms and intermediate states are employed for some sounds.

Surprisingly, even a simple two-dimensional model of the pigeon syrinx produces basic features of pigeon vocalization, such as the correct fundamental frequency and nonlinear phenomena. Clearly it should be extended to a 3-dimensional model and compared to a physical model with known mechanical and acoustic properties. Such work is now in progress (Elemans et al., 2002).

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S26-4 Nonlinear phenomena and song evolution in *Streptopelia* doves

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Abstract The production of complex bird song is commonly achieved through neuromuscular activity of respiratory, syringeal and craniomandibular systems. According to nonlinear dynamics theory, however, complexity can also emerge spontaneously from very simple and deterministic systems, without any external control. Thus far, studies linking bird song complexity with nonlinear dynamics are very rare. Here we explore the possibility that a number of complex acoustic phenomena in vocalizations of *Streptopelia* doves are caused by nonlinear dynamics intrinsic to their vocal organ. We show that the complex acoustic phenomena in species-specific coos resemble the nonlinear phenomena described earlier for mammalian vocalizations. These phenomena include the different attractor states that have been found in mammalian phonation (limit cycle, folded limit cycle, torus, and chaos), and sudden transitions within and between those states (bifurcations). We argue that large, qualitative differences between species-specific song in *Streptopelia* doves may correspond to different attractor states of the same type of dynamic system. If so, dramatic acoustic differences between species sounds do not necessarily reflect large differences in sound production mechanisms or evolutionary differentiation, but may be due instead to relatively small differences in syringeal structure and control mechanisms.

Key words Vocal production, Nonlinear dynamics, Chaos, Syrinx, Evolution, *Streptopelia*

1 Introduction

One major challenge in the study of bird song is to explain the mechanistic origins of its complexity and diversity. Birds in general share the same basic mechanism for vocal production. The avian vocal organ, the syrinx, produces sound through the vibration of pairs of opposing labia or membranes that are driven by respiratory air flow (Larsen and Goller, 1999). Modulation of the sound generated comes about by changing the physical properties of this acoustic source, or of the vocal tract filter that shapes the source signal (Hoese et al., 2000). Such changes are often achieved through neuromuscular activity of respiratory, syringeal and craniomandibular systems. It is not surprising, then, that the identification of neuromuscular correlates of acoustic modulation in birds has received considerable attention over the years (see Suthers et al., 1999).

Recent findings, however, show that simple nonlinear systems can also exhibit complex dynamics without any external, complex control. This is true even if the underlying mechanisms are simple and completely deterministic. Systems in nature are often nonlinear, meaning that the equations describing them include squared and higher-order terms; and the study of such systems using concepts developed in nonlinear dynamics theory has led to a better understanding of their behavior in such diverse fields as ecology, physics, and economics. Because the primary

sound generators in birds are nonlinear oscillators, it seems logical to hypothesize that nonlinear system dynamics also contribute to the complexity of bird vocalizations. Surprisingly, the concept of nonlinear dynamics has been mostly ignored in the study of bird song (cf. Fee et al., 1998; Fletcher, 2000).

In this paper, we explore the possibility that part of the complexity in species-distinct coo vocalizations in the genus *Streptopelia* (turtle-doves) can be explained by nonlinear dynamics intrinsic in the sound-producing organ. The genus *Streptopelia*, family Columbidae, consists of 17 species with a known phylogenetic history (Johnson et al., 2001), each of which has its own specific species perch-coo (Slabbekoorn et al., 1999). Between species, coo sounds can differ qualitatively in tonal structure, a characteristic that is used by turtle-doves to discriminate between species coos (Beckers et al., 2003), and may be used for species recognition. If qualitative differences in tonal structure represent different states of the same nonlinear dynamic system, as opposed to qualitatively different production mechanisms, this has serious implications for our understanding of the kind of mechanistic changes that may be involved in the evolution of song in these birds.

We show that acoustic characteristics of the coos of *Streptopelia* match dynamics known to occur in nonlinear systems, and resemble those found in mammalian vocalizations, the production of which is better understood in terms of the dynamics of coupled, nonlinear oscillators

(Herzel et al., 1995; Wilden et al., 1998; Riede et al., 2000; Neubauer et al., 2001). First, therefore, we recapitulate the different types of nonlinear phenomena identified in mammalian vocalizations.

2 Dynamics of nonlinear oscillators in mammalian vocalizations

The following summary of nonlinear dynamics in mammalian vocalizations is necessarily brief, and is based on Wilden et al. (1998) and Fitch et al. (2002). Voiced sounds in mammals are produced by the vocal folds, which are set into vibration by the effects of subglottal pressure, the viscoelastic properties of the vocal folds, and the Bernoulli effect (Titze, 1994). Nonlinearities in glottal pressure-flow relations, stress-strain-relations of vocal fold tissue, and the collision of vocal folds into each other constitute the nonlinearities of the system. This system consists of multiple coupled, nonlinear oscillators, and has been shown to exhibit qualitatively different types of vibratory dynamics that correspond to three different attractor types in nonlinear dynamics theory (Wilden et al., 1998): limit cycle, torus, and chaos attractors.

2.1 Limit cycle

In the simplest state, the behavior of the system is periodic, i.e. repeats itself in time. The resulting sounds are called harmonic sounds in acoustics, and correspond to a limit cycle in nonlinear dynamics theory. This is the normal state: vocal folds vibrate synchronously and periodically, and produce voiced sounds in humans and other mammals. Spectrographic representation of harmonic sounds shows acoustic energy in discrete bands, composed of a fundamental frequency, corresponding to the inverse of the vibration period, and zero or more integer multiples of the fundamental frequency. Sometimes, additional spectral components called subharmonics appear in the harmonic stack, usually at multiples of 1/2 or 1/3 of the fundamental frequency. Subharmonic regimes correspond to folded limit cycles, and occur, for example, when one of two vocal folds oscillates at exactly half or one-third the frequency of the other.

2.2 Torus

In a more complex attractor, there are two oscillations that are not harmonically related. In human vocal production this has been termed biphonation, and the corresponding object in nonlinear systems theory is a torus. Biphonation can be identified in a spectrogram as two simultaneous, non-parallel energy bands, and occurs, for example, when two vocal folds that are normally entrained to vibrate harmonically at the same frequency, become desynchronized and vibrate at their own individual, different frequencies (Neubauer et al., 2001). In nonlinear systems, this not only gives rise to two independent frequencies f and g , but also to linear combinations of these frequencies: $n \cdot f + m \cdot g$, where n and m are integer numbers.

2.3 Chaos

In a very complex attractor called a chaotic state, or 'chaos', oscillations are very irregular. This results in particularly complex sounds, the spectrographic representation of which exhibits irregular patterns of energy over wide frequency bands, even though some residual energy may still be concentrated in discrete bands. It is easy to misidentify chaotic sounds as noise, because chaos and noise resemble each other superficially in spectrograms. Mechanistically, however, they are very different (Tokuda et al., 2002). The complexity of chaotic sounds originates from the intrinsic behavior of a low-dimensional dynamics system (say, less than 10 components), and is completely deterministic. Noise, in contrast, originates from a very high-dimensional system of random components. Noise is a normal component of human speech, and is not produced by vibrating vocal folds but by a vocal tract constriction that creates turbulence in the flow of air (Stevens, 1998). Deterministic chaos, in contrast, is produced by vibrating vocal folds, in pathological human speech and in the normal vocalizations of other mammals (Wilden et al., 1998; Fitch et al., 2002).

2.4 Bifurcations

Apart from the above qualitatively different dynamical states, coupled nonlinear oscillators can also exhibit another characteristic behavior, namely sudden transitions from one dynamic state to another. These are called bifurcations. Typical examples in mammalian vocalizations are the sudden transitions from harmonic to subharmonic regimes (period-doubling bifurcation), from harmonic to biphonation (secondary Hopf bifurcation), or from harmonic to chaotic regimes. Sudden transitions within one type of attractor are also bifurcations. Examples of this are mode-locking transitions, in which harmonic vibrations instantaneously jump from one frequency to another. Mode locking occurs when a nonlinear interaction constrains two oscillating components of a system to maintain a small integer ratio of frequencies; it is known to occur in the song of zebra finches (Fee et al., 1998). Mode-locking transitions may arise when the characteristic frequency of one component is changed relative to the other, and the oscillation frequency suddenly jumps to achieve a new stable integer ratio.

3 Nonlinear dynamics in the song of *Streptopelia doves*

We used recordings of perch-coo vocalizations that had been collected for earlier studies (Slabbekoorn et al., 1999; Beckers et al., 2003) to search for phenomena linked to nonlinear dynamics. All of the above-described nonlinear phenomena in mammalian vocalizations (Wilden et al., 1998; Fitch et al., 2002) appear in the perch-coo vocalizations of *Streptopelia doves*.

3.1 Limit cycles

Fourteen of the seventeen species have pure-tonal perch-coos, the simplest form of a limit cycle (Fig. 1a). Seven of these have trill-like coos, which consist of fast, repetitive pulses of pure-tone sound, and could therefore be regarded as amplitude-modulated and interpreted as a torus in nonlinear dynamics theory. The repetition rate of these pulses, however, is relatively low (< 30 Hz); they do not give rise to multiple frequencies in human and probably dove perception, and their production may not be intrinsic to the dynamics of the syrinx.

Subharmonics (folded limit cycles) do not occur normally in coo sounds emitted by *Streptopelia* doves, but vocalizations recorded in the interclavicular air sac of ring doves, *S. risoria*, occasionally do (Fig. 1b; Beckers et al., 2003), even though the harmonic and subharmonic components are filtered out before the sound radiates.

3.2 Torus

Two harmonically unrelated frequencies, “biphonation”, occur in the normal perch-coos of at least one species, *S. orientalis*. An example is the third sound element, labeled “B” in Fig. 2. In this example, a multi-harmonic signal with a fundamental frequency of 460 Hz (f) is modulated by a lower signal (g) of about 180 Hz, leading to the “side-bands” of 180 Hz at each harmonic of f .

3.3 Chaos

In three species (*S. orientalis*, *S. tranquebarica* and *S. lugens*), normal coo vocalizations consist completely or partly of elements with a chaotic structure. The *S. orientalis* sound elements labeled “C” in Fig. 3 are examples. Slabbekoorn et al. (1999) classified these vocalizations as “noisy”, but we believe that they are true chaotic sounds because there is often some harmonic structure within the irregular patterns, as described for mammalian chaotic sounds by Wilden et al. (1998). The regular sudden transitions from harmonic or biphonic sound to very irregular regimes (element ‘B/C’ in Fig. 2), and the varying degrees

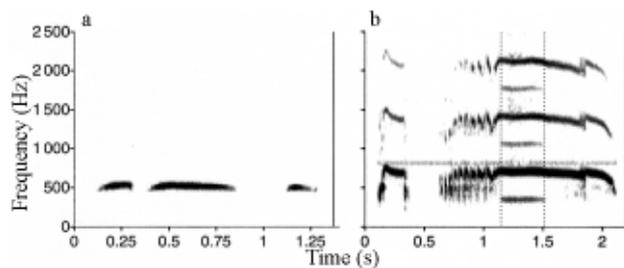


Fig. 1 Perch-coos of *Streptopelia decaocto* (a) and of *S. risoria* (b) Perch-coo (a) is harmonic sound corresponding to a limit cycle. Perch-coo (b) is recorded in the interclavicular air sac inside the vocalizing dove, near the syringeal sound source. Normally this source sound is a multi-harmonic signal, only the fundamental frequency ($300 < f < 800$ Hz) radiating from the dove. This particular individual (b) shows subharmonic regimes (between dotted lines) in its perch-coos, corresponding to a folded limit cycle. The continuous frequency band around 825 Hz is an artifact due to electronic interference during recording.

of irregularity in time-frequency patterns, are consistent with this interpretation. In an exceptional case, we found short chaotic regimes in the perch-coos of *S. risoria*, a species that normally produces harmonic coos. Although it is hard to prove the chaotic nature of sounds from acoustic analysis alone, some mathematical tools can be helpful in its identification (Fletcher, 2000; Tokuda, 2002).

3.4 Bifurcations

Frequency jumps are common sudden dynamic state transitions in all *Streptopelia* species with harmonic vocalizations. At these transitions, the gradual time-frequency contour is momentarily disrupted, as the fundamental frequency jumps almost instantaneously to a different frequency range without interrupting phonation (the first element in Fig. 1b). Such frequency shifts probably reflect mode-locking dynamics. In *S. orientalis*, transitions from harmonic to chaotic states are common (Fig. 2), and in *S. risoria*, coos showing subharmonics, transitions from harmonic to subharmonic regimes, and vice versa, occur suddenly without a stop in phonation.

4 Implications for evolution of song

One of the key features of nonlinear systems is that small and gradual changes in control parameters can cause large, sudden, and qualitative changes in dynamics. If true in bird song, the intrinsic dynamics of the sound production organ itself would provide a source of major and qualitative acoustic variation. Presence of transitions within species shows that these can be readily achieved. Such transitions may also be at the basis of vocal differences between species. Seemingly strong interspecific differences, e.g. between the tonal coos of *S. risoria* and the noisy ones of *S. orientalis* or *S. tranquebarica*, might thus have resulted from minor changes in underlying mechanisms of vocalization, without the need for large changes in syringeal structure or control mechanisms.

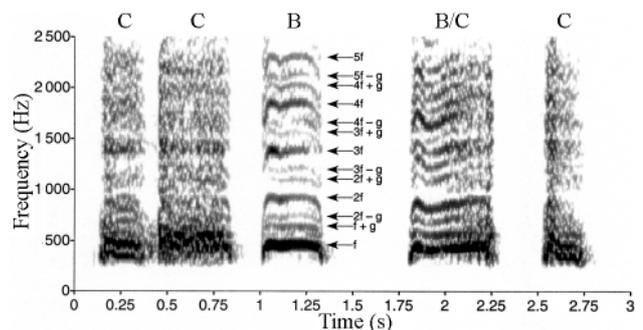


Fig. 2 Part of a coo bout of *Streptopelia orientalis* C = chaotic regime, B = biphonation regime. In the third element, a harmonic signal (f , first five harmonics shown) is modulated by a lower frequency component (g), which causes a side-band pattern around each harmonic of f . Note that in the fourth element, the regime changes from biphonation (or perhaps subharmonic) to chaotic.

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S26-5 Vocal sacs and their role in avian acoustic display

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Abstract Much progress has been made in understanding the fundamentals of the avian voice in general and the workings of the syrinx in particular. As well, there is growing understanding that the rest of the avian vocal tract plays an important accessory role in sound production. Here we examine the role that one such secondary structure, the avian vocal sac, may play in shaping the avian voice, addressing its function in chamber resonance, membrane resonance, acoustic coupling, directionality, and percussion. Special attention is given to the greater sage grouse, *Centrocercus urophasianus*, with its paired vocal sacs and unique strut display.

Key words Vocal sac, Sound production, Acoustic display, Greater sage grouse

1 Introduction

Birds produce most of their sounds with their syrinx; and physiologists have spent decades determining how this uniquely avian voice-box works. Having only recently solved the long-standing riddle of how vibrations are produced in the syrinx, the field has now turned to the role of ancillary structures that modify, radiate, and spatially configure those vibrations. It is already clear that these secondary adaptations are even more diverse than the structures creating the initial vibrations.

It has long been realized that the upper vocal tracts of both mammals and birds can act as resonance filters, increasing the tonal quality of song (Greenewalt, 1968; Nowicki, 1987); in humans, this filtering is an essential precondition for speech. Recent work on mammals has shown that vocal tract resonances can also feed back on the non-linear dynamics of the vibrating glottis, and alter the kinds of vibration patterns produced (Mergell and Herzel, 1997; Riede et al., 2000). Birds also modify their vocal tract geometries, and thereby are likely to produce similar effects during vocalization. The best example of this to date comes from studies of changes in beak posture (Westneat et al., 1993), which demonstrated a tight association between beak movements and vocalization. Moreover, differences in vocal tract morphology among species can create species specific differences in sound production. Differences in beak morphology, in particular, have been shown to be important in the diversification of sound signals (Podos, 2001). Hence, in recent years, it has become increasingly apparent that the secondary structures associated with sound production and radiation in birds may have quite profound evolutionary and behavioral significance.

2 Secondary acoustic structures in birds

Given the newly recognized importance of upper vocal tract structure, it is useful to compare the relevant acoustrements that are present in various avian groups. Examples include the tracheae of cranes and swans that form multiple loops within the breast bone, and the upper trachea of ducks that is enlarged to form a chamber (Dorst, 1974). These significantly lengthen or enlarge the path between the syrinx and the outside world. Many such vocal modifications have been described but few have yet had their function rigorously examined. Almost without exception, these structures are presumed to function as “resonators”; but no tests have been done to justify this conclusion. One such trait, one that has evolved many times in birds yet has received no attention as a general phenomenon, is the vocal sac. While all birds have air sacs as part of their respiratory system, and many birds puff up these sacs, their esophagus, and/or their gular region to some extent when vocalizing, only a subset have exaggerated and externally visible sacs. It is this latter group that is the focus in this review.

3 Types of avian vocal sacs

Most avian vocal sacs are bare with few or no feathers. Such bald sacs are found in at least five avian families, including the North American grouse (Tetraonidae) and the Neotropical cotingas (Contingidae) which have perhaps the most striking examples of bare vocal sacs found in birds. In grouse and cotingas, the vocal sacs are only inflated to their largest extent in acoustic display. The vocal sacs are brightly colored in most of these species, and therefore probably involved in concurrent visual signaling. The pantropical frigatebirds (Fregatidae), and two storks, the Old World marabou (*Leptoptilos crumeniferus*) and New World jabiru (*Jabiru mycteria*), also inflate their necks and phonate but not always at the same time. In these species, the

air sac is often held fully inflated for lengthy periods in a strictly visual display and is only used occasionally in sound production. The African pink-backed pelican (*Pelecanus rufescens*) has been reported to make a loud “blowing sound” when it inflates its gular pouch (Serle, 1943), but it is unclear from the description just how vocal the birds are.

Three other groups have vocal sacs that are equally impressive but not devoid of feathers. Perhaps the most striking is the kakapo (*Strigops habroptilus*), an endangered flightless parrot from New Zealand that seems to inflate its whole body when booming. Many medium to large bustards (Otididae) inflate sacs which are often covered in elaborate feathering; and some but not all inflating bustard species vocalize while inflated. Buttonquails (Turnicidae), which inflate as well, are unique insofar as they are the only group in which females, not males, have the vocal sac.

4 Vocal sac functions

What role do vocal sacs play in sound production in birds? Here we examine the various functions that any vocal tract accoutrement might fulfill, and assess their relevance to vocal sacs.

4.1 Chamber resonance

Sets of natural resonant frequencies result from the size and shape of the vocal tract. Introduced vibrations that match the resonant peaks of the vocal tract will experience a relative gain while others will be selectively filtered out. The addition of any air filled space can, in principle, alter the resonant spectrum of the vocal tract and change the character of the voice. This is thought to be the explanation associated with opening and closing the beak (Westneat et al., 1993). Manipulations of beak gape lead to a mismatch between this filter and syringeal output, and the result is less tonal sound (Hoese et al., 2000).

Does the addition of a “balloon” change the resonant properties of the chamber? Certainly the size and shape of the airway are changed with inflation of such a sack, and this in turn should result in a change in the resonant peaks. However, there is some doubt whether a flexibly walled sac can act as an efficient chamber resonator because the transfer of sound across the membrane is so easy that independent vibrations might not be supported (Watkins et al., 1970). When a frog, for example, is made to vocalize in a helium atmosphere in an assay for this kind of resonance, there is no evidence that it plays a significant role (Capranica and Moffat, 1983; Rand and Dudley, 1993).

That the vocal sac of a frog does not amplify or filter its laryngeally-produced sound through selective chamber resonance does not necessarily mean that all air sacs are incapable of such sound modification. If the flexibility of the walls of the anuran vocal sac make it unsuitable for chamber resonance, then perhaps other air sacs consist of materials more suited to the task. Alternatively, the air sacs

of frogs may just be too small to effectively alter the frequency composition of the relatively low frequency sounds that they produce (Ryan, 1988). If so, other animals that use air sacs may have a more appropriate match between frequency output and the size of their inflated air sacs. Many birds call at higher fundamental frequencies than frogs, which would also tend to make chamber resonance a more viable function for their air sacs. Therefore, it is inappropriate to rule out chamber resonance as air sac contribution without appropriate experimentation.

4.2 Selective radiation and coupling

In most tetrapods, internally produced sound is transmitted to the surrounding medium through the nose or mouth. This seemingly simple process is complicated by the impedance mismatch of the apertural air way and the environment. Depending on the shape of the aperture, much of the sound may actually be reflected back into the vocal tract. One way that animals can avoid such problems in transference is to pass the sound through a membrane which has an intermediate impedance value (Bradbury and Vehrencamp, 1998). An inflated air sac has a more favorable impedance match with surrounding air, and therefore is able to transfer sound energy to the environment more efficiently.

This type of trans-membrane sound transfer is frequency dependent since the membrane itself has resonant frequencies. The precise nature of this frequency dependence is determined by the size, shape, and micro-anatomical makeup of the membrane tissue. It is likely that selection has acted to bring the natural resonant frequencies of membranes that couple sounds to the environment into line with important components of species-specific vocalizations.

To understand how relevant this may be for avian vocal sacs we can again learn from research done on the better-studied anuran vocal sac. Frogs call with mouth and nares closed so that all sound must pass across some biological membrane for transmission. Purgue (1997) showed that various anurans have membrane transfer functions with peaks that are aligned with key components of species-specific vocalizations. Thus, the anuran vocal sac is an important selective resonator; but it is the transfer function of the membrane that matters, not that of the chamber. This helps to explain how such small animals can make such low frequency sounds so loudly. It also suggests that selective radiation and coupling might be an important feature of air sacs in many birds, specifically those that, like the greater sage grouse (*Centrocercus urophasianus*) and the kakapo, vocalize at very low frequencies.

4.3 Rapid modulation of resonance

Westneat et al. (1993) showed that rapid movement of the beak during vocalization can have profound effects on the signal emitted. Rapid changes in sac volume or shape might also cause fluctuations in resonance which create qualitatively novel sounds. Such an effect is likely to be found in animals that use their sacs in a dynamic fashion such as sage grouse or the bare-necked umbrellabird

(*Cephalopterus glabricollis*). Through rapid body movements and muscle contractions, these birds modify the shape of their vocal sacs wildly during display, creating rapid changes in the shape of the sac which might alter chamber resonant profiles. This also modulates tension on the membrane which affects its resonance profile. The bare-necked umbrellabird has a fleshy projection attached to the middle-bottom of its air sac (Crandall, 1945) that might serve to amplify both types of modulation.

5.4 Directionality

Air sacs which are used to couple sound to the environment have the potential to modify more than just the frequency composition of those sounds. This mode of radiation also alters the shape of the sound field significantly. An animal that relies on expired air to carry the pressure waves to the environment will have an acoustic field shaped very much like that of a horn. The intensity of the waves will be much greater in line with the opening, and have frequency-dependent lobes of lower intensity to the sides and rear. A single air sac, however, might act much more like an acoustic monopole where pressure waves are of nearly equal intensity in all directions. This is generally what has been found in anurans with a single vocal sac (Gerhardt, 1975). It is less clear what pattern would be radiated from paired sacs.

We examined the directionality of a two sac system in our work on the greater sage grouse (Dantzker et al., 1999). As noted above, adult male sage grouse in breeding condition develop a pair of bare vocal sacs on their breasts. These sacs inflate and deflate many times during each two-second strut display. The display consists of noisy wing sounds followed by several low frequency notes ("coos"), a loud broadband pop, a frequency-modulated high frequency note, and a final pop. Males repeat this same display over and over for hours when lekking. We found that the lower frequency and broadband components of the strut display radiate in a monopole or unidirectional pattern, while the higher frequency components radiate in a variable dipole pattern (Dantzker et al., 1999). This suggests that paired vocal sacs may be used to create spatially variable interference patterns. At least for the greater sage grouse, this produces sounds that are broadcast more laterally than frontally, and are thus unlike any animal sounds previously measured.

5.5 Percussion

In some cases, air sacs may serve not only in the modification of syringeally produced sounds, but also in the production of novel vibrations. The mode of such production is most likely percussion of the inflated air sac. The bare-necked umbrellabird and the sage grouse appear to offer two very different examples of air sac percussion. In one, the male umbrellabird shakes its body from side to side, and the fleshy projection on its vocal sac slaps rhythmically back and forth against the inflated sac to produce a rapid drumming sound (Crandall, 1945). In the sage grouse there are no projections to bang against the inflated air sacs. Instead, the paired air sacs are slapped against each other, possibly producing the loud

"pop" components of the display. These seem to be clear examples of percussion but it is important to bear in mind that the sound produced by percussion may not be the primary reason for the behavior. Rather, the behavior might serve more to start rapid movement of the air sac membrane to lead to the dynamic modulation of resonant and/or radiation patterns described above.

5 Conclusion

Evolutionary biologists see convergence as a signpost for adaptation. The vocal sac appears to be an excellent example of such convergent evolution given that it has evolved independently at least eight times in birds. However, the complexity and diversity of the ways that vocal sacs are used, and the different physical processes that seem to be invoked in different species, suggest that considerably more research on different vocal sac systems will be needed to determine whether this, and other secondary acoustic structures in birds, follow common rules.

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Symposium 27 Morphological integration and modularity

Introduction

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Organisms are complex systems built up in a biological hierarchy, from genes to expressed morphology, physiology and behavior, with networked correlations within and between the respective traits bound by a framework of heritability and phylogenetic constraint. The role of function as a key factor in avian morphology is deeply implicated. In an ongoing process of coevolution, form and function are blended in the body plan to constitute functional complexes. These may be explained as correlated morphological mechanisms that accomplish common biological roles such as locomotion or feeding. They are the main modules in the architecture of bird design. Bound by morphological integration they can only be modified together. How these modules are turned on and off has been poorly understood until now. During the last decade, the Hox genes, with their func-

tions of constraint, have been discovered as the “master regulators” for the organization of body pattern and form. The morphological expression of developmental genes in vertebrates, especially in birds, is a very recent research field. Their ecological, behavioral and phylogenetic determinants are yet to be explored, as well as their portion of phylogenetic load as the counterpart of evolution.

This symposium reviewed several aspects of morphological integration, from basic trait evolution and its underlying molecular modules to its expression in flight and behavior and interaction with ecological factors. Hypotheses arising — how developmental morphological integration may affect the response of traits to selection pressures from the environment and behavior over time — have yet to be tested.

S27-1 Integration and modularity in biological systems: a review

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Abstract Olson and Miller (1951, 1958) coined the term “morphological integration” to describe the observation that particular subsets of morphological traits tend to covary strongly over development and evolution, while other subsets are more weakly associated. Traits forming such subsets are said to be “integrated”. Such patterns of association, they argued, are a reflection of underlying developmental and functional demands on organismal phenotypes. Olson and Miller reasoned that characterizing such patterns and exploring the causes and consequences of integration would lead to interesting insights about phenotypic evolution. In current usage, such sets of integrated traits are termed “modules”. An expanded view of integration focuses not only on patterns of phenotypic covariation but considers the implications of modular patterns of organization over a wide range of biological problems. Theoretical, experimental, and methodological advances have increased our understanding of how and why modular systems are likely to evolve. I briefly review contributions from a variety of fields including quantitative genetics, studies of multivariate selection, developmental biology, and systems biology, and discuss why modularity is likely to be a key concept for advancing our understanding of complex biological systems.

Key words Morphological integration, Covariation, Modularity, Selection, Evolution

1 What is modularity?

Precise definitions of what constitutes modularity are surprisingly elusive (Chernoff and Magwene, 1999; Magwene, 2001). This, in part, may reflect the diversity of biological systems and the types of data for which the concept was introduced. While explicit criteria for defining or delimiting modularity are sometimes hard to come by, the key property of modular systems is that they exhibit strong interactions within themselves and weak interactions with others (Cheverud, 1982; Wagner and Altenberg, 1996; Magwene, 2001; Winther, 2001). A modular system is therefore one that can be broken down into a set of independent or semi-independent subsystems, each of which is integrated. In a biological context we often demand other criteria as well. For modularity to be of evolutionary relevance, for example, it must have a genetic basis (Cheverud, 1996; Wagner, 1996).

The idea that biological systems are fundamentally modular has been evoked to explain a variety of observations such as population level patterns of covariation among traits, mosaic patterns of evolution, and the compartmentalized effects of environmental, developmental and genetic perturbations (e.g., Olson and Miller, 1958; Kirschner and Gerhart, 1998; Bolker, 2000). How modular systems evolve and how modularity affects selection are currently the focus of a great deal of conceptual research, mathematical modeling, and experimental and observational inquiry.

2 Historical overview

The study of patterns of covariation among pheno-

typic traits as a tool for understanding the evolutionary and selective constraints on populations and species has a long history. Karl Pearson, one of the key founders of the biometric school, provided some of the earliest examples of using trait correlations to study populations and the effects of selection (Pearson, 1903).

Quantitative approaches focusing on the study of trait covariation also emerged from the work of population and quantitative geneticists. Chief among these was Sewall Wright (Wright, 1918, 1932). Wright’s method of path analysis was applied to the study of phenotypic correlations among traits. Using exploratory path analyses, Wright made the case for the existence of general and special factors that explained patterns of correlation. General factors, such as size, contribute to patterns of correlation among most traits. Special factors correspond to explanations for correlations among particular subsets of traits. Often these special factors correspond to presumed functional or developmental modules (Wright, 1932, 1934; also Bookstein et al., 1985).

Developmental biologists have long been interested in patterns of integration and modularity among phenotypic traits. Early quantitative work includes Huxley’s studies of allometry (Huxley, 1932). Needham’s (1933) work on the dissociability of development, and subsequent studies of heterochrony, also support the concept that phenotypes, and the developmental processes that build them, are modular. Additional conceptual treatments relevant to modularity and integration can be found in Schmaulhausen (1947).

Olson and Miller drew from this background in developing their concept of Morphological Integration (Olson

and Miller, 1951, 1958). Olson and Miller never gave a formal definition of integration. Perhaps their most succinct statement is the following “...there exist groups of highly associated morphological dimensions within most organisms...such groups have important biological and evolutionary meaning” (Olson and Miller, 1960). Starting with their 1951 paper, Olson and Miller began to develop a conceptual and methodological basis for studying morphological integration. In particular, they laid out a statistical methodology for testing hypotheses of integration that they called the ρ F model. The ρ F model involved testing a set of empirically derived clusters of traits (ρ -groups) against trait sets derived by qualitative assessment of function or development (F-groups). In their book *Morphological Integration* (1958), Olson and Miller argued that there was sufficient evidence for the validity of ρ -groups such that a comparison with F-groups was no longer a necessary part of their model. They also described there a complex method for discovering sets of correlated traits.

What distinguished Olson and Miller’s work, however, was not their statistical methodology but rather the scope of their research program. They explicitly advocated a quantitative approach, based on multidimensional phenotypes; they analyzed and considered both neontological and paleontological data; and they provided perspectives on both the micro- and macro- evolutionary consequences of morphological integration.

Despite continued conceptual and theoretical interest in the concepts of modularity and integration (e.g. Riedl, 1978), relatively little empirical work addressing the issue directly appeared in the 1960s and 1970s. This situation began to change in the early 1980s when James Cheverud and coauthors suggested a quantitative genetics framework for studying the evolution of integration (Lande, 1979; Cheverud, 1982, 1984; Cheverud et al., 1983). This work put the concept of integration on a firmer theoretical basis, and also suggested more appropriate statistical tools for quantifying and assessing integrative patterns. Many of these developments are summarized in Chernoff and Magwene (1999).

3 Types of integration and modularity

Different categories of modularity have been defined to distinguish between explanatory hypotheses for modularity and integration. Common sets of categories are functional, developmental, genetic, and evolutionary modularity (Cheverud, 1996). Functional modules are sets of traits that are presumed to form a module because they interact to accomplish some function or task (Cheverud, 1996; Winther, 2001). Developmental modules are those that result from developmental processes which induce patterns of modularity such as common tissue origin or similar regulatory control (Atchley and Hall, 1991; Nemeschkal, 1999; Bolker, 2000). Genetic modules are sets of traits that are modular due to pleiotropy or linkage disequilibrium (Cheverud, 1996; Wagner, 1996). An evolutionary module is a set of traits

that covary together over evolution, either because they are jointly inherited (due to genetic modularity) and/or jointly selected (Cheverud, 1996). A given set of traits may form a module of one or more of these types, and the extent to which these different explanations overlap can vary.

4 Measuring modularity

How is modularity in biological systems measured and quantified? This was one of the fundamental questions that Olson and Miller (1951, 1958) tried to address. Other workers have proposed a variety of statistical methods for quantifying modularity. These techniques include cluster analysis (Van Valen, 1965; Cheverud, 1982), matrix similarity tests (Cheverud et al., 1989), and path and confirmatory factor analyses (Zelditch, 1987, 1988). Concerted trait evolution over phylogenies may also be indicative of integration (Nemeschkal et al., 1992; Roth, 1996). A recent novel approach has been the use of fluctuating asymmetry to study developmental integration (Klingenberg and Zaklan, 2000; Klingenberg et al., 2001).

Recently, Magwene (2001) proposed the use of a statistical technique called Graphical Modeling as both an exploratory and confirmatory tool for studying modularity. Graphical modeling, and related methods such as Bayesian networks, are based on the statistical notion of conditional independence (Whittaker, 1990). A pair of traits is conditionally independent if their statistical interaction disappears upon conditioning (statistically) on some other trait or set of traits. Modules then correspond to sets of traits which all show strong conditional interactions with each other. This approach has a number of strengths, two of which are worth highlighting. Magwene (2001) shows that (1) conditional independence can be used to provide an unambiguous criterion for delimiting modules, and that (2) conditional independence among traits can be related to standard models of multivariate selection. This argument is similar to one made by Pearson nearly a century before (Pearson, 1903). Pearson argued that marginal correlations among traits were not the most informative type of interaction to study; rather, he saw that conditional interactions were fundamental to understanding the association of traits within populations and species.

5 Evolution of modularity

What is the “unintegrated state”? Do phenotypes typically evolve from a state of overall strong correlation among traits, or is the ancestral state one in which most traits are independent. The idea that modularity evolves by breaking down interactions among traits has been labeled the “Fission” model; modularity built up from initially independent traits has been termed the “Fusion” model (Riska, 1986; parcellation and integration *sensu* Wagner, 1996). Riska (1986) argues: “high genetic correlation is simpler than and antecedent to zero genetic correlation.” There is, however, little empirical evidence to support either view. While that evidence may be sparse, a variety of mathematical treat-

ments provide some insights into the types of genetic architectures and selective regimes which may favor the evolution of modularity or lead to changes in modularity (Cheverud, 1984; Wagner, 1984, 1988; Bürger, 1986; Rice, 1998, 2000).

6 Systems biology

In the past, methodological difficulties usually limited studies of modularity and integration to the consideration of a limited number of traits; even in the most ambitious studies usually less than 50 variables of interest were considered. Technological advances over the last decade have begun to change this as high-throughput technologies allow researchers to assay the state of hundreds, even thousands, of variables simultaneously (Brown and Botstein, 1999). The richness of such data has begun to be exploited by researchers interested in the organizational properties of biological systems. The concepts of modularity and integration have begun to be exploited in this context, in analyses of systems such as metabolic pathways (Ravasz et al., 2002) and genetic regulatory networks (Magwene, unpublished).

From a practical point of view, modularity is a useful concept for breaking down a complex system into sets of smaller subsystems, each of which can be studied in isolation. If the break down is consistent with the actual patterns of (semi) independence, then little or no information about the behavior of the system as a whole is lost. Modularity therefore provides an important conceptual and experimental handle for dealing with the complications faced when we study complex biological processes.

7 Relation to other concepts

Modularity and integration have been related to other phenomena of evolutionary interest such as buffering and canalization and the evolvability of biological systems (Altenberg, 1995; Wagner and Altenberg, 1996; Kirschner and Gerhart, 1998). For example, it has been argued that modular patterns of organization help to buffer against developmental noise and mutation. Modularity may therefore be an important mechanism which helps to produce normal phenotypes in the face of imprecise regulatory control (Kirschner and Gerhart, 1998; von Dassow et al., 2000).

8 Outlook

Modularity and integration have emerged as key concepts for studying organismal phenotypes and the molecular, developmental, and evolutionary processes which affect them. The research cited above represents only a small portion of the growing body of work that bears on our understanding of modularity and integration. Future research, in particular the development of experimental tools to test hypotheses of modularity and techniques for quantifying modularity with diverse types of data, will contribute to a greater understanding of the organizational properties of complex biological systems.

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S27-2 Trait evolution, morphological integration and functional complexes

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Abstract A salient feature of bird morphology is the design of adaptive functional complexes. These complexes have evolved as a response to selection for function, which has led to integration of sets of traits that act evolutionarily as one coherent unit rather than as independent parts. For understanding the ecological importance and the evolution of these functional complexes, research needs to focus on three areas of analysis. At the basic level, it must unravel the quantitative genetics of trait complexes to understand the potential for evolutionary change. It can be shown that the magnitude of genetic correlations determines to a large extent the evolutionary trajectory of a population, almost irrespective of selection. So far, little is known about this in birds. Secondly, the ontogenetic basis of trait complexes needs appreciation, together with the variation in ontogenies in populations. This area is tightly linked to understanding the basic morphological interactions among parts in order to learn which parts constitute a functional complex. The ontogeny of birds is also poorly known. Thirdly, patterns of selection acting on the complexes need to be understood, in addition to the selection on means and variances. For the future, it is of importance to learn how many parts can be involved optimally in a functional complex, and how separate complexes evolve. This will have a profound impact on our understanding of avian evolution: how new complexes and new taxa evolve.

Key words Genetic variance-covariance matrix, Size, Growth trajectories, Selection, Optimal integration, Carduelid finches

1 Introduction

In birds, most morphological variation among species within a genus, or among genera within a family, is confined to size (Björklund, 1991, 1994a). Differences in shape are usually minor such that species are commonly larger or smaller copies of one another on a common line of allometry. Thus, of all the theoretically possible phenotypes, only a few actually exist. Functional complexes are one of the reasons for this pattern, producing, for example, the different bills in cardueline and nectar-feeding birds, without which such birds cannot function properly in their environment. These complexes have evolved in response to strong selection for function, and, as a result, sets of traits have evolved to function as a single unit rather than a number of independent parts. For understanding the ecological importance and the evolution of functional complexes, research needs to focus on three areas of analysis and to integrate them into a common framework based on basic evolutionary principles. Those three areas — genetic, ontogenetic and functional (ecological) — are evaluated here. I also discuss briefly recent theoretical attempts to understand the evolution of integration by means of neural networks.

2 Genetics

One way to analyze genetic patterns of integration is through the genetic variance-covariance matrix (\mathbf{G}), which

describes the genetic variance for each trait and the genetic covariance (correlation) among traits. This matrix can provide vital information concerning the future paths of evolution because \mathbf{G} appears in the standard equation for evolution, $d\mathbf{z} = \beta\mathbf{G}$, where $d\mathbf{z}$ is the change in trait means and β is the selection gradient vector (Lande, 1979). One way of analyzing the possible paths of evolution is through the eigenvalues of the \mathbf{G} -matrix. A matrix with high correlations among traits has one eigenvalue that is much greater than the rest, producing a large variance in eigenvalues (Wagner, 1984). A matrix with low correlations has eigenvalues of about equal magnitude, and thus low variance. Vectors shed light here. Each eigenvalue corresponds to an eigenvector, and these have directions as do all vectors. The eigenvalue is a measure of the length of the associated eigenvector.

In biological terms, the eigenvalue measures the amount of variation that is associated with each combination of traits. If the correlations are high and positive, then the eigenvector associated with the largest eigenvalue can be interpreted as a size vector, and the magnitude of the eigenvalue represents a measure of the variation in size in the population. The importance of knowing the structure of \mathbf{G} can be illustrated by the fact that the response to selection is determined by the length and the direction of the eigenvectors of \mathbf{G} (Björklund, 1996a). In other words, the \mathbf{G} -matrix biases the future evolutionary paths of a population. Biologically, this means that if the largest eigenvalue is very

large, almost all variation in the population is confined to a certain dimension. Since selection can only act on the variation that is available, this will direct the response to it. It can be shown that if the leading eigenvector is very long, indicating considerable variation, then the response is almost always in the direction of the eigenvector rather than the selection vector. Thus, if the largest vector is one of overall size, almost all selection for shape will nevertheless result in a response in size (Björklund, 1996a).

Only when selection is collinear with other vectors will the variables respond according to those vectors. This pattern has been described by Schluter (1996) as “the trajectory of least resistance”. It is an unfortunate label because it suggests freedom of movement when it is actually a brute force process of constraint. This finding has two important evolutionary implications: first, selection against the leading eigenvector is very ineffective, and thus the structure of the **G** matrix can act as a true constraint with a strength determined by the strength of the correlations among traits. Secondly, it can be shown that the response to selection in the direction of the leading eigenvector is much larger than if selection were to act on each trait independently, as would be the case if there were no correlations among traits (Björklund, 1994b, 1996a). In short, the pattern of integration can promote evolutionary change in some cases, but also constrain it in others.

Data bearing on these issues in natural populations of birds is limited, especially with respect to the same traits. I found six species — three of *Geospiza* (Grant, 1986), *Melospiza melodia* (Schluter and Smith, 1986), *Ficedula albicollis* (Merilä et al., 1994), and *Pyrenestes ostrinus* (Smith and Griman, 2000) — in which bill length, depth and width, tarsus length and wing length were all included. To describe the level of integration, I used the variance of the eigenvalues of the genetic correlation matrix and expressed that as a percentage of the maximum possible (equals the number of traits for correlation matrices). Integration varied between 85 % in *Geospiza fortis* to 36 % in *Melospiza melodia*. To analyze the pattern of variation, I compared the direction of the longest eigenvector to an isometric size vector. The correlation between these two vectors varied between 0.906 and 0.998 across species.

This reveals variation among species in the level of integration, from quite low to quite high, and that in all cases the variation involves size. Thus the response to selection is one of overall size change, even though selection may act on shape. The same pattern emerges from analysis of the three bill traits alone, only even more strongly, with level of integration at 53%–94 % and correlation with isometry vector at 0.985–1.0. It shows that the size-alone response to selection is the by far most likely outcome of selection on bill form in these species. Unfortunately, sample sizes were generally low, ranging from 12–84, with *Ficedula* an exception with 744. The most general conclusion that can be drawn from this analysis is that more data are needed from more species. Given the logistic problems inherent

these kinds of studies, this will take time.

3 Ontogeny

At the mechanistic level, any evolutionary change in morphology is rooted in change during ontogeny, particularly in timing and rate of growth (McKinney and McNamara, 1991). For example, an increase in size can arise through either prolonged growth or increased growth rate or both. Changes in shape will occur if timing and rate of growth change in one trait but not the other. Therefore, it is of fundamental importance to analyze the amount of variation in these growth parameters. Such variation may be of two kinds: variation in the elevation of growth curves which result almost exclusively in changes in size, and variation in the shape of growth curves which can lead to changes in shape. Studies of variation in elevation of growth curves abound, but those on the actual shape of growth curves are rare. There are almost always differences in growth curves among individuals in a population, and in some cases these can be substantial. Such variation not only has an environmental basis but also a genetic one, the extent of which, however, is unknown for most bird populations.

Thus, Björklund (1993) found very little variation in the shapes of growth trajectories among three species of cardueline finches. Variation was confined almost exclusively to elevation trajectories, representing size. Furthermore, correlations among the trajectories for the different traits were very strong, indicating that the only variation available for selection to act on is in size and so predicting evolutionary change only in size. This analysis was repeated for two species of tits, with the same result (Björklund, 1995, 1996b).

4 Selection

The analysis of patterns of multivariate selection gives considerable insight into the functional properties of phenotypes. For example, where selection acts consistently to stabilize a particular trait combination, then the correlations among the traits should become strengthened. The pattern of integration, i.e. the correlational structure, is itself the result of past selection, and may today be reinforced or broken down by current selection. Questions about current selection now emerge: is current selection concordant with the pattern of integration, or is it pressuring in other directions? An analysis of this will give answers to the more general question of whether the pattern of integration is acting to facilitate or constrain future evolution.

There are, however, few studies of multivariate selection on birds. There are a number of reasons for this, one of the most important being that very large sample sizes are needed if the statistical machinery of selection analyses is to be fully utilized. Another is that the literature and techniques in this area are not easy reading, and researchers may avoid more appropriate analyses for this simple but sad reason. It cannot be stressed strongly enough, however,

that, if the data are available, a full multivariate analysis of selection is worthwhile because information concerning the correspondence between phenotype and environment is of enormous value.

Analyses of selection involve three steps: selection on trait means, selection on trait variances, and selection on trait covariances. Completing all three steps allows multivariate fitness surfaces to be estimated (Phillips and Arnold, 1989; Schluter and Nychka, 1994; Arnold et al., 2001), providing much important information. The first two steps have been employed in a large number of studies. Kingsolver et al. (2001) list more than a dozen; and there are more as they confined their meta-analysis to studies published in general journals without searching the ornithological literature.

For example, in an analysis of survival in the serin (*Serinus serinus*), Björklund and Senar (2001) found that probability of survival increased with increasing wing and tail length in males. There was, however, significant selection against the correlation between tail and wing, leading to a fitness surface with a valley between two peaks and most individuals in the valley. The reason for this might be a consequence of both traits developing in the same way — energy allocated to wing growth going to the tail as well, hence the correlation of 0.69 in males. If energy is insufficient to increase both tail and wing length, then the consequent compromise is likely to be medium-sized birds with a suboptimal fitness. Another example taken from the same study showed a distinct difference in fitness surface between males and females in bill traits: whereas males were close to an adaptive peak, females were positioned on a slope well away from theirs. Such inferences could not have been reached without detailed multivariate analysis, using sample sizes in the hundreds; simple univariate analysis would have even been misleading.

5 Optimal integration

At a general theoretical level in functional trait evolution, one must ask the following questions: how many elements should be integrated? Under what ecological conditions are large complexes favored? And under which conditions are small complexes favored? These questions relate closely to an issue addressed in theoretical physics: the stability-flexibility dilemma. It observes, in short, that large complexes, networks or organizations are able to perform many tasks but are slow and costly to maintain, whereas small complexes are fast and cheap but cannot perform many tasks. Thus, depending on the demands imposed by the environment, different organisms may evolve different levels of integration or networks.

To test this, Reppilber et al. (unpublished) used neural networks of different size to compete in a genetic algorithm under a wide variety of ecological conditions. A neural network is a general construction where “something” is put in, and the construct is trained to handle the input in such a way that a certain output is delivered. This is a very

general and flexible model that can handle all levels of organization, from the strictly molecular to ecosystems. In this context, the network or complex can be thought of as an individual that is given a certain amount of resources and which uses the energy from the resources in a way to maximize reproductive output (or Darwinian fitness). Thus, complex networks correspond to individuals with a high level of integration (many parts, strong correlations), while small networks correspond to individuals with a low level of integration.

In the study of Reppilber et al., the ecological environments comprised between three and eight different habitats each with different resources. Networks of sizes three to ten were then allowed to compete within these environments. The results were clear, and show that in the short run, smaller networks out-compete (have higher fitness) than larger ones, but that in the long run, after hundreds of generations, the larger ones won. A correlation was also found between the size of the optimal (“winning”) network and the degree of environmental heterogeneity such that larger networks were more successful in more heterogeneous environments. Thus, at a given level of heterogeneity, a certain size of network is the most successful, and larger and smaller networks at a disadvantage.

The biological conclusions to be drawn from this study are that smaller networks are favored in unpredictable environments, and larger networks in predictable ones. Thus, the levels of integration can be predicted to vary according to the long-term properties of the habitat in which each species has evolved. In this context, the model relates both to the number of traits that should optimally be included in each module of integration, and to the number of different modules that would be optimal.

6 Conclusions

The main conclusions of this paper are that, first, more data are needed on the structure of the genetic variance-covariance matrix in natural bird populations for understanding and predicting future evolutionary change, and to learn how and when patterns of integration aid or constrain that change. Secondly, more data are needed to assess natural variation in the shape of growth trajectories, since this is the raw material for selection at different levels of integration. Thirdly, more data are needed concerning the pattern of selection on integration itself, in addition to selection on trait means and variances. Needless to say, the basis for all this is a firm understanding of the actual patterns of morphological integration and functional complexes of birds, knowledge of which is still rudimentary today.

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S27-3 Interaction between morphological integration and ecological factors

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Abstract Closely related species may have similar traits not because these traits are adaptive but because they are strongly intercorrelated and inherited from a common ancestor. We examined how intraspecific morphological integration (first principal component within each species) relates to the direction of interspecific divergence in species of two passerine genera (*Oenanthe*, *Ploceus*). We used thirteen traits to describe external morphology, more than have been analyzed in any previous study. Ecological data on migration distances, food type, habitat type and type of locomotion were used to interpret interspecific variation. For pairwise comparisons we used closely related species within the set of species studied. In all cases examined, interspecific differences affected several correlated characters at the same time. The direction of interspecific change did not coincide with the main direction of intraspecific variation described by common principal components. In another finding, the main axis of intraspecific variation was not determined solely by variation in size. We used data on six *Ploceus* species with resolved molecular phylogeny to examine the relationship between morphological integration, morphological differentiation, ecological differentiation and phylogeny. The main direction of morphological integration changed slowly over phylogenetic time and not as a response to immediate adaptive needs. Our main conclusion is that the three different domains of correlated variation (intraspecific, interspecific, ecological) are only loosely interdependent.

Key words Ecomorphology, Line of least resistance, Multivariate evolution, Size, Shape

1 Introduction

The concept of morphological integration emphasizes the fact that characters co-vary. From such covariance, resistance to change in certain directions may ensue. Basically, two kinds of model of microevolutionary divergence have been put forward. One, the constraint model, stresses that selective forces can produce correlated responses only in the directions set by morphological integration. The other model type holds that inherited patterns of covariation are overridden easily in the course of adaptive divergence (Björklund and Merilä, 1993).

In our previous studies of integrated ecomorphology, we concentrated on the fit between morphology, environment and behavior among closely related species, involving interspecific comparisons (e.g., Leisler et al., 1989; Gamauf et al., 1998; Winkler and Preleuthner, 1999). In our comparisons, we used (1) species means, which were analyzed with respect to allometric shape rather than size, and (2) traits of known function and suspected ecological relevance. From this approach we found that subtle morphological differences among species in shape had profound ecological effects (Leisler and Winkler, 1985).

Here we examine how phenotypic patterns of covariation within and between species correspond to ecol-

ogy in two song bird genera, *Oenanthe* and *Ploceus*.

2 Material and methods

2.1 The taxa

Wheatears (*Oenanthe*) are morphologically very uniform, and live year-round under extreme ecological conditions in which food (terrestrial insects) is scarce or not permanently available (Potapova and Panov, 1977). Molecular data indicate that the wheatear lineage, as currently understood, is monophyletic (A. Helbig, pers. comm.). The study species comprise three migrants (*O. oenanthe*, sample size = 30; *O. pleschanka*, 63; *O. isabellina*, 56) and two residents (*O. (lugens) lugubris*, 31; *O. pileata*, 18) that all coexist during the northern winter in Africa, where their ecology has been studied in detail (see below).

In contrast, the species of the genus *Ploceus* studied are members of a group that has undergone remarkable adaptive radiation, its members separately occupying a wide spectrum of habitats, feeding on a variety of food types and developing different modes of locomotion (Moreau, 1960). Although the species of *Ploceus* have acquired diverse life-styles, morphological differentiation is rather moderate.

The following species were used in our comparisons:

P. baglafecht, 52; *P. bertrandi*, 15; *P. pelzelni*, 44; *P. ocellaris*, 38; *P. nigricollis*, 40; *P. alienus*, 42; *P. subaureus*, 28; *P. xanthops*, 45; *P. aurantius*, 25; *P. castanops*, 15; *P. nigerrimus*, 63; *P. weynsi*, 32; *P. jacksoni*, 37; *P. rubiginosus*, 42; *P. tricolor*, 31; *P. philippinus*, 24; *P. hypoxanthus*, 17; *P. bicolor*, 40; *P. insignis*, 33.

2.2 Ecological data

To describe the ecological requirements of the five *Oenanthe* species, we used fifteen characteristics of diet, foraging and migratory behavior (Leisler, 1990; Flinks and Leisler, unpubl.): prey size (four categories), food type (percentage of ants, beetles, Isoptera, others), foraging speed, percentage of time spent on perches vs. ground, number of ground-stays per minute, distance covered by running vs. flying, number of runs per minute, number of sallies per minute and distance of migration. Information for the species of *Ploceus* was drawn from Leisler et al. (1997) and unpublished data, and uses four categories of food type on a gradient from granivory to insectivory, four habitat type categories from open savannah to forest, and four types of locomotion on a gradient from ground-hopping to climbing with frequent upside-down hanging.

2.3 Morphometric analysis

We used thirteen morphometric characters to describe external morphology: wing length, tail length, tarsus length, bill length, bill width, bill height, hind toe, middle toe, hind claw, middle claw, tarsus diameter in *Ploceus*, plus primary projection, notch length, rectal bristle length in *Oenanthe*.

2.4 Data analysis

From these data, which were not corrected for size but log-transformed, we computed covariances. To determine major axes of morphological variation within the lineages, we used principal component analysis (PCA). We determined the ecological relevance of the trait combinations from interspecific comparison, and assumed that they held for species at intraspecific level. To describe relationships of within- and between- species covariation, we used canonical discriminant analysis (DA), and combined those analyses with common principal component analysis (CPCA; Flury, 1988). The discriminant analysis was used to represent morphological divergence between species in correspondence with the model of multivariate evolution of adaptive change (Lande, 1979; Schluter, 2000). The common principal components reflect best the ideas put forward in models of constraint evolution by morphological integration. This statistical model assumes that two populations share common components of variation (eigenvectors) which, however, may differ in their relative contribution (eigenvalues) to total variation (Steppan et al., 2002).

3 Results

3.1 Interaction in wheatears, *Oenanthe*

Our first example deals with the species of *Oenanthe*.

PCA of the external morphological variables resulted in two axes that together explained 97% of the total interspecific variance. The first factor (54%) was not a pure size factor, since characters of the flight apparatus were not correlated with this factor. The second component (43%) represented a contrast between wing length, primary projection and tarsus length (positively correlated), and tail length and rectal bristle length (negatively correlated). Both components were correlated with ecological factors. Migration distance and the second component explained 98% of the variation in the first component (F -value = 52.106, $P < 0.02$, $df = 2.2$).

This may seem surprising because principal components are, by definition, not correlated with one another. In a multivariate context that includes other predictors, however, such a result does make sense. The second component acts as a suppressor variable and suppresses irrelevant variation in the other predictor (Tabachnick and Fidell, 2001). Almost 100% of the second component was explained by the proportion of 5–8 mm food size items in the diet, and percent distance covered by running vs. flying during foraging. These results show that one can relate morphological integration at the interspecific level to ecological factors.

In the next step, pairwise comparisons were made between species according to the following procedure. First a DA of the morphological variables was run. Then we ascertained that the differences found corresponded to ecological differences. The same morphological data were also used for a CPCA. The subsequent analyses were based on species pairs presumed to be recently diverged. According to the predictions of the constraint model, morphological differences associated with ecological divergence should be highly correlated with the main component of intraspecific variation. This component is furthermore thought to represent mainly variation in allometric size (Björklund, 1994). In terms of our analyses, scores along the major common principal component would be highly correlated with the individual scores along the discriminant axis under the constraint model. These correlations could be either negative or positive as the vector of “least resistance” represents a line rather than a directed ray (Björklund and Merilä, 1993). Under a pure adaptive model such correlation should occur only accidentally and hence be rare.

For the pairwise comparisons, we begin with *O. isabellina* vs. *O. oenanthe*. Both are closely related but represent an old divergence (A. Helbig, pers. comm.). Both are long-distance migrants and highly terrestrial, but *isabellina* feeds on larger insects, flies more and hunts more by sitting-and-waiting. These differences correspond to a longer tarsus, larger bill and greater overall size in *isabellina* (Fig. 1a). The same morphological data for individuals were used in a CPCA. There was no correlation between the first principal component and scores of the DA in either species (Fig. 1a). Both species, however, showed significant correlation between CPC5 (explaining 6.2% variance in *Oenanthe* and 4.4% variance in *isabellina*, and comprising mainly

variation in bill length and height) and the discriminant axis (Fig. 1b). Thus these two species did not diverge along the line of least resistance.

Other tested species pairs showing no correlation between DA and CPC scores were *O. isabellina* vs. *O. pileata* and *O. pileata* vs. *O. pleschanka*. A different pattern was found in the resident *O. lugubris* and long-distance migrant *O. oenanthe*. They differ little in diet but substantially in foraging behavior, the latter running more and perching less. Accordingly, the discriminant axis represents differences in wing length, primary projection, rictal bristle length and tail length, with *O. oenanthe* being the species with the longer and more pointed wings, short tail and short rictal bristles. First inspection of the CPCs showed that two axes had high loadings in these variables. The DA and two most important CPCs were correlated in *O. oenanthe* but not in *lugubris*.

3.2 Interaction in weaver finches, *Ploceus*

PC analysis of the external morphological variables of the 19 species of *Ploceus* produced two axes. The first factor was a size factor and all characters correlated positively with it. However, it also contained shape information, as correlations varied from 0.56 (claw 1) to 0.88 (thickness of tarsus, wing length), and from 0.49 to 0.77 for respective traits when the very small *P. pelzelni* was omitted. The second component was correlated with measurements of the hind limb (long claws and middle toe, thin tarsus). Principal component 1 was only weakly related to ecology, namely type of habitat (one-way ANOVA, $P < 0.05$), whereas component 2 was significantly associated with habitat ($P < 0.001$) and locomotion ($P < 0.05$).

In pair-wise comparisons, we begin with a pair of very closely related species, *P. nigricollis* vs. *P. ocularis* (Moreau, 1960). *P. nigricollis* forages in higher strata in

forests, and *ocularis* more on the edge and lower in bushes. The DA axis represents differences in bill width, primary projection and wing length, more arboreal *nigricollis* having a wider bill, longer, more pointed wings and smaller feet. Multiple regressions with the CPCs show that the DA axis is not related to them, as expected. The relationship is significant, but the contribution of the CPCs becomes more important as their contribution to the within-species variation falls. As in the case of *Oenanthe lugubris* vs. *O. oenanthe*, such significant relationships were found only in one species, namely *Ploceus ocularis*.

In the pair *P. aurantius* vs. *P. castanops* (subgenus *Textor*, Moreau, 1960), the latter occurs in reed-like vegetation, is insectivorous to a substantial extent, and clings frequently on vertical structures; *P. aurantius* is less specialized. In this pair, *castanops* has larger and rounder wings, and has longer legs and larger feet. The DA and CPC scores were not correlated.

3.3 Interaction among morphology, ecology and phylogeny

We also used data on six *Ploceus* species with resolved phylogeny (*pelzelni*, *ocularis*, *castanops*, *jacksoni*, *rubiginosus*, *bicolor*) to examine the relationship between morphological integration, morphological differentiation, ecological differentiation, and phylogeny. Morphological integration was represented by the first PC within each species. The corresponding differences between species were calculated as $1 - \cos\theta$, with θ representing the angle between the PCs. Morphological differentiation was based on the Mahalanobis-distance, which bears close relationship to discriminant analysis. Ecological differentiation was recorded by Euclidean distances between species with the scores of the habitat, food and locomotion discriminant axes as variables. Phylogenetic distances were based on Kimura distances of cytochrom-*b* data.

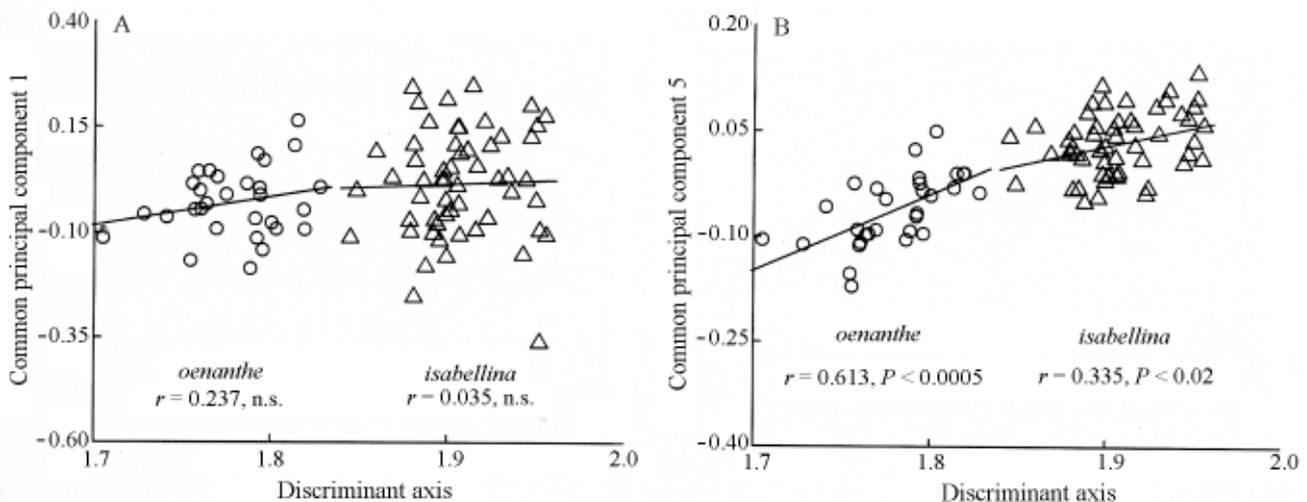


Fig. 1 Correlation between scores of a discriminant and a common principal component analysis of morphological traits in two species of wheatears, *Oenanthe*

O. oenanthe = circles, *O. isabellina* = triangles. The discriminant axis represents differences in tarsus length, bill dimension and overall size that pertain to ecological differences. A = correlation with CPC1, B = correlation with CPC5.

We then tried to unravel the interactions between these four domains of differentiation in the fifteen possible combinations. Unexpectedly, morphological distances and ecological distances were not correlated (0.17), which may be due to the rather unspecific ecological information. Morphological distances and genetic distances were correlated (0.62). Morphological distances and divergence of PCs were only weakly correlated (0.48). This correlation may be mediated by the common relationship to phylogeny. Genetic distances and divergence of PCs were highly correlated (0.75) as shown in Fig. 2.

4 Discussion

The main objective of this study was to examine how intraspecific morphological integration relates to interspecific adaptive radiation. The prediction of the constraint hypothesis is that both should be closely correlated. In our examples, we found very little evidence for this notion. Even in closely related species, adaptive changes affected several characters at the same time. These correlated changes, however, did not take place along the so-called line of least resistance. Rather, the main direction of morphological integration changes slowly with phylogenetic time. Thus morphological integration appears to be subject to phylogenetic inertia. Such inertia was not found in our analysis of interspecific variation.

Another finding of the study is that the main axis of intraspecific variation is not solely attributable to variation in size. Likewise, adaptive changes are mainly changes in shape (Schluter, 2000). Thus we conclude that the three

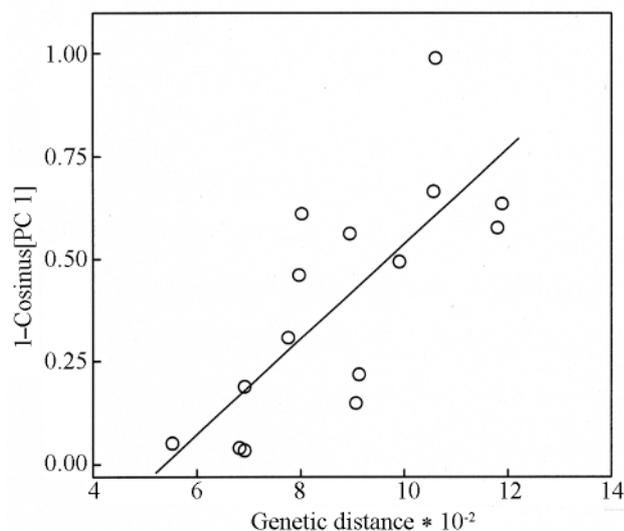


Fig. 2 Correlation between genetic distances (Kimura distances) and divergence of PCs (13 morphological characters) in 5 *Ploceus* species (15 possible combinations).

different domains of correlated variation (intraspecific, interspecific, ecological) are only loosely interdependent.

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S27-4 Patterns among avian flight style, nesting biology, development, body size, and locomotor modularity

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Abstract Morphological investment emphasizing either the hind limb or forelimb module varies predictably with trends in: (1) parental care, as in nest construction and placement, feeding and protection of young, (2) developmental hatchling stage, as in the precocial-altricial spectrum, (3) body size, and (4) flight style, as in weak, one-paced or maneuverable. Simultaneous comparison of these life history variables within a five-parameter model is presented here to better understand the evolutionary history of avian diversity, focusing on locomotor biology.

Key words Locomotor modules, Flight styles, Parental care, Precocial-altricial spectrum

1 Introduction

Aspects of avian biology such as nesting strategy, flight style, body form, and hatchling type are usually studied as separate topics, but rarely addressed as integrated and mutually dependent variables. Herein, I suggest that it is also particularly insightful to compare range and expression among each of these variables together, within an integrated matrix. Consistent trends are then observed among suites of traits for locomotor and life history features when surveying primitive and derived avian taxa, for which predation pressure appears to be the primary selective force triggering and molding the changes. To begin, I briefly review the five model parameters involved.

2 The five parameters

Avian body plans can be viewed as a composite of three discrete locomotor modules — forelimbs, hind limbs, and tail — which are differentially elaborated according to specializations in life-style (Gatesy and Dial, 1996). Unique among vertebrates, these three avian locomotor modules are operated by separate muscle groups, thus permitting each module to function without necessarily impinging on the other. A differential investment in the hind limb or forelimb module results in predictably distinct flight styles and behaviors.

Nest building varies from a simple accumulation of materials on the ground to elaborately built structures placed in secluded and elevated positions (Collias and Collias, 1984). The progression from simple to complex nest construction appears to correlate with an increasing effort to protect young from predators (Nice, 1962; Skutch, 1985; Martin, 1988). An increase in the complexity of nest building, as well as in the feeding and protection of young, correlates

with morphological emphasis on the anatomy of the forelimb and, to a lesser degree, tail.

The precocial-altricial spectrum ranges from the megapodes, whose advanced well-feathered hatchlings are virtually flight-capable from day one, to the Passeriformes, the chicks of which are nearly embryonic, hatching naked, blind, thermally dependent, and essentially incapable of movement (Ricklefs, 1983; Starck and Ricklefs, 1998). The spectrum is unevenly distributed, altricial developmental stages predominating in the great majority of birds today (Starck, 1993). Precocial development may be considered a primitive condition while altricial development correlates with advances in parental care.

Most altricial species are small in body size while precocial taxa are relatively large. Birds span over five orders of magnitude in body size, extant species ranging from the 5 g Cuban bee hummingbird to the ostrich, exceeding 150 kg (Peters, 1983; Calder, 1984). The relationship between body size and power output means that smaller birds can make more of their environment on the wing. While many small species within an order are capable of vertical flight, the larger members can only rise at shallower angles, as in the Psittaciformes.

The range and diversity of flying abilities among birds is extraordinary (Savile, 1957; Norberg, 1990; Warrick, 1998). Specific morphological attributes facilitate high maneuverability and linear acceleration. Generally, species that are intrinsically maneuverable possess larger wings relative to body mass; and species that are facultatively maneuverable have the ability to generate high mass-specific power at slow speeds by creating large force asymmetries between the two wings (Warrick, *l.c.*).

3 Five-way comparison of the parameters

Inspection of the trends among primitive and derived taxa in the above five variables provides insights into a fairly straightforward evolutionary trajectory (Fig. 1). The more primitive groups possess the following characters: large body size, superprecocial to precocial young, locomotor morphology dominated by the hind limb module, minimal parental care, flightlessness or capacity for only brief, episodic flight, and simple ground nesting (e.g., megapodes, most other Galliformes, some Anseriformes). The next taxonomic cluster exhibits relatively large body size, precocial young, constricted flight styles, ground or platform nests, and increased propensity for parental care (e.g., Podicipediformes, Gruiformes, Gaviiformes, and some Anseriformes). The next level of complexity comprises taxa with medium-to-large body size, a more evenly balanced locomotor arrangement involving tail, hind limb and forelimb, simple elevated nests, altricial young with increased parental care, and increased flight machinery with more diverse flight styles (e.g., Columbiformes, Ciconiiformes, Falconiformes).

The most morphologically, ecologically, and versatile fliers are the highly derived and speciose Passeriformes, characterized by small body size, well-balanced investment in hind limb, tail, and forelimb modules with diverse wing

and tail designs, a wide range of feeding and nesting habits, intense parental care, and altricial-to-superaltricial young. Positioned at the terminus in this schema are the aerial cursors (e.g., Apodidae, Trochilidae, Hirudinidae), endowed with extraordinary flight capabilities. This group exhibits small body size, atrophic hind limb modules and pronounced forelimb musculoskeletal investment, elaborately constructed and secluded nests, (or simple nests placed within predator-free environments), intense parental care, and superaltricial young.

Taken together, the trends in the five variables are coherently linear and unidirectional, the more derived species sequestering young in a secured nest and providing significant parental care, thus permitting a morphological trajectory towards reduced hind limb and increased forelimb investment for increased flight capacity (Fig. 1). These observations suggest that bipedal, hind limb-dominated proto-avian theropods were relatively large, hatched precocial young, provided rudimentary parental care, and had forelimbs to assist incline running as they escaped to elevated refugia (Dial, 2003). This interpretation is consistent with most, if not all, of the recently discovered proto-avian paleontological material in China and Asia (e.g., *Caudipteryx*), as these fossils represent long-legged, cursorial bipeds with partial wings (Norell et al., 2002; Ji et al., 1998).

4 Conclusions

Among vertebrates, birds possess a unique modular anatomical arrangement permitting different modes of locomotion from regionally specific musculoskeletal modules (forelimbs, hind limbs, and tail). Body size, developmental stage at hatching, flight style, nesting biology and locomotor modularity appear to be intimately correlated. Simultaneous inspection of trends among these attributes suggests that primitive taxa are relatively large, cursorial, hind limb-dominated species building crude ground nests and providing relatively unsophisticated parental care. In contrast, derived taxa possess complex flight capabilities in which forelimb and tail dominate, are physically small, and exhibit complex parental care in order to sequester helpless young within a complexly engineered, elevated nest. The evolution of birds may thus be viewed as a morphological shift from hind limb locomotor machinery, consistent with primitive extant species as well as proto-avian theropods, to forelimb-powered flight stimulated primarily by predation pressure and motivated secondarily by filling niches to exploit diverse food resources.

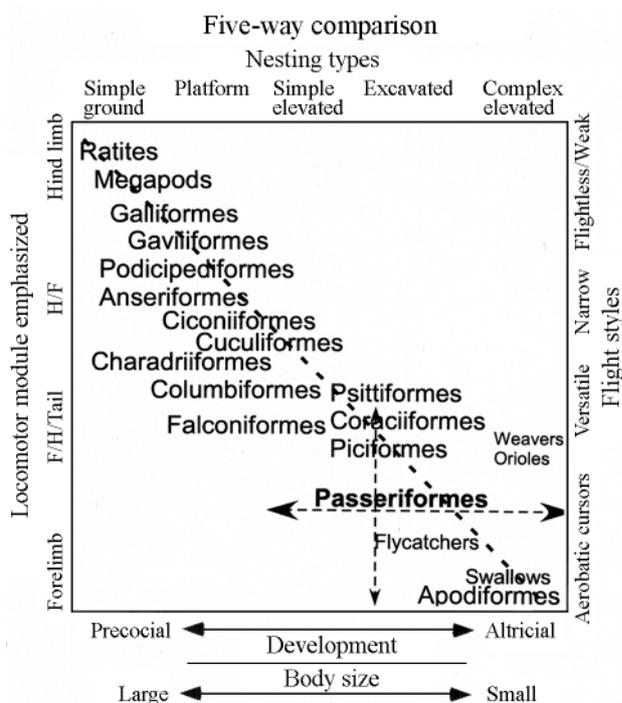


Fig. 1 Five-way comparison of variables associated with avian locomotion and the evolution of life-history traits

Note the nearly linear progression in the suite of traits associated with primitive bipedal cursors towards aerial cursors. Passerines exhibit the greatest diversity in form and flight styles by attaining small body size, substantial forelimb and tail modular investment, and complex nesting biology (H=hind limb-, F=forelimb-, Tail=tail-modules).

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S27-5 Molecular modules and morphology

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Abstract We present a phylogenetic perspective on morphological and molecular characters and character complexes and their properties at different hierarchical levels, using both examples from literature and case studies in carduelid finches and pigeons. Phylogenetic hypotheses inferred from both molecular (cytochrome-*b*) and morphological characters (plumage ornamentations), and combined analyses in carduelids, indicate that in both datasets corresponding patterns occur at particular nodes and systematic levels. A new method is introduced to partition and quantify correlation in cladogenetic, anagenetic and environmental signal, to estimate by their degree of similarity the underlying factors producing that correspondence.

Key words Cladogenesis, Anagenesis, Environmental signal, Matrix similarity, Cytochrome-*b*, Plumage ornamentation

1 Introduction

One approach towards realizing a holistic view of organismal structure and evolution is the concept of morphological integration (Olson and Miller, 1958). Its tools are morphometrics, the quantitative study of changes in the size and shape of the organism during ontogeny and evolution (Crowe, 1994). Patterns of trait correlation are traced to identify the underlying processes that produce corresponding structures. In the modern formulation of the concept of morphological integration (Cheverud, 1982, 1988; Wagner, 1996; Wagner and Altenberg, 1996; Chernoff and Magwene, 1999; Magwene, 2001), the importance of pattern correspondences and of the evolution of modularity are stressed, and principles of quantitative genetics (Steppan et al., 2002) as well as aspects of developmental biology (Nemeschkal, 1999) are included.

Phenotype-genotype mapping are a focus in current research, testing also the involvement of ecology (Marroig and Cheverud, 2001), life history (Roff, 1996) and other environmental factors, as well as physiology (Villani et al., 1992) and behavior (Bloemer and Crowe, 1998). Both the ideas of “morphological integration” and “modularity” are now being used at the molecular genetic level (Raff, 1996; Wagner and Altenberg, 1996) to describe hierarchical levels and interactions within and between biological domains. Most investigation into morphological integration and modularity, however, has focused on morphological or phenotypic (Badyaev et al. 2001) characters at the microevolutionary level, in analyses of character coupling or decoupling within or between populations. At the macroevolutionary level, trans-specific exploration of characters or character

modules are the tools to explore the frameworks of phylogenetic effect.

2 Molecular and morphological modularity in phylogenetics

For phylogenetic inference, the most frequently used exploratory gene is cytochrome-*b*, a protein-coding mitochondrial gene. Analogous to morphological evolution, molecular evolution is affected by its own constraints, such as the genetic code, secondary and tertiary structure, and replication rate or gene or protein function (for an overview, see Mindell and Thacker, 1996). In an analysis of falcons and caracaras, the extent of substitution saturation in cytochrome *b* was correlated with functional modules in its structure (Griffiths, 1997). In several species of carduelid finches, productive change in aminoacids occurs solely (van den Elzen, 2001) or preferredly (Arnaiz-Villena et al., in press) within the transmembrane region of the cytochrome *b* molecule. That region has been found to be hypervariable in mammals too (Irwin et al., 1991).

Results from our investigations add to the phylogenetic perspective. In two disparate bird families (Fringillidae-Carduelinae and Columbidae), infraspecific analyses of skeletal characters exhibited patterns of character correlation that corresponded with developmental requirements, and may be taken as modules of the body plan (Nemeschkal, 1999). And a trans-specific investigation of the same species (van den Elzen et al., 1987; Nemeschkal et al., 1990) identified several units of character complexes that reflect patterns of shared biological roles. These character modules tend to coevolve and are clade specific (Nemeschkal et

al., 1992). Finches and pigeons differ in their levels of morphological integration and in the variance of phenotypic characters, as well as in the numbers of characters integrated within covarying units. Such differences reflect phylogenetic effect, the geological age of pigeons probably doubling that of finches. Yet phylogenetic effect has scarcely been considered in phenotype-genotype matching, even though there is a comprehensive literature dealing indirectly with it.

3 Alternative perspectives on the phenotype-genotype match: the phylogenetic approach

Phylogenetic methods estimate relationships on the basis of change in homologous, novel characters, which in cladistic terminology are synapomorphies, or shared derived characters inherited from a common ancestor. In the cladistic approach to phylogeny, characters are not evaluated by quantity (=measurements) but quality (=occurrence of characters and their states). These are transformed into a numerical distance matrix to link taxa by parsimony (=minimal number of steps in character change) and/or degrees of distance (extent of differences in characters). Cladogenetic (=speciation) events are then mapped on to a dichotomously bifurcating branch-pattern.

This phylogenetic model rests on the assumption that both phenetic and genetic distance matrices include a module of identically or similarly structured cladogenetic information (patterns of speciation, phylogenetic signal), and a module of anagenetic information (number of evolutionary steps within a species or lineage not associated with speciation). Phylogenetic estimates of relationships among taxonomic groups are thought to improve in precision with the combination of different datasets. In the concept of total evidence (Kluge, 1989), all relevant character information is combined in a single phylogenetic analysis. The total evidence approach has been practised successfully in diverse organismal groups at various systematic levels (e. g., Eernisse and Kluge, 1993; Mattern and McLennan, 2000; overview in Chippindale and Wiens, 1994), including birds (e. g., Zink and Blackwell, 1996; Griffiths, 1999; Johnson and Sorensson, 1999).

A restricted, conditional combination approach (Bull et al., 1993; Gatesy et al., 1999) only allows the combination of data sets that are not significantly contradictory when tested for congruence. In cases of incongruence, comparisons of single data sets can elucidate the underlying evolutionary phenomena (McCracken and Sheldon, 1998). If phylogenetic tree-length is accepted as a measure of evolutionary change, incongruence between trees built from different data sets may be interpreted as differences in evolutionary steps manifested in these characters.

In the Carduelinae, we have inferred phylogenetic hypotheses from siskins (van den Elzen et al., 2001) and serins (Arnaiz-Villena et al., in press) using both molecular

(cytochrome-*b*) and morphological characters (plumage features) and a combination of both data sets. Results indicate that corresponding patterns of characters occur at particular nodes and systematic levels in both species-groups. Tempo of diversification in plumage characteristics precedes that of molecular change. In siskins, moreover, phenotypic change is faster in male than female ornamentation, but not in serins.

To quantify similarity patterns between these different taxa and data sets, matrix comparison can be used. This approach has been used successfully in birds in genealogical comparisons of phenotypic and genetic differentiation in the South American antwrens (Hackett and Rosenberg, 1990). Distance matrices for plumage features, morphometrics and genetic distance based on protein electrophoresis were compared by Mantel's (1967) test. General patterns of genetic diversification paralleled those of both sets of morphological traits, and rate of plumage feature divergence again exceeded that for the protein genes screened; rates for morphometric change were slowest. To quantify phylogenetic relationships and effect, pattern correlations may be tested by application of cladistic principles.

4 Separating cladogenetic and anagenetic signal in phylogeny

Accordingly, we outline here a new approach to statistically separate cladogenetic from non-cladogenetic signal in phenotypic and molecular distance matrices. We compared distance patterns between these matrices and their separated portions and to environmental parameters, to estimate the underlying factors producing correspondence. A detailed description of the method and its material is in preparation. Three hierarchical datasets for siskins were built for comparison: one phenetic from plumage ornamentation of the phenotype, another molecular from DNA sequences of the mitochondrial cytochrome *b* gene, and the third environmental from such information such as geography, climate and habitat.

Distance matrices were calculated in the same way for the three datasets by the phylogenetic software package PAUP* (Swofford, 2001). Mean character differences (uncorrected pairwise character distance, mean character difference) as offered by PAUP* were taken as distance measures for all but the single character datasets. Phylogenetic distance (cladogenesis) was estimated from the topology of a cytochrome *b* gene NJ-bootstrap tree based on maximum likelihood, counting branching points between each species-pair. This is here referred to as the cladistic matrix, because it includes cladogenetic information derived from cladistic principles.

Using a modified Mantel's test (Nemeschkal, 1991, 1999), significant correspondence was found between basic molecular and phenotypic distance matrices, and between both of them and the cladistic matrix (ZEISUO-MOLZM, $r=0.77352$, $P<0.0016^{**}$, ZEIPHYLL-ZEISUO, $r=$

0.5153854, $P < 0.02^*$, ZEIPHYLL-MOLZM, $r = 0.4876437$, $P < 0.0001^{***}$). We interpret these findings as indicating that cladogenesis is the underlying factor inducing proportionality of character change in both phenetic and molecular characters. The observed congruence among cladistic, phenetic and genetic distance matrices is not unexpected, being concordant with other observations of pattern congruence between phenotypic and genetic matrices mentioned above. It also agrees with similarities in tree topology among morphological- and molecular- based phylogenies at different systematic levels from species to class (e. g., Smith et al., 1992; Potter and Doyle, 1994; Bridge et al., 1995; Griffiths, 1999; Titus and Frost, 1996; Frost et al., 2001; but see Baker et al., 1998 for conflicting results).

The hypothetical environmental matrix also exhibited significant pattern similarity with the rest. Mantel's test revealed significant congruence between body mass (SIZE-ZEISUO, $r = 0.50283$, $P < 0.0438^*$), the complete environmental matrix (ENVIR-ZEISUO, $r = 0.57275$, $P < 0.0125^*$), and its respective its biogeographic and topographic portions (GEOG-ZEISUO, $r = 0.57227$, $P < 0.0298^*$, AREA-ZEISUO, $r = 0.68307$, $P < 0.0012^{**}$), but not with habitat nor climatic data. Molecular distance (MOLZM) exhibited fewer (two instead of four) significant similarities in pattern, matching phenetic matrix correspondence in biogeographical and topographic attributes (GEOG-MOLZM, $r = 0.52038$, $P < 0.0013^{**}$, AREA-MOLZM, $r = 0.69395$, $P < 0.004^{***}$), but not in body mass (SIZE) nor the complete environmental dataset (ENVIR). The cladistic matrix ZEIPHYLL, as expected, resembled the genetic matrix from which it had been extracted (GEOG-ZEIPHYLL, $r = 0.52938$, $P < 0.02^*$; AREA-ZEIPHYLL, $r = 0.52042$, $P < 0.009^{**}$).

Our results from siskins in general corroborate already well-known interrelationships between geographic distribution and phylogeny, especially in distribution pattern and cladogenetic events. The results also encourage application of Lande's (1979) model for assessing phenotypic variance-covariance to distance measure analysis. This will open the way for integrating cladogenetic, biogeographical and ecological information into the explanations of morphogenesis over the interface of quantitative genetics theory (Steppan et al., 2002).

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Symposium 29 New developments in the study of seabird foraging

Introduction

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The inception of new technologies for studying the behavior of seabirds in their natural environment, coupled with the large size of the birds and the relative ease with which they can be captured, has led to seabirds pioneering a recent thrust in understanding animal foraging ecology. Although seabirds may travel thousands of kilometers or dive to depths in excess of several hundred meters on a single foraging sortie, new technologies now make it possible to monitor and quantify their behavior precisely. This is in stark contrast with previous studies, where inability to gather rigorous quantitative data from free-living birds meant that testing theoretical models of foraging decisions rested largely on laboratory studies.

This symposium reviews progress in the field, and evaluates the strategies that seabirds use to enhance chances of finding food while minimizing energy expenditure. This includes assessments of how procellariiforms use olfaction in hunting (Gabrielle Nevitt), how remote sensing technology can track decision-making

in diving penguins (Rory Wilson), what biomechanical and physiological constraints there are to diving in foraging penguins (Katsufumi Sato and colleagues), and how great cormorants (*Phalacrocorax carbo*) maintain minimum energetic costs during foraging despite living in thermally taxing environments (David Grémillet and colleagues). A fifth paper, integrating data and predictions about the seasonal distribution of seabirds and their prey from ship- and colony-based studies, was presented as an oral only. Titled 'Seabirds foraging in a heterogeneous environment' (George L. Hunt and Henri Weimerskirch), its abstract is published in the Abstract volume for the Congress.

Seabirds forage over the oceans of the world, at the top of the food chain. Combining remote sensing and ship- and colony- based studies of them with measurements of oceanic parameters can be expected to tell us a great deal about the functioning of the marine environment and its temporal and spatial variability.

S29-1 Olfactory foraging strategies of procellariiform seabirds

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Abstract The study of olfactory foraging ability in procellariiform seabirds is now beginning to explore how species are morphologically and behaviorally adapted to track odor plumes, and to relate these findings to models of odor transport in natural situations. According to the models, odors in atmospheric flow tend to be dispersed laterally and downwind in turbulent plumes. Because turbulent transport processes operate more rapidly than molecular diffusion, plumes of airborne odors have an irregular, patchy distribution of concentrations. For a foraging seabird, tracking the distribution of high concentration, scented eddies over the ocean to a source is thus a complex problem. This paper explores this topic, first by reviewing current understanding of olfactory foraging by procellariiform seabirds at large and small spatial scales. I then discuss different behavioral mechanisms that procellariiform species use to track odors, and show that adaptive solutions to this problem vary considerably between species, depending on olfactory ability and flight style. I also review how different olfactory and visual modalities mediate intra- and inter-specific interactions between foraging seabirds at small spatial scales.

Key words Olfaction, Procellariiform seabirds, Foraging strategies, Petrel

1 Introduction

Antarctic procellariiform seabirds roam over the oceans of the world in search of patchily distributed food resources. Satellite telemetry and other remote monitoring techniques have now proven that many species routinely travel distances ranging from hundreds to thousands of kilometers during foraging trips (Weimerskirch, 1998). While satellite telemetry has provided substantial information about where species forage, little is known about the underlying sensory and behavioral mechanisms that contribute to foraging success. How do procellariiforms know where to forage, or recognize productive areas on the open ocean? While other sensory modalities should not be overlooked, well-developed olfactory systems, and the ability to detect odors associated with potential prey, has been well established for several species (Bang, 1965, 1966; Bang and Cobb, 1968; Grubb, 1972; Hutchison and Wenzel, 1980; Nevitt, 1999a; Nevitt et al., 1995; Wenzel, 1967; reviewed by Nevitt, 2001; Warham, 1996). There is an emerging picture that a keen sense of smell is fundamental to foraging success in many species; yet the strategies used to hunt prey by smell are more complex than simply tracking odors of target prey.

This paper provides a brief overview of some of the new developments in our understanding of olfactory foraging by procellariiform seabirds and offers some ideas for future investigation. I first address a new conceptual model which suggests that olfactory foraging occurs at different spatial scales over the ocean. I then review several underlying issues indicative of adaptations for optimizing olfac-

tory search at small spatial scales. Finally, I review how different olfactory and visual modalities mediate intra- and inter-specific interactions between foraging seabirds at small spatial scales.

2 Foraging at different spatial scales

Based largely on studies conducted in the southern oceans, current understanding perceives olfactory foraging as occurring at both large and small scales. This model has been reviewed in detail elsewhere with a more comprehensive explanation (Nevitt, 1999b, 2000, 2001). According to it, procellariiform seabirds use changes in the odor landscape at large scales of hundreds or thousands of kilometers to alert themselves that they have arrived at a productive area for foraging. Elevations in scents associated with primary production such as dimethyl sulfide (DMS) have been implicated as landscape indicators of productive foraging grounds (Nevitt, 1999a, 2000; Nevitt et al., 1995). The new model suggests that birds do not track changes in odor gradients over great distances, but rather that potentially rich feeding grounds share an olfactory signature which the long distance forager recognizes upon arrival.

Once a seabird has arrived at a productive area, the problem becomes one of locating exploitable prey patches (Fig. 1). A change in the large-scale olfactory landscape may trigger a bird to begin a relatively small-scale area-restricted search of the region using a combination of visual, olfactory, and other sensory cues to pinpoint a prey patch (Nevitt and Veit, 1999). Once an odor plume is detected, some species may zigzag upwind to sense out the odor

source of the prey patch (Hutchison and Wenzel, 1980). Other species are more likely to use visual cues to locate prey patches, either by spotting prey directly or by seeing aggregations of other foraging seabirds at the patch.

3 Tracking the plume to its source: optimizing search at small spatial scales

We are now beginning to explore the morphological and behavioral adaptations that different species use to track odor plumes, and to relate them to conceptual models of odor transport in natural situations. It is generally assumed that odors in atmospheric flow tend to be dispersed laterally and downwind in turbulent plumes. Because turbulent transport processes operate more rapidly than the dissipating eddies of molecular diffusion, plumes of airborne

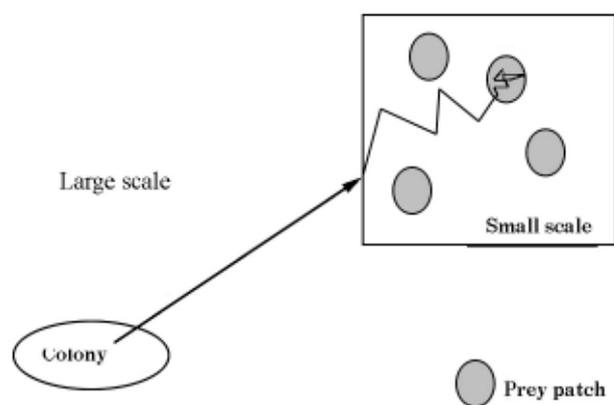


Fig. 1 Large and small scale search strategies
 Shaded (grey) areas indicate prey patches in a productive area (square outline) far from the colony. Lines with arrowheads indicate the theoretical flight trajectory of the seabird. As the seabird arrives at the foraging area, the changing olfactory landscape is predicted to trigger an area-restricted search (Nevitt and Veit, 1999).

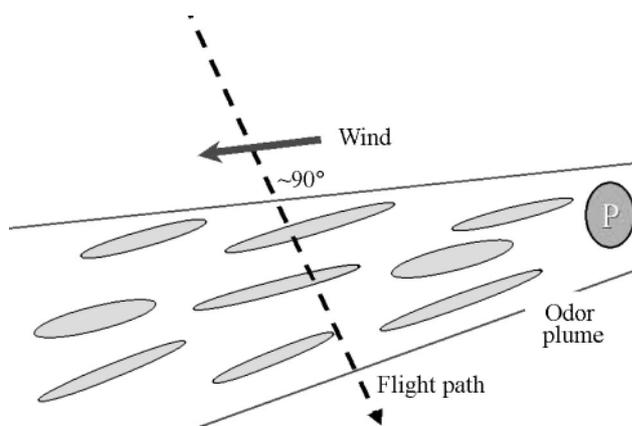


Fig. 2 Encountering the odor plume
 This diagram shows an odor plume emitted by a theoretical prey patch “P” on the right-hand side of the diagram. Scented eddies are indicated as grey ovals streaming downwind from the prey patch. For a foraging petrel, the probability of encountering the odor plume is maximized by flying directly cross-wind. This flight path is indicated by a dashed line perpendicular to the direction of the wind.

odors have an irregular, patchy distribution of concentrations. For a foraging seabird, tracking the distribution of high concentration, scented eddies over the ocean to a source is thus a complex problem that may be solved in different ways.

The basic algorithm for olfactory search is diagramed in Figs. 2 and 3 (Dusenbury, 1992). Odors emitted from a prey patch will disperse downwind and become subject to turbulent mixing. The odor plume is spatially discontinuous, presenting the bird with odor patches (eddies) that can be almost as concentrated as at the source. Energetic considerations aside, a bird foraging by smell should maximize its chances of encountering a random odor plume by flying directly crosswind (Fig. 2; Dusenbury, 1992). Once a scented eddy is encountered, the bird will travel upwind within that eddy until it loses the scent (Fig. 3). The bird then turns directly crosswind again to cast about for the odor. Such casting behavior is common among animals that track odor plumes (e.g., Carde, 1996 for moths) because it maximizes the likelihood of re-encountering a plume. Upwind, zigzag flight is commonly seen in many of the smaller procellariiforms in association with odor traces at sea (Hutchison and Wenzel, 1980; Warham, 1996).

Despite its simplification, the model shows that species adapted to search by olfaction should also be adapted to flying directly crosswind, simply because this behavior maximizes the chances of encountering an odor plume. Although our laboratory has not studied this issue, data reported by others support it. For example, Spear and Ainley (1997) made shipboard observations of flight direction relative to wind direction for a variety of procellariiform species. They found that storm-petrels tended to fly perpendicular to, or across, the predominant wind direction. These birds are highly olfactory, and commonly zigzag upwind towards odor patches deployed experimentally at sea (reviewed in Nevitt, 1999b).

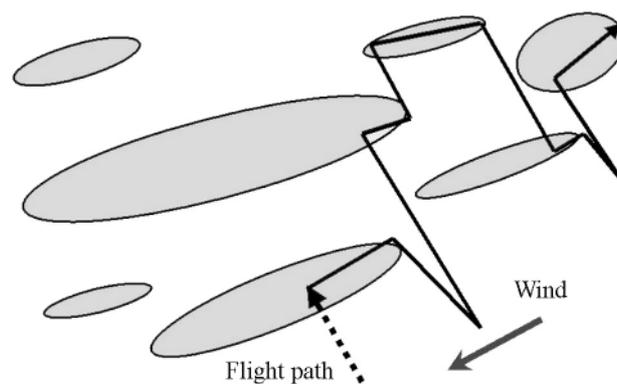


Fig. 3 Locating the source of the odor plume
 The figure shows the zigzag flight path used to track an odor plume to its source (upper right hand corner, not shown). Scented eddies are indicated as gray ovals, as in Fig. 2. The initial crosswind flight path is indicated by a dotted line. The solid line indicates the flight path once the odor plume is encountered.

In contrast, Spear and Ainley's data indicate that dynamic soarers, such as albatrosses, fly more obliquely crosswind. Energetic considerations notwithstanding, this result is consistent with a foraging strategy that is less reliant on olfactory cues, in that constraints on the flight style may lessen the chances of encountering an odor plume. Elucidating the relationship between flight energetics and sensory ecology in driving different foraging strategies is clearly a ripe area for future study.

Incorporating technologies to track fine-scale movements of individual foraging birds gets over many of the limitations of shipboard observational studies (Weimerskirch et al., 2002). Although sample sizes are smaller, the fine scale resolution of the flight trajectories that individual birds follow allows for more refined predictions about search behavior under different foraging conditions. For example, Spear and Ainley's data (1997) indicate that albatrosses tend to fly obliquely to the wind, yet that behavior could change during active foraging events. Birds might choose flight directions that are energetically more costly if the chance of finding prey is high.

Fine-scale monitoring will help to elucidate such questions, and further determine when different sensory strategies are likely to be employed for finding prey. Species such as the wandering albatross (*Diomedea exulans*), for example, forage opportunistically, presumably on both dead and live prey, using a combination of sensory strategies including olfaction and sight. Because wandering albatrosses are sensitive to prey-related odors, detailing fine-scale flight trajectories with respect to wind direction should be useful in distinguishing olfactory from visual or multimodal search strategies (Fig. 4). Casting behavior may thus be restricted to highly productive areas, and to particular types of prey (e.g., squid carrion), or to foraging areas where specific prey types are likely to be found. Casting behavior may also vary with weather condition, or with the type of foraging trip being made, short or long (Weimerskirch, 1998). There are clearly a multitude of ques-

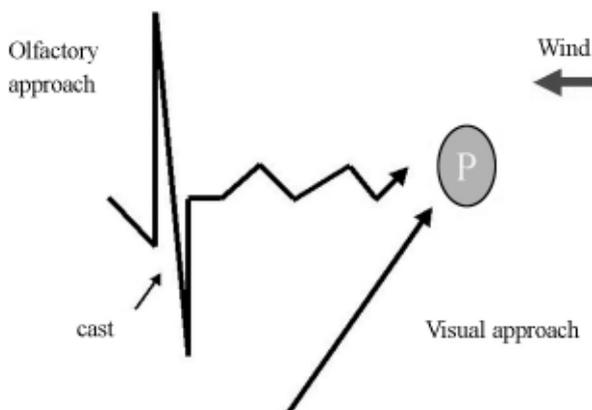


Fig. 4 Fine scale flight paths indicate differences between the sensory modalities used to locate a prey patch

The characteristic olfactory “cast” is indicated by a broad zig-zag sweep perpendicular to (across) the direction of the wind.

tions that will be intriguing to explore with GPS technology.

4 Interspecific Interactions

It is becoming recognized that different olfactory abilities mediate intra- and inter-specific interactions among foraging seabirds at small spatial scales. Controlled behavioral experiments show that different species of procellariiforms are sensitive to a variety of naturally scented compounds associated with prey. Responses have been detailed for approximately 20 species of Antarctic procellariiforms to the following odors: krill (crude extract, trimethyl amine, pyrazine, 2,3-dimethyl pyrazine), squid, cod liver oil, herring oil and phenyl ethyl alcohol (Cunningham et al., submitted; Nevitt, 1999a, b; Nevitt et al., 1995), as well as to biogenic sulfurous compounds associated with phytoplankton (dimethyl sulfide, DMS) (Nevitt et al., 1995), and krill (Daly and DiTullio, 1996). I now review several basic trends that have been identified, particularly with respect to how different odor sensitivities are linked to foraging at mixed-species feeding aggregations near South Georgia Island (Nevitt, 2000; Nevitt and Veit, 1999).

The term “mixed-species feeding aggregation” is used to describe large gatherings of birds — often numbering hundreds — which exploit ephemeral food bonanzas, such as a krill swarm near the surface. How these aggregations form is not known, but results from empirical studies investigating the sensitivity of various procellariiform species to prey related odors near South Georgia Island suggest use of two competing strategies: “early detection” and “late detection”.

For early detectors such as storm-petrels, olfaction provides a means of opportunistically exploiting small prey patches or larger krill swarms before late detectors arrive to displace them. These species are highly sensitive to DMS and will track DMS plumes in experimental trials. As well as serving as a general indicator of high primary productivity, DMS emissions increase as phytoplankton are grazed by krill, particularly when krill swarms aggregate (Nevitt, 1999a). Thus the ability to detect and respond to DMS and other odors may give highly olfactory species such as storm-petrels an advantage in locating and exploiting available food resources quickly and efficiently.

In contrast, late detectors such as albatrosses and giant petrels take their cues from the activity patterns of other seabirds. In experimental trials, late detectors do not track DMS, but instead recruit to scents associated with macerated krill and are highly responsive to the activity of con- and heterospecifics (Nevitt, 1999a, 1999b). These species probably arrive after aggregations have started to form, and are primarily attracted by visual cues. Late detectors tend to be highly visible and aggressive at mixed-species feeding aggregations, and a nuisance for smaller species (Nevitt, 1999a). It is not surprising that late detectors often dominate mixed-species feeding aggregations (Harrison et al., 1991), and probably represent a threat to smaller, early detectors that could fall prey to them.

These patterns are significant because they suggest that procellariiform species have evolved different strategies for foraging based partly on sensory factors. Some species are clearly more highly adapted to exploit olfactory cues, and others better fitted to combine visual and olfactory cues, according to the situation. Because species that tend to be olfactory also nest in burrows, we are currently exploring whether the environment of the burrow predisposes chicks to learn olfactory cues brought back by the parents early in life. These and other questions suggest productive areas for future research.

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S29-2 Fishing made easy: tips and tricks on decisions for optimal foraging in Magellanic penguins, *Spheniscus magellanicus*

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Abstract Diving and foraging in Magellanic penguins was studied at Cabo Virgenes and San Julian, Argentina, by equipping the penguins with loggers recording swim speed, heading and dive depth, together with beak angle to determine when prey were ingested. Gross dive parameters (maximum depth, duration, descent and ascent speeds) conformed with patterns described for penguins in general, and were primarily dependent of the maximum depth of dives. Maximum depth was 11 m (*SD* 9), duration 50 s (*SD* 24), and descent and ascent rates both 0.8 m/s (*SD* 0.5). Based on their characteristics, dives could be grouped into different types with three different primary functions: traveling, searching or feeding. Dives followed a smooth, predictable course in heading, depth and speed (smooth dives), unless changed by suspected external stimuli, marked by abrupt inflections in measured parameters denoting a decision to change strategy (inflected dives). Comparison of parameters in smooth and inflected dives reveals how the behavioral strategy adopted enhances prey encounter and capture.

Key words Magellanic penguin, Foraging strategies, Diving, Prey capture

1 Introduction

The success of a foraging organism depends on the ability of that organism to determine the whereabouts of food and on its ability to make quick appropriate decisions that lead to efficient ingestion of that food. Most studies investigating predator-prey relations in this context have come from terrestrial animals (Goss-Custard, 1977; cf. Pyke et al., 1977). Foraging conditions for terrestrial predators tend, however, to be simpler than those of diving endotherms because access to oxygen is unlimited and so plays no central role in decision-making. There have been a number of studies theorizing about which such factors might be important in foraging marine endotherms (Mori, 1998; Thompson and Fedak, 2001), but such studies have been hampered by a paucity of data on, first, the behavior of the study animal underwater, and, secondly, the point at which decisions actually occur there. The development of new technology for attaching remote-sensing devices to free-living animals now allows major insights to be gained in both these areas.

This paper presents information from the use of such technology to examine the foraging behavior in free-living Magellanic penguins *Spheniscus magellanicus*, and addresses when and where decisions are made and their consequences for foraging success.

2 Methods

The results presented here stem from field work conducted on Magellanic penguins (*Spheniscus magellanicus*) brooding small chicks at Cabo Virgenes (52°24'S, 68°26'W) and San Julian (49°16'S, 67°42'W) in Santa Cruz, Argentina,

during November–December, 2000 and 2001. Remote sensing technology was used on a total of 47 birds by attaching to them three types of device, produced by Driesen and Kern GmbH, Bad Bramsted, Germany. The devices were:

Speed/depth gauges, which recorded speed (via a moment arm linked to a pressure transducer corrected for depth) and depth (via a simple medium-separated transducer) with 16 bit resolution logging at intervals of either 0.5, 1 or 5 Hz in a 4 mbyte flash RA memory (44 deployments). Details are given in Wilson et al. (2002a).

Inter-mandibular angle sensors (IMASEN) which recorded beak angle in diving birds (14 deployments). Here, a Hall sensor attached to the upper mandible responded to the magnetic field produced by a small, rare earth magnet glued to the lower mandible, such that changed magnetic field with changing beak angle is perceived by the sensor (Wilson et al., 2002b). Sensor output, calibrated to derive beak angle, was recorded with 10 bit resolution by a logger with a 4 mbyte memory at intervals of 8 to 20 Hz. Measurement of bill angle at high frequencies enables elucidation of prey capture as well as respiratory frequency (Wilson et al., 2002b) and tidal volume (unpubl. data).

Integrated movement assessing sensory units (IMASU) which recorded flipper angle at a frequency of 30 Hz (18 deployments). These units were modified IMASEN systems (see above), using Hall sensors glued to the penguin axillar to sense the position of penguin flippers via a wing-attached magnet. Full details are given in Wilson and Liebsch (2003).

The devices were attached singly as well as in combination on birds brooding the chicks and were left in place

for a single foraging trip, typically lasting for between 12 and 30 h. On five occasions, all three units were deployed on the same bird. Logging units were attached to the center of the lower back to minimize drag (Bannasch et al., 1994) and fitted with tape as described by Wilson et al. (1997). Thin (0.8 mm diam.) cables run under feathers linked the Hall sensors to the logging units. On recovery, the data were downloaded and assessed using the MT-flip program (Jensen Software Systems, Laboe, Germany), which simultaneously displays data from various devices with differing logging regimes.

The work here discusses initial patterns apparent in the data, without exhaustive analytical treatment. In order to identify foraging decisions, data were examined for points of inflection over recording time. Although birds may decide to continue with a particular strategy resulting in no obvious change in monitored data, such points of inflection signal a marked change in behavior that probably follows a decision. For rigorous assessment of such changes, it is desirable that inflection points be definable mathematically. This can be undertaken, for example, by deriving running means of values and examining the points at which the means intersect limits based on defined confidence intervals (Wilson and Peters, 1999). The treatment presented here ignores such an approach because the mathematical definition is often modified until it conforms with common sense and requires considerable analysis for each of the variables. As this study uses a number of such variables, I have limited myself to reporting, however subjectively, what I consider to be obvious points of inflection.

Two types of decision are distinguished here. The first is of binary, yes/no decisions, dictating whether a particular behavior is undertaken or not. An example is the decision to dive or remain at the surface. The second is of analogue decisions, which modify a particular behavior, as, for example, in the decision to increase swimming speed to capture prey.

3 Results and discussion

3.1 Initiation of diving

If the dive is assumed to begin at the surface, several points of inflection in the electronic record indicate its initiation, the most obvious of these being cessation of breathing followed by a sudden increase in depth (Fig. 1A). Although the decision to submerge is binary, the extent to which the penguin should inhale is not. Air in the penguin respiratory system contributes to overall oxygen storage (Kooyman, 1989) and can thus potentially extend dive duration, although this is tailored by energy expenditure (Wilson et al., 1992; Lovvorn et al., 1999). The situation is further complicated by depth, because air is compressed with increasing hydrostatic pressure which reduces upthrust.

Generally, however, it is to be expected that birds that

dive deep will benefit by inspiring larger air volumes prior to diving because they may profit from the additional oxygen while reducing the costs associated with upthrust. In this context, it appears that Magellanic Penguins regulate the air inspired in the last breath according to this principle; there is a significant relationship between the beak angle in the last breath preceding a dive (a proxy for volume of air inhaled) and the depth of the dive (Fig. 1B). This indicates that the overall course of the dive is, to a large extent, predetermined at the surface.

3.2 Descent through the water column

That much of the course of the dive is predetermined before it happens is also apparent as the bird begins its descent because the rate of descent for the first few meters is correlated positively with maximum dive depth (Fig. 2A). Making the correct decision about the rate at which to descend has energetic advantages. Birds that inhale deeply should not waste time near the water surface where upthrust, and consequently energy expenditure, are high. The decision about the depth to reach is presumably based on foraging success or perhaps cues in the water (cf. Wilson and Peters, 1999; Wilson, 2002); but once this decision has been made, there are optimum ways to reach the depth, all involving swim speed and angle of descent. Culik et al. (1994b) report that penguins should generally swim at minimum energetic cost of transport.

Accordingly, penguins are somewhat limited in the speeds at which they normally swim, excluding prey chase (Fig. 2B - inset; Wilson, 1995), and so changes in descent rate are primarily brought about by variability in descent angle. Thus, penguins diving deeply minimize energy expenditure near the surface by simply diving at a steeper angle which takes them down the water column faster. However, the typical U-form of the cost of transport versus speed curve (Culik et al., 1994b) may be shifted according to current and upthrust conditions (Wilson et al., 2001; cf. Pennycuik, 1997). In this context it is interesting that there is a slight increase in swim speed with increasing depth. This may result from capacity in the penguins to invest a higher proportion of their propulsive efficiency in movement rather than simply working against upthrust.

3.3 Ascent through the water column

Both initial submergence and return to the surface are accompanied by a point of inflection in flipper angle (Fig. 3A) because the normal flipper beat underwater involves phases where the flipper is above the midline of the longitudinal axis of the body (Bannasch, 1995), a position which could not occur on the surface without the flippers coming out of the water. However, both flipper amplitude and flipper beat frequency tend to decrease with time underwater (Fig. 3A; Wilson and Liebsch, 2003). This is related to two factors, one being the angle at which the bird swims with respect to the surface, and the other the upthrust which varies with depth. As penguins are positively buoyant at most of the depths (Wilson et al., 1992), any

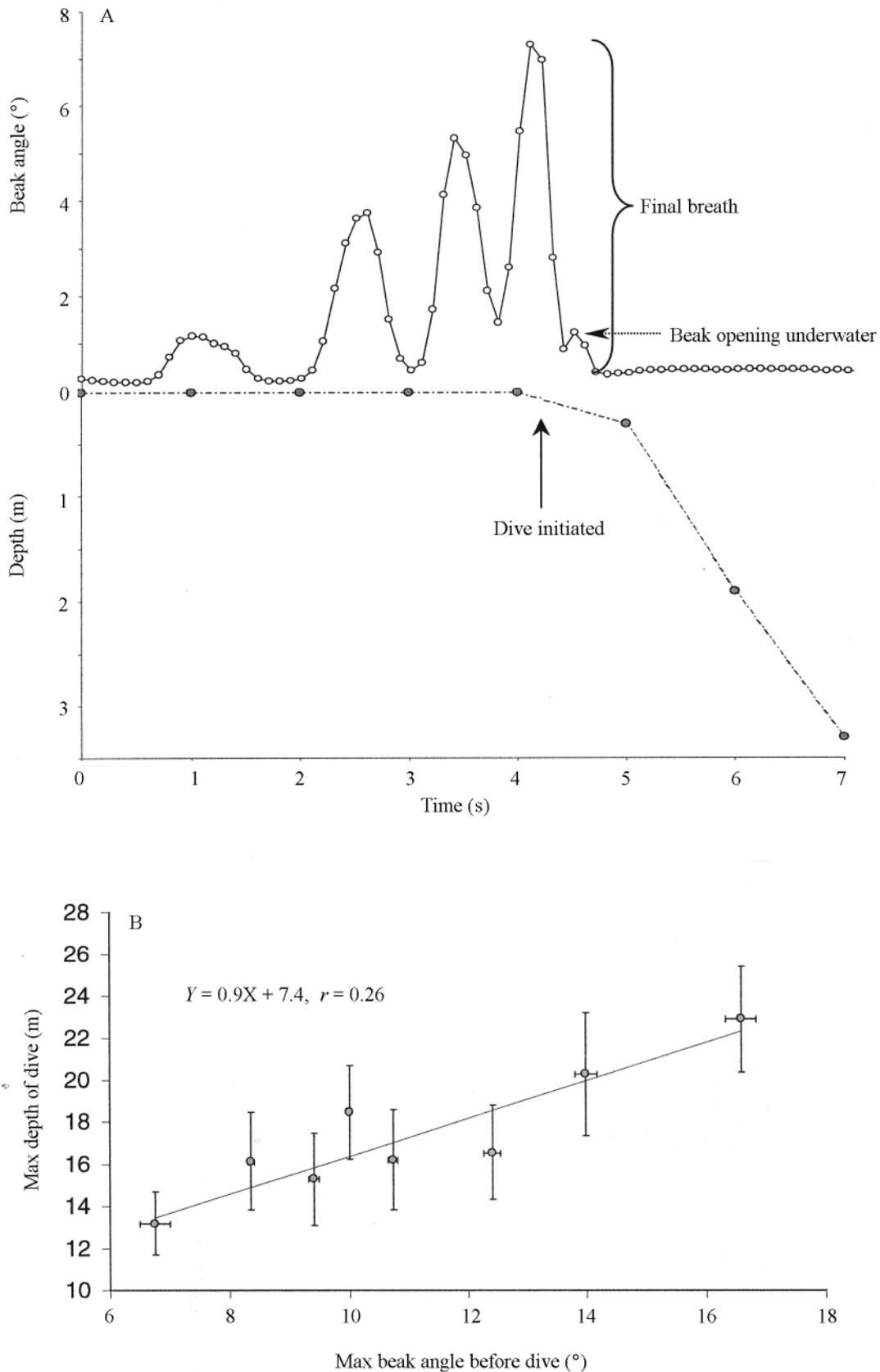


Fig. 1 (A) Breathing (denoted by rhythmic changes in beak angle) in a free-living Magellanic penguin at the surface just prior to diving; (B) Maximum beak angle in the last breath before submergence versus maximum depth of the ensuing dive. In A, the final breath has the largest beak amplitude. In B, dots (comprising at least 17 data pairs) show mean values, and associated bars = SE ($F = 11.87 > 11.23$; $P < 0.001$).

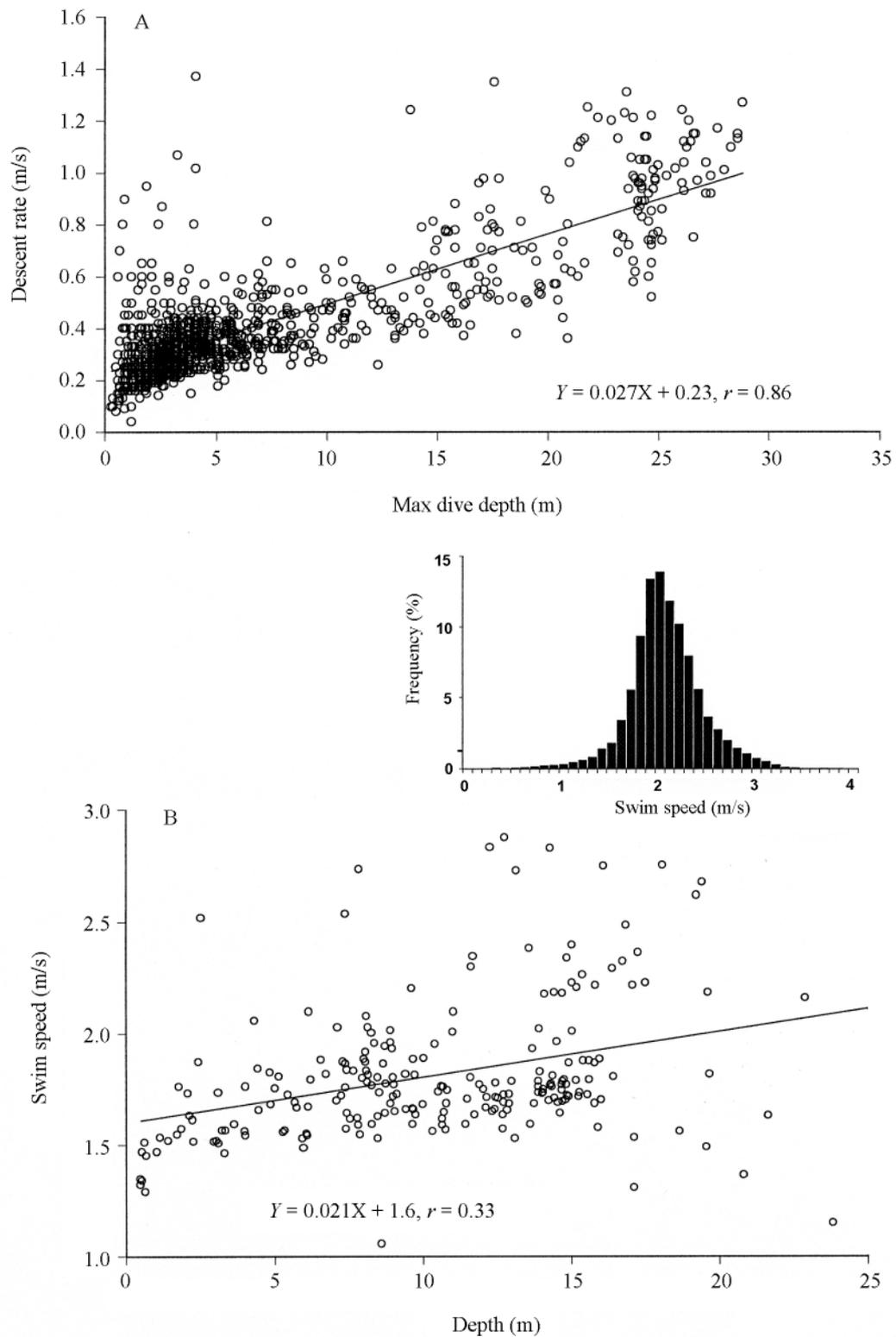


Fig. 2 A. Relationship between rate at which a free-living Magellanic penguin descends and the maximum depth reached in a dive; B. Swim speed of a penguin during descent as a function of depth over 22 consecutive dives during which no prey were caught

For A, $F = 1404 > 10.96$, $P < 0.001$; for B, $F = 27.58 > 11.11$, $P < 0.001$. The speed frequency distribution for total foraging trips by this bird (upper right box in B) shows that swim speed is remarkably constant at around 2 m/s.

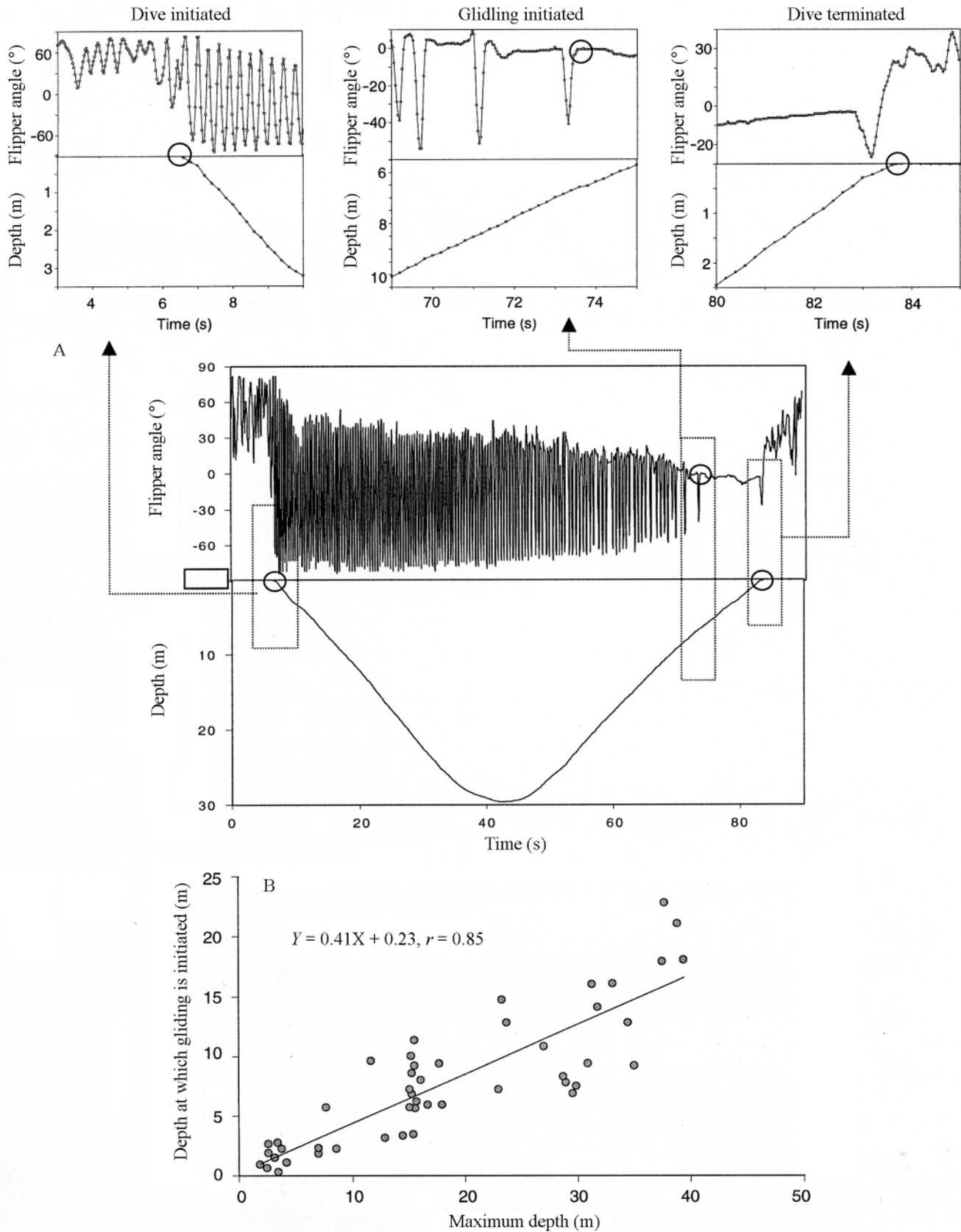


Fig. 3 (A) Flipper angle (showing flipper beat frequency and amplitude) in relation to dive depth for a single parabolic dive by a free-living Magellanic penguin; (B) Depth at which gliding is initiated and maintained to the surface as a function of maximum depth reached during the dive

In (A), features considered to be indicative of decisions (circles) are based on points of inflection in the time series of either depth or flipper angle. For (B), $F = 129.1 > 12.35$, $P < 0.001$.

forward motion at angles between 90 and 0° to the surface will necessitate flipper beating. During the ascent, however, positive buoyancy can be used to drive the birds to the surface (Sato et al., 2002), and there is a point at which the penguins decide to cease flipper beating altogether, buoyancy force being enough. This allows penguins to reduce energy expenditure as they glide to the surface (cf., Williams et al., 2000). Because Magellanic Penguins inhale more air for deeper dives, the depth at which gliding begins is not surprisingly a function of maximum dive depth (Fig. 3B).

3.4 Dive types

Three main dive types, based on depth as a function of time, have been recognized in penguins. They are parabolic, U- and V-dives (Wilson, 1995). They are evident in Magellanic Penguin dive profiles and have, in their execution, a number of points of inflection which indicate decisions.

Excluding prey pursuit and cessation of flipper beating on ascent, parabolic dives show points of inflection only at the beginning and end of dives. Otherwise there is an essentially linear change in the rate of change of depth from negative to positive over the course of the dive (Fig. 4, top). It thus appears that the execution of the dive is predictable from the moment it is initiated, with few or no decisions being made from beginning to end. It seems likely that parabolic dives are used during foraging when depth of prey distribution is unclear because this pattern leads to a slowly increasing proportion of time spent per meter water depth rather than a concentration of time at a particular depth (Wilson et al., 1996). Such dives may thus be seen as exploratory.

V-, or bounce, dives have a single point of inflection at the deepest point of the dive where the rate of change of depth, which is approximately constant during the descent, changes abruptly to a constant positive value which is maintained throughout ascent (Fig. 4, middle). As swim speed is essentially constant, such dives result in a constant time spent per meter water depth, and thus are unselective with respect to decisions about the likely depth distribution of prey. Some factor apart from the sea bed (Wilson et al., 1989), however, must lead to the abrupt turnabout at the bottom of the dive.

U-dives may be regarded, in some senses, as modified V-dives. The rate of change of depth is constant down to a specific depth before changing abruptly. Instead of becoming positive, however, it changes to *ca.* 0 m/s for some period before changing abruptly again to a new constant value which is maintained from this point to the surface (Fig. 4, bottom). The first point of inflection at the deepest point may stem from a decision that occurs as a result of the sea bed, but may also be due to perceived changes in oceanographic cues for locating prey or even simply the re-visitation of a depth known to be particularly profitable for foraging (Wilson and Wilson, 1995).

The bottom period results in extended time spent at

selected depths and is an appropriate strategy for birds concentrating their search, for whatever reasons, at such depths (Wilson et al., 1996). The decision to terminate a bottom phase is presumably determined by body oxygen levels. It is notable here that the rate at which oxygen is used during normal swimming is a function of inhaled air volume and depth (see above), and during prey capture a function of pursuit speed (Wilson et al., 2002a). Because energy expenditure increases as the cube of swim speed, the decision to end the bottom phase should occur sooner in birds pursuing prey than in penguins simply searching (Wilson et al., 2002a).

3.5 Prey pursuit

The process of prey capture in Magellanic penguins is complex. The birds engage in co-operative group hunting (Boswell and MacIvor, 1975; Wilson et al., 1987) which results in a confusing pattern of changes in direction and swim speeds not addressed here. There is, however, a fairly straightforward pattern apparent in the capture of lone prey items, and this appears typified by a number of points of inflection. Initially, there is a change in regular flipper beating which is due either to a pause when the bird perceives prey or becomes concerned with implementing a change in swim heading (Fig. 5A); presumably this is the point at which the bird decides whether to pursue or not. This is followed by a short period of usually less than 1.5 s when both frequency and amplitude of flipper beat change, usually together with depth; this is likely to be the pursuit phase (Fig. 5A). It terminates with a virtual cessation of flipper beating while the prey is swallowed, as evidenced by beak opening (Fig. 5A), after which regular flipper beating begins again.

The decision to pursue prey is binary, but the actual pursuit has analogue features. For example, Wilson et al. (2002a) analyze the speed at which penguins should pursue prey, pointing out that the cubed increase in oxygen with increasing swim speed makes very high speed chases disadvantageous; penguins should select their speed so as to catch prey with a minimum of energy expenditure. It is a requirement often met by a more extended, low-speed chase. But because larger prey tend to swim faster (Peters, 1983), penguins should have to work harder and swim faster to secure them (Wilson et al., 2002a); and this seems to be the case in Magellanic penguins.

Data from mean flipper angular speed during pursuit, which incorporates a measure of flipper amplitude and beat frequency, and thus can be used as a proxy for energy expenditure (cf. Skrovan et al., 1999), shows that birds do indeed work harder to catch larger prey (Fig. 5B). It is notable here that flipper angular speed does not systematically increase over the pursuit phase (cf. Fig. 5A), indicating that penguins do not match speed with that of the prey, but rather decide on the appropriate speed at the moment of prey perception. The relationship between flipper angular speed and prey size, though significant, incorporates considerable scatter, presumably due to upthrust and swim

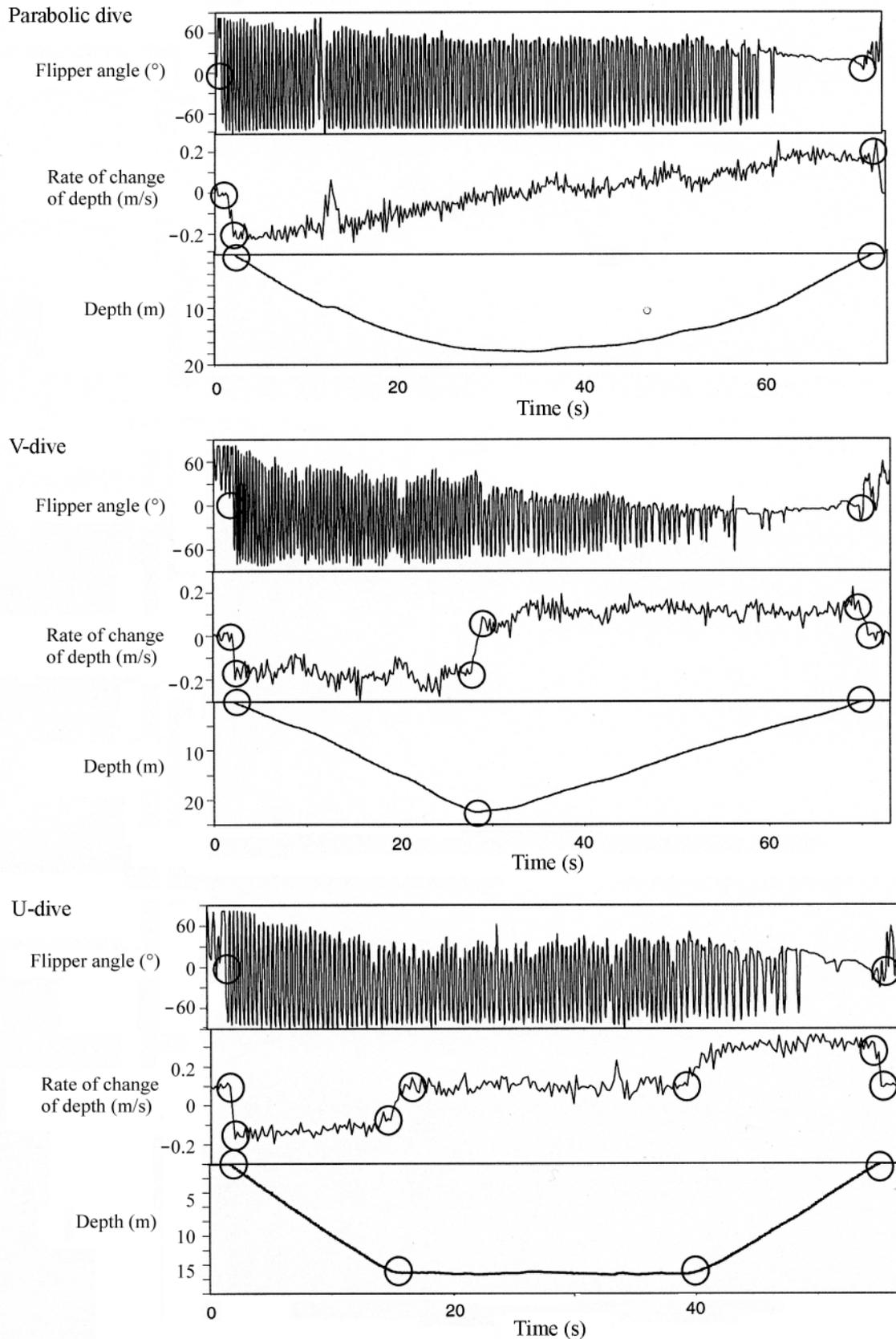


Fig. 4 Three major types of dive of Magellanic penguins showing points of inflection in measured parameters indicative of decisions made by the birds

The upper graph shows a parabolic dive where the only points of inflection are associated with submergence and return to the surface. The center and bottom graphs show V- and U-dives, respectively. In addition to the dive and surfacing points of inflection, sudden changes in the rate of change of depth indicate decisions that occurred underwater.

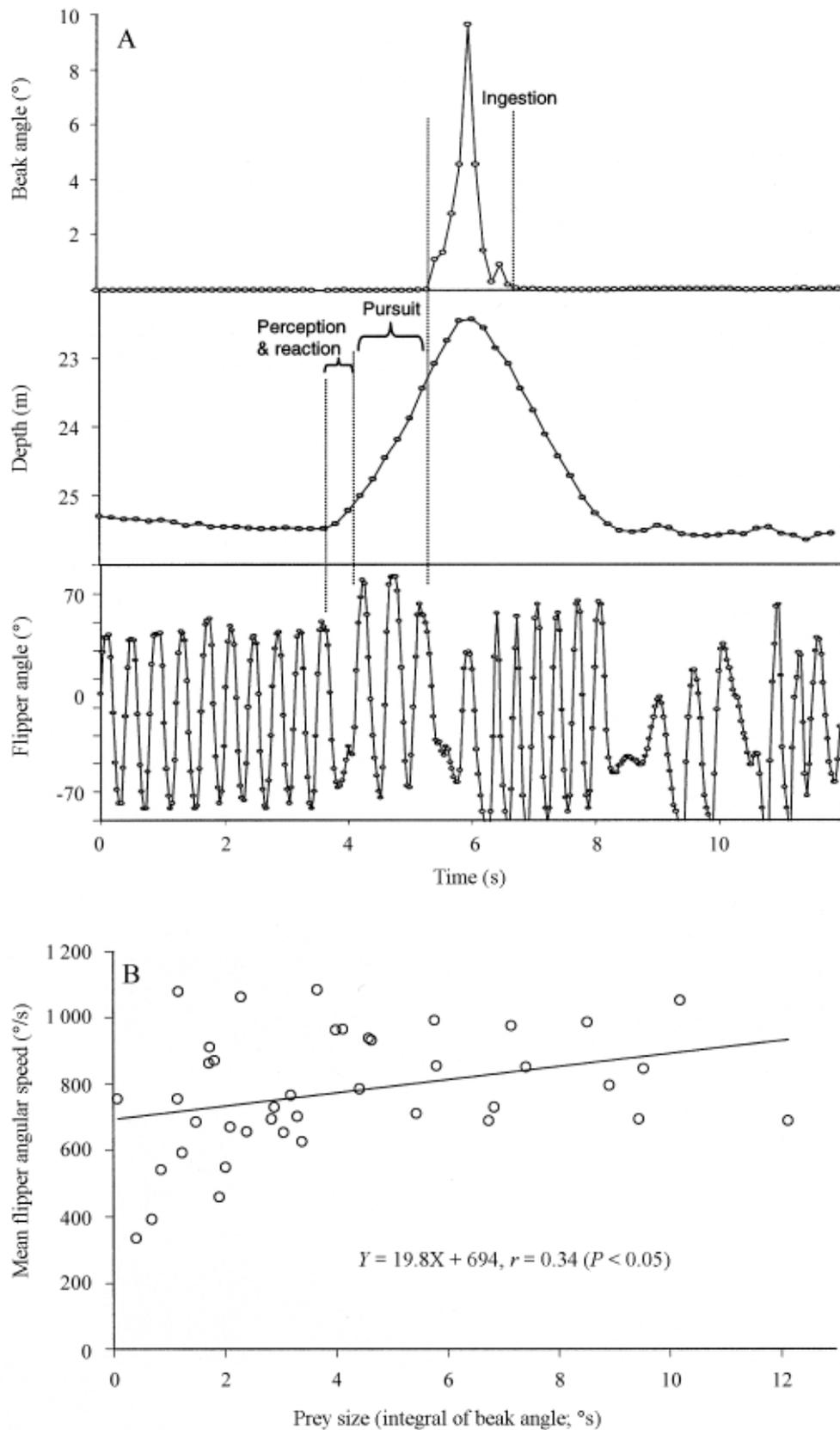


Fig. 5 A. Sequence of prey pursuit and capture in a free-living Magellanic penguin, as marked by changes in beak angle, depth and flipper movement over time; B. Relationship between mean flipper angular speed and prey size for a Magellanic penguin feeding on lone prey

In B, the line shows the best linear fit ($F = 4.75 > 4.09, P < 0.05$).

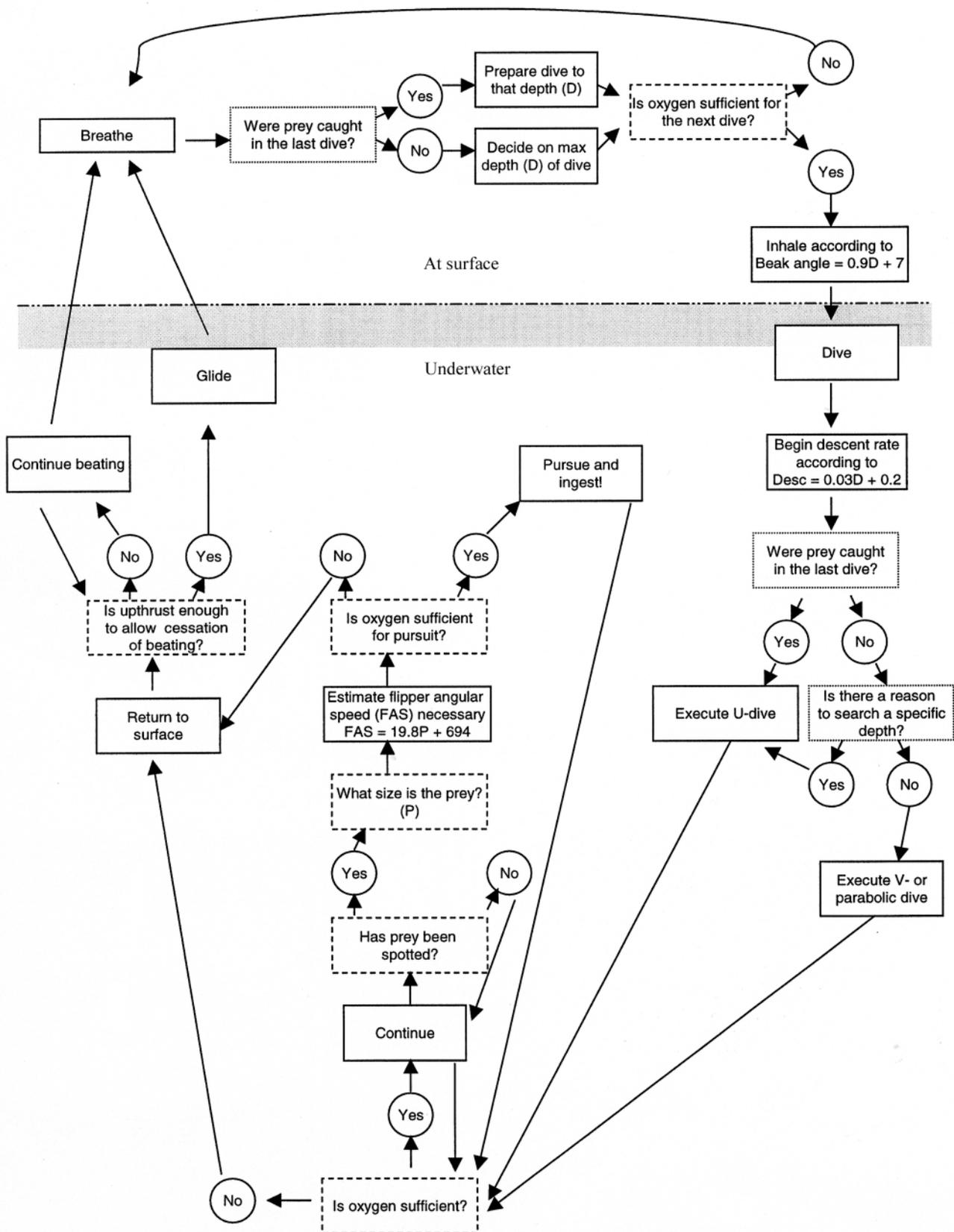


Fig. 6 Simplified schematic diagram showing the types of decisions made by Magellanic penguins during a single foraging dive. Relationships shown in the boxes are taken from the data shown in previous figures.

angle factors. Over and above this, however, it would be interesting to know whether pursuit speed is and has been modified by prey type.

3.6 Foraging decisions

The data presented here, though preliminary, demonstrate that foraging penguins make decisions of both analogue and binary nature (Fig. 6). That they do so to enhance their chances of long-term reproductive success ties in well with optimality theory (Perry and Pianka, 1997). Perhaps most surprising, however, is the complexity of decisions that these birds have to make, and their frequency. This makes it clear that our studies of optimal foraging, which often focus on particular aspects of foraging, are just a tiny part of the large, sophisticated decision-making process. Future use of devices attached to free-living animals will undoubtedly make it clear just how ill-informed we are about the way animals acquire prey and perhaps go some way to explaining how they do it so efficiently against seemingly insurmountable odds.

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S29-3 Evidence for regulation of air volume in the respiratory system of diving Adélie penguins, *Pygoscelis adeliae*

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Abstract Penguins are outstanding divers. That they dive on inspiration is particularly intriguing because as it increases oxygen stores it also increases buoyancy. Buoyancy is a major factor determining the energetics of shallow diving birds, and there is a positive correlation between estimated air volume in the body (respiratory system and feathers) and the maximum depth in the dive of free-ranging penguins. However, it is not known whether variation in total air volume is caused by variation in the volume of air in the respiratory system or plumage. In the present study, underwater weights of restrained Adélie penguins *Pygoscelis adeliae* ($n=27$) were measured continuously. The birds lost much air from their feathers within 1–2 min of submergence. Maximum weights in the water were used to calculate the minimum air volumes that diving birds are expected to hold in the body. These volumes were compared with estimated air volumes from two free-ranging Adélie penguins. Most estimated values were larger than values in the restrained birds, which indicates that variation in total air volume is probably caused by variation in the air in the respiratory system. Penguins seem to adjust the volume of air inhaled to the maximum depths of their dives.

Key words Diving physiology, Buoyancy, Data logger, Biomechanics, Respiratory regulation

1 Introduction

Breath-holding diving birds must divide their time between obtaining two basic resources: oxygen at the surface and prey under water (Dunstone and O'Connor, 1979). When submerged, they must balance the energetic demands of movement with conservation of their limited oxygen store (Castellini et al., 1985). High levels of movement under water lead to shorter dives as oxygen reserves are depleted more rapidly. Several studies have shown that buoyancy is a major load for shallow-diving birds (Dehner, 1946; Stephenson et al., 1989; Lovvorn et al., 1991; Lovvorn and Jones, 1991a,b; Wilson et al., 1992; Stephenson, 1994). Buoyancy in birds is strongly affected by the volume of air in the respiratory system and plumage. Some flying birds such as cormorants and ducks have been observed to dive following expiration (Ross, 1976; Butler and Woakes, 1979; Tome and Wrubleski, 1988). Yet penguins apparently dive on inspiration (Kooyman et al., 1971), which, although it enhances oxygen stores, also increases buoyancy. In 1971, however, no means had been devised for measuring either respiratory or plumage air volume in birds during natural, unrestrained dives (Lovvorn and Jones, 1991a).

Sato et al. (2002) used newly-developed acceleration data loggers on king (*Aptenodytes patagonicus*) and Adélie (*Pygoscelis adeliae*) penguins to monitor their flipper movements underwater. According to the data, the penguins flapped continuously as they descended, but after the first half of the re-ascent, stopped flipper beating and took ad-

vantage of natural buoyancy to glide back to the surface. Biomechanical calculations indicated that the air volume of the birds (respiratory system and feathers) could provide enough buoyancy for passive ascent.

Comparison of passive ascents from shallow and deep dives shows a positive correlation between estimated air volume and the maximum depth of the dive (Fig. 1). Sato et al. (2002) proposed that penguins inhale according to dive depth, reducing air volume so as to avoid buoyancy resistance during shallow dives. According to measurements of restrained penguins (Kooyman et al., 1973), it has been assumed that most of the air (more than 90 %) is held in the respiratory system (Sato et al., 2002). To date, however, it has not been shown definitively that air volume is actually adjusted in the respiratory system. To elucidate this, we conducted an additional experiment on Adélie penguins.

2 Materials and methods

The underwater weights of Adélie penguins were measured at Hukuro Cove (60°00'S, 39°39'E) south of Syowa station, Antarctica, during the 1999–2000 breeding season. Adult Adélie penguins ranging in body mass from 3.0 to 5.75 kg ($n = 27$ birds) were used. When penguins returned to nests from foraging trips, they were captured and caged in a penguin holder made of stainless steel mesh (Fig. 2). The head of the bird was covered with a mask of dark cloth to keep it calm, and the feet were fixed with the toes pointing down. Belts on the holder were used to restrain movements

of the flippers, which were bound close to the body. Body weight (Ma) was first measured in air.

Then the bird was slowly submerged to eye-level in a tank filled with seawater, with care taken to ensure that ventilation was not impaired. Bird weight in seawater (Mw) was continuously measured to the nearest 5 g with a digital balance until the value equilibrated (Kansai Scale, KHS-7.5 kg). The bird could breathe through a hole at the top of the mask. Weight was attached to the holder to adjust the total weight of the system plus penguin in the water so that it was within the measuring range of the balance (from 0 to 7.5 kg). The value displayed on the scale together with the appearance of the bird was recorded by a digital video camera (SONY DCR-PC1). After measurements were taken, all penguins were released near the breeding colony. They immediately returned to their own nests where normal interaction with their partners was observed. No birds abandoned their nests after the experiment.

After measurement, weight values were read every five seconds from the video records. Minimal and maximal values during the equilibrated period were used to calculate the total air volume in the body using following equation:

$$Va = (Ma - Mw)/\rho_w - Ma/\rho_t,$$

where Va is air volume in the penguin (m^3), Ma is the penguin weight in air (kg), Mw is the penguin weight in water (kg), ρ_w is sea water density ($kg\ m^{-3}$) which was measured using a hydrometer, and ρ_t is the density of penguin tissue ($= 1.02 \times 10^3\ (kg\ m^{-3})$) (Wilson et al., 1992).

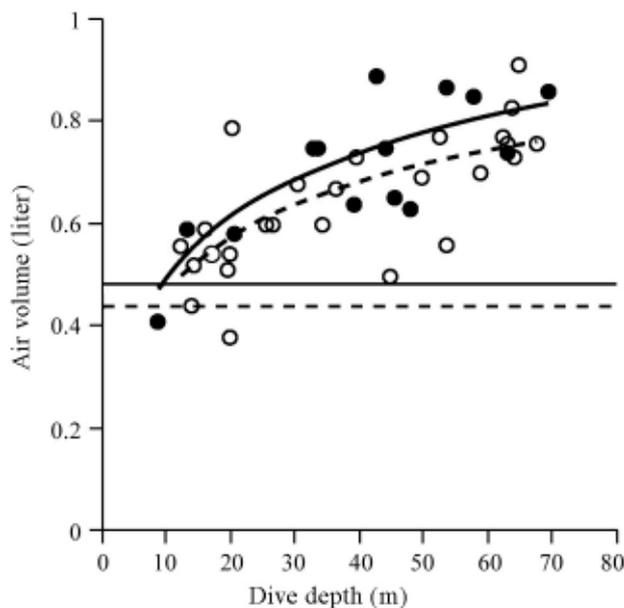


Fig. 1 Relationship between the maximum depths of dives and estimated air volume in the Adélie penguin

Open circles and dotted curve = 4.0 kg penguin; closed circles and solid curve = 4.5 kg penguin. Redrawn and modified from Sato et al. (2002). Horizontal lines are calculated minimum air volumes for each bird (solid = 4.5 kg, dotted = 4.0 kg).

3 Results

Fig. 3 illustrates continuous measurement of the underwater weight of a penguin. Total weight in the water increased rapidly at first when small bubbles came from feathers (Fig. 3). After 1–2 min, the base line of the weight began to equilibrate. During the period when the total weight was being equilibrated, abrupt increases in weight were recorded several times (Fig. 3). The video recordings indicated that these increments corresponded to breathing; rapid exhalation and subsequent inhalation were separated by apneas. The mean frequency of breathing counted from video records ranged from 12.0 to 25.3 breaths/min ($n = 24$ birds). The minimum air volume, which was calculated from the maximum weight in the water, ranged from 337.0 to 593.2 ml in the studied penguins (Fig. 4). The relationship between body weight in air Ma and minimum air volume Va was

$$Va = 87.3 Ma + 86.0$$

$$(R^2 = 0.455, n = 27, F = 20.8, P < 0.0001)$$

The maximum air volume, which was calculated from the minimum weight in the water, varied above the regression line for the minimum air volume (Fig. 4).

4 Discussion

According to the underwater weight measurements (Fig. 3) and video observations, penguins lost much of the air in their plumage within 1–2 min of submergence. We consider that a diving penguin actively stroking with its flippers under natural conditions would lose almost all plumage air immediately. Kooyman (1973) demonstrated that air in plumage of restrained Adélie penguins was not more than

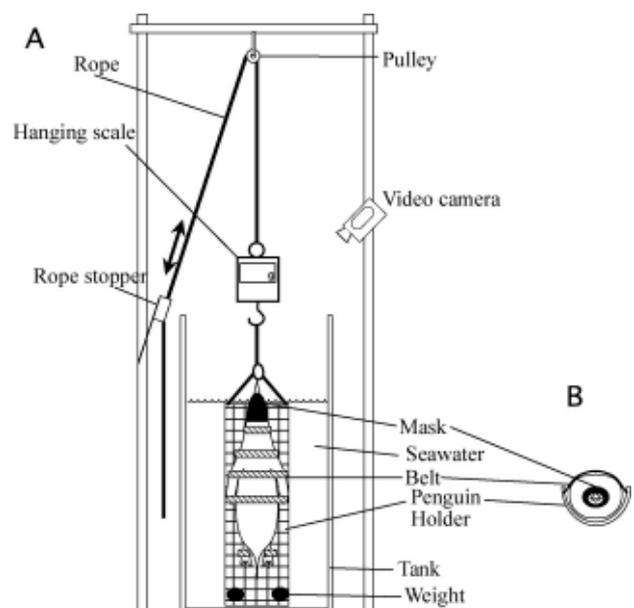


Fig. 2 Schematic diagram of construct for underwater mass measurements

A = side view, B = view from above.

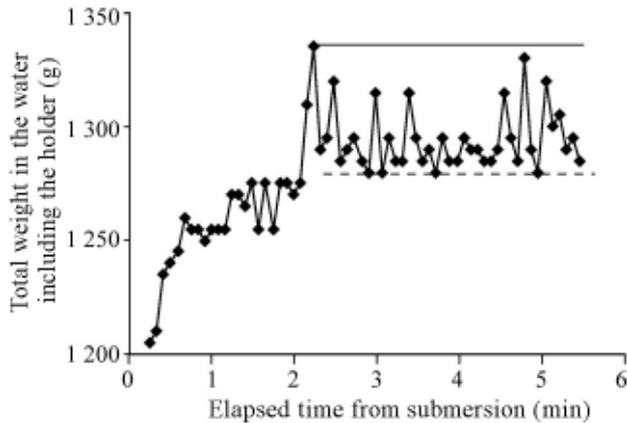


Fig. 3 Underwater weight measurements of an individual Adélie penguin

The solid horizontal line corresponds with maximum values and the dotted with minimum.

10 % of the total air volume in the body, and Sato et al. (2002) assumed that most of the air (> 90%) at the end of dives would be in the respiratory system. This assumption seems acceptable under natural conditions.

The minimum air volume measured in our study incorporates both the air volume in the respiratory system and residual air in the plumage. The calculated minimum air volumes for two penguins (4.0 and 4.5 kg) are represented by horizontal lines in Fig. 1. Most estimated air volumes are larger than measured minimum volumes (Fig. 1), which indicates that variation above the lines was mainly caused by the variation in the air volume in the respiratory system. This means that the free-living penguins studied by Sato et al. (2002) are indeed likely to have adjusted their inhaled air volume in response to the depths of dives. We predict that when penguins make deep dives, they spend much of the dive time deeper than the critical depth at which air is so compressed that buoyancy is zero. They can therefore hold considerable amounts of air in their respiratory systems as oxygen stores. In contrast, shallow diving penguins reduce the volume of air in their respiratory system so as to avoid buoyancy. Biomechanical considerations, together with the data obtained from free-ranging penguins under natural conditions, indicates that penguins may adapt their diving strategy to their own biomechanical and physiological constraints.

If penguins indeed regulate inhaled air volume, how might this affect diving effort? To answer this question, swimming activity must be measured. Swim speed alone is a relatively poor indicator of aquatic effort, and may be inadequate for assessing energetic costs in diving animals because, in buoyant gliding penguins rising to the surface, it is sometimes faster than normal speed from flipper propulsion (approximately 2 m/s) (Sato et al., 2002). Although several studies have investigated the stroke pattern of diving birds (Clark and Bemis, 1979; Hui, 1988; Johansson and Aldrin, 2002), these experiments were conducted at shallow depths in aquaria, and it is unclear how reduced buoyancy

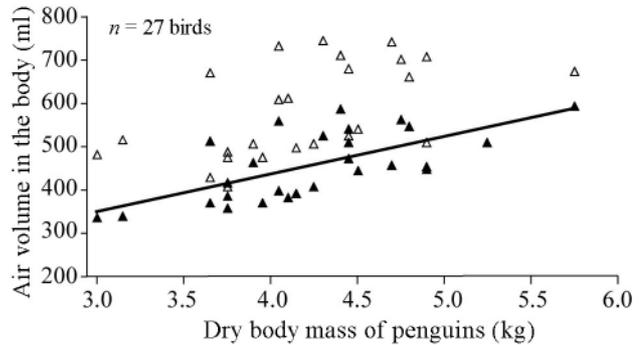


Fig. 4 Relationship between dry body weight and air volume Minimum = closed triangles, maximum = open triangles. A regression line was calculated for minimum air volume.

at greater depths might affect force requirements (Johansson and Aldrin, 2002). This may yet be resolved by acceleration-measuring data loggers, which have already been used on a variety of free-ranging animals to monitor their behavior under natural conditions.

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S29-4 The relative importance of physiological and behavioral adaptation in diving endotherms: a case study with great cormorants

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Abstract Extensive morphological and physiological adjustments are assumed to underpin the adaptations of diving birds to high thermoregulatory costs. However, the role of behavioral adaptations has received little consideration. We have assessed the relative importance of physiological and behavioral adjustments in aquatic endotherms by studying the case of the poorly insulated great cormorant (*Phalacrocorax carbo*) in two contrasting thermal environments: Normandy (water temperature 12°C) and Greenland (water temperature 5°C). Major differences were found in the feeding behavior of birds breeding in the two regions. Greenland birds showed a 70% reduction in time spent swimming relative to those in Normandy. Reduction in Greenland was achieved first by reducing time spent on the surface between dives and secondly by returning to land in between intensive bouts of diving. Total daily energy intake of cormorants was similar in both areas but prey capture rates in Greenland were 150% higher than those in Normandy. Our study shows that in a cold foraging environment, poorly insulated great cormorants significantly increase their foraging efficiency. To do this they rely on ecological adaptive patterns (minimization of time spent swimming in cold water and increased prey capture rates) far more than physiological adaptations (minimizing instantaneous costs). This finding supports predictions by Grémillet and Wilson (1999) that great cormorants can cope with a wide range of abiotic parameters despite their morphological handicaps, provided they can adjust their distribution to exploit dense prey patches.

Key words Diving endotherms, Great cormorant, Behavioral adaptation, Physiological adaptation, Energetics, Foraging behavior

1 Introduction

Although diving seabirds colonized the oceans rather recently (less than 100 million years ago), they possess highly developed and diverse morphological and physiological adaptations for diving (Kooyman, 1989). These attributes enable them to play a major role at the top of aquatic food chains (Ainley et al., 1994; Croll et al., 1998; Pauly et al., 1998). As endotherms, they also experience much greater heat losses to water than to air, such that their thermoregulatory mechanisms are more developed than those of land birds. Such capabilities have motivated numerous studies of warm-blooded diving animals, with at least 2 200 articles published since 1981 (SCI, 2000). Few of these studies, however, have considered the capacity of marine endotherms to compensate for high living costs via food intake (Guillemette et al., 1992).

The aim of the present paper is to assess the relative importance of physiological and behavioral adaptations in a poorly insulated endotherm diving in cold water, namely the great cormorant (*Phalacrocorax carbo carbo*), which

has wettable plumage (Rijke, 1968; Wilson et al., 1992) and which experiences particularly high heat losses to water (Schmid et al., 1995; Grémillet et al., 1998a). Great cormorants were considered more likely than any other diving endotherm to display specific strategies enabling them to deal with such constraints.

The great cormorant additionally has a wide breeding range (Johnsgard, 1993). We used this characteristic to compare the foraging energetics of birds breeding in temperate (Normandy, water temperature 12°C) and polar (Greenland, water temperature 5°C) environments using radio tracking, qualitative and quantitative dietary analysis, stomach temperature records and time-budget analysis. Previous investigations showed that, despite the colder aquatic environment, daily food intake of Greenland birds was similar to that in Normandy (Grémillet et al., 1999). This finding suggests that Greenland birds have developed specific physiological and/or behavioral adaptations which enable them to compensate for increased heat losses. What those are is investigated here.

Table 1 Comparison of foraging parameters for great cormorants breeding in Greenland ($n = 6$ males, 5 females) and Normandy ($n = 8$ males, 6 females)

	Foraging trips per day	Duration of foraging trip (min)	Foraging range (km)	Time in water per trip (min)	Time in water per day (min)	Mean dive time (s) ($n=5$)	Food load (g fish/ foraging trip)	Catch per unit time (g fish/min underwater)
Males Greenland	3.1±0.8	140 (85–200)	7.4±2.0	13.9± 6.1	43.1	25.5±3.6	305±40	35.1 (0–770)
Males Normandy	2.4±0.7	165 (110–226)	9.7±6.0	52.2±16.7	125.3	38.2±9.4	430±120	15.2 (0–820)
Females Greenland	3.1±0.8	155 (80–185)	6.0±3.0	15.8±10.2	49.0	24.2±3.7	340±140	24.8 (0–480)
Females Normandy	2.3±0.3	180 (130–325)	17.1±10.0	74.5±18.6	171.4	38.8±10.5	425±75	9.0 (0–1060)

Means are given with \pm standard deviation, and medians with range values. Time in water per day is the product of the time in water per foraging trip and the number of foraging trips per day.

2 Materials and methods

Our two study colonies of the great cormorant are located on inshore islands: Chausey in Normandy, France, at 48°55'N, 01°45'W (346 pairs in 1996) and Qeqertaq, Disko in Greenland at 69°30'N, 54°05'W (179 pairs in 1998). Normandy birds bred between March and July when water temperature averaged 12°C and Greenland birds bred between April and August (average water temperature 5°C; Grémillet et al., 1999). We studied adult birds raising young chicks in April and May 1995 and 1996 (Normandy) and in June and July 1998 (Greenland). Due to discrepancies in body mass and foraging patterns, males and females were considered separately. Statistical tests were performed using Minitab 11; means are \pm one standard deviation.

2.1 Greenland study

Foraging behavior: eleven adult cormorants were caught at the nest site and equipped with VHF transmitters (TW3 transmitters, Biotrack, 52 Furzebrook Road, Wareham, BH20 5AX, UK; mass 18 g). Individual birds were subsequently radio-tracked for at least 10 foraging trips chosen at random. Foraging data recorded were location of foraging area, time and duration of each dive plus subsequent recovery phase on the surface, and total time spent swimming per foraging trip in comparison with nest attendance. This gave an estimate of the total time spent on water per day. To compare dive/pause ratios, radio-tracking data (Grémillet, 1997) were pooled as follows: for 5 individuals of each sex and each location, a set of 5 dive bouts was analyzed, within which 5 dive times and ensuing recovery times were pooled. Individuals, dive bouts and dive cycles were chosen at random.

Food intake: using automatic nest balances, adult body mass and food intake rates were determined concurrently with foraging patterns in the same 11 adult birds (after Grémillet et al., 1996, 1999). Food loads were then corrected for the effect of digestion (Grémillet et al., 1996) using radio-tracking data and assuming a mean prey mass of 108 g calculated from stomach temperature measurements. Predation efficiency was assessed by calculations of catch per unit effort (CPUE), where CPUE values are expressed in

grams of fish taken per minute spent underwater (after Grémillet, 1997).

Body temperature patterns: stomach temperature patterns and concurrent activity data (via radio-tracking) were recorded in 6 birds for a total of 10 days using gastric probes (SICUP, Grémillet and Plös, 1994; Wilson et al., 1998). Deployment of such stomach temperature loggers is not detrimental in any way (Wilson et al., 1998). Recorded stomach temperatures were analyzed following Grémillet and Plös (1994) and Wilson et al. (1995) to calculate the mass of individual prey items to an accuracy of 15%. Potential body cooling in diving birds was assessed following Grémillet et al. (1998a), using these stomach temperature records (after Grémillet et al., 1996, 1999).

Diet: prey spectrum was determined and identified via pellet analysis following Harris and Wanless (1993) and from fish regurgitated at the nest site. A total of 52 pellets containing 1 490 otoliths were analyzed. The average energy values of the different prey species were obtained from literature. Using frequency of occurrence of the main prey species in diet, their average specific mass and calorific content, we then calculated the average calorific values of food taken.

2.2 Normandy study

All data for Normandy birds were derived from previous studies performed during the same breeding phase (early to mid chick rearing) and using the same methodology as that used in Greenland (Grémillet et al., 1996; Grémillet, 1997; Grémillet et al., 1998b).

2.3 Modeling

We used respirometric measurements by Schmid et al. (1995) and a thermo-energetics model developed by Grémillet and Wilson (1999) to predict energy costs as a function of water temperature and dive depth. The poor body insulation of great cormorants, and the resulting relationship between water temperature and dive costs, has been recently confirmed experimentally (Grémillet et al., 2001). The calculations were performed for mean water temperatures of 12°C and 5°C, and a mean dive depth of 8 m and 3 m at respective Normandy and Greenland study sites (Grémillet

et al., 1999). Dive depths of Normandy birds were measured by time-depth recorders; and those of Greenland birds were derived from mean dive times presented in Table 1 using a relationship given in Grémillet et al. (1998b).

The increase in the energy costs of diving for Greenland birds was determined as follows. Because cormorants in Normandy and Greenland take similar quantities of similar energy value (Grémillet et al., 1999) and maintain a constant body mass throughout the breeding season (Grémillet, 1997), comparison of the time-energy budgets in the two areas should indicate that energy requirements are similar. If the total daily energy budget for each location is then calculated as if the energy costs of diving are the same in both, the difference should represent the additional energy allocated to diving in Greenland birds.

To determine this, we used the behavioral data presented in Table 1 and the energetics data from Grémillet et al. (2000). We assumed that all activities performed at the nest site had similar energetic costs at both locations. This

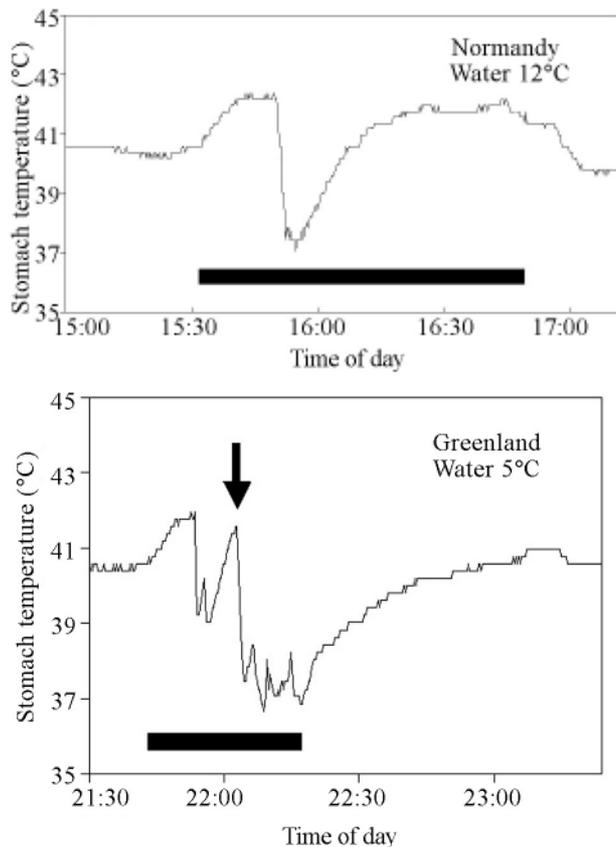


Fig. 1 Examples of stomach temperature patterns in individual great cormorants foraging off Normandy (top) and Greenland (bottom)

The black bar shows the time spent in the water. The initial temperature increase comes from heat generated by diving activity. Precipitous drops in stomach temperature are caused by the ingestion of fish. Note that birds in Normandy keep high, stable body temperature for long periods when swimming and after warming ingested fish. Greenland birds stayed in water for shorter periods, and, while swimming, also rapidly warmed ingested prey to temperatures higher than resting values (arrow).

assumption is valid as long as the temperature regimes are similar, which is not the case when the Greenland colony is shaded by nearby cliffs. To correct for this effect, we applied data recorded by Storch et al. (1999), which predict an increase of 63% in resting metabolic rate (RMR). Differences in flying time periods and brood biomass were also taken into account.

3 Results

3.1 Foraging behavior

Radio-tracking data show that for both sexes, the total times spent swimming per foraging trip and per day were significantly lower in Greenland than in Normandy (average decreases 73% and 65% respectively in males, and 79% and 71% in females, Table 1). Foraging bouts of Greenland birds were not only shorter, but also organized differently. Their recovery times were significantly shorter, and they further reduced contact with cold water by performing significantly briefer dives (Table 1). Great cormorants sometimes rest in the middle of a foraging trip, leaving the water to stand on nearby rocks. In Normandy, males and females have an average of 0.26 ± 0.14 and 0.59 ± 0.19 breaks per foraging trip respectively, i.e. no breaks at all or just one. In Greenland, the mean number of breaks per trip is greater at 1.9 ± 0.64 and 1.8 ± 0.35 in males and females respectively, the birds making up to three breaks per trip.

3.2 Diet and food intake

Although fish mass intake is similar in Normandy and Greenland (Grémillet et al., 1999), the two populations prey upon different species. In Normandy, great cormorants feed on 22 different fish species, mainly labrids, and in Greenland 14, mainly sculpins. The average calorific of the intake was calculated as 4.0 kJ g^{-1} in Greenland (Table 2), and is the same in Normandy (Grémillet and Argentin, 1998). Combining dietary and behavioral data to estimate CPUE (mass prey taken per time spent underwater) showed clearly that, for both sexes, predation efficiency was significantly higher in Greenland than Normandy: twice as high in males and nearly three times as high in females (Table 1).

3.3 Body temperature patterns

Previous studies detected no abnormally low body temperature levels in great cormorants diving off Normandy (Fig. 1, top), even during prolonged periods in the water of up to 158 minutes (Grémillet et al., 1998a). In Greenland, where dive bouts were much shorter (Table 1), cormorants have similar temperature patterns (Fig. 1, bottom). In both groups, body temperature rises rapidly at the start of swimming and then is kept stable until the ingestion of cold prey, which initiates a precipitous drop in temperature (Wilson et al., 1992). Ingested food is subsequently warmed, and stomach temperature returns to initial, high levels.

3.4 Modeling

The algorithm proposed by Grémillet and Wilson

Table 2 Diet of great cormorants breeding in Greenland, from 52 regurgitated pellets containing 1 490 otoliths

Main prey species	Mean calculated mass (g±SD)	Proportion in diet (% of total fish number)	Proportion in diet (% of total fish mass)	Mean energy value (kJ.g ⁻¹)
Sculpins	185±8.0	39.4	79.6	3.8*
Capelin	45±4.0	15.2	7.4	4.1**
Gadids	90±6.5	12.8	12.6	4.9§
Sand eels	2.8±0.2	10.8	0.4	7.1§§
Others		15.7		
Undetermined		6.1		
Mean total calorific value (kJ.g ⁻¹)				4.0

See material and methods for calculations. Mean calorific values are taken from * Grant (1984), ** Van Pelt et al. (1997), § Brekke and Gabrielsen (1994) and §§ Hislop et al. (1991).

(1999) predicts increases of 28% and 36% in the energy costs of diving for male and female cormorants in Greenland. In theory then, the overall costs of diving in Greenland should be 169 W in males and 146 W in females (Fig. 2). However, present calculations based on the time-energy budgets of birds from Normandy and Greenland (Table 3a and b) show that the field energy costs of diving off Greenland may be as high as 257 W in males and 250 W in females. The actual heat losses experienced by birds diving in Greenland may thus be 50%–70% higher than the predicted values, and 98% and 165% higher than in Normandy for male and female cormorants, respectively (Fig. 2).

4 Discussion

Great cormorants have not evolved specific morpho-

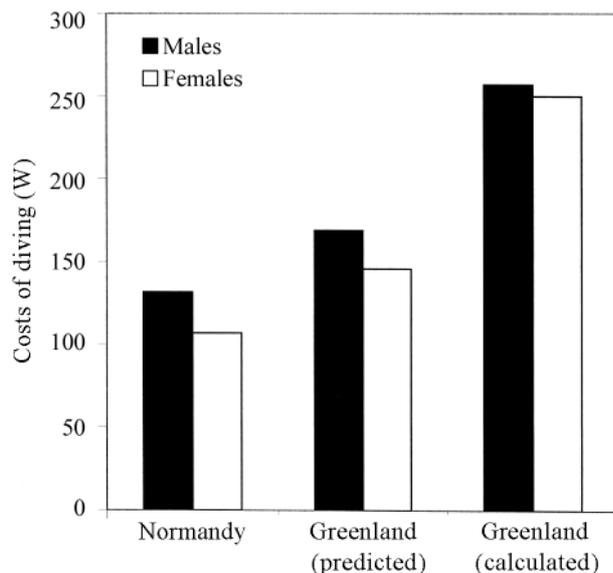


Fig. 2 Comparison between the energy costs of diving in great cormorants

Comparisons based on gas respirometry data from Schmid et al. (1995) for Normandy in 12°C water, on the costs of diving predicted by Grémillet and Wilson (1999) in Greenland in 5°C water (Greenland predicted), and on the energy costs of diving determined *in vivo* for Greenland birds in this study (Greenland calculated).

logical adaptations for diving in cold water (Rijke, 1968; Johnsgard, 1993; Grémillet et al., 2001). Our estimations suggest that the energy costs of diving off Greenland may be as high as 95 W kg⁻¹, more than six times those of Adélie penguins (*Pygoscelis adeliae*) foraging in a similar thermal environment (Culik et al., 1994; Schmid et al., 1995) and comparable with average flight costs (calculated after Pennycuik, 2001). Despite this, our empirical data on prey quantity and quality indicate that the daily energy intake of birds breeding in Greenland does not differ from those breeding in temperate Normandy (Grémillet et al., 1999; Table 2). Taken together these findings suggest that the allocation of energy resources must differ in the two regions. The relative importance of physiological and behavioral adaptations within this unexpected strategy is discussed below.

4.1 Physiological adaptation

Heat loss experienced by diving endotherms is critically influenced by the temperature differential between body and surrounding medium. For Greenland great cormorants, then, a straightforward solution would be to reduce the differential by dropping body temperature. Other diving birds and mammals respond by cooling extremities or larger parts of the body (Butler and Jones, 1997); and hypothermia, which has been claimed to increase foraging efficiency, has been found recently in two cormorant species, the bank cormorant *Phalacrocorax neglectus* (Wilson and Grémillet, 1996) and the blue-eyed shag *Phalacrocorax atriceps* (Bevan et al., 1997). But do great cormorants use these pathways to reduce diving costs?

Grémillet et al. (1998a) showed that this was not the case for great cormorants in Normandy, which kept a constant body temperature for long periods when swimming in water at 12°C (Fig. 1, top). Even at the lower water temperatures experienced by Greenland birds there was no evidence of drastic body cooling (Fig. 1, bottom). Food intake rates calculated for Normandy and Greenland birds using stomach temperature levels confirm these findings, because these estimates are similar for both groups. We thus conclude that hypothermia is unlikely to play a major role in minimizing heat loss in great cormorants diving off Greenland. Our

Table 3a Nominal time-energy budget for male great cormorants breeding in Normandy and Greenland

Activity	Costs per second (W)		Duration (h)		Total costs (kJ d ⁻¹)	
	Normandy	Greenland	Normandy	Greenland	Normandy	Greenland
Overnight resting*	11.9	19.6	7.90	9.16	338	647
Daytime activities on land**	16.4	16.6	13.50	13.70	798	821
Flight***	252	258	0.50	0.38	454	353
Diving§	130.3	132.0	2.08	0.72	977	341
Reproduction§§					536	616
Total (kJ d ⁻¹)					3 103	2 778
Difference between total costs for Greenland / Normandy (kJ d ⁻¹)						325
Related potential increase in dive costs (W and % costs at 12°C)						125 (95%)

Calculations were performed assuming that the energy costs of diving were the same in both regions. The difference between total costs in the two locations thus allows calculation of the potential increase in diving cost in Greenland (see Results).

Table 3b Nominal time-energy budget for female great cormorants breeding in Normandy and Greenland

Activity	Costs per second (W)		Duration (h)		Total costs (kJ d ⁻¹)	
	Normandy	Greenland	Normandy	Greenland	Normandy	Greenland
Overnight resting*	8.6	15.9	7.9	9.17	245	525
Daytime activities on land**	11.9	13.5	12.37	13.70	530	666
Flight***	148	180	0.88	0.32	469	207
Diving§	94.5	107.0	2.85	0.82	970	315
Reproduction§§					536	616
Total (kJ d ⁻¹)					2 750	2 329
Difference between total costs for Greenland / Normandy (kJ d ⁻¹)						421
Related potential increase in dive costs (W and % costs at 12°C)						143 (134%)

Calculations were performed assuming that the energy costs of diving are the same in both regions. The difference between total costs for both locations thus allows calculation of the increase in diving cost in Greenland (see Results).

* Night time in Normandy and time when the colony was in shade in Greenland. ** All these activities have similar energy costs, range 5 to 7 W kg⁻¹ (Storch et al., 1999). *** Flight costs calculated for body masses according to procedures in the Methods; input values for cormorants stated in Pennycuik (2001), using the computer program available on <http://detritus.inhs.uiuc.edu/wes/pennycuik.html>. § Diving costs for great cormorants diving in water at 12°C (Schmid et al., 1995). §§ Calculated from Grémillet et al. (2000) for 1.5 chicks in Normandy and 1.7 chicks in Greenland.

field measurements have been corroborated in recent trials with captive great cormorants, which showed that birds kept constant, high body temperature even when swimming in water at 1°C for 30 min (Grémillet et al., 2001).

4.2 Behavioral adaptation

Great cormorants breeding in Greenland face increases of more than 100% in metabolic costs over those in temperate Normandy while diving for prey, yet eat no more food (Grémillet et al., 1999). To remain in energy balance, then, they have to either drastically reduce the metabolic costs of activities other than diving or increase the energy gained (prey capture) per unit time spent underwater. Except for their diving rhythms, the time-energy budgets of Normandy and Greenland cormorants were very similar (Table 2). Only two significant differences were recorded. First, females spent less time flying in Greenland than in Normandy due to a short foraging range. Secondly, Greenland cormorants raised 30% more chicks than in Normandy (Grémillet, unpubl. data). These effects are in-

cluded in the overall energy budget discussed below.

In contrast, there were major differences between Normandy and Greenland cormorants in diving behavior. In particular, Greenland birds spent much less time foraging both per bout and per day (Table 1). Furthermore, the dive/pause ratios in Greenland birds were significantly higher, indicating that they spent less time in recovery between dives, thereby maximizing foraging time underwater. In addition, dives series made by Greenland birds were more likely to be interrupted by periods spent ashore when the birds were presumably resting, digesting and/or recovering from a potential oxygen debt accumulated during series of intense dives (Ydenberg and Clark, 1989; Butler and Jones, 1997). Dive durations in Greenland birds were also significantly shorter, suggesting that they were shallower (Wilson and Wilson, 1988). By searching for prey in shallow waters, Greenland cormorants avoid increased compression of plumage air volume and consequent increased heat loss to the water as well (Wilson et al., 1992).

In combination, these behavioral strategies allow Greenland birds to catch the same amount of fish of similar calorific value as Normandy birds in only a third of the time. Greenland great cormorants, in fact, have the highest feeding efficiency recorded so far for a marine predator of its size: 35 and 25 g fish caught per minute spent underwater in males and females respectively (Grémillet, 1997).

4.3 Relative importance of physiological and behavioral adaptations

This case study on great cormorants demonstrates that the capacity of diving endotherms to acquire energy and compensate for a costly way of life via specific, flexible foraging techniques should not be underestimated. Our field data and subsequent modeling highlight the major role played by behavioral adaptations in shaping the energy budgets of great cormorants foraging in cold water, especially in comparison with both morphological and physiological adaptations. Knowing that cormorants from both Normandy and Greenland have similar daily energy intakes, it follows that birds from Greenland are likely to lose even more energy when diving than previously thought.

This confirms that great cormorants in Greenland do not have particular morphological or physiological energy saving features. Further modeling presented in Wilson and Grémillet (1996) and Bevan et al. (1997) for bank cormorants and blue-eyed shags also shows why hypothermia is not a good option. These theoretical relationships show that a 3.2 fold increase in prey density at the feeding site (and a proportional increase in bird CPUE values) in great cormorants allows them to fully compensate for a decrease in water temperature from 12°C (Normandy) to 5°C (Greenland). A decrease in body temperature from 41°C to 22°C throughout the time spent swimming, on the other hand, would be necessary to save the same amount of energy. This is not possible for great cormorants diving in Greenland, whose lowest recorded stomach temperature was 25.0°C, an effect due in any case to the ingestion of cold food and not hypothermia (Fig. 1, top).

Our results also indicate that great cormorants from boreal and arctic regions, which have the highest foraging rates so far recorded for any group of diving birds, are nonetheless unlikely to deplete local prey stocks because they can only operate when prey densities are above a certain threshold. Fish resources have to be both abundant and reliable for this energy-maximizing process (Schoener, 1987; Guillemette et al., 1992). This may explain why great cormorants breeding in Greenland feed on sedentary, bottom-dwelling sculpin, a predictable resource rather than on shoaling capelin of higher density per unit area but of more erratic occurrence (Montevecchi and Piatt, 1984). Individual birds are also likely to adjust their distribution patterns then in order to exploit dense prey patches.

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Symposium 30 Interactions between coastal aquaculture, fisheries and birds

Introduction

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Coastal aquaculture and fisheries are expanding industries, and their further development is accepted by society. With increasing industrialization of the landscape, it has also become important to protect ecologically important habitats from further human impact. Therefore, international directives have been set up with the objective of protecting areas that are especially valuable for their habitat and wildlife, including birds. Aquaculture and fisheries are conducted in many such areas along coasts, and thus have potential to impact on wildlife and contravene the international directives. This symposium canvassed these issues.

The important question posed was: can coastal aquaculture and fisheries operate compatibly with the habitat requirements of birds and other wildlife? The answer depends on a number of factors. First, the form of aquaculture and the manner in which it is executed, whether extensively or intensively, needs to be defined. For example, shrimp aquaculture, such as the intensive system identified in south-east India by R. Nagarajan and K. Thiyagesan in this symposium, probably has a negative impact, whereas traditional, extensive systems may have either no impact, or even an indirect beneficial one (Young, 1997).

In order to achieve economic yields without compromising the conservation status of protected areas, information on the interactions between aquaculture, fisheries and birds are needed. Such information, and the studies providing it, are missing for most parts of the world except Europe (Hilgerloh et al., 2001). Effects of different modes of exploitation and production in different areas of the world have to be identified and quantified in order to develop guidelines for sustainable exploitation without damage to the

environment. Coastal sites and habitats where birds are especially vulnerable have to be identified, with modeling to predict the impacts of three particular effects: (1) habitat loss, including bird enclosures, (2) competition for food between humans and birds, and (3) disturbance, as addressed by R. Stillman and J.D. Goss-Custard in this symposium. Behavior-based models employing optimal decision rules are needed to make predictions on the fitness of birds, quantified in terms of survival rate and body condition.

In areas where large areas of valuable habitat have been destroyed by intensive aquaculture, and monitoring and effect data are lacking, awareness has to be increased and politicians advised on how to limit the damage to the natural environment while sustaining local industry. If land reclamation is severe, as in Hong Kong, extensively managed fishponds may even act as a buffer zone against further urbanization and help to maintain bird populations.

In this symposium, papers given by Llewellyn Young and Yun-Jin Wang on the interaction between coastal fisheries and bird conservation in southern China, and by Kenneth Norris on competition between fisheries and oystercatchers for cockles in English estuaries, were presented as orals only. Abstracts of their papers are published in the Abstract volume for the Congress.

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S30-3 Using behavior to predict the effects of environmental change on shorebirds during the non-breeding season

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Abstract There is widespread concern over the damage that humans are inflicting upon the environment. To assess future impacts of industrial development and changes in the intensity or type of land use, and to evaluate the cost effectiveness of proposed mitigating measures, ecologists must be able to provide accurate predictions under altered environmental conditions. The difficulty with predicting new circumstances is that there is often no way of knowing whether the empirical relationships upon which models are based will hold under the altered conditions; and so predictions are of uncertain accuracy. Behavior-based models have been developed in an attempt to overcome this problem. These models follow the behavioral responses of individual animals to changes in the environment and predict variables such as population mortality rate from the fates of all individuals. Animals in the models use optimal decision rules to determine their behavior, which means that model animals are likely to respond to environmental changes in the same way as real ones would. They are therefore thought to provide a reliable means of predicting how animal populations will be influenced by environmental change. We describe how we have used a behavior-based model to predict the mortality rate of shorebirds accurately during the non-breeding season and to predict the consequence of environmental change for shorebirds in a number of European estuaries.

Key words Coastal development, Disturbance, Habitat loss, Habitat quality, Shellfishing

1 Introduction

Coastal areas provide vital feeding areas for migratory shorebirds, particularly outside the breeding season. Because they breed and overwinter in different countries, and often different continents, they are of international conservation concern, and many local, national and international measures have been taken to protect them. Many human activities potentially damaging to shorebird populations are carried out on the coast: land reclamation, salt production, resource harvesting, and recreation. Decisions are frequently required on how best to maintain these bird populations and to reconcile their protection with economic and other developments. In order to do this, policy makers need to know how bird populations will respond to environmental change, ideally before the change happens. The difficulty with predicting such circumstances is often that there is no way of knowing whether the empirical relationships upon which models are based will hold under the new conditions. Until recently, there have been few, if any, adequate methods for making such predictions.

Shorebird conservation aims, in the least, to maintain present bird population size. Environmental change on a non-breeding site can impact on population size by affecting (1) the store of fat reserves needed for migration and successful breeding, and (2) the chance of starving during the non-breeding season. If an environmental change is not expected to affect present-day rates of fat storage or

survival, there would be no reason to be concerned. If, on the other hand, fat storage and survival are predicted to decline, population size would be expected to fall, to an extent dependent on the strength of any compensatory reproduction on the breeding grounds (Goss-Custard and Durell, 1990) and the availability of alternative wintering or passage sites (Pettifor et al., 2000).

We have developed and field tested a behavior-based model designed specifically to predict the influence of environmental change and different policy options on the survival and body condition of shorebirds (Stillman et al., 2000, 2001). The model predicts the changed food intake rates of birds forced by environmental change to alter their diet and/or to redistribute themselves over resource patches of varying quality (Goss-Custard et al., 2000). It does this by using foraging and game theory which are thought to provide a reliable basis for prediction (Goss-Custard, 1996; Sutherland, 1996; Goss-Custard and Sutherland, 1997). The behavioral responses of model birds to environmental change are based on decision principles, such as maximization of intake rate, that are unlikely to be affected by change, even if the particular choices made by individuals do change in the interests of survival. Model birds are therefore believed likely to respond to environmental change in the same way as real birds. We describe how this model is being applied in a range of European sites to predict the effects of habitat quality, coastal development, shellfishing and disturbance on the mortality rate and body condition of shorebirds.

2 The model

The model is individual-based and tracks the foraging location, body condition and ultimate fate of each individual within the population. During each day, each bird in the population must consume enough food to meet its energy demands. It attempts to do this by feeding in those locations and at those times of the day where its intake rate is maximized. Although all individuals decide on the same principle, to maximize intake rate, the actual decisions made by each may differ. Their individual choices depend on their particular competitive ability which in turn depends on two factors. One is interference-free intake rate, and the other is susceptibility to interference.

Interference-free intake rate is the rate at which an individual feeds in the absence of competition and is a measure of basic foraging efficiency. Susceptibility to interference measures how much the interference from competitors reduces intake rate as population density rises. Survival is determined by the balance between rates of energy expenditure and consumption. Energy expenditure depends on metabolic costs plus costs of thermoregulation at low temperatures. Energy consumption depends both on the time available for feeding and intake rate while feeding. When daily energy consumption exceeds daily expenditure, individuals accumulate energy reserves or maintain them if a maximum has been reached. When daily energy requirements exceed daily consumption, individuals draw on their reserves. If reserves fall to zero, an individual starves, the only source of mortality in the model. Stillman et al. (2000, 2001) describe the model in detail, and Stillman et al. (2000) perform a sensitivity analysis of it.

3 Testing the model

The model was originally developed for oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus*

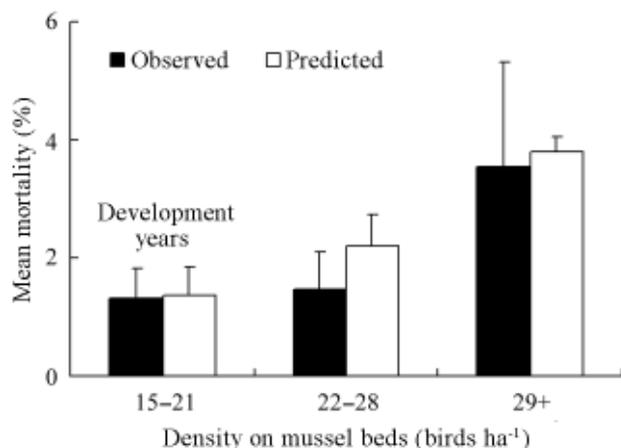


Fig. 1 Test of the Exe estuary oystercatcher model

Bars show the mean and standard error of observed and predicted mortality rates within years of different oystercatcher population size. The model was developed using data collected in years when the density of oystercatchers on the mussel beds ranged from 15–21 ha⁻¹. Adapted from Stillman et al. (2000).

edulis) in the Exe estuary, UK, and has been tested most thoroughly for this system (Stillman et al., 2000, 2001). The model was developed by comparing its predicted mortality rate with the observed rate on the Exe estuary during 1976–1981. Successive components were added or removed until the discrepancy between prediction and observation was reduced. By the end of development, the model described the system with reasonable accuracy (Fig. 1). This could have arisen, however, because too many parameters had been added such that the model had become over-fitted to the data. To test the model, its predicted mortality rate was compared with the observed rates during 1981–1991, a period when the oystercatcher population increased with concomitant density-dependent increase in the mortality rate. The model successfully predicted this increase, even though it was only developed to predict the mortality rate when population size was lower (Fig. 1).

Furthermore, the Exe model predicted, with reasonable accuracy, underlying oystercatcher behavior, such as the amount of time spent feeding on mussels, the distribution of birds throughout the estuary and the changes in body mass through the season (Stillman et al., 2000). This demonstrates the potential for this model in particular, and behavior-based models in general, to predict new circumstances accurately outside the range of conditions for which they are parameterized. We are currently testing the predictive power of the model in a number of other estuaries.

4 Applications of the model

Although developed for oystercatchers on the Exe estuary, the model is now being applied to a range of other species and estuaries, to address a number of conservation issues (Fig. 2), such as the following.

4.1 Habitat quality

The quality of a non-breeding site can be measured by the numbers of birds that survive the non-breeding season and leave for breeding grounds in good condition. The number of birds arriving at a site is not necessarily a reliable measure of site quality as it may depend on factors beyond the site itself, such as the quality of the breeding grounds or neighboring non-breeding sites.

We have used the model to determine how site quality is related to the number of birds arriving at the start of the non-breeding season and the amount of food available (Goss-Custard and Stillman, 1999). The model of the Exe estuary oystercatcher population was used to predict how mortality rate and body condition was related to the quantity of food supply at the start of the non-breeding season. The simulations showed that mortality rates were low and body condition high when more than 50 kg of mussels were available per bird. If availability dropped below this, mortality rate increased and body condition fell. Significantly, birds started to die before the entire food supply was used up; each bird only consumed 8 kg of food during the non-breeding season. This happened because some birds were less

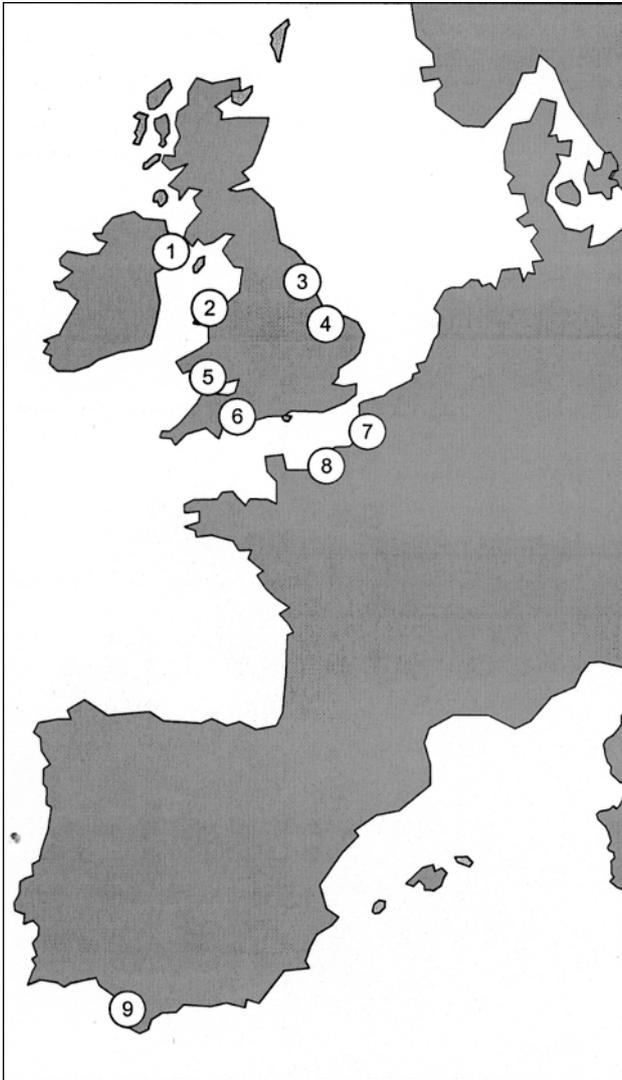


Fig. 2 Sites where the behavior-based model has been used to predict the effects of environmental change on shorebirds

1. Strangford Lough: oystercatchers and shellfishing
2. Menai Straits: oystercatchers and shellfishing
3. Humber estuary: shorebirds and industrial development
4. The Wash: waders, habitat quality and shellfishing
5. Burry Inlet: oystercatchers and shellfishing
6. Exe estuary: shorebirds, shellfishing and disturbance
7. Baie de Somme: shorebirds, shellfishing, and hunting
8. Baie de Seine: shorebirds, industrial development and mitigation
9. Bahia de Cadiz: shorebirds, aquaculture and salinas intensification

efficient foragers and also because interference kept others from the food supply, due to food stealing (Goss-Custard, 1980).

The model showed how a simple measure of food supply and the number of birds can be used to determine site quality. The quality of a site can therefore be monitored by measuring the food supply and bird population at regular intervals. We are currently applying this approach to other species and estuaries to determine how the required amount of food per bird is related to climate, human activi-

ties and bird body mass.

4.2 Coastal development

A wide variety of human developments may potentially affect coastal birds. Developments range from small extensions to existing harbors and marinas to extensive land reclamation, new ports, oil terminals and tidal barrage schemes. The potential effects of these developments on bird habitats, and so the birds themselves, are wide ranging. Both feeding and roosting habitat may be lost when ports are extended, or when dredging occurs to improve port access. The quality of the habitat lost is likely to depend on the shore level influenced by the development. The availability and type of feeding habitat may be changed when the tidal range of an estuary is altered by tidal barrages.

Our behavior-based model separates habitat into a number of patches of varying size and quality. Predictions of the effect of habitat loss can be made by simply reducing the size of one or more patches. Conversely, the effect of proposed mitigation schemes to create habitat to compensate for habitat loss can be predicted by increasing the area of one or more patches or by creating new patches. Because model patches vary in quality, the model can predict the effects of removing or adding habitat of either above or below average quality. When habitat is lost or created within the model, the model birds alter their behavior in order to maximize their chances of surviving in the new habitat. The model has been used to predict the effect of habitat loss and mitigation of a suite of shorebirds on the Humber estuary, Britain, and on the Baie de Seine, France.

4.3 Shellfishing

Shellfishing has a range of effects on coastal birds, some negative and some positive (Goss-Custard et al., 2000). Mussel and cockle (*Cerastoderma edule*) fishing removes the large-sized shellfish which are also eaten by birds such as oystercatchers, and hence reduces the food available to them. If shellfishing occurs at low tide when shorebirds are feeding, it can also disturb birds and force them to waste energy flying away or to move to poorer quality habitat. In contrast, when artificial shellfish beds are created in the intertidal zone by dredging mussels from deep waters, the amount of food available to birds is increased. Damaged shellfish left on intertidal areas after harvest can also provide feeding for birds. Our model can simulate all such effects from shellfishing.

We have used the model to predict the effect of current intensities of shellfishing on the Exe estuary and Burry Inlet, Britain (Stillman et al., 2001). In both estuaries, the model predicted that current low intensity shellfishing was highly unlikely to increase the mortality rate in oystercatcher populations (Fig. 3). However, the model also predicted the points of fishing intensity that would increase those rates (Fig. 3).

4.4 Disturbance

Human disturbance has a number of effects on shore-

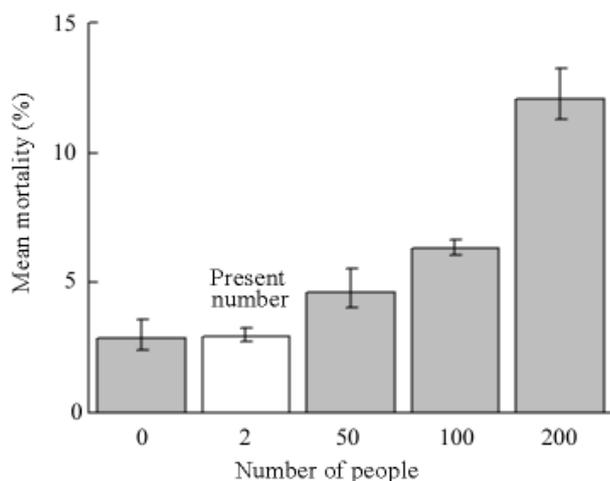


Fig. 3 Predicted effect of shellfishing on the mortality rate of oystercatchers on the Exe estuary

Bars show the mean, minimum and maximum predicted mortality rates from different quantities of fishing. The fishing technique modeled was hand raking of mussels from mussel beds at low water on spring tides: fishing both depleted mussels and disturbed birds. Adapted from Stillman et al. (2001).

birds during the non-breeding season. It excludes birds from areas which would otherwise be used for feeding or roosting, increases energy demands by causing the birds to take flight, and reduces the time for feeding. The behavioral responses of birds to the presence of humans in coastal areas are often obvious; large bird flocks may be seen flying away from people, and areas where people occur often have few birds. These overt behavioral responses, however, do not necessarily mean that more birds will die, as they may have spare time in which to compensate or may simply move to another feeding area. Our behavior-based model incorporates all such effects of disturbance, and can predict whether more birds will die, or body condition drop, as a result of disturbance.

We have used the model to predict the effect of disturbance on oystercatchers on the Exe estuary (West et al., 2002). As for shellfishing, the model predicted that the current level of human disturbance had no influence on oystercatcher mortality or body condition, but would if it increased.

5 Discussion

We have focused on our own work, but other behavior-based models have been developed (reviews in Sutherland, 1996; Goss-Custard and Sutherland, 1997; Pettifor et al., 2000; Norris and Stillman, 2002). Several spatial depletion models have been used, in particular, to address a number of shorebird and wildfowl conservation issues (e.g., Sutherland and Anderson, 1993; Sutherland and Allport, 1994; Percival et al., 1996, 1996). Although based on the same general principles, our model differs from spatial depletion models in three main ways. First, it includes food competition from interference as well as depletion. Secondly, individuals in our model may differ in foraging

efficiency and susceptibility to interference, whereas all individuals are assumed to be equal in spatial depletion models. Thirdly, our model includes the storage of reserves whereas fat reserves are not incorporated in spatial depletion models. The main consequences of these differences are that our model is able to predict how environmental change influences mortality rate and body condition in birds, and, in turn, how these trends affect population size. In contrast, spatial depletion models are not used to predict mortality or body condition, but instead the number of bird-days that a site can support.

To date we have only applied our model to European sites. The conflicts that the model is designed to address, however, occur worldwide; and the fundamental principles on which the model is based also apply globally. Therefore, the model can be applied to any site anywhere, provided that sufficient data are available or can be collected. All that it requires in basic information is the quantified food supply at the beginning of the non-breeding season, its availability throughout the non-breeding season and the numbers of birds present through the non-breeding season.

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S30-4 The effects of coastal shrimp farming on birds in Indian mangrove forests and tidal flats

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Abstract Large areas of mangroves in India are disappearing rapidly due to booming shrimp aquaculture along its coasts. Such losses, pollution and direct conflict with aquafarmers has resulted in a decline in the number and diversity of birds along the coastal wetlands of India. In the Pichavaram mangroves, species numbers have fallen from 30 in 1995 to 24 at present. At the Point Calimere sanctuary, the flamingo (*Phoenicopterus minor*) population has dropped from 20 000 to a mere 5 000 birds. The Sunderbans wilderness of West Bengal is being eroded by shrimp farms and its bird life is also declining. In brackish Pulicat Lake, north of Madras, the flamingo population has dropped from more than 10 000 to just 1 000 due to pollution of feeding grounds by shrimp farm effluents. In natural tidal flats on the Nagaipattinam and Karaikal coasts, the waterbird population of 45 species averages 400 per tidal flat, while in the areas adjacent to shrimp farms, only 9 species of birds were recorded at an average of 80 birds per similarly sized area. Analysis of data from the Asian Midwinter Waterfowl Census over the past 10 years also reveals negative impacts on coastal bird life after aquaculture expansion. Guidelines for the construction of aquafarms by the National Environmental and Engineering Institute of India (NEERI) and Coastal Authority of India, and rulings from the Supreme Court of India, could form the basis for redressing such impacts.

Key words Aquaculture, Birds, Mangrove, Tidal flats, Population, Interaction

1 Introduction

India has a long coastline of over 7 500 km, with numerous brackish water lakes, estuaries, lagoons and backwaters suitable for shrimp farming. Aquaculture underwent rapid growth worldwide between the 1970s and early 1980s, and expanded along the coasts of India during the 1990s. Global aquaculture production has been steadily increasing over the last decade, in a boom reflected in shrimp production figures for India which increased from 0.78 million mt in 1987 to 1.77 million mt in 1996 (126%), with a corresponding increase in value from US\$ 0.83 billion to US \$ 1.98 billion (139%) (FAO, 1998). The major states in India where aquaculture is practiced are, in the order of importance: West Bengal, Gujarat, Andhra Pradesh, Maharashtra, Orissa, Kerala and Tamil Nadu. Traditional paddy cum shrimp farming continue to be carried out in West Bengal, Kerala, Karnataka and Goa over about 50 000 ha. The total area under cultivation rose from 65 100 ha in 1990–1991 to 141 837 ha in 1998–1999. Production rose similarly from 35 500 to 82 634 tonnes over the same period.

The increase in aquaculture in India has brought it into conflict with users of natural aquatic resources, and organizations concerned about its ecological effects. The report of an investigation by the National Environmental Engineering Research Institute (NEERI, 1995) of India found that many coastal aquafarms were not scientifically designed and located, resulting in excessive ecological and social

damage that far exceeded economic benefits. Damage extended to the spread of brackish water, loss of potable water, loss of traditional fishing grounds for fishermen, and loss of mangrove ecosystems which provide both protection against cyclones and other natural hazards and natural habitat for spawning of natural biota (Reddy, 1995). Further, indiscriminate destruction of mangroves resulted in loss of natural breeding grounds for the shrimps themselves.

Satellite data from the National Remote Sensing Agency (NRSA) show the extent of mangrove destruction, revealing that less than 10% of mangroves survive in Gujarat today (Qasim, 2000). In coastal Andhra Pradesh, mangroves covering 4 411 ha and 5 884 ha in Guntur and Krishna areas respectively in 1973 declined to 3 454 ha and 5 479 ha in 1992 (Reddy, 1995). Large scale conversion of mangroves and agricultural lands to aquaculture has taken place along the sides of the Vellar and Coleron Rivers, and in and around Pichavaram and Muthupet (Ramachandran et al., 1998; Jayanthi and Ramachandran, 2000; Ravichandran and Ramachandran, 2001). According to a report from CIBA (1997), many potential wetlands of avian importance in the coastal districts of Tamil Nadu have been lost to shrimp farms.

In addition to the effects of waste released from aquafarms, the physical pressure of high biomass shrimp and human activity can interact with wildlife in a number of ways (Gowen and Rosenthal, 1993). Thus aquafarming has impacted on predatory birds in particular (Anon, 1988;

Wilde, 1990), attracting them with convenient sources of fish and shellfish, often close to natural wintering grounds (Pillay, 1992), and then destroying them as pests (Pillay, 1990). Bird predation on shrimp ponds is reported to have decreased production by about 75% in Texas, USA (Pillay, 1992). Cormorants, fish eagles, herons, and kingfishers are considered to be the most destructive; other groups of relevance are grebes, gulls, and terns (Stickley, 1990).

Birds can also transmit disease. Herons appear to be the final host for fish tapeworms (cestodes) and herons, gulls, grebes, and geosanders the final hosts for fish flukes (trematodes) which infect both wild and farmed fish in lar-

val stages. Birds are mechanical carriers of viruses as well; and other pathogenic organisms, such as salmonellae, faecal coliforms and the bacterium *Edwardsia tarda*, might be transmitted through the contamination of water bodies by bird faeces. Grebes, fish-eating eagles and crows are thought to be agents for the white spot virus (systemic ecto-meso dermic baculo virus — SEMBV) which caused extensive damage to the aquaculture industry along the coasts of Tamil Nadu and Andhra Pradesh in 1995.

Thus aquafarmers treat birds as pests and take measures to thwart them. Diverse deterrents are used, from antipredator nets to scaring devices, but those with most impact are entrapment and killing. Yet the greatest impact of aquafarming on birds is the disruption of natural habitat, however attractive it may be for opportunistic predatory species (Pillay, 1992). Accordingly, this paper examines the impacts of aquafarms on bird life along the east coast of India.

2 Materials and methods

Figure 1 shows areas of mangroves along the east coast of India discussed in this paper. Avian nomenclature follows Grimmett et al. (1999) except for the little green heron (*Butorides ardeola*) and herring gull (*Larus argentatus*) which are according to Ali and Ripley (1983). The data on waterbird populations in different wetlands was collected from various sources such as census and research reports (Perennou et al., 1990; Lopez and Mundkur, 1997), as well as dissertations and published papers. We also include our own field data from Pichavaram mangroves and adjacent wetlands, collected from 1989 on except between 1996–1999. Information on aquaculture, changes in land use pattern in the Pichavaram and Muthupet mangroves, and land reclaimed for aquaculture farming was collected from published papers.

The total number of birds present in the different wetlands was counted. The total number of species was also counted for estimations of species richness using the Shannon-Wiener diversity index (Shannon and Wiener, 1949) calculated by the formula

$$H' = - \sum p_i \log_e p_i$$

where p_i is the proportion of the i th species in the sample.

3 Results

Asian mid-winter waterbird census data from 1990 to

Table 1 Asian mid-winter waterbird census results from selected wetlands along the east coast of India in 1990 and 1995

Wetland	1990	1995
Pichavaram	12 299	5 559
Chembarambakkam	24 560	12 075
Kalyani Lake	2 777	893
Ballarpur Wildlife Sanctuary	5 663	2 640

Data from Perennou et al. (1990) and Lopez and Mundkur (1997).



Fig.1 Map of India and Tamil Nadu showing study areas

2000 were analyzed, and the information from 1990, when aquaculture started to grow, was compared with that from 1995 for selected wetlands on the east Indian coast (Table 1). Over the 1990–1995 period, there has been a consistent decline in the number of waterbirds in each of those wetlands.

3.1 Avifaunal changes at the Pichavaram mangroves

Total numbers of birds rose from 5 156 in 1987 to 13 097 birds in 1992 but declined thereafter as the area under aquaculture increased (Fig. 2; Table 2). Shrimp farming peaked in 1995 and in that year 5 091 birds were recorded. By 2001, the bird population had fallen to a low of 1 278 individuals, followed by a slight increase in 2002. The number of species present (i.e., species richness) followed the same pattern. A total of 50 species was recorded in 1987, which increased to a maximum of 63 in 1990 and then declined rapidly to a low of 23 in 2001 (Fig. 2; Table 2).

Nagarajan and Thiyagesan (1998) found that adjoining croplands played an important role in attracting the birds to the Pichavaram mangroves. Aquafarm development, however, moved into them as well as the mangroves, requiring their assessment, together with adjacent abandoned fields, mudflats, marshes and open waters in the period between 1990 and 2001, based on Nagarajan (1990) with wetlands classified according to Nagarajan and Thiyagesan (1996). In 1990, bird density was highest at 105.63 individuals/ha in cropland but declined to 42.5/ha in 2001 (Table 3). There was reduction in waterbird density in all the habitats between 1990 and 2001, a trend most pronounced in the croplands.

3.2 Avifaunal changes in Point Calimere Wildlife Sanctuary

The total number of waterbird species at Point Calimere Wildlife Sanctuary (Fig. 1) between 1986 and 1999 is given in the Table 4. A total of 60 075 birds was present in 1986 which declined to 7 170 in 1999. Species richness was at 28 in all the years, but diversity indices declined from 1.0045 to 0.4582 between 1986 and 1999 (Table 4). The flamingo (*Phoenicopterus* spp.) population which usually con-

sisted of around 20 000 individuals declined from 3 351 in 1986 to 350 in 1995.

3.3 Status of the Sunderbans mangroves

The Sunderbans wilderness of West Bengal, where the mangrove forest extends across 10 000 sq km (Fig. 1), is being eroded at its edges by the development of shrimp farms which have already reclaimed ca. 10 000 ha (Anon., 1993). According to Qasim (2000), the fish catch has been declining annually and this will affect endangered bird species. Tutu (2001) found that industrial shrimp cultivation is causing disturbance to migratory birds in the area.

3.4 Status of Pulicat and Chilka brackish water lakes

The Pulicat and Chilka lakes (Fig. 1) are important brackish water bird areas on the east coast of India. Both of them appear to be threatened by aquaculture expansion and there have been several incidences of conflict (Goss, 1992; Vivekanandan and Kurien, 1998; Anon, 1999; Mohanty, 1999; Noronha, 1999; Pearce, 1999; Pattnaik, 2000). The Asian Waterfowl Census 1994–1996 (Lopez and Mundkur, 1997) found that Chilika Lake, the largest brackish water body in India and a declared sanctuary and Ramsar Site, is being threatened by aquaculture. According to Patel (1996), the Pulicat Lake flamingo populations that numbered more than 10 000 in 1993 had declined to 1 000 in the following year due to pollution of their breeding grounds by aquafarm effluent.

3.5 Comparisons between bird populations on aquafarms and adjacent tidal flats

The avifaunal composition of seven mudflats along the east coast of Tamil Nadu — Mahenderapalli, Pazahayar, Thirumullaivasal, Chinnangudi, Tharangampandi, Karaikkal and Niravai — ranges from 146 birds to 795 birds on different mudflats; and the number of bird species ranges from 7 and 23, with a total richness of 45 species (Table 5). Bird species diversity indices range between 0.944 and 2.351. Avifaunal density in and around three selected areas containing three aquafarms in the midst of these mudflats are enlightening (J. Pandian, unpublished data). In 1999, the

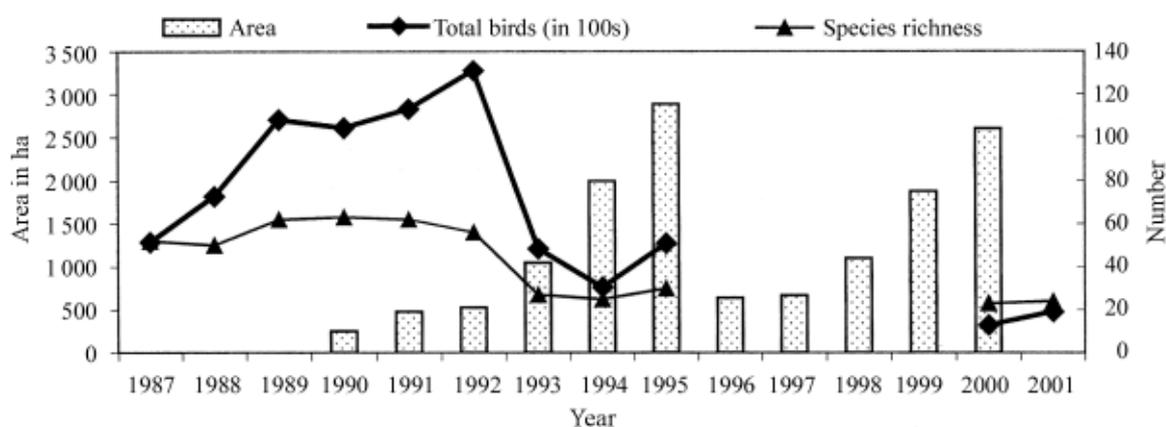


Fig. 2 Changes in bird numbers and species richness in the Pichavaram mangroves. The spotted bars indicate the area covered by aquaculture in Tamil Nadu across years.

Table 2 Waterbird population numbers in the Pichavaram mangrove forests, Tamil Nadu, between 1987 and 2001

Common name	Species	1987	1988	1989	1990	1991	1992	1993	1994	1995	2000	2001
Gray heron	<i>Ardea cinerea</i>	15	33	45	48	39	52	12	2	18	2	6
Purple heron	<i>Ardea purpurea</i>	2	2	6	9	13	19	4	0	8	0	2
Indian pond heron	<i>Ardeola grayii</i>	90	240	105	72	85	0	1 600	1 100	1428	257	754
Great bittern	<i>Botaurus stellaris</i>	90	0	0	68	0	0	0	12	8	6	0
Cattle egret	<i>Bubulcus ibis</i>	17	145	180	215	165	240	150	128	210	0	0
Little green heron	<i>Ardeola grayii</i>	35	0	0	0	0	0	22	48	56	6	14
Little heron	<i>Butorides striatus</i>	0	90	80	0	0	82	0	0	0	0	0
Western reef egret	<i>Egretta gularis</i>	14	18	15	25	18	32	0	0	0	0	0
Great egret	<i>Casmerodius albus</i>	6	80	40	22	28	47	182	58	162	48	63
Little egret	<i>Egretta garzetta</i>	135	375	450	415	380	415	1 250	898	1 300	359	520
Intermediate egret	<i>Mesophoyx intermedia</i>	65	290	160	140	160	315	0	0	0	0	0
Pacific reef heron	<i>Egretta sacra</i>	0	0	0	0	0	0	0	2	0	0	0
Cinnamon bittern	<i>Ixobrychus cinnamomeus</i>	4	6	6	0	0	0	0	0	0	0	0
Black bittern	<i>Dupetor flavicollis</i>	2	3	4	2	4	12	0	0	0	0	0
Yellow bittern	<i>Ixobrychus sinensis</i>	0	0	1	0	0	0	0	0	0	0	0
Black-crowned night heron	<i>Nycticorax nycticorax</i>	1 500	1 800	1 800	2 100	2 300	2 100	262	102	186	36	59
Asian openbill	<i>Anastomus oscitans</i>	30	18	377	43	46	17	68	52	182	158	163
White stork	<i>Ciconia ciconia</i>	19	0	5	8	17	38	0	0	0	0	0
Painted stork	<i>Mycteria leucocephala</i>	15	35	15	8	19	0	10	4	62	9	2
Crab-plover	<i>Dromas ardeola</i>	0	0	0	0	4	7	0	0	0	0	0
Small pratincole	<i>Glareola lactea</i>	0	15	6	3	5	0	0	0	0	0	0
Kentish plover	<i>Charadrius alexandrinus</i>	93	140	55	70	88	225	112	72	128	62	45
Little ringed plover	<i>Charadrius dubius</i>	35	85	70	95	120	170	220	180	316	109	0
Greater sand plover	<i>Charadrius leschenaultii</i>	7	0	6	4	6	9	12	0	18	0	0
Lesser sand plover	<i>Charadrius mongolus</i>	190	365	600	820	1 115	1 725	0	0	0	0	0
Pacific golden plover	<i>Pluvialis fulva</i>	165	180	215	280	190	220	0	0	0	0	0
Grey plover	<i>Pluvialis squatarola</i>	29	45	75	45	79	130	0	0	0	0	0
Red-wattled lapwing	<i>Vanellus indicus</i>	22	17	32	18	22	43	128	102	212	28	16
Yellow-wattled-lapwing	<i>Vanellus malabaricus</i>	6	0	0	8	0	31	0	0	0	0	0
Eurasian oystercatcher	<i>Haematopus ostralegus</i>	0	0	4	6	3	6	0	0	0	0	0
Pheasant-tailed jacana	<i>Hydrophasianus chirurgus</i>	0	0	5	0	0	0	0	0	0	0	0
Whiskered tern	<i>Chlidonias hybridus</i>	60	195	225	160	220	160	28	13	22	11	0
Gull-billed tern	<i>Gelochelidon nilotica</i>	37	85	160	95	130	185	8	0	12	0	0
Herring gull	<i>Larus argentatus</i>	130	28	80	50	45	24	0	0	0	0	0
Brown-headed gull	<i>Larus brunnicephalus</i>	835	160	150	225	190	230	0	0	0	0	0
Pallas's gull	<i>Larus ichthyaetus</i>	0	0	0	13	28	0	0	0	0	0	0
Black-headed gull	<i>Larus ridibundus</i>	145	49	85	125	180	150	0	0	0	0	0
Little tern	<i>Sterna albifrons</i>	40	45	94	90	110	96	68	49	122	28	52
River tern	<i>Sterna aurantia</i>	0	6	0	5	9	25	0	0	0	0	0
Lesser crested tern	<i>Sterna bengalensis</i>	0	0	0	120	0	0	0	0	0	0	0
Great crested tern	<i>Sterna bergii</i>	0	0	65	0	140	170	0	0	0	0	0
Caspian tern	<i>Sterna caspia</i>	0	17	15	30	47	55	42	18	47	18	0
Common tern	<i>Sterna hirundo</i>	75	130	95	65	110	140	0	0	0	0	0
Black-winged stilt	<i>Himantopus himantopus</i>	650	750	480	550	615	820	280	32	168	0	0
Pied avocet	<i>Recurvirostra avosetta</i>	15	19	15	8	14	26	0	0	0	0	0
Common sandpiper	<i>Actitis hypoleucos</i>	26	29	22	17	22	62	72	26	88	33	51
Ruddy turnstone	<i>Arenaria interpres</i>	0	4	28	15	6	0	0	0	0	0	0
Eurasian thick-knee	<i>Burhinus oedicnemus</i>	0	0	0	0	0	0	0	4	0	0	0
Dunlin	<i>Calidris alpina</i>	7	0	35	325	35	46	0	0	0	0	0
Curlew sandpiper	<i>Calidris ferruginea</i>	34	375	450	325	475	560	0	0	0	0	0
Little stint	<i>Calidris minuta</i>	250	680	2 800	2 250	2 415	2 600	124	87	186	50	62
Temminck's stint	<i>Calidris temminckii</i>	0	8	15	20	35	45	0	0	0	0	0
Common snipe	<i>Gallinago gallinago</i>	45	55	42	65	80	0	26	11	32	3	9
Broad-billed sandpiper	<i>Limicola falcinellus</i>	18	18	40	35	48	68	0	0	0	0	0
Asian dowitcher	<i>Limnodromus semipalmatus</i>	0	0	0	2	4	0	0	0	2	0	0
Bar-tailed godwit	<i>Limosa lapponica</i>	0	0	15	8	19	38	0	0	0	0	0
Black-tailed godwit	<i>Limosa limosa</i>	9	0	400	320	290	330	0	0	0	0	0
Whimbrel	<i>Numenius phaeopus</i>	25	35	42	25	36	57	0	0	0	0	0
Eurasian curlew	<i>Numenius arquata</i>	17	28	30	38	43	0	0	0	0	0	2
Ruff	<i>Philomachus pugnax</i>	35	0	250	127	95	155	0	0	0	0	0
Spotted redshank	<i>Tringa erythropus</i>	0	0	6	0	0	26	0	0	0	0	0
Wood sandpiper	<i>Tringa glareola</i>	20	0	22	6	11	39	16	8	10	0	0
Common greenshank	<i>Tringa nebularia</i>	0	42	25	20	18	22	0	0	0	25	15
Green sandpiper	<i>Tringa ochropus</i>	33	0	0	7	15	0	64	48	58	24	33
Marsh sandpiper	<i>Tringa stagnatilis</i>	45	275	550	620	715	840	25	16	18	2	14
Common redshank	<i>Tringa totanus</i>	63	155	85	115	65	85	58	0	14	0	6
Terek sandpiper	<i>Xenus cinereus</i>	0	8	7	15	9	8	0	0	0	0	2
Great thick-knee	<i>Esacus recurvirostris</i>	0	0	0	2	0	4	0	0	0	0	0
Little grebe	<i>Tachybaptus ruficollis</i>	0	0	25	0	0	0	0	0	0	0	0
Darter	<i>Anhinga melanogaster</i>	4	2	0	3	0	0	0	0	0	0	0
Great cormorant	<i>Phalacrocorax carbo</i>	6	18	0	0	0	0	0	0	0	0	0
Little cormorant	<i>Phalacrocorax niger</i>	17	2	30	15	3	8	0	0	0	0	0
Lesser flamingo	<i>Phoenicopterus minor</i>	6	0	28	0	0	0	0	0	0	0	0
Greater flamingo	<i>Phoenicopterus ruber</i>	13	0	0	28	24	36	0	0	0	0	0
Eurasian spoonbill	<i>Platalea leucorodia</i>	0	0	22	31	26	29	0	0	0	0	0
Black-headed ibis	<i>Threskiornis melanocephalus</i>	0	0	23	9	11	23	0	0	14	2	8
Total birds		5156	7290	10813	10435	11292	13097	4843	3060	5091	1278	1904
Species richness		52	50	62	63	62	56	27	25	30	23	24
Diversity index (H')		2.684	2.921	2.885	2.888	2.858	2.949	2.207	2.016	2.376	2.296	1.900

overall number of birds ranged from 62 to 115. Only six different species of waterbirds and three of terrestrial birds — *Milvus migrans*, *Haliaster indus*, and *Halcyon smyrnensis* — were observed on the farms; bird species diversity indices ranged between 1.389 and 1.896. Thirty-three species of aquatic birds present on the mud flats were not recorded on adjacent aquafarms.

4 Recommendations

The data reported here indicate clearly that extensive alienation of mangrove and other coastal wetlands has resulted in a marked quantitative and qualitative fall in bird numbers and diversity along the east coast of India. Towards redressing the trend, a number of observations and recommendations are pertinent.

The shrimp farming industry needs to seriously consider its effects on the environment. This, in general, should include better planning and management of coastal aquaculture developments, integrated coastal area management (ICAM), implementation of Environmental Impact Assessments (EIA) recommendations, monitoring of pollution, and environmental legislation. For shrimp culture, in particular, these measures include management of pond effluents, regulation of species introductions and chemical use, and rehabilitation of wild habitats and populations.

Detailed guidelines have been issued for the construction of farms by the National Environmental and Engineering Research Institute of India, the Coastal Authority of India and the rulings of the Supreme Court of India. These offer a base for the integrated use of coastal wetlands by people, birds and the environment. The goal of this plan, Integrated Coastal Area Management or ICAM, is to ensure sustainable use of coastal natural resources, maintenance of biodiversity and conservation of critical habitats by coordinating the initiatives of various economic sectors toward long-term optimal socio-economic outcomes, including resolution of conflicts (Clark, 1992). In addition to aquaculture, there are multiple users of the coastal zone, including urban settlement, industrial development, waste disposal, ports and marine transportation, fisheries, forestry and tourism. All are implicated in the ICAM plan.

Table 3 Waterbird densities (no./ha) in different habitats at Pichavaram, Tamil Nadu, in 1990, 2001 and 2002

Habitat	Year		
	1990 ^a	2001 ^b	2002 ^b
Agricultural land	105.63	44.38	42.5
Abandoned field	21.5	22.0	18.0
Mudflats	7.13	8.25	3.0
Swamps	18	4.50	6.0
Marshy areas	8.25	4.50	5.25
Open waters	24.75	10.50	18.75

^a Data from Nagarajan (1990); ^b Nagarajan, unpublished data

For mangrove areas in particular, priorities can be designated now (Bird and Kunstader, 1986):

- a) preservation-conservation for biodiversity and ecological function, including natural exchanges and storm buffering;
- b) sustained yield of fisheries and silviculture;
- c) reforestation; and
- d) conversion to culture ponds, salt beds etc., preferably on previously altered sites.

Land use mapping of the entire coast is urgently needed, followed by on-the-spot assessment of bird use of each and every coastal wetland, for designing a coastal management plan to conserve both avian diversity and enable sustainable aquaculture.

Environmental Impact Assessments (EIA) are required to ensure compliance with site selection criteria that include not only standard grow-out parameters such as salinity and land elevation, which treat the farm as an isolated unit, but also the potential effects on the environment including wildlife.

Integrated programs are needed to manage mangrove vegetation to maintain functions such as storm protection, and nutrient/particulate export to near-shore communities. Remaining mangroves should be conserved and there should be enforcement of existing legislation that prohibits further conversion and allows for greenbelt areas. Abandoned ponds should be allowed to regenerate back to mangroves by breaking down dikes. Large-scale reforestation should be undertaken in severely degraded areas. Lessons can be learned from the experience of Bangladesh where a total of 120 000 ha have been afforested since 1966 to protect and stabilize coastal areas from cyclone damage (Saenger and Siddiqi, 1993). These mangroves can be managed silviculturally to produce up to \$11 000/ha/yr (Primavera, 1993). Integration of forestry, fisheries and aquaculture in mangrove habitats has also taken place in the *tambak tumpang sari* of Indonesia (Naamin, 1986) and traditional mangrove-shrimp ponds in Vietnam.

Concerning management of pond effluents, intensive aquaculture has been recommended as an alternative to

Table 5 Comparison of water bird abundance, richness and diversity from seven mudflats on the east coast of Tamil Nadu

Locality	Total birds	Species richness	Diversity index
Mahendrapalli	343	18	1.7705
Pazhayar	146	15	2.0883
Thirumullaivasal	570	24	2.1349
Chinnangudi	795	14	1.7711
Tharangambadi	414	8	0.9439
Karraikkal	610	19	1.9618
Niravi	239	17	2.3799
Total	3 117	45	2.3596

From J. Pandian, unpublished data.

Table 4 Total counts of waterbird species at Point Calimere Wildlife Sanctuary, Tamil Nadu, in 1986, 1998 and 1999

Common Name	Species name	1986 ^a	1998 ^b	1999 ^b
Grey heron	<i>Ardea cinerea</i>	235	64	20
Indian pond heron	<i>Ardeola grayii</i>	0	0	45
Cattle egret	<i>Bubulcus ibis</i>	0	61	0
Great egret	<i>Casmerodius albus</i>	6	18	299
Little egret	<i>Egretta garzetta</i>	307	0	296
Pacific reef egret	<i>Egretta sacra</i>	12	0	2
Black-crowned night heron	<i>Nycticorax nycticorax</i>	0	1	0
Kentish plover	<i>Charadrius alexandrinus</i>	856	0	0
Asian openbill	<i>Anastomus oscitans</i>	0	31	26
Painted stork	<i>Mycteria leucocephala</i>	1 017	1 018	156
Little ringed plover	<i>Charadrius dubius</i>	0	31	207
Greater sand plover	<i>Charadrius leschenaultii</i>	0	2	0
Lesser sand plover	<i>Charadrius mongolus</i>	394	0	0
Grey plover	<i>Pluvialis squatarola</i>	0	3	2
Pacific golden plover	<i>Pluvialis fulva</i>	2	7	0
Red-wattled lapwing	<i>Vanellus indicus</i>	0	2	14
Ruddy turnstone	<i>Arenaria interpres</i>	92	0	0
Whiskered tern	<i>Chlidonias hybridus</i>	109	0	0
Gull-billed tern	<i>Gelochelidon nilotica</i>	11	0	5
Caspian tern	<i>Sterna caspia</i>	604	8	4
Little tern	<i>Sterna albifrons</i>	643	972	153
River tern	<i>Sterna aurantia</i>	0	34	101
Common tern	<i>Sterna hirundo</i>	330	1 363	858
Black-headed gull	<i>Larus ridibundus</i>	0	24	0
Herring gull	<i>Larus argentatus</i>	90	4	0
Brown-headed gull	<i>Larus brunnicephalus</i>	0	525	5
Black-winged stilt	<i>Himantopus himantopus</i>	19	0	92
Avocet	<i>Recurvirostra avosetta</i>	2	0	0
Common sandpiper	<i>Actitis hypoleucos</i>	0	199	90
Curlew sandpiper	<i>Calidris ferruginea</i>	4 437	0	20
Little stint	<i>Calidris minuta</i>	46 666	237	4 184
Broad-billed sandpiper	<i>Limicola falcinellus</i>	9	0	0
Bar-tailed godwit	<i>Limosa lapponica</i>	0	0	3
Eurasian curlew	<i>Numenius arquata</i>	1	13	19
Common greenshank	<i>Tringa nebularia</i>	55	0	57
Marsh sandpiper	<i>Tringa stagnatilis</i>	21	425	3
Common redshank	<i>Tringa totanus</i>	351	51	17
Wood sandpiper	<i>Tringa glareola</i>	0	15	0
Terek sandpiper	<i>Xenus cinereus</i>	2	0	0
Spot-billed pelican	<i>Pelecanus philippensis</i>	89	14	13
Flamingos	<i>Phoenicopterus</i> spp.	3 351	250	350
Eurasian spoonbill	<i>Platalea leucorodia</i>	364	46	129
Black-headed ibis	<i>Threskiornis melanocephalus</i>	0	7	0
	Total birds	60 075	5 451	7 170
	Species richness	28	28	28
	Diversity index (H')	1.0045	0.4195	0.4582

a = Data from Sankar (1989).

b = Unpublished data from Tamil Nadu Forest Department Census Records.

extensification that would exploit wide mangrove areas. Such intensification, however, will only be viable if pollution levels in effluents are minimized and salinization of outlying areas prevented.

A research and information network is an ongoing imperative to coordinate research effort for mangrove evaluation and delineation of greenbelts, and to determine impacts of exotic species on biodiversity, common methodologies for evaluating environmental impact, nutrient requirements of species and quality standards for feeds, and impacts of drugs and chemicals (Briggs, 1993; FAO/NACA, 1994). The information network should include exchange of technicians and sharing of technology and experience gained in other areas, such as mangrove reforestation in Bangladesh, mangrove silviculture in the Matang Forest of Malaysia and shrimp restocking in Japan.

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Symposium 31 Bird population explosions in agro-ecosystems: common factors in case histories

Introduction

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Explosions of particular bird species in agro-ecosystems is a common phenomenon throughout the world. Well known cases include the eared dove (*Zenaida auriculata*) in South America, European starling (*Sturnus vulgaris*) in Europe, North America and Australia, and quelea (*Quelea quelea*) in Africa. In most cases, such birds are considered pests by farmers, who commonly call for control measures. Understanding the factors underlying these population outbreaks, therefore, has important practical implications.

Bird explosions in agro-ecosystems are closely associated with changes in land-use or crop technologies. Being amongst the most drastic and widespread alterations imposed by man on the natural environment, these changes may also be viewed as large-scale experiments in habitat and food supply change. Unfortunately, proper studies at this level are very difficult, since it is virtually impossible to systematically manipulate whole landscapes. For the present at least, the only alternative is to accumulate corroborated evidence from repeated observations for different species in different regions and at different times. Although somewhat unsatisfactory, it is often the only practical approach at the scale considered here.

This symposium follows this approach by analyzing several case histories for different species from different regions of the world. Historical cases of eared dove explosions in South America are reviewed, as well as its novel irruption in São Paulo, Brazil. The symposium also canvassed the quelea problem in Africa, population changes of the European starling in Great Britain, and the effects of habitat change and agricultural development on crane populations in India.

Enrique Bucher and Ronald Ranvaud found that historical eared dove outbreaks in South America appeared in areas where agricultural frontiers expanded into previously forested areas, particularly wherever sorghum became the main crop. A significant increase in food availability from sorghum crops, wasted grain, and weed seeds catalyzed a rapid population increase and a shift in breeding habits from isolated to colonial nesting in remnant forest fragments. This generalized model, developed from explosions studied in semi-arid regions, was confirmed in Ranvaud and Bucher's

analysis of a completely new situation in São Paulo, Brazil, where, under more humid conditions, eared dove colonies are establishing themselves in sugar cane plantations.

In the case of the starling in Britain, Robert Robinson and colleagues found that for this formerly very abundant species, food supply is a key determinant of local population density, mostly through its effect on first year winter survival. Recently declines in farmland populations have been associated with large scale changes in the management of both pastoral and arable systems, including a greater spatial separation between the two. Although decline has been driven largely by the drop in food in winter, the farmland population may have also been limited by the numbers of nest sites in woodlots, also drastically reduced by recent changes in land-use.

According to Clive Elliot, on the other hand, cycles in quelea populations appear to occur independently of agricultural change, populations fluctuating primarily according to rainfall in their breeding areas. There is no evidence of a population explosion and little evidence even to support any general trend towards increasing population levels other than temporary irruptions, despite repeated claims to the contrary. A completely different situation arose when irrigation programs created new wetlands associated with croplands, which provided both appropriate habitat and increased food for aquatic birds, as detailed by Aeshita Mukherjee for India.

The general conclusion drawn from the symposium was that land management, through its impact on food availability and breeding habitat, explains most of the bird explosions known. This generalization, however, clearly does not apply to species whose habitat is only marginally encroached on by agro-ecosystems, as in the case of African quelea. Attempts at lethal control, by whatever means, commonly have negligible impact because such mortality usually falls within the compensatory range. The factors and principles underlying population explosions also underpin population declines in agro-ecosystems, a situation that is becoming increasingly common as technology reduces grain spillage and weed abundance to a minimum while habitat becomes more and more uniform.

S31-1 The population decline of the starling, *Sturnus vulgaris*, in Great Britain: patterns and causes

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Abstract Although the starling has the capacity for explosive population growth, its population in Britain has declined by two-thirds over the last 40 years. Here we summarize a major study (Crick et al., 2002) which investigates the reasons for this. The starling is commonest in urban and farmland habitats, though density in the latter is much lower; the total breeding population is estimated at 9 million birds. In general, breeding productivity has increased, while survival, particularly of juveniles, has shown periods of decrease. The decline on farmland has been greater in pastoral areas, and is probably linked to reduced foraging opportunities associated with more intensive agricultural management. There is some evidence for a decline in urban populations, but data are scant and possible reasons for decline there are unclear.

Key words Avian demography, Agricultural intensification, Pastoral farming, Survival

1 Introduction

The European starling, *Sturnus vulgaris*, is one of the most successful birds in the world. Indigenous to Europe and western Asia, it has been introduced successfully on to three continents (Feare, 1984). The population increase in North America has been particularly explosive. Around 60 birds were released in Central Park, New York, in 1890, and although initial spread was slow, the starling has now become one of the most numerous birds on the continent, numbering over 200 million individuals.

Even in its native range, the starling has expanded in historical times. Thus, in Britain in the early half of the 19th century, it was absent from much of mainland Scotland, southwest England and western Wales. Through the middle of the 19th Century and into the 20th Century, it spread north and west, becoming common in all except the most exposed upland areas (Holloway, 1996). Amelioration in climate, increased agricultural utilization of marginal upland areas and spreading urbanization are all likely to have played a role. The starling had become a pest in agricultural lands and its huge, fouling roosts, sometimes numbering in the millions, created public health hazards in urban areas (Feare et al., 1992). Starling populations are capable of expanding rapidly, their success attributable to a catholic diet, wide habitat tolerance and an aggressive attitude towards ownership of nest holes.

Because of the problems caused by large starling flocks and their ubiquity, the British government issued a general licence allowing their killing, and the destruction of their nests and eggs, in the interests of public health and safety and to prevent serious damage to crops or livestock.

This licence was re-issued in January 1993 under a derogation of the European Directive on the Control of Wild Birds (EC/79/409), which imposed the added responsibility of monitoring population trends nationally.

But all is not well for the starling. In Britain and elsewhere in northwest Europe, starling populations have declined over the last three to four decades. The decline has been so severe that the starling has recently been placed in the highest category of conservation concern in Britain (Gregory et al., 2002). In October 2000, the government's Department for Environment, Food and Rural Affairs (Defra) commissioned a comprehensive report on its status to ensure that legal control measures were not contributing locally to the national decline in numbers (Crick et al., 2002). We summarize the key findings of the report to examine why a population of such an apparently successful bird should decline so dramatically.

2 The status of the starling in Britain

Robinson et al. (2002a) quantified, for the first time, the size of the starling population breeding in Britain. It totaled some 9 million birds in the late 1990s. Although the density of birds breeding on farmland (typically about 30 birds.km⁻²) is much lower than in human-associated habitats (180 birds.km⁻²), a significant proportion of the total population occurs there because farmland forms the major land-use in Britain. Together, farmland and urban habitats account for the vast majority (87%) of the British breeding population. No data were available on the size of the wintering population, which includes immigrants from continental northern and eastern Europe, predominantly from around the Baltic Sea, that may equal or exceed the numbers of the

breeding population (Feare, 1984).

The breeding population of starlings has been monitored since 1962 by the British Trust for Ornithology's (BTO) Common Birds Census (CBC), a scheme based on territory mapping, mainly in woodland and farmland habitats, that counts around 200 sites each year. While populations have declined generally since 1962 (68%), the decline has been greatest in woodland (>90%). This is likely to reflect the fact that woodland is sub-optimal habitat for breeding starlings, but could also be due in part to a decline in the number of nest holes available. The population on farmland has declined by two-thirds, and mirrors the national trend, as this is where the bulk of birds occurs. Even within farmland, population declines differ: those breeding on pastoral farms have declined more than those on agricultural farms. Declines have been greatest in the south west of Britain where the rural industry is livestock-based.

Very little is known about the winter dispersal and habitat use of British breeding starlings, though virtually all of the breeding population remains in the country, most of it within a few tens of kilometers of where it breeds (Feare, 2002). The wintering populations of immigrant starlings in different areas of Britain originate from different breeding populations, and the habitat used by the immigrants while in Britain is unknown. Few long term data are available on numbers in winter, though there is evidence of at least local declines, particularly in urban areas (Robinson et al., 2002b).

3 Demographic processes

Breeding productivity was quantified by using the archives of the BTO's Nest Record Scheme (NRS), which can be used to assess the success of individual breeding attempts (Siriwardena and Crick, 2002). The breeding performance of starlings, in common with many other British passerines, has increased over the last forty years. Such a pattern may represent a density-dependent response to a reduction in numbers, but could also occur if starlings have become more concentrated in more favorable habitats.

The NRS can only be used to investigate the number of fledgling birds produced in each nesting attempt. Productivity summed across the entire season is also important for understanding the population dynamics of a species. This was quantified from a study of a suburban colony in southern England (Feare and Forrester, 2002). The study ran from 1975 to 1997, covering the major period of decline in the national population and some immediately preceding years when the population index was largely stable. Although the number of birds fledged varied significantly from year to year, there was no overall trend in productivity. The proportion of birds laying second clutches also varied annually, being largely dependent on the date of laying of the first clutch. There was no systematic temporal trend in these variables either, nor in inter-clutch interval, an indicator of environmental stress.

Survival was quantified from numbers of birds ringed in Britain during the breeding season and subsequently

reported dead (Freeman et al., 2002). Survival during the 44 days immediately following fledging was estimated at 38%, that over the first winter for fledged birds at 39% and that for adults annually at 67%. Thus, birds were much less likely to survive their first year than any subsequent year. These estimates are comparable to those for other birds of similar size (Siriwardena et al., 1998). Juvenile survival, in particular, declined markedly through the 1980s, from 50% in 1980 to just 31% in 1991, but subsequently increased to around 45%. The decline in survival rates nationwide coincided with the major period of population decline. A population modeling exercise, whereby the demographic rates were held constant and each one allowed to exhibit time-dependent variation in turn, suggested that changes in first-year over-winter survival rates could best account for the observed population change, and were sufficient, on their own, to explain the broad pattern of decline (Freeman et al., 2002).

The potential impact of lethal control was assessed using a questionnaire survey of landowners and local governmental authorities (McKay et al., 2002). The vast majority of owner/occupier respondents and all Local Authority respondents had undertaken no lethal control. It was estimated that around 75 000 starlings were culled each year, mostly during the non-breeding season, when large numbers of immigrants are present. Most of this mortality is likely to be compensatory and the impact on the population negligible.

4 Starlings on farmland

On farmland, starlings are very much birds of pastoral and livestock systems. Their main prey are soil and ground-dwelling invertebrates, particularly leatherjackets (Tipulidae) and earthworms (Lumbricidae), although they also eat a wide range of other foods (Tinbergen, 1981). Densities of soil invertebrates are highest in pasture fields, particularly those which are undisturbed by cultivation (Whitehead et al., 1995). Although there is little published evidence that the density of tipulids has changed over time (Wilson et al., 1999), the area of permanent pasture has declined and the use of insecticides on them has increased. Starlings also often forage in association with livestock, particularly cattle, which create a heterogeneous sward in which starlings prefer to forage. The British cattle herd has decreased by 18% since 1970, mostly since 1980.

Concurrent with increased use of general insecticides has been a growing use of anthelmintics in livestock (McCracken, 1993). Although starlings rely predominantly on subterranean invertebrates, they turn to surface-dwelling invertebrates if the former are scarce or unavailable due to drought or hard frost (Feare, 1984). Starlings will also utilize other food sources at such times, including invertebrates in dung. The importance of this source has not been established but, if it is important, depletion through the action of anthelmintics is likely to impact on the survival of individual birds, especially when subsurface prey is unavailable and birds are stressed.

Fertilization levels have increased and, although this seems to have little effect on leatherjacket numbers, the number and diversity of other insects taken by starlings may decrease (Paoletti, 1999). Fertilizer use also tends to promote taller, denser swards, in which starlings have greater difficulty foraging, and is likely to be associated with increased levels of grazing and/or mowing, which all tend to reduce invertebrate numbers. Starlings frequently forage around cattle feeding stations, where they may take significant amounts of food, particularly cereal grains (Feare, 1984). It is often the most dominant birds (primarily adult males) that use this food source, other individuals continuing to forage on grassland. The tendency to keep cattle indoors may have reduced foraging opportunities for them, though this needs to be quantified.

5 Starlings in towns

Relatively little is known about starlings in towns and cities. Their urban roosts are spectacular, sometimes numbering in excess of a million birds, as the birds wheel into them around stands of large trees in the darkening skies. A major finding of the Crick report (Crick et al., 2002) is just how important suburban and urban habitats are for starlings. For breeding, starlings require a suitable cavity for nesting with some short grass fields close to the nest; adults rarely forage more than 500 m from the nest (Feare, 1984). Such situations are widespread in many towns and cities, although the quality of the urban and suburban habitats in terms of food provisioning for nestlings is unknown. Nesting attempts in urban and suburban areas produce fewer young than rural areas, due to lower clutch sizes and hatching success (Siriwardena and Crick, 2002).

Lawns, parks and sports fields should provide an attractive alternative foraging habitat to preferred pasture fields. Although large numbers of starlings frequently forage in these areas, their quality and quantity of food production remains unquantified. Also unknown is the extent to which starlings use these resources. The ecology of urban starlings remains a woefully neglected area.

6 Discussion

In order to appreciate the causes of population decline, and to plan effective countermeasures in amelioration, one needs to understand the demography of the species concerned. Freeman et al. (2002) clearly show that changes in survival have driven the population decline in British starlings. There have been large-scale changes in the management of both pastoral and arable systems, and greater spatial separation of the two (Vickery et al., 2001; Robinson and Sutherland, 2002). These changes are likely to have resulted in decreased foraging opportunities in the non-breeding season, primarily in autumn when leatherjackets are scarcest. With their mobility and catholic diet, starlings seem less affected by spells of cold weather than other birds. Encouraging mixed farming practices through agri-environment schemes, and measures such as

the introduction of pockets of grassland cultivation in arable areas, should benefit the starling and other species.

Although the population decline has been largely driven by changes in survival, the farmland population may have been limited by the numbers of nest sites too. Providing extra nesting-sites within good areas of farmland may have the potential to increase the size of the breeding population in these areas, but this requires that sufficient foraging resources are available to support the increased numbers (Bruun, 2002). Careful monitoring would be needed to check that birds were not simply moving in from other sites.

The starling clearly has the ability for explosive population growth, and populations in Britain have expanded in historical times. Today, however, the starling population is declining. In the wider countryside, this appears to be due a reduced food supply; the population dynamics of urban populations are simply not known. Food supply is a key determinant of local population density, as many studies have shown (Newton, 1998). Changes in food supply because of agricultural intensification have been implicated in the declines of other farmland species which had attained population highs in the 1960s (Robinson and Sutherland, 2002). Thus it seems that the fortunes of the starling, as of other birds which live in close proximity to man, are destined to fluctuate according to the vicissitudes of his land management.

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S31-2 Bird population explosions in agroecosystems — the quelea, *Quelea quelea*, case history

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Abstract There is some evidence to suggest that the quelea, probably the world's most numerous bird, has existed for centuries in enormous populations in sub-Saharan Africa, subsisting mainly on the seeds of annual grasses in semi-arid savannas. Large populations occur because their staple food is abundant and because they can move opportunistically to areas that have received good rain and breed. The quelea is a highly visible pest of small-grain cereal crops: wheat, rice, sorghum and millet. Farmers often perceive quelea as more of a menace than it really is. Farmers also claim that quelea populations are increasing at the expense of their crops, but seldom have supporting evidence. The few quelea population estimates that have been made have not been repeated or tested for accuracy, and it is thus difficult to establish trends. Indirect population information includes atlasing and government records of the numbers killed in control operations. Distribution data suggest that drought can be a major factor in limiting distribution. There is, however, evidence for range expansion in South Africa, but the reasons for it are uncertain and do not necessarily imply population increase. Data from control kills show fluctuations but no consistent upward trend. A review of the changes in African agro-ecosystems in relation to their possible influence on quelea populations suggests that natural food sources in regional savannas still greatly exceed the food available from an agriculture that is dominated by maize, a crop not eaten by quelea. In the next few decades, quelea population levels are likely to continue to be controlled by rainfall/wild grass seed production in their breeding habitats. In the longer term, human population expansion and cutting of acacia bush for charcoal could affect those populations negatively.

Key words Quelea, Bird populations, Agro-ecosystem changes

1 Introduction

The red-billed quelea (*Quelea quelea*) is a prime example of a gregarious bird adapted to semi-arid habitats that has a significant impact on agriculture. It occurs exclusively in sub-Saharan Africa, typically in *Acacia* savannas where it sometimes gathers in vast flocks of several million, and where it breeds gregariously in colonies that sometimes cover more than 100 ha and include about 30 000 nests per hectare. It is thought to be the most numerous bird in the world, totaling about 1 500 million at the end of the breeding season (Elliott, 1989). The enormous populations of quelea are generally thought to occur for two main reasons. First, their staple diet of wild annual grass seed, given sufficient rain, is abundant but patchily distributed over extensive semi-arid habitats. Gaston (1976) showed that over 2t/ha could be produced in natural quelea habitat with an annual rainfall of about 450 mm. Secondly, the ability of quelea to follow movements of the Inter-tropical Convergence Zone, and consequent rainfall, allows them to breed itinerantly two or three times per year wherever conditions are most favorable (Ward, 1971; Jaeger et al., 1986; Elliott, 1990).

In the context of bird population explosions in agroecosystems, this paper will review the evidence for popula-

tion explosion in quelea and, where there is evidence of population change, consider the factors that may have been involved.

2 Quelea as an agricultural pest

Because the quelea is an agricultural pest, official statements are often made that its populations are increasing, or are causing serious damage to crops, or are becoming permanently resident in agricultural areas. Such reports may be made to induce a sense of urgency or to encourage national treasuries or donors to fund quelea control. The statements are also sometimes repeated in scientific publications, but usually without supporting data (Mundy and Herremans, 1997). Obtaining supporting data is laborious and costly. Quelea can and regularly do cause severe damage locally to crops, and objective data exist in which the levels of losses have been measured (Jaeger and Erickson, 1980; Elliott, 1989). The high visibility of quelea flocks, and the fact that most quelea control involves the aerial spraying of pesticides at Government cost, often encourages farmers to exaggerate their problems. On the other hand, farmers have to scare the birds from their fields all day long during the period covering the crop's milky stage to harvest. This is a demanding task for a smallholder and an expensive activity for large farms. Because quelea are there when crops

are ripe, farmers assume they are resident. Such perceptions should be treated with scepticism except when properly substantiated

Serious quelea damage to crops is not a recent phenomenon. One of the earliest records is of a famine in Central Tanzania in 1881 (Brooke, 1967), attributed at least in part to quelea. Maize was introduced by the Portuguese in West Africa in the 16th century and probably in East Africa in the 17th century. It apparently became a staple crop partly because of its resistance to bird damage (Miracle, 1965; Reader, 1998). This implies that quelea was also a pest in those times as it cannot peel the maize cob. Great flocks of quelea are supposed to have existed for centuries; nor is there any reason to suppose that their staple food, wild grass seed (Ward, 1965; Erickson, 1989), has been in short supply during the last few hundred years, except during widespread droughts. Quelea were recorded in 1836 in southern Africa (Layard, 1867; Whittington-Jones, 1997), but their association with agricultural damage was only mentioned in the early 1900s (Johnston, 1907; Schlupp, 1922; Whittington-Jones, 1997). Large flocks of quelea were first reported in the Sudan in 1914 by the naturalist Abel Chapman (C.E. Wilson, pers. comm.) who noted the potential threat to agriculture. Following increasing numbers of complaints by farmers in South Africa, Government intervention to control quelea began in 1952 (Whittington-Jones, 1997).

3 Estimates of quelea populations

To my knowledge, only South Africa and Zimbabwe systematically collect and estimate the numbers of quelea killed during control operations. In Tanzania, indirect estimates were made during the 1980s, but this practice no longer continues. In the other 14 countries in which quelea are controlled, figures given are not reliable as the teams have a vested interest in maximizing reports. Crook and Ward (1968), while describing the numbers reported killed as "fantastic", concluded that the total quelea population might lie between 1 000 million and 100 000 million. Elliott (1989) attempted to estimate regional populations by reviewing information on the breeding distribution and the number of breeding colonies found using a helicopter, the most efficient means of locating colonies. From the number of colonies found and an estimate of the percentage of the potential breeding area actually searched, an estimate was made of the total number of breeding colonies present and hence the total breeding population. The post-breeding population was assumed to be double that figure, i.e. 1 500 million, based on a survival rate of 2.2 fledglings per nest (Jones, 1989b), indicating that the quelea is the most numerous bird in the world.

The detailed results suggested that there was a post-breeding population of 124 million in Tanzania, 534 million in the Sudan, and about 380 million in southern Africa.

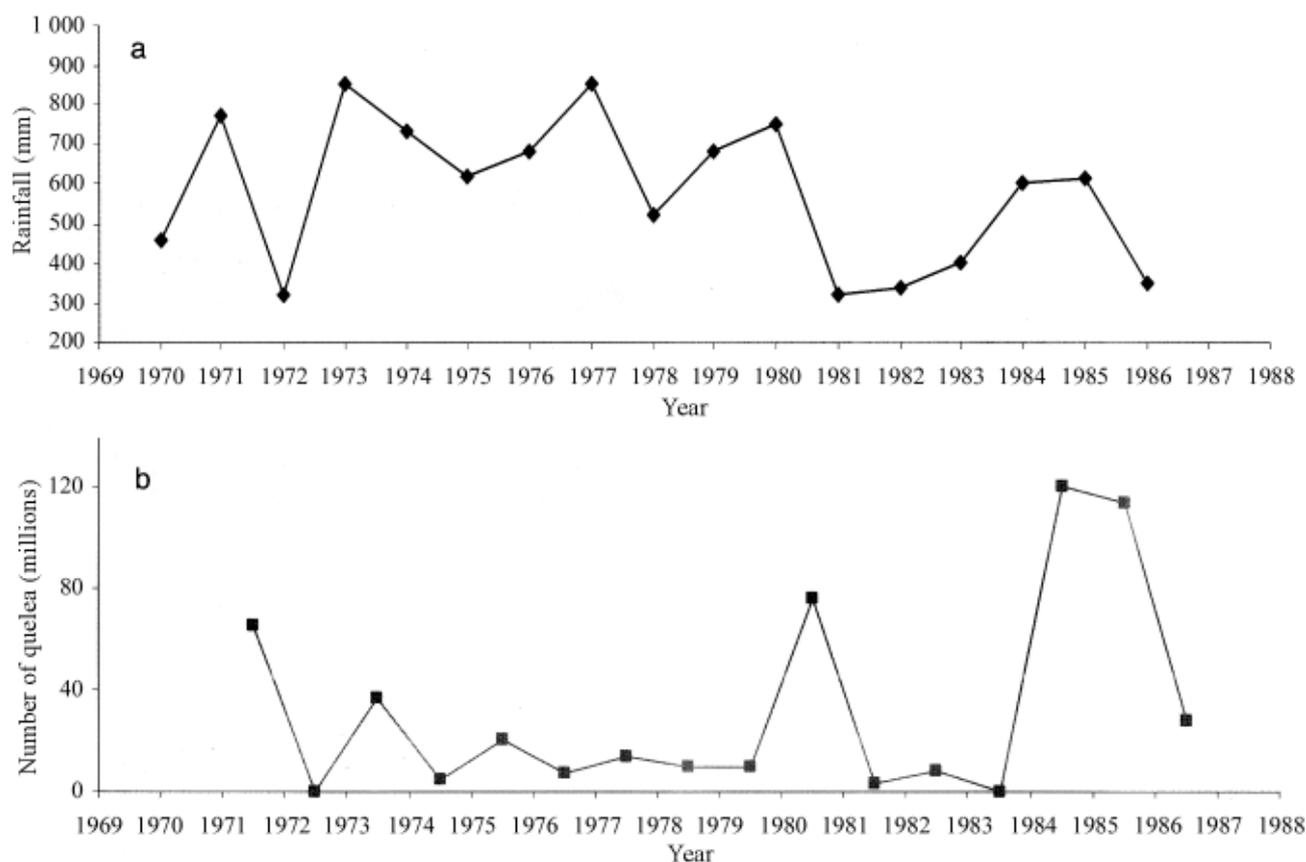


Fig. 1 Numbers of quelea controlled in Zimbabwe in winter compared with rainfall in the breeding areas in the previous summer. Data from La Grange (1989).

Mundy and Herremans (1997) estimated that between 65 and 180 million quelea are killed annually by control operations in the southern African region, but do not give details. If correct, it would mean that up to half the total post-breeding population is being exterminated annually, which seems unlikely given its wide distribution in the region and the low level of control in Namibia, Botswana and Mozambique. Nevertheless, a re-examination of the estimated population in southern Africa would clarify the situation.

4 Changes in quelea populations: numbers killed

La Grange (1989) presented data on the numbers of quelea controlled in Zimbabwe from 1972 to 1987 in relation to total rainfall in the main breeding areas (see Fig. 1). Kills fluctuated from 120 million to zero during this period, while the control effort was more or less constant. There is no evidence of a gradual increase over this 16 year period, even less of a population explosion. La Grange's claim of a loose correlation between rainfall in the breeding areas and subsequent population size is not supported by a re-plotting of the data and statistical analysis (Fig. 2). Zimbabwe contains a quelea population which is part of the southern Africa subspecies *Q.q.lathamii* (Jones, 1989a). Rainfall in Botswana, Mozambique and Angola would influence its breeding rate in those countries such that close correlation with rainfall should not be expected in Zimbabwe. An extensive winter wheat agriculture in Zimbabwe, the protection of which is the objective of most of the control operations, does not seem to have had any serious impact on quelea survival.

In South Africa control efforts have varied, partly for economic reasons and partly because of political changes. In the last ten years or so, "green lobby" pressure has led to use of environmentally-cleaner firebombs, rather than organophosphate pesticides; but the bombs are more expensive so that fewer targets can be tackled with the same level of funding. Political change is also putting more effort into protecting smallholder sorghum rather than wheat produced by commercial farmers. In the period 1956 to 1960, 400 million quelea were destroyed. Since then, the numbers have varied annually between 112 million in 1966/1967 (Crook

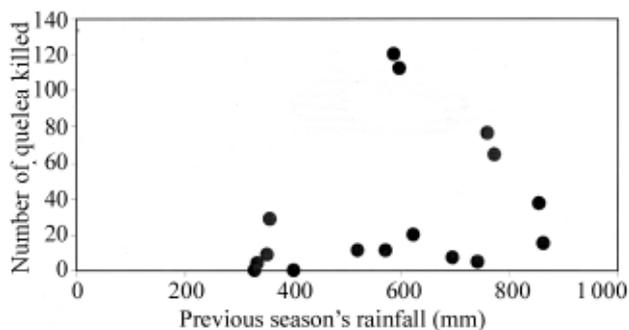


Fig. 2 Correlation of rain (mm) and number of quelea killed

$r = 0.300$, $P = 0.259$, n.s.; $Y = -4.37 + 6.31E-02X$, $R^2 = 9.0\%$

and Ward, 1968) and 39 million in 1999/2000. Although the data are incomplete, it appears that numbers fluctuate, and that while there is probably some correlation between numbers destroyed and the population level, there is no general upward trend in the population, as in Zimbabwe.

In Tanzania, reports on control effort were compiled by Magor (1970) for the period 1960 to 1969, and updated by P.J. Jones to 1976, as shown in Fig. 3. No information is provided as to how numbers were estimated, and they are probably exaggerated. Again there is evidence of large fluctuations, with no upward trend.

The final example comes from Nigeria where Ward and Jones (1977) estimated the numbers of birds destroyed over about 19 years, with a ten-year gap in the records (Fig. 4). The marked decline in the number of colonies found was ascribed to the drought afflicting the Sahelian region at that time, and not to control because similar declines were reported from nearby countries where there was absent. Once again, climatic factors, especially rainfall, were the main influence on quelea population size.

5 Changes in quelea populations: distribution

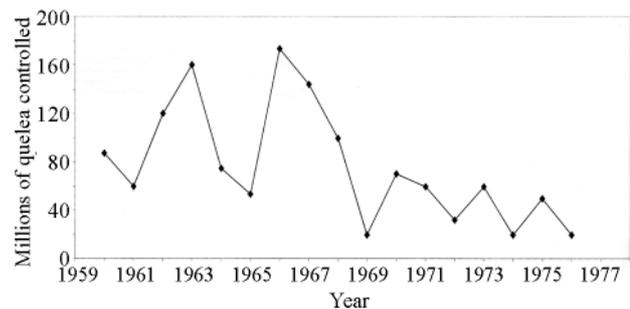


Fig. 3 The number of quelea controlled in Tanzania from 1960 to 1976

During the last four years, quelea were controlled only when threatening crops directly (data from Magor, 1970; updated by Jones, 1977).

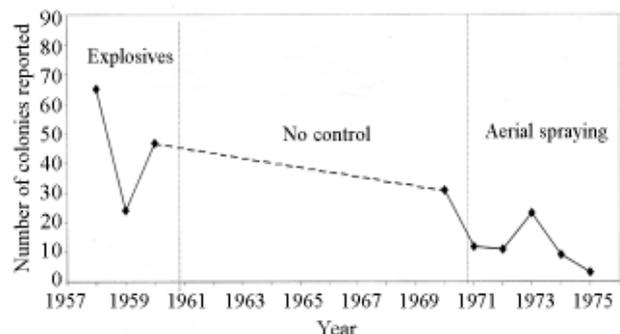


Fig. 4 The number of quelea breeding colonies found in Nigeria during two periods between 1958 and 1975 under different regimes of control

Those in 1958–1960 were found by ground survey and are underestimated. Those in 1970–1975 were found by ground/helicopter surveys, but, although more accurate, were sampled during drought (data from Ward and Jones, 1977).

It is possible that expanding and changing agro-ecosystems in Africa may be providing quelea with food during periods when it would otherwise be short, thereby encouraging overall growth in quelea populations.

The quelea was included in the South African Bird Atlas Project (SABAP) that sought, over a period of about ten years, to plot all observations of different bird species in quarter-degree squares in southern Africa. Although the quelea is not easy to identify out of breeding plumage, SABAP vetted records carefully and its published results should be reasonably reliable (Mundy and Herremans in Harrison et al., 1997). Whittington-Jones (1997) investigated the SABAP results in the light of historical accounts from 1910 to 1984, and concluded that the known distribution of the quelea had changed rapidly and dramatically from 1985 onwards. From an irregular visitor to the Eastern Cape, it had become widespread through most of that province. The coincidence of apparent expansion with the initiation of the SABAP in 1986 suggested that at least some of the expansion might have resulted from increased search effort. Even so, Whittington-Jones (1997) also investigated changes in agro-ecosystems as possible causes, as reviewed below.

In KwaZulu-Natal, in 1994–1995, Berruti (2000) reported quelea numbers in one area as 10 to 100 times higher than found by T.B. Oatley in 1970. However more information on rainfall in the two periods is needed to be sure that similar rain years are being compared. The only other recorded change (Ward and Jones, 1977) comes from the Lake

Chad Basin from the late 1950s to early 1970s, and also involves the whole Sahel. Large areas that had been used extensively for breeding in the 1950s in Nigeria bordering Lake Chad became desiccated by drought which began in 1965 and continued to 1972. The northern limit for breeding moved from just south of 15°N to just north of 13°N. The southern limit of the population appeared to remain the same, so the effect of the drought was to squeeze the quelea population into a narrower band of country. According to Ward and Jones (1977), the reduction in distribution was accompanied by a reduction in population size to 10% of the level it had been in 1960.

6 Changes in quelea populations: effects of agro-ecosystems

Over the past 100 years in Africa, agro-ecosystems have changed most in South Africa where organized commercial farming has long been established. Data on crop production are available by country on the agriculture statistics section of the FAO website (www.fao.org) for the period 1961 to 2001; and the areas under cultivation in South Africa are tabulated in Fig. 5. They show remarkably little shift over the last 40 years. Maize is the dominant cereal under about twice the hectareage of all other cereals together. The areas under wheat and sorghum have dropped in the last four years, too recently to have had an effect. Areas under millet and rice have apparently remained remarkably stable over the whole period, without any marked change in

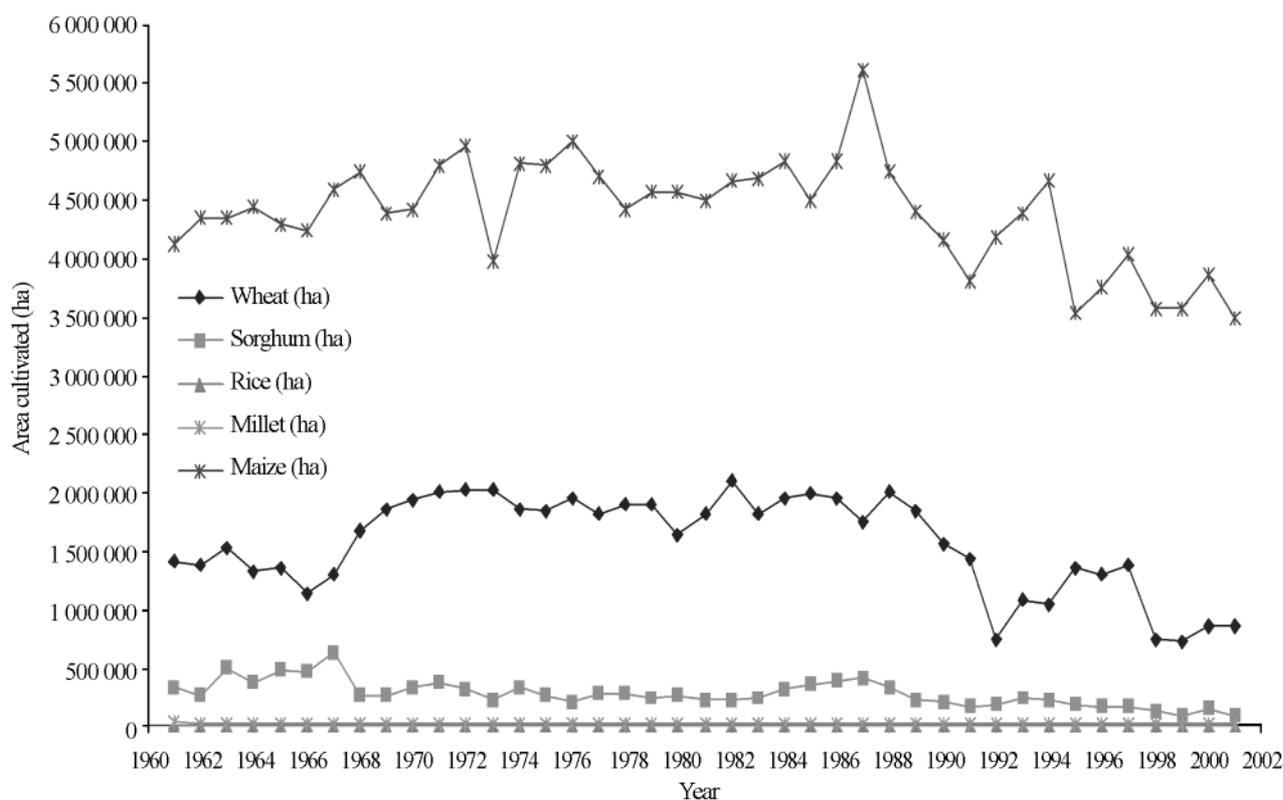


Fig. 5 Areas (ha) of cereal crops cultivated in South Africa from 1961 to 2001
Data from FAO website on agricultural statistics.

productivity or practices. From the quelea's point of view, inedible maize cultivation probably had a negative impact by replacing natural grasslands. Winter wheat or irrigated rice expansion, on the other hand, might have been positive.

Whittington-Jones (1997) noted that in the Eastern Cape, farming focused on livestock production up to the 1960s, then gradually changed to more intensive farming over the last three decades. Eight-fold and eleven-fold increases in wheat plantings were recorded in two districts, although the areas under cultivation are tiny in comparison with the province as a whole. He also addresses the possible influence of intensive livestock farming through supplementary feeding with crushed cereals including maize. Quelea have been seen consuming broken maize grain at cattle feedlots and at feeding trays put out for domesticated ostriches. In KwaZulu-Natal, sampled quelea show that crushed maize is the single most important food for the species outside the breeding season (Berruti, 1995). The question is whether these favorable micro-habitats have a significant bearing on the overall population.

Quelea have to drink at least twice, if not three times, a day. Flocks leaving roosts at first light often go first to water before going to feed. When it is hot, i.e. $> 40^{\circ}\text{C}$, flocks usually form day roosts near water in the heat of the day, during which they drink. They also drink in the evening on the way to roost. Whittington-Jones (1997) mentions the influence of the Orange-Great Fish River water transfer scheme that converted the Great Fish River from an intermittent to permanent water source. Allan et al. (1997) mention that in South Africa, 517 major reservoirs had been constructed by 1986 and that there are many tens of thou-

sands of earthen dams and boreholes on farms or other private land in southern Africa. These water sources allow quelea to exploit land that would not have been available before.

Whittington-Jones (1997) further mentions the possible influence of overgrazing through which woody species such as *Acacia karoo* have encroached into grasslands in the Eastern Cape. The acacia provides ideal nesting and roosting habitat and may have aided the spread of quelea into that province. In the same context, Crook and Ward (1968) cite the often repeated idea that overgrazing encourages annual grasses to flourish in place of perennials, to the advantage of quelea populations. While such an advantage may be occurring, it is not known if there is any published information that quantifies the extent to which this has happened.

Evidence from other countries is much less complete. Fig. 6 shows the changes in hectareage in principal cereal crops grown in a typical quelea country, Tanzania. Unlike circumstances in South Africa, some significant long-term changes are noticeable. Thus the staple and preferred food crop is maize and the 40 years from 1961 to 2001 have seen a quadrupling of the area under cultivation. In contrast, the number of hectares under sorghum has fluctuated after a steady increase from 200 000 to 550 000 ha by 1976. Rice cultivation has grown six-fold but wheat, after an initial surge to 60 000 ha in 1970, has also fluctuated.

Maize is unlikely to have had any positive influence in Tanzania, quelea only occasionally eating it as spillage when it has been pounded in villages. Rice is regularly eaten by quelea both before and after harvest, and control opera-

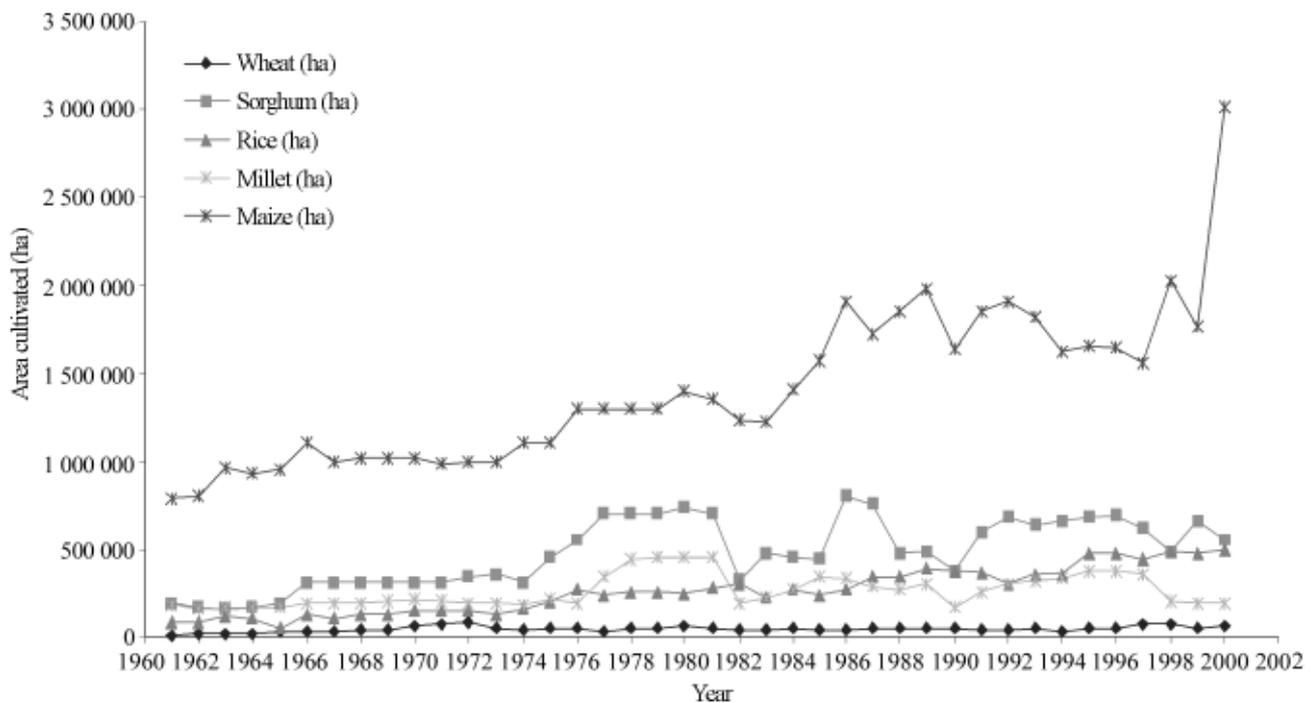


Fig. 6 Areas (ha) of cereal crops cultivated in Tanzania from 1961 to 2000
Data from FAO website on agricultural statistics.

tions try to reduce quelea numbers around major rice farms during vulnerable stages of the crop. However, flocks of quelea in the middle of Tanzanian irrigated rice farms often feed on wild grass seed (pers. obs.). Of 1 454 quelea sampled in a roost adjacent to rice farms in Cameroon, 64% were found to be feeding exclusively on rice and 22% exclusively on wild grass seed and insects (Elliott, 1979). Luder (1985) found that quelea in Tanzania caused more damage to wheat fields that had been badly weeded than those which were clean, indicating that quelea were attracted as much by associated weed seed.

Tanzania covers about 71 one-degree squares; quelea have been recorded in 47 of them, and a further 17 contain vegetation that is probably suitable for the species (Magor and Ward, 1972). Given this wide distribution, it must be questioned what effect a million hectares, roughly a single one-degree square, of small grain production grown during the rainy season when natural food is widely available, is likely to have on the quelea population. In contrast, human demographic pressure may be generating a negative impact that could balance out any benefit from changes in agro-ecosystems. For example, the human population in South Africa has increased from 12 million in 1951 to 39 million in 1991 (Reader, 1998). A parallel increase can be expected in Tanzania. In the latter, two effects are evident to the casual observer: the penetration of village communities deeper and deeper into the countryside, and the cutting of small trees for fuel. Most Tanzanian quelea establish breeding colonies well away from villages in patches of thorn trees. They need peace and quiet and trees to breed successfully.

7 Discussion

There is no shortage of statements that quelea populations are increasing and that the main reason for this is the extra food provided by agriculture (Lourens, 1963; Gaudchau, 1967; Mundy and Herremans, 1997; Brown and Tinney, 1998; Berruti, 2000). Some have also drawn attention to population reductions caused by drought, especially in the Sahel in the 1960s (Ward and Jones, 1977; GTZ, 1987). This paper has attempted to take a dispassionate view of the evidence, and to draw conclusions accordingly.

The first point to make is that it is not an easy task to assess population size in a bird as numerous as the quelea. Breeding colonies are conspicuous, and can be seen from the air several kilometers away. They are best searched for by helicopter, supported by information from local populations or farmers who have been encouraged to report colonies. Resources for such surveys and to maintain local networks are increasingly scarce, with the result that repeating surveys to standard is difficult. Indirect measurements of population sizes have been made from the kills achieved by control teams on the assumption that control effort is more or less constant. Where control effort changes, comparisons will be less valid.

All the evidence so far indicates that quelea populations fluctuate, influenced strongly by favorable rainfall for

breeding. During widespread drought, large declines can be expected. If drought is localized, emigration is likely to diminish any effect. If conditions are good over a large part of the range, breeding is not only likely to be successful but will often be repeated itinerantly in several different places as well (Jaeger et al., 1986).

Information from South Africa that suggests that the range for the quelea has expanded there (Whittington-Jones, 1997); but this is not necessarily evidence for a larger quelea population. It is possible that changes in agro-ecosystems, or simply human pressure, may be forcing the quelea to range further to survive. The numbers reaching the Eastern Cape are, by quelea standards, small; flocks seldom exceed a few hundred birds, and their contribution to overall numbers insignificant. Even the evidence given by Berruti (2000), that quelea are now 10–100 times more abundant in one part of KwaZulu-Natal than they were in the 1970s, is probably an indication of distributional change rather than exponential increase in overall population levels.

Changes in agro-ecosystems have been relatively minor with respect to cereal crops, even in South Africa, and have had little effect on quelea. Although quelea attack on small-grain crops is impressive, and causes much anguish to farmers and Governments, its impact compared to the vast tracts of savanna grassland that form the quelea's natural food source is still very small. On an even smaller scale are impacts on livestock feedlots and domestic ostrich feeding troughs that provide a ready source of food to a few quelea during the dry season. While such food sources might sustain small local populations of quelea, they are hardly likely to affect overall regional totals. Agro-ecosystems have probably had a positive effect on quelea in another area: the building of farm dams and larger scale reservoirs. As quelea can range about 30 km from a daily water supply, the presence of such dams should open substantial new areas for foraging. On the other hand, the presence of water without wild grass seed would have little benefit.

Demographic changes involving increasing human population and its exploitation of trees for fuel and the countryside for agriculture are probably acting as a counter-pressure to any tendency for agro-ecosystems to increase quelea populations. It is possible that if human population continues to increase in Africa as it has over the last 40 years, and HIV/AIDS does not reverse the trend, it is likely that suitable breeding habitats may gradually disappear. Unless it can become more tolerant of humans, the quelea could, in the long run, follow the fate of another highly gregarious, colonially-nesting species, the passenger pigeon (*Ectopistes migratorius*).

Thus it appears that, while quelea populations fluctuate primarily according to rainfall in their breeding areas, there is no evidence of a modern population explosion and little evidence even to support any general trend towards increased regional population levels.

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S31-3 The effect of irrigated agriculture on bird populations on the Mahi Right Bank Canal System, India

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Abstract Most bird explosions in cultivated areas are correlated with dry-land agro-ecosystems. Agriculture under irrigation, however, is expanding rapidly around the world, and, as in the case of dry-land agriculture, irrigated areas have also spawned explosions in bird populations. I discuss interactions between irrigation development and birds in India using the Mahi Right Bank Canal System as a case study. After a rapid initial expansion, water logging and soil salinization resulted in loss of cultivable areas that became marshlands dominated by wetland vegetation, providing excellent habitat for many wetland birds. As these wetlands developed next to agricultural fields, crops became a potential target for bird damage. At the same time, a marked increase in food availability resulted from spilled rice and wheat grains, particularly after the introduction of machine harvesting. The sarus crane, a globally threatened species, expanded and increased in irrigated areas, causing some agricultural damage. Bird population increases in the study area bore striking similarities to those in dry-land agro-ecosystems, driven by the same key factors. Habitat became available because irrigation created artificial wetlands, and extra food, at least for granivorous birds, was provided by crops and quantities of spilled grain.

Key words Agricultural expansion, Irrigation, Wetland birds, Land degradation, Habitat change, Colonization, Crop impact, Opportunistic food

1 Introduction

Most bird explosions in cultivated areas are correlated with dry-land agro-ecosystems. Agriculture under irrigation, however, is expanding rapidly around the world, and, as in the case of dry-land agriculture, irrigated areas have also spawned explosions in bird populations. In principle, the same factors driving bird population growth in dry-land agro-ecosystems also operate in irrigated areas, i.e. increased food supply from standing crops, wasted grain and the creation of favorable habitat. Therefore, analysis of such factors may become extremely important when searching for general processes underlying population explosions in agro-ecosystems.

In this paper, I analyze bird-land management interactions in irrigated areas in India where marked increases in bird numbers have occurred, in some cases associated with crop damage. The analysis will focus on the following aspects: habitat change, effects of wasted grain, raw growth in bird populations, and crop damage problems.

2 Habitat changes

2.1 Irrigation in India

Agriculture is the mainstay of the Indian economy; almost three quarters of the country's working population is engaged in agriculture and about half of the gross national product is generated by agricultural production. Ag-

ricultural development depends on water, but a large part of the subcontinent is arid, and rainfall often cannot ensure even a single crop. Irrigation, therefore, is indispensable to the welfare of Indian agriculture. Its use can be traced back to prehistoric times, but it gained momentum after Independence (1950). The gross area under irrigation in 1950–1951 was already 22.6 million ha. Multipurpose irrigation projects have since been launched, such as the Bhakra Nangal in Punjab, Damodar Valley in Bihar, Hirakund in Orissa and Mahi Right Bank in Gujarat, the study area of this paper.

The adoption of irrigation techniques increased areas under crop production, but unforeseen problems arose. End users, for example, often got too much water, either because they had no choice or deliberately took it as they wished and often more than was needed. The cropping pattern employed, often very different from the designed pattern due to diverse circumstances, also contributed to low irrigation efficiency.

2.2 The Mahi Right Bank Canal System, Gujarat

The Mahi Right Bank Canal System was begun in 1955 to increase crop production, both in variety and by two annual harvests. Canal irrigation is available to most of the region through the Mahi Right Bank Canal (MRBC) which links fifteen man-made reservoirs. The reservoirs are filled periodically for agricultural use, and so are essentially perennial wetland. Extensive waterlogging, however, soon followed, resulting in soil salinization. Other factors such

as poor natural drainage and lack of incentives for community use of water have added to the problem. In a total area of 212 694 ha, as much as 138 676 ha is now affected by salinity. The lost agricultural area became marshlands dominated by wetland vegetation, particularly *Typha angustata*, *Ipomoea aquatica*, and *Phragmites* sp., providing excellent habitat for many wetland-dwelling birds. As these wetlands are adjacent to agricultural fields, crops there have become potential targets for bird damage.

When irrigation was introduced, the major crops in Gujarat were paddy rice and wheat; others in more arid areas included sugar cane and tobacco. Market forces then complicated matters, applying pressure to replace the food crops of rice and wheat with the cash crops of tobacco, cotton and sugar cane. As a result, a drastic change in land use and cropping pattern happened, causing a negative impact on the overall bird community as well as those farmers who continued growing cereal crops and suffered from bird concentrations on them. Furthermore, increasing use of harvesters scattered and shattered larger proportions of grain in the field, increasing the food available for granivorous birds and mammals.

3 Waste grain availability

3.1 Food supply: crop production and grain spillage in wetlands

Increases in food availability in irrigated land are due mostly to spilled rice and wheat grain, as shown from measurements made late mid harvest in the study area in 1997. Twelve fields were sampled soon after the harvest by 1 m × 1 m quadrats fixed randomly in 5 m × 5 m quadrats in the center of each field. All loose grains and small pieces of seed heads (ears) with less than 10 grains were collected from the small quadrat, and whole seed heads or parts with more than 10 grains were collected from the larger quadrat. Grain samples were oven dried for 48 hours at 48°C and weighed. Sampling was repeated weekly on four successive weeks to evaluate the depletion rate of spilled grain.

An estimate of total field grain available was calculated for each plot using the formula of Frederick et al. (1984):

$$\text{Total kg/ha} = (25 K + E) / 2.5$$

where K (g/m²) = weight of loose grain + grain from small seed heads of less than ten grain, and E (g/25 m²) = weight of grain from seed heads with more than ten grains. Bird species seen feeding on scattered grains in harvested field during the study were also recorded and are listed below. The results of grain depletion estimations are as follows.

Paddy rice: The quantity of rice grain scattered on the ground from harvesting was estimated for twelve fields on the day of harvesting. Mean grain loss due to scattering was 107 ± 11 kg/ha. There was wide variation in the amount of grain scattered, ranging from 49 kg/ha to 197 kg/ha. Nearly 60% of the grain was depleted within one week of harvesting. Of the remainder, 38% was taken over the next three weeks. The reduction rate of both loose grain and

seed heads was similar throughout the study period.

Wheat: The quantity of scattered wheat grain left on the ground after harvesting was estimated from eleven fields. Mean grain loss due to scattering was 183 ± 17 kg/ha. The quantity of grain scattered was much higher than for ears. There was wide variation in total grain scattered, ranging from 97 kg/ha to 264 kg/ha. Nearly 40 % of the grain was depleted within the first week of harvesting. Of what was left, 54 % was taken within the next three-weeks. The reduction rate of loose grain and ears was similar throughout the study period.

4 Bird population increases

More than 200 species of birds have been recorded in Gujarat. Because of the aridity of the region, these birds need man-made wetlands directly or indirectly for survival. In the last two years, the bird population has increased significantly, particularly in passerines, although reliable numeric data are not available. A total of 67 species of birds have been recorded on the wetlands, and at least 39 are confirmed to eat rice and 15 species wheat from the stubble. Relative abundance below is denoted by the acronym RA.

Ruff (*Phylomachus pugnax*) (RA 52%) were the first to concentrate in large numbers in harvested paddy fields, followed by the eastern skylark (*Alauda gulgula*) (RA 14%); and large flocks of black-tailed godwit (*Limosa limosa*) have since been recorded feeding on rice. Other important species frequently present on the fields in large flocks include the short-toed lark (*Calendrella cinerea*), blackthroated weaver (*Ploceus benghalensis*), and three cranes: sarus (*Grus antigone antigone*), demoiselle (*Anthropoides virgo*) and common (*Grus grus*).

The Indian sarus crane is a true wetland species. Because of its restricted distribution and small population size it has been included in the list of globally threatened cranes (Meine and Archibald, 1996). Its decline is related to the loss of natural wetlands and marshlands, many of which have been degraded or drained. Recently, sarus cranes have expanded into paddy wetlands, which has led to conflict with farmers (O'Connor and Shrub, 1986; Conner and Decker, 1991). In Gujarat, fields are inundated during most of the cropping season (July–October) and thus form temporary wetlands with very high productive potential, menaced by the cranes. My observations indicate a marked increase in sarus cranes in the Mahi Right Bank Canal System area. The population there increased from 252 individuals (density of 0.13 pairs/km²) in 1989 to 414 birds (density of 0.36 pairs/km²) in 2000 (Mukherjee et al., 2002).

Due to the availability of inundated paddy fields, breeding performance has also increased. A total of 70 sarus crane nests were monitored over the period 1996–1998. The study revealed that 68 nests were in the agricultural marshland and only two in the non-agricultural area. Of the 68 nests in agricultural land, 31 were built in paddy fields and the rest in inundated fallow wasteland lost due to water

logging (Mukherjee, 2000).

Sarus cranes are highly conspicuous, and therefore readily perceived by farmers as a threat to crops. In recent years, reports of damage by cranes have increased world wide (Sugden et al., 1988; McIvor and Conver, 1994; Pivovarov, 1995; Swanberg and Lundin, 1995; Vaverins, 1995; Katondo, 1996; Mukherjee, 2000). However, very few detailed assessments of crop loss are available (McIvor and Conver, 1994; Parasharya et al., 1998).

5 Crop damage problems

Reliable estimates of damage and damage potential are important for understanding the impact of birds on crop yield and subsequent economic loss to farmers. To assess grain loss in rice and wheat, the study area was visited weekly to identify crane damage throughout crop development, from June to November. Precise measurements were made in 10 fields (0.09–0.35 ha), including those of damage caused by trampling and uprooting at harvest time.

Crane damage was easy to differentiate from damage caused by other birds, being characterized by the type of seed head damage, and presence of large pale gray feathers and toe prints on the ground. Sarus cranes also use paddy plants for constructing nests and other platforms for raising chicks, especially if both chicks survive. They either uproot the whole plant or cut the tillers just after transplanting. As a result, the whole area around nests is cleared of plants.

Paddy rice loss from the standing crop was always negligible, but loss due to trampling was high, ranging from 0.02% to 4.39%. Trampled areas where all seed heads were damaged ranged from 10.1 to 210 m², mainly around nests. I estimated the overall yield loss in five fields as being between 5% and 14%.

Wheat damage was assessed just before harvesting in one field at Sojitra. Plant loss ranged from 1.5% to 15.2%, and yield loss from 14 kg to 120 kg/ha.

6 Discussion

Bird population increases in Indian wetlands bear striking similarities to those in dry agro-ecosystems in terms of driving processes. Habitat is made favorable because irrigation creates artificial wetlands. Favorable habitat is increased by mismanaged areas that are abandoned to production. Extra food, at least for granivorous birds, is provided by significant amounts of spilled grain which become even more copious when modern machinery is used.

Damage caused by birds, particularly by sarus cranes, results from direct grain consumption, trampling, and plant uprooting.

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S31-4 Eared dove outbreaks in South America: patterns and characteristics

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Abstract Information on eared dove (*Zenaida auriculata*) outbreaks in South America is analyzed towards finding common factors and processes for developing a conceptual model that may help to predict future outbreaks. Between 1950 and 2000, eared dove populations exploded in a number of regions in Argentina (Córdoba, Entre Ríos, San Luis, Chaco, and Salta), Colombia (Cauca valley), Uruguay, Bolivia (Santa Cruz) and Brazil (Sao Paulo and Paraná). We found a consistent association between the outbreaks and particular habitat characteristics at the landscape level caused by agricultural expansion in forested areas. Specifically, dove populations respond to (1) increased availability of grain from crops, spilled harvest grain and weed seeds, (2) forest fragments suitable for colonial breeding, and (3) handy water sources. Eared doves appear to shift from isolated nesting to colonial breeding once the local population passes a particular threshold. Predation, and control measures based on massive killing, do not appear to affect population levels in all studied cases. The observed ability of the doves to take advantage of landscape-scale changes is linked to several adaptations in *Zenaida* doves, including crop-milk production, colonial breeding, and nomadism.

Key words Sorghum, Forest fragmentation, Agricultural expansion, Colonial breeding

1 Introduction

The eared dove (*Zenaida auriculata*) is a widespread species in South America that occurs in nearly all types of ecosystems except tropical rainforest. Prior to 1950, it was a common, though not particularly abundant dove throughout its range except in Caatinga in northwest Brazil where it had been breeding in large colonies for a long time (Bucher, 1982). At the end of the 1950s, a rapid and large growth in numbers was recorded in Córdoba, Argentina, accompanied by the development of large breeding and roosting colonies of up to 1–5 million birds (Murton et al., 1974).

This initial upsurge was followed by further population outbreaks and colony development in other regions of Argentina, including the provinces of Entre Ríos, Chaco, and Salta from 1970 to 1990. Moreover, similar explosions were also recorded in other countries, notably Uruguay, Colombia, Bolivia, and Brazil. In all cases, these outbreaks happened in areas of developing agriculture (Bucher, 1990). In all cases, too, crop damage caused by the doves reached significant proportions. It led to the implementation of massive killing campaigns using poisoned baits and other lethal methods, without achieving any significant reduction in population levels (Murton et al., 1974; Bucher, 1990).

Agricultural changes are amongst the most drastic and widespread man-induced alterations of land, and may thus be seen as unplanned, large-scale environmental experiments. Unfortunately, detailed studies to elucidate the impacts at the regional level are often hindered by meth-

odological and practical difficulties. In their absence, all that can be done is to accumulate corroborating evidence from repeated observations of modifications resulting from changes in land-use patterns. From this aspect, eared dove outbreaks, being restricted to specific areas and times as well as closely related to agricultural expansion, provide a unique opportunity to advance understanding about the catalysts and processes underlying bird population explosions in agro-ecosystems.

Here we analyze available information on Eared Dove outbreaks in South America to find common factors and patterns that will help to develop conceptual models capable of predicting possible future outbreaks.

2 Eared dove population outbreaks

Between 1950 and 2000, eared dove population outbreaks occurred in several regions of South America: Argentina, Colombia, Uruguay, Bolivia and Brazil. Information on them differs considerably, from abundant in a few to scarce in most. The available data allow, nevertheless, a general comparison of the historical aspects of the outbreaks, agro-ecosystem dynamics, and eared dove breeding and feeding habits. In the following sections we analyze the known outbreaks in each of the countries where they were recorded.

2.1 Argentina

Córdoba: Eared dove outbreaks in Córdoba devel-

oped on a semi-arid plain, originally covered by dry woodland. Annual rainfall is about 600–700 mm, concentrated in the summer months (October–March). During the 1950s, grain sorghum was introduced and its area under agriculture increasing rapidly. As a consequence, agriculture expanded into previously forested areas, creating a mosaic of croplands and fragments of original woodland (Murton et al., 1974).

Eared dove colonies occupied forest fragments there that ranged between 100 and 600 ha, the doves preferring patches with dense secondary thorn-scrub. From there they dispersed in daily movements of up to 100 km to obtain food. All colonies lived near water sources such as rivers or irrigation channels. Nest density averaged between 1 000 and 2 000 nests/ha, reaching in some cases over 4 000 nests/ha in some patches. Active nests were found in all months of the year, the colonies being eventually abandoned only for short periods (Bucher and Orueta, 1977).

Population increase and colony development did not include, however, the whole region planted to sorghum. Instead, it was restricted to a well defined zone of mosaic landscape where food patches (sorghum cropland) and breeding habitat (patches of secondary thorn-scrub woodland) were present in obviously suitable proportions.

Colonies neither developed to the east, where sorghum was abundant but without intermingled woods, nor to the west, where woodland was predominant (Murton et al., 1974). More specifically, colonies were confined to forest patches of some 100 ha or more, located at distances no greater than 100 km from food sources and less than 10 km from water sources. In the affected areas, the proportion of land covered with crops was in nearly all cases higher than 10%. In those cases where total cropland was less than 10%, the area under grain sorghum reached at least 3%.

The sorghum-planted area and eared dove popula-

tion continued to increase in parallel. In 1972–1973, sorghum expansion peaked at 1 044 000 ha, ranging from 6% to 15% of the landscape in the dove-affected area, where eight colonies were developing (Bucher, 1990). In subsequent years, soybean became more and more attractive to farmers and consequently the sorghum-planted area began a steady decline which continues today. This inflection was closely followed by the dove population, which was reduced to only two colonies by the 1990s (Fig. 1; Bucher, 1990). The connection between eared doves and cultivated grain was eventually made evident when dove crop contents were analyzed. In the early 1970s, most of the diet comprised the seeds of cultivated plants, particularly sorghum, wheat, millet, and secondarily weed seeds (Murton et al., 1974).

The eared dove has become a major pest of agriculture in Córdoba, particularly of grain sorghum (Murton et al., 1974). Although the birds can damage standing plants, they prefer to feed on spilled grain in harvested crops. Due to the inefficiency of mechanical harvesters, a considerable amount of wasted grain (between 160 and 500 kg/ha in the case of sorghum) remains in the fields and supports a huge dove population. Weed seeds are important at certain times of the year, particularly early spring when cultivated grains are not available. Grain sorghum has nevertheless proved to be a key factor in maintaining a substantial level of food availability during a time of shortage of other food sources, given that its stubble remains for 5–6 months before being ploughed at the start of the next spring (Bucher, 1990). Following reports of severe damage, local authorities implemented massive control campaigns during the 1960s and 1970s, using poisoned baits distributed around the roosts. Although millions of doves were killed (pers. obs.), there was neither a noticeable reduction in overall population level, nor in colony numbers (Bucher, 1990).

2.2 Other outbreaks in Argentina

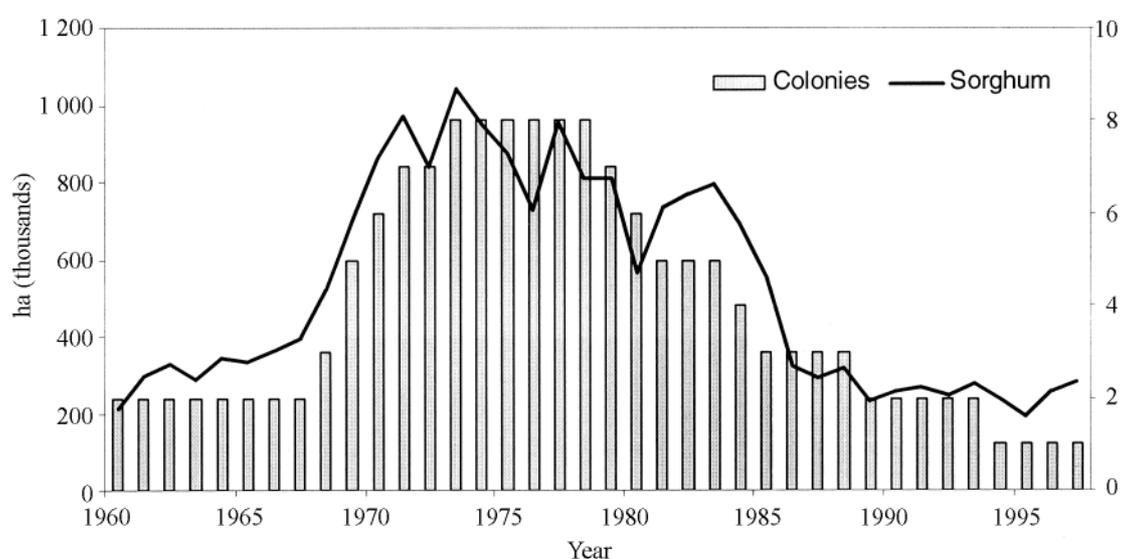


Fig. 1 Temporal changes in sorghum-cultivated area and numbers in eared dove colonies (< 1 million birds) in Córdoba, Argentina

Population outbreaks similar to those in Córdoba developed elsewhere in Argentina after 1960. In Entre Ríos province, at least two huge colonies developed in the riparian vegetation of the Paraná River, close to Paraná city. Main crops affected were sorghum, sunflower, and to a lesser extent rice (Bucher, 1985). Another significant outbreak occurred in Chaco province at the end of the 1960s, where at least two colonies were detected. This population exploded following a dramatic increase in the area cultivated with sorghum, which increased from 23 000 ha in 1966 to 150 000 ha in 1987, though remaining stable for more than a decade afterwards (E.H. Bucher, unpublished data).

The agricultural frontier continued expanding west in most of Argentina from the late 1980s, associated with a marked increase in rainfall and irrigation that allowed cultivation of new areas previously covered with woodland and thorn-scrub. In San Luis province, development of commercial seed production farms, mostly sorghum and maize, coupled with non-tillage practices that allowed seeds to remain on the ground for a long time, catalyzed a rapid increase in eared and spotted (*Columba maculosa*) doves.

In Salta province, a rapid and massive expansion of soybean cultivation in previously forested areas resulted in the development of at least one eared dove colony. In this case, it is possible that the reduced area dedicated to sorghum has limited dove expansion (E.H. Bucher, unpublished data).

2.3 Uruguay

At least six significant eared dove colonies developed in western Uruguay in the 1970–1980s. All were located in gallery forests along the coast and main rivers, particularly the Uruguay and Negro (Bucher, 1985). Agricultural land in Uruguay is restricted to the western part of the country. Sorghum is far less widespread than in Argentina, with only 42 000 ha planted (2% of the land in some places) (Bucher, 1990). Cultivated crop seeds made up over 70% of dove diet, dominant items being wheat, sunflower, sorghum, and barley (Bucher, 1990). Offsetting the limited area of sorghum were inefficient farming practices which left year-round food for the doves. Of particular importance was the significant proportion of seed left uncovered during wheat and barley sowing, as well as the many sunflower fields left unharvested in marginally suitable land (Bucher, 1985). Damage control was based on dispersion of poisoned baits, which failed to reduce population levels despite achieving high mortality on occasion (Bucher, 1985).

2.4 Colombia

An upsurge in eared dove populations was first noticed in the Cauca Valley during the 1960s. The Cauca Valley in southwest Colombia is one of the major agricultural areas in the country. Elevation is about 1 000 m asl. Average annual temperature is 23°C with little seasonal variation. Annual rainfall is around 800 mm, with two dry seasons, one in winter, the other in summer. The original vegetation

was a semi-deciduous forest, but today most of the land has been cleared for agriculture and cattle breeding.

Eared doves were first reported as a serious problem during 1969–1970 after a buildup during the previous five years. This upsurge coincided with a period of marked expansion in the amount of land devoted to crops. From 1960 to 1984, cultivated areas under soybean in the Cauca valley increased from 7% to 23%, and under sorghum from 0 to 20%, whereas maize decreased from 23% to 5% and rice from 9% to 4%. By 1984 the area dedicated to grain crops was around 50 000 ha, including soybean (48%), sorghum (41%), and rice (11%). The proportion of crop plantation in relation to total valley area was around 7% for soybean, 6% for sorghum and 2% for rice, but the two harvests per year there may almost double productivity per hectare. Moreover, the harvesting of the crops is staggered throughout the year, making substantial amounts of waste grain available to birds in all months (Bucher, 1990).

Seeds of cultivated plants constituted 92% by volume of eared dove diet in 1973–1974. Maize, rice, and sorghum were most important, in high frequency and volume throughout the year. At the same time, the thorny xeric vegetation, which the doves seem to prefer for nesting sites, also increased as a result of overgrazing and deforestation, particularly in the foothills and river canyons. The limited evidence available from periodic samples of testis weight and crop milk gland activity indicates that there is at least some breeding in all months, with two peaks shortly after rainfall maxima (July–August and December–February). This coincides with the two annual harvests produced in the area.

The population outbreak in Colombia may be attributed to an increase in year-round availability of food that results from expansion of suitable crops (mostly sorghum), together with an expansion of preferred nesting sites as a consequence of deforestation of the tropical forest and its replacement by scrubland (Aguilera and Hoyos, 1986; Bucher, 1990).

2.5 Bolivia

In Bolivia, a significant eared dove outbreak was recorded in the eastern lowlands (Departamento de Santa Cruz) during the 1990s. This upsurge coincided with a rapid and intense process of deforestation and agricultural expansion. Dominant crops today include soybean, sunflower, sorghum, maize, rice, and wheat. About 15 colonies were identified in the area. Recorded dove food is dominated by cultivated grains (84%), including sunflower (31%), sorghum (26%), soybean (25%), maize (2%), and rice and wheat (<1%) (Rojas and Davies, 2001). Here again, the eared dove explosion is associated with a marked rise in food availability due to agricultural expansion into areas where adequate breeding habitat is still available.

2.6 Brazil

Explosions in southeast Brazil are a relatively recent

event, with unique characteristics that separate them from other known outbreaks. Most significant is the development of breeding colonies in sugarcane plantations, instead of fragments of scrubland or dry woodland as elsewhere. This situation, which has been studied in detail, provides an opportunity for testing the conceptual model developed in this paper from the analysis of previous outbreaks. It is therefore analyzed separately in the final paper in this symposium.

3 Common factors and patterns in eared dove outbreaks

The cases analyzed here suggest a consistent association between dove outbreaks and particular habitat characteristics at landscape level driven by agricultural expansion in forested areas. More specifically, dove populations appear to be controlled by the following key factors:

(1) an increase in food (grain) availability that is relatively stable throughout the year. Sustained availability is usually the consequence of wastage caused by poor harvesting practices, stubble left for long periods for grazing, multiple harvests during the year in tropical irrigated areas, and weed seed availability, at least until weed control measures improve;

(2) availability of adequate areas for colonial breeding. These are secondary patches of the original woodland or natural forest land unsuitable for cultivation, such as gallery forests or mountain slope forests. In some if not all cases, the available patches may eventually disappear, preventing the development of large colonies. However, even non-woody vegetation may be used, as has been recorded in Sao Paulo, Brazil, where colonies nest in sugarcane plantations (Ranvaud and Bucher, this symposium);

(3) availability of water for drinking, usually from rivers, ponds, or irrigation canals.

To become effective, the above three factors each need to reach a threshold before colonies develop. Specifically, a minimal proportion of the landscape surface has to be converted to cropland, which can be estimated, from recorded data, as follows:

(i) a minimal proportion of land covered with crops of at least 3% of grain sorghum, or 10% of other suitable grain crops combinations; (ii) patches of breeding and roosting habitat of at least a hundred ha and at distances no greater than 100 km from the food source; and (iii) water sources at a distance no further than 10 km from roosts.

Given the above mentioned conditions, increases in dove colonies are apparently independent of other environmental factors, such as rainfall, land relief, and vegetation composition. Predation and control measures so far do not appear to check population levels significantly. A detailed analysis of the Brazilian population outbreak in Sao

Paulo supports this preliminary model (Ranvaud and Bucher, this symposium).

From the perspective of population regulation, the direct correlation between dove numbers and food supply provides circumstantial evidence supporting the hypotheses that food is the limiting factor in eared dove outbreaks, providing that breeding habitat requirements are satisfied. The importance of the present evidence lies in the fact that it involves regional scale manipulations of supplementary food, under different geographic scenarios. Moreover, it reveals a direct correlation between resource and population both when food increases and decreases (Fig. 1). On the other hand predation, either by natural predators or by man, does not seem to play a primary role in checking population growth when food availability increases.

The relationship between agricultural land-use and the dove has important practical implications. First, our conceptual model predicts that expansion of grain-crop agriculture in originally wooded areas will favor a marked increase in eared dove populations, providing that enough breeding habitat is available. Many potential situations of this kind are widespread in Latin America, where agricultural frontiers are still expanding. Secondly, the same predictive approach can be applied in conservation problems. There are indications, for example, that eared doves in north-east Brazil are declining (Bucher, 1982). Accordingly, protective measures have been proposed based on the preservation of woodland patches where the doves breed. These measures, however, will not work unless a food supply of adequate proportion and quality is conserved too. Information gained from the study of eared doves, moreover, may provide important insights into the understanding of the causes of population crashes, such as that which caused the extinction of the passenger pigeon (*Ectopistes migratorius*), a closely related species.

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S31-5 Explosions of the eared dove: the unique case in southeast Brazil

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Abstract The unique environmental conditions in which eared dove populations exploded in southeast Brazil recently has enabled verification of a general hypothesis that had been put forward to explain earlier dove explosions elsewhere in South America. Large-scale deforestation followed by a sequence of land use developments in different parts of the State of São Paulo, southeast Brazil, produced landscapes that favored, in varying degrees, the presence of doves in high densities. Applying knowledge of dove biology gained from prior experience, it was possible to predict, at least approximately, where and when dove populations might be expected to explode or implode. Observed patterns were surprisingly consistent with predictions after a key feature of local adaptation was taken into account, namely the novel adoption of sugarcane plantations for colonial breeding. Previously, breeding had only been recorded in semiarid natural woodland and forest patches, habitats unavailable in the new area of outbreak.

Key words Soybeans, Deforestation, Agricultural expansion, Colonial breeding

1 Introduction

At the time of European settlement, the forested habitat of the State of São Paulo, Brazil, was unsuitable for eared doves (*Zenaida auriculata*). Early in the 20th century, the human population started to spread and forest clearing began in earnest (Victor, 1975), mostly for pasture, coffee groves and subsistence farming. The new landscape favored eared doves, and by the 1940s their numbers had grown sufficiently for some grain farmers to become alarmed. The problem was not serious, however, and the doves still bred separately in dispersed pairs, mostly in trees.

Real change, however, came about in the late 1960s and early 1970s when generous government policies favored the mechanization of agriculture and fostered a switch to large-scale planting of grain crops valuable on the international market. As a result, the size of fields increased and rotation was introduced for a second annual crop. Under these conditions, eared dove populations exploded, the birds becoming a real nuisance in soybean fields at seedling emergence and wheat and rice fields at harvest. This coincided with the establishment of several vast breeding colonies, covering areas of between 40 and 1 000 ha, with up to 5–10 million breeding birds, all located in sugarcane fields.

Earlier agricultural development in the Argentinean Chaco had also resulted in eared dove outbreaks and colonial breeding (Bucher and Ranvaud, this symposium), so the events in southeast Brazil, a humid tropical environment, offered an opportunity to test whether ideas developed to explain prior outbreaks had wider applicability. In spite of several differences (climate, grain crops and crop rotation practices, number of harvests per year, type of vegetation

present), several key factors were common to the situations in both Brazil and Argentina. Principal among them was the waste from mechanical harvesting, providing grain food for most of the year, and a mosaic landscape with large homogeneous patches of dense vegetation (sugarcane) suitable for colonial breeding not far from the crop fields.

2 Materials and methods

The information here reported was obtained through a combination of literature search, questionnaires and oral history from local informants, and personal surveying of three active colonies in the State of São Paulo. In addition, the largest and most persistent of the breeding colonies, near Tarumã (50°30' W, 23°15' S) was the focus of a quantitative study of diet in which more than 6 000 crop contents were analyzed between 1994 and 2002.

3 Results

Information from literature, questionnaires and oral history, together with our own records, enabled the following reconstruction. As dove numbers increased gradually through the late 20th century in southeast Brazil, solitary nesting in trees gave way to colonial breeding in sugarcane. Evidence was obtained of a total of ten breeding colonies in sugarcane fields in the States of São Paulo and Paraná then, most no longer active.

The first colony was established in the early 1970s, near Tarumã SP. This was also the largest, reaching 1 000 ha on occasion, and the most persistent; it still survives. The time of its establishment coincided with a ten-fold increase in the area devoted to soybeans and wheat in the surround-

ing region. Around that time farmers adopted the practice of two harvests per year, providing abundant food for the birds year round, both through waste at harvest times and from weeds in the fields. Weed seeds were found to be important in the diet of the birds, especially at times when grain crops were ripening prior to harvest and unavailable. Land use has been relatively stable in the region, and, unlike plantings in the rest of the state, the area under sugarcane did not increase after the 1980s. About equal areas are devoted to sugarcane and to soybean-maize production on yearly rotation.

The other colonies were established within about a decade of the first, but all but one had disappeared by the late 1990s. In the region around the town of Ribeirão Preto, which was studied in some detail, the appearance of the colonies correlated with increased areas dedicated to maize (+50%) and to a lesser extent rice (+30%). The extinction of these breeding colonies correlated with a crash in the crops to levels lower than before the colonies had formed. During this time sugarcane continued to expand there, almost doubling from the late 1970s to the mid 1990s, and occupying more land than all other crops combined.

The sizes of the two active colonies in São Paulo today, at Tarumã and Penápolis about 170 km further north, are more than an order of magnitude different from each other, 1 000 ha versus 60 ha respectively. This correlates well with the area dedicated to annual crops within a radius of 50 km of the two colonies. Fifty kilometers is a distance that the birds are known to cover to feeding grounds each day

Dove diet at Tarumã over 8 years of study was entirely of grain and seeds from agricultural lands, consisting almost exclusively of waste grain, mainly wheat and maize, and weed seeds (Ranvaud et al., 2001; De Freitas, 2002). Mean dry weight of dove crops correlates with estimated grain availability, obtained through the monthly summaries of cooperative accounts. Dry weight also correlates with breeding and its intensity. Crop weights pass through a minimum in December and January, 2–3 g compared to 5–7 g at other times (Ranvaud et al., 2001; De Freitas, 2002); and these are months in which breeding, if any, is much reduced.

4 Discussion

Once sugarcane is recognized as a substitute for colonial breeding habitat, the recent natural history of eared doves in southeast Brazil is consistent with the hypothesis put forward by Bucher and Ranvaud (this symposium) to explain population explosions elsewhere in South America.

Establishment, survival and extinction of the breeding colonies together correlate with food available from ag-

ricultural activities. Colony size also correlates with food from the same sources. Diet was found to be entirely dependent on agriculture, especially waste grain and associated weeds. The mean weight of dove crops was found to go through a minimum at times of vegetative growth in grain crops, when agriculture provides little food; these are also times when breeding all but stops. Food is thus the key factor in dove demography.

The picture that emerges is one of growing dove populations as soon as food becomes easily available in open country, a common situation under the regime of expanding agriculture and improved mechanization through the 20th century in South America. Quantity of food available is increased by inefficiency in agricultural mechanical harvesting and by extended asynchronous or double cropping made possible by climatic conditions. At some threshold in population density, solitary nesting gives way to colonial breeding in dense, uniform patches of vegetation of particular size, if these are available. It is then that the populations explode. For this, the ideal ratio of areas dedicated to sugarcane and annual crops appears to be around 1:1, with patches of sugarcane above a regional minimum of 20 000 ha for breeding and roosting. When these conditions change or desynchronize, the doves appear to respond accordingly, dropping in numbers and reverting to solitary nesting.

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Symposium 33 Competition and hybridization from introduced waterbirds: a rising political issue

Introduction

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Although the introduction of animals such as the common pheasant (*Phasianus colchicus*) and rabbit (*Oryctolagus cuniculus*) outside of their range began as early as the 12th century (Lever, 1977), human activities have greatly increased such movements since the 1800s. Whether deliberate or accidental, the translocation of species beyond their native range is a major cause of loss of biodiversity throughout the world (IUCN, 1997) and of economic damage to agriculture, forestry, aquaculture and other industries (Williamson, 1996). In the United States alone economic costs are estimated at \$97 billion (Bright, 1998).

If a single waterbird issue motivated this symposium, it was the extensively researched and topical case study of the ruddy duck (*Oxyura jamaicensis*) and white-headed duck (*O. leucocephala*). In the short time since its introduction in England in the early 1960s, the ruddy duck has become a minor national embarrassment. By January 2000, it had increased to 6 000 birds (Kershaw and Hughes, 2002), by which time some birds had dispersed into the breeding grounds of the globally endangered white-headed duck. There the ruddy duck threatened this already vulnerable species through hybridization, a threat so real that it led to cross-governmental consensus on tackling the problem (Baz Hughes and colleagues, this symposium) and may have contributed to recent improvements in legislation relating to the introduction of nonnative organisms (K.A. Shaw, this symposium).

However high the ruddy duck issue may be on the political agenda, it is not unique. Introduced nonnative waterbirds are considered such an ecological threat to endemics, including Meller's (*Anas melleri*) and African yellow-billed (*A. undulata*) ducks that the recently drafted African Eurasian Waterfowl Agreement specifically considers the issue. Symposium papers presented by Murray Williams and Britta Basse, and Judith Rhymer, describe how

mallards (*A. platyrhynchos*) introduced to New Zealand and released for hunting in Florida could lead to the possible extinction of native species through hybridization, introgression and competitive displacement.

However there may be solutions. Baz Hughes and colleagues demonstrate that it is probably possible to extirpate even such well-established introductions as the ruddy duck, and K.A. Shaw suggests that a solution to the ongoing problem of introduced waterbirds exists in international legal frameworks which provide the means for the banning importation of nonnative species and for their control if they threaten native biodiversity. Yet it is perhaps wise to end on a note of caution. The opening paper of the symposium by Mark Rehfish and colleagues, in a brief overview of the generally negative impact of introduced birds on native fauna globally, note that an unfortunate by-product of increasing first and second world human wealth is the growing tendency for waterbirds to be held in captivity with attendant risks of accidental or deliberate release.

The consensus of opinion from the symposium was that existing legislation should be used to stop the deliberate or accidental introduction of species outside of their natural range, with the possible exception of species threatened by global extinction. Even that should not be done until appropriate research had cleared such introductions of posing a threat to native species of conservation value in the region of introduction. Such an approach has proved successful in conserving stocks of the New Zealand saddleback (*Philesturnus carunculatus*) and Hawaiian goose (*Branta sandvicensis*) (Lever, 1985).

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S33-1 The impact and status of introduced waterbirds in Africa, Asia Minor, Europe and the Middle East

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Abstract As part of a British government-funded project, the number and distribution of introduced waterbird species in 77 of the 116 countries in the African-Eurasian Migratory Waterbird Agreement (AEWA) was determined from responses to questionnaires sent to government officials and ornithologists. Meeting predefined criteria, 112 species of introduced waterbirds were recorded. European countries held the most, with an average of 7.7 species per country. Across the AEWA area, the most common introductions were the mandarin duck (*Aix galericulata*)—17 countries, Canada goose (*Branta canadensis*)—16, and mallard (*Anas platyrhynchos*) and mute swan (*Cygnus olor*)—15. The costs of introductions normally outweigh benefits, and we recommend that existing legislation for controlling introductions be augmented and better enforced.

Key words Introduced waterbirds, Distribution, Africa, Europe, Asia

1 Introduction

The African-Eurasian Migratory Waterbird Agreement (AEWA) under the Convention on the Conservation of Migratory Species (Bonn Convention) aims to create a legal basis for a concerted conservation and management policy for the 172 species of birds ecologically dependent on wetlands for at least part of their annual cycle in its 116 states in Europe, Africa, NE Arctic Canada, Greenland, Asia Minor, the Middle East, Kazakhstan, Turkmenistan and Uzbekistan. The AEWA agreement encourages member states to assess the impact of introduced and nonnative species on their native migratory waterbirds. The species of waterbirds covered include, amongst others, pelicans, storks, flamingos, swans, geese and ducks.

Article III General Conservation Measures Section 2 (g) states that "... the Parties shall prohibit the deliberate introduction of nonnative waterbird species into the environment and take all appropriate measures to prevent the unintentional release of such species if this introduction or release would prejudice the conservation status of wild flora and fauna; when nonnative waterbird species have already been introduced, the Parties shall take all appropriate measures to prevent these species from becoming a potential threat to indigenous species." In the AEWA Annex 3 Action Plan it is further stated that "Parties shall, if they consider it necessary, prohibit the introduction of nonnative species of animals and plants which may be detrimental to the populations listed ...", that "Parties shall, if they consider it necessary, require the taking of appropriate precautions to avoid the accidental escape of captive birds belonging to nonnative species", and that "Parties shall take

measures... to ensure that when nonnative species or hybrids thereof have already been introduced into their territory, those species or their hybrids do not pose a potential hazard to the populations listed ...".

There is an extensive literature on the translocation of nonnative species, their consequences for biodiversity conservation, their economic impacts and the control strategies available for pest and problem species outside of their original ranges (Williamson, 1996; McLean, 2001). Apart from a few high profile species, however, it is surprising how little is known about the number and distribution of nonnative waterbirds in most countries, and their ecological interactions with native species. Studies have often been driven by economic imperatives and have related to species that have obvious economic impacts in the country of introduction. In only few countries, such as New Zealand, has there been a greater long-term interest in the ecology and competitive abilities of such introductions (Williams and Basse, 2006).

This paper summarizes some of the information obtained from a survey of government officials and ornithologists that sought to assess the status of introduced and nonnative waterbird species and the extent to which these species affected native species in AEWA countries (Blair et al., 2000). Using four of the most commonly introduced waterbirds in the AEWA area as exemplars, we then detail some of the issues arising out of the introductions.

2 Materials and methods

Introduced species are those satisfying one of the five categories defined in Table 1.

Table 1 Definitions of non-native birds

Naturalized introduction	Established species that would not occur naturally without introduction by man
Naturalized establishment	Species that have become established in an area where previously they had occurred but had not bred naturally, having been a vagrant, passage migrant or winter visitor.
Naturalized re-establishment	Species successfully re-established in areas of former natural occurrence
Naturalized feral	Domesticated species established in the wild
Vagrant naturalized species	Species from established naturalized populations in a neighbouring country

After Holmes and Simons (1996), and Holmes et al. (1998).

Much of the information presented here about species numbers was collated from responses received to questionnaires sent to the 116 AEWa countries (Blair et al., 2000). The questionnaire sought information on the identity of each introduced species, its location, habitat and history in the country, whether it exhibited sedentary or migratory behavior, its breeding and population status, hybridization, disease, habitat changes, escape recruitment, and threat to other waterbird species. Only considered in detail were the 112 species that fulfilled at least one of the following criteria in the country of introduction: minimum of three records of escape or release since 1960, survival for a year in the wild, and breeding successfully. Information also gathered from the completed questionnaires, but not discussed here, covered national conservation measures and legislation relating to introduced nonnative waterbirds, their effectiveness in stopping entry, countermeasures taken for control and against spread, and the extent of waterbird trading and keeping of live waterbirds and free-flying stock.

The information used in the four case studies below was extracted from the AEWa questionnaires and a review of the literature.

3 Results

AEWa questionnaires were returned from 77 countries. The number of introduced species of waterbirds per country was greatest in Europe (Table 2). Within Europe, Britain reported 72, Switzerland 43, Germany 21, The Netherlands 20, France and Italy 17, Austria 16 and Belgium 15 species. Outside of Europe, the United Arab Emirates and South Africa, with 24 species each, also reported unusually high numbers.

The most commonly introduced species in the AEWa area, the mandarin duck (*Aix galericulata*), is recorded for South Africa and 16 European countries. Canada goose (*Branta canadensis*), mallard (*Anas platyrhynchos*), mute swan (*Cygnus olor*), black swan (*Cygnus atratus*), bar-headed goose (*Anser indicus*), ruddy duck (*Oxyura jamaicensis*), wood duck (*Aix sponsa*), ruddy shelduck (*Tadorna ferruginea*), greylag (*Anser anser*), and Egyptian goose (*Alopochen aegyptiacus*) are all recorded in 10 or more countries.

4 Discussion

The results of the questionnaires were startling, and

the unexpected scale of the problem demonstrated clearly how little the issue had been investigated. Comments in the questionnaires about four of the most commonly introduced species are summarized below to illustrate the diverse yet particular issues raised by introduced species.

Because of its beauty, the mandarin duck is the most widely introduced waterbird within the AEWa area and perhaps in the world. It has been living in the wild in Britain since 1866 (Lever, 1987). Its status is classified as “Insufficiently Known”, and some of its native habitat in China is threatened by habitat loss. It has hybridized with at least four species of duck in captivity including the very closely related wood duck, and destroys the eggs of other cavity nesting species in the wild. It can be argued that there is benefit in having self-sustaining feral populations of this duck as insurance against major declines in its wild populations in China. Lever (1987) had suggested that the estimated 1 000 pairs in Britain could exceed the numbers present in its natural range outside of Japan.

The Canada goose is the second most widely introduced waterbird within the AEWa area, having been released in 16 European countries. Unlike the mandarin duck, this species is not globally threatened. It was first introduced in Britain and France in the 17th Century for wildfowl collections, food and hunting (Lever, 1977). Since the late 1960s its numbers have increased by a factor of six in Britain to a minimum of 82 000 birds (Musgrove et al., 2001; Rehfish et al., 2002); and yet much suitable habitat appears to be unused still (Graham Austin, unpublished). In captivity or in the wild, Canada geese are known to have hybridized with 16 species of Anatidae, including barnacle (*Branta leucopsis*), greylag (*Anser anser*), and white-fronted (*A. albifrons*) geese (Delany, 1993), as well as mallard.

Table 2 The average number of introduced species of waterbird per country in the AEWa area

Africa	1.2 species in 29 countries
Asia	0.3 species in 4 countries
Asia Minor and Middle East	4.3 species in 7 countries
Europe	7.7 species in 37 countries
NE Arctic Canada and Greenland	0 species in 2 countries

From Blair et al. (2000).

Canada geese are considered to be a potential threat to native greylag geese in Scotland through hybridization and introgression (Welch et al., 2001), and if their eastwards spread continues in Europe they could threaten the endangered red-breasted goose (*Branta ruficollis*). Canada geese are aggressive towards native wildlife, cause ecological disturbance and habitat damage and can be an agricultural pest (Anon., 1973; Lever, 1977, 1987; Watola et al., 1996; Blair et al., 2000; Welch et al., 2001).

The mallard is the third most widely introduced species of waterbird within the AEWa area, having been introduced into seven European, five African, one Asian and two Middle Eastern countries for wildfowl collections, food and hunting; some 400 000 are released annually in Britain. In captivity or in the wild, it has hybridized with two species of geese, three species of shelduck, 38 species of duck, guineafowl and chicken (Lever, 1987; Blair et al., 2000). Within the AEWa area it has produced fertile offspring with the threatened African yellow-billed duck (*Anas undulata*) and perhaps the endemic Meller's duck (*Anas melleri*) of Madagascar. Elsewhere it has hybridized with a range of regionally threatened species, including the New Zealand grey duck (*Anas superciliosa*) (Williams and Basse, 2006) and Florida mottled duck (*A. fulvigula*) (Rhymer, 2006), potentially leading to local extinction of native species.

No summary of the impact of introduced species within the AEWa area would be complete without the ruddy duck, a species that has triggered governmental action to control its numbers (Hughes et al., 2006). This porcelain-billed duck, widespread in the Americas, is popular in wildfowl collections. In Britain, it apparently filled an unexploited niche and increased dramatically following its accidental release in the early 1960s (Sir Peter Scott in Lever, 1987). Had it remained in Britain it would not have become such a conservation issue. Unfortunately, it spread into 11 European countries, including Spain, Morocco and Turkey that constitute part of the restricted breeding range of the "Globally Threatened" white-headed duck (*Oxyura leucocephala*). There the ruddy duck has hybridized with the white-headed duck and could contribute to its possible extinction (Hughes et al., 2006).

Clearly, the level of ornithological interest in a country will determine the number of waterbird species that it introduces. Although the number reported in the AEWa area is a minimum, it is unlikely to be artificially inflated. There is a broad relationship between the wealth of a country and the introduction and keeping of waterbird species. The greater collections and captive breeding of birds in the wealthier countries make it much more likely that accidental escapes or releases will occur there. The increasing popularity of bird collections has increased the demand for exotic waterbirds, and this has been accompanied by ever more escapes.

5 Conclusions

Introductions of waterfowl may confer two major

benefits. First, they can be of economic value in providing human employment, food and sport. Secondly, they may help ensure the conservation of relic populations of endangered species, even though releasing them into a totally new habitat is usually not the only way to ensure their continued survival (Lever, 1987).

These benefits are normally much outweighed by the costs. Across many taxonomic groups, introductions have led to the extinction of native species, contributed to genetic pollution and caused economic and environmental damage. Whereas competition between species is a natural part of evolution, it can be argued that competition should not be so strongly directed by human influence on nature. The ruddy duck is an example of a species that is most unlikely to have reached Britain in sufficient numbers to establish itself without human assistance.

Our research has shown that considerable numbers of waterbirds have been introduced into the AEWa area. Many more waterbird species escape today than in the 1980s, because many more exotic species are being bred in captivity. A single recent issue of *Aviornis* (143), a journal aimed at breeders of captive birds, listed over 58 000 exotic birds for sale, 1 051 collections and many commercial breeders in Belgium and The Netherlands alone. Reducing escape events should become a high priority towards stopping introduced species from establishing themselves. To enable this, the marking of all captive birds with individual rings or transponders registered at a central data base should become a legal requirement. The recovery of such markers in the wild can then be used to impose heavy fines on the owner, rated at a level to reflect the risk posed to indigenous wildlife and the environment. As it stands, existing legislation can, if fully implemented, stop or at least severely restrict the further spread of introduced waterbirds throughout the world (IUCN, 1997; Shaw, 2006).

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S33-2 Conservation of the globally threatened white-headed duck, *Oxyura leucocephala*, in the face of hybridization with the North American ruddy duck, *Oxyura jamaicensis*: results of a control trial

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Abstract The North American ruddy duck, introduced into Europe in the 1960s, threatens the globally endangered white-headed duck with extinction through hybridization. A regional control trial, conducted in three areas of Britain, killed over 2,600 birds and led to a significant regional reduction in ruddy duck numbers. Control using firearms was effective but trapping ineffective. Population modeling suggests that the ruddy duck population in Britain can be reduced to fewer than 175 individuals in four to six years using year-round control if access is available to the principal wintering sites. The likely cost of the program is between £3.6 m and £5.4 m.

Key words Ruddy duck, White-headed duck, Competition, Population control

1 Introduction

In recent years, there has been a growing appreciation of the need to prevent the introduction of, and to control, nonnative organisms that threaten native biodiversity. At the global level, the Global Invasive Species Program was established in 1997 to address threats posed by nonnative species that disrupt ecosystem processes and hence threaten biodiversity, health and economies. The International Union for the Conservation of Nature and Natural Resources (IUCN) has established an Invasive Species Specialist Group that has published guidelines on the prevention of biodiversity loss caused by invasive alien species. At the European level, the Bern Convention has addressed invasive species issues by producing various policy documents, and by holding workshops to increase awareness amongst policy makers. In Britain, a review of the Government's policy on nonnative species is due to report in late 2002.

2 Status and distribution of the white-headed duck

The white-headed duck (*Oxyura leucocephala*) is a globally "endangered" species. Numbers in the main central Asian population have declined from around 100 000 to less than 10 000 birds since the 1930s (Green and Hughes, 2001). The Spanish population fell to 400 birds in 1950, then to just 22 birds in 1977. Destruction of habitat and excessive hunting were the main causes. Habitat protection, protection from hunting, and captive breeding have subsequently led to increased numbers in Spain to over 2 500 birds (Hughes, 2006).

3 Status and distribution of the ruddy duck

3.1 Britain

Ruddy ducks (*Oxyura jamaicensis*) are common and widespread in their native habitat in North and South America, where there is an increasing population of over half a million birds. It was introduced into Britain from captive collections in the 1950s. In summer, the birds are widely dispersed, but in autumn and winter they congregate on a limited number of large inland water bodies. In January 2000, for example, the top ten sites for ruddy ducks held approximately 67% of the wintering population and the top 25 sites 83%. The total January 2000 winter population was estimated at 6 000 birds, but the rate of increase is now slowing, from 39% per annum between 1966 and 1980, to 8%–9% during the 1980s and to 6%–7% subsequently (Kershaw and Hughes, 2002).

3.2 Europe

In 1965, the first record of a free-flying ruddy duck outside of Britain was reported from Sweden. As population numbers increased in Britain, so did the number of sightings abroad. These came initially from countries closest to Britain, such as France, the Netherlands, Belgium and Ireland, countries which still hold the greatest numbers of records. There have now been over 900 reports of some 1 500 ruddy ducks in 19 western palearctic countries (Hughes et al., 1999). The number of sightings, moreover, is increasing at a mean annual rate of 21% since 1976 (Hughes et al., 1999). Records are concentrated along the North Sea coasts

of The Netherlands, Belgium and Germany, and in France and Spain.

During the breeding season the ducks are now present in eight countries; and annual breeding attempts probably take place in five: Belgium, France, Ireland, The Netherlands, and Morocco, but not Spain where most birds are shot. The number of ruddy ducks that currently attempt to breed annually in continental Europe is still low — less than 10 pairs in 1998–2000 (Wetlands International, unpubl. data). Flocks of wintering birds have recently appeared in Spain and France. In January 1997, about 30 were recorded in northern Spain following a freeze across northern Europe, and 30–80 birds have wintered annually at Lac de Grand-Lieu in northern France since 1995. The feral population in Britain is the most likely source of these birds.

4 The threat to the white-headed duck

The biological, social and economic threat caused by nonnative species can be immense. In the USA, for example, nonnative species have contributed to the decline of 42% of threatened species; and exotic animals and plants have been estimated to cost the USA \$137 billion per year (Pimentel et al., 2000). After habitat loss and over-hunting, the impacts of nonnative species are the third most important factor threatening globally endangered waterbirds.

Introduced waterbirds are already known to threaten native populations with extinction through both hybridization and competition. Naturalized mallards (*Anas platyrhynchos*) now threaten seven distinct species or subspecies of other members of the genus *Anas* through introgressive hybridization (Rhymer, 2006). Ruddy duck x white-headed duck hybrids are known to be fertile to at least the second generation, indicating that hybrid breakdown, where F2 hybrids are infertile, does not occur. Wild introgressants to at least second generation have been observed in Spain.

5 Conservation control action

5.1 International

White-headed duck conservation action plans have been produced at a global (Anstey, 1989), continental (Green and Hughes, 1996; Li and Mundkur, 2002), and national levels. In 1996, the Council of Europe published 23 action plans for globally threatened birds in Europe, including the white-headed duck (Green and Hughes, 1996). The white-headed duck action plan urged Britain, *inter alia*, to “undertake its planned regional control program as soon as possible. If the results suggest that it is possible to control ruddy ducks on a large scale, the U.K. should undertake countrywide control measures for ruddy ducks as soon as possible.” The Bern Convention has since produced a strategy for the eradication of the ruddy duck in the western palearctic region (Hughes et al., 1999).

The number of countries taking action against ruddy ducks has increased in recent years. By 2002, at least 11 countries in the western palearctic (excluding Spain and

Britain) were taking, or preparing to take, action against ruddy ducks. This compares with only six countries in 1999. Birds have been controlled in six countries: France, Iceland, Morocco, Portugal, Spain and Britain; and Spain and France have national ruddy duck eradication strategies in place. By the end of 2001, 101 pure ruddy ducks and 58 hybrids had been killed in Spain, and 107 ruddy ducks in France.

5.2 Britain

In 1992, a three-phase ruddy duck control program began in Britain. The first phase investigated a range of lethal and nonlethal control techniques and concluded that reduction and control of numbers was possible. Population modeling suggested that shooting during the breeding season could reduce ruddy duck numbers to under 50 individuals in 3–10 years, without significant disturbance to other species or habitats (Hughes, 1996).

The second phase, a regional control trial conducted in three areas of Britain, began in April 1999 and ended in May 2002. The trial aimed to determine whether it was possible to reduce the British population to fewer than 175 individuals within ten years; to determine the likely cost of the program; and to determine whether ready access to control sites could be obtained on a voluntary basis (Central Science Laboratory, 2002). Three regions thought to be representative of the different challenges facing the project were selected for the trial. At Anglesey and in the Western Midlands control was carried out all year round while at Fife it was limited to autumn and early winter. Limited control also took place on waters in Avon, Leicestershire, Northamptonshire because of the need to test control methods on large wintering sites, and in Gloucestershire where breeding season traps were tested (Central Science Laboratory, 2002).

At Anglesey we aimed to reduce the breeding population by the maximum possible, and at least by 70% within three years. The original breeding population of 200 birds was reduced by over 70% within the first twelve months of the trial, and by an estimated 93% within sixteen months. It was achieved by shooting a total of 515 birds (158 females, 225 males and 132 immatures). In the Western Midlands we attempted to reduce the immediate pre-breeding population by the maximum possible. Counts on a subset of 17 sites showed reductions of 28% in the first twelve months. Counts on a subset of 23 sites showed a further 54% reduction in the second twelve months of the trial. These figures represent an overall reduction of 66% in the first two years of the trial. It was achieved by shooting a total of 1 715 birds (495 females, 743 males and 477 immature birds). The aim of the trial in Fife was to kill the maximum number possible of the post-breeding (autumn) population. A total of 216 ruddy ducks were removed during the trial (33 in 1999, 163 in 2000, and 20 in 2001).

Permission to carry out control of ruddy ducks was sought on a voluntary basis for a total of 153 sites, requiring approaches to 193 owners/occupiers. Of those

contacted, 58% gave permission, enabling control to be carried out on 52% of the 153 sites. Shooting was allowed on 48% of all sites, and trapping on a further 4%.

Shooting proved effective on breeding sites and on a range of post-breeding and wintering sites. On average 47% of the ruddy ducks present on breeding sites were killed per visit, with a staff input of 1.98 hours on site per bird killed. On post-breeding and wintering sites less than 1 km², 54% of birds present were shot per visit on average, with a staff input of 1.1 hours per bird killed. On larger waters, the percentage of birds killed was reduced (mean 19%) but staff input only 0.8 hours per bird.

Three traps were constructed at three post-breeding/wintering sites, and fourteen on three breeding sites. Approximately 900 hours of staff effort in construction, maintenance and driving of ducks during the autumn and winter failed to produce any captures. During the breeding season, another ca. 750 hours of staff effort resulted in a total of 17 ruddy ducks (five females and twelve males) being caught, all on just one of the three sites. The results of this work suggest that post-breeding and winter trapping is ineffective, but that breeding season trapping, although far less efficient than shooting, could be effective on some sites.

The overall trial on breeding, post-breeding and various sizes of wintering sites, with over 2 600 birds killed, resulted in a significant reduction in ruddy duck numbers regionally. Control by firearms was effective, and trapping ineffective, in taking large numbers of birds.

A stochastic Monte Carlo simulation model was constructed to project the national ruddy duck population from January 2000 under a variety of control strategies. Three variables were included: efficacy per person (how much one staff could reduce the British population per year), numbers of staff, and changes in ruddy duck population growth rate. Although there may be as many as 1 000 breeding sites across Britain, the forty or so key post-breeding and wintering sites where most of the population concentrates is the key; and access to them will be critical for progressing an effective eradication scheme. If access is gained, modelling suggests that there is an 80% certainty that the popula-

tion can be reduced to fewer than 175 birds in between four and six years, at a cost of between £3.6 m and £5.4 m.

Acknowledgements The regional control trial was carried out under contract to the UK Department for the Environment, Food and Rural Affairs, and is published with the Department's agreement.

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S33-3 Indigenous gray ducks, *Anas superciliosa*, and introduced mallards, *A. platyrhynchos*, in New Zealand: processes and outcome of a deliberate encounter

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Abstract Three hypotheses — demographic and competitive ascendancy, genetic assimilation, and habitat destruction and disturbance — have been advanced to explain the demise of the gray duck and rise of the mallard in New Zealand subsequent to the introduction of the mallard a century ago. We modelled relative population change over the past 50–60 years, based on hunter kills, and evaluated the competing hypotheses. We conclude that capacity for survival, greater fecundity and productivity, physical domination of gray duck, and willingness to exploit novel feeding opportunities in man-disturbed environments, have contributed most to the present numerical dominance of the mallard. An apparently extensive hybrid swarm may be dominated by a mallard phenotype, but evaluation of genetic exchange based on phenotype alone remains problematic. Gray ducks and the gray duck phenotype may soon disappear from New Zealand.

Key words Hybridization, Ecological displacement, New Zealand, *Anas superciliosa*, *Anas platyrhynchos*

1 Introduction

The Anatidae feature commonly among animals now established in free-living populations beyond their native ranges. For example, 27 species were deliberately introduced to New Zealand with the intention of establishing populations for sport (Thomson, 1922; McDowall, 1994) and two, the mallard (*Anas platyrhynchos*) and Canada goose (*Branta canadensis*), are now among the most common birds in that country. Mallards have been introduced almost worldwide (Lever, 1987), including Australasia (Marchant and Higgins, 1990). The introductions there dropped the mallard directly into the core of the native range of the gray or Pacific black duck (*Anas superciliosa*), which extends from eastern Indonesia through Australia, New Zealand and New Guinea to Micronesia and Polynesia.

From 1867 to 1886, only occasional pairs or small numbers of mallards were imported into New Zealand, but from 1895 on, serious attempts were undertaken to propagate and release them (Thomson, 1922). Hunter organizations and acclimatization societies persisted with breeding and release of British game farm mallards for about 20 years, eventually establishing feral populations sufficient to permit hunting. The slow spread of these populations, and the ongoing decline of the gray duck in New Zealand, especially on the North Island, prompted importation of mallards from North America in 1937. The ensuing breeding program continued to 1963, releasing over 20 000 mallards nationwide (McDowall, 1994).

Subsequent expansion of the mallard in New Zealand coincided with (1) a nationwide decline of the gray duck, and (2) the appearance of birds of obvious hybrid ancestry (Williams, 1981; Gillespie, 1985). Three hypotheses have been advanced to explain these changes: (1) demographic and competitive ascendancy of the mallard which outbred and outlived the gray duck, and displaced and dominated it in competition for essential resources (Williams, 1981); (2) genetic assimilation, a consequence of widespread interbreeding between the two species that created an extensive hybrid swarm in which the mallard phenotype dominated (Gillespie, 1985); and (3) habitat depletion and disturbance that forced the gray duck, with its apparent preference for wild and remote wetlands and wooded environments, to retreat as forest was replaced by pasture and natural wetlands were drained. In contrast, the mallard readily exploited wetlands and other resources available within the pastoral landscape, and tolerated human-induced disturbance much better (Caithness, 1982).

In this paper we examine some predictions arising from each of these hypotheses.

2 Materials and methods

Patterns of historic mallard population growth were deduced from changes in the relative proportions of mallards and gray ducks in hunter kills. Records in available diaries from hunters mostly cover the period 1968–1990, although one extends back to 1933 (Caithness, 1980). Nationwide telephone surveys of hunters provided similar data

annually for 1992–2000 (NZ Fish and Game Council, unpubl. data). We also used regional banding studies (see Table 1) and field surveys (1963–1995; M. Williams, unpubl. data) to provide further measures of the mallard-to-gray duck ratio over time and species-specific survival and productivity estimates.

We used regional changes in mallard-to-gray duck ratios in hunters' kills to establish models of population trend for the two species, namely a continuous model:

$$dG/dt = b_G(t)G(t) - (1 - s_G(t))G(t);$$

$$dM/dt = b_M(t)M(t) - (1 - s_M(t))M(t);$$

and a discrete model:

$$G(t+1) = s_G(t)G(t) + b_G(t)G(t);$$

$$M(t+1) = s_M(t)M(t) + b_M(t)M(t),$$

where $s_{G/M}$ = species-specific annual adult survival, $b_{G/M}$ = species-specific recruitment rate (proportion of young per adult surviving one year), and G and M are the numbers of gray duck and mallard respectively. By substituting field-derived estimates of survival and/or productivity, we estimated likely changes in regional species populations over varying time periods.

3 Results and discussion

3.1 Demographic and competitive ascendancy hypothesis

This hypothesis predicts, first, differential survival, fecundity, productivity and recruitment rates for the two species, and, secondly, that mallards are physically dominant at shared feeding and breeding sites.

Survival Contemporaneous estimates of survival of mallard and gray ducks are shown in Table 1. Balham and Miers (1959) reported that survival rates for mallards averaged significantly (10%+) higher than for gray ducks in all sex and age categories examined. Reanalysis of their data sets using MARK (White and Burnham, 1999) confirmed their comparative findings but lowered their survival estimates. Caithness et al. (1991) reported no statistically significant differences in mallard and gray duck survival in the decades after the Balham and Miers (1959) analysis.

They reported, however, that low banded sample sizes yielded tests of low power, and only for males could they have detected large (40%+) differences in survival had they existed.

Both studies reported recovery rate estimates (15%–25%) for gray ducks that are among the highest yet recorded for wild ducks, indicating that they were 1.3–2.0 times more likely to be shot than sympatric mallards. Barker et al. (1991) concluded, from the same data, that such hunter-induced mortality was mostly additional to natural mortality rather than compensatory, thereby implicating hunting as an important determinant of gray duck survival. The lower survival and higher recovery rate estimates for 1949–1954 than those subsequent suggest significant over-exploitation and hunting as an understated contributor to gray duck decline.

Subsequent analyses of mallard survival (Nichols et al., 1990) have identified significant regional variation, especially for males. Within regions, the greater temporal variations in survival were in adult females. However, for neither sex were the differences indicated in Table 1 significant (Nichols et al., 1990; P. Taylor, pers. comm.).

Fecundity, productivity and recruitment The most frequently reported clutches for mallards and gray ducks are 10–12 and 8–10 respectively (Balham, 1952; Balham and Miers, 1959; Marchant and Higgins, 1990; M. Williams, unpubl. data). These records do not discriminate between initial clutches and re-nesting attempts. Broods of near-fledged mallard young are generally reported as larger than those of gray duck: 5.7 vs. 5.0 in a Manawatu wetland (Caithness, 1970), 5.8–6.9 vs. 3.9–4.8 in the Waikato wetlands in 1963–1970 (M. Williams, unpubl. data). None of these records indicate the percentage of ducks successfully raising young, and there are no data on the frequency with which each species re-nests. The mallard starts breeding earlier each season than the gray duck and ends later (Caithness and Pengelly, 1973), which implies more re-nesting by mallards.

Balham and Miers (1959) determined that the average productivity required of mallard and gray duck females to replace annual losses during the 1950s was 2.9 and 4.4

Table 1 Mean survival estimates (S) for adult mallard and gray duck, 1947–1990

Period	Male mallard S ± SE	Male gray duck S ± SE	Female mallard S ± SE	Female gray duck S ± SE	Region	Source
1949–1954	0.62 ± 0.05	0.39 ± 0.02	0.44 ± 0.03	0.32 ± 0.02	Waikato and Manawatu, female estimates adult + young combined	Balham and Miers (1959), reworked using MARK (White and Burnham, 1999)
1957–1965	0.69 ± 0.02	0.51 ± 0.02	0.59 ± 0.08	0.57 ± 0.05	Waikato	Caithness et al. (1991)
1966–1974	0.59 ± 0.03	0.58 ± 0.09	0.53 ± 0.07	0.52 ± 0.25	Waikato	Caithness et al. (1991)
1979–1983	0.66 ± 0.06 0.49 ± 0.03	* *	0.44 ± 0.05 0.41 ± 0.04	* *	Waikato Manawatu	Nichols et al. (1990)
1986–1990	0.48 ± 0.09	*	0.45 ± 0.09	*	Manawatu	P. Taylor (pers.comm.)

* Too few for reliable estimation.

fledglings, respectively. The many possible solutions in our models for relative population change in the Waikato region during 1960–1970 suggest that average mallard productivity then was not less than 3.1 fledglings per female, and for gray ducks not greater than 1.6. There are no direct field estimates of recruitment, that is, the number of progeny per duck surviving to breeding age. Applying known juvenal survival estimates (Caithness et al., 1991) to our models suggests that annual mallard recruitment was 0.58–0.71 per female and only 0.38–0.5 for gray duck in the Waikato region. These solutions indicate that annual mallard recruitment in the 1960s and 1970s averaged approx. 15% above replacement, and gray duck approx. 5% below.

Competitive displacement Mallards are 15%–20% heavier than gray ducks, and up to 10% larger in bill, wing and leg (Marchant and Higgins, 1990). They use their size advantage to physically displace and exclude gray ducks at feeding sites. In mixed species flocks at urban parks, for example, mallards dominate public feeding sites and physically prevent gray ducks from accessing the food: on one occasion, mallards initiated 413 interactions and won all but 3 (M. Williams, unpubl. data). Mallards also usurped gray duck breeding sites. Between 1963 and 1970, the numbers of gray duck pairs in the Waikato wetlands declined by 70% as numbers of mallard pairs rose by 145%; gray duck declined from 78% to 28% of the combined duck population then (M. Williams, unpubl. data). Specific sites previously used by gray ducks for loafing or waiting for mates became occupied by mallards. Pair and brood densities of gray ducks declined 22% and 17% respectively as mallard numbers increased, implying greater preoccupation of space by mallards.

3.2 Genetic assimilation hypothesis

Mixed species pairings and birds of apparent hybrid phenotype were observed soon after the initial mallard introductions (Thomson, 1922). Consistent with the reported dominance of the mallard, a mallard-like phenotype can be expected to prevail within the hybrid swarm. Progeny of mixed species pairings superficially resemble the paternal species (Williams, 1981). Although genuinely intermediate phenotypes may arise, more mallard-like than gray-like phenotypes result from mixed species, F1 hybrid-hybrid and backcross pairings. For mallard-like phenotypes to dominate in hybrid swarms, the initial mixed species pairing should involve primarily mallard drakes and gray ducks.

Despite experimental evidence that females of both species mate assortatively when given a choice (B. Bakker, pers. com), field observations indicate no courtship interaction among mixed species (Hitchmough et al., 1990). Yet breeding studies on the Waikato wetlands between 1963–1970 (M. Williams, unpubl. data) recorded 1%–4% of pairs as mixed species. Of 92 pairs observed in 1967, all but five were mallard drake × gray duck. Rhymer et al. (1994) confirmed, nevertheless, that mixed species matings of both types occur, and identified introgression of gray duck mtDNA into the mallard population as well as the reverse.

Phenotypic criteria discriminating between F1–F3 hybrids and parental species are not reliable (Green et al., 2000). Thus wing and face plumage characters and wing length could together only discriminate F1 hybrids from parental species with 85% confidence. Progeny of F1 hybrids backcrossed with gray ducks could be distinguished from gray ducks in 90% of specimens, but no comparable resolution of mallard-like hybrids and mallards was possible. The lack of plumage specificity in mallards may be a legacy of the inbred, game-farm stock from which the introductions were derived.

Using plumage characters, Green et al. (2000) estimated the gray-like hybrid component of the combined mallard-gray duck population. They identified varying levels of F1 and gray-like hybrids within regional duck populations, and recorded gray duck-like hybrids as more numerous than “pure” gray ducks in regions where the mallard phenotype comprised >80% of the total anatid population. This finding is consistent with rising hybridization as conspecific mates become difficult to find; but it does not preclude forced copulations as an important mechanism also.

3.3 Habitat depletion and disturbance hypothesis

The New Zealand landscape has been significantly modified during 150 years of European settlement. In little more than a century, indigenous forests on 26% of New Zealand’s land area were felled and replaced by grassland and pastoral farming (Wards, 1976). By 1970, almost 90% of the original wetlands had been reduced to inconsequential vestiges or converted to farmland (Cromarty and Scott, 1996). The ubiquitous gray duck found much of its native habitat obliterated, and as a direct consequence its populations declined (Balham, 1952).

Attributing the relative change in mallard and gray duck populations in the 20th century to the destruction of wild wetlands implies mallard and gray duck have different habitat preferences, the latter keeping more to remote or unmodified wetlands. This is not, however, the contemporary observation. Mallards have dispersed to and settled remote and uninhabited Auckland and Campbell Islands, 300–500 km south of New Zealand, from which gray ducks have subsequently disappeared. Mallards are presently expanding their presence in remote and forested Fiordland, the sole remaining region of New Zealand in which they have yet to achieve numerical dominance. It is now possible to find mallards at all sites where gray ducks presently survive: river headwaters, mountain tarns, high country lakes, and coastal stream mouths.

We are not aware that the hypothesis of differential tolerance of mallard and gray duck to human disturbance has been evaluated experimentally. However, we have observed that gray ducks feed and breed on created habitats on farmland with abundant marginal cover and/or riparian trees; that gray ducks were formerly conspicuous on lakes in urban parks as they are in Australia today; that areas where gray ducks formerly occurred in close proximity to

humans are now populated exclusively by mallards; and that mallards exploit agricultural habitats such as field drains and streams without riparian cover, and grain, grass and brassica crops, from which gray ducks are rarely reported.

4 Conclusion

There is clear evidence that the mallard has demographic ascendancy over the gray duck. The higher productivity and higher survival attributes of mallards fuelled their rapid expansion, especially following the persistent post-1937 releases. Being larger than gray ducks and thus able to physically dominate them, mallards were able to usurp the remaining lowland wetland habitat in which gray ducks persisted while concurrently exploiting new habitats and feeding opportunities within the expanding pastoral landscape. At the same time, gray ducks appear to have been hunted excessively (Balham and Miers, 1959). Such combined demographic and competitive ascendancy appears to be a particularly important contributor to mallard success.

Not so clear is the role of hybridization in the demise of gray duck. Until nuclear markers for discriminating gray duck and mallard from their hybrids have been identified, quantitative assessment of gray-mallard hybridization based on plumage characters alone must remain conjectural (cf., Gillespie, 1985; Green et al., 2000). Nevertheless, if mixed species pairings have occurred as frequently as described above, the introgression recorded by Rhymer et al. (1994) demonstrates that the genetic integrity of both species in New Zealand, particularly that of the gray duck, has already been compromised.

Loss of wild wetlands characteristic of pre-human New Zealand certainly impacted on the gray duck population. On its own, however, it does not explain its stunning displacement by the mallard. Gray ducks formerly occurred on lakes in urban parks, as they presently do in Australian cities and towns. Their present-day absence from pastoral and urban wetlands may be due to their physical or competitive displacement by mallards rather than to their inability to colonize or exploit these modified environments. Mallards have proved successful opportunists and ecological generalists worldwide. These traits have enabled them to occupy the full range of gray duck habitats in New Zealand. Given their demographic and competitive ascendancy over the past 60 years, mallards can be expected to continue to displace gray ducks everywhere; a further retreat of the gray duck phenotype appears inevitable. Whether a gray duck-like phenotype will persist alongside that of the mallard awaits further evaluation of the present hybrid swarm. Yamashina (1948) identified two hybrid phenotypes within the only other population reportedly derived from these two species, the so-called Mariana mallard (*Anas oustaleti*), but its extinction has precluded evaluating their stability.

What future for *Anas superciliosa* in its stronghold of Australia? Although mallards are mostly confined to urban parks there (P.J. Fullagar, pers. comm.), the post-1970s

expansion of mallards in rural South Australia (Marchant and Higgins, 1990) is reminiscent of past New Zealand events. Left unchecked, this expansion has the potential to repeat the New Zealand experience and to extend throughout southern Australia and Tasmania.

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S33-4 Extinction by hybridization and introgression in anatine ducks

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Abstract Non-indigenous species can bring about a form of extinction in native fauna through hybridization and introgression, as a result of human introduction or habitat modification bringing previously isolated species into contact. This process can be especially difficult for rare species that are brought into contact with congeners that are more abundant and aggressive. The best-known examples among the Anatinae involve the ubiquitous releases of mallard (*Anas platyrhynchos*) and its subsequent hybridization with the American black duck (*A. rubripes*), Florida mottled duck (*A. fulvigula*), and Hawaiian duck (*A. wyvilliana*) in North America, and gray duck (*A. superciliosa*) in New Zealand and Australia. Similarly, invasion of the European continent by escaped, captive-reared American ruddy ducks (*Oxyura jamaicensis*) has contributed to regional declines in the endangered white-headed duck (*O. leucocephala*). Use of molecular technology focuses attention on the extent of this under-appreciated problem that is not always apparent from morphological observations alone. Although some degree of gene flow is a normal, evolutionarily constructive process, hybridization with or without introgression may, nevertheless, threaten the genetic integrity and fitness, and so existence, of rare species.

Key words Introgressive hybridization, Introduced species, Genetic mixing, Extinction, Anatine ducks

1 Introduction

The most often cited causes of extinction are habitat destruction and/or fragmentation, cascade effects, overkill and the impact of introduced species. The impact of introduced species is usually approached from an ecological perspective, involving such negative effects as predation or competition. Another negative impact, often overlooked but also important, is hybridization and introgression, which can dissipate the unique gene pools of native taxa and, in effect, exterminate them (Rhymer and Simberloff, 1996). Modification of gene pools via hybridization can occur through purposeful or accidental introductions of exotic species, or through habitat changes that bring previously isolated native species into contact. Once this has happened, the risk of genetic extinction then depends on the strength (or weakness) of reproductive barriers between taxa, the vigor and fertility of hybrids, relative and absolute sizes of parental populations, and relative competitive ability (Levin, 2002).

For the purpose of this study, hybridization is defined as the interbreeding of individuals from genetically distinct populations irrespective of taxonomic status, and introgression as gene flow (genetic mixing) between populations whose individuals hybridize. Identification of hybrids based only on morphological analyses can be quite difficult because, after several generations of backcrossing, phenotypes of hybrids tend to converge on those of the parental species (Rhymer et al., 1994). Genetic analyses are required to unequivocally identify all hybrid individuals. The direction of hybridization can be determined using mitochondrial DNA (mtDNA) analysis. mtDNA is inherited only from the female parent, so it is possible to trace taxic

and sexual inputs into the parentage of hybrids, that is, whether matings occur consistently between the females of one species and males of the other, or in both directions (Rhymer et al., 1994). To determine the extent of introgression, analysis of bi-parentally inherited nuclear DNA markers, such as microsatellites, is required.

Recognizing that introgressive hybridization can also be an evolutionarily constructive process (Arnold, 1997), Allendorf et al. (2001) distinguished between natural forms of hybridization in wild populations and those that have been induced by anthropogenic activities. Here only anthropogenically-induced hybridization in anatine ducks is considered.

2 Hybridization through introductions

Taxic mixing resulting from animal introductions can be purposeful or accidental. Extensive hybridization between the endangered European white-headed duck (*Oxyura leucocephala*) and American ruddy duck (*O. jamaicensis*), for example, was initiated by the accidental escape of ruddy ducks from captivity in Britain, with near disastrous results (Hughes, 1996). On the other hand, mallard (*Anas platyrhynchos*) introductions have been purposeful and extensive throughout the world, contributing to the decline of closely related native species in North America, Hawaii, New Zealand, South Africa, and Madagascar. Hybridization with mallards has been implicated in the decline of American black ducks (*A. rubripes*) in eastern North America (Kirby et al., 2001). Purposeful introductions of mallards for hunting, in addition to changing land use, have brought these two previously isolated

species into contact (Callaghan and Kirby, 1996).

In southern Florida, escaped mallards from parks, backyard ponds and hunting clubs have hybridized with the mottled duck (*A. fulvigula*) to such an extent that the public is being warned that this could lead to the demise of their indigenous species (Mazourek and Gray, 1994). Another example is the endangered Hawaiian duck (*A. wyvilliana*) or koloa, which is threatened by hybridization with released mallards such that the population on Kauai is now the only one remaining unimplicated in a hybrid swarm (Rhymer, 2001).

In New Zealand, the gray duck (*A. superciliosa superciliosa*) was considered a game species until the 1990s, but is now listed as endangered. It is on the verge of disappearing as a distinct species, due to introgressive hybridization with introduced mallards (Williams and Basse, 2006). There is concern in Australia that a similar situation could develop for the gray (Pacific black) duck there. Meller's duck (*A. melleri*), an endangered species endemic to Madagascar, is also threatened by hybridization with game-farm mallards kept by indigenous people on Lac Alaotra, the primary location for Meller's duck (Young and Rhymer, 1998). Mallards have been introduced both deliberately and accidentally into South Africa as well, threatening the integrity of the yellow-billed duck (*A. undulata*) through extensive hybridization (Cape Nature Conservation, 1994; Owen et al., 2002).

3 Hybridization through habitat change

Changing land use practices in the southwestern United States facilitated contact between mallards and the

Mexican duck (*A. diazi*) (Hubbard, 1977). Extensive hybridization between these taxa well into northern Mexico led to the Mexican duck being determined as conspecific with the mallard in 1983 (AOU, 1983), preventing its listing as endangered. This decision was made despite the fact that pure populations of Mexican ducks remain in central Mexico and that the species is as distinct genetically from the mallard as other recognized species in the complex in North America (McCracken et al., 2001; Rhymer, unpubl. data). Habitat change due to agricultural expansion and increased urbanization has also contributed to the exposure of the American black duck to mallards (Johnsgard and Disilvestro, 1976; Heusmann 1974, 1988).

4 Mechanism of decline

Hybridization can lead to the decline of species through either outbreeding depression or genetic mixing and consequent genic dilution and dispersion. Outbreeding depression is expressed in lowered fitness in offspring and can arise whether hybrids survive or not. Low survivorship results either from embryonic inviability (one or both sexes) or the inability of young to cope with local environmental conditions. Even if hybrids do survive well, they may be sterile or the offspring of one cross or the other may be sterile. Thus, hybridization with or without introgression can contribute to extinction of rare species, because relatively more reproductive effort is dissipated in hybrid matings (Fig. 1). This phenomenon led Wolf et al. (2001) to declare that "hybridization is the most rapidly acting genetic threat to endangered [plant] species, with extinction often taking place in less than five generations".

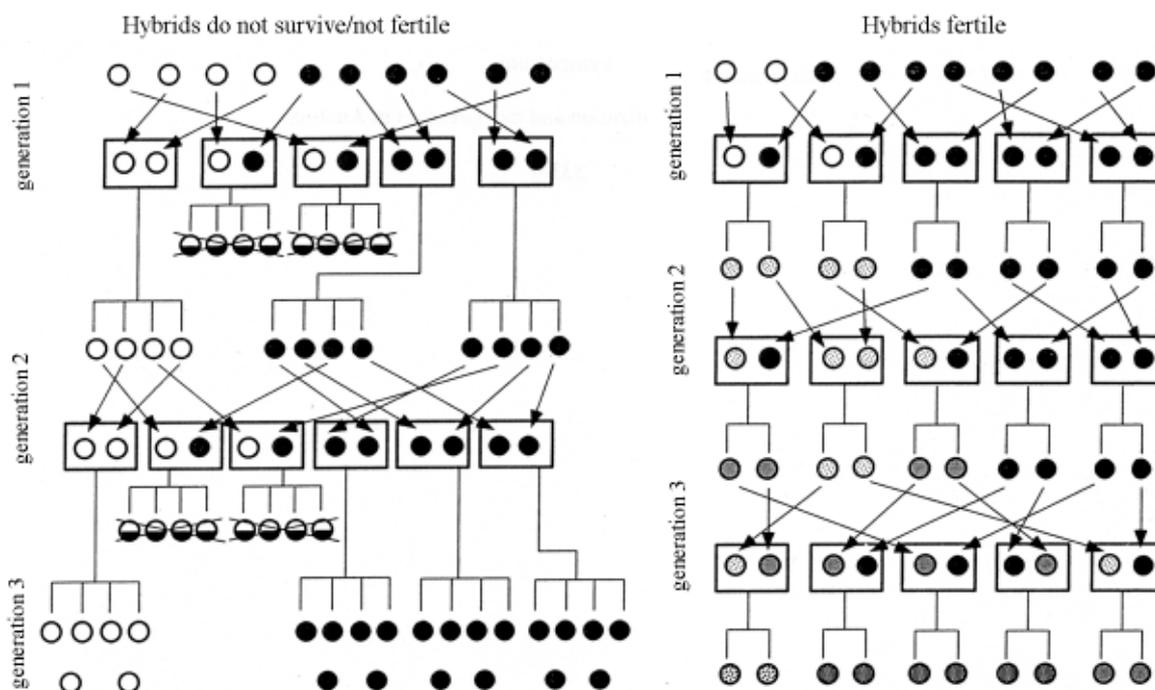


Fig. 1 Hybridization can lead to the decline of the rarer species (white circles) whether it results in fertile offspring or not. Left: although the number of individuals has increased after three generations, the proportion of the rarer species has declined. Right: a hypothetical example in which hybrids are fully viable and fertile, and form a hybrid swarm with complete genetic mixing (after Levin, 2002).

5 Solving the problem

Helbig et al. (2002) discuss the taxonomic implications of hybridization due to secondary contact, suggesting that taxa should be considered as separate species if the level of divergence between them indicates that they will remain distinct. The example given is the ruddy duck and white-headed duck. Unfortunately, even highly divergent congeneric species are capable of forming a fertile hybrid with complete admixture, despite being separated for long periods of time (Price, 2002). The retained ability of taxa to hybridize and introgress is not indicative of conspecificity. Rather, the emphasis should be put on protecting species, especially rare species, from the hazards of hybridization.

Possible solutions are the isolation or translocation of endangered species or the culling of hybrids. The former is often impractical and care must be taken to ensure that species are not being relocated to environments to which they are not adapted. This approach has been suggested for the Laysan duck (Rhymer, 2001) and gray duck (Rhymer, et al., 2004), but careful consideration of the consequences is essential. Culling ruddy ducks has been recommended to control the increase in hybridization between this species and the white-headed duck (Hughes et al., 1999, 2006).

In some cases, it will ideal to cull hybrids as well, but they may contain some of the last remaining genetic record of a species on the verge of extinction. As a last resort, hybridization with a closely related subspecies could even be used to help salvage distinctive characteristics, as has been done with the Florida panther (*Felis concolor*) (Hedrick, 2001). Allendorf et al. (2001) recommended protecting anthropogenic hybrids when they contain the only remaining genetic information of a taxon otherwise lost through genetic mixing, as well as taxa that have arisen through natural hybridization.

Thus, when planning translocations and reintroductions, it is essential to heighten awareness of possible deleterious consequences to prevent possible extinctions of native species through hybridization and introgression.

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S33-5 A review of legislation concerning introduced non-native waterbirds

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Abstract Non-native waterbirds have been introduced either intentionally or accidentally into many parts of the world. Some of the introductions have created problems, where nonnative birds either compete or hybridize with indigenous species or cause extensive damage to agricultural crops and fisheries. Environmental legislation is promulgated to protect indigenous animal species of respective countries; yet despite legislation, introductions of nonnative waterbirds still occur. Current international, national and, where possible, provincial environmental legislation was evaluated to determine the effectiveness thereof in preventing introductions and controlling introduced species where they have become established. Information was gathered by interviews and by scrutinizing relevant legislative documents. Sufficient legislation occurs at the international level in the form of conventions, treaties, agreements and policies. Legislation at national and provincial level is, however, inadequate. It is clear that, despite strict and specific guiding principles developed at international level, very few signatories to international agreements incorporate their principles into relevant national and provincial legislation. While legislation is not the only solution to the problem, it does set a standard, it indicates the stand taken by the respective authorities, and it gives support to conservationists concerned with nonnative waterbirds.

Key words Legislation, Exotic, Non-native, Waterbirds, Waterfowl, International agreements

1 Introduction

Environmental legislation is promulgated to protect the biodiversity of respective countries. One of the biggest threats to biodiversity is invasive alien species. Furthermore, these species also impose enormous costs on human enterprises such as fisheries and agriculture, as well as on human health. The most cost effective method for controlling invasive alien species is to prevent their introduction outside their natural range of distribution. Legislation is one of the preventive measures that can be used to avoid such introductions. Nonnative waterbirds have been introduced either intentionally or accidentally into many parts of the world. Some of the introductions have created problems, where nonnative birds either compete or hybridize with indigenous species or cause extensive damage to industries such as agriculture. Despite existing legislation, introductions of nonnative waterbirds still occur. This implies that the legislation is inadequate either due to the lack thereof, or because of unsatisfactory enforcement, or both. To investigate the issues, an evaluation of current international, national and South African provincial environmental legislation was undertaken to determine their effectiveness in preventing introductions and controlling introduced species where they have become established.

2 Methodology

The definition of legislation is restrictive and usually

confined to laws, acts and regulations. Initially, only such provisions were reviewed. There are, however, a substantial number of instruments that play an important role in legislation for nonnative waterbirds. To take account of these instruments, the concept of legislation was broadened here to include policies, codes of conduct, guidelines, conventions and protocols. Extensive use was made of the Internet to acquire a large percentage of the information. Interviews, either in person, by telephone or by email, were also carried out with ornithologists and officials implementing legislation in various countries, as well as all nine provinces within South Africa. The British Trust for Ornithology Research Report No. 229 (Blair et al., 2000) was used to improve and corroborate the assimilated information.

3 Results

The documents reviewed were grouped into the following categories: international, national, provincial or state, and municipal or city legislation. Municipal or city legislation is concerned centrally with people living close together, and those sections relating to animals revolve around aspects of health and noise pollution; it was therefore excluded from evaluation.

3.1 International legislation

Forty-five legislative instruments dealing with invasive alien species were found. These included conventions, protocols, codes of conduct and guidelines. Twenty-nine

of the instruments are applicable to waterbirds, the majority of them rather localized. The Convention on the Conservation of European Wildlife and Natural Resources is, for example, applicable only to European countries, while the Agreement for the Preparation of a Tripartite Environmental Management Program for Lake Victoria is between Kenya, Tanzania and Uganda.

There are, however, three instruments that are pertinent on a global scale. They are the Convention on Biological Diversity (Anon., 1992), the Convention on Wetlands of International Importance Especially as Waterfowl Habitat (Anon., 1971) and the Convention on Migratory Species of Wild Animals (Anon., 1979). The number of countries (parties) that have joined these three conventions are 183, 130 and 83 respectively. Parties to these conventions are expected to include the principles and guidelines adopted at the various conferences of the parties (COP) into relevant national legislation.

All three conventions have very clear principles in terms of alien species. Article 8 (h) of the Convention on Biological Diversity requires parties to prevent the introduction of alien species that threaten ecosystems, habitats or species. At the 1999 COP Convention on Wetlands of International Importance, a resolution (Resolution VII.14) was passed on Invasive species and Wetlands. While the entire resolution concerns invasive species, paragraph 16 (b) refers to the role of the Scientific and Technical Review Panel of the Convention in legislation and other management practices. The Convention on Migratory Species of Wild Animals, moreover, has two articles dealing with invasive species: one protecting those species listed on Appendix I (Article III(4)(c)) and the other protecting those species listed on Appendix II (Article V(5)(e)). For convenience, the precise wording of most respective articles is included here in an addendum.

3.2 National legislation

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES — 158 parties) requires parties to the convention to issue import and export permits for species listed in the appendices of the Convention. There are, for example, 30 species of Anatidae listed in the Appendices of the Convention. A number of countries, however, apply this principle to all imports irrespective of whether the species concerned is listed in one of the Appendices or not. It was the one piece of legislation that was shared among a substantial number of countries.

Once a species had entered a country, however, legislation varied from no control to fairly rigorous control. To illustrate this aspect, several examples are given below: (1) Belgian legislation protects its feral populations of introduced species; (2) legislation in Botswana, Zimbabwe and Israel has no provision for control once a species is allowed entry; (3) Namibia allows certain species of anatids into its country but they must be kept in enclosed cages; (4) Slovenia, where a potential threat exists, may allow a spe-

cies into its country but prohibits introduction to the wild; and (5) legislation in the Netherlands makes provision for the identification of exotic species and the control thereof.

3.3 Provincial legislation

Legislation at this level is in much the same predicament as national legislation, or even more so where guidance at national level in policy and legislation is lacking. It was not practical here to evaluate provincial legislation on a global scale, and so practice in South Africa will serve as its exemplar.

At the national level, South Africa currently has very little biodiversity legislation. Prior to 1994 there were four provinces and seven self-governing homelands, each with its own legislation. The homelands were subsequently abolished and South Africa has now been divided into nine provinces. Unfortunately, no revision of provincial legislation has taken place since, and modifications of pre-1994 legislation are used in its stead. It was also found that, despite similarities in legislation, different provinces interpreted different sections differently, which resulted in variations in application. A survey of legislation concerning waterbirds revealed: (1) all provinces require permits to keep indigenous waterbirds, which must be obtained via a legal source; (2) none of the provinces allow the release of exotic waterbirds into the wild; (3) seven of the provinces require no permits to keep exotic waterbirds, although one province did make an exception concerning the mallard (*Anas platyrhynchos*), for which strict captivity conditions were laid down; and (4) five provinces have regulations for waterbirds that concern captivity requirements. These regulations apply to both indigenous and exotic waterbirds in two of the provinces, but only to indigenous waterbirds in the other three.

4 Discussion

Although there is scope for improvement, sufficient legislation exists at the international level to protect native biodiversity from introduced nonnative waterbirds. At the national and provincial level, however, legislation varies between countries and provinces to such a degree that it becomes functionally inadequate. Waterbirds are able to move over long distances. A country with inadequate legislation can therefore affect and threaten biodiversity in neighboring countries, irrespective of whether these countries have adequate legislation or not. Zimbabwe, for example, has reported that the ruddy duck (*Oxyura jamaicensis*), an invasive species with capacity to hybridize (Hughes, 1996), has been introduced into the wild, due to either accidental or deliberate release (Blair et al., 2000). This poses a threat to neighboring countries because Zimbabwe has no legislation concerning introduced nonnative species, nor does it have an action plan for the identification and removal of introduced species. There is a possibility, therefore, that the maccoa duck (*Oxyura maccoa*) of Africa could be facing the same situation as the white-headed duck (*O.*

leucocephala) in Europe.

It is apparent from the wide variation in legislation at both national and provincial levels that a number of countries, although signatories to various international instruments covering introduced nonnative species, have not incorporated the principles, guidelines, and directives of those instruments into their respective legislation. Not only should the secretariats of these instruments persuade negligent governments to ratify the instruments, but the governments of countries need to realize their commitment to international obligations through ratification. Furthermore, in order to gain uniformity in legislation between countries concerning nonnative waterbirds, specific guidelines need to be compiled.

Guidelines in this respect are being drafted and, if suitable, can be adopted by conventions. Aspects that must be addressed in such a document include, *inter alia*, the type of legislation required to prevent and control introductions of nonnative species, conditions and requirements for keeping waterbirds in captivity, schedules of species that have the potential to threaten biodiversity should they escape or be released, schedules of species that can safely be released for hunting purposes, and the methodology for controlling and eradicating invasive species.

Information on waterbirds, specifically the threats that they pose when introduced into areas outside their natural range, is not easily accessible. There are a number of databases that contain information on some species, but none are adequate. A data system needs to be established, in conjunction with existing programs, that will supply such needed information as invasive potential, regions and effects of introduction, and the economies of countries into which waterbirds are introduced.

The discrepancies in implementation of legislation among South African provinces is but one example of how legislation can be interpreted differently. Interpretation of legislation from appropriate policy documents will vastly improve such situations, and will not only make for easy implementation but also help affected stakeholders, such as bird keepers and the hunting lobby, to understand it. It is imperative that information concerning legislation is fed through to the affected parties so that they are aware of the legislation and understand the reasons and necessity for it.

Prevention, of which legislation is but one approach, is the most cost effective method of controlling invasive alien species. The number of introductions of invasive nonnative waterbirds to date would have been curtailed to a large extent had adequate legislation been in place and correctly applied. It is hoped that this review will encourage governments, convention secretariats and other international organizations to seriously examine existing legislation and initiate new collaborations and partnerships.

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Addendum

Relevant sections concerning invasive species in the three conventions referred to in the text

1. Convention on Biological Diversity

Article 8, paragraph (h): “Each Contracting Party shall, as far as possible and as appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species”.

2. Convention on Wetlands of International Importance Especially as Waterfowl Habitat

Resolution VII.14, paragraph 16(b): “The Conference of Contracting Parties DIRECTS the Scientific and Technical Review Panel to consult with relevant parties to prepare, for the benefit of the Contracting Parties, guidance on legislation or other best practice management approaches that incorporate ‘risk assessment’, in order to minimize the introduction of new and environmentally dangerous alien species into a jurisdiction, and the movement or trade of such species within a jurisdiction”.

3. Convention on Migratory Species of Wild Animals (Bonn Convention)

Article III (4)(c): “Parties that are Range States of a migratory species listed in Appendix I shall endeavour to the extent feasible and appropriate, to prevent, reduce or control factors that are endangering or are likely to further endanger the species, including strictly controlling the introduction of, or controlling or eliminating, already introduced exotic species”.

Article V (5)(e): “Where appropriate and feasible, each Agreement should provide for but not be limited to conservation and, where required and feasible, restoration of the habitats of importance in maintaining a favourable conservation status, and protection of such habitats from disturbances, including strict control of the introduction of, or control of already introduced, exotic species detrimental to the migratory”.

Agreements referred to in Article V (5)(e) are instituted to conserve and manage migratory species, which have an unfavourable conservation status. These species are listed under Appendix II of the convention.

Symposium 34 Optimality in bird migration — the role of stopover ecology

Introduction

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Bird migration has many components, and varies among species, populations, age classes and sex. Yet its causes, adaptive significance, and consequences are only now being explored. This has and will only become possible by taking advantage of comparative and integrated studies that combine theory, field observation and laboratory experiment, and link mechanical physics, physiology, ecology and behavior.

Stopovers to refuel are a crucial component because they largely determine the speed and success of migration. When replenishing energy stores at stopover sites, migrants have to forage in unfamiliar habitat with unknown food resources and predation risk in competition with others under unpredictable weather. Furthermore, the flight bout just completed may have affected capabilities entailing behavioral and physiological constraints; and the prospective bout may affect duration and fat accumulation at the site. Although models predict the optimal way in which migrants should fatten up under given selective pressures, there are few empirical studies of this process. So this symposium attempts an overview of current optimality models in avian migration and of recent findings in behavioral and physiological ecology during stopovers.

Anders Hedenström and Thomas Weber address modeling that integrates fuel loading with the mechanics of flight and energy use for determining optimal flight times,

distances and speeds. Volker Dierscke breaks ground by synthesizing a range of intrinsic and extrinsic (environmental) factors affecting departure decisions in small passerines from empirical studies of northern wheatears and other migrants. Nikita Chernetsov and Casimir Bolshakov report the development of small temporary home ranges in some species and individuals at stopovers, but not in others, which has implications for body condition and refueling and affects departure decisions. Michael Schaub completes the symposium by presenting a methodological framework for comparing and rating the importance of extrinsic and intrinsic factors affecting departure decisions from simple capture-recapture data. It is yet another step forward towards understanding stopover ecology and managing migrants at stopover sites. One paper by Frank Moore and colleagues, which addressed mainly the physiological aspects of stopover ecology, was given only as an oral. Its abstract is published in the Abstract volume for the Congress.

More detailed knowledge of variation in migration and its mechanisms and regulatory processes is crucial for understanding the role of migration within the complete life cycle of migrant species, for understanding how natural selection moulds migratory life-histories, and for elucidating the evolution of those life-histories.

S34-1 Current optimality models in avian migration

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Abstract Optimality models of bird migration are reviewed. The principal approach to simple optimality theory is presented, as well as main predictions and tests. We also discuss flight mechanical theory because migration theory builds extensively on such principles. This approach to the study of bird migration has proven very successful, and generated new directions of experimental work.

Key words Time, Fuel loading, Flight mechanics, Stopover decisions, Optimality modeling, Wind effects

1 Introduction

During the last decade, a migration theory has been developed as a theoretical foundation for understanding migration strategies and behaviors (Alerstam and Hedenström, 1998; Houston, 1998). This theory comprises a framework for predicting optimal policies regarding the process of migration, such as the length of stopover, at what fuel load to depart, and the influence of current winds on departure decision. It relies on the range equation, which is derived from the lift:drag ratio, and gives the potential flight range as a function of fuel load. Flight mechanical theory provides a model framework to analyse the forces and power components of birds in flight. Aerodynamic analysis leads to the so-called power curve, which is a relationship between the power required to fly and speed (Pennycuick, 1989). From this relationship it is possible to derive predictions about flight behavior.

A related analysis for gliding flight gives the glide-polar, relating sink rate to forward speed at force equilibrium to provide the input for predictions concerning soaring flight migration (Pennycuick, 1972). From analysis of the effect of winds, as the vector triangle between airspeed, ground speed and wind, predictions about optimal behavior of drift and compensation can be deduced (Alerstam, 1979; Alerstam and Hedenström, 1998). These are the main constituents of what we will loosely define as “optimal migration theory”: theory concerning the process and behavior of migration. Issues regarding the evolution of migration, and partial and differential migration patterns, may also be analysed from a theoretical viewpoint (Alerstam and Hedenström, 1998), but we do not consider such theoretical aspects in this paper. Figure 1 presents an overview of the components of migration theory and their relationships.

2 Fundamental equations

The flight range provided by a certain fuel load can

be derived from the effective lift:drag ratio, the energy density of fuel and the conversion efficiency of fuel (Pennycuick, 1975). The range shows a diminishing return function for added fuel because flight cost increases with body mass including added fuel, assuming that fuel energy density is constant; and flight cost will also increase due to increased pressure drag because fat stored subcutaneously increases the frontal area of the bird. Hence, flight range can be expressed as

$$Y = c \left(1 - \frac{1}{\sqrt{1+f}} \right),$$

where f is the relative fuel load ($f = (m/m_0) - 1$, where m is total body mass and m_0 is lean body mass), and c is a coefficient with distance dimension (Alerstam and Lindström, 1990; Alerstam and Hedenström, 1998). If the frontal area is unaffected by added fuel (an unrealistic assumption), the flight range is

$$Y = \frac{c}{2} \ln(1+f)$$

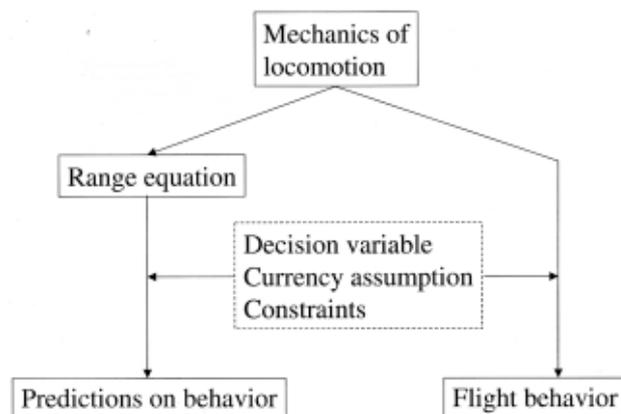


Fig. 1 Overview of bird migration theory and the interrelationship among its components

which is a curve of lesser penalty for carrying extra fuel than the first equation (Weber and Houston, 1997a; Alerstam and Hedenström, 1998). Both equations represent useful approximations of the relationship between range and relative fuel load. If the first range equation is rearranged to express fuel load as a function of potential flight distance f (Y), a useful relationship emerges for calculating the fuel load of a bird arriving overloaded at a new site, that is, a bird that had departed with more fuel than needed to fly the distance. Assuming a constant fuel deposition rate k and a constant energy density of fuel, and substituting kt for f in the range equation, the potential range can be expressed as a function of fuelling time $Y(t)$. Differentiating gives the instantaneous migration speed of the bird as

$$S = \frac{dY}{dt} = \frac{c}{2} k \cdot \frac{1}{(1+f)^{3/2}}$$

This equation gives the marginal rate of gain in flight range for a bird depositing fuel at a rate k , where S declines with increasing fuel reserves.

3 Predictions and tests about migration behavior

The optimal stay at a stopover site raises a fundamental question. Here we assume that the bird is accumulating fuel at a rate k , and that birds experience search/settling time and energy costs when arriving at a new stopover site (Rappole and Warner, 1976). A direct application of the range equation for two alternative fueling rates is shown in Fig. 2. For the two rates shown ($k=0.04, 0.08$) and a search/settling time cost $t_0 = 3$ days and no energy cost ($f_0 = 0$), it appears that the optimal stopover period is $t^* = 13.2$ days for the low fueling rate and $t^* = 9.6$ days and $f^* = 0.77$ for the high fueling rate if both have a fuel load of $f^* = 0.53$ at

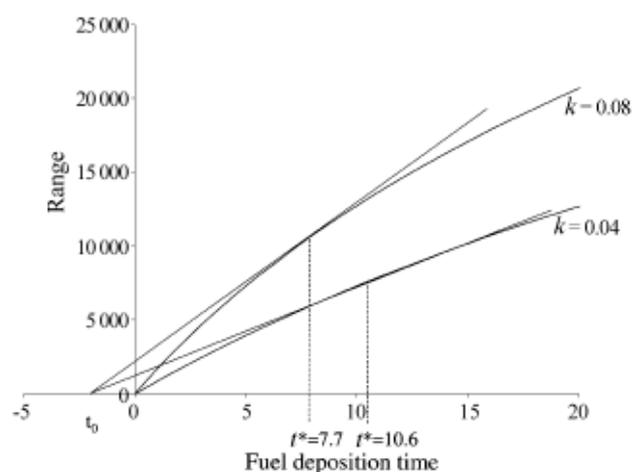


Fig. 2 Flight range as a function of fuelling time (t) at a stopover site

Two range curves representing $k = 0.04$ and $k = 0.08$ are shown, where the fuel load expressed as a proportion of lean body mass is $f = kt$. The optimal departure time for the two illustrated examples and $t_0 = 2$ days are: $t^* = 7.7$ days at $f^* = 0.62$ and $t^* = 10.6$ days at $f^* = 0.42$.

departure. Hence, with a high fuel deposition rate the bird should leave the stopover site with a higher fuel load than at low fuel deposition rates, but the fuelling time will be shorter at high deposition rates. The baseline model assumes an infinite total migration distance, whereas if migration is modelled as finite, the optimal departure load in relation to fuel deposition rate will increase in a stepwise manner, not as a continuous curve (Weber and Houston, 1997b). Hence, there will be windows where no change can be expected in departure fuel load across an interval of fuel deposition rates.

These general predictions have been tested several times by providing birds with food at artificial stopover sites, where mass gain and departure timing are monitored using color marked individuals and a remote-controlled balance. A few studies have reported data in qualitative, but not quantitative, agreement with the prediction (Lindström and Alerstam, 1992; Fransson, 1998), while similar experiments found no relationship between fuelling rate and fuel load at departure from the stopover (Dänhardt and Lindström, 2001). A number of possible explanations have been suggested for the mismatch between prediction and experimental data: (1) individual variation in expected migration speed (Lindström and Alerstam, 1992); (2) lack of response within intervals of fuel deposition rates, according to the step model of Weber and Houston (1997b); (3) birds may individually update expected migration speeds according to conditions experienced at the current site (Weber et al., 1999), (4) increased fuel loads that affect metabolic costs and reduce effective fuel deposition rate (Klaassen and Lindström, 1996); (5) applicable currencies other than time minimization, such as minimizing the total energy cost of migration (Hedenström and Alerstam, 1997); (6) variation in the expected speed of migration along the route (Lindström and Alerstam, 1992).

If birds use discrete stopover sites along their flyway, then one can predict scenarios for overloading and bypassing, depending on the relative quality of the stopover sites (Gudmundsson et al., 1991). If birds minimize the transport energy cost, they should stop at all useful sites along the route in order to carry the smallest possible fuel loads. On the other hand, skipping certain sites and overloads may become optimal for minimizing time. These predictions are derived from the third equation above. The predictions have not been tested experimentally, but observations of site use and nonzero fuel loads in birds arriving at stopovers are consistent with the predictions. Conditions and patterns of overloads and bypasses have been investigated theoretically by Weber et al. (1994), Weber and Houston (1997a) and Weber et al. (1998a, b).

More recently, Alerstam (2001) investigated optimal detours in birds using flapping flight. Since it is cheaper to fly with low fuel loads, it may be optimal to fly along a detour allowing frequent stops for refueling, rather than flying across an ecological barrier with a large fuel load at departure. Alerstam (2001) derived predictions for break-

even detours in birds, and provided numerous examples of birds taking a detour predicted by theory.

When accumulating fat before migratory flights, birds also seem to accumulate protein, mainly as increased flight muscle mass (Lindström et al., 2000). Weber and Hedenström (2000) derived predictions regarding the conditions when such physiological flexibility could be expected.

4 Flight behavior

The mechanical properties of flight have been modeled by various approaches, ranging from direct estimation of the forces acting on the flapping wing to characterization of the vortex wake (a bird's aerodynamic footprint) of the flying bird (Hedenström, 2002). In a popular approach, Pennycuick (1989) used an actuator disc, in which the bird is replaced by a circular disc of diameter equal to the wingspan. The oncoming airflow is considered as a circular tube, which is deflected downwards by the actuator disc and obtains an induced velocity. The induced power (P_{ind}) is inversely proportional to flight speed (U) and wing span (b). Another important power component arises from the pressure drag of the bird's body, usually called the parasite drag because it is not involved in generating any lift. Parasite power is proportional to U^3 and body frontal area and shape. There is as well a profile drag on the wings that has been shown to vary relatively little in the normal range of flight speeds, and is therefore usually considered as constant in that speed range. By adding together the three main power components of bird flight we get the power curve

$$P = \alpha + \beta \cdot U^{-1} + \gamma \cdot U^3,$$

where α , β , and γ are parameters that include bird morphology, body mass and certain physical constants. The power curve is illustrated in Fig. 3, where the characteristic U-shape is shown, and which immediately suggests several optimal flight speeds. First, from $dP/dU=0$ we get the minimum power speed which is associated with the cheapest flight cost per unit time. This is the best flight speed if flight duration is the main concern, irrespective of distance covered. Secondly, from $dP/dU=P/U$ we get the maximum range speed, which is associated with the minimum cost of transport. This is the best speed if energy expenditure per unit distance moved is important. Further optimal flight speeds can be derived from different currency assumptions (Hedenström and Alerstam, 1995).

5 Predictions and tests of flight behavior

It might be thought that the most straightforward approach here is to measure power output for a bird over a range of flight speeds by analyses of flight mechanics. Indeed, this has been tried several few times, but mainly by measuring the metabolic rate of flying birds (Butler and Bishop, 2000), which includes also the overall heat production by the bird. Thus changes in mechanical power output

may be masked. A few such studies do show a U-shaped relationship between metabolic rate and forward speed, while others show it as surprisingly flat. Direct measurement of mechanical power output has proven quite difficult to accomplish, but some recent technological advancements have made this possible (Dial et al., 1997; Pennycuick et al., 2000). Even though theory and experiments disagree in these studies, further experimentation is required for a critical evaluation of flight mechanics theory.

An alternative approach is to test the validity of predictions derived from the power curve. Depending on ecological context, we can expect birds to select one or other of the optimal flight speeds derived above. Skylarks (*Alauda arvensis*) seem to fly near their U_{mp} during song display while on migration their speed is $\geq U_{mr}$ (Hedenström and Alerstam, 1996). Such tests provide at best an indirect test of flight mechanics theory.

The power curve can also be used to derive predictions about flight speed adjustment in relation to head and tail winds. With a tail wind increment, a bird should reduce its flight speed from that in still air (Fig. 3), while in head winds it should increase it to remain at the optimal U_{mr} . That migrating birds actually do adjust their airspeed in relation to winds, as predicted, has been shown several times (Hedenström et al., 2002). Flight speed should also change with altitude because air density changes with altitude, a behavior also supported by recent radar tracking of migrating birds in the high Arctic (Hedenström et al., 2002). For a summary of different predictions about flight behavior on the basis of flight mechanics, see Hedenström (2003).

6 Prospects

The development of optimal bird migration theory over the last decade has been catalytic for bird migration research. Even if aspects of the theory are found to be wrong, it will have still served its purpose of pointing out

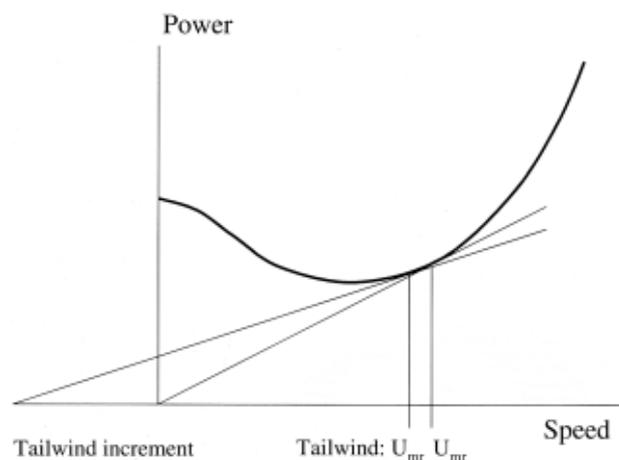


Fig. 3 Power in relation to forward air speed

This is a graphical representation of the last equation. How the optimal speed, U_{mr} , is affected by a tail wind increment is also shown.

what critical studies and experiments are needed. Studies on flight mechanics and the physiology of bird flight have also entered a new era with the deployment of modern low-turbulence wind tunnels (Pennycuik et al., 1997). New techniques for measuring the mechanical power output from birds, in particular, will be invaluable for evaluating flight mechanics theory.

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S34-3 Factors determining stopover decisions in migrating passerines on an offshore island

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Abstract Factors influencing decisions in small migrating passerines to stopover on small islands or press on were investigated in a five-year study on Helgoland Island in the North Sea, using the northern wheatear as the focal species. Assessment of foraging opportunities focused on rate of prey intake and the related effort of finding food. Northern wheatears prolonged their stopovers and defended territories whenever rich food patches occurred. The density of passerines also affected departures due to crowding and interference. Raptors, as a measure of predation, played little part in departure decisions, but cloud cover and head winds seemed to hold up departures, particularly in Greenlandic wheatears in spring before their sea crossing to breeding grounds. Body condition was not a factor in forcing birds to land on Helgoland, judged by its uniformity in early departing and resting birds. Because the number of migrants passing over Helgoland annually is unknown, it is difficult to assess its importance as a stopover. Stopovers seem to occur randomly, but in favorable conditions, migrants will take the opportunity to refuel.

Key words Stopover ecology, Departure decision, Foraging opportunity, Climatic factors, Crowding, Northern wheatear

1 Introduction

The migration of birds between breeding and wintering areas is generally controlled endogenously (Berthold, 1996). Many environmental factors, however, modify the behavior of birds during migration, particularly weather (Richardson, 1990) and the quality of stopover sites for refueling in transit (Rabøl and Hansen, 1978; Bibby and Green, 1981). Because most time and energy is spent at stopover sites during migration (Hedenström and Alerstam, 1997), such sites play a major role in successful migration. For birds, the choice of whether to use a stopover site or not involves balancing refueling conditions, flight conditions and body condition (Jenni and Schaub, 2003). After landing in any environment, a bird has to check quickly whether the site is suitable for a stopover and to decide between staying or moving on. Such decisions are best observed on small, isolated stopover sites where it is easy to separate those that stay and those that move on. That is why I chose the small offshore island of Helgoland in the North Sea to determine factors influencing stopover decisions in migrating passerines. The results are summarized here.

2 Methods

The island of Helgoland (1.5 km²) is situated 50 km off the German North Sea coast (54°11' N, 07°55' E). For more than 90 years, migrating birds have been trapped regularly there during stopovers by a daily trapping routine of seven rounds using three large funnel traps (for details, see Moritz,

1982). In a field study from 1998 to 2002, northern wheatears (*Oenanthe oenanthe*) were trapped with spring traps outside the funnel-trap site and marked with individual combinations of color-rings (Delingat and Dierschke, 2000). All birds trapped or re-trapped during spring and autumn migration were measured and weighed (Dierschke and Bindrich, 2001); visual fat stores were scored according to a nine-class scale (Kaiser, 1993). Birds were treated as staying on the island if recaptured or resighted on days following the day of ringing, but were considered to have departed if not recaptured or resighted after the day of arrival. Strong fluctuations in the daily number of birds present (Delingat and Dierschke, 2000) suggest that most birds were trapped on their day of arrival. The very low rate of recaptures elsewhere on the island (< 1% away from the funnel traps, Dierschke and Bindrich, 2001), and the high search effort for color-ringed wheatears, make these estimates of length of stay highly reliable.

3 Results

3.1 Body condition

On both spring and autumn migration, passerines generally cross the southeastern North Sea with low or intermediate fat stores; high fuel loads are rarely observed in trapped birds (Dierschke and Bindrich, 2001). In the funnel traps, recapture rates are much higher for lean birds (fat scores 0–1) than for birds with larger amounts of visible fat stores (Fig. 1). Therefore, the degree of fuel store depletion is a considerable factor in the decision to skip or stopover.

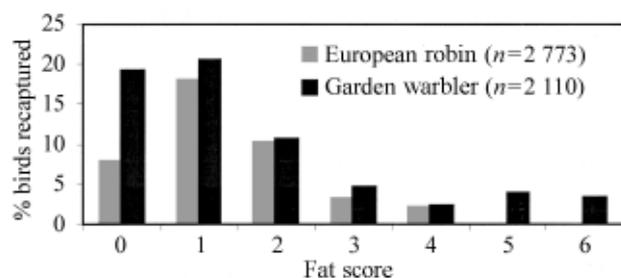


Fig. 1 Proportion of birds recaptured in relation to visible fat stores at initial capture during autumn migration (1996–2001)

Note that fat scores 5 and 6 were not found in European robins.

3.2 Season

Northern wheatears of the nominate subspecies which breeds in Scandinavia showed a much higher tendency to stay on Helgoland during the first part of spring migration (20%–80% of individuals staying in early and mid April) compared to the period from late April to late May (0%–10% of individuals staying) (Dierschke and Delingat, 2001). Comparison with other migratory passerines is needed to determine whether this is a general pattern for passerine spring migration.

3.3 Foraging conditions

A fundamental component of foraging conditions is the availability of food. Its presence or absence should thus have an impact on stopover decisions. During post-breeding migration, many European passerines are frugivorous, and berries of Black Elder *Sambucus nigra* have been found to be a very profitable food source for them (Simons and Bairlein, 1990). On Helgoland, large quantities of elder berries become available from early September onwards, but are nearly completely depleted by birds by mid October. In two highly frugivorous species, the garden warbler (*Sylvia borin*) and the blackcap (*Sylvia atricapilla*), recapture rates in funnel traps are much higher during periods of high avail-

ability of berries (Table 1). The importance of food supply in the stopover decision is further illustrated by those northern wheatears that visited grassland habitats poor in invertebrate food, to linger there for a much shorter time than conspecifics in food-rich wrack beds on the beach (Delingat and Dierschke, 2000). In a field experiment, a much higher proportion of northern wheatears stayed on in the poor grassland when they were offered mealworms ad libitum (Table 2).

The effects of foraging conditions are not only explained by food availability, but also by competition for food among the birds stopping over. It was expected that at least interference competition would act when high bird densities occurred. For funnel trapping, no absolute values of bird density are available; instead, the number of birds trapped per day was used as an estimate. For a number of species, the proportion of birds recaptured on days after ringing decreased with increasing bird density, most clearly so in pied flycatchers (*Ficedula hypoleuca*) which are territorial during migration (Table 3). This is consistent with observations during big fallouts, when most of the thousands of grounded birds leave by morning (Dierschke and Bindrich, 2001). In such circumstances, it appears that the food supply for frugivorous birds is not sufficient to allow refueling for all birds present at one time; the number of birds exceeds the carrying capacity of the island. In the color-ringing study with northern wheatears, high bird density and concomitant interference competition was also identified as a factor leading to early departures (Dierschke and Delingat, 2001).

3.4 Predation risk

Predation risk was quantified as the number of sparrowhawks (*Accipiter nisus*) and various falcons (*Falco* spp.) flying over the study site per hour. In both spring and autumn migration, the rates of raptor flights did not differ for northern wheatears on or leaving on the day of arrival

Table 1 Effect of high and low availability of elder berries

	No/few elder berries available		Copious elder berries available		χ^2	<i>P</i>
	<i>n</i>	Recapture rate	<i>n</i>	Recapture rate		
Garden warbler, <i>Sylvia borin</i>	732	6.3%	878	14.9%	31.6	<0.001
Blackcap, <i>Sylvia atricapilla</i>	483	0.8%	2226	9.0%	38.3	<0.001

Proportion of birds recaptured after 1 day during periods of high availability (1 September to 10 October) and low availability (1–31 August, garden warbler; 11 October to 30 November, blackcap).

Table 2 Proportion of color-ringed northern wheatears resighted in grassland habitat with and without additional food

	No additional food		Mealworms ad libitum		χ^2	<i>P</i>
	<i>n</i>	Resighting rate	<i>n</i>	Resighting rate		
Spring migration	174	11.5%	226	33.2%	25.5	<0.001
Autumn migration	170	5.9%	178	32.0%	38.2	<0.001

Table 3 Proportion of birds recaptured during autumn migration (1990–2000) in relation to bird density

Bird density (number of birds trapped)	Garden warbler, <i>Sylvia borin</i>		Pied flycatcher, <i>Ficedula hypoleuca</i>	
	<i>n</i>	Recapture rate	<i>n</i>	Recapture rate
1–10	1 247	11.4%	771	10.0%
11–20	658	8.8%	173	4.0%
21–30	365	9.6%	70	2.9%
31–50	189	4.2%	129	0.0%
>50	242	2.1%		

Proportion expressed as the number of conspecifics trapped on the day of ringing

(Dierschke and Delingat, 2001). Because freezing in response to raptors lasted up to 30 minutes, however, there may be an indirect effect through reduced foraging time and thus lower fuel deposition rate.

3.5 Weather

Apart from stopover site characteristics, the decision to take off on migratory flight is influenced by weather: strong headwinds or drift will increase fuel consumption and overcast conditions can compromise orientation. During spring migration, wheatears tended to stay when cloud cover was high (Dierschke and Delingat, 2001). Whereas nominate birds breeding in Scandinavia with a short flight to the next stopover left regardless of weather conditions, those of the subspecies *O. o. leucorhoa*, which breed in Iceland and Greenland and face a long nonstop flight, stayed on much longer when wind and overcast combined in adverse conditions (Dierschke and Delingat, 2001). Nevertheless, much more information is needed to understand the effect of weather on patterns of landing and departure.

3.6 Migration route

Migration route may be involved too in the decision-making of migrating birds. In order to combine the effects of the factors analyzed above, logistic regressions were calculated using the observed departure decision of color-ringed northern wheatears as the dependent variable (0 = staying, 1 = departing). The regressions were calculated separately for groups of birds facing a long-flight (*O. o. leucorhoa* in spring) and those facing a short flight (*O. o. oenanthe* in spring, all birds in autumn). For both groups, data are available for unmanipulated situations as well as for experiments with food offered ad libitum. The factors involved affected the two groups significantly. Whereas birds facing long flights focused on site use with respect to factors reflecting foraging conditions and weather, those facing short flights were more diverse in their decision making. In contrast to the first group, moreover, the second factored in body condition and, in spring, the time of the season, early or late (Table 4). The significance of predation

risk for Greenlandic/Icelandic spring migrants was probably related to weather conditions, which favored migration (and thus departures) in both wheatears and raptors (Dierschke and Delingat, 2001).

4 Discussion

The results of field studies and field experiments on the offshore island Helgoland demonstrate that a number of factors play a role in the stopover decisions of migrating passerines. So far, only single factors have been shown to be important in experiments: food supply for refueling (Gwinner et al., 1985), overcast as a factor influencing orientation (Åkesson and Bäckman, 1999), tail wind for helping migratory flight (Åkesson and Hedenström, 2000), and fuel loads as crucial energy stores for the crossing of ecological barriers (Biebach, 1985; Sandberg et al., 1991). Predation risk has also been shown to influence departures (Fransson and Weber, 1997), but seemed to be negligible for northern wheatears on Helgoland, both in field studies (Dierschke and Delingat 2001, this study) and in an indoor experiment (V.D. and A. Walter, unpubl.). Beyond these factors, a seasonal component, reflected in early spring migrants staying on, and, more importantly, foraging and thus refueling conditions, was also found to be incorporated into decision-making.

Given appropriate body condition, opportunity for refueling as a combination of food supply and competition seems to be the most important factor in the stopover decision for migrating passerines. This fits well with a strategy of time-minimization which incorporates departure from a stopover site if the fuel deposition rate is equivalent to an instantaneous speed of migration below the expected average (Alerstam and Lindström, 1990). Accordingly, factors decreasing the fuel deposition rate directly (low food supply, high density of competitors) were found to promote early departures in this study. However, the indirect impacts of weather (Schaub and Jenni, 2001), and predation risk which hindered foraging, were not investigated or did not prove to be significant, respectively. The minor influence of predation risk on departure decision and the emphasis on refueling is in accord with other studies (Metcalf and Furness, 1984; Moore, 1994). Despite the underlying significance of refueling factors, flight and orientation conditions affected by local weather can dictate decisions, even preventing departures. This was especially the case for wheatears facing a long flight from Helgoland.

The importance of refueling conditions writ small in Helgoland may be writ big on large continental landscapes. Fragmentation of habitats suitable for stopovers will lead to a higher concentration of birds at local sites and thus to increased competition for and exploitation of resources (Moore and Yong, 1991; Ottich and Dierschke, in prep.). High concentrations of passerines on Helgoland created an imbalance between food supply and energy demand, with carrying capacity overloaded more than four-fold (Ottich and Dierschke, in prep.). Because habitat availabil-

Table 4 Results of logistic regressions using departure or stay in color-ringed northern wheatears as the dependent variable and physiological and environmental factors as independent variables

Flight faced	Long-distance flight			Short-distance flight		
	Spring	Spring	Spring	Spring	Autumn	Autumn
Subspecies	<i>leucorhoa</i>	<i>leucorhoa</i>	<i>oenanthe</i>	<i>oenanthe</i>	both	both
	field obs.	experiment	field obs.	experiment	field obs.	experiment
Season						
five-day period	no	no	yes	no	no	no
Body condition						
fat score	no	no	yes	yes	no	
body mass/fuel load	no	no	no	no	no	yes
Foraging conditions						
rate of successful pecks					yes	
fuel deposition rate						no
total number wheatears	yes	no	no	no	no	no
aggression rate					no	
Predation risk						
rate of raptor flights		no	no		no	no
total number raptors	yes		no			
Weather						
cloud cover	no	no	no	no	no	yes
wind velocity	no	yes	no	no	no	no
tail wind component	yes	no	no	no	yes	no

“Yes” or “no” indicate variables that are significant or not. Results are split into birds facing long-distance flights in spring (*O. o. leucorhoa*) and those facing short-distance flights in spring and autumn (*O. o. oenanthe* in spring, both subspecies in autumn) from Helgoland. “Field obs.” refers to unmanipulated conditions, and “experiment” to birds offered food ad libitum.

ity on a landscape-scale is a central issue in conservation (Simons et al., 2000), understanding of processes at stopover sites becomes important, despite high flexibility in habitat use by passerine migrants (Bairlein, 1981).

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S34-4 Spatial behavior of some nocturnal passerine migrants during stopovers

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Abstract Capture-recapture analysis of the pattern of movements of some passerine migrants during stopovers suggest that some species, such as European robins and winter wrens, establish small home ranges which could potentially be defended as territories, whereas others, such as the European reed warbler, sedge warbler and blackcap, move rather broadly across the stopover site. Telemetric study of stopover behavior in European robins during spring migration confirms that these birds hold very small home ranges once they establish themselves at a stopover site. Before that, they move broadly about for some time (up to two days) which is probably the search/settling time of optimal migration models. The small home ranges are, however, not exclusive territories as conspecifics are tolerated even in core areas. The potential reasons underlying the different spatial behaviors of nocturnal passerine migrants during stopovers are discussed.

Key words Stopover, Spatial behavior, Home range, Fuel deposition

1 Introduction

Spatial behavior is an important aspect of stopover ecology in migrants. Some passerines, such as pied flycatchers (*Ficedula hypoleuca*), European reed warblers (*Acrocephalus scirpaceus*), rufous hummingbirds (*Selasphorus rufus*) and grey-streaked flycatchers (*Muscicapa griseisticta*) (pers. obs.) are known to occupy temporary territories during stopovers (Bibby and Green, 1980, 1981; Kodric-Brown and Brown, 1978; pers. obs). So, in some cases, do northern wheatears (*Oenanthe oenanthe*) as well (Delingat and Dierschke, 2000). Other migrants, obviously, move broadly across a stopover site, or share it with others as reported for the sedge warbler (*Acrocephalus schoenobaenus*) (Bibby and Green, 1981).

The aim of our study was to compare patterns of spatial use in several nocturnal passerine migrants, and their variation during the stopover. In one species, the European robin (*Erithacus rubecula*), we were able to use telemetric data to test conclusions derived from analysis of captures and recaptures. We also attempted to discover the reasons underlying the different patterns found in different species.

2 Materials and methods

We analyzed data from a standardized banding project run at Rybachy, Courish Spit, Russia (55°09'N, 20°52'E) in 1994–2000. A total of 73 mist-nets were used. At each (re) capture, the number of the mist-net where the bird was caught was recorded. This enabled the creation of a frequency distribution of distances between capture localities for each individual bird. Its purpose was to test whether multiple captures of the same individual occurred indepen-

dently of one another. To do this, a simulation model was built which assumed that captures are independent of each other, and from it the frequency distribution of distances between capture points was calculated. The resulting distribution was then compared with the distribution of recaptures of real birds. Were the two distributions to show no significant difference, there is no reason then for interpreting the pattern of real recorded movements as nonrandom.

If, however, recaptures occur significantly closer to a site of previous capture than predicted by the neutral model, then there is evidence that birds retrapped had kept to a limited home range that was smaller than the whole trapping area. If recaptures occur farther away than predicted, there is also evidence of avoidance of the site of previous capture. To run the simulations, the real net numbers were replaced by numbers generated by a random numbers generator. The probability of “capture” in a certain virtual net was related to the capture probability in the real net with this number, i.e. species-specific habitat selection was taken into account (model 2 from Titov, 1999a).

In a telemetric study, we followed the movements of European robins stoppingover at the same site during April 2002. We used LB-2 transmitters produced by Holohil Systems Ltd. The transmitters were fitted on the back of the robins by Rappole harness; their weight with harness was 0.7 g. Battery life was 10 days or slightly more. The birds were tracked by hand-operated receivers with Yagi antennae. We tried to obtain a location from each bird once per hour during the whole period between the onset of activity at dawn until the end of activity in dusk. The locations were plotted on a digitized map of the study area. We tagged the birds soon after their presumed arrival, judged by arrival

waves. Migratory waves are very pronounced on the Baltic coast in spring and sometimes in fall, and seniority analysis showed that on the first day of a wave of arrivals, the probability that newly banded European robins had been present undetected at the site is low (Chernetsov and Titov, 2000).

3 Results

For European robins in autumn, distribution of distances between capture localities did not differ between the simulation model ($n = 7\ 064$) and actual recaptures within the first two days of initial capture ($n = 7\ 064$) (Fig. 1; Wilcoxon matched pairs test, $z = 0.63$, $P = 0.53$). However, in birds recaptured on the third and later days after first capture ($n = 4\ 082$), the recaptures were strongly biased towards shorter distances, significantly different from the simulation model (Fig. 1; Wilcoxon matched pairs test, $z = 2.72$, $P < 0.01$). This means that during the first two days, the movements of European robins across our study area were not significantly different from random, but that those that remained for longer became confined to a much smaller area.

A similar pattern was found in winter wrens (*Troglodytes troglodytes*), but they did not keep to a confined area until the fourth day after the initial capture (Titov, 1999b). The situation in European reed and sedge warblers and in blackcaps (*Sylvia atricapilla*) was different: even when they kept to an area smaller than the whole stopover site, its size was too large for it to be exclusive (Chernetsov and Titov, 2001; Chernetsov, 2002). The same area was shared by several individuals, such that territoriality was out of the question.

The results of radio tracking the robins during spring

stopovers were in line with the capture-recapture results in autumn. Of the 22 individuals tracked just after arrival, seven did not remain in a small home range but moved on. Their stopover duration varied from less than one day to two days, on average: 1.4 ± 0.6 (mean \pm SD). Two birds of this group left the site by slow daytime movements through scrub, one after a stopover of less than one day, and the other after 1.5 days. The other five robins departed by nocturnal flight during the first or the second night after arrival.

Eleven individuals remained, each within a small home range usually up to 40–50 m in diameter, but as small as 10 m in diameter; one had initially been a floater but it subsequently occupied a small range. Stopover duration of home range owners varied between 2 and 12 days, averaging 6.9 ± 3.6 days. The difference in stopover duration between floaters and home range owners was statistically significant (Mann-Whitney test, $z = 3.2$, $P < 0.002$). Ten individuals with a small home range took off at night, but one bird departed at dawn. Departure at dawn was recorded again in a bird of an uncertain territorial status. This mode of migratory departure has not been reported before for the European robin, even though “special morning flights” are known for other nocturnal passerine migrants (Gauthreaux, 1978; Bingman, 1980; Moore, 1987). Three individuals were tracked for too short a time to determine their territorial status; and one bird with a small home range was probably a local individual, not a migrant.

As shown by the spring telemetric data, home ranges of residents were not defended as territories. We have frequently observed untagged conspecifics (intruders) in the core areas of known home ranges of marked birds. No at-

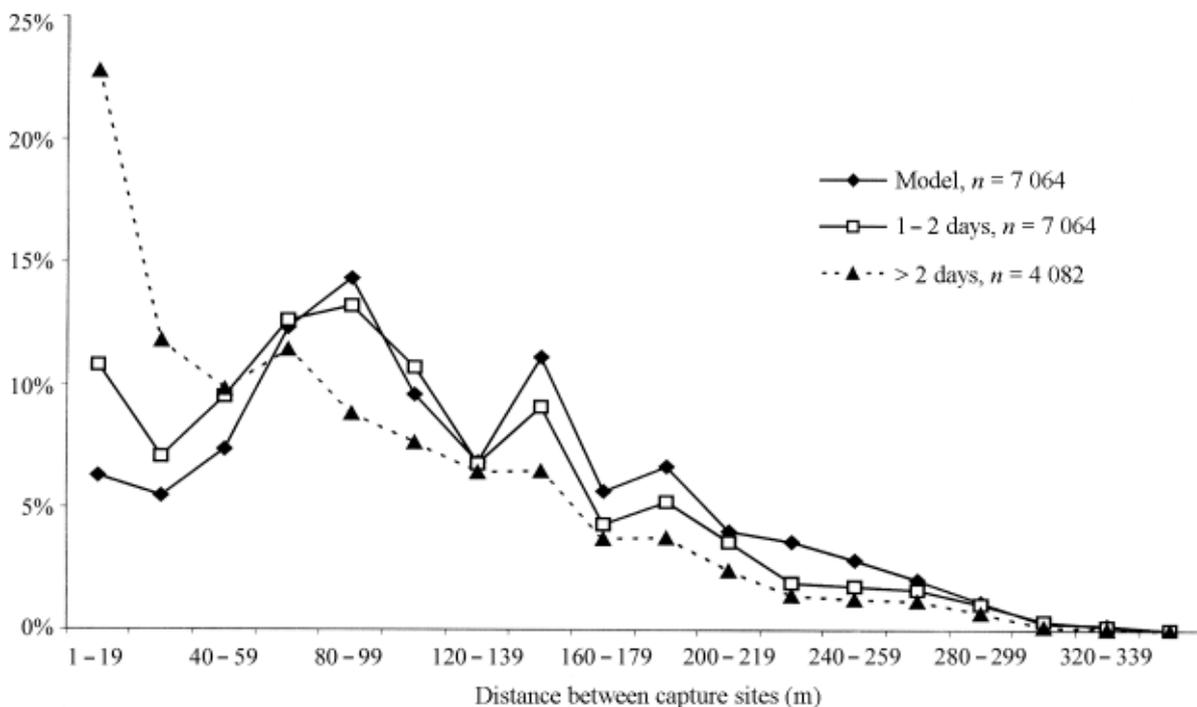


Fig. 1 Distribution of distances moved between capture localities by European robins retrapped within 1–2 days of initial capture, and more than two days after

tempts to evict the intruders were recorded. When the density of European robins at the stopover site was high, moreover, no territorial behavior was involved.

4 Discussion

The analysis of recaptures in fall suggested, and the telemetric data from spring confirmed, that European robins need some time to establish themselves at novel stopover sites. The period between actual arrival and gaining a small home range — not a defended territory, *pace* Titov (1999a) — may be between several hours and two days. Individuals which fail to gain a small home area — or decide not to — leave the area, either by nocturnal flights or by daytime movements through vegetation. The scale of these diurnal movements is difficult to estimate. Telemetric data suggest that they may cover at least 1.0–1.5 km; they are certainly less than 11 km, the distance to the next permanent trapping site. Many thousands of European robins have been captured at the second site during both spring and fall migrations, but no exchange with the first site has been recorded in 10 years of parallel work. The diurnal movements are not necessarily oriented in the migratory direction and are probably related to habitat selection and foraging optimization; their scale probably does not exceed several kilometers.

It has been shown that in autumn, European robins gain mass at stopover sites when they have a small home range, at least those that arrive with depleted fuel stores and need to refuel (Titov, 1999b). It is most likely that the period needed for gaining a small home range represents the search/settling time of optimal migration models (Weber and Houston, 1997; Houston, 1998). Search/settling time is an important parameter in the models which assume stochastic variation in fuel deposition rate at stopover sites (Chernetsov et al., in prep.). Thus the empirical data obtained in this study are particularly valuable. Time costs of settling may be the cause of the low initial refueling rate, but the latter was not demonstrated directly in our study (cf. Schilch and Jenni, 2001). Our data suggest that in European robins, the search/settling costs are due at least partly to behavioral and ecological factors, even though physiological factors cannot be ruled out.

Our data suggest that different species of nocturnal passerine migrants show varying spatial behavior at stopovers. The pattern of spatial distribution of migrants may be related to the distribution of preferred food (Chernetsov and Titov, 2001; Chernetsov, 2002). Birds that utilize more or less evenly distributed resources occupy restricted home ranges, whereas those that forage on superabundant but unpredictable prey move broadly. It remains unclear whether migrants which have large and broadly overlapping home ranges, such as the warblers, need some time to establish themselves at a new site, as

European robins or winter wrens do. Knowledge of this aspect could provide clues as to whether it indeed represents the time costs of settling, or is used rather to estimate refueling potential at the site, i.e. site quality.

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S34-5 How to study departure decisions of migrants from stopover sites using capture-recapture data

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Abstract Environmental factors (weather conditions, predation risk, competition) as well as intrinsic factors (innate rhythm, fuel deposition rate, body mass) have been shown to be taken into account by birds when they decide to depart from a stopover site on the next flight bout. Only a few empirical studies, however, have evaluated more than one of these factors simultaneously. The relative importance of these factors, as well as possible interactions among them, are therefore largely unknown. The reason for this is the difficulty of observing birds and knowing their condition at departure. Here I present a methodological framework for circumventing these problems when capture-recapture data are available from a stopover site. It shows how multi-state capture-recapture models can be used to test which factors are the most important for departure decisions.

Key words Migration, Stopover, Departure, Capture-recapture, Statistics

1 Introduction

Migrating birds usually divide their journeys into several flight steps with intermittent stopovers. At stopover sites, fuel for flight is accumulated and during flight it is used up. During their journeys, migrants are faced with two main challenges that determine the spatiotemporal pattern, and hence the overall success, of their migrations. The first is when the bird should end the stopover period (departure decision), and the second is when and where the bird should end the flight bout (landing decision). The focus of this paper is on the departure decision.

The decision to depart from a stopover site on the next flight bout may be governed by environmental factors (weather conditions, competition, predation risk) and by intrinsic factors (fuel accumulated, fuel deposition rate, time program). Theory-based predictions about how birds should react to variation in each of these factors already exist (Liechti and Bruderer, 1998; Weber, 1999). Moreover, their effects on departure decision have been studied empirically by a number of workers. Jenni and Schaub (2002) recently reviewed results of empirical studies. The main conclusions were that departure readiness was higher on days/nights when weather was favorable, when food was scarce and hence fuel deposition rate low or negative, and when the risk of predator attack was high. The influence of actual fuel stores was not always clear: some studies found that birds with low fuel stores stayed longer at the stopover site and others did not. To my knowledge, no empirical study that relates departure decision to competition has yet been carried out.

Such results came from studies that used different methods (laboratory or field experiments, observational field

studies), and which were sometimes conducted at special stopover sites such as oases. They are therefore difficult to compare, and cannot be extrapolated readily to situations at more typical stopover locations. Some conclusions were even based on the restrictive assumption that birds departed immediately after the last observation.

What is needed for the next step are studies that overcome these shortcomings, and which use the same methods to investigate several factors affecting departure decision in order to rank their importance. My main objective here is to offer methodological solutions for achieving this goal using capture-recapture data obtained in the field. I will not discuss experiments and telemetry studies. It is assumed that the reader has some basic knowledge about open population capture-recapture statistical methods (Lebreton et al., 1992; Cooch and White, 2001).

2 Capture-recapture and departure decision

Standardized ringing (Bairlein, 1995) is a common method for gathering data to study various aspects of stopover ecology (Kaiser, 1996; Schaub and Jenni, 2000, 2001). Each time a bird is captured, its condition (body mass, fat score) is recorded and it is ringed or its ring number noted. Such data can be stored in an $n \times m$ matrix of individual capture histories, where m is the number of capture days and n is the number of birds caught. An element $I_{n,m}$ of the matrix is either 0 if the n th bird was not caught at the m th day, and 1 if it was caught. Additional information about the condition of the bird at the capture event may be stored as well. These capture histories contain information about the times when the birds leave stopover sites, even though

departure may not have been observed directly.

A typical capture history is $\{1\ 0\ 1\ 1\ 0\}$: the bird was caught on days 1, 3 and 4, and not on days 2 and 5. Traditionally, this would infer that the bird left the site on the night between day 4 and 5. However, the bird was not caught at day 2 even though it was there. Recapture probability thus was not 1, and the bird may well have been still present at day 5 but was not detected. What is needed from such data is a method that estimates recapture probability and the probability that the bird remained at the site for one more unit of time. The Cormack-Jolly-Seber model (Lebreton et al., 1992), originally developed to estimate survival rates, is such a method. If it is assumed that mortality during stopover is negligible, estimated local survival probability (ϕ) is the probability of remaining at the site. The complement to one is the probability that the bird has left the site (emigration probability, $\varepsilon = 1 - \phi$). Emigration probability is thus the focus parameter for investigating the departure decision.

Estimated emigration probability is the probability that the bird has left the area covered by the trapping program. It does not necessarily mean that the bird has actually begun its next flight — the bird may just have moved to an adjacent area. The position and number of traps (mist-nets) within the stopover site should be optimized such that birds remaining at the stopover site are readily detected (Chernetsov and Titov, 2000). Additional information on the movement of the birds that stop over (Titov, 1999) helps with the design and the interpretation of the results. The violation of the assumption that there is no mortality during stopover is not a serious problem because daily mortality probabilities are usually an order of magnitude lower than daily emigration probabilities. Other assumptions that apply to these methods are the same as those for the ordinary capture-recapture statistical methods, and some of them can be tested statistically (Lebreton et al., 1992). All models that I will describe can be fitted with program MARK (White and Burnham, 1999) that is freely available at www.phidot.org/software/mark.

3 How to study single factors

3.1 Environmental factors

If weather conditions, predation risk and competition are taken into account by departing birds, they can be expected to affect the departure decision in all individuals in the same way. Temporal variation of emigration probability then becomes the focus. Whether this variation can be explained by temporal variation in the environmental factor requires evaluation. Different models have to be fitted in which emigration probability is either a function of the environmental factor (ε_{env} ; i.e., ultrastructural model, Lebreton et al., 1992) and varies independently of it (ε : emigration probability is different each day), or is constant over time (ε). Each of these models represents a working hypothesis, and information-theoretic approaches can be used to rank them according to their support in the data (Burnham and

Anderson, 1998).

Environmental factors can be categorical or continuous. Examples are daily measures of wind speed, cloud cover, or rain at time of takeoff, daily estimates of predator density (daily count of raptors), and daily estimates of the number of competitors.

The number of competitors can be estimated with capture-recapture methods as well (Jolly-Seber model; Schwarz and Seber, 1999). The Jolly-Seber model estimates population size (number of competitors) and local survival rate. A significant negative process covariance between local survival probability and population size, which needs to be extracted from the total covariance and sampling covariance (Burnham and White, 2002), is an indication that emigration is higher when population size — and thus competition — is high.

3.2 Intrinsic factors

Different approaches have to be used to test whether birds take their actual condition (innate rhythm, fuel deposition rate, amount of fuel stores) into account for departure. If they do, emigration probability is not the same in all birds at a given time, but it is the same in all birds for a particular condition irrespective of time. Each intrinsic factor requires a different testing approach.

Innate rhythm The innate rhythm hypothesis (regular phases of flights and stopovers) is difficult to test. If it is real, we would expect that all birds have the same stopover duration and hence also emigration probability. In principle, models in which emigration probability is constant over time (ε) represent this hypothesis. However, as birds usually arrive in waves at stopover sites, emigration probability may still appear to be time-dependent if all birds stay for exactly the same time at the site. On the other hand, if the constant emigration model turns out to be the best fit, it does not yet give proof of the innate rhythm hypothesis. The power to detect variation in emigration probability may have simply been low. High sample size protects against low power here.

A different, but perhaps more appropriate approach is to estimate stopover duration for birds in different conditions and at different times of the migratory season (Schaub et al., 2001). There is strong evidence that innate rhythm is important for regulating stopover duration if stopover duration is the same under different conditions.

Fuel deposition rate Fuel deposition rate (FDR) is estimated as the difference in body mass between first and last capture divided by the number of days between the captures. In capture-recapture analysis a difficulty arises here: FDR can only be estimated for birds caught at least twice, whereas for capture-recapture statistics, all birds, even those caught only once, must be included. There exists, nevertheless, a simple practical solution to this problem: just delete the first capture (i.e., replace the 1 by a 0) of *all* birds in the input file. The new file then comprises only birds that were caught at least twice. Now emigration prob-

ability assesses only birds that stayed at least one day at the stopover site against the non-transients (Pradel et al., 1997). As our aim is to examine the emigration of that fraction of birds that really stops over at the study site, this is not a constraint but a benefit. A more serious problem is the reduction in the sample size, and thus precision of the parameter estimates and test power.

The birds must be allocated into groups according to their FDR. The hypothesis that departure depends on FDR is translated into a model in which the emigration probability of each group is different (ϵ_{fdr}). The alternative hypothesis is that emigration is the same in each of these groups (ϵ).

Fuel stores (body mass) Body mass, fat scores and other indicators of the amount of fuel stored are all considered together here because their significance for departure is tested with the same models. I will use “body mass” for all indicators of the quantity of fuel stores. For capture-recapture analysis, a further problem emerges. Birds change body mass from day to day, and hence also from capture to capture. If emigration probability is related to body mass at one particular (e.g., first or last) capture, we do not really test whether *actual* body mass is decisive for departure decisions — rather we test whether body mass at first or at last capture is decisive. As the body mass of each bird at each capture event is known, capture histories can be adapted to contain this information.

It is necessary to define classes of body mass, and each bird at each capture event is then assigned to a specific class. An original individual capture history of {1 0 1 1 0} may then be replaced by the following {low 0 high high 0}, that is, the bird had low body mass at first capture and high body mass at second and third. Multi-state capture-recapture models (Hestbeck et al., 1991) are suited to estimate emigration probability for each class from such data. Compared to the one-state models presented so far, multi-state capture-recapture models contain an additional parameter type, the daily probability of change in body mass class. This can be interpreted as an estimation of fuel deposition rate. The hypothesis that departure decision depends on actual body mass is translated into a model where state (class)-specific emigration probabilities differ (ϵ_{mass}). This model may be compared to a model in which the state-specific emigration probabilities are constrained to be the same (ϵ).

4 How to study multiple factors

As shown above, the study of single factors requires different models: one-state models with or without groups and multi-state models. I now propose a framework within which all these different factors can be tested simultaneously. First I describe the preparation of the data and secondly the statistical analysis.

First, FDR over the time interval previous-actual capture event is estimated and allocated to the actual capture event. (Alternatively, individual FDR may also be estimated

over time interval first-last capture, as shown above, and its value allocated to each capture event. It depends on the focus of the study whether *actual* or *overall* FDR is used.) The first capture in all capture-histories is then deleted (1 replaced by 0) in the capture-recapture data file such that only birds that were recaptured at least once remain. Next, a suitable number of classes (not too many) representing combinations of FDR and body mass at actual capture is created, and allocated to each capture event. The result is a matrix of multi-state capture histories. The procedure is summarized in Table 1.

The states represent different combinations of body mass and FDR, so specific hypotheses about their relationship to departure can be tested by appropriate constraints of state-specific emigration probabilities. With estimates of the unconstrained model ($\epsilon_r \neq \epsilon_s \neq \epsilon_3 \neq \epsilon_4$, where ϵ_r is the emigration probability of state r , see Table 1), interaction between FDR and body mass can be evaluated. To test whether the interaction is significant, we compare the former model with models where emigration is only a function of FDR ($\epsilon_1 = \epsilon_2 \neq \epsilon_3 = \epsilon_4$), only a function of body mass ($\epsilon_1 = \epsilon_3 \neq \epsilon_2 = \epsilon_4$), or dependent on neither FDR nor body mass ($\epsilon_1 = \epsilon_2 = \epsilon_3 = \epsilon_4$). By allowing for temporal variation of state-specific emigration probabilities, it can be assessed whether an environmental factor is taken into account in the departure decision. Models in which state-specific emigration probabilities are time-dependent need to be compared with models in which time-specific emigration probabilities are a function of an environmental factor. If the state-specific emigration probabilities are different functions of environmental factors, it is an indication of interaction between environmental and intrinsic factors. Appropriate model selection can become quite complicated when all aspects are considered, in particular because the recapture and the transition probabilities need to be modeled as well. Burnham and Anderson (1998) describe how model selection is done most efficiently. They emphasize the importance of creating a small list of working hypotheses prior to data analysis based on results from former studies.

5 Recommendations

The price of this framework is a large number of recaptured birds. Although ringing under standardized conditions has been carried out for years and will continue, problems may arise from sample sizes. If data are insufficient, there is a risk that some parameters in the models cannot be estimated, that the iteration process does not find the maximum of likelihood function (Lebreton and Pradel, 2002), or that parameter estimates are imprecise. Solutions to the problem of sample size may be either to analyze only one factor at once, or to analyze all factors except FDR. If FDR is excluded, all birds, not just those recaptured, can be used without reducing the sample size. As the sample size from one migration season may be too small, data for several years can then be pooled in a single analysis.

Acknowledgements I thank Franz Bairlein and Lukas Jenni

Table 1 An example of how to prepare a capture history needed to test simultaneously the significance of environmental and intrinsic factors that regulate departure

1. Original capture history	0	10	0	11	12	0	12	0	0
2. Calculate fuel deposition rate		0.5		1.0		0.0			
3. Delete first capture	0	0	0	$\begin{pmatrix} 0.5 \\ 11 \end{pmatrix}$	$\begin{pmatrix} 1.0 \\ 12 \end{pmatrix}$	0	$\begin{pmatrix} 0.0 \\ 12 \end{pmatrix}$	0	0
4. FER-body mass states		FDR/mass		<11.5		>11.5			
		≤ 0		1	2				
		> 0		3	4				
5. Final capture history	0	0	0	3	4	0	2	0	0

In the original capture history, capture is indicated by the body mass of the individual at time of capture, i.e., 10 = 10 g. FDR = fuel deposition rate.

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Symposium 35 Bird minds

Introduction

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Higher cognition is one of the more controversial fields in avian research. This symposium presents results of new laboratory and field research in this area, showing that characteristics usually associated with the great apes are present in birds, and thus present without an increase in brain size or a neocortex. These findings suggest that some avian species do not merely respond to effects but are capable of planned action and intentional communication.

The speakers cover a substantial range of behaviors once thought to be unique to humans. Giorgio Vallortigara discusses the very topical issue of spatial cognition and learning of abstract rules in birds, based on the domestic chicken as a model. Irene Pepperberg analyses processes of acquisition of language in grey parrots. Gisela Kaplan discusses alarm calls of the Australian magpie showing that

they may use referential alarm calling for predators. Martine Hausberger and colleagues have proved experimentally that social conditions in raising starlings influence vocalizations, perception and even neuronal selectivity in the brain. Gavin Hunt and Russell Gray provide evidence of sophisticated manufacture of tools by New Caledonian crows, now among the very few confirmed examples of the manufacture of tools by animals.

Evidence of use of referential communication, complex learning, manufacture of tools and problem-solving in avian species suggests that it may no longer be possible to dismiss these cases as rare. We may need to consider that these traits demonstrate higher cognitive abilities approaching, perhaps even rivaling, those of primates.

S35-1 Spatial and object cognition in the domestic chicken

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Abstract The ability of the chicken to encode different aspects of spatial layout were investigated. In a first series of experiments, chickens were disoriented in a rectangular environment, where they proved able to reorient themselves using both geometric and non-geometric properties of the environment. In a second series of experiments, chickens were trained to find the central position of an arena using only the spatial arrangement of the walls for orientation. When subsequently tested in an arena of identical shape but a larger area, chickens displayed searching behavior at two different distances, one corresponding to the original distance (i.e., center) in the smaller, training arena, the other to the actual center of the test arena. When training was performed in the presence of a conspicuous landmark at the center of the arena, animals searched at the central location even after the removal of the landmark. Chickens are thus able to encode information about absolute and relative distance from the walls of the arena, even when orientation by a single landmark suffices for spatial localization. Temporary occlusion of the left or the right eye during testing revealed that the right hemisphere (served by the left eye) is primarily concerned with encoding geometric and relational spatial information, whereas the left hemisphere (served by the right eye) is concerned with absolute metric information, possibly as part of an encoding strategy based on local spatial and non-spatial information.

Key words Cognition, Spatial memory, Cerebral lateralization, Domestic chicken, *Gallus gallus*

1 Introduction

When considering spatial cognition in birds, cognitive ethologists usually think of the surprising feats of food-storing birds or of the remarkable orienting abilities of homing pigeons. In contrast, the protagonist of my paper is the humble domestic chicken (*Gallus gallus*). I shall report on the ability of the chicken to make use of different features of spatial layout in its environment for orientation, and on the way in which these different features are encoded separately in left and right hemispheres of the brain.

2 Encoding of geometric and non-geometric information

My analysis begins with the ability of the chicken to use so-called purely geometric information, namely the information provided by the spatial arrangement of surfaces as surfaces. In a rectangular space similar to that used by Cheng (1986) for rats and Hermer and Spelke (1994) for children, a filled dot in corner A indicates the location where the chicken can find visible food (Fig. 1). After several trials, the food is progressively hidden until it becomes completely invisible. At the same time, the chicken is disoriented by slow rotation on a chair, and then is replaced in the rectangular arena. In the absence of topographical cues, there is no way that it can relocate the correct corner. Nevertheless, if it can encode and use geometric information, a partial solution to its problem is possible. There is only one other

location that is truly indistinguishable from corner A, and that is its rotational equivalent, corner C (empty dot). Corners B and D can be discarded on the basis of geometric information alone. We found that chickens, after brief training, could learn to choose the correct corners A and B. Surprisingly, it has been found that human infants (Hermer and Spelke, 1994) and adult rats (Cheng, 1986) failed to reorient. They tended to use only purely geometric information, persisting in confusing corners A and C.

These findings have been interpreted as suggesting that spatial reorientation depends on an encapsulated, task-specific mechanism, a “geometric module” (Cheng, 1986). Such a module would encode only the geometric properties in the arrangement of surfaces as surfaces. In the case of the spatial reorientation task in the rectangular environment, for instance, the geometric module would use only “metric properties” (i.e., the distinction between a long and a short

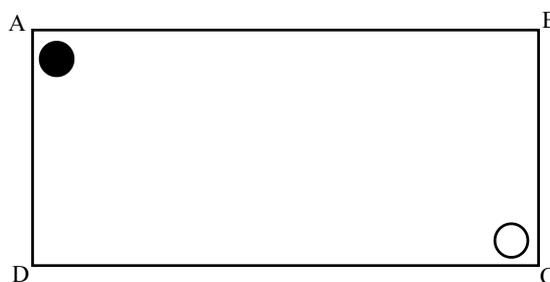


Fig. 1 Rectangular space for testing encoding of geometric information by the chicken

wall) and what is known in geometry as “sense” (i.e., the distinction between right and left).

It was found that chickens, in contrast to rats and young children, can easily learn to reorient by combining geometric and non-geometric information (Vallortigara et al., 1990). Rats showed the clearest evidence of informational encapsulation of the geometric module when tested with geometric transformations of the arrangement of panels, particularly with transformations that modify the geometric relations between the target and the shape of the environment (Cheng, 1986).

Chickens behave very differently. We studied the effects of two geometric transformations: the diagonal transposition and the affinal transformation. Both transformations alter the original spatial arrangement of the panels; the affinal transformation, however, also modifies geometric relations between the target and the shape of the environment, whereas the diagonal transposition does not. Results showed that chickens were completely unaffected by these transformations. They searched on the basis of featural information alone, making virtually no errors at the locations specified by geometric information. Thus, chickens perform better than rats and young children in such spatial reorientation tasks, encoding and combining geometric and non-geometric information to position themselves (also Sovrano et al., 2002 for fish).

Recently, the possibility that different processing modules in the two cerebral hemispheres encode these different spatial processes has aroused interest. The avian brain provides an excellent model for analyzing brain lateralization in the vision domain, because there is complete crossing (decussation) at the optic chiasma, and the two visual pathways, the thalamofugal and tectofugal, ascend in the main contralaterally. This means that by occluding one eye temporarily, we can study how information is stored in the left and right parts of the brain.

Chickens were first trained in the rectangular-cage test, with four panels at the corners, as described before, and then tested with one eye covered in the affinal transformation test. Although chickens oriented mainly on the basis of non-geometric information whatever the eye condition, left-eyed chickens made more errors in the geometrically correct corners and tended to choose incorrect panels more often. This would suggest that purely geometric information, based on large-scale spatial information, is processed by the right hemisphere (left eye), whereas object-centered, local information is processed by the left hemisphere (right eye).

3 Learning to localize the center of an environment

An even more striking example of dissociation between position-specific and object-specific cues has been obtained in a different task. Young chickens were trained to find food hidden below sawdust on the floor by ground

scratching in the center of a closed uniform arena: the center was indicated by a conspicuous landmark (a red stick). After learning, the landmark was shifted to a novel position and chickens were tested with both or only one eye uncovered. It was found that chickens with both or only the left eye uncovered searched at the center, ignoring the landmark, whereas chickens using only their right eye searched at the corner centered by the landmark, ignoring purely spatial information. It is interesting to note that here global cues prevailed over local cues in binocular and left-eye viewing conditions. The reason for it is unclear at present, but even so, whatever cues dominate in binocular conditions, the left eye tends to attend to global geometric cues and the right eye to local, non-geometric cues.

Our investigations then turned to a search for the neural bases of these spatial processes in the brain, in particular for specific areas in the left and right hemispheres that could be involved in these tasks. The hippocampus is very important for spatial memory in mammals, and patterns of connectivity suggest that its function could be homologous in birds. To test this, chickens were trained to find the center of an arena with a central landmark. Lesioned birds learned the task as well as sham-operated controls. Then the landmark was removed. Chickens lesioned bilaterally or at the right hippocampus appeared to be completely disoriented; lesions to the left hippocampus, in contrast, were ineffective.

In a second experiment, the landmark was not removed but transferred to a different position. Control, sham-operated chickens behaved as binocular chickens, searching in the center and ignoring the landmark. Bilateral- and right-hemisphere lesioned chickens (but not left-lesioned chickens), in contrast, searched near the landmark. In the absence of the right hippocampus, then, chickens could only use local information (i.e., the landmark), and were unable to process large-scale, geometric spatial information.

A similar dissociation between object-specific and position-specific cues has been observed in a working memory task. Young chickens were confined to a transparent cage through which they could see their “mother” (an imprinted object) at a distance. The mother object was then moved and hidden behind one of two different opaque screens. After a delay of 30 seconds, the cage was opened and the chicks allowed to search for the mother object behind the screens. In each trial, the position of the screen behind which the mother object was hidden was changed at random such that the task for the chicken was to remember the “correct” screen.

The chickens managed this task quite well. In one version, however, an opaque partition was placed in front of the transparent cage during the 30-second delay, and the experimenter, not visible, changed the left-right position of the screens so as to produce contradictory spatial and object-specific information. The chicken was thus faced with the dilemma of choosing the screen in the correct position but with the wrong color, or of choosing the screen in the

wrong position but with the right color. It was found that left-eyed chickens searched behind the screen in the correct position, and right-eyed chicks behind the screen of the correct color. Once again, the right hemisphere (left eye) attends to position, and the left hemisphere (right eye) to visual characteristics.

The finding that birds are capable of using the metric configuration of distances between surfaces in the environment opens the door to the previously uninvestigated field of spatial performance. Take, for example, the task of localizing the perceptual center of a closed environment, and orienting by it, a task easily accomplished by humans. If the environment lacks distinctive landmarks, localization of the center would require the use of abstract metric information concerning spatial relations and distances between surfaces in the environment. We trained young chickens to find food by ground scratching in the center of a closed square-shaped uniform arena, and then tested them in arenas of similar size but different shape. The birds showed localized searching behavior in the square arena, and maintained it when placed in circular or triangular arenas. In a rectangular arena formed by doubling the original square, chickens dispersed their searching more along the major axis, yet searching tended to be concentrated around the centers of the composing squares and around the center of the rectangle itself.

When trained in a square-shaped arena and then tested in an arena of the same shape but larger area, chickens displayed searching behavior at two different distances from the wall, one corresponding to the original distance (i.e. center) in the smaller, training arena, the other to the actual center of the test arena. The same was found in triangular-shaped arenas. In circular arenas, however, chickens searched mainly at a distance midway between the radius of the small, training and large, testing arenas when moved to the latter. These results suggest that, during training, the

chickens encoded information about both the absolute and relative distances of the food from the walls of the arenas, the latter information being more accurate when the arena provided identifiable features such as corners.

This task was used to investigate the way in which distances from the center were encoded in the two hemispheres. Left- and right-eyed chickens were strikingly different: chickens using their left hemisphere (right eye) searched only at absolute distances, whereas chickens using their right hemisphere (left eye) searched only at relative distances.

4 Conclusion

Overall, these results suggest that, for vision, the right hemisphere of the avian brain is concerned primarily with encoding relational spatial information, and the left with absolute metric information, possibly as part of an encoding strategy based on local spatial and non-spatial information.

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S35-2 Simultaneous development of vocal and physical object combinations in the gray parrot (*Psittacus erithacus*): parallels with primates

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Abstract Some cognitive abilities of gray parrots (*Psittacus erithacus*) — birds with walnut-sized brains organized differently from those of primates, mammals, and even songbirds — match those of marine mammals, nonhuman primates, and 4–6 year old humans (Pepperberg, 1999); but little attention has been paid to their development. I review a study of co-emergence of communicative and physical object combinatorial skills in parrots (Pepperberg and Shive, 2001) and discuss neurobiological implications.

Key words Avian cognition, Comparative cognition

1 Introduction

After the “cognitive revolution”, researchers began to accept that nonhuman and human intelligence formed a continuum, to study a wide range of behavior using many techniques in various species, and to overturn negative beliefs about avian cognition (Pepperberg, 2001). Evolutionary theories of intelligence were, however, still built upon analyses of present-day social and cognitive skills in non-human primates that could be ancestral to unique human abilities. But similar abilities may evolve in different ways. Skills comparable to those of primates exist in birds and cetaceans, creatures with different evolutionary histories and differently wired brains (Pepperberg, 2004). Focus on primates will miss insights into the evolution and development of complex cognitive processes, on how development relates to brain function, and how such issues impact on search for analogous/homologous neural bases of behavior. The development of combinatory behavior provides one such caution (Pepperberg and Shive, 2001).

2 Co-emergence of object and label combinations

Young children almost simultaneously begin combining objects, behavior supposedly controlled initially by one neural structure (roughly Broca’s area) that, as a child matures, differentiates into specialized areas for language and physical combinations (Greenfield, 1991). After finding that co-emergent spontaneous physical and communicative combinatorial acts of “language”-trained apes (*Pan paniscus*, *P. troglodytes*) were similar to those of young children, Greenfield (1991) proposed that such behavior derives from a homologous structure predating ape and

hominid divergence (Deacon, 1992).

Greenfield (1991) also proposed uniquely primate cognitive connections in seriation (hierarchical) tasks, rule-governed behavior, and early language. Simple seriation, that of putting smaller items into bigger ones, demonstrates elementary ordinality and may relate to grammatical constructs. More complex forms, such as putting C into B, then placing the unit into A, which shows knowledge that B is smaller than A and larger than C, involve multiple, two-way relationships underlying advanced abilities. These include phoneme/word combinations, rudimentary language and syntax (Greenfield, 1991). Such arguments support ideas that spoken language is derived from gesture without major neural restructuring (Hewes, 1973). Co-development of communicative/physical combinations purportedly controlled by one neural center might thus be viewed as unique to primates. But what if Aves exhibited such combinatory behavior?

Study of gray parrot vocal and physical hierarchical combinations began after we observed spontaneous two-object combinations by a bird that had already combined two human vocal labels (Pepperberg and Shive, 2001). Two-item physical and vocal combinations thus are not limited to primate brains. In June 1999, I began examining the nature, extent, and time lines for advanced hierarchical combinations in gray parrots (*Psittacus erithacus*).

3 Parrot combinatory behavior

The following summary is drawn from Pepperberg and Shive (2001). The subject gray parrot, Griffin, had never seen humans stacking the items used in the study nor been trained to combine labels or objects. It was being taught single labels (for objects, colors). It heard “want X” and

“wanna go Y” (X and Y, respectively, were items or locations) from another gray parrot (Pepperberg, 1999) and as untrained queries from students. It routinely uttered, “want X” and “wanna go-back” (go back sounded like “g-back”) and untrained color-object phrases.

For object combinations, we used colored plastic or metal bottle caps and lids that Griffin had manipulated previously. Trials initially involved three items; and seven later trials, one per session, involved four. We randomly placed items simultaneously on the counter where it sat, then manually recorded spontaneous behavior. Its actions were never rewarded. A trial ended when Griffin tossed items off the counter. We replaced items and recorded until it began another activity (e.g., eating, preening). Sessions ended when the substitution of new items failed to reengage the bird. Thus its interest dictated the number of trials per session, and trial and session length; it received 50 sessions. A proportion of trials was videotaped, testing transcriptions for inter-observer reliability.

Following Johnson-Pynn et al. (1999), we noted whether and how often Griffin (a) paired two items (pair); (b) put two items successively into a third or placed a third on to a pair (potting); (c) put two-object units into a third (subassembly); (d) combined units out-of-order; (e) picked up new objects versus further manipulation of old; (f) performed other multiple object manipulations; and (g), like apes and *Cebus* but unlike children in Greenfield’s (1991) study, dismantled units. All combinatory efforts were classed as “Attempts”. Successful assemblies stayed together; failures did not fit or fell apart.

In July 1999, a month after the parrot’s first, and for some time only, successful three-item combination, we began training with shape labels, such as “x-corner y”, where $x=2.5$ and $y=\text{wood or paper}$; a pine pentagon was “5-corner wood”. We recorded vocal combinations outside of training, calculating percentages of two- and three- label combinations. Griffin mostly combined objects in silence;

thus notation of utterances occurred outside those sessions.

4 Results

Using its beak, Griffin consistently combined two of three objects, rarely three (Pepperberg and Shive, 2001). Of 233 attempts, 217 pairings succeeded (93%; binomial test, $P \ll 0.001$). On 65% of trials (141 trials, binomial, $P < 0.05$), he picked units up in his beak, carried them around, threw them off the counter, or, with his beak, flipped the internal object over. Only 38% of successes were not serial ($P=0.08$). Successful potting was rare (7 times; 3% of total attempts, 58% of potting attempts, $P=0.06$), but his first success was in the first month. Subassemblies failed (Pepperberg and Shive, 2001) but co-emerged with spontaneous three-label utterances in early 2000 (Fig. 1).

On 7 trials with four items, Griffin always combined two. Four times it tried but failed at further combinations: it picked up and threw each unit or took it apart to recombine successively. Further attempts were correct but unsuccessful, seemingly because of a lack of dexterity rather than an understanding of seriation.

Other object manipulations (Pepperberg and Shive, 2001) replicated those of children and apes (Greenfield, 1991). Many primate acts, such as the simultaneous lifting of two objects independently, are either prohibited or made difficult by parrot anatomy; but Griffin often simultaneously picked up two objects with sides touching. It also often performed acts of older children (Langer, 1986): transformations (e.g., placing a cap into a ring makes the ring a receptacle) and combinations (e.g., fitting a ring inside a cap), both related to serial actions.

Griffin’s frequency of spontaneous label combinations paralleled physical ones (list in Pepperberg and Shive, 2001). Two-label combinations occurred more often (61%–93% of the time) than single labels. Most two-label combinations (~92%) were hierarchical (e.g., “want+X”, “wanna+X”); others (e.g., “green+X”) might be termed so.

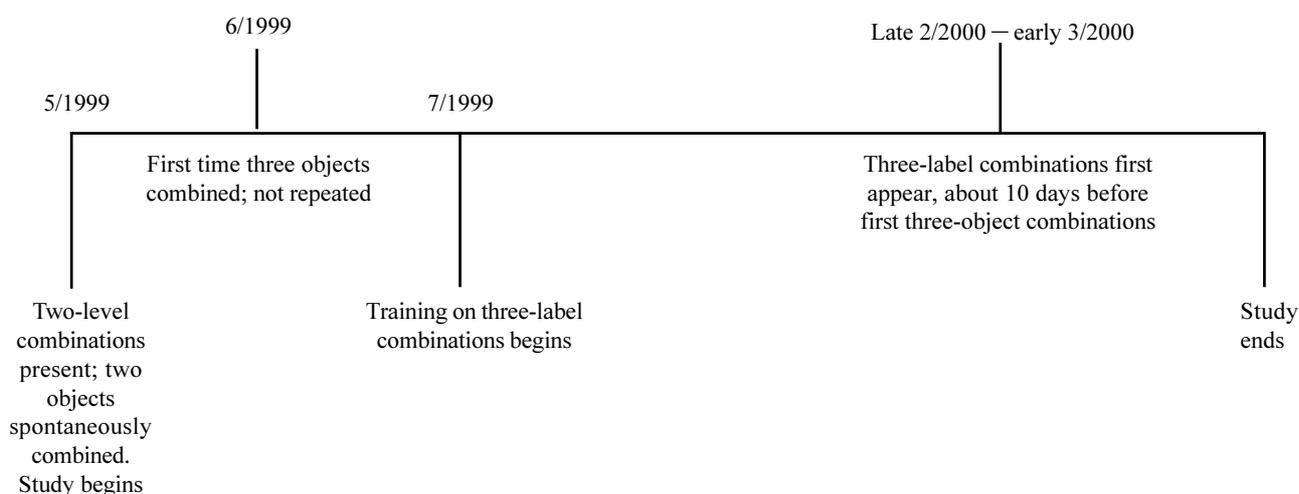


Fig. 1 Timeline for vocal and object combinations
From Pepperberg and Shive (2001).

In late February 2000, after eight months exposure, three-label combinations arose (6%–10% of totals), but were rarely those trained. Inter-observer reliability was ~85%; disagreements involved phonetically similar single labels.

Greenfield (1991) also considered phonemic combinations relevant to seriation and syntactical development. Griffin's common phonemic recombinations (e.g., cork/corn) predated this study, but others (e.g., beeper from paper, green, and /b/) developed in early 2000 (list in Pepperberg and Shive, 2001). Notably, Greenfield would consider "Want corn", "Want cork" as three-element serial combinations.

5 Discussion

Co-emergence of physical and label combinations is not limited to primates. Griffin simultaneously initiated three-item and -label combinations. Note that (a) percentages of physical and vocal combinations roughly match; (b) despite months of training on x-corner wood/paper, three-label utterances emerged only as Griffin began combining three objects; (c) vocal combinations were rarely those trained; and (d) it executed physical combinations with beak and tongue, not feet. Thus a mammalian brain is not necessary for such behavior, and physical combinations need not be manual.

5.1 Manipulative and vocal combinations

Griffin predominantly paired; potting was limited compared to primates. Pottings, successful slightly more than half the time, probably failed because the bird lacked physical dexterity. Subassembly failures did involve impossible combinations.

Humans introduced only a framework for vocal combinations. Of Griffin's spontaneous three-label combinations, only 2-corner wood was trained (1/14); no other trained combinations appeared. Phrases were generally novel, or reproduced what was heard from trainers, not taught by them. Some novel utterances lacked clear syntactic, hierarchical form and were unlikely to have come from trainers.

Might both types of combinations continue developing? Behavior in other gray parrots, as interpreted by Greenfield (1991), suggests that this is likely (Pepperberg and Shive, 2001).

5.2 Neural Issues

Mirror neurons might explain co-emergence of primate object and grammatical combinations; avian data are preliminary (see below). Monkey F5 Manes (MNs) are activated by both action and observation of hand and mouth gestures, supporting theories of gesture origins for speech because similar human MNs occur in Boca's area of the brain, including gesture function (Parsons et al., 1995). For monkeys, in which complex hierarchical behavior must be trained (Johnson-Pynn et al., 1999), the observed action is already fixed in the repertoire and is

goal-oriented (e.g., Chaminade et al., 2002; Rizzolatti et al., 2001); great ape MNs have not been studied. Human MNs, however, probably evolved to analyze and developmentally recreate actions to which they are exposed, including speech, where neurons react to activate unobserved muscles.

What might act like MNs in a parrot, an animal that cannot recreate human vocalizations or primate actions in exactly the same manner as humans, even if it achieves the same results? Does exposure to human speech and behavior initiate patterns in the parrot brain analogous or homologous to those of humans? Interestingly, electrophysiological studies in frontal neostriata of awake budgerigars show activity in production of and response to calls (Plumer and Striedter, 2000); evidence also exists for additional auditory-vocal pathways.

Further research must determine what, if any, avian neural substrates mediate co-emergent vocal and physical combinations and if there are differences between bird groups. Neural vocal control pathways differ in oscines and psittacids and, although their vocal learning supposedly arose independently (Jarvis and Mello, 2000), the structures responsible may have been derived from a common ancestor and then lost in some descendants. Interestingly, physical and vocal combinations in both wrens and parrots involve beak and tongue, closer vocal and physical ties than in primates. Such data, and arguments concerning gestural origins for speech without major neural restructuring, support a motor control theory for the origin of song (Nottebohm, 1991) which involves neural substrates similar to those proposed for primates. Arguably, emphasis in future research is best placed on coordinated neuronal activity linking brain areas (Deacon, 1997), and on how alternative neurological means can achieve the same end (Jarvis and Mello, 2000).

6 Implications

Co-emergent vocal and physical combinations so far documented in the gray parrot resemble those of primates. Clearly, the behavior of gray parrots is not isomorphic with the language of children or complex combinatory behavior. Nevertheless, (a) combinatory behavior in the gray parrot resembles that of nonhuman primates, (b) parallel communicatory and physical development is not limited to primates, and (c) involved neural structures are unlikely to be unique to primates. How avian neuroanatomy evolved is not yet well enough understood to determine parallels among oscines, psittacines, and primates. The search for such parallels should thus be of high priority.

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S35-3 Alarm calls, communication and cognition in Australian magpies (*Gymnorhina tibicen*)

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Abstract Alarm calls have served a model function to test hypotheses about intentional signaling as an integral, if not key element, in the expression of higher cognition. The alarm signals of some avian species, including alarm and distress calls, may be generalized and so be understood by mammals and other birds. Some species, including primates and ground-dwelling mammals, have developed specific alarm calls that convey meaning beyond communicating a general state of arousal or fear. They indicate specific types of predators, for example ground or aerial. Similar distinctions in alarm calls had been shown only in one avian species, the domestic chicken. I investigated the alarm calls of Australian magpies in the field and found that magpies may use as many as eight well-defined types of alarm calls, only one of which is used for a general alert. This was used in playback experiments. I also identified a specific alarm call that seemed to be reserved for birds of prey alone; recordings of them were taken in response to wedge-tailed eagles. The same alarm calls were then used experimentally in playbacks to other groups of magpies. The results demonstrate that magpies respond differently to this alarm, suggesting that they may also use referential signaling.

Key words Alarm calls, Cognition, Communication, Australian magpie

1 Introduction

Alarm calls are a class of vocalizations of significance to research into the evolution of signal structure and function because they warn receivers of the appearance of threat, such as a predator. The question concerning higher cognition is whether species can actually discriminate between classes of threat and demonstrate this by selective use of alarms. To be regarded as intentional, one expects alarms to be given only in the presence of an audience of conspecifics. This would demonstrate that the sender was acting not merely on impulse (expressing a state of emotion), but with intent to communicate a specific message to conspecifics within auditory range. Hence, an intentional raptor alarm call should be emitted after sighting a bird of prey, and a snake alarm call after the sighting of a snake, only when others are present.

It has been argued that alarm calls are simply an automatic, unintentional signal of emotional state, because predators induce a state of fear (Rogers and Kaplan, 2000). An aerial predator might elicit more fear than a ground predator (or vice versa), and different calls for either might thus reflect the differences in perceived danger. In fact, even switching from one call to another may indicate increased fear, and this does seem to occur in some species. For instance, two types of alarm calling have been reported in black-winged stilt (*Himantopus himantopus*), the type of call depending on the distance of the predator (Emlen, 1972).

Since renewed interest in cognition in animals and

the work by Seyfarth, Cheney and Marler (1980), Greene and Meagher (1998), Manser (2001), Blumstein and Armitage (1997) and Zuberbühler (2000), it has been confirmed that the ability to discriminate between different alarm calls signaling threat from different predators is present in a variety of species, and that such signals lead to predictable behavioral responses in the receivers. Research has also established that domestic chickens (*Gallus gallus*) have different alarm calls for ground and aerial predators (Marler and Evans, 1996; Evans, 1997). Thus, alarm calls may be intentional and convey meaning beyond a simple “readout” of the emotional state of the sender (Kaplan and Rogers, 2001).

2 Vocalization research on the Australian magpie

There is good information available on the biophysical properties of alarm calls in Australian birds in general, including the Australian magpie (*Gymnorhina tibicen*) (Jurisevic and Sanderson, 1994, 1998; Wood et al., 2000). Yet there have been only two major published studies on magpie vocalizations so far, one concentrating on group interactions between territorial owners and neighbors (Brown et al., 1988, 1991) and the other on mimicry (Kaplan, 2000). Australian magpies (Fig. 1) are territorial and communal ground-feeders, foraging in loose groups of diverse hierarchy and engaging in extensive communication that is context-dependent (Farrabaugh et al., 1992). Both visual and vocal signals are used. As Brown and Farrabaugh (1991)



Fig. 1 The Australian magpie (*Gymnorhina tibicen*), one of Australia's foremost songbirds

Song is not used in breeding display, and males and females sing almost equally all year round.

have shown, some geographic variation occurs in alarm calls.

3 Methodology

I undertook extensive field observations on Australian magpies over a three year period, collecting a range of vocalizations including alarm calls in inland and coastal New South Wales and, as far as possible, establishing the context in which the calls were made. The calls of 20 different magpie tribes (only established territorial groups or pairs, not bachelor groups) were collected. Alarm calls elicited by the presence of an eagle were recorded in two separate geographical locations, inland and coastal, involving unrelated tribes.

Three types of calls formed the basis for playback experiments. One sequence comprised the “eagle” alarm call alone (Fig. 2C). The second call was the most commonly- heard alarm call through eastern Australia; it comprises repeats of the same call and is referred to as the “generic” alarm call (Fig. 2B). The third call, used as a control, was a short segment of song or “warble” (Fig. 2A). In addition to these calls, two extra types were generated from the existing samples: (1) the “eagle” alarm call was reversed in note order with maintenance of its temporal integrity (spacing between syllables); and (2) the “eagle” alarm call was mixed with the generic “alarm” in a semi-randomized blend. The “generic-plus-eagle-alarm” call was used to test whether a composite call elicited stronger responses; and the reversed “eagle” alarm was used to test whether chronological sequence is essential for its message.

Initial tests varied the duration of playbacks to test responses, establishing that the five-minute playback was the most effective. That five minutes in turn determined an observational period of 15 minutes per playback experiment: five minutes pre-playback silence, five minutes playback, and five minutes post-playback silence. Behaviors recorded

during the 15 minutes of playback covered foraging, walking, standing, running, vocalizing, looking down, scanning and, in particular, looking up, i.e. overhead. Because of the lateral position of the eyes, looking up was defined as raising the head so that the beak was above horizontal, with or without tilt of the head.

Playback experiments were carried out in five different magpie territories in different areas and in different seasons. Each magpie group was exposed to the five types of calls in semi-randomized order on every second day for eight days at three times a day (8 am, 12 noon, 4 pm). The portable cassette unit had two loudspeakers producing 68 dB at 10 m attenuation and was placed on the ground. Observers were placed ten meters away from the sound source, and recorded any change in magpie behavior. The results were weighted for number of magpies in each group.

4 Results

Across all playback tests, the “eagle” alarm call yielded

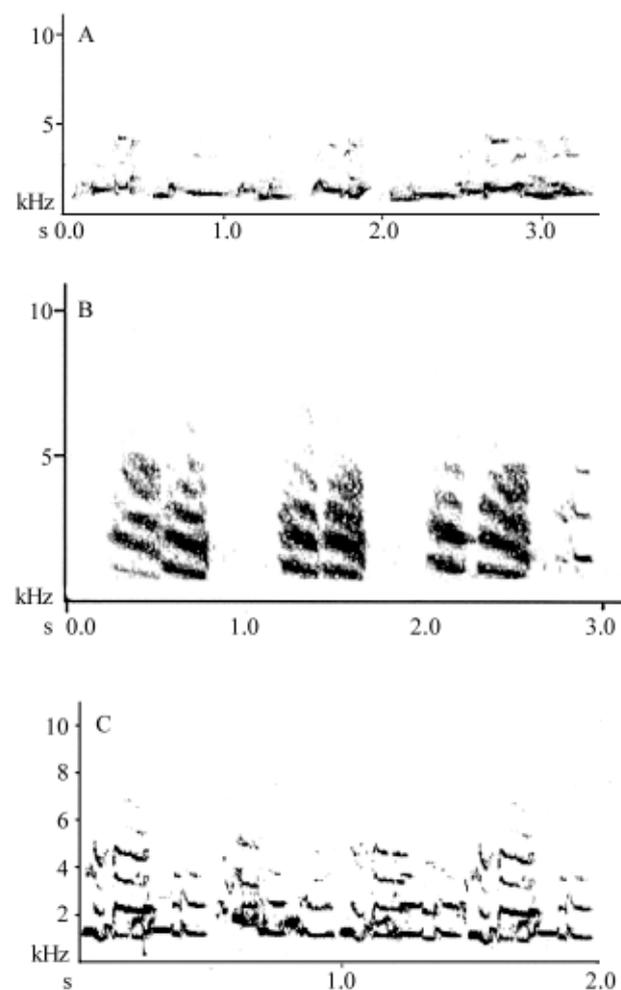


Fig. 2 Three specific vocalizations of an Australian magpie A. Typical song, sometimes called “warble”, usually in the frequency range 500 Hz–2 kHz; B. “generic” alarm call, shared by magpie populations across eastern Australia, in a frequency range of 5–7 kHz; C. “eagle alarm call”, almost always in excess of 6 kHz and with complex structure and layers of harmonics.

the strongest response. The most conclusive single response was undoubtedly the “looking up” behavior, which would scan for an aerial predator, even though the sound source was at ground level. Results for mean numbers of recorded events of “looking up” are presented below (Fig. 3).

It is noteworthy that playback of normal song yielded negligible looking up in any trials for any of the five groups. This behavior was usually absent in most trials using control song (warble) or the generic (nonspecific) alarm call. Some looking up occurred in the phase of playback of “generic” calls but was significantly enhanced once the “eagle” alarm call was added. For all call types, looking up is higher during playback than before playback and remains elevated after the “eagle” alarm call has been played, and also after the reversed “eagle” call. Indeed, the post-playback period was as important as the actual playback period. For reasons of space, the results of overall reactivity scores have not been presented here but they are statistically significant in the post-playback period. Generally, the post-playback period indicated high levels of arousal and very watchful behavior that subsided only gradually; it sometimes took over half an hour before activities returned to normal foraging patterns.

5 Discussion

It is too early yet to say whether “eagle” alarm calls are intentional signals because I have not yet tested their use in the absence of an audience. It can be suggested, however, that that alarm call has a specific meaning, since magpies respond to it not just by general arousal but by

looking overhead as they would only for an aerial predator. As magpies respond to the “reversed eagle” alarm call equally strongly, it seems that they may obtain meaning from the frequency ranges of the overtones in the call and not from the chronological sequence of notes.

This project will continue to address the important question of referential signals, contributing as it does to cognition in the wider sense. Intentional communication is an integral, if not key, element in the expression of higher cognition. Debate on higher cognitive abilities has tended to focus on the great apes, often tacitly assuming that many traits associated with higher cognition first evolved in the great apes linked to the development of a large neocortex and a complex social life-style. However, some higher cognitive characteristics have also evolved in avian species, on a different evolutionary trajectory than in apes; birds do not have a neocortex. Recent research shows that many of the traits once considered unique to humans, and later also to great apes, are shared with similar ability by some birds. Examples are tool using, problem solving, deception, concept development, and spatial abilities, as discussed in other papers in this symposium. Referential signaling is another important piece in the puzzle of cognitive abilities in birds.

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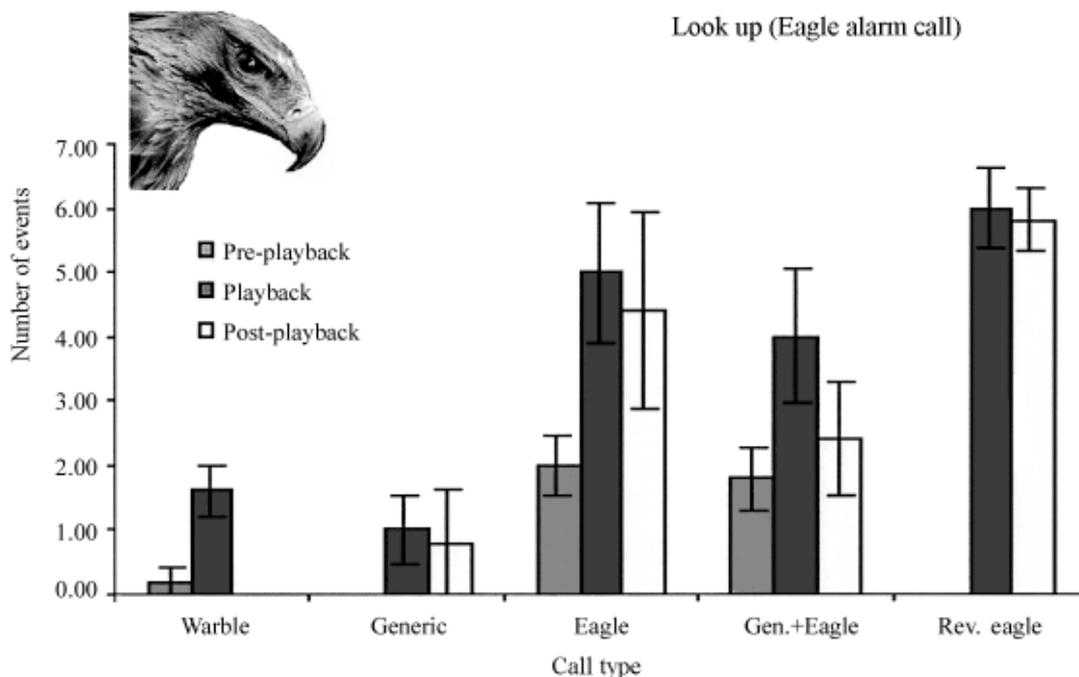


Fig. 3 Australian magpie responses to playbacks of three different types of their calls, and two experimental modifications of them. The y-axis shows the mean number of events for all magpie groups tested. The x-axis shows the responses during the three phases of the experiment. All “looking up” responses are significantly higher during playback of “eagle” alarm calls than prior to playback.

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S35-4 Social experience, vocal learning and social cognition in the European starling, *Sturnus vulgaris*

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Abstract European starlings are well known for their rich and varied social life. Recent studies reveal a social organization based on same-sex preferences, spatial proximity and vocal sharing in captive groups. Much less is known about social cognition and the possible role of social experience on the development of cognitive abilities. Experimental results described here show how the social conditions under which starlings are raised affect not only the quality of vocal copying (for the same auditory experience), but also perception of mirror images, relationships to people and organization of neuronal selectivity in the brain. Thus hand-raised birds placed either in groups with adults, or in pairs as young naive birds, or in isolation, react very differently when confronted with familiar or unfamiliar humans. Intraspecific social experience, therefore, influences the relationships of birds with their environment, including interspecific interactions. Different modalities are involved and include the visual and auditory worlds, as revealed by a mirror test and electrophysiology respectively..

Key words Social learning, Vocal learning, Cognition, Starlings

1 Introduction

Despite an apparently less sophisticated brain structure, birds have been shown to be capable of cognitive tasks generally considered restricted to mammals. A number of examples have been revealed through exhaustive studies on the African gray parrot (e.g., Pepperberg, 1990). Another remarkable feature of avian ability is the vocal complexity of song, which led Marler (1970) to suggest parallels between song learning in birds and language development in humans. Long-term memory, categorization, discrimination and recognition have all been found to be involved in learning and perception in birdsong (Hausberger et al., 1999).

Complex vocal learning is often involved in social contexts (Baptista and Gaunt, 1997). Many songbird species spend at least part of their lives in social situations: colonies, foraging groups, wintering flocks, leks. Therefore, social cognition in songbirds, although little investigated, should be a fruitful field for study. Birds, through song signatures, discriminate neighbors from unfamiliar birds (Beecher, 1982), evaluate distance (Wiley and Godard, 1996), and form preferential social associations (Freeberg, 1999). In many species, song learning appears to be modeled under social influences, although the precise modalities involved (auditory-visual-physical contact) remain unclear. Moreover, birdsong has led to fascinating discoveries in neuroethology revealing a complex system where learning, plasticity and therefore, experience, play a role in modeling brain structure (e.g., Doupe and Solis, 1997).

It is still difficult, however, to integrate these differ-

ent lines of knowledge, especially where social cognition is involved. Essential questions concerning perceptions of conspecifics or social partners, why a young bird chooses a particular tutor, the roles that vocal versus visual channels play in communication, and the neuronal bases involved, must all be solved in order to understand how birds view their social world. In the present study, we present evidence of social cognition in European starlings and investigate the effects of social experience on the development of social perception and brain structure.

2 Behavioral evidence

Song characteristics enable starlings to gather information about species, population and individual identities. Playback experiments in the field reveal clear dialectal discrimination as well as an ability to recognize specific song types despite variation (Adret-Hausberger, 1982). Studies on captive groups indicate that social organization is reflected best in spatial proximity and that song-sharing is a sign of social affinity: pairs of females and groups of males emerged that shared most of their song repertoires (Hausberger et al., 1995).

Social affinities tend to remain stable for long periods. It is possible that birds may have an image of some kind in their memory for a preferred social partner. Thus we devised an experiment to investigate whether shared songs had special meaning for the sharers and whether separation affected their memory. Playback experiments were performed on female starlings. We broadcast their own songs (unique

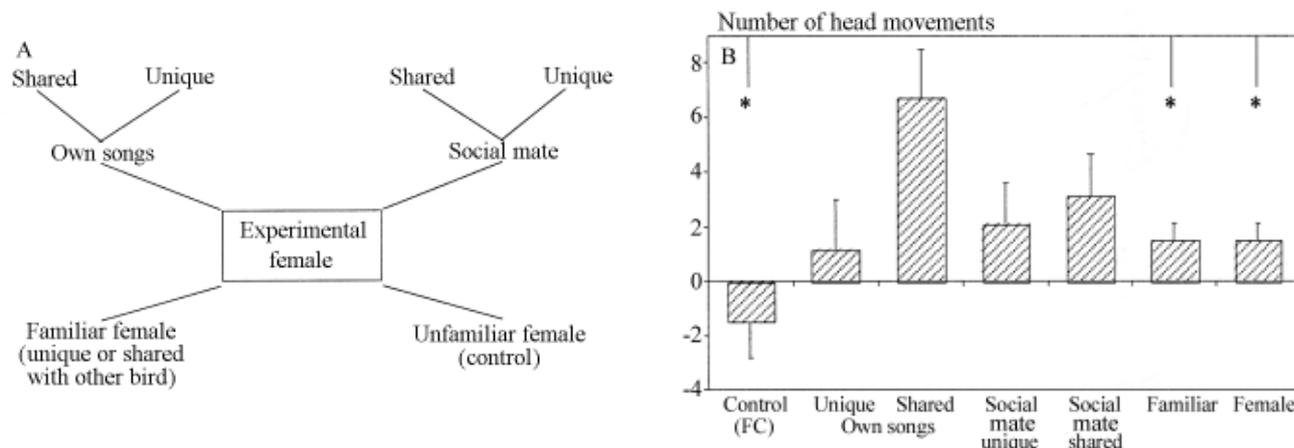


Fig. 1 Responses of the three social types of European starlings to broadcast song

A: the categories of songs broadcast to experimental females; B: head movements after playback of female whistles to females — means and *SD* (from Hausberger et al., 1997).

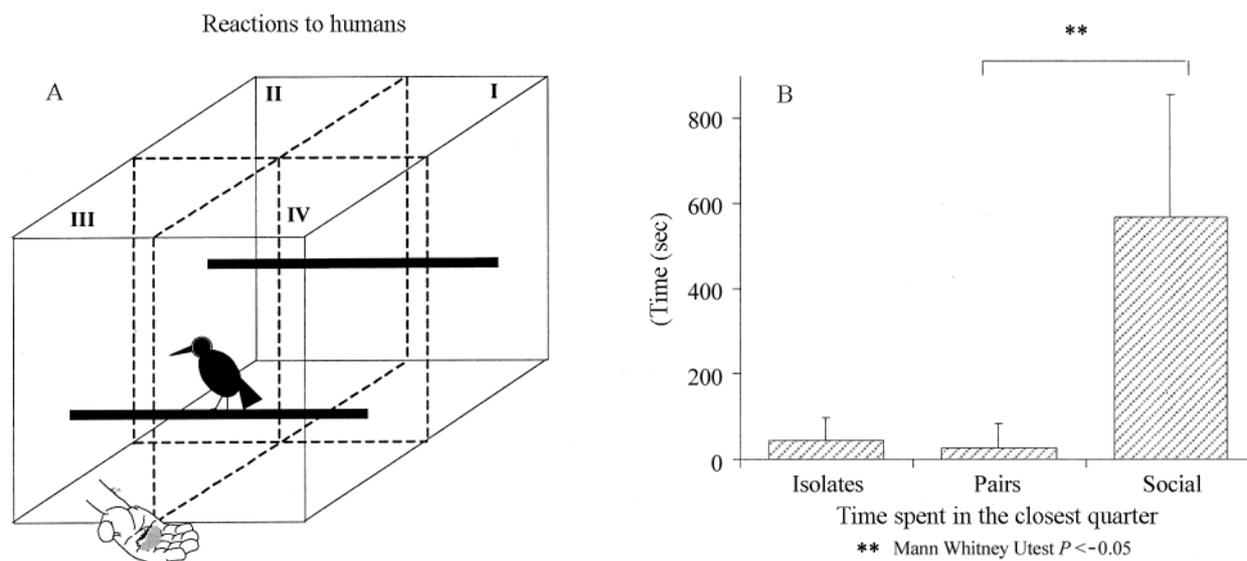


Fig. 2 Responses of the three social types of European starlings to humans

A: experimental setting to assess reactions in male birds raised in their first year in different social contexts in aviaries (1) with adult males and other young birds (social), (2) in pairs of inexperienced birds (pairs), and (3) in isolation. Pairs and isolated birds were kept in soundproof chambers (Poirier et al., submitted). Appetizing food was presented at the door of the cage. The cage was divided in four parts: I and II = back of cage, III and IV = front of cage. B: average time spent by birds in the front part of the cage (III and IV). Clear differences appear between birds raised socially, in pairs or in isolation.

or shared), the songs of partners (unique or shared), and songs of familiar or of unfamiliar females, and recorded all behavioral responses (Fig. 1A). The females increased their head movements (changes in orientation, gazes) for some stimuli more than for others. Whereas the songs of a strange female inhibited head movements, shared songs (own and partner's) elicited a significant increase (Fig. 1B). Obviously, shared song had special meaning for the birds which seemed to exhibit searching behavior through visual cues. Interestingly, the females had been separated from their social partners for several months before being tested, suggesting that shared songs may recall a perception of a social bond.

Social experience has important effects on vocal

sharing. Thus young females raised only with adult male tutors shared only their warbling motifs (Table 1). It also affects visual perception. Reactions to mirror images differed according to whether starlings have been raised in social groups, in pairs as naive birds, or in isolation. Birds raised in pairs appeared less disturbed, whereas those that had been isolated or raised in social groups were more active in response, gazing or pecking at the mirror (Henry et al., in prep.). The perception of what is a conspecific clearly differed among the three groups, a perception probably most difficult for the birds raised socially.

We then asked the question: could the perception of a nonspecific individual be affected by experience and, moreover, if that perception differed according to social

experience? So reactions to humans were tested by presenting appetizing food to birds at the door of their cage (Fig. 2A). We compared time spent by birds in the back of their cage (parts I and II) and in the front of their cage (parts III and IV) close to humans. Social experience clearly affected their reactions to humans. Socially-raised birds spent longer than isolated and pair-raised birds in the parts of their cages closest to humans (Fig. 2B). Thus in starlings, social experience affects both the perception of conspecifics and non-conspecifics, including humans.

3 Neuroethological evidence

Playback experiments clearly indicate capacities for categorization and generalization in starlings (Hausberger and Cousillas, 1996). We investigated the neural bases of these abilities. Thus, a study on wild-caught adult male starlings, involving single cell electrophysiological recordings of field L, the main auditory area of the brain, revealed that about 80% of over 300 auditory neurons responded only to whistles (Hausberger et al., 2000). Thus, many neurons appear to select precise elements in songs, which were also identified as key elements for categorizing songs in behavioral experiments. A mapping method, using multicellular recordings, indicated that such selectivity is organized spatially (Cousillas et al., submitted).

Both neuronal selectivity and their spatial distributions appear to depend on social experience. Comparisons revealed that most auditory neurons in birds raised in isolation responded to any sound (e.g., on/off responses), those in paired birds were intermediate in selectivity, and only those in birds raised in social groups were proportionally similar to those in adult wild animals (Cousillas et al., in prep.).

Thus these data indicate that, even though they may hear adult songs, birds raised in isolation develop poor perceptual abilities that certainly affect the way they view, categorize and memorize their social world. Social experience obviously plays a major role, auditory experience in solitary starlings preventing them from constructing a "normal" auditory field.

4 Discussion

Both behavior and neuro-ethological data converge to show that social cognition does exist in starlings, and that it depends very much on social experience acquired during development. Social organization differs between males and females, and this difference is reflected in the stronger reactions of females to shared songs.

Moreover, female starlings do not seem to learn from male models. Song learning along sexual lines has been described in a few species (review in Baptista and Gaunt, 1997), and in particular in the Indian hill mynah (*Gracula religiosa*), another sturnid (Bertram, 1970). This is particularly intriguing, as here the young females had no adult female model. Baptista et al. (1993) did not succeed in tutoring young female white crowned sparrows; this may have been due to the fact that only male models were available

Table 1 List of motif types found in the repertoire of 3 adult males and four one-year old females

	Wild birds			Experimental birds		
	M1	M2	M3	Social birds		
				S3f1	S3f2	S3f3
W1		+				
W2		+	+			
W3		+	+			
W4		+	+			
W5		+	+			
W6		+	+			
W7		+	+			
W8		+	+			
W9		+	+			
W10		+	+			
W11		+	+			
W12		+	+			
W13		+	+			
W14		+	+			
W15		+	+			
W16		+	+			
W17		+	+			
W18		+	+			
W19		+	+			
W20		+	+			
W21		+	+			
W22		+	+			
W23		+	+			
W24		+	+			
W25		+	+			
W26		+	+			
W27		+	+			
W28		+	+			
W29		+	+			
W30		+	+			
W31		+	+			
W32		+	+			
W33		+	+			
W34		+	+			
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W49						
W50						
W51						
W52						
W53						
W54						
W55						
W56						
W57						
W58						
W63				+	+	+
W64				+	+	+
W65				+	+	+
W66				+	+	+
W67				+	+	+
W68				+	+	+
W69				+	+	+
W70				+	+	+
W71				+	+	+
W72				+	+	+
W73				+	+	+
W74				+	+	+
W75				+	+	+
W76				+	+	+
W77				+	+	+
W78				+	+	+
W79				+	+	+
W80				+	+	+
W81			+			
Within each pair						
Non shared motif types	19	32	26	3	1	1

The four females were housed with male M3 from fledging and could hear and see males M1 and M2 living in adjacent aviaries. Note song sharing among males and among females respectively, but no overlap between them (from Poirier et al., submitted).

(Baptista, pers. com.). Song sharing seems to be linked to social affinity in a variety of species, including starlings (Hausberger et al., 1995; Mann and Slater, 1995; Brown and Farabaugh, 1997; Smith et al., 2002). We also found that female starlings form close bonds. Therefore, the cues used for learning a song may be correlated with cues used to develop social affinities (West et al., 1997).

As it is, sharing a song seems to give particular status to the song and to elicit long-term memories. Exactly what sort of perceptivity this is is difficult to assess but, in our experiments, females clearly responded with searching behavior when a shared song was broadcast. Moreover, socially-raised birds approached humans more readily. Social experience in early life affected perception of non-conspecifics as well.

Social experience appears to build both the visual and auditory worlds of starlings. Mirror images elicit very different responses in birds raised socially, in pairs or in isolation. Only those individuals habituated to one companion settled down rapidly; both solitary and socially-raised groups appeared disturbed. At least the paired and socially-raised birds seemed to recognize a conspecific (some social males were even aggressive), but birds raised in isolation spent much more time looking at the mirror image and did not resume feeding during the experiment (Henry et al., in prep.). Parrots also respond to mirror images (Pepperberg et al., 1995).

The construction of social cognition through social experience requires plasticity. This emerges clearly in our investigations of song perception. Developmental plasticity has been demonstrated in field L in the brain of starlings (Cousillas et al., submitted), and has been shown to exist in a variety of song nuclei and species (Doupe and Solis, 1997). Here we have demonstrated that social experience is a key in the development of complex selectivity in auditory neurons in field L.

The nature of social experience appears crucial in the development of the perceptual world of birds. Being raised with another naive young bird is sufficient to elicit a higher quality of song than when raised in isolation (Chaiken et al., 1997), but this is nothing compared to the effect from being raised with adult models, whatever the auditory experience.

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S35-5 Tool manufacture by New Caledonian crows: chipping away at human uniqueness

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Abstract New Caledonian crows have evolved relatively sophisticated tool manufacture. We identify ten complex aspects that occur in their toolmaking, which is more similar to human toolmaking than that of any other nonhuman species, including chimpanzees. Crows provide living animal subjects for investigating those behavioral, cognitive and neural adaptations that allow species to move beyond chimpanzee-like tool manufacture.

Key words New Caledonian crow, Tool manufacture, Cognition

1 Introduction

A wide range of animals, from insects to humans, use tools (Beck, 1980), but we still know very little about how complex tool manufacture evolves. This is because toolmaking in nonhuman species has so far been found to be very simple. Skills considered necessary to move beyond chimpanzee-like toolmaking include a good understanding of, first, the physical relationships and functional properties of objects, and secondly, the intentions and goals of others (Heyes, 1993; Tomasello and Call, 1997; Povinelli, 2000). Research in the last 10 years has shown that New Caledonian crows (*Corvus moneduloides*) are complex toolmakers. We briefly summarize the complexities of their

toolmaking, then compare them with those found in tool manufacture in other animals. An expanded version of this paper will appear in Hunt (2003).

2 Aspects of complex tool-manufacture in crows

2.1 Types of tools

New Caledonian crows make two distinct types of tools: stick tools and pandanus-leaf tools (Hunt, 1996). Stick-type tools consist of lengths of a range of stiff raw materials. The materials identified so far are twigs, bamboo stems, fern stolons, compound leaf stems, a slither removed from the stem of a palm leaflet and leaf petioles (Hunt, 1996, 2000a; Hunt and Gray, 2002).

Pandanus-leaf tools, on the other hand, are very flexible lengths of material that the crows cut and rip from the leaves of *Pandanus* spp. trees (Hunt, 1996). The manufacture of pandanus tools preserves a unique record for the study of toolmaking, because of the associated artifact of matching tool “counterparts” on leaves. These counterparts provide a complete artifactual history of the number and finished shapes of pandanus tools made at a site over the four years or so that leaves stay on trees (Hunt, 2000b).

2.2 Species-wide manufacture

New Caledonian crows use stick-type tools and pandanus tools throughout their range (Hunt and Gray, 2002, 2003). To April 2002, Hunt had collected 34 stick-type tools directly from birds on Grande Terre (10 sites) and Maré (2 sites), excluding tools collected in direct association with experimental work. Although a systematic survey of stick-type tools has not been carried out, our observations and information from local people indicate that the use of stick-type tools is widespread. Most of the stick-type tools were of material that



Fig. 1 New Caledonian crows use and manufacture tools

had been modified to some degree (Hunt, 1996, 2000a; Hunt and Gray, 2002). Simple modifications include the breaking-off of dead twigs or the picking-up of fallen leaves and removing their petioles. When selecting live twigs, crows usually remove any associated leaves and sometimes shorten material before using the finished tool. More involved manufacture is required to make hooked tools (see hook tools). Birds may also simply pick up petioles and dead twigs from the ground to use as tools without modification.

Our survey of counterparts in 2000 showed that pandanus-leaf toolmaking is common as well as widespread (Hunt et al., 2001; Hunt and Gray, 2003). We sampled 21 sites and recorded 5 550 counterparts, generally collecting well over 100 counterparts at each site. These counterparts were only a small percentage of those on pandanus trees throughout New Caledonia; tens of thousands are probably present at any one time. All pandanus tools are manufactured.

2.3 Diversification

The making of stick-type and pandanus-leaf tools must have developed independently of one another once crows began to use tools. Within each of these tool-types, crows make tools to distinctly different designs (Hunt, 1996; Hunt and Gray, 2002, 2003). Crows have developed two distinct groups of stick-type tools: hooked tools (see hook tools) and non-hooked tools. Use of both types is widespread. Hooked-twig tools and non-hooked tools probably have a common historical origin, given the similarities in base material: all are stiff and stick-like in nature. The lack of hooked toolmaking in species like chimpanzees (*Pan troglodytes*) and woodpecker finches (*Cactospiza pallida*) also suggests that the initial form of a stick-type tool, in an evolutionary sense, is likely to have been non-hooked (Beck, 1980). Hooked-twig tools most probably represent a population-level diversification of stick-type tools.

The range of diversification in pandanus-leaf tools is greater. Our 2000 survey of tool counterparts showed that crows manufacture them to three distinct designs: wide tools, narrow tools and stepped tools (Hunt and Gray, 2003). Similarities in material and manufacture techniques, and the continuous geographical distribution of each design type which overlaps in the southeast of the Grande Terre (main island), together suggest that all three designs are closely related and have a common historical origin. It is very likely that there has been population-level diversification in the making of pandanus tools. The finished designs of both hooked-twig tools and pandanus tools are probably transmitted, not invented individually.

2.4 Hook tools

We have found three types of hooked stick-type tools: one made from twigs, another from the thorny stems of the compound leaves of a leguminous vine (*Caesalpinia schlechteri*), and one from the stolons of a *Nephrolepis* fern (Hunt, 1996; Hunt and Gray, 2002). A material-specific technique is required to make each of these hook-types. Hooked-twig tool manufacture is by far the most complex

because it involves the creation of a hook where there had been none (see sculpted tools). Examination of hooked stick-type tools collected directly from crows, and observations of birds using them, indicates that the main working ends are the hooked ends.

The leaf-edge barbs on stepped pandanus tools only very rarely face the narrow working end of the tool. Therefore, stepped tools are hooked tools in which the hooks are natural. We know little about how crows use wide and narrow pandanus tools.

2.5 Targeting raw materials

Crows select material (pandanus leaf, fern stolon, thorny vine) that has naturally-occurring hooks (see hook tools). The birds do not need to use these materials to make non-hooked tools because suitable material for such tools is much more abundant in local rainforest. Crows also select specific tree species for material for hooked-twig tools. Eight of the nine hooked-twig tools that we collected at Pic Ningua between 1993 and 1995 were made from *Elaeocarpus dognyensis* (Hunt, 1996), whereas a family of crows that we observed in Parc Rivière Bleue in 2002 preferred to make theirs from *Cunonia vieillardii* (Hunt and Gray, 2003.). At both these sites the preferred tree species did not appear to be overly common in the rainforest. The advantages, if any, of using *E. dognyensis* and *C. vieillardii* are not known, but these trees have an abundance of forked twigs that are suitable for making hooked-twig tools. Crows also use the common, tougher-leaved pandanus species for toolmaking more often than material from less common, more fragile-leaved species (Hunt, pers. obs.).

2.6 Different tools for different foraging tasks

Crows appear to have developed different tools and associated manufacturing techniques to meet site-specific foraging needs. At Sarraméa in grazed woodland, crows commonly extract large cerambycid larvae with non-hooked tools (Hunt, 2000a). Tools there consist of a range of materials from leaf petioles to twigs that seem to be obtained mostly at the site of use. The crows commonly use them to “fish” for larvae in artificial holes drilled in dead logs, often extracting larvae clasped by their mandibles on to the ends of the tools.

High densities of large cerambycid larvae are restricted to areas outside primary rainforest where the softwood *Agathis moluccana* grows. In primary rainforest, invertebrate prey appear to be generally much smaller and without large mandibles. Here crows search in the multitude of places where prey cache themselves, as in the ends of broken branches and bases of pandanus and palm leaves (Hunt, pers. obs.). Hooked tools seem to offer advantages in this habitat, and this is where we have collected most of them. We do not know whether individual birds use different tools for different foraging tasks.

2.7 Sculpted tools

Sculpting tools involves modifying raw material to arbitrary shapes. The shapes are arbitrary because they are

formed largely by the toolmaker and little constrained by the raw material. Crows sculpt regular, two-dimensional tool shapes from the edges of pandanus leaves (Hunt, 1996, 2000b). There are obvious constraints on the finished shapes because of the two-dimensional nature of pandanus leaf, the narrowness of leaf edges and the strong parallel fibers. Nevertheless, that crows make wide, narrow and stepped tools from the same raw material demonstrates that each of these distinct designs is arbitrary.

The hook tools that crows make out of live twigs often have pointed hooks on their wide ends (Hunt, 1996; Hunt and Gray, 2002). These hooks cannot be created by simply pulling twigs off adjoining stems. Instead, the hooks on hooked-twig tools are sculpted out of the forks at the stumps with adjoining stems, which the birds then sharpen and refine with the bill (Hunt and Gray, in prep.).

2.8 Rule systems

At any one site, pandanus-tool designs are usually quite similar in shape (Hunt, 2000b; Hunt and Gray, 2003). Crows therefore manufacture them to regular, arbitrary designs from some kind of instruction stored in memory (Hunt, 2000b). We do not have the same comprehensive data for hooked-twig tools as we do for pandanus toolmaking. However, an adult and its dependent offspring observed over two weeks both followed the same basic steps when making them (Hunt and Gray, in prep.). So we suspect that hooked-twig tools are also manufactured to some kind of rule system stored in memory. Experiments are required to determine the nature of the rule systems that crows use and whether this behavior is goal-directed.

2.9 Lateralization

The manufacture of stepped pandanus tools is lateralized, not only at population level (Hunt, 2000b) but also at species level (Hunt et al., 2001). We looked at the position of stepped-tool counterparts on leaves at 19 sites throughout Grande Terre and found that birds preferred to make these tools on the left edges of leaves rather than the

right. We speculated that left-edge bias might be caused by the specialization of the right-eye/left-hemisphere system for complex sequential tasks in birds (Rogers, 2002); but the contralateral visual system responsible for the bias needs to be established experimentally. We have not investigated laterality in the toolmaking of individual crows or in the way they use the tools.

2.10 Cumulative change

Cumulative change in tool manufacture is indicated when three criteria in the design of different tools are met: (i) the designs belong to the same lineage, (ii) they have non-recapitulating manufacture techniques, and (iii) they vary in complexity and/or adaptive characteristics as improvements are incorporated over time. Such criteria are met in the stone tools produced by early humans (Tomasello et al., 1993; Foley and Lahr, 1997). The pandanus tools of the New Caledonian crow also appear to meet them (Hunt and Gray, 2003). We have already presented evidence for a common lineage in wide-, narrow- and stepped-pandanus-tool designs (see Diversification). There is also no recapitulation in the making of the three designs, that is, at no stage in the process is one design modified from another. Furthermore, stepped tools are more complex than either wide or narrow tools: (i) they are both sturdy and narrow-ended at the working end, in contrast to wide and narrow tools which are either sturdy or narrow-ended, but not both, and (ii) the technique of their manufacture is more complex than that for wide or narrow tools. Stepped tools have probably developed through the following series of evolutionary changes: non-tapered tools led to one-step tools, which in turn led to multi-step tools. The functional differences associated with these different tool shapes still need to be determined.

3 Comparison with other tool users

A comparison of toolmaking in animals shows that crows have a wider range of complexities in their tool manufacture than reported for any other species except humans (Table 1).

Table 1 Specialized features of tool manufacture at taxon level in free-living vertebrates

	Brown-headed nuthatch	Woodpecker finch	Crow	Orangutan	Chimpanzee	Humans
Distinct types of tools	---	---	+	---	---	+
Species-wide manufacture	?	?	+	?	+	+
Diversification	---	---	+	---	---	+
Hook tools	---	---	+	---	---	+
Target tool material	---	?	+	---	?	+
Different tools for different tasks	---	?	+	?	+	+
Making tools to rule systems	---	---	+	---	---	+
Lateralization	---	---	+	---	---	+
Sculpted tools	---	---	+	---	---	+
Cumulative evolution in tool design	---	---	+	---	---	+
Social transmission	---	---	?	+	+	+
Cultural variation	---	---	?	+	+	+

Reference sources in Hunt (2003). + = attribute present; ? = attribute might be present.

4 What mechanisms underlie toolmaking in crows?

Many of the specialized features in crow toolmaking have parallels elsewhere only in the cultural behaviors of humans. Is crow toolmaking therefore based on social transmission of information and complex tool-related cognitive capabilities? The nature of crow tool manufacture, involving a diversity of tool types, raises the possibility that its complexity may be the consequence of a well-developed understanding of the physical world. This is supported by recent experimental work suggesting that crows may have considerable tool-related cognitive abilities (Chappell and Kacelnik, 2002; Weir et al., 2002; Pain, 2002). There is also circumstantial evidence that transmission of tool know-how in crows involves social learning. First, it is unlikely that the different tool designs that crows use are “extended phenotypes” reflecting underlying genetic differences. Significant genetic differences even between crows at distantly separated sites on Grande Terre seems a remote possibility because the island is relatively small (ca. 400 km long and 50 km wide), and crows, although not great flyers, are still highly mobile and young are dispersive. Woodpecker finches, which can develop tool use even without social contact, still rely heavily on individual learning (Tebich et al., 2001).

Secondly, crow pandanus-tool manufacture appears to meet criteria used to identify traditional behavior (Whiten et al., 1999; Avital and Jablonka, 2000). It is habitual, the shapes of pandanus tools are generally quite similar at individual sites compared to differences between sites, the complement of pandanus-tool designs differs between sites in ways that suggest they have a common historical origin, and the shape variation in a pandanus-tool design, and consistency of shape at a site, lacks an obvious ecological explanation (Hunt, 2000b; Hunt and Gray, 2003).

Moreover, the case for both individual and social learning in the development of crow tool manufacture is plausible considering shared characteristics between *Corvus* species and primates. These include highly encephalized areas of the brain that seem to deal with so-called “intelligent” behavior (Rehkämper and Zilles, 1991), behavioral flexibility and considerable cognitive capabilities (Heinrich, 1995; Zorina, 1997; Fritz and Kotrschal, 1999), and social behavior that can provide substantial parental care for offspring (Heinrich, 1999).

5 Conclusion

There is still much to be learnt about the evolution, development and natural history of tool manufacture in New Caledonian crows. Nevertheless, our research over the last 10 years has shown that they have evolved sophisticated toolmaking skills. This is scientifically interesting not only because of what it says about crow cognition and capabilities, but also because of the insights that might be gained about the evolution of complex tool manufacture and cognition. Crow tool manufacture has already demon-

strated that capacity for making hook tools and regular, arbitrarily-shaped instruments does not require large brains, manipulatory limbs or symbolic attributes.

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Symposium 36 Energetics, physiology and biochemistry of bird flight

Introduction

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Although flight is the most characteristic and conspicuous feature of birds, its study under controlled conditions has been meager. Recently, however, major advances in facilities for performing such research have become available in the form of high quality wind tunnels. Using the large wind tunnel of the Birmingham/Bangor group in Britain, Charles Bishop and co-workers present data here on heart rate and rate of oxygen uptake in barnacle geese (*Branta leucopsis*) during flight. The long-term objective of this study is to make possible the use of heart rate as an indicator of metabolic rate in free-flying geese and other migrants. Marcel Klaassen has also used a tunnel in Lund, Sweden, to augment his findings here on the effect of size on energy and water use during migratory flight, together with problems associated with their modeling.

The three remaining papers were only presented orally. Herbert Biebach and Ulf Bauchinger discussed changes in the composition of the breast muscles in response to long-distance flights, making direct measure-

ments of energy expenditure, body mass and breast muscle performance in barn swallows (*Hirundo rustica*) and rosy starlings (*Sturnus roseus*) in the wind tunnel at Andechs, Germany. The two final papers reported on the flight physiology of the smallest of birds, the hummingbirds. Hummingbirds have the highest mass-specific rates of aerobic metabolism among vertebrates. Ingenious experiments and painstaking morphometric and biochemical studies have enabled determination of their power output and its biochemical basis. Robert Dudley, from Austin, Texas, addressed the ecological and evolutionary physiology of hovering in hummingbirds, including the relation of power output to body mass and altitude. In the final paper, Raul Suarez, from Santa Barbara, California, also discussed power output and the biochemical basis of hummingbird metabolism, demonstrating that flight in hummingbirds is at the very upper limits of performance. Abstracts of the last three papers are published in the Abstract volume of the Congress.

S36-1 The flight energetics of barnacle geese (*Branta leucopsis*) under wild and captive conditions

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Abstract Experimental data on the relationship between mean heart rate (f_H) and mean rate of oxygen consumption (VO_2) of captive barnacle geese during flights in a wind tunnel are reviewed in terms of their capacity to predict the mean VO_2 of wild barnacle geese, based on recordings of their f_H during autumn migratory flights between Spitsbergen (78°N) and Scotland (55°N). f_H increased linearly with simultaneously recorded VO_2 in a single barnacle goose flying in the wind tunnel ($VO_2 = 1.42 f_H - 304$, $r^2 = 0.82$, $P < 0.001$, $N = 12$ flights). The mean f_H of wild migratory barnacle geese was 253 beats min^{-1} . Substitution of this value into the above calibration equation results in an unrealistically low value for mean migratory VO_2 of only 55 $ml\ min^{-1}$. Factors such as difference in heart mass, selective tissue perfusion, environmental temperature and formation flight may account for some of the difference in f_H between the captive and wild geese.

Key words Migration, Energetics, Geese, Heart rate, Oxygen consumption, *Branta leucopsis*

1 Introduction

It is not easy to obtain cardiovascular, respiratory and energetic data from animals during flight, either under captive or wild conditions; and very few techniques are applicable to both situations. No single approach can adequately give all of the necessary information required for a full analysis of the physiological responses to flight. The respiratory and cardiovascular systems of birds and mammals are primarily designed to enable gas exchange and molecular flux between the circulating blood supply and various organs and tissues and the external environment (Schmidt-Nielsen, 1997). This process is especially demanding during sustained locomotor activities, in order to support the prolonged metabolic activity of the muscles by continuously oxidizing stored fuels to yield high energy bonds within molecules of ATP. The rate at which oxygen is taken up by the lungs and delivered to the working muscles is closely correlated with the rate of circulation of blood (and hence, oxygen) around the body, and with its eventual utilization in oxidative phosphorylation (Weibel et al., 1991). Thus, the rate of oxygen consumption (VO_2) gives an indication of the rate of fuel oxidation required to sustain locomotor activity and associated aerobic physiological processes.

Recent technological advances have enabled the development of biotelemetry and data logging devices which have been successfully deployed in studies of the physiology and behavior of free-flying birds (Butler and Woakes, 1980; Butler et al., 1998; Weimerskirch et al., 2000). For

running, swimming and gliding, in particular, it has been demonstrated that, when properly calibrated and when mean data are used from a number of individuals, heart rate (f_H) can be measured and used as an indicator of VO_2 in free-living birds (Nolet et al., 1992; Bevan et al., 1994, 1995a,b; Green et al., 2001). However, the relationships between f_H and VO_2 during resting, walking and running, or during swimming, may not necessarily be the same as when the birds are flying (Gessaman, 1980; Nolet et al., 1992; Butler et al., 2000). In general, it is recommended that, where possible, the range of f_H values recorded in the field should not exceed the range of f_H measured during calibration. Thus, f_H should be calibrated against VO_2 for birds during flapping flight before the method can be used reliably to determine the VO_2 of free-flying birds in the wild, as f_H during flight can be much greater than that during hind limb exercise (Nolet et al., 1992; Butler et al., 1998; Butler et al., 2000).

The general relationship between f_H and VO_2 is described by the Fick equation

$$VO_2 = f_H \times V_s \times (C_a O_2 - C_v O_2) \quad (1)$$

where V_s is cardiac stroke volume, $C_a O_2$ the oxygen content of arterial blood, and $C_v O_2$ the oxygen content of mixed venous blood. This relationship can be used as a basis to model predictions for the VO_2 of birds during forward flapping flight (Bishop and Butler, 1999; Bishop, 1997, 1999), or used in conjunction with data obtained from calibration studies.

The increased use of wind tunnels over the past few decades has greatly increased our understanding of the

physiology, biomechanics and aerodynamics of birds during gliding and flapping flight (Butler et al., 1977; Butler and Woakes, 1990; Norberg, 1990; Pennycuik et al., 1996; Dial et al., 1997; Kvist et al., 1998; Rosén and Hedenström, 2001). The wind tunnel itself may influence bird behavior and wing kinematics during flight, so it is important where possible to compare these data with those from free-flying birds (Butler et al., 1977; Rayner, 1994). Given such potentially direct effects from experimental conditions, and the indirect effects of captive husbandry on attributes such as physical fitness, it would be valuable to compare data collected from animals living in the wild with that from animals in captivity. In this paper we will review the experimental data on the relationship between mean heart rate (f_H) and mean VO_2 of captive barnacle geese during flights in a wind tunnel (Ward et al., 2002), in terms of their capacity to predict the typical VO_2 of wild barnacle geese, based on recordings of their f_H on autumn migratory flights between Spitsbergen (78°N) and Caerlaverock, Scotland (55°N) (Butler et al., 1998).

2 F_H and VO_2 of captive barnacle geese flying in a wind tunnel

Ward et al. (2002) trained young barnacle geese (1.6 to 2.3 kg) to fly in a large wind tunnel, and to walk on a treadmill while covered by a respirometry chamber. They simultaneously measured the VO_2 and f_H of 5 individuals on the treadmill ($N=50$) and 4 individuals in the wind tunnel ($N=15$), although in the latter case one bird made almost all the flights ($N=12$). A full description of the wind tunnel is provided in Ward et al. (2002). Following 6 weeks of training, heart rate data loggers which stored f_H as averages over 30 s intervals (Woakes et al., 1995) were implanted into the abdomens of the geese under sterile conditions (Butler et al., 2000). The birds were given one week to recover before a further 3 weeks of experimental flights (Ward et al., 2002). In order to measure the rate of oxygen consumption and heart rate during flight, geese were flown wearing a lightweight, clear polyurethane mask (4.4 g) which covered the beak and nares. Data where both f_H (beats min^{-1}) and VO_2 (ml min^{-1}) were recorded simultaneously are presented in Fig. 1, but only the data from goose B-B are used to calculate the regression relationship between f_H and VO_2 . Data are presented as the overall mean values recorded over complete flights ($N=12$ flights).

Ward et al. (2002) show (Fig. 1) that the linear regression equation for 5 barnacle geese walking/running on a treadmill (i.e. terrestrial locomotion) was

$$VO_2 = 0.32f_H - 11, r^2 = 0.70 \quad (2)$$

while that for goose B-B flying in a wind tunnel was

$$VO_2 = 1.42f_H - 304, r^2 = 0.82 \quad (3)$$

The slopes and intercepts of the relationship for the calibration of f_H and VO_2 during flight are significantly different from those during terrestrial locomotion (ANCOVA: intercept $F_{1,22} = 9.2, P = 0.007$; slope $F_{1,22} = 7.9, P = 0.01$).

3 Heart rate from other studies of wild and captive barnacle geese

The values for f_H measured in other experiments and observations of captive and wild barnacle geese during flight in a wind generator or during free-ranging flights are shown in Fig 2. Using data loggers, Butler et al. (1998) measured the f_H of four geese flying on autumn migration between Spitsbergen and Scotland. Mean f_H at the beginning of the flight from Spitsbergen was 317 ± 9 beats min^{-1} . As it progressed, mean f_H gradually declined until it reached a low point of 226 ± 10 beats min^{-1} , after approximately 70% of the mean total journey time had elapsed (61.3 ± 2.5 h; Butler et al., 1998). Mean f_H for the entire migratory flight was 253 ± 10 beats min^{-1} . The values for f_H from the wild geese are substantially lower than the mean values of 512 ± 4 beats min^{-1} for geese (body mass $M_b = 1.7$ kg) trained to fly behind a truck (Butler and Woakes, 1980) and 378 ± 15 beats min^{-1} for geese ($M_b = 1.7$ kg) trained to fly in front of a wind generator (WG) in Toronto (Butler et al., 2000). A mean value for f_H of 451 ± 23 beats min^{-1} ($N=4$ birds) was recorded in barnacle geese flying unencumbered by respirometry masks in the Birmingham wind tunnel (WT; Ward et al., 2002). In the latter study, f_H was measured from birds flying at a distance of more than 1 m away from the trainer, where the trainer had no detectable effect on f_H .

4 Discussion

4.1 Calibration of f_H and VO_2 during walking and flight

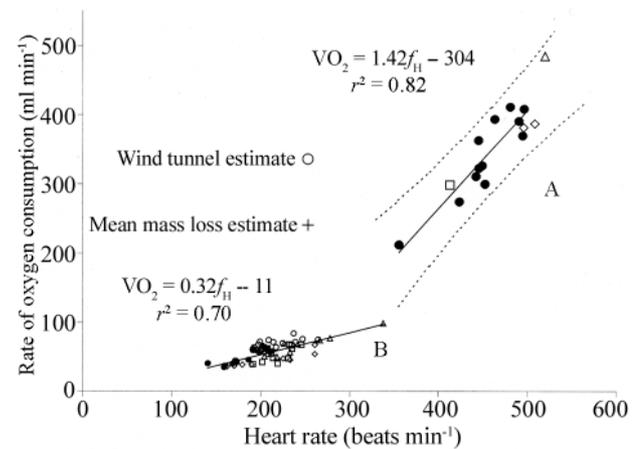


Fig. 1 Linear regression relationships between mean heart rate (f_H , beats min^{-1}) plotted against mean rate of oxygen uptake (VO_2 , ml min^{-1}) of barnacle geese flying in a wind tunnel (A) and walking on a treadmill (B)

The filled dots represent mean values for individual exercise bouts for one barnacle goose (B-B), from which most data on the relationship between f_H and VO_2 during flight were obtained ($N=12$ flights). The open symbols represent mean values from 3 additional birds during flight ($N=4$) and 4 additional birds during walking ($N=50$). The dotted lines = 95% prediction intervals for goose B-B during flight. Data from Ward et al. (2002). Also presented are estimates for mean VO_2 of wild migrating geese based on wind tunnel data (large open circle) and minimum mass loss data (large cross) plotted against mean f_H during migration.

in captive barnacle geese

Nolet et al. (1992) suggested that the f_H/VO_2 relationship in barnacle geese during terrestrial locomotion could not be the same as that during flight. This suggestion is clearly confirmed by the results presented in Fig. 1, where the extrapolation of regression equation (2) for running geese does not predict realistic values of VO_2 from the values of f_H recorded for flying geese, and vice versa. At an f_H of around 350 beats min^{-1} , the VO_2 of the flying geese is approximately twice as great as that during running, and this is likely to result from both a relative increase in cardiac stroke volume and so cardiac output (Bishop and Butler, 1995), and an associated increase in oxygen extraction from the blood (Butler et al., 1977). This might be expected because barnacle geese have flight muscles that are approximately twice as large as the total musculature of the legs (Bishop et al., 1996) and, in addition, a higher aerobic capacity (Bishop et al., 1995).

4.2 Predictions of VO_2 in wild migrant barnacle geese

Using the f_H and VO_2 calibration of captive birds flying in the wind tunnel In principle, it should be possible to use the calibration relationship for f_H/VO_2 during flight in the wind tunnel to estimate VO_2 in wild migrant flying barnacle geese, based on recordings of f_H made using data loggers during migration (Butler et al., 1998). However, the ability to predict mean VO_2 in wild migrating geese from the calibration of f_H in the wind tunnel is based on the assumption that the captive-bred birds do not differ from wild birds in wing morphology, in the physiology and morphology of the heart and the major locomotory muscles, nor in the major constituents of the blood. An additional assumption is that there is no large difference in physiological and environmental variables, such as air temperature, that might influence the peripheral resistance of the blood vasculature. Large changes in any of these variables could alter the relationship between f_H , stroke volume and oxygen extraction, and hence that between VO_2 and f_H .

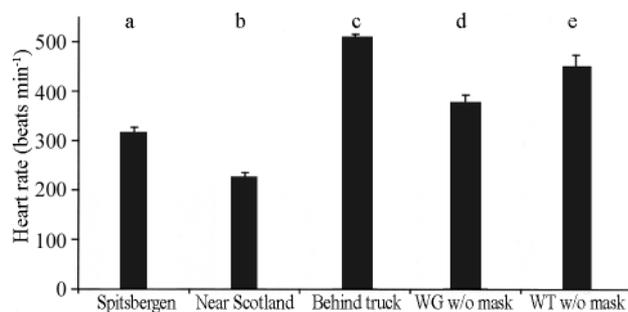


Fig. 2 Mean $f_H \pm SE$ recorded from wild barnacle geese (a) flying at start of autumn migration from Spitsbergen and (b) flying on approach to Scotland, and from captive barnacle geese (c) flying behind a truck, (d) flying without respirometry mask in front of a wind generator (WG), and (e) flying without respirometry mask in a wind tunnel (WT) Data from Butler and Woakes (1980), Butler et al. (1998), Butler et al. (2000) and Ward et al. (2002).

Fig. 2 shows that the mean f_H of captive geese flying in the wind tunnel was generally much higher than that of migrating wild geese. Thus, when using the mean f_H recorded during migratory flights in equation (3), the prediction of VO_2 in wild, migrating geese is unrealistically low (55 ml min^{-1}). Therefore, the f_H/VO_2 relationship for captive geese during flight must be different from that in wild migratory geese (Butler et al., 1998). This suggests that a number of the assumptions mentioned above are not fulfilled.

Using the VO_2 of captive birds flying in the wind tunnel Taking the value of f_H (451 beats min^{-1}) obtained for captive barnacle geese during flights in the wind tunnel without a respiratory mask (Fig. 2), we can use regression equation (3) to predict the VO_2 of captive birds in unencumbered flight (Ward et al., 2002). Equation (3) yields a prediction for VO_2 for geese flying in the wind tunnel of 336 ± 31 ml min^{-1} (mean body mass 2.06 kg, $N = 4$). This gives a mass-specific value of 163 ml min^{-1} kg^{-1} . Over the range of speeds (16–19 m s^{-1}) that barnacle geese were usually prepared to fly for 6–10 minutes in the wind tunnel, there was no significant effect of flight speed on VO_2 (Ward et al., 2002). Therefore, the above estimate of VO_2 probably represents the minimum power required for forward flapping flight in the wind tunnel.

This estimate for minimum VO_2 during flight in a wind tunnel should reasonably be considered to be a slight overestimate for the minimum power required by barnacle geese during free-ranging flight. Although the f_H of the birds in the wind tunnel was recorded during unencumbered flight and without help from a respiratory mask and trainer, any relatively unstable posture (e.g., head turning), turbulence in the wind tunnel and stress associated with the laboratory environment, would all tend to increase flight costs. In addition, the primary feathers had become abraded by aviary conditions.

Mass loss estimates During field studies conducted by Bishop et al. (1996), four birds were caught in Hornsund, southern Spitsbergen, towards the end of the premigratory period. Average body mass was 2.302 ± 0.099 kg compared to an average of 1.746 kg for 13 geese caught in Scotland on 4th October (Owen and Ogilvie, 1979). Assuming no evolutionary shift in the mean size during this period, these data give a mean body mass difference of 556 g between pre- and post-migratory geese. This figure represents our best estimate for minimum body mass loss in barnacle geese performing the complete migration of around 2 500 km between Hornsund and Scotland. Total flying time for this migration is, on average, 61 h. (Butler et al., 1998). Assuming that the metabolic energy consumed during the migration comes from 96% lipid stores and 4% from proteinaceous tissue (Le Maho et al., 1988; Butler et al., 1998), the average VO_2 required to metabolize 556 g of body tissue during 61 h of flight is 241 ml min^{-1} .

This estimate for minimum mean mass loss during migratory flight should reasonably be considered a slight underestimate, as the birds caught in Hornsund were still

premigratory, and it is possible that they could have had at least another week to continue gaining weight before migration. The mean difference in body mass between pre-migratory geese in Hornsund and post-molting adult geese caught earlier in the season at their normal breeding site in Spitsbergen (1.825 ± 0.057) can be accounted for by an average body mass increase of 24 g per day (Bishop et al., 1996). Thus, an extra week of pre-migratory feeding could theoretically have resulted in an average body mass difference of up to 723 g between pre- and post-migration. Moreover, some birds require as little as 5 days to complete the migration between Spitsbergen and Scotland, while others take 2 or 3 weeks (Butler et al., 1998). One possible explanation for this is that only the fattest birds are in sufficiently good condition to fly for around 61 h in the space of 5 days, as there would be little chance for significant refueling during that time. If geese do take opportunities to take on additional fuel, then this yields a final prediction for the maximal body mass change over a migration period of 5 days of up to 783 g. The average VO_2 required to metabolize 783 g of body tissue during 61 h of flight is 339 ml min^{-1} . This figure is very similar to the predicted value for unrestrained flight in the wind tunnel ($336 \pm 31 \text{ ml min}^{-1}$), which we have argued above is probably a slight overestimate of the cost of flight for free-flying wild birds.

As stated, we would expect the energetic cost of flight for captive and wild barnacle geese of a given morphology and body mass to be similar. Thus, we will use the above wind tunnel value (336 ml min^{-1} ; $M_b = 2.06 \text{ kg}$) as an upper estimate, and the minimum mass loss value (241 ml min^{-1}) as a lower estimate, for the mean costs of migratory flight between Spitsbergen and Scotland. The four wild pre-migratory geese had an average M_b of 2.3 kg so, assuming no extra increase in mass, this would give an approximate mean body mass for the migratory flight of around 2 kg, similar to the mean mass in wind tunnel birds. These estimates for mean migratory VO_2 and body mass can then be associated directly with the measured mean value for the migratory f_H ($253 \text{ beats min}^{-1}$) recorded from four barnacle geese during autumn migration (Butler et al., 1988).

Fig. 1 shows these predictions for the maximum and minimum mean VO_2 s in wild migrant barnacle geese, calculated respectively from f_H in the wind tunnel and field data for mass loss, plotted against the mean value for f_H during migration, and alongside the power equation calibrating f_H and VO_2 for the captive geese flying in the wind tunnel. If wild and captive geese were physiologically and morphologically similar, and flew in similar environmental conditions, it would be expected that the values for the predicted maximum and minimum mean migratory VO_2 s for wild barnacle geese would lie close to the f_H/VO_2 calibration line. As this is not the case, then some or all of these conditions or assumptions must differ between the two populations.

4.3 Modeling the cardiovascular responses of captive and wild migrant geese

The heart mass (M_h) of wild pre-migratory barnacle

geese (22.1 g; Bishop et al., 1998) was 30% greater than that of captive geese (17 g) flying in the wind tunnel (unpublished data). Bishop and Butler (1995) and Bishop (1997) used the Fick relationship in equation (1) to model predictions for the VO_2 of birds during forward flapping flight. Bishop (1997) showed that for mammals, maximum sustainable cardiac output (V_b) was a function of heart mass, and calculated that

$$V_b = 212.7 M_h^{0.879 \pm 0.036} \quad (4)$$

The highest sustained mean f_H recorded during a single flight by a captive barnacle goose was $520 \text{ beats min}^{-1}$. Thus, assuming that cardiac muscle in birds has a similar physiological and biomechanical performance to that in mammals (Bishop, 1997), equation (4) predicts that for a captive barnacle goose, maximum cardiac stroke volume (V_s) = 4.96 ml. If the maximum f_H of wild geese is similar to that of captive geese, then the predicted V_s for wild migrants is 6.24 ml.

Grubb (1983) showed that the V_s of birds at rest ($V_{s,\text{rest}}$) scaled as

$$V_{s,\text{rest}} = 0.18 M_h^{1.05} \quad (5)$$

This would suggest a $V_{s,\text{rest}}$ for the captive barnacle geese of 3.53 ml, compared with the estimate for V_s during flight ($V_{s,\text{flight}}$) of 4.96 ml from equation (4). The prediction that $V_{s,\text{flight}}$ may be larger than $V_{s,\text{rest}}$ by 1.4 fold is consistent with the results of Bishop and Butler (1995), who reanalysed data from the study of Butler et al. (1977) and suggested that $V_{s,\text{flight}}$ of pigeons could be approximately 1.4-fold greater than $V_{s,\text{rest}}$. If a similar increase in V_s also occurred in barnacle geese during flight, this would contribute to the difference in the relationship between the f_H/VO_2 in walking and flying geese (Fig. 1; Nolet et al., 1992; Butler et al., 2000). In addition, the greater cardiac output could be associated with a larger value for oxygen extraction (see below), so there would be a further increase in VO_2 for a given value of f_H when flying.

We can investigate and visualize the possible effect of an increase in V_s between flying and walking, and a further increase in $V_{s,\text{flight}}$ between wild migrating geese and their captive counterparts due to their larger hearts, by estimating values for cardiac output (V_b) and plotting them against the measured values of VO_2 . Fig. 3 plots the estimated relationship between the V_b and VO_2 of walking and flying captive barnacle geese, calculated by multiplying the measured values for f_H during walking by the estimated $V_{s,\text{rest}}$ using equation (5), and multiplying the values for f_H during flying by the estimated $V_{s,\text{flight}}$ using equation (4). The linear regression for the estimated relationship between V_b and VO_2 during flight then is

$$\text{VO}_2 = 0.287 V_b - 304.4, \quad r^2 = 0.82 \quad (6)$$

In theory, we would expect equations (4) and (5), which are based on an allometric function of M_h , to be applicable to wild and captive birds and, therefore, that equation (6) would also be similar for both captive and wild barnacle geese if heart mass alone varied between the two

groups. Thus, using the measured value for mean f_H from the wild, migrating geese, we can estimate their V_b , using the $V_{s,flight}$ of 6.24 ml based on their heart mass. The estimate for V_b in the wild geese is plotted in Fig 3 against the maximum and minimum mean VO_2 s, calculated from f_H in the wind tunnel and field data on mass loss, respectively. The higher estimate for minimum VO_2 in the migrants is well above the calibration line for captive birds, while the minimum estimate of VO_2 lies close to the 95% prediction interval of the data for wind tunnel birds. It is clear from Fig. 3 that, while the larger hearts of the wild geese will have a major impact on the relationship between f_H and VO_2 , our current data cannot account for all of the apparent differences between wild and captive geese.

4.4 Additional factors affecting the f_H/VO_2 relationship of geese during flight

There are various confounding variables that could be taken into account. Any possible reduction of peripheral circulation experienced during flight, or selective vasoconstriction to other tissues, would tend to divert blood towards the working muscles (Butler et al., 1988; Bevan and Butler, 1992) and could also increase oxygen extraction for a given value of f_H and V_b , thus shifting the f_H/VO_2 and V_b/VO_2 curves further to the left. Selective perfusion of tissues vital for support of flight could possibly occur in wild migrants as a physiological strategy to maximize flight performance, and account for much of the remaining differ-

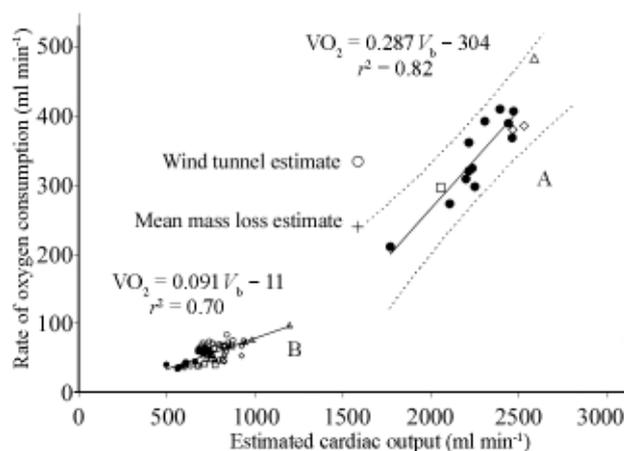


Fig. 3 Linear regression relationships between estimated mean cardiac output (V_b , ml min^{-1}) plotted against mean rate of oxygen consumption (VO_2 , ml min^{-1}) of barnacle geese flying in a wind tunnel (A) and walking on a treadmill (B). The filled dots represent mean values for individual exercise bouts for one barnacle goose (B–B), from which most data on the relationship between f_H and VO_2 during flight were obtained ($N=12$ flights). The open symbols represent mean values from 3 additional birds during flight ($N=4$) and 4 additional birds during walking ($N=50$). The dotted lines = 95% prediction intervals for B–B during flight. Also presented are estimates for mean VO_2 of wild migrating geese based on wind tunnel data (large open circle) and minimum mass loss data (large cross) plotted against estimated mean V_b during migration.

ence between f_H recorded in the wild and in the wind tunnel. The barnacle geese flying in the wind tunnel experienced higher air temperatures that those in the Arctic and may have been relatively heat stressed, leading to a potential increase in blood flow to the legs and feet and a consequent reduction in overall oxygen extraction for a given value of f_H and V_b .

It has also been suggested that migrant birds such as geese may gain significant aerodynamic advantage by flying in flock formation (Lissaman and Shollenberger, 1970; Hummel, 1995). In theory, the consequent effect of reducing both the f_H and VO_2 of geese flying in formation could be considerable. Weimerskirch et al. (2001) have shown that pelicans when flying in formation have values of f_H that are around 11%–14% lower than those in birds flying alone. If a similar reduction occurs in barnacle geese flying in formation, this would equate to a potential energy saving of approximately 25%, according to calibration equation (3). There is, however, no evidence at present that the wild migrant barnacle geese actually flew in such flocks for much of their migration, or that they obtained any such aerodynamic advantage during flapping flight.

Clearly, it is necessary to conduct further wind tunnel- and field- based studies in order to clarify the detailed relationship between f_H/VO_2 and investigate the differences, particularly in f_H , between wild and captive birds. Even so, both the wind tunnel and mass-loss data for barnacle geese, and the inter-species allometric relationship of VO_2 for 9 different species of birds (mass-specific minimum $VO_2 = 173$, $M_b^{-0.224}$, $r^2 = 0.848$; Bishop et al., 2002), support the conclusion that the mass-specific minimum power cost of forward flapping flight for larger species of birds appears to be remarkably low. For barnacle geese, this value lies between a minimum of 121 and a maximum of 163 $\text{ml min}^{-1} \text{kg}^{-1}$.

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S36-2 The effect of size on water and energy balance during migratory flight: empirical data versus theory

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Abstract In the absence of sufficiently reliable empirical data, theoretical models for estimating the costs of flight have had to serve ecology. This has led to general insights, such as the finding that power requirements for flight increase rapidly with size. As maximum fuel loads decrease with size, potential flight range decreases too. Because water balance also needs to be maintained during flight, the potential problems for large migrants only seem to grow. This has significant implications for migratory flight. With every gram of fuel added, the more can returns in distance flown diminish. The physiological challenges of long flight in birds, however, can now be studied with greater accuracy than ever before because of the development of wind tunnels. Here, the latest findings are used to update previous predictions on energy and water use in migrating birds in relation to inter- and intra-specific variations in size. These findings are then placed into a more comprehensive ecological context by considering some of their consequences for avian migration strategies, stopover ecology and breeding performance.

Key words Flight, Migration, Energy, Water, Body size

1 Introduction

Although migration is widely associated with migratory flight, approximately 90% of migration time is actually spent going nowhere at stopover sites (Hedenström and Ålerstam, 1998). Thus, judged by time allocation, migration is more a matter of foraging. It is estimated that approximately one third of all energy expenditure during migration, however, is spent in the relatively short period of migratory flight (Hedenström and Ålerstam, 1998). Flight costs, therefore, loom large in the energy budget of migratory birds. This has caused much interest in energy levels, and in how flight costs change both across species and individuals of different mass and morphometry as they empty their fuel stores en route. To estimate flight costs empirically, nevertheless, is difficult, as a result of which many researchers have relied on aerodynamic theory and allometric equations for estimating the costs.

The preference for the aerodynamic model of Pennycuik (1989) as an explanant can be explained by the flexibility that it offers. Variations in flight altitude, body mass, morphometry, air density, etc., can all be taken into account in flight cost estimates. Unfortunately however, the choice of model, including the alternative empirical flight cost estimates model of Masman and Klaassen (1987), can lead to quite different outcomes. In Fig. 1, I provide an overview of empirical flight cost estimates in unrestrained birds during prolonged flight, and compare them with two aerodynamic predictions: one from Pennycuik's original 1989 model (Pen89) and another from the same model with a much lower body drag coefficient, after Pennycuik, Klaassen,

Kvist and Lindström (1996) (Pen96). Although the match on the depicted log-log scale may look impressive, predictions according to aerodynamic theory may vary considerably from empirical findings: on average 13% (range 50% to 99%) and 28% (range 66% to 51%) for Pen89 and Pen96 respectively.

Using repeated-measures ANCOVA, the effect of the model employed was significant ($F_{2,30} = 3.33, P < 0.05$). In a post-hoc comparison, this appeared to be due mainly to the large differences between Pen96 and the other estimates. Flight-power requirement estimates often serve an important role in "higher-order" models of migration, such as the prediction of flight range and optimal departure fuel loads from stopover sites. In this paper, I will focus on the effects of the discrepancies between empirical and aerodynamic flight cost models on the outcomes of higher-order migration models. It appears that these discrepancies can sometimes be huge, indicating that flight cost models need to be selected extremely carefully, and that studies using them should be accompanied at least by sensitivity analyses.

Not only energy balance but also water balance is thought to limit migratory performance in birds (Carmiet al., 1992; Klaassen and Biebach, 2000; Klaassen et al., 1999; Liehti et al., 2000). These predictions are based on rather complicated physiological migration models with a large number of parameters. Some of the parameter values are based on scanty empirical data. For one of the most critical parameters — exhaled air temperature — new data have now surfaced, and I review their impact here on the extent to which water deficit may limit flight range.

2 Water balance

In a sensitivity analysis of their water-budget model, Klaassen et al. (1999) identified two parameters that largely determined outcomes from the model: exhaled air temperature and power requirements for flight. These parameters are also often poorly understood and surrounded by much uncertainty. Below I discuss power requirements for flight in more detail and here only focus on exhaled air temperature. When a bird inhales air, the temperature of the air increases to near body temperature, and in the lungs becomes saturated with water. As the volume of water that air can contain increases exponentially with temperature, a flying bird try-

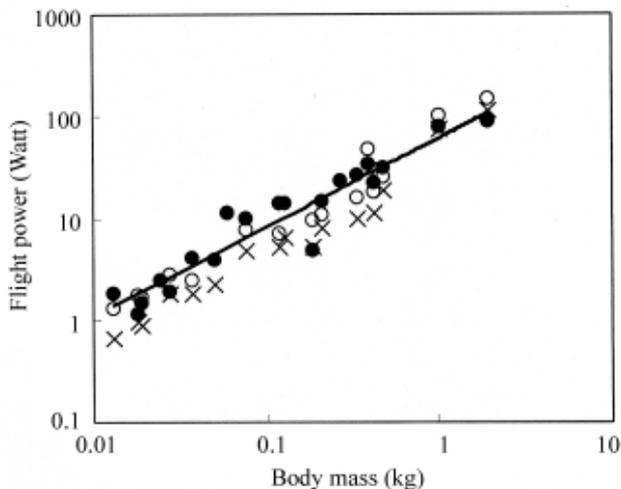


Fig. 1 Empirically estimated power requirements for flight for 20 species of birds in relation to body mass

Black dots — $Y = 10^{1.780 \pm 0.073} X^{0.868 \pm 0.065}$, $R^2 = 0.908$; error terms are standard errors. In the same graph are predicted power requirements according to Pennycuick (1989): circles — $Y = 10^{1.790 \pm 0.060} X^{0.914 \pm 0.055}$, $R^2 = 0.948$, $N = 17$; and Pennycuick (1996): crosses — $Y = 10^{1.644 \pm 0.060} X^{0.975 \pm 0.055}$, $R^2 = 0.954$, $N = 17$. Predictions from aerodynamic models were based on birds flying at sea level and with species-specific wing characteristics and flight speeds. Most empirical flight cost studies provided information for these parameters, but data on wing morphometrics were also obtained from Robbins et al. (1966), Masman and Klaassen (1987), Tobalske and Dial (1994), Pennycuick et al. (1996), Butler et al. (1998), Bruderer and Boldt (2001), and some internet sources. Additional flight speed data came from Bruderer and Boldt (2001). Taxa covered: *Anas rubripes* (Berger et al., 1970), *Branta leucopsis* (Butler et al., 2000), *Calidris canutus* (Kvist et al., 2001), *Columba livia* (Butler et al., 1977; Gessaman and Nagy, 1988; LeFebvre, 1964; Rothe et al., 1987), *Corvus cryptoleucus* (Hudson and Bernstein, 1983), *Delichon urbica* (Hails, 1979; Westerterp and Bryant, 1984), *Falco sparverius* (Gessaman, 1980), *Falco tinnunculus* (Masman and Klaassen, 1987), *Hirundo rustica* (Hails, 1979; Turner, 1982a, 1982b), *Larus atricilla* (Tucker, 1972), *Larus delawarensis* (Berger et al., 1970), *Luscinia luscinia* (Klaassen et al., 2000), *Melospittacus undulatus* (Tucker, 1966), *Progne subis* (Utter and Levebre, 1970), *Riparia riparia* (Turner, 1982a, 1982b; Westerterp and Bryant, 1984), *Sterna fuscata* (Flint and Nagy, 1984), *Sturnus vulgaris* (Torre-Bueno and LaRochelle, 1978; Ward et al., 2001; Westerterp and Drent, 1985). Only the least square fit through the empirical data points is depicted.

ing to conserve water should attempt to cool down exhaled air as far as possible through heat exchange in the nasal passage. The extent to which a bird is successful in doing this largely determines its water loss.

Although this is a crucial determinant of water loss, only data from flights of seven American black ducks (*Anas rubripes*), which lasted no longer than 18 seconds anyway, were available for its estimation (Berger et al., 1971) — until recently. Over the past few years, the data set has expanded considerably (Fig. 2), with measurements from pigeons (*Columba livia*) flying from 1.5 up to 3 h (Michaeli and Pinshow, 2001) and Eurasian widgeon (*Anas penelope*) and teal (*Anas crecca*) flying from 4 up to 38 min. (R. Klaassen et al., unpubl). These new estimates, from advanced measuring techniques on different birds flying for much longer periods, appear to deviate only slightly from the black duck data. Thus, there still seems to be a strong case for earlier predictions that, under specific conditions, migratory flight may indeed be constrained by water budgets (Klaassen et al., 1999).

3 Estimating maximum flight range

Maximum coverable distance is an important parameter when migrating birds have to migrate across inhospitable oceans and deserts; and it is a paramount constraint on birds that use discontinuously distributed food resources and are bound to specific habitats on stopovers. The flight range of birds is generally considered to decrease with increasing bird size (Klaassen, 1996). That contention, however, is based solely on aerodynamic theory. Maximum flight range (m) can be derived by taking the maximum fuel load of an animal (J), dividing it by power requirements for flight (Watt or J/s) and multiplying that with its flight speed

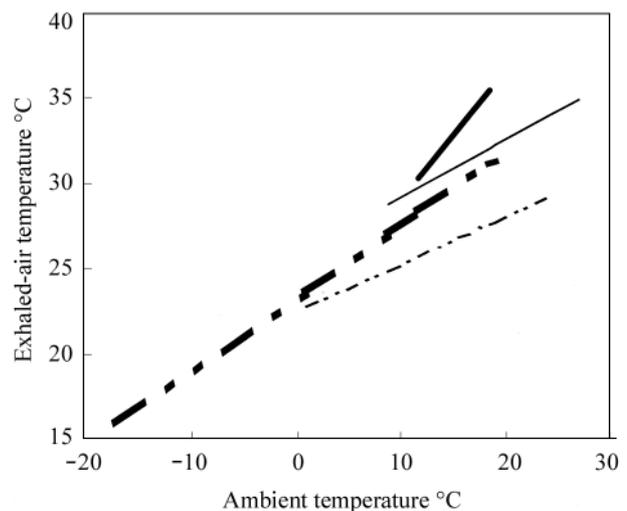


Fig. 2 Exhaled air temperature as a function of ambient air temperature in different birds

Heavy dashed line: American black duck (*Anas rubripes*); thin line: rock dove (*Columba livia*); thin dashed line: common teal (*Anas crecca*); heavy line: Eurasian widgeon (*Anas penelope*).

(m/s). Using Pennycuick's aerodynamic model, maximum flight range will decrease significantly with an increase in size. Using the empirical flight cost model of Masman and Klaassen (1987), however, will result in far smaller changes with size. According to it, changes will initially be positive and only slightly decrease at body masses of more than a kg (Klaassen, 2002).

4 Size-dependent breeding strategy in arctic breeding birds

"Capital" and "income" breeding are two extreme strategies that lie on a continuous scale, the first relying exclusively on body stores and the second on local food sources for all nutritional requirements during breeding. Klaassen (2002) investigated size-dependency in the use of capital breeding strategy in arctic breeding migrants. Employing allometric equations, I evaluated migratory time and energy costs associated with carrying extra stores to the breeding grounds. It appeared that the outcome of this modeling depended critically on the power requirements for migratory flight.

As stressed earlier, maximum flight range predictions by the Pennycuick models and the empirical flight cost model vary greatly, being much shorter under the Pennycuick models. It can be expected that a capital breeder would want to take along extra reserves to the breeding grounds for egg production and incubation, and will thus need to be able trade distance for capital. According to the aerodynamic model, however, the scope for large birds to trade distance for extra reserves for investment in egg production upon

arrival on their breeding grounds is very small. In contrast, the empirical flight cost model predicts that the scope for capital breeding will only increase with size (Klaassen, 2002).

Striking differences between the two models appeared again in comparisons of estimated time required to acquire reserves for migratory flight or for egg synthesis and catabolism on the breeding grounds. Fuelling times for migratory flight predicted by aerodynamic theory were much longer than those based on the empirical flight cost model (Klaassen, 2002). Thus, if the Pennycuick predictions of power requirements are indicative for arctic breeding birds, a capital breeding strategy will be extremely difficult to realize for large birds given their short flight range and long refuelling times. If the empirical flight cost model is closer to the truth, capital breeding is probably less of a marginal life-style for large birds. Support for the empirical flight cost model comes from various sources that have found a capital breeding strategy in large but not small arctic breeding birds (Klaassen, 2002; Klaassen, Lindström, Meltofte and Piersma, 2001).

5 Departure fuel load

Conceivably, the flight costs for a bird on migration will decrease while fuel stores are being catabolized. Aerodynamic theory provides predictions for this. These predictions have now been challenged by a study by Kvist et al. (2001) on knots (*Calidris canutus*) flown in a wind tunnel. In Fig. 3, their findings are plotted against Pen89 and Pen96 predictions. The empirical data suggest that flight costs decrease at a much slower rate with a decrease in fuel load

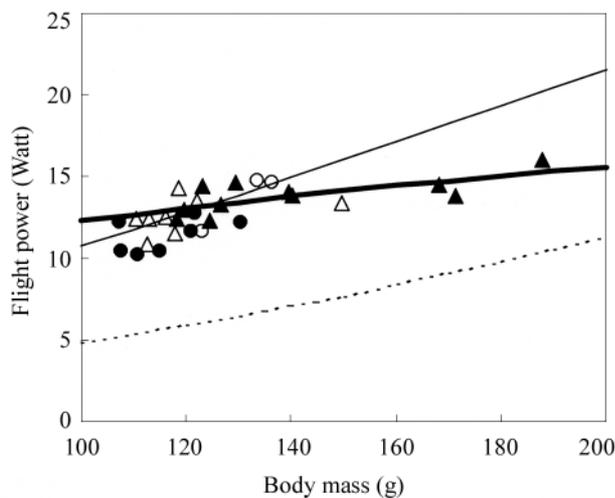


Fig. 3 Flight costs in relation to body mass for individual red knots (*Calidris canutus*)

Measurements according to Kvist et al. (2001), shown by original data points and the heavy line, and predictions by aerodynamic models (Pennycuick, 1989: thin line; Pennycuick, 1996: dashed line). For the aerodynamic models, the default settings of Pennycuick's (1989) program were used. For the model calculations, knots were assumed to have a lean mass of 100 g, a wing span of 0.512 m, an aspect ratio of 8.35, an energy density of fuel stores of 30 kJ/g, and to fly in air with a density of 1.25 g/L.

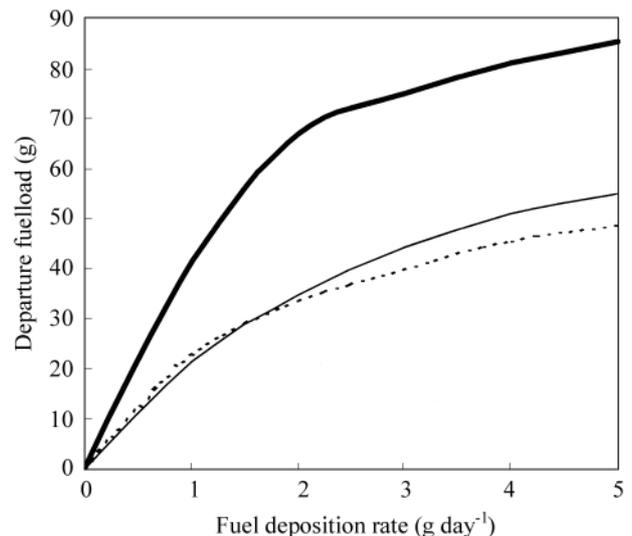


Fig. 4 Optimal departure fuel load in relation to fuel deposition rate (or site quality) for red knots (*Calidris canutus*) exhibiting the three different flight cost curves depicted in Fig. 2

Empirical flight cost model according to Kvist et al., 2001 (heavy line) and the Pennycuick 1989 (thin line) and 1996 (dashed line) aerodynamic flight cost models. Optimal departure fuel loads were calculated according to Alerstam and Lindström (1990), assuming a search/settling time of 2 days.

than indicated by the aerodynamic models. As for both airliners and refuelling birds at stopovers, the precise relationship between body mass and flight costs are of essential concern. Here the differences between empirical findings and aerodynamic models have an impact on maximum flight range.

Aerodynamic models have been used widely to predict stopover behavior (Alerstam and Lindström, 1990; Klaassen and Lindström, 1996; Weber and Houston, 1997; Weber et al., 1998), yielding, *inter alia*, estimates of optimal staging time, optimal range and optimal fuel load. It is of interest to see how such predictions change when one adopts alternative flight cost models. Using the optimal migration model advocated by Alerstam and Lindström (1990), for example, I calculated the departure fuel loads for knots in relation to fuel deposition rate (site quality; Fig. 4). Extrapolating the data of Kvist et al. (2001) to these optimal migration models yields much higher predictions of optimal departure fuel load than the Pennycuick models.

6 Conclusions

In principle, aerodynamic theory should be able to predict accurately the requirements of mechanical power for flight. However, in the transformation of mechanical power to chemical or total power, which is the parameter of concern to ecologists and physiologists, assumptions have to be made about overall muscle efficiency and power requirements for basal life functions, in addition to respiration and circulation during flight. On top of that, the values for some parameters in the calculation of mechanical power are in dispute, such as the coefficient of body drag (Hedenström and Liechti, 2001; Pennycuick et al., 1996). Such complications led Rayner (2001) to the conclusion that aerodynamic models cannot yet be extended reliably to predict total flight power. This notion is directly opposed to the views of Weber and Houston (1997) who advocate the use of aerodynamic rather than empirically derived models. They varied the parameter estimates of allometric flight cost equations within confidence limits and found considerable effects on departure fuel load and flight range. The lack of error terms in aerodynamic models, however, should not be taken to mean that the many parameters in those models are error free.

Models should be used primarily to put empirical findings into context and to guide empirical results. Clearly, measuring the actual flight costs of focal species under appropriate conditions is the most ideal alternative for any study relying on flight cost estimates. Yet, this is seldom feasible, forcing researchers to use empirical or theoretical models to generate predictions. The analyses presented by Weber and Houston (1997), Klaassen (2002) and here indicate that the choice of model may have a marked effect on the outcome and that sensitivity analyses of studies involving flight cost predictions should thus be standard procedure.

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Symposium 37 Global seabird conservation: threats and opportunities

Introduction

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Seabirds are rarely tied to boundaries: in contrast to land birds, there are few national endemic species. Such low level endemism requires a global approach to seabird conservation, because lessons learned in one sea or ocean are likely to be applicable elsewhere. Many of the threats facing seabirds are themselves global in nature: marine pollution, climate change, fishery interactions, and, on breeding islands, introduced predators and human exploitation and disturbance. Although there are still very few long-term studies of seabirds which allow for assessment of popu-

lation trends over generations, it is evident from the literature that many seabird species have decreased in abundance over the last century as a result of impacts from the identified threats. This symposium presented specific case studies to summarize some of the conservation threats and opportunities facing seabird populations generally around the world. Examples include threatened bird species, direct and indirect interactions with fisheries and human exploitation.

S37-1 Fishery impacts on the food supplies of seabirds

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Abstract Commercial fisheries can impact on seabirds by taking fish and other seafood that the birds might otherwise harvest. We compare, at global scale, the quantities of prey taken by fisheries and seabirds from information of global seabird populations and available metabolic equations. From two case studies in the tropical east Pacific Ocean and North Sea, we give examples of circumstances in which fisheries can impact deleteriously on seabird populations or can be beneficial through effects on the marine food chain.

Key words North Sea, Pacific Ocean, Prey consumption, Tuna, Sand-eels, Seabirds, Commercial fisheries

1 Introduction

Seabirds and commercial fisheries that harvest the same prey are affected mutually by their food supply. Noting this two-way interaction, we begin by comparing, at a global scale, the quantities of prey taken by fisheries and seabirds. The latter can be calculated using improving knowledge of the global populations of seabirds (del Hoyo et al., 1992, 1996; Gaston and Jones, 1998; Brooke, 2003), and available equations for their metabolic requirements (Nagy, 1987). We find that the annual take by seabirds and fisheries is of the same order of magnitude, in the range 50–100 million tonnes a year. Among seabirds, dominant consumers in order of consumption are penguins, procellariiforms and auks. Pre-eminent among the top 20 species, and responsible for 74% of seabird consumption, are the macaroni penguin (*Eudyptes chrysolophus*) and thick-billed murre (*Uria lomvia*). Under current conditions, neither interact significantly with commercial fisheries.

At global level, this conclusion masks distinct regional differences in bird-fishery interactions, as illustrated by two case studies here. One hints at a potentially deleterious impact of fisheries on seabirds, whereas the other documents a beneficial effect mediated through changes in the wider marine ecosystem.

2 The case studies

In the eastern tropical Pacific Ocean, the most widespread and abundant nekton-feeding seabirds are the Juan Fernandez petrel (*Pterodroma externa*), wedge-tailed shearwater (*Puffinus pacificus*), sooty tern (*Sterna fuscata*), and red-footed booby (*Sula sula*). All feed at or close to the surface, where they are largely dependent on predatory tu-

nas (*Thunnus* spp.) to drive smaller prey fish to the surface (Au and Pitman, 1986; Ballance et al., 1997). These four bird species consume 83% of prey caught above an average tuna shoal, the remaining 17% being captured by other, less numerous seabirds. The regional annual consumption of the four species combined is 350 000 tonnes, suggesting that the annual consumption of all seabirds is about 430 000 tonnes. This total is similar to the annual catch of the tuna fishery of 420 000 tonnes (IATTC 2000). Whereas the seabirds themselves do not consume any tuna, the impact of commercial fisheries on tuna populations could affect seabirds indirectly by diminishing the tuna schools, and so reducing available prey patches for the seabirds. This potential impact is not currently recognized in tuna management decisions.

In the temperate North Sea, one important impact of commercial fisheries on seabirds has been via ecosystem links. From a very small-scale fishery in the early 1950s, a million-tonne a year industrial fishery for sand-eels (*Ammodytes marinus*) has developed. Over the same period many seabird populations have increased. This counter-intuitive result may be explained by huge reductions in food-fish consumption by overfished stocks of predatory fish, notably gadoids and mackerel (*Scomber scombrus*). This has resulted in decreased predation of sand-eels, despite the increase in fishing and birds (Furness, 2002). The overwhelming importance of food-fish consumption by predatory fish in determining food web structure appears to be a common feature of shelf food webs. Consumption of offal and discards from trawlers, especially during winter, also sustains seabird populations, particularly the scavenging species (Ojowski et al., 2001). The imbalance in seabird community composition caused by decades of provid-

ing offal and discards can lead to severe predator-prey interactions if discard volumes are subsequently reduced (Oro and Furness, 2002).

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S37-2 Conservation of rare and endangered seabirds in Australia

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Abstract There is an urgent need for the conservation and management of several rare and endangered seabird species in Australia. The initial problem in attempting to conserve or recover these species is, in most cases, a lack of basic ecological information. We use several case studies to highlight the need for baseline studies to inform the management of seabirds in Australia. Gould's petrel (*Pterodroma leucoptera*), the providence petrel (*P. solandri*), sooty tern (*Sterna fuscata*), little tern (*S. albifrons*) and a threatened population of little penguins (*Eudyptula minor*) have all been the subject of recent research designed to provide information for management and recovery. In most cases, management decisions have been delayed while information on nesting requirements, foraging behavior and the effects of limiting factors and human disturbance is obtained. Because long-term studies of threatened species are rare, such studies of more common species provide important information about environmental changes and population fluctuations that inform management of the issues concerning rarer seabirds.

Key words Threatened species, Conservation research, Adaptive management, Species recovery, Long-term studies, Seabirds

1 Introduction

There are 74 species of seabirds (penguins, albatrosses, petrels, shearwaters, gannets boobies, tropicbirds, frigatebirds, skuas, jaegers, gulls and terns) breeding within Australian territories (Marchant and Higgins, 1990; Higgins and Davies, 1996). Of these, 48 (65%) are currently threatened (Garnett and Crowley, 2000) and face a range of impacts both on land and at sea, almost all of which are human in origin (Ross et al., 1996; Garnett and Crowley, 2000; Baker et al., 2002). There are an additional 59 seabird species that visit Australian waters regularly; 16 of them are of global conservation concern (BirdLife International, 2000).

Each year, tens of thousands of seabirds are killed accidentally by longline fishing when birds, attracted to fishing vessels by discards and baits, ingest baited hooks during line setting, or less commonly, hauling-in of the longlines (Baker et al., 2002). Hooked birds are then pulled underwater by the weight of the line and drown. This global threat, which affects predominantly albatrosses and giant petrels, is being addressed at both the national and international level. Threats to the smaller, less charismatic species have not received the same degree of attention. Consequently, there remains an urgent need for informed conservation and management of several rare and endangered seabird species in Australia.

In attempting to address the management of these

seabirds, we have invariably encountered a lack of basic ecological information, including population size and demographic trends, diet and foraging requirements. Even the most fundamental aspects of the ecology of many common Australian species are poorly known. For example, it is only recently that the short-tailed shearwater (*Puffinus tenuirostris*), of which some 23 million breed in Australia each year, was found to provision chicks with food obtained from waters around Antarctica (Klomp and Schultz, 2000). The implications for management arising from this are profound. Clearly, Australia needs to look and act beyond its territorial waters to ensure that adequate food resources are maintained for the seabirds that breed within its national boundaries.

Here we present several case histories of successful seabird management in Australia. Each of these cases highlights an initial lack of baseline information for developing management strategies and recovery plans. In some instances, management decisions had to be delayed until very basic information on nesting requirements, foraging behavior and threatening processes was obtained. Whereas research has been pivotal to these programs, many of them have also benefited from adaptive management during the research phase. The experimental management actions implemented during the adaptive phase were largely developed from knowledge obtained from studies of common seabird species.

The case histories illustrating the issues are those of

Gould's petrel (*Pterodroma leucoptera leucoptera*), providence petrel (*P. solandri*), little tern (*Sterna albifrons*), sooty tern (*S. fuscata*), and a threatened population of the little penguin (*Eudyptula minor*). Along with conservation outcomes, we present some of the more intriguing findings of recent research. Many of the threats that we have unearthed were predictable, but others have been surprising. We also outline long-term studies of two common seabirds, the short-tailed shearwater and wedge-tailed shearwater (*Puffinus pacificus*), that have provided basic information relevant for the management of rarer species.

2 Case histories

2.1 Gould's petrel

The nominate race of Gould's petrel is endemic to Australia and breeds on two small islands off the east coast of New South Wales (Priddel and Carlile, 1997a). In 1990, only 250 pairs were recorded breeding, and less than 20% of eggs laid produced fledglings (Priddel et al., 1995). In 1992, a recovery program was commenced (Priddel and Carlile, 1997b), and proved successful. Today there are more than 800 breeding pairs, and breeding success generally exceeds 50%.

Research began with baseline studies of population size, breeding ecology and mortality factors. Threats were identified, and their experimental amelioration implemented and evaluated (Priddel and Carlile, 1997b). Once information on diet, meal size delivered to chicks, and feeding frequency had been obtained, techniques for translocation were developed, tried and assessed (Priddel and Carlile, 2001). Subsequently, we successfully completed a translocation of 200 fledglings to another island. This process included the creation of artificial habitat by installing nest boxes that were specifically developed for the purpose (Priddel and Carlile, 1995a). The second colony provides a buffer and safeguard for the species should the main colony on the main island suffer catastrophic loss due to wildfire or the arrival of alien predators such as cats or rats. We also undertook a European rabbit *Oryctolagus cuniculus* eradication program on the main island that included an assessment of the effectiveness of each of the three mortality agents used (Priddel et al., 2000). Monitoring, together with research into recruitment, longevity and the energetics of breeding, continues.

The main threats discovered were plumage entanglement with the sticky fruit of a native shrub, the birdlime tree (*Pisonia umbellifera*), and predation of nesting adults by a native bird, the pied currawong (*Strepera graculina*) (Priddel and Carlile, 1995b). The reason why these native species, which had presumably coexisted harmoniously with Gould's petrel in the past, had now become a threat was perplexing. The key to the riddle was the degradation of vegetation caused by the rabbit since its introduction some 90 years earlier (Priddel and Carlile, 1997b). This degradation had opened up the rainforest to such an extent that

birdlime tree and currawong were now having a significant impact on a habitat where previously their influence had been minimal. Until the rainforest fully regenerates, currawongs will continue to be controlled and emergent seedlings of the birdlime tree removed from within petrel nesting areas (New South Wales National Parks and Wildlife Service, 2001).

2.2 Providence petrel

The providence petrel is endemic to Australian waters. The species was exterminated from Norfolk Island by a colonial settlement that ran short of food after their supply ship was wrecked in the 1790s (Hutton, 1991). At least 84 000 birds, and an unknown number of eggs, were eaten in the first year alone. The species now survives within the Norfolk Island Group in only very small numbers on Philip Island. The stronghold, and only other breeding locality, for this species is Lord Howe Island where there are approximately 40 000 breeding pairs. These nest predominantly on the summits of two mountains: Mount Gower (875 m) and Mount Lidgbird (777 m). As late as 1998, almost nothing was known about the biology of this species. Our recent research has focused on breeding ecology, foraging strategies, the extent of nesting distribution on Lord Howe Island, population size and the identification of threats.

Although several threats have been recognized, breeding success is high and the species appears secure. Inundation of burrows during heavy rain is a major cause of egg loss. Ship rats (*Rattus rattus*) are present but take few eggs. Providence petrels almost certainly benefit from the baiting of rats, conducted to protect endemic mountain flora. This action is motivated by commercial interest rather than for biodiversity conservation, as the endemic plants are a potential export resource for Lord Howe Island. The most surprising threat comes from the endangered Lord Howe woodhen (*Gallirallus sylvestris*). Normally restricted to a diet of invertebrates, in dry times these flightless rails will take petrel chicks up to 800 g in mass. Woodhens capture petrel chicks by repeatedly plunging their bills through the roof of the nesting chamber to create a hole through which they can extricate their prey.

Initial results from satellite-tracking studies of providence petrels have revealed foraging ranges of hundreds of kilometers in all directions from Lord Howe Island, with one bird flying 1 500 kilometers from the colony on a single foraging trip. Providence petrels are known to interact with fishing vessels that operate in the region, but the level of interaction and the implications for their conservation are still unknown.

2.3 Little tern

Within Australia, there are three discrete populations of little terns, one breeding on the east coast, another one along the north of the continent, and a third a palearctic non-breeding migratory population present during the austral summer (Higgins and Davies, 1996). The east coast breeding population is the smallest and most threatened,

primarily because it breeds on estuarine sand-flats and beaches which are subject to all manner of disturbances in a country famed for its beach culture. By the 1980s, the population had declined to just 220 breeding birds (Smith, 1990). Intensive management of breeding colonies since 1990 has seen the population increase to more than a thousand birds. Principal recovery actions included predator control and the erection of temporary fences to deter humans and vehicles from entering nesting colonies.

Sited just above the mean high tide mark, the nests, eggs and chicks of little terns are threatened by spring tides, sunbathers, beach anglers, four-wheel-drive vehicles, hovercraft and other beach-oriented activities. There are a number of native bird species that, given the chance, will prey heavily upon the eggs of colonies. Predation occurs most often when the terns have been disturbed from their nests by humans. Crabs also prey on the eggs by undermining the sand beneath an incubating adult and drawing the egg into the sand below. Inserting a metal sheet into the sand below the nests prevents such losses from occurring. Despite their cryptic nature, little tern chicks are particularly vulnerable to predation from introduced European foxes (*Vulpes vulpes*), feral domestic cats (*Felis catus*) and unrestrained domestic dogs (*Canis familiaris*). Ants also set upon wet, newly hatched chicks. We have been able to protect vulnerable nest sites from ants by spraying the surrounding sand with a liquid pesticide.

2.4 Sooty tern

Sooty terns present some challenging management problems on islands such as Lord Howe Island, where they nest on sand dunes near the airport runway, creating potential for aircraft bird-strike. This has necessitated baseline study of the breeding ecology of the tern there in order to manage the species responsibly.

Our studies have shown that sooty terns on Lord Howe Island, the most southerly colony in the world, have a breeding success that is highly variable between years. In some years, they raise more than twice the young reported for colonies elsewhere. Such success is achieved despite the presence of ship rats, which elsewhere have either caused colonies to decline or to be driven to extinction. In other years, very few chicks survive to fledge. It appears that the extent, timing and success of breeding on Lord Howe Island all fluctuate in response to local availability of food. This information has useful application in the management of the 10 other species of threatened seabirds that breed on Lord Howe Island.

2.5 Little penguin

Little Penguins are relatively common in Australia and its waters. They are one of few seabirds that still breed on the Australian mainland, and a small remnant population survives in Sydney Harbour. In 1995, the State of New South Wales introduced legislation, the *Threatened Species Conservation Act 1995*, to protect such endangered populations of relatively common species.

Only in the last four years has there been a coordinated research effort to catalogue the basic ecological requirements of the Sydney population. It is now known that there are some 70 pairs in this endangered population, many of which nest within the gardens and backyards of a busy suburb. The birds forage in the harbor as well as out to sea. They compete for baitfish with commercial fishers and compete for swimming space with huge numbers of watercraft every day. Marine pollution and debris are also causes for concern, although recent initiatives to improve the water quality in Sydney Harbour have been very successful. Although the size of the population appears to be relatively stable, and breeding success is high for the species, dog and fox attacks have taken 5%–10% of the entire breeding population on at least two occasions in recent years.

Notwithstanding its limited conservation value for the species as a whole, the research on this small endangered population has engendered great community support and publicized the plight of seabirds widely.

3 Discussion

The case histories outlined above highlight instances where research has contributed to the successful management or recovery of threatened seabirds in Australia. These species include surface-nesting seabirds (little and sooty terns), burrow nesters (providence petrel) and cavity nesters (Gould's petrel and little penguin). The case histories demonstrate that it is possible to manage or recover a wide range of seabirds, each with very different breeding strategies. Each species faced a unique suite of threats, and each successful management or recovery program entailed the application of a unique set of management actions. These successes have been achieved despite an initial lack of basic ecological information.

Several of the recovery programs have also involved coordination of adaptive management with research. Many adaptive management decisions have been based on information and knowledge obtained from studies of other, more common, seabird species. Long-term studies of common seabirds can provide important information about environmental changes and population fluctuations which can then be applied to the management of rarer species.

Harvesting of short-tailed shearwaters on the islands of Bass Strait, between Tasmania and the Australian mainland, has provided the impetus for long-term monitoring of this particular species. Comparative studies are also being conducted on wedge-tailed shearwaters breeding on inshore islands along Australia's east coast. Whereas short-tailed shearwaters make regular foraging trips to Antarctica, wedge-taileds feed within a few hundred kilometers of their breeding grounds (Schultz and Klomp, 2000). By comparing two similar sister species with radically different foraging strategies, we are beginning to tease out the effects of change in local and more distant marine environments.

On Montague Island, off the coast of southern New

South Wales, a 30-year study continues to document the effects of short-term climatic events and long-term El Niño cycles on both short-tailed shearwater population size and chick production. Such long-term studies not only provide benchmarks against which fluctuations in the rarer species can be gauged, but also indicate how the shearwaters and other, rarer seabirds are likely to respond to major perturbations in the marine environment. The value of long-term studies of common species, and the applicability of their data to rarer seabird species, should not be underestimated.

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S37-3 Reducing longline mortality in seabirds: a South African perspective

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Abstract Longline mortality is the most significant factor causing population decline among several seabird populations. South Africa has three major longline fisheries operating in its Exclusive Economic Zone (EEZ). Over the last six years, we have quantified the impacts of these fisheries. The success of mitigation measures to reduce seabird bycatch has varied among fisheries. For the Patagonian toothfish (*Dissostichus eleginoides*) fishery, operating around the sub-Antarctic Prince Edward Islands, a well-controlled licensed operation has shown excellent reductions in bird bycatch, rates falling from 0.2 to <0.05 birds per 1 000 hooks. However, illegal, unreported and unregulated (IUU) fishing remains a significant problem due to the distant-water nature of this fishery. The longline fishery for hake (*Merluccius* spp.) in continental shelf waters around South Africa has a much lower observer coverage, and resultant poor compliance with mitigation measures. Fortunately it kills relatively few birds. The most damaging fishery is the pelagic tuna (*Thunnus* spp.) fishery, which includes South African and foreign vessels operating inside the EEZ and in international waters. Estimates of the numbers of birds killed are complicated by a paucity of observers, especially on foreign vessels, but bycatch rates are high and compliance with mitigation measures required by permit is poor. The ease with which mitigation can be implemented depends on the type of fishery, its history, location and number of operators. We find that well-trained fishery observers play a crucial role in reducing longline mortality among seabirds.

Key words Longline fishing, Seabirds, Mortality, Mitigation, Fishery observers, South Africa

1 Introduction

Longline fishing is widely acknowledged as the cause for population declines among several albatross and petrel populations (Gales, 1998). Birds are killed when they pursue baited hooks during setting, and are drowned when they are dragged underwater either after swallowing hooks or becoming entangled. Smaller numbers of birds are also killed or injured during hauling operations. Because of the conservative life-history traits of the affected seabirds (single-egg clutches, delayed maturity and sometimes biennial breeding), only relatively few birds have to be killed to precipitate population declines. As a result, longline fishing is cited as a significant threat to 24 species listed as Threatened and a further six listed as Near-threatened (BirdLife International, 2000).

Fortunately, there is a suite of relatively simple mitigation measures that can be implemented to limit bird bycatch on longlines (Brothers et al., 1999). These include setting exclusively at night to avoid diurnal foragers such as albatrosses, adequate line weighting and slow setting speeds to maximize line sink rates, underwater setting through funnels or chutes to preclude bird access to baits, use of bird-scaring or *tori* lines over the setting line, and

appropriate management of discards to reduce the risk of entanglement during hauling, the attractiveness of fishing vessels and the risk of hooks being obtained from discards. Another option is to declare closed seasons or areas in especially sensitive situations, for example at seabird breeding colonies. Together these measures can reduce seabird bycatch to acceptable levels (see Discussion).

The main challenge today is to ensure that fisheries adopt the mitigation measures promulgated. In this paper we report progress made in implementing the measures in three longline fisheries operating off South Africa. We measure the success of implementation in terms of change in bird bycatch rates. The main aims of the paper are to identify problem areas and to share lessons learned from attempts to reduce bird bycatch in South African fisheries.

2 Materials and methods

There are three major longline fisheries operating in waters off South Africa. One is a widespread pelagic fishery for tunas (*Thunnus* spp.) and broadbill swordfish (*Xiphias gladius*), which sets *c.* 12 million hooks a year. The other two are demersal fisheries, one in continental waters for hake (*Merluccius* spp.), which sets 15 million hooks, and

the other around the Prince Edward Islands for Patagonian toothfish (*Dissotichus eleginoides*), which sets three million hooks. Fishing is conducted by South African vessels and, in the case of the tuna fishery, by Japanese and Taiwanese license holders. The foreign licenses will not be renewed at the end of 2002. All fisheries have mitigation programs designed to limit seabird bycatch as part of their permit requirements, and Japanese and Taiwanese vessels licensed for tunas in South African waters also fall under the guidelines set out in their National Plans of Action — Seabirds (FAO, 1999).

Most of what is known about the numbers of birds killed in these fisheries comes from observer programs (Barnes et al., 1997; Ryan and Boix-Hinzen, 1998, 1999; Nel et al., 2002; Ryan et al., 2002), although some data is also available from observations of the quantities of fishing tackle brought back to breeding colonies by seabirds (Nel and Nel, 2000). We also obtained information from the Taiwanese tuna fishery in South African waters by inspecting vessels and interviewing captains (Ryan and Boix-Hinzen, 1998). Data presented in this paper include updates of bycatch estimates based on observer data subsequent to these published accounts. Additional information came from voluntary programs that ask boat captains to return any birds killed to port; such data, however, are not comprehensive.

3 Results

The longline fishery for toothfishes is the best documented of the South African fisheries, with almost complete observer coverage since the sanctioned fishery commenced operating in 1996 (Nel et al., 2002). Large numbers of birds were killed in the first year of operations, when compliance with prescribed mitigation measures was poor (Table 1). Since then more stringent implementation of mitigation measures and a shift in fishing effort away from the immediate vicinity of breeding islands have combined to reduce bycatch rates to a point where fewer than 0.05 birds have been killed per 1 000 hooks over the last four years (Table 1). There has thus been a more than 10-fold drop in bycatch rates, with the lowest rate in 2001/2002 when compliance

with mitigation measures was all but complete.

The hake longline fishery started in 1983, but ceased in 1990 due to excessive targeting of the more valuable kingklip (*Genypterus capensis*). The fishery recommenced in 1994, when fishery observers collected the first data on seabird bycatch. They reported substantial mortality among white-chinned petrels *Procellaria aequinoctialis* (0.44 birds per 1 000 hooks set), with small numbers of other species being caught and released during hauling (Barnes et al., 1997). Based on these findings, mitigation measures were made part of the permit requirements for the fishery. Fortunately, fish catches are highest on lines set at night, resulting in good compliance with this measure and greatly reducing the risk of killing species other than those of *Procellaria*. Compliance with other key mitigation measures is relatively poor, probably in part because of the currently low observer coverage (9%). Despite these problems, the bycatch rate is a more moderate 0.14 birds per 1 000 hooks set (Marine and Coastal Management unpubl. data for 2000/2001), which is a three-fold improvement since the start of observations in 1994.

The pelagic fishery for tunas, and more recently swordfish, is the oldest longline fishery off South Africa, dating back to the 1950s. Until the later 1990s, there was little direct evidence to assess the numbers of birds killed, because prior to 1997, most fishing within the South African Exclusive Economic Zone (EEZ) was conducted by vessels from Japan and Taiwan (Ryan and Boix-Hinzen, 1998). Since then, an increasing number of South African vessels have entered the fishery, making it easier to deploy observers. As a result, observer coverage on domestic vessels is a commendable 17%, whereas that for foreign vessels remains woefully inadequate at 1% for Japanese boats and none for Taiwanese (Ryan et al., 2002). The poor observer coverage precludes an accurate assessment of compliance with permit requirements, creating uncertainty about the impacts of this fishery.

Within the domestic pelagic fishery, seabird bycatch inside the EEZ averages 0.34 birds per 1 000 hooks ($n=294\ 000$ hooks observed). This is substantially lower than

Table 1 Changes in annual seabird bycatch rates compared with compliance with the ban on daytime sets in the Patagonian toothfish fishery off the Prince Edward Islands

Year	Bycatch rate (birds per 1000 hooks set)			% daylight sets*
	Procellaria	Other birds	All species	
1996/1997	0.210	0.079	0.289	55
1997/1998	0.111	0.006	0.117	15
1998/1999	0.012	0.004	0.016	18
1999/2000	0.034	0.002	0.036	19
2000/2001	0.008	0.001	0.009	16
2001/2002	0.001	0.000	0.001	1

* Proportion of hooks set during the day (nautical dawn to dusk), excluding experimental sets through a Mustad underwater funnel (see Ryan and Watkins, 2002). "Other birds" are predominantly albatrosses (*Thalassarche* spp.) and giant petrels (*Macronectes* spp.).

the 2.64 birds per 1 000 hooks recorded by observers on two Japanese vessels fishing off South Africa (Ryan et al., 2002). Data from observers in the Japanese Real Time Monitoring Programme reported bycatch on tuna longliners off southern Africa in the 1990s at 0.360 birds per 1 000 hooks (Ryan and Boix-Hinzen, 1998), closer to the domestic fishery catch rate; but this includes fishing in oceanic waters where bycatch rates are much lower. South African vessels fishing in warm oceanic waters outside the EEZ caught only 0.02 birds per 1 000 hooks ($n=222\ 000$ hooks observed, all north of 30°S). Even within the EEZ, bycatch rates vary greatly, with few birds killed off the east coast (0.02 per 1 000 hooks) compared with south and west coasts (0.45 per 1 000 hooks) where bird numbers attending vessels are substantially higher (Ryan et al., 2002). Of particular concern is the high proportion of albatrosses killed by this fishery, 70%–80% of them within the EEZ. Irrespective of uncertainties surrounding the data, it is clear that current bycatch by the tuna fishery is unacceptably high.

4 Discussion

Despite the fact that all three longline fisheries are subject to similar mitigation measures as part of their permit requirements, levels of compliance and concomitant rates of seabird bycatch vary greatly. Both demersal longline fisheries have shown significant improvements in seabird bycatch rates since monitoring commenced in the 1990s. However, only the sanctioned fishery for Patagonian toothfishes has attained the interim target of 0.05 birds per 1 000 hooks deemed “operationally acceptable” (Environment Australia, 1998), even though the target may be demographically faulty with respect to sustainability of seabird populations. Three factors probably account for the success of mitigation in the toothfish fishery, despite its proximity to a globally-important breeding site for a large number of longline-affected seabird species. First and foremost, the fishery has had 100% observer coverage since its inception. Secondly, the fishery has had only six license holders, which simplifies outreach to the operators. Thirdly, as a newly-established fishery, its operators were more open to alter fishing practices. Together, these factors allowed rapid and effective implementation of mitigation measures laid down in the permit requirements for the fishery.

The main remaining issue concerning the toothfish fishery is illegal, unreported and unregulated (IUU) fishing, presumably with little if any mitigation measures to reduce seabird bycatch. This problem is especially serious because of the great distance of the fishery from South African ports (some 2 000 km), coupled with the virtual absence of long-range patrolling. Control of IUU fishing is problematic for remote fishing areas and for fisheries where access for large numbers of potential fishers is easy. In the case of the toothfish fishery around South Africa’s Prince Edward Islands, IUU effort is fortunately in decline because of the rapid drop in fish catch rates.

The demersal fishery for hake could potentially

achieve a target of 0.05 birds per 1 000 hooks in the near future, provided there is improved compliance with mitigation measures. At present, compliance is poor partly because fishers are ill-informed of the problem, and partly because there is no enforcement of permit conditions pertaining to seabird bycatch, even when vessels carrying observers flout the regulations. Increasing observer coverage in this fishery (planned for 2003) will probably help the situation, provided that the observers are well trained. Action also needs to be taken against license holders known to repeatedly ignore mitigation measures. Compliance in this fishery is also complicated by the large number of license holders operating from numerous harbors, so making fisher education and outreach a formidable task.

The pelagic fishery for tunas and swordfish remains the most problematic fishery, in part because of the greater difficulty in limiting bird bycatch on pelagic longlines (Brothers et al., 1999), and in part because of the history of the fishery. This foreign-based fishery has been long established, resulting in considerable resistance to change in practices (Robertson, 1998). Moreover, many of the foreign-licensed vessels only call once in South African ports, making it extremely difficult to deploy fishery observers. The announced halt to licensing of foreign vessels by the end of 2002 should go some way towards reducing the problems, but it remains to be seen whether this merely results in foreign vessels taking on local partners in joint-ventures. Foreign vessels may also transfer their fishing effort farther offshore into international waters, where the lower densities of birds are likely to reduce bycatch rates but increase pressure on threatened oceanic species.

Although the South African pelagic fishery has a much lower bycatch rate than that of the few foreign vessels which have carried observers, there is still a need to reduce its rates further. These are currently more than six times the interim target of 0.05 birds per 1 000 hooks. Compliance is moderate among vessels carrying observers, but given the low observer coverage, compliance overall could be poor. Most of the bycatch is taken in the south, where the numbers of birds attending vessels are greatest (Ryan et al., 2002). Special care is needed when fishing in that area, and the development and deployment of effective underwater setting devices is a priority if this fishery is to attain its target.

South Africa is currently developing a National Plan of Action — Seabirds to reduce seabird bycatch on longlines, as called for by the Food and Agriculture Organization of the United Nations (FAO, 1999). This includes a broad participatory program that should help to expose the problem. We hope to use the process both to educate fishers and to ensure that mitigation measures are implemented effectively.

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S37-4 Are current harvests of seabirds sustainable?

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Abstract This paper reviews seabird harvests towards evaluating whether monitoring, research and management are adequate to assess their sustainability. The low productivity of adult seabirds makes their populations extremely vulnerable to overharvest unless only eggs and chicks are taken. A critical lack of information on density dependence and other potential compensatory mortality adjustments makes assessment of sustainability very difficult even in the few cases where adequate monitoring and population research are underway. Research must be very long-term for robust demographic predictions. There is neither evidence for unsustainability of most current seabird harvests, nor evidence that harvesting is sustainable.

Key words Seabirds, Harvesting, Sustainability, Conservation, Compensation, Regulation

1 Introduction

Seabird eggs, chicks and adults have been harvested for food in nearly all parts of the world in the recent past. Wing or tail feathers have been gathered for personal adornment, and down for bedding as well. Humans continue to consume eggs, flesh, proventricular oil and fats for sustenance, medicine and aphrodisiacs. There are also occasional uses of seabirds for fish bait and pet food, while large scale collection of guano for fertilizer potentially disrupts breeding success (Croxall et al., 1984; Nettleship et al., 1994). The high adult survival, low reproductive rate and delayed maturation of seabirds make them especially vulnerable to overharvest. Humans can easily exploit dense breeding colonies, which are often established on remote islands where monitoring or regulation of harvest is extremely difficult.

Reliance on agriculture and declines in hunter-gathering since the industrial revolution and associated urbanization have led to fewer harvesters and declining markets for seabird products. Protective legislation, harvest prohibition and land reservation became much more common around the world from the 1970s onwards. Poaching and the impossibility of enforcing harvest prohibitions (Croxall et al., 1984, Nettleship et al., 1994) make it clear, nevertheless, that these legislative restrictions and reservations are not sufficient safeguards to halt ongoing risk to seabirds. Much of the ongoing seabird harvesting is sporadic and unobserved.

The relatively development of population ecology and a growing awareness of the need for environmental sustainability globally are new reasons for hope that unsustainable seabird harvests will diminish. But is science applied well enough to guide most seabird harvests and can it adequately predict sustainability? What are the main complexities in seabird population dynamics that make the

application of science difficult?

2 Assessing risk step one: measuring harvest intensity

Most current seabird harvesting goes unmeasured. The norm is typified by the situation described by Bergur Olsen (*in litt.*, August 2002) from the Faroe Islands which has closed seasons on seabird harvesting but no bag limits and no intensive monitoring. Annual harvests of northern fulmar (*Fulmarus glacialis*) by Faroese are approximately 5 000–10 000 eggs, 50 000–100 000 juveniles caught from the water and 5 000–10 000 adults caught with a “fleyg” (net on a pole). About 5 000–10 000 guillemots or common murres (*Uria aalge*), 5 000–10 000 razorbills (*Alca torda*) and 1 000 Atlantic puffins (*Fratercula arctica*) are shot. 50 000–100 000 puffins are taken each year by fleyg. In addition, there is a take of 3 000 Manx shearwater (*Puffinus puffinus*) chicks, 500 northern gannet (*Morus bassanus*) chicks, 500 European shags (*Phalacrocorax aristotelis*), as well as 1 000–5 000 black-legged kittiwakes (*Rissa tridactyla*) taken from fishing boats and 500–1 000 young gulls (*Larus* spp.).

Estimation of the sustainability of these harvests is a huge undertaking for a relatively small scientific community. The large number of species involved and consequent differences in the spatial and seasonal distribution of the take makes it extremely difficult to assess harvest size. The very round figures and wide range of the “guesstimates” underscore their uncertainty. There are few reliable estimates of population size and productivity for most of the harvested species, so even a preliminary estimate of harvest intensity is not possible. The situation is paralleled in Greenland, Iceland, Canada and many other parts of the world where it is simply not practicable to apply science to assess risks.

Research into the traditional harvest of “titi” or sooty shearwaters (*Puffinus griseus*) chicks by Rakiura Maori in

New Zealand illustrates the more unusual end of the continuum, where a single species harvest is monitored with reasonable diligence. Initiation of research into the sustainability of titi harvests in 1994 is enormously encouraging and apparently unique (Taiepa et al., 1997). There are no other records in the literature of an indigenous people initiating and directing their own scientific research project to ensure that the birds remain plentiful enough for their grandchildren to harvest (Moller, 2001). The Rakiura project aims to determine what limits should be set on titi harvests and to develop monitoring tools that will enable the community itself to monitor long-term trends and changes.

3 Assessing sustainability by monitoring population trends

Monitoring trends in population abundance could provide a rough measure of harvest impacts, especially if trends in harvested and unharvested populations could be compared. However, there are several difficulties besetting such methods: (1) reliable measurement of a population trend can be extremely difficult, especially for burrow-nesting alcid and procellariiforms (Hamilton, 2000); (2) extraordinarily long data runs are needed to monitor trends reliably because of the long generation times in seabirds; (3) broad-scale changes in ocean ecology are occurring, so past population trends may not apply in future even if harvest pressure does not change; (4) differential migration between harvested and unharvested populations may remove evidence of harvest effects; and (5) unharvested colonies may be very different from those harvested in location and ecology in ways that affect population dynamics.

Population trends may be imperceptible or slight when viewed over short time spans, and trends in the first decade of a monitoring program may have been determined by the ecological events prevailing over the 20 years prior to it. Lag effects are likely if the age structure of the population has been affected by past events because seabird breeding and survival are age dependent.

In assessment of sustainability, the monitoring method on its own should only ever be used by researchers and environmental managers as a prioritization tool for choosing which species and populations to study intensively by a combination of other approaches. For example, declines in thick-billed murre (*Uria lomvia*), when coupled with knowledge that adults sustain heavy harvest pressure in Greenland and Canada (Falk and Durinck, 1992), signaled the need for urgent management of that particular harvest. A decline in sooty shearwaters coupled with large-scale harvesting is another potential case (Scofield and Christie, 2002).

4 Spatial comparisons of density for estimation of harvest impact

A quick test of large-scale harvest impacts could come from comparisons of the density of birds breeding in har-

vested and unharvested colonies. This approach, however, makes a critical assumption that density would have been the same in both colonies if harvest had not been imposed. Thus, in the case of breeding colonies of the sooty shearwater, unharvested Titi Islands tend to be smaller and have different vegetation than harvested ones, so any observed differences in density may not relate to harvest.

5 Demographic prediction approach

The “demographic prediction” approach assesses sustainability from calculations of inputs (reproduction and immigration) and outputs (mortality and emigration) and knowledge of the way density affects these parameters (density dependence). Demographic models can be built relatively quickly, so they can offer a first, best guess, of likely outcomes.

The main challenge in developing prediction models for seabirds such as the titi is the long time required to obtain good estimates of population parameters. Marine systems, and consequently the productivity and survival of seabirds, are extremely variable between years and decades, so accurate estimation of mean parameters is difficult. For example, Bradley et al. (1989) estimated the annual adult survival of short-tailed shearwaters (*Puffinus tenuirostris*) to be 0.912 ± 0.011 . This may seem to be a very accurate estimate, and fitting reward for 40 years of research because the 95% confidence interval for annual survival is only 2.4%. However, if the confidence interval is expressed in terms of mortality, which is the rate at which adults fall out of the population, the confidence interval rises to 25%.

6 Compensatory, additive or exacerbated harvest effects: the key complexities for estimation of sustainability?

Even if demographic parameters can be measured accurately, the crucial assumption in constructing demographic models is whether harvest mortality is compensatory, additive or exacerbated. Re-laying after harvest is a simple example of compensation for smaller seabirds that can re-lay within the same breeding season, such as terns in the Seychelles (Feare, 1976).

Most potential compensatory mechanisms could operate through density dependence. If a pool of birds is prevented from breeding because of insufficient space, then harvest of eggs or chicks would have little effect on population numbers because “floaters” or “queuers” (mature birds waiting for space to breed) can reproduce earlier whenever harvest occurs. Reduction of populations of wandering albatrosses (*Diomedea exulans*) because of fishery bycatch has already led to earlier onset of reproduction (Tuck et al., 2001). Raising of young is energy sapping and time-consuming for seabirds and therefore risky (Weimerskirch, 2002). Harvesting of eggs or chicks could reduce the probability of the parents skipping breeding in the next season because curtailment of the current season

relieves pressure on adults. It is also possible that adult survival will be enhanced if breeding is artificially disrupted. Density-dependent settlement rates may occur.

If metapopulation decline is triggered by harvesting, reduced density locally within a colony could release neighbors from interference competition and lead to increased egg and chick survival. Chick growth in less crowded colonies could improve fitness of fledglings and improve juvenile survival. Reduction in density may concentrate breeding in more high-quality areas of the colony so that per capita productivity or survival increases (Kokko et al., 2002).

Density dependence presents two related problems for demographers seeking to predict harvest effects. First, it is not known for most seabirds if the parameters measured on current populations are constrained by or released from density effects — it is usually impossible to know if the population under study is near carrying capacity or not. Secondly, measurement of the way parameters change over a range of densities is extremely difficult, especially when natural population change is slow or driven by fluctuation in environmental factors that alter carrying capacity itself. Researchers wanting to estimate density-dependent effects must measure vital rates when the population has been forced away from carrying capacity by some artificial perturbation, not simply when density varies in response to changing carrying capacity. The strongest inferences of density-dependent regulation effects in albatrosses come from putative fisheries bycatch impacts, but even here the perturbation is set against a background of generally warming seas since 1960 (Weimerskirch, 2002). This makes it difficult to partition effects of density *per se* from potential influences of changes in food or wind patterns that could affect foraging and chick provisioning.

The impacts of harvesting could in some circumstances exacerbate simple additive mortality. For example, disturbance of pre-breeders at nesting sites by harvesters can increase emigration. Selective harvesting of the larger chicks could increase impacts because such chicks are those most likely to be recruited (Hunter et al., 2000a). Many procellariids tend to switch mates if breeding fails, so harvesting could reduce mate fidelity. There may be delays in finding another mate and breeding is usually less successful when a new pair forms (Bradley et al., 1990), so overall productivity of the colony may be reduced by harvest. Humans walking on the breeding ground can collapse burrows and compact the substratum as well.

The traditional demographic approach to assessing risk is to calculate a “reproductive value” for estimating the relative impact of harvesting. According to calculations for such K-strategists as seabirds (slowly reproducing, long-lived species), removal of an egg or chick is likely to have much less impact on future population size than removing an adult. I suggest that an hierarchy of risk is driven partly by scope for compensatory effects and the parameter calculations embodied in reproductive value. If an egg is harvested, the chain of potential compensatory effects that

could reduce harvest impact is long, such as re-laying, reduced disturbance, earlier onset of breeding. If a young breeding adult is harvested, there will be less opportunity for compensation, and so further exacerbation of harvest impact is possible.

Perturbation analyses are used to focus on the key parameters that effect population change. Apart from setting priorities for relative accuracy in measures of population parameters (Hunter et al., 2000b), elasticity and sensitivity analyses can guide researchers to the life stages most important for determining whether compensatory or additive mortality effects result from harvesting.

7 The need for corroboration from several different approaches

The above complexities potentially reduce the reliability of the demographic prediction method for assessment of sustainability. Demographic modeling, however, is not constrained by the fundamental weakness of monitoring and density comparison approaches that cannot predict what will happen if ecological conditions or harvesting changes in future. Monitoring and spatial comparisons look backward, demographic modeling looks forwards. The most reliable predictions will use a combination of the three approaches. Monitoring can be used to test the accuracy of the demographic prediction approach by providing an “external check” on predicted trends. Managers should be sceptical of any model that predicts a rate of population change different from that observed by monitoring, or if predicted densities between harvested and unharvested colonies are different from those actually observed.

8 General discussion: are current harvests sustainable and can science help?

It has taken eight years of hard work by an annual team of two to three scientists and three students assisted by six field volunteers to establish the Rakiura titi harvesting research project. First predictions of sustainability are expected in 2006, 13 years after starting research. Many communities would not have the time, resources or scientific capacity to mount such a project to assess the sustainability of their local seabird harvests, even of just one species.

The complications associated with compensatory, additive or exacerbated harvest effects will make even preliminary predictions of harvest sustainability very approximate. And should researchers be able to model current dynamics satisfactorily, long-term prognosis for harvest sustainability may yet be determined by global environmental changes that are even harder to predict. For example, there is correlative evidence that more frequent and intense El Niño climate fluctuations depress adult titi survival, the key determinant of population trajectory with or without harvest (Lyver et al., 1999). Anthropogenic climate change may be increasing the intensity and frequency

of El Niños and become the key determinant of sustainability. Our team of population ecologists has therefore had to shift the emphasis of research to climatology and oceanographic systems, subjects well beyond their own expertise. The complexity of oceanic and climate systems and the multitude of threats encountered by far-ranging seabirds demands a multi-disciplinary approach for guiding seabird conservation.

The expense, duration and complexity of the necessary research entail strict prioritization, and it is the harvests themselves that deserve most scrutiny. Declining populations merit immediate attention, particularly where life stages with the greatest reproductive value are taken, in the order of young adults > old adults > pre-breeders > juveniles > fledglings > chicks > eggs.

More scientific research into harvests, and incorporation of the traditional environmental knowledge of the harvesters, can help guide management and reduce environmental and cultural risks. In nearly all ongoing seabird harvests, there is neither evidence for unsustainability, nor evidence that harvesting is sustainable. Premature conclusions that harvests are sustainable, or that they are causing declines, must be avoided. Attempts to impose harvest restrictions from outside the harvesting community on false or unproven claims of unsustainability are likely to fail and alienate the key people involved: the seabird harvesters themselves.

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S37-5 Understanding global trends in seabirds — are there winners and losers?

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Abstract We review the lessons provided by long-term studies of seabirds. The literature holds few examples of long-term studies and exposes major gaps in the knowledge required for making sound conservation decisions. Sufficient long-term data for assessing population trends is available for few species. The northern fulmar (*Fulmarus glacialis*) and the gannets (*Morus* spp.) have increased or remained stable, but several albatrosses have declined, the cause for which has often been attributed to impacts from human fisheries, although direct links are seldom demonstrated. Declines in grey-headed albatrosses (*Thalassarche chrysostoma*) and rockhopper penguins (*Eudyptes chrysocome*) at Campbell Island have been correlated with environmental change, a factor that is often overlooked. Such changes do occur; and to understand their effects on seabird populations fully, seabirds need monitoring at sea as well as on breeding grounds.

Key words Seabirds, Long-term studies, Populations, Longevity

1 Introduction

For seabirds, changes in the marine environment or breeding grounds may result in either “winners” or “losers”. We define a “winner” as a species that is able to maintain or increase its population size and prevail within its environment in spite of human induced and/or natural change. Conversely, a “loser” is one consistently unable to cope in the face of change.

Determining “winners” or “losers” requires detailed information on global population size and trends for each species. Good data on population trends can only come from long-term study, ideally over 40–50 years. The coloniality of many seabirds makes them accessible subjects for such study (Wooller et al., 1992), yet little is known about the size and demographic trends in most of their populations. Moreover, there is a paucity of long-term studies, a phenomenon not restricted to seabirds. Although there was a move away from long-term monitoring for several decades (Krebs, 1991), seabird ecologists are now re-discovering their importance (Woehler et al., 2001). Trends in populations are needed for finding out whether observed threats to individuals have impact on populations.

Of 328 seabird taxa, 28.7% have been identified as critical, endangered or vulnerable by IUCN, with a further 10% categorized as at lower risk/near threatened or data deficient (BirdLife International, 2000). The list may well provide a guide to the species thought to be declining rapidly, the presumed “losers”, but current information is

too coarse to identify gradual declines in other species.

2 How well are seabird populations known?

To assess data on size and trends in seabird populations, we used recent handbook summaries of relevant information on 328 species of Sphenisciformes, Procellariiformes, Pelecaniformes and seabirds from the Charadriiformes (Marchant and Higgins, 1990; del Hoyo et al., 1992; BirdLife International, 2000). From these sources, we grouped the methods by which global population size was determined for each species, whether by direct counts, partial counts or guesstimates from brief visits, or unknown.

In Sphenisciformes (penguins), population estimates are available for 82% of the 17 species; those for the remainder are guessed. In Procellariiformes (petrels and albatrosses), direct estimates are available for 60% of the 108/128 species, 29% are guessed, and 11% lack information. In Pelecaniformes (gannets, frigatebirds, cormorants and allies), direct estimates are available for 38% of the up to 58 species, 36% are guessed, and a surprising 26% lack information. In the marine Charadriiformes of up to 125 species (gulls, terns, alcids, skuas, and plovers and allies), direct estimates are available for only 31%, 48% are guessed and 21% lack adequate information.

Data on population trends are considerably fewer. Although long-term studies are a prerequisite, almost all information on trends comes from short-term studies or

anecdotal reports. It seems that the lack of knowledge about population trends in seabirds has been greatly underestimated.

Of the 328 seabird species, 127 are listed under categories of threat by IUCN (Birdlife International, 2000); and of these, no global population trends are available for 28% in Procellariiformes, 21% in Pelecaniformes and 18% in Charadriiformes. In the 201 species not listed as threatened, global population trends are unknown for 18% of Sphenisciformes, 54% of Procellariiformes, 64% of Pelecaniformes and 63% of Charadriiformes. How can risk be assessed reliably from such a dearth of information?

This analysis reveals that current knowledge of seabird population sizes and trends is poor. However, some long-term studies do exist, and we now examine them for the factors and threats that cause some species to “win” and others to “lose”.

3 Long-term seabird case-studies

3.1 Declining species

Taxa in decline may demonstrate some of the threats being faced. The Campbell albatross (*Thalassarche impavida*), grey-headed albatross (*T. chrysostoma*) and rockhopper penguin (*Eudyptes chrysocome*) all breed on Campbell Island, southeast of New Zealand. Populations there have all declined over the at least the last 50 years, due to different factors.

The Campbell albatross population appears to have been stable until 1966 (Waugh et al., 1999). Then the numbers breeding declined rapidly during the 1970s and early 1980s. This decline was correlated with the impact of fisheries bycatch. Since at least 1984, numbers have increased, coincident with a reduction in longline fishing (Waugh et al., 1999). A correlation between fishing effort and the decline of Campbell Albatrosses is evident, and demographic models show good agreement with observed numbers in nest counts.

In contrast, grey-headed albatrosses appear to have been affected predominantly by factors other than longlining. They declined steadily at about 3.7% a year at Campbell Island between the early 1940s and mid-1980s (Waugh et al., 1999). Between 1992–1996, the rate of decline was similar. Because the drop before and after the advent of longline fishing is much the same (Murray et al., 1993; Klaer and Polacheck, 1995), it cannot be explained by that factor alone. Waugh et al. (1999) attribute the cause instead to low and variable breeding success, together with low juvenal survival, driven by environmental factors. Longline fishing may only be a recent contributor, because some grey-headed albatrosses have been taken in the New Zealand and Australian bycatch (Gales et al., 1998).

Rockhopper penguins have also declined steadily at Campbell Island, by 94% over *c.* 45 years (Cunningham and Moors, 1994). They are not caught on longlines. The decline has probably resulted from changes in the marine en-

vironment about Campbell Island, associated with a substantial increase in sea temperature. Cunningham and Moors (1994) suggest that warmer waters were most likely to affect rockhopper penguins through altered availability of their food. Average sea temperatures throughout the southern ocean have risen by 0.5°C since the 1950s (Allan et al., 1996).

3.2 Stable species

Few seabirds are known to have stable populations, probably due to the short-term nature of most population data. Viewed long-term, rises and falls in some populations may actually reflect a stable but fluctuating pattern. Cape gannets (*Morus capensis*) around southern Africa appear to have fluctuated in numbers over the past 40 to 50 years (R. J. M. Crawford, pers comm.). They declined markedly in Namibia, following the collapse of the sardine (*Sardinops*) fisheries in the 1970s, but there followed an increase in the South African colonies during the 1980s, perhaps caused by first-time breeders moving to colonies with a better food supply (Crawford, 1999). This may well be a species with a stable population able to respond to environmental change, and therefore be one of the “winners”. Yet it is currently listed as Vulnerable, with a rapidly declining population.

3.3 Increasing species

Over the past 200 years, the northern fulmar (*Fulmarus glacialis*) has undergone one of the most spectacular population increases of any seabird, both in distribution and numbers (Warham, 1990). Although well studied, there is still argument about the cause of the increase. Greater food supply from fisheries waste appears likely to have had an effect, but adaptation to changes in the marine environment may have contributed also. Hence, we cannot predict the impact of declining fisheries and environmental change, and so must class it as a “winner” for the time being.

In contrast to the Cape gannet, both the northern gannet (*Morus bassana*) and Australasian gannet (*M. serrator*) have increased markedly. Populations of the northern gannet grew steadily at *c.* 3% a year for most of the last century. Nelson (2002) attributes this to cessation of exploitation by humans. The Australasian gannet has also increased in New Zealand, and, since the late 1980s, in Australia, after exploitation of its breeding colony on Cat Island, Tasmania, was stopped (cf. Warham and Serventy, 1978). Early exploitation by Maori in New Zealand may have led to an earlier decline, so the recent increase there may also be due to a release from hunting pressure.

Changes in both northern and Australasian gannet populations show a relatively smooth rate of increase. Census points are at least a decade apart. However, this does not represent the real fluctuations in their populations accurately.

4 Conflicts in seabird studies

Short- and long-term studies offer conflicting perspectives on trends in seabird populations. Short-term studies

indicate that many species are in decline. Yet there is often no historical baseline for determining what such trends mean in the long-term, or what is causing them.

Considering the smooth line phenomena in some population data, we reviewed the long-term Australasian gannet data at Cape Kidnappers in New Zealand. There, the Plateau colony shows an annual increase of just over 4%. This study, which began in 1945, is an excellent example of a long-term data set, involving annual counts of breeding pairs at one colony. There is much inter-annual variation, both in the numbers of breeding pairs and productivity, yet a trend line drawn between data points spaced a decade apart does not show this. Much of the inter-annual variation detected appears to be related to environmental factors.

Without the benefit of such a long-term data set, the results could be very different. It is possible to choose periods of three to four years from within the Cape Kidnappers data set, normal for a University-type study, that give decreasing, stable, and steeply increasing population trends. Population models based on such short-term data would be unlikely to reflect the real long-term population trend. Data collected long-term are required to model seabird populations accurately and so determine correctly the effects of various threats.

5 What are the threats and what are we studying?

Longlining is often said to be the single greatest threat to seabirds and responsible for widespread declines in seabird populations across the world. Yet, to put the impact of longlining into perspective, only some 10% of seabird species are caught regularly in longline bycatch, and some of them appear to be declining for other reasons. Unfortunately, precise demographic reasons for the declines are known for only a few (Weimerskirch et al., 1997; Waugh et al., 1999), due to the lack of long-term studies (Wooller et al., 1992). Some studies have linked population declines circumstantially with fisheries (Weimerskirch and Jouventin 1987, 1998; Croxall et al., 1990, 1998), even though little or no data on population size or parameters existed before the fisheries started. Campbell and Buller's (*Thalassarche bulleri*) albatrosses are still represented in fisheries bycatch, but their populations appear to be increasing (Sagar et al., 1999).

Research into recruitment factors, knowledge of foraging zones (especially for juveniles, immatures, and non-breeding adults), and data relating to fisheries outside national fishery zones are needed to resolve questions of "winners" and "losers" (Wooller et al., 1992; Waugh et al., 1999). Relatively little attention has yet been paid to bycatch in other fisheries. The effects of other anthropogenic threats such as pollution, introduced predators at breeding grounds, disturbance and human exploitation have also received little attention.

Environmental factors may well be the most important of impacts, yet recent reviews of seabird threats have

either ignored them or addressed them superficially (e.g., Baker et al., 2002). From the case studies presented here, it is clear that environmental factors affect seabird populations. Long-term environmental changes, such as the increase in Southern Ocean sea surface temperatures, are almost unstudied. The impact of events such as the El Niño Southern Oscillation on seabird populations are evident even in the short-term (Schreiber and Schreiber, 1984; Lyver et al., 1999); but there is little understanding of its importance long-term.

Short-term environmental perturbations, such as storms, have also affected seabird populations and breeding habitat, as in the case of the northern royal albatross, *Diomedea epomophora sanfordi* (Robertson, 1998). The faster breeding, shorter-lived brown noddy *Anous stolidus*, however, has been found to compensate for high mortality after storms (Morris and Chardine, 1995), possibly by drawing upon birds from within a "strategic reserve" (Warham, 1996). Thus there may well be an inherent resilience to cope with short-term events, but there is little understanding of what this means in the long-term.

6 Where do we go from here?

To understand the threats facing seabirds, more information is needed on birds at sea. Most of the threats impacting on them happen there, yet until recently almost all have been studied on land. The technological advances in transmitters and data-loggers will facilitate measuring seabird activities at sea. Such research, however, should not be conducted at the expense of long-term land-based studies. Only long-term monitoring can provide the information on population trends that will allow us to understand the demographic consequences of the threats to seabirds.

So, are there "winners" or "losers"? Based on long-term studies, there are clearly some current "winners", such as northern fulmars and northern and Australasian Gannets. Yet we still do not fully comprehend why these species have done so well, nor can we make predictions about their continuing success. What about current "losers"? At this stage, there is not enough long-term information on trends to declare as "losers" most species currently on the IUCN threatened list. Many of them may be fluctuating in the short-term within normal population cycles. There certainly are some seabirds which, with assistance, appear to be returning from the brink of extinction; but these are few: Chatham Island taiko (*Pterodroma magentae*), Bermuda petrel (*P. cahow*) and short-tailed albatross (*Phoebastria albatrus*).

Seabird ecologists, managers and modelers will not win the conservation battle until they can provide the information required to understand the ecology and demography of the seabirds they study. At the very least, this requires a precise knowledge of seabird populations and trends, and an understanding of the wider links between seabird threats and human population change.

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Symposium 38 Phenotypic plasticity and early developmental conditions in birds

Introduction

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The phenotype of any animal is determined only partly by its genotype. The environment in which it develops can also play a major role. Phenotypic plasticity is the ability of a genotype to produce different phenotypes under different environmental conditions. During recent years there has been increasing recognition that environmental factors play an important role during early development in determining the phenotype of adults and adult fitness of offspring. The aim of this symposium was to review the

current state of knowledge on phenotypic plasticity and its evolutionary significance for birds. The papers cover such questions as how the quality of parents can influence the quality of the eggs which they lay, and the consequences for the young. They also review the influences that parental incubatory behavior has on embryonic development, and how the growth pattern of nestlings can have implications for their future fitness.

S38-1 Maternal effects through the avian egg

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Abstract There are many ways in which parents impact on the phenotype of their offspring, independently of genetically transmitted traits. Although such impacts are commonly known as maternal effects, they can be influenced by either parent. In this review we discuss maternal effects in birds in relation to the egg. Sealed from the external environment, the avian egg is a complex structure that has to provide all resources that a growing embryo needs to survive. The resources are deposited maternally over a short, but well defined, period immediately prior to laying. Allocation of resources to the egg has significant consequences for the phenotype and fitness of the offspring. First, we discuss experimental protocols for demonstrating maternal effects. This involves showing (1) that egg characteristics change with parental phenotype, and (2) that these changes in turn affect offspring phenotype. Such changes in egg characteristics in response to variation in parental phenotype may or may not be adaptive. We then provide an overview of the effects of maternal state on egg characteristics, such as size and other key components that shape the development of offspring in lesser black-backed gulls (*Larus fuscus*).

Key words Egg composition, Egg production, Maternal effects, Offspring fitness, Phenotypic plasticity

1 Introduction

The causes and consequences of variation in phenotype are of fundamental interest to evolutionary biology because that variation fuels evolutionary change. The phenotype is the product of a combination of genetic factors (the genotype) and environmental influences where, depending on the environment, each genotype can give rise to different phenotypes (Stearns, 1989). This is the concept of phenotypic plasticity which provides a useful framework for bringing together such disparate fields as genetics, ontogeny, ecophysiology, evolution and ecology (Stearns, 1989).

An individual phenotype is not only influenced by its own environment, but sometimes also by the environmental experience of others in the same population. Most often, but not exclusively, such effects result from interaction between parent and offspring: transgenerational phenotypic plasticity (Mousseau and Fox, 1998). Offspring phenotype resembles parental phenotype not only because of the genes transmitted, but also because of the parental investment, and therefore the environment, that parents provide for offspring growth and development independent of parental genotype. Such non-genetic effects are known as maternal effects (Arnold, 1994), although they can be influenced by either parent. Knowledge of maternal effects may contribute significantly to an understanding of the evolution of traits (e.g., Wolf et al., 1998), sexual selection (Gil et al., 1999; Qvarnström and Price, 2001) and speciation (Badyaev et al., 2002). Here we present a short over-

view of maternal effects on offspring phenotype and fitness acting through the avian egg.

Studies on maternal effects in birds have so far considered maternal effects mainly during the post-hatching period (reviewed in Price, 1998). Here focus is placed instead on the environmental conditions encountered by an organism during embryonic development. It has been suggested that variation in conditions during early embryonic development can have long-lasting effects on adult phenotype (Lindström, 1999; Metcalfe and Monaghan, 2001). However, parental investment in egg formation is costly (Monaghan and Nager, 1997; Monaghan et al., 1998; Nager et al., 2000, 2001; Visser and Lessells, 2001). Therefore, it is likely that parents within a population may differ in their ability to produce high quality eggs; and this ability may depend on their phenotype. Many recent studies have demonstrated a much greater variability in egg characteristics than previously thought, as well as in relationships between egg and parental phenotype.

Sealed from the external environment, the avian egg is a complex structure that has to provide all resources that a growing embryo needs for successful development. These resources are deposited maternally over a short, but well defined period immediately prior to laying. Quantitatively, the most important resources are protein, lipids and water, and the volume included is usually related to egg size (Williams, 1994). Larger eggs typically give rise to larger hatchlings that may have an advantage because of larger nutrient reserves at hatching (Parsons, 1970) or which have better thermoregulatory abilities (Rhymer, 1988). It is there-

fore often assumed that egg size, as a parameter of egg quality, is a good measure of the probability of producing surviving offspring. Yet egg quality may not only be affected by the volume of macronutrients but also their own quality. Thus the diet of laying females has been shown to affect both protein (Houston, 1998) and lipid quality (Surai et al., 2001).

Eggs also contain other resources, such as hormones (Schwabl, 1997), antioxidants and immunoglobulins (Ig), that are transferred maternally in small quantities unlikely to affect egg size. Such components can also be expected to affect offspring phenotype and fitness. Here we consider carotenoids and Ig. Carotenoids as antioxidants that play an important role in protecting embryonic tissue from oxidative stress (Blount et al., 2000). As animals cannot synthesize these compounds, the embryo depends on their provisioning in the egg. Carotenoids have therefore been suggested as the cause for a number of maternal effects on egg quality in wild birds (Royle et al., 1999; Blount et al., 2000). Female birds also transmit Ig into the egg to provide offspring with passive immunity (Smith et al., 1994; Lung et al., 1996; Gasparini et al., 2000). Embryos and hatchlings are unable to synthesize Ig and therefore depend on passive immunity until their own immune system becomes effective (Apanius, 1998).

In this contribution, we provide an overview of effects of parental phenotype on egg characteristics such as egg size and other key components that shape the development of offspring, drawing from field experiments carried out on the lesser black-backed gull (*Larus fuscus*).

2 Methods

In mediating maternal effects through the egg, individual females can be expected to vary in their ability to produce high quality eggs, and that this ability is related to phenotype. Hence the experimental protocol needs to address two questions. First, is parental phenotype related to egg characteristics, such as egg size or egg composition? And secondly, are these characteristics related to offspring phenotype and fitness?

We addressed the questions in field experiments on lesser black-backed gulls. The lesser black-backed gull is a common, colonial breeding seabird along coasts and lakes in Scotland. The gulls typically lay a clutch of three eggs, the third of which is significantly smaller than the first two (Cramp, 1983). They are also indeterminate layers, replacing any eggs lost during laying (Monaghan et al., 1995; Nager et al., 2000). If a first-laid egg is removed from the nest within a few hours of laying, then the female lays a clutch of four rather than three eggs (Monaghan et al., 1995). Continuous egg removal of every freshly laid egg within ca. 8 hours of laying induces the gulls to extend laying sequences (Nager et al., 2000). Egg removal therefore allows manipulation of production effort.

Tackling the first question required manipulation of the parental phenotype independently of its genotype. In

the lesser black-backed gull, we concentrated on maternal nutritional state. Many bird species, including gulls, use endogenous reserves to contribute to egg production (Houston, 1998). Increasing egg production effort from three to four eggs by removal of the first egg reduced maternal nutrient reserves significantly at clutch completion and ability to rear young to fledging (Monaghan et al., 1998). Nutrient reserves were measured as body mass corrected for body size, as well as by measuring protein reserves in pectoral muscle in females, their main protein reserves (Bolton et al., 1991). We also enhanced female nutritional state experimentally by the provision of a carotenoid supplement during egg formation (Blount et al., 2001). We then related maternal condition to egg size and measures of egg composition in terms of protein, lipids, carotenoids and Ig (Nager et al., 2000; Blount et al., 2001, respectively).

To address the second question, the consequences of variation in egg characteristics on offspring fitness, we needed to eliminate the effects of manipulating parental rearing ability. This was achieved by cross-fostering eggs laid by manipulated and control parents to unmanipulated foster parents. On the assumption that foster parents did not differ significantly in their ability to rear young, we concluded that differences between treatment groups in offspring phenotype and fitness would be due to differences between eggs alone.

3 Results and discussion

Through continuous egg removal, lesser black-backed gulls were induced to lay extended sequences of on average 8.6 ± 0.6 eggs (Nager et al., 2000). Eggs laid late in the sequences came from experimental females in which nutritional state had been reduced. In order to test for differences in egg quality, the induced additional eggs were fostered to unmanipulated parents (Monaghan et al., 1998). Each egg was fostered singly in order to avoid effects of sibling competition. A strong relationship was found between the position of the egg in the laying sequence and fledging success: eggs laid at the end of the sequence were three times less likely to produce fledglings than eggs laid early (Nager et al., 2000). Obviously, eggs laid at the end of extended sequences hatched later than eggs at the start, but we verified that all foster parents were able to raise single control chicks irrespective of date. Therefore, differences in fledging success between eggs laid early and late in the sequence were interpreted as differences in egg quality.

Thus females in reduced body condition laid eggs of poorer quality with lowered chance of producing a fledgling. A similar trade-off between egg size and experimentally enlarged clutch size has also been found in zebra finches (*Taeniopygia guttata*) in captivity (Williams, 2001). In the gulls, eggs laid at the end of the sequence had a lower fresh mass than eggs laid at the beginning, but did not weigh less than the average size of a third egg in control clutches laid at the same time (Nager et al., 2000). Fresh egg mass,

therefore, is unlikely to explain the three fold lower fledging success of last-laid eggs in the sequences; other factors of egg quality must be involved.

Accordingly, we analyzed the content of macronutrients in eggs from the laying sequences (Nager et al., 2000). Only lipid content declined relative to egg size through the laying sequence, not protein content. Water content, however, increased. Hence, important changes occurred in nutrient content that were not directly reflected in egg size. Young of eggs late in the sequence came from eggs with a reduced lipid content, and were thus likely to have been at an energetic disadvantage (Parsons, 1970). The absolute quantity of specific amino and fatty acids declined within extended laying sequences too, but remained at the same concentrations relative to egg mass (Fidgett, 2002). Hence the relative composition of lipid and protein reserves in the egg was maintained, while the quantity of lipid reserves declined as maternal condition fell. Increased water content may be a factor favoring chick survival (Finkler et al., 1998), but it did not overcome the effects of changes in nutrient content in this study.

These data suggest that, in birds, nutrient content is likely to be more important in determining egg quality than egg size per se. So far, studies have focused on the lipid and protein content of eggs. Yet there are many more components in eggs that may mediate between parental and offspring phenotypes. In order to test whether carotenoid content is influenced by carotenoid availability during egg formation, a carotenoid supplement was given to female lesser black-backed gulls in that period (Blount et al., 2001). Supplemented females developed increased carotenoid-based coloration in the integument, as well as higher blood plasma concentrations of carotenoids and higher antioxidant activity. In turn, carotenoid-fed females produced eggs containing higher carotenoid concentrations compared to control females. This result suggests that, in the wild, carotenoids may be a scarce, limiting resource during egg production.

As carotenoids also have immunomodulating properties (Møller et al., 2000), they may influence the levels of Ig in maternal circulation. Indeed, supplemented females had lower blood plasma levels of Ig than control females, which was mirrored in the Ig content of the eggs that they laid (Blount et al., 2001). These results suggest that carotenoid and Ig deposition in the eggs is a function of their maternal circulating levels. Levels of carotenoids and Ig also vary within clutches. In unmanipulated clutches, female lesser black-backed gulls deposited lower levels of carotenoids in the third egg compared to the first (Royle et al., 1999; Blount et al., 2001). Similarly, Ig levels declined from the first to the third egg in unmanipulated clutches (Blount et al., 2001). In the experimentally extended laying sequences, the last egg contained significantly less Ig than control eggs (Fidgett, 2002). This suggests that transmission of passive immunity may also depend on maternal condition. No such effect was found in the carotenoid con-

tent of eggs laid late in extended laying sequences (Fidgett, 2002).

There is thus potential for maternal effects to be passed through the avian egg. Egg size and composition is influenced by maternal phenotype in lesser black-backed gulls, in contrast to studies of other species showing that egg characteristics are affected by paternal ornamentation (Gil et al., 1999; Cunningham and Russell, 2000; Saino et al., 2002a,b). The physiological mechanisms of differential allocation of resources to eggs according to maternal and paternal phenotype remain unclear, but resources may come from body reserves and/or daily food intake (Meijer and Drent, 1999). Although there may be considerable variation in nutrient composition between and within clutches, the consequences of these differences for offspring phenotype and fitness also remain unclear. The observed changes in egg content in response to variation in parental phenotype may not necessarily be adaptive; it can also represent a constraint. Too few studies have yet attempted to relate variation in egg characteristics to offspring fitness, and those that have, have focused mainly on the nestling stage. To understand the adaptiveness of these maternal effects, an understanding is also needed of the long-term consequences of embryonic rearing condition on offspring performance later in life. More experimental studies that elucidate the direct effects of variation in egg characteristics on offspring fitness are needed.

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S38-2 Developmental phenotypic plasticity in embryos during incubation

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Abstract Bird embryos depend on the attendance of parents to provide the optimal temperature for development. When parents cannot incubate optimally, the embryos need to adjust rates of growth and modes of development to compensate. I review data on the plasticity of embryo growth in birds, and relate this to mode of incubation, climate, nest insulation, and the continuum between precocial and altricial species. I also review the effects on hatchling survival of ensuing suboptimal growth trajectories. In several precocial species that require hatching synchrony, growth rate and mode of growth in embryos can be accelerated or retarded depending on the position of the embryo in the laying sequence. Communication between embryos in eggs late in incubation conveys information on the degree of maturity and time to hatching of each. This makes it possible for embryos in eggs produced after the start of incubation to accelerate growth in order to hatch at the same time as their siblings. I evaluate the circumstances under which such acceleration (or retardation) will occur, and how this affects the mode of growth and hatchling performance and survival.

Key words Embryo development, Incubation, Accelerated hatching, Embryo communication

1 Conditions for embryonic development in the wild

Developing avian embryos depend on their parents for food and nutrients in the egg, supplied by the female during egg formation, and the right temperature and humidity in the egg, provided by parental incubation. This review centers on the role and effects of parental incubation.

Through more-or-less continuous contact with the eggs, parents provide a benign environment for developing embryos. As a rule, species that are precocial or biparental in incubation are more attentive than altricial species and those in which only one sex incubates (Deeming, 2002). Recently, evidence for significant parental costs in incubation has come to light (Monaghan and Nager, 1997; Thomson et al., 1998; Visser and Lessells, 2001), suggesting that optimal incubation performance is not always possible. What happens then? In such cases, embryos need to adjust their rate of growth or mode of development to try to cope with the thermal environment. Such developmental plasticity has its limits as well as its costs for both embryos and hatchlings forced to follow growth trajectories other than the norm.

To evaluate embryo performance under suboptimal conditions, knowledge is needed of the optimal thermal environment for embryonic development. The development of chicken embryos, which have served as a model for all avian species, stops below 26°C, the so-called physiological zero temperature. Even between 26 and 36°C, the rate of development and growth is reduced; and long exposure to these temperatures may cause developmental abnormali-

ties and death. The thermal range between 36 and 40 °C is considered optimal for optimal development of most avian embryos. Embryos are generally very sensitive to temperatures above 40 °C with a rapid increase in risk of mortality (Lundy, 1969; Conway and Martin, 2000). Thus, whereas developmental plasticity seems to be very low at high temperatures, embryos at suboptimal temperatures seem able to cope with a range of thermal environments.

What then are the incubation temperatures found in nature? Data from four avian orders (Fig. 1) show that avian embryos are commonly incubated at temperatures below the optimal thermal range for growth and development (Webb, 1987). Clutches of more precocial orders are incubated at a little higher mean temperature, consistent with the higher levels of attentiveness in precocial species (Fig.

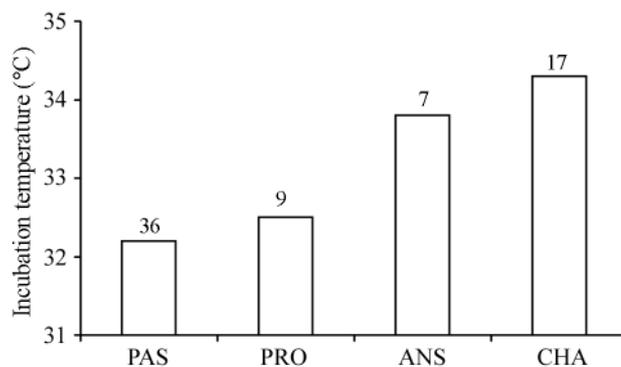


Fig. 1 Mean incubation temperature for clutches of four avian orders

PAS = Passeriformes, PRO = Procellariiformes, ANS = Anseriformes, CHA = Charadriiformes. Number of species screened stated above each bar. Compiled after Webb (1987).

1). Thus, the avian embryo does not have to cope with suboptimal incubation temperatures now and then, but most of the time. Such deviations from optimal incubation efficiency may therefore call for well-developed response plasticity in embryos.

2 Developmental limits in response to suboptimal incubation

Ambient temperature is an obvious factor affecting incubation efficiency. Here the northerly expansion of the breeding range of the pied flycatcher (*Ficedula hypoleuca*) into harsh and variable environments provides an illustrative example. This migratory species started to breed in northern Finland in 1957 (Järvinen, 1989), and has continued to do so. Mean ambient temperature during incubation was found to influence hatching success significantly each year. A reduction in mean temperature of 5 °C resulted in a 50 % fall in hatching success (Järvinen, 1983). Low ambient temperatures resulted in reduced incubation efficiency which increased the length of the incubation period (Järvinen, 1990). Concordant with this, most embryo deaths happened during the final days of incubation (Ylimaunu and Järvinen, 1987). The total metabolic rate of embryos increases as incubation temperature decreases (Booth, 1987) and the duration of incubation increases (Vleck and Vleck, 1996). This may then deplete energy-rich nutrients in the yolk before the embryos can hatch. Thus, increase in the duration of incubation can quickly fall outside the response range of embryos.

Looking for limits to developmental plasticity, I used field experiments to both increase or decrease incubation efficiency. The experiments included manipulative enlargement and reduction of clutch sizes, supplemental feeding, and the removal of courtship-feeding males. To measure the extent to which the experiments affected incubation efficiency, I used reported lengths of incubation period from the literature. Results showed that quite small increases in incubation time reduce hatching success (Fig. 2), indicating that some embryos are sensitive to increases in the length of the incubation period to a point where they are not plastic enough to survive. Increased hatching success in the treatments with shortened incubation period shows that normal incubation efficiency in the species investigated is suboptimal for the growth and development of embryos (Fig. 2).

3 Developmental costs in response to suboptimal incubation

Concerning post-hatching costs to those embryos that succeed in changing development and growth trajectories, data interpretation precipitates several issues. Clutch size and other manipulations must be restricted to the incubation period, otherwise fitness-related effects that arise later in hatched young cannot be separated from those resulting from the manipulation. Even then, poor nestling

condition can be explained either by deviations from optimal embryonic development or by reduced parental ability to provision the nestlings (Monaghan and Nager, 1997; Reid et al., 2000a). What is needed are records of hatchling condition, which is a direct consequence of embryonic development. Few studies meet these criteria.

Two out of four studies, in which a decrease in hatching success had been manipulated by clutch size enlargement, reported significantly reduced mass among young hatched from enlarged clutches (Sanz, 1997; T. Lislevand, pers. com., for the lapwing, *Vanellus vanellus*). The third study reported reduced growth rates in young hatched from enlarged clutches (Heaney and Monaghan, 1996), whereas the fourth found no such effects in enlarged clutches of the starling, *Sturnus vulgaris* (Reid et al., 2000b). In all these studies, however, a reduction in fledgling mass was found in clutches with low hatching success.

Another study on starlings is also relevant because measures of mass are available just after hatching (Reid et al., 2002). In this study, single-parent incubation was compared with biparental incubation. Hatching success and hatchling mass were significantly lower in clutches incubated by one parent (Reid et al., 2002). Thus, direct effects on hatchlings reported in some of the studies can be interpreted as the consequence of reduced incubation efficiency. The more general finding of reduced fledgling mass in these studies has been interpreted as the consequence of reduced rates of provisioning by females due to increased incubation costs. That some of the explanation lies in carry-over effects from suboptimal embryonic development, however, cannot be eliminated.

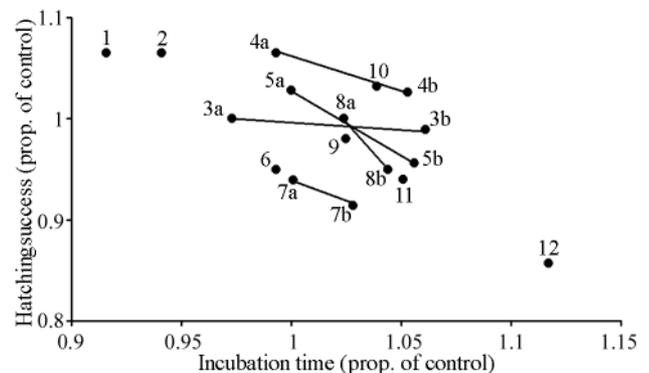


Fig. 2 The relation between length of incubation period and hatching success in experimental studies designed to test incubation efficiency

Both incubation period and hatching success are expressed as the ratio of experimental to control clutches. Values larger than 1 denote an increase in the length of incubation and hatching success, respectively, due to the experiment. Points connected with a line denote studies where data is presented for both reduced (a) and enlarged (b) clutches. Data from: Moreno (1989) = 1, Nilsson and Smith (1988) = 2, Moreno and Carlson (1989) = 3, Møller (1993) = 4, Siikamäki (1995) = 5, Heaney and Monaghan (1996) = 6, Sanz (1997) = 7, Moreno et al. (1991) = 8, Cichón (2000) = 9, Smith (1989) = 10, Baltz and Thompson (1988) = 11, Lyon and Montgomerie (1985) = 12.

4 Developmental costs in response to accelerated and delayed hatching

Another approach for assessing the costs of suboptimal embryonic development is through an evaluation of the post-hatching effects of accelerations or delays towards the end of embryonic development in precocial species. Females of many precocial species continue to lay eggs after the start of incubation, thus generating developmental asynchrony within the clutch (Wilson and Verbeek, 1995; Persson and Andersson, 1999). This is paradoxical because synchronization of hatching is vital for rapid and coordinately chick departure from the nest, to limit exposure to predation (Clark and Wilson, 1981; Spencer et al., 2001). It is also important for individual embryos to hatch simultaneously in the frequent case of females that abandon the nest soon after hatching, even if unhatched eggs remain (Björvall, 1968). To overcome this problem, embryos click to communicate their stage of development to one another through the egg towards the end of incubation (Vince, 1969; Brua, 2002). From such sounds, individual embryos can correct their hatching date coordinant with the perceived development of other embryos in the clutch. This correction may be accomplished either by shortening or prolonging incubation (Vince, 1964, 1968; Persson and Andersson, 1999).

In an experiment, artificial clutches of pheasants (*Phasianus colchicus*) and mallards (*Anas platyrhynchos*) were incubated in an incubator to produce embryos that had to either accelerate or delay hatching to synchronize their hatching with the bulk of their siblings (Nilsson and Persson, in prep.). This resulted in pheasant embryos having to accelerate by two days in a shortened incubation period, and mallard embryos having to hold back for up to 2.5 days longer than the normal incubation period. Both of these experimental groups had higher mortality rates after hatching, indicating that deviations from the normal incubation period had detrimental effects noticeable soon after hatching. Reducing the length of incubation, in this case, seemed to be more serious than prolonging it, as accelerated embryos suffered from reduced growth rate and impaired balance as well.

These costs, due to deviations from the normal incubation period, may help in evaluating possible constraint mechanisms in the development of precocial chicks, at least. Precocial chicks already possess functional sensory, neuromuscular and thermoregulatory systems at hatching (Starck, 1998), as they may be exposed to stressful environmental conditions requiring them to walk considerable distances soon after hatching. It is suggested that the maturation of these systems takes place late in embryonic development (Ricklefs and Starck, 1998), during the plateau phase. As this is the time when chicks appear able to communicate with each other (Vince, 1969), acceleration and delay of hatching must also take place during that phase (Cannon et al., 1986). Thus, chicks that have shortened this phase of

organ maturation may have to pay the cost of less developed or impaired body systems: hatching earlier than normal should make it harder for precocial hatchlings to find and handle food items, which has consequences for survival.

5 Conclusions

Embryo growth and development within species thus appears to be regulated rather strictly. Small deviations from normal incubation efficiency increase the risk of embryo mortality. Reduced incubation efficiency, resulting in longer incubation periods, seems to increase metabolic rates in embryos, and thereby cause starvation in late stages. In precocial species, this may lead to a delayed cost due to decreased residual yolk reserves, which are important for the survival of newly hatched chicks. In both precocial and altricial species, embryos are assumed to follow similar growth trajectories until late in embryogenesis when the two types need different lengths of time to pass through developmental stages (Ricklefs and Starck, 1998). This gives rise to variation in functional maturity of tissues, which seems to be more plastic than growth *per se*. How plasticity in the functional maturity of important tissues, for example the brain and nervous system, is related to fitness, early or late in life, is still largely unknown, especially in wild populations.

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S38-3 Evolution and expression of genetic variation in nestling traits

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Abstract Environmental conditions experienced during early life are known to impact upon the development of passerine nestlings, as well as on their performance and fitness as adults. Nevertheless, little is yet known about the relative importance of different types of maternal, environmental and genetic effects as proximate determinants of variation in nestling traits, and in particular, how the relative importance of these components is affected by the characteristics of the growth environment. Evidence from a number of studies suggests that the expression of both genetic and maternal effects can be highly environment-dependent, together with their impact upon fitness variation among individuals. Again relatively little is known about how selection acts upon this variation. According to one popular scenario, selection acts mainly on environmental, not genotypic variation. Using data from a long-term study of collared flycatchers (*Ficedula albicollis*) from the Swedish island of Gotland, we demonstrate that: (1) common environmental/parental effects have a strong influence on variation in nestling traits, and (2) different traits are affected differentially by early vs late effects. We further demonstrate that (3) selection acts on genetic, as well as environmental, variation. These results suggest that common environmental/parental effects may be more important sources of variation in nestling traits than previously acknowledged, and that the time-window for these effects differs for different traits. Furthermore, our analyses reinforce the conclusion that selection on environmental deviations cannot alone explain the lack of expected selection responses in heritable nestling traits under directional selection.

Key words Genetic variation, Maternal effects, Environmental effects, Selection, *Ficedula albicollis*

1 Introduction

How do environmental conditions influence individual growth? How does individual variation in growth translate into variation in individual fitness? What are the evolutionary implications of fitness variation stemming from environmentally induced effects on individual growth performance? These all appear to be fairly trivial and unproblematic questions because it is known that: first, poor environmental conditions have a negative impact on individual growth (Gustafsson and Sutherland, 1988; Merilä, 1997); secondly, poor growth performance is often associated with reduced likelihood of survival to adulthood (Alatalo et al., 1990; Lindén et al., 1992); and thirdly, poor growth can translate into other kinds of problems with cascading effects on future performance such as lowered fecundity (Gustafsson and Sutherland, 1988). Furthermore, poor growth performance often leads to lowered heritability of growth related traits in birds (Larsson, 1993; Merilä and Sheldon, 2001), and thereby reduces the efficiency of selection and expected evolutionary response to directional natural selection (Hoffmann and Merilä, 1999).

An idea intimately related to low heritability under poor environmental conditions is ‘selection on environmental deviations’ (Alatalo et al., 1990). The kernel of this idea is the perception that when environmental variation causes

individual variation in growth, and reduced growth is selected against, then selection will predominantly weed out individuals deviating negatively from the “genetic ideal” (Fig. 1). In other words, selection is considered to be “soft” in the sense that it acts mainly against negative environmental deviations from genotypic (breeding) values (Fig. 1a), rather than “hard” in the sense that it acts mostly on absolute trait values irrespective of the genetic details (Fig. 1b). This argument has been repeatedly evoked as an explanation for the lack of evolution (or expected selection response) in heritable traits under directional selection (Merilä et al., 2001a).

Returning to the opening questions, it is clear that there is now a fairly good understanding of how environmental conditions influence individual growth and how this translates into fitness variation (cf. Stinchcombe et al., 2002). It is not at all clear, however, whether our understanding of the evolutionary implications of environmentally induced variation in individual fitness is adequate (cf. Merilä et al., 2001a). First, evidence for lowered heritability of growth-related traits under poor environmental conditions is somewhat mixed, and although there seems to be a tendency for size-related traits to express less genetic and more environmental variance under such conditions, the evidence is equivocal (Hoffmann and Merilä, 1999; Merilä and Sheldon, 2001). Secondly, although arguments for selection on envi-

ronmental deviations have been made frequently, it is unclear whether this is actually a plausible mechanism in nature: none of the early studies have explicitly tested for selection on environmental deviations. Thirdly, due to the ubiquity and persistence of maternal and common environment effects (Rossiter, 1996; Mousseau and Fox, 1998), it is still unclear how much of the variation attributed to additive genetic effects in the wild can be explained by common environmental and parental effects.

The aim of this paper is to describe work that addresses the following three questions. First, is there evidence that the heritabilities measured in earlier studies of wild bird populations could be upwardly biased due to persistent maternal or common environmental effects? Secondly, how much scope is there for parents to influence the performance of their offspring through these effects? Thirdly, is there evidence that selection may be acting on variation in environmental/parental effects, rather than on breeding values per se? The answer to the last question is valuable also because it can shed light on the debate as to why heritable traits under directional selection fail to show the evolutionary responses predicted by quantitative genetic theory (Merilä et al., 2001a).

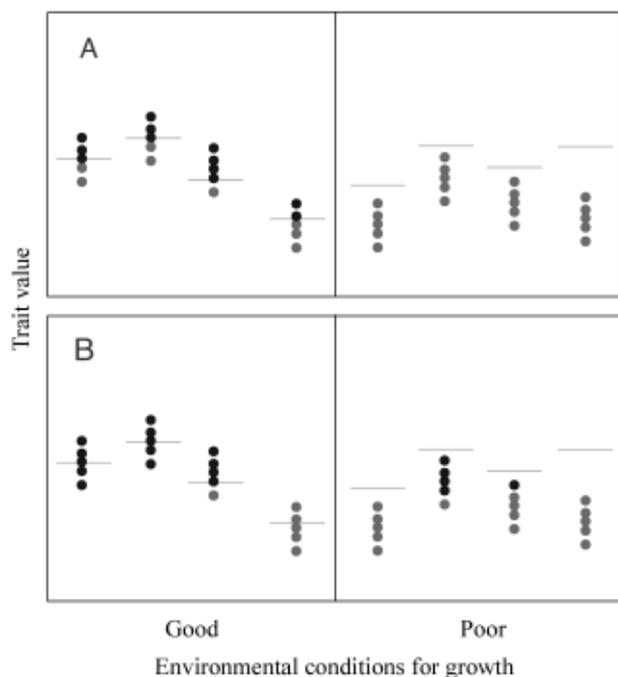


Fig. 1 Schematic illustration of the concepts of (A) “selection on environmental deviations” and (B) “conventional selection” under two different environmental conditions

Environmental conditions are poor vs. good growth conditions, respectively. Each point represents the phenotypic value of an individual, and the horizontal line the expected breeding value for a brood (group of points). The distance and direction between expected breeding value and individual phenotypic value represents the environmental deviation for a given individual. The effect of selection is depicted by red circles: under a given scenario, individuals marked with grey are destined to die (selected against), whereas individuals in black are destined to survive (selected for).

2 Materials and methods

The data for the analyses here derive from a long-term study, between 1980 and 1999, of the collared flycatcher (*Ficedula albicollis*) on the Swedish island of Gotland (Gustafsson, 1989; Merilä, 1997; Kruuk et al., 2001). Every year, nearly all adults and their offspring were captured and banded with individually numbered aluminium rings for their subsequent identification and construction of pedigrees. All banded nestlings were also measured for tarsus length (mm) and body weight (g). Nestling tarsi are full grown at fledging, and can be used as a measure of general body size (Merilä, 1997). Body condition index in nestlings is defined as the mass relative to general body size, as obtained from the linear regression of nestling body weight on tarsus length (Merilä, 1997; Merilä et al., 2001b). Both of these traits are known to be influenced negatively by poor feeding conditions (Merilä, 1996; Merilä, 1997), and to be under positive directional viability selection (Lindén et al., 1992; Merilä et al., 2001b; Kruuk et al., 2001). Yet for one reason or another, they have not shown the phenotypic evolution expected over the study period (Merilä et al., 2001a,c; Kruuk et al., 2001).

To analyze the relative contributions of different genetic and environmental factors to nestling tarsus length and condition, two different data sets were used. These were a data set consisting of all nestlings ($n = 17\,769$) that had been reared by their biological parents between 1980 and 1999, and a data set consisting of nestlings cross-fostered two days after hatching during the same period ($n = 5\,567$). These data sets were subjected to “animal model” analyses of variation, which are generalized linear mixed models utilizing pedigree information and allow the partitioning of variance in phenotypic traits into additive genetic effects and other random and fixed effects (Knott et al., 1995; Milner et al., 1999; Merilä et al., 2001a).

These models were also used for BLUP (Best Linear Unbiased Predictor) estimation of the individual breeding values used in the analyses of natural selection on individual breeding values and environmental deviations, respectively. Environmental deviations here were defined as residuals of regressions of phenotypic values on individual breeding values. All animal model analyses were performed using the programs PEST (Groeneveld and Kovacs, 1990; Groeneveld et al., 1992) and VCE (Groeneveld, 1995) running on UNIX-platform. Selection analyses used to estimate linear standardized selection differentials (S) were performed using the methods of Arnold and Wade (1984a,b) with SAS statistical package (SAS Institute, 1996). More details about the data and analyses can be found in Merilä et al. (2001b) and Kruuk et al. (2001).

3 Results and discussion

3.1 Sources of phenotypic variation in nestling traits

“Animal model” analyses of variation in tarsus length and the condition index of non-fostered nestlings revealed

that both traits were significantly heritable (tarsus length: $h^2 = 0.35 \pm 0.021$; condition index: $h^2 = 0.30 \pm 0.023$; Table 1a). After controlling for additive genetic effects, however, large amounts of environmental (*sensu lato*) variation still remained in both traits. This was largely accounted for by a common nest environment effect, and to a minor degree by year and area effects (Table 1a).

The common environment effect could be genuine, due for example to territory quality; but it could also be attributable to parental effects. To explore this, we fitted models where the common environment effect was replaced with maternal and paternal identity effects. The results revealed that the combined effect of the maternal and paternal identities was about the same as the common environment effect for each trait (Table 1b), suggesting that variation captured by the latter in the original models (Table 1a) reflect a genuine common environment effect. For both tarsus and nestling condition traits, however, the maternal identity effect was slightly but significantly larger than the paternal identity effect by ca 5%, suggesting a small maternal effect contribution to both traits (Table 1b).

When the analyses were repeated using data from cross-fostering experiments (Table 2), which allowed fitting the effects of origin and rearing environments together with additive genetic effect, the following intriguing points emerged. First, heritability estimates were lower than those recovered from the analysis of non-fostered nestlings (cf. additive genetic variance in Tables 1a and 2). This suggests that the heritability estimates from non-fostered nestlings may be inflated by unaccounted common environment or parental effects, especially so in the case of tarsus length. Secondly, even after accounting for additive genetic effects, there was a substantial (16.1%) nest of origin effect on tarsus length (Table 2). This further suggests a substantial

early-life common environment or parental effect on variation in tarsus length. In the case of nestling condition, the nest of origin effect was small (ca 2%), whereas the nest of rearing effect was about twice as large (ca 43%) as the additive genetic effect (22%; Table 2). Hence, in contrast to tarsus length, nestling condition seems to be determined mainly by the environment experienced late in the nestling phase, with little or no influence from the early environment.

3.2 Selection on environmental vs genetic components of phenotype

Concerning the action of survival selection, analyses of selection over the study period revealed strong and consistent directional selection on the phenotypic values of both tarsus length ($S = 0.18 \pm 0.02$ standard error) and nestling condition ($S = 0.23 \pm 0.02$). Similar analysis of estimated breeding values revealed that selection was acting on breeding values as well (tarsus length: $S = 0.13 \pm 0.02$; condition: $S = 0.14 \pm 0.02$). These analyses suggest that selection is acting not only on environmental deviations, but also on genotypic variation. This conclusion is corroborated by two further lines of evidence. First, comparisons of variance components attributable to additive genetic and environmental effects before and after selection reveal that both are significantly reduced by natural selection (Merilä et al., 2001b; Kruuk et al., 2001). Secondly, analysis of survival selection on offspring deviations from the midparent tarsus length, together with selection on midparent tarsus length, reveal that both midparent values and the offspring deviations from them are subject to selection (Kruuk et al., 2001). Both of these analyses reinforce the conclusion that selection is acting not only on environmental deviations, but also on additive genetic variance.

4 Conclusions and implications

The results above lead to three main conclusions. First, “animal model” analyses of phenotypic variation return lower heritability estimates than traditional midparent-midoffspring regressions, at least for tarsus length ($h^2 =$

Table 1 Sources of variation in nestling condition and tarsus length in collared flycatchers as revealed by “animal model” analyses applied to data (1980–1999) of non-fostered nestlings

Source of variance	Condition	Tarsus
	var% \pm SE	var% \pm SE
a. Nest of rearing		
Additive genetic	29.9 \pm 2.3	35.3 \pm 2.1
Nest of rearing	48.5 \pm 1.4	29.7 \pm 1.4
Year	7.5 \pm 1.7	13.9 \pm 2.6
Area	0.6 \pm 0.4	2.1 \pm 0.7
Residual	13.5	19.0
b. Maternal and paternal identity		
Maternal identity	28.5 \pm 1.1	18.6 \pm 1.0
Paternal identity	23.7 \pm 0.9	12.2 \pm 0.8
N (nests)	3 836	3 844
N (fledglings)	17 717	17 769

Var = variance component as a percentage of total phenotypic variance. N = sample size. Adopted from Merilä et al. (2001b) and Kruuk et al. (2001).

Table 2 Sources of variation in nestling condition and tarsus length in collared flycatchers as revealed by “animal model” analyses applied to data (1984–1999) of cross-fostered nestlings

Source of variance	Condition	Tarsus
	var% \pm SE	var% \pm SE
Additive genetic	21.9 \pm 2.9	28.0 \pm 4.4
Nest of rearing	42.8 \pm 2.2	15.2 \pm 2.2
Nest of origin	2.2 \pm 1.3	16.1 \pm 1.3
Year	10.4 \pm 3.0	12.2 \pm 3.2
Area	4.8 \pm 2.3	2.8 \pm 1.5
N (nests)	1 044	1 044
N (nestlings)	5 565	5 567

Var = variance component as a percentage of total phenotypic variance. N = sample size. Adopted from Merilä et al. (2001b) and Kruuk et al. (2001).

0.48, Merilä, 1997; $h^2 = 0.65$, Merilä et al., 1998). This suggests that traditional estimates of heritability in wild animal populations might often be overestimated. Such a difference between the methods can be attributed to the ability of “animal model” analyses, which are based on extensive pedigree information, to remove environmental correlations between relatives more efficiently. The reduction in heritability estimates between the two sets of analyses, non-fostered vs. cross-fostered nestlings, nevertheless suggests that even “animal model” estimates of heritabilities might be to some degree inflated by early common environment or parental effects.

Secondly, the large common environment/parental effects recovered by these analyses suggest ample scope for parental performance to influence the fitness of their offspring. In the case of tarsus length, moreover, the effects of both early and late parental environments (cf. Table 2) seem to be equally important, whereas in the case of the condition index, any effects from the early environment are overwhelmed by late nestling period effects (Table 2). Thus, selection acting on environmental variation, whether due to parental or common environment effects, can in theory act differently on early and late effects of caretaking, depending on the trait concerned.

Thirdly, environmental and parental sources of variation in offspring performance are under directional natural selection, as revealed by selection analyses demonstrating that both genetic and environmental components are under directional selection. The lack of expected response in these traits over time (Merilä et al., 2001c; Kruuk et al., 2001) thus cannot be explained simply as the failure of selection to act on the relevant underlying variation; alternative explanations should be considered. Consideration of further mechanisms, as well as further partitioning of phenotypic variance into its causal components, particularly those attributable to direct and indirect maternal genetic effects (Roff, 1997: 248), remains a challenge for future studies.

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S38-4 The effect of environmental conditions on early growth in geese

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Abstract Geese, one of the few avian herbivores, face a combination of unique constraints during growth. Goslings must feed by themselves; they must reach a large size during a short growing season; they grow in the Arctic under harsh climatic conditions; and, despite their high nitrogen requirement for growth, they feed only on plants, which are low in protein. We examined how these constraints shape growth strategy in the greater snow goose (*Anser caerulescens atlanticus*). Growth rates of goslings are among the highest reported in precocial birds. Goslings maintain a very high resting metabolic rate throughout growth and are fully competent homeotherms soon after hatching: they seem to prioritize maintenance of optimum internal conditions for biosynthetic activity over energy conserving strategies. Such an expensive life-style can only be sustained by feeding at a very high rate on high-quality food. The consequence is that growth rate is highly sensitive to environmental conditions encountered in early life. Although the developmental pattern in goslings shows some phenotypic plasticity when environmental conditions deteriorate, it is not sufficient to compensate for factors such as a seasonal decline in plant quality. Therefore, goslings that hatch late or grow slowly must fledge at a smaller size, and this may have serious fitness consequences for survival and adulthood.

Key words Snow geese, Growth, Food, Thermoregulation

1 Introduction

One of the most important factors affecting growth patterns in birds is the developmental mode of the hatchling, i.e. the altricial-precocial spectrum (Starck and Ricklefs, 1998). Geese are precocial birds that have been the focus of some growth studies, although they have been ignored in comparisons of altricial-precocial birds. Yet geese are subject to a series of unique ecological circumstances that affect their growth patterns different from other precocial birds. Here we review some of these factors and how they affect the energetics and growth patterns in geese, using our research on greater snow geese (*Anser caerulescens atlanticus*) as a case study.

Geese are one of the few herbivorous groups of birds (Sedinger, 1997). Because of the relatively low quality of their diet (low protein, high fiber), herbivores must hold large quantities of food in the gut for long periods for digestion. These conditions, however, are incompatible with the avian digestive system which is small in volume and short in retention time to minimize mass. That is why herbivory is found in so few bird taxa, such as grouse and ratites, which are large in body and poor flyers or flightless. Geese are also relatively large in body but are unique in having retained the capacity for strong flight. Consequently, the goose alimentary system is typically avian with limited digestive capacity. To cope, geese have developed behavioral adaptations to improve nutrient uptake, such as discriminating food selection, prolonged feeding time and long

migrations to exploit highly seasonal environments such as the Arctic.

Breeding in the Arctic confers some advantages, such as access to high quality food and almost continuous daylight for feeding during the summer. It also imposes severe constraints. The Arctic is a cold and windy environment, and subjects goslings to high thermoregulatory costs. Although the relatively large body size of goslings may provide some thermoregulatory relief, it also lengthens the growth period, which is a major constraint where summers are short. The most severe constraint faced by goslings, however, is undoubtedly their strictly herbivorous diet. This is unusual, as the chicks of most leaf- or seed-eating birds are fed on an animal diet (e.g., insects) to meet their high energy and protein requirements. Therefore, a herbivorous diet is likely to impose a strong limitation on growth in geese.

2 Growth rates in geese

Despite being herbivorous and self-feeding, goslings also have remarkably high growth rates (Aubin et al., 1986; Sedinger, 1986; Lesage and Gauthier, 1997). In Table 1, we compare the growth constant of the logistic equation (K), an index of growth rate, for a number of goose species. Ricklefs (1979) described the relationship between K (logistic growth constant) and M (asymptotic body mass) in birds by the following allometric equation:

$$K = 1.10M^{0.34}.$$

We used this equation to calculate the value of K predicted (K_{pred}) for each species in Table 1. Among the 14 studies compared, all but two reported higher empirical growth rates than predicted by the equation, which is surprising because the allometric equation is based largely on altricial birds that should have higher growth rates than precocial birds. These results suggest that selective pressure for fast growth is very strong in geese.

Goslings achieve very high growth rates despite their well-developed legs and mobility from hatching, which have their own energy costs. In greater snow geese, for example, we found that the more mature organs at hatching, such as legs, gizzard and gut, developed early and grew more rapidly than other parts of the body (Lesage and Gauthier, 1997; also Sedinger, 1986). Such results indicate that embryonic constraints at the tissue level are not the primary factor limiting growth rate in geese, as predicted by the tissue-allocation hypothesis (Ricklefs et al., 1994).

3 Metabolic rate and energy expenditure of goslings

In order to grow, the balance between energy intake and energy expenditure for maintenance must be positive. For a self-feeding precocial bird in the Arctic, maintenance of metabolic rate is likely to be high and dependent on environmental conditions. As the expenditure side of the equation increases, surplus energy may decrease if not matched by an increase in food intake, and thus lead to retarded growth.

We conducted experiments on the metabolism of captive-reared goslings hatched from eggs collected in the wild. Over 1 to 40 days, we exposed them to various ambient temperatures and measured O_2 consumption, CO_2 production, and internal body temperature (T_b ; Ratté, 1998). We also evaluated the cost of thermoregulation using heated taxidermic mounts of goslings of 4 different ages (5, 10, 20 and 30 days; Fortin et al., 2000b). The mounts were calibrated in the laboratory using live goslings, and then exposed to field conditions in the Arctic to measure heat loss under various environmental conditions (temperature, wind, and solar radiation; Renaud, 1999).

One- to two-day old goslings maintained their T_b at around 39.7°C when exposed for 1 hour to temperatures ranging from 5 to 25°C (Ratté, 1998). At -5°C , however, they had difficulty, as their T_b dropped to 37.8°C over the same period; but by day 10 this had been overcome (Ratté, 1998). Under field conditions, four day old goslings living in average air temperatures of 7.7°C already have a T_b of 40.4°C , very close to that of adults (Fortin et al., 2000a). Therefore, newly-hatched goslings are fully homeothermic and able to maintain their T_b near adult values over a wide range of environmental conditions, as has been observed in other Anatidae (Visser, 1998).

In line with their high T_b , goslings also have high thermoneutral metabolic rates at rest (RMR). Throughout

growth, the RMR of goslings is more than twice the predicted basal metabolic rate (BMR) of adult birds of similar size (Fig. 1). It should be noted that the RMR of growing goslings, unlike the BMR of adults, includes the cost of biosynthesis for growth. The RMR of neonate goslings 1–2 days old (body mass: 77 g) already averages 1.25 W (Fig. 1), just over twice the value predicted for nonpasserine adults of similar size (Lasiewski and Dawson, 1967). This is the highest reported RMR value for neonates, even when compared to such cold-hardy neonates as common eiders, *Somateria mollissima* (Steen and Gabrielsen, 1986). Peak metabolic rate (PMR) of goslings, defined as the metabolic rate at -5°C , is also very high, averaging $1.5 \times \text{RMR}$, or $3.8 \times \text{BMR}$ of adult birds of similar size (Fig. 1).

Despite their high RMR, goslings are exposed to significant thermoregulatory costs as average air temperature during the growth period at our study site on Bylot Island, Nunavut, Canada (73°N , 80°W) is only 5.7°C (Renaud, 1999). The corresponding standard operative temperature, an effective environmental temperature that takes the influence of wind and solar radiation into account (T_{es} ; Bakken, 1976), is only 5.3°C . This value declines with the season from 11.3°C at hatching to 1.1°C at 40 days of age. These temperatures are well below the thermoneutrality zone of goslings, as their lower critical temperature is $15\text{--}20^\circ\text{C}$ (Ratté, 1998). Regulatory, cold-induced thermogenesis therefore represents a significant portion of energy expenditure in goslings. Using heated taxidermic mounts calibrated on live goslings, Renaud (1999) estimated that thermogenesis represented on average 31% of the maintenance metabolism of

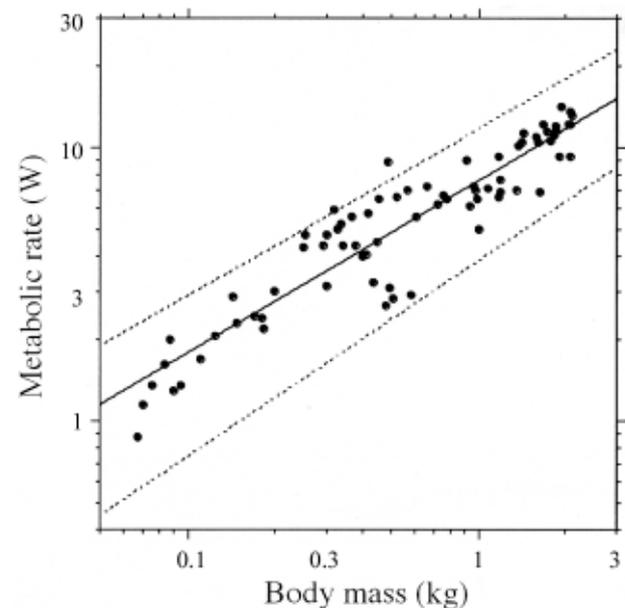


Fig. 1 Relationship between resting metabolic rate (RMR) or peak metabolic rate (PMR) and body mass of greater snow goose goslings

RMR is the solid line, measured at 25°C , within the thermoneutrality zone; PMR is the upper stippled line, measured at -5°C . The lower stippled line is the predicted basal metabolic rate for adult non-passerine birds of similar size (from Lasiewski and Dawson, 1967).

growing goslings between 1 and 40 days of age: 42% in newly hatched goslings, declining to 22% at day 40.

Self-feeding in goslings clearly imposes very high maintenance costs. In particular, their high RMR is probably an adaptation that enables individuals to sustain a high growth rate. High PMR also allows them to maintain a high T_b during cold periods, as foraging goslings do not commonly use hypothermia as an energy-saving mechanism (Fortin et al., 2000a). Thus they must prioritize the maintenance of optimum internal conditions for biosynthetic activity over strategies of energy conservation.

4 Food intake, food quality and body growth

Such an expensive life-style can only be sustained by feeding intensively on high-quality food. Yet even though food quality is high in the Arctic, there is much evidence that growth rate in geese is commonly food-limited. In an experiment where captive goslings were reared in the field, those that received a high quality food-supplement grew faster and were larger at fledging (Lindholm et al., 1994). Similarly, Lepage et al. (1998) found a direct and positive correlation between the availability of high quality food and growth in wild goslings.

Plants begin a steep seasonal decline in quality, with dropping protein, around the time of gosling hatching (Manseau and Gauthier, 1993; Lepage et al., 1998). Even

though regrowth of grazed plants may be of high quality, this may not be sufficient to compensate for the reduction of biomass due to grazing (Piedboeuf and Gauthier, 1999). Goslings hatched earlier in the season thus exploit higher food quality than those hatched later; hence they grow faster (Sedinger and Flint, 1991; Cooch et al., 1991; Lepage et al., 1998). Because of the short Arctic summer, goslings that hatch late may not be able to complete their growth, and as a result survive less well during the following autumn migration (Schmutz, 1993; Cooch, 2002); those that do survive become small adults (Cooch et al., 1991).

Given the serious fitness consequences of reduced growth rate, it could be expected that late-hatched, slow-growing goslings may adjust their growth pattern to maximize their chances of fledging. This we examined by collecting goslings shortly before fledging and comparing organ development between early- and late-hatched goslings (Lesage and Gauthier, 1998). Late-hatched goslings carried less total body protein than those hatched early (Fig. 2). Deficiency was greatest in breast muscle, indicating that when faced with a diminished food supply, goslings prioritize development of the energy supply organs (digestive tract, legs) over other organs such as wings.

In a laboratory experiment, we also examined the effect of variations in food quality on growth, digestive efficiency and organ development. We found that diet quality had a strong effect on growth (Fig. 3). Even though food intake was higher for the goslings on low-quality food, this

Table 1 Growth coefficients in geese

Species	Env.	Sex	Body mass	K_{obs}	K_{pred}	Reference
<i>Anser caerulescens caerulescens</i>	W	-	1 890	0.151	0.085	Aubin et al., 1986
	C	-	1 890	0.115	0.095	Ankney, 1980
<i>Anser caerulescens atlanticus</i>	W	M	2 666	0.096	0.075	Lesage and Gauthier, 1997
	W	F	2 391	0.090	0.078	Lesage and Gauthier, 1997
	C	-	2 525	0.132–0.168	0.077	Lindholm et al., 1994
	C	-	2 525	0.112–0.131	0.077	Fournier (unpubl. data)
<i>Anser anser</i>		M	3 400	0.098	0.069	Heinroth and Heinroth, 1928 (in Starck and Ricklefs, 1998)
		F	2 930	0.109	0.073	Heinroth and Heinroth, 1928 (in Starck and Ricklefs, 1998)
<i>Anser indicus</i>	W	-	2 600	0.065	0.076	Würdinger, 1975 (in Sedinger, 1992)
	C	-	2 600	0.094	0.076	Würdinger, 1975 (in Sedinger, 1992)
<i>Branta canadensis atlantica</i>	C	-	3 800	0.079	0.067	Würdinger, 1975 (in Sedinger, 1992)
<i>Branta canadensis moffitti</i>	C	M	5 075	0.075	0.061	Yokum and Harris, 1966
	C	F	4 111	0.068	0.065	Yokum and Harris, 1966
<i>Branta canadensis minima</i>	W	M	1 341	0.106	0.095	Sedinger, 1986
	W	F	1 223	0.120	0.098	Sedinger, 1986
<i>Branta bernicla nigricans</i>	W	-	1 237	0.081	0.098	Sedinger and Flint, 1991
<i>Branta bernicla orientalis</i>	C	-	1 273	0.125	0.097	Morehouse, 1974 (in Sedinger, 1992)
Domestic goose	C	M	3 640	0.095	0.068	Laird, 1965 (in Ricklefs, 1973)
	C	F	3 750	0.078	0.067	Laird, 1965 (in Ricklefs, 1973)

Growth constant, K , from the logistic curve and minimum winter body mass, Env. = environment (W = wild, C = captivity), K_{obs} = observed value, K_{pred} = predicted value by allometric equation.

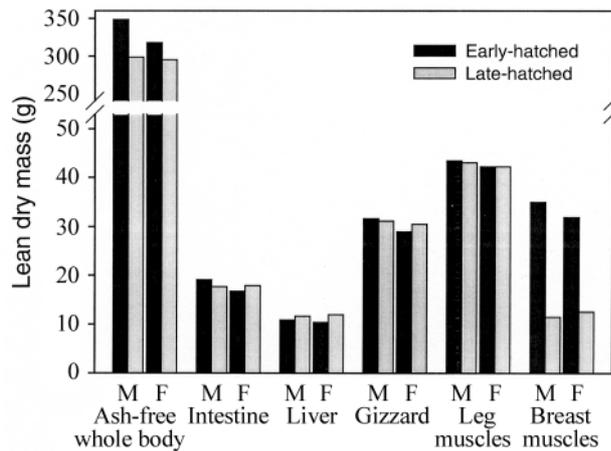


Fig. 2 Lean dry mass of various organs and ash-free lean dry mass of whole body in early- and late-hatched male (M) and female (F) greater snow goose goslings collected shortly before fledging on Bylot Island

$n = 24$ for each combination of hatch period and sex. All values are standardized to a common value of total body ash to correct for differences in body size and age at capture (details in Lesage and Gauthier, 1998).

was not sufficient to prevent a slowing of growth rate. At the end of 45 days, goslings reared on a low-quality diet for all or part of the experimental period had enlarged digestive organs and reduced breast muscles compared to goslings reared for the entire period on a high-quality diet.

Overall, these experiments show that goslings can adapt their developmental pattern to mediate the impact of a decreasing food quality. Despite these adjustments, however, it appears that the capacity of goslings to buffer the effects of variations in food quality are limited, probably because their gut is always working near maximum capacity (Manseau and Gauthier, 1993).

5 Conclusion

Our results suggest that optimal allocation of energy and nutrients to growth and maintenance is critical for achieving high growth rates in young geese. Their self-feeding mode, herbivorous diet, and high maintenance costs are all ecological factors that nevertheless contribute to limiting growth rate. Although developmental patterns in goslings show some phenotypic plasticity when environmental conditions deteriorate, they are not enough to compensate for such factors as natural decline in plant food quality and availability. Thus, we conclude that growth rates in wild geese are limited more by environmental conditions than by embryonic constraints at the tissue level.

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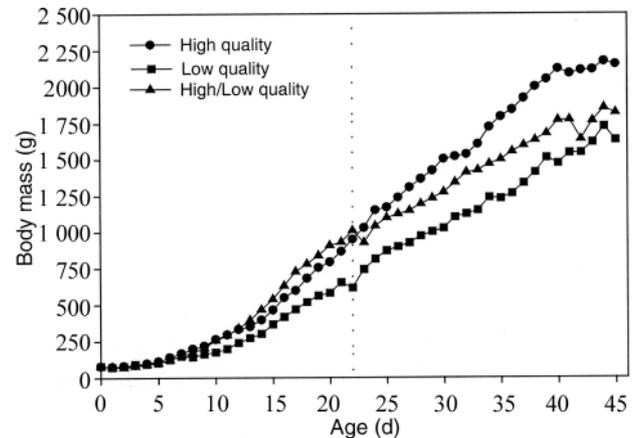


Fig. 3 Body mass of greater snow goose goslings reared on different diets as a function of age

The first group fed on high-quality diet (2/3 goose chow: 1/3 alfalfa, $n = 6$), the second group fed on low-quality diet (1/3 goose chow: 2/3 alfalfa, $n = 5$), and the third group started on high-quality diet but was switched to low-quality diet (stippled line) during the growth period ($n = 5$).

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S38-5 Are unseen effects of early environment negligible? Three examples in great tits (*Parus major*)

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Abstract Three case studies failed to demonstrate impacts of early environment or maternal effects on breeding in situations where they could have been expected. This leads to a number of methodological questions about the resolving power required to detect such impacts, but above all else to the conclusion that maternal effects and homeotic control are opposites. When assessing potential maternal effects, one has to consider not only the developmental period in which they occur but also the later stage of life of concern, because, with age, maternal effects may become less and less important or disappear altogether. The only real measure that there is of the relative importance of early environment and maternal effects is their proportion in phenotypic variance in the traits of interest.

Key words Environmental effects, Maternal effects, Breeding, Great tit

1 Introduction

There is abundant evidence from invertebrates that environmental conditions during early development have effects that last throughout life (Prout, 1984, and references therein). Yet homeostatic regulation and compensatory growth processes may lead to the disappearance of early effects, particularly in homeotherms with finite growth. Thus, in searching for lasting effects from early environment, we have to consider not only the traits of concern and environmental factors during the period of development under investigation, but also those later stages of life that may express the effects. For morphological traits including body size, regulation of growth determines the time window for environmental effects on the phenotype, because, in animals with determinate growth, there can be no compensatory growth after growth has stopped (van Noordwijk et al., 1988; Alatalo et al., 1990; Larsson, 1996).

Demonstrating that effects are absent requires the capacity to demonstrate their presence with sufficient power to find the smallest effects of concern. This is more difficult than demonstrating simple presence, for a number of reasons: first, the adequacy of the methods required is more critical, secondly, the specificity of the effects sought is more critical, and thirdly, it is more difficult to find a good frame of reference for the negligibility of the effects. I present here three examples where three different aspects of the early environment could have, but did not, explain a significant part of phenotypic variation (Table 1).

2 Example 1: laying date of females hatched in a second brood

A number of studies have shown a heritable compo-

nent in the timing of reproduction in the great tit, *Parus major* (van Noordwijk, 1981; van der Jeugd and McCleery, 2002); but in contrast to factors such as clutch size, the environmental component is complex and heritability estimates are sensitive to outliers (van Noordwijk, 1981). Opportunities to test the effect of early environment on subsequent timing of reproduction are provided by females that produce a second clutch. Second clutches are always produced by early laying females (Verboven and Verhulst, 1996). Thus, great tits recruited from a second clutch should be genetically early, but very late in terms of juvenile environment. In mainland European populations, the number of local recruits from second clutches is very low. This may be a consequence of lower post-fledging survival or a higher tendency to disperse or both (Dhondt and Hubble, 1968). However, in the island population on Vlieland, the number of local recruits from second broods is quite high (van Balen et al., 1987). In the period between 1956 and 1995, 91 females hatched in second broods were recruited into the breeding population.

In order to evaluate the reasons for this, I compared the laying dates of females hatched from a second clutch with those hatched in a first brood (Table 1). The females hatched in second broods were found to be early breeders. Their advancement was related to the extent to which females producing a second clutch are early relative to the total population (van Noordwijk, in prep.). We can characterize the difference in first clutch laying dates between females producing a second clutch and the total population as a selection differential, and the deviation of laying dates in second brood-hatched females from the total population as a response. This allows calculation of realized heritability for the group.

Table 1 Summary of examples from studies of the great tit (*Parus major*)

Trait	Environmental effect	Age of effect	Age of testing for effect	Type of test
Laying date	rearing environment in early May versus late June	whole nestling period	first year breeders	difference in laying date between individuals hatched in 1st or 2nd brood
Fledging weight	quality of pair or territory related to clutch size	nestling period	prior to fledging	comparison of fledging weights, balanced for date between broods differing in original clutch size
Behavior score	feeding behavior of foster pairs	1–10 days after hatching	40 days after hatching	behavior scores of birds from up and down selection lines raised together

The values obtained for realized heritability varied from 0.55 to 0.22, depending on whether outliers were included or ignored. The values, however, are the same as for heritability based on daughter-mother similarities in recruits from first clutches. The conclusion that there are no detectable effects from being hatched six weeks late is thus quite strong, as second-hatched females could have been expected to lay many days late, but not one day early. There may thus be a buffer period in the annual cycle that is long enough to absorb the effects of hatching six weeks late.

3 Example 2: fledging weights in relation to parental clutch size

In the context of a selection experiment on clutch size in a natural population of great tits, large numbers of clutches were raised by pairs which had produced either bigger or smaller clutches (van Noordwijk et al., in prep). In this reciprocal selection experiment, about 35 broods were cross-fostered each year and then matched for laying date with broods raised by the biological parents. There was a systematic difference of two eggs in the clutch sizes of donor and foster parents. Had clutch size been indicative of the quality of the pair and or their territory, substantial differences in fledging weights could have been expected. In none of five years, nor in either of the two directions (lighter or heavier nestlings), was there any significant difference (Table 1). In fact, in five out of the ten cases, what small difference there was was in the direction of parents of larger clutches producing lighter rather than heavier fledglings when raising broods of the same size, contrary to expectations. In two cases no difference was found, and only in three was the difference in the expected direction. Although potentially detectable difference in each individual replicate was limited because of the standard error of the average of brood means (0.2–0.4 g), the combined power of the ten replicate tests would have allowed detection of average differences in the order of 0.15 gram or about one per cent of average fledging weight.

4 Example 3: rearing environment scored on behavior

Great tits were selected for exploration behavior, measured around 40 days after hatching (Drent et al., 2002).

Chicks raised in broods in the field were mixed between up and down selection lines, so that all chicks grew up in an environment with sibs of both types (Table 1). The chicks were then taken to the laboratory at ten days after hatching for hand-raising, where they remained in mixed groups. Thus, if their early environment, and in particular their feeding during completion of brain growth, had had a strong effect on later behavior, one would have expected an effect from foster brooding in their behavior score. Although such an effect has been found in mice (Benus and Henkelman, 1998), no effects of a fostering environment were found in this case.

5 Conclusions

In each of these examples, we may conclude that aspects of early environment did not explain a biologically and statistically significant part of phenotypic variation at specified later stages in life. There may well be other aspects of the environment that do have a lasting effect, even for the same traits. These effects will have to be investigated one by one. It is therefore crucial to tease out the potentially important impacts of early environment into a number of testable components (van Noordwijk, 1989). In order to do this, guidelines are needed for determining which effects to test on what traits. It seems to me that the only reasonable guideline is provided by observed phenotypic variance in traits under natural environmental conditions. In explanations of such variance, the proportions that can be attributed to maternal or early environmental effects then serve as a measure of the importance of those effects.

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Symposium 39 Ecological forestry and avian communities

Introduction

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Although forest covers more than 35% of global land, and harbors more biodiversity than any other habitat, the increasing human demand for land and timber is accelerating deforestation in many countries. The rate of forest loss is particularly high in South America; and the proportion of forest birds that are endangered is equally high in South America and Asia. Sometimes forest clearing and conversion to monoculture plantations has been justified on the basis that younger forests, which grow faster, store carbon at higher rates than old-growth forests. They are said to be better at counteracting global warming. Many studies, however, show that young plantations have depauperate bird communities.

In forests that are not clear-cut but harvested silviculturally, the demand for timber and other forest products still can cause habitat degradation. Such forestry practices include various types of forest thinning, selective logging, and management for crops or for grazing in the understory. Ornithologists have been concerned about habitat loss through clear-cutting, but the effects of these other types of management also impact on bird communities, and have received less attention. Much of the literature focus too, so far, has been on forestry practices affecting bird communities in North America and Europe.

Considering the problems globally, there is clearly a great need for impact-finding research on other continents. Accordingly, the papers in this symposium report on work in Japan, India and Taiwan, in addition to research in the United States and Canada. Chin-kuo Lee and coauthors compare a bird community in an old-growth broadleaf forest in Taiwan with a second community in a forest subject to timber stand improvement (TSI) program and a third community in a cedar plantation. Teruaki Hino assesses the state of bird communities in 12 study areas in Japan that carry different densities of deer and thus undergo different impacts from browsing. Susan Hannon describes a large program in the boreal forest of Canada that is trying to provide managers with guidelines for ecologically sustainable forest management. That program evaluates the effects of forest fragmentation, the effects of prescribed burning, and of various methods of timber harvest. Lalitha Vijayan and Gokula V summarize an extensive study of the effects of human disturbance on bird communities in a variety of wooded habitats in India. Todd Engstrom and Richard Conner conclude the symposium with a discussion of the impact on bird communities of two types of timber harvesting in pine forests in the southeastern United States.

S39-1 The impact of forest management on bird communities in Taiwan

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Abstract Many forest-management practices have negative impacts on forest birds. Here we compare the bird communities between, first, an old-growth forest and a 30-year-old monoculture conifer plantation, and secondly, an old-growth forest and an old-growth forest that was “improved” silviculturally 9 years earlier. We collected data on tree species composition and variables important for analysis of forest structure. We sampled breeding birds using variable-distance transect and variable circular-plot methods, and recorded the microhabitat and food habits of each species. Results showed that the monoculture plantation held only 51.5% of the species found in old-growth forest. Bird species richness and density in the silviculturally improved forest were also lower than that in old-growth forest. Examining the avian guilds of these forest communities, we found that upperstory flycatching insectivores, upperstory gleaning insectivores, and ground-feeding omnivores all suffered severely in the managed forests, whereas upperstory trunk-probing insectivores and understory gleaning insectivores increased in numbers. Although the effects of forest improvement are less drastic for forest birds than conversion to monoculture, the alteration of forest structure still changed microhabitat and available resources. The implications of these findings for birds in southeast Asia and forestry practices elsewhere are discussed.

Key words Forest bird communities, Monoculture plantation, Natural forest, Forest improvement

1 Introduction

Many studies have documented serious impacts on bird communities from forest clear-cutting and conversion to monocultural plantations. Although alternative techniques have been developed commercially to reduce the impacts, such methods can still result in significant disruption and decline (Johns, 1988; Thiollay, 1992; 1997; Mason, 1996; Marsden, 1998). Forests cover 59% of Taiwan Island, but only 72% of these are natural (Taiwan Forestry Bureau, 1995). From 1965 to 1971, under the support of FAO, many stands of natural broadleaf forest were clear-cut and replaced with monoculture softwoods, mostly Japanese cedar, (*Cryptomeria japonica*), a fast-growing exotic.

From 1983 to 1989, in step with international forestry practices, a Timber Stand Improvement (TSI) program was implemented to increase the volume of commercial timber in natural broadleaf forests in Taiwan. This program involved the removal of subcanopy and understory vegetation, including saplings, vines, shrubs, and snags, and planting of seedlings of native commercial tree species (Taiwan Forestry Bureau, 1995). The effects of such forestry practices on bird communities in Taiwan have not been examined before. Accordingly, our studies compare the bird communities of, first, a Japanese cedar plantation and an old-growth broadleaf forest, and secondly, a TSI stand and an old-growth broadleaf forest. Our aims were to quantify the change in vegetation structure in conifer plantation and TSI stand, to analyze the effects of forestry practices on

breeding bird communities, and to determine the responses of individual bird species and guilds.

2 Materials and methods

2.1 Study sites

Our study area was located at Lalashan in northern Taiwan (24°49'00"N, 121°25'00"E, elevation 800–1 300 m). Average annual temperature is 16°C, and average annual precipitation over 3 000 mm (Wang, 1987). The monocultural Japanese cedar plantation was about 30 years old; and the control broadleaf forest was 2 km from that plantation. The TSI stand had been treated 9 years before; its understory had been cleared and saplings of *Chamaecyparis formosensis* and *Calocedrus formosana* planted. Subsequently, the understory was cleared another 11 times, at a little more than once a year, and the canopy thinned once. In 1994, sapling densities in TSI stands were 320–470 per hectare. A natural forest 5 km away was used as the control site for this study. Neither natural broadleaf forest sites had ever been harvested; their dominant trees included *Persea thunbergii* and *Litsea acutivena hayata* (Lauraceae) and *Castanopsis borneensis* and *Cyclobalanopsis acuta* (Fagaceae).

2.2 Methods

The variable line transect method was used to survey bird communities in the plantation study, whereas, because of steep slope and rugged topography, the variable circular-plot method was used in the TSI study. We identified

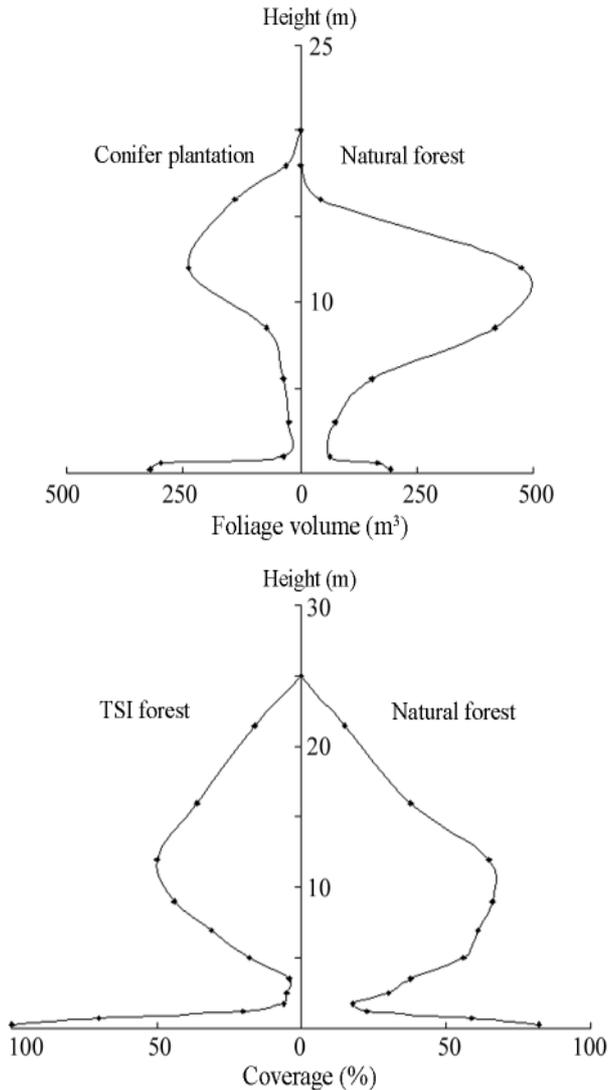


Fig. 1 Foliage coverage and volume for the four forest stands sampled

each bird species and recorded the number of individuals seen, their distances to the transect line or to observer, and their foraging behaviors. Foraging behavior included food type, foraging stratum, foraging substrate, and foraging method.

We sampled 30 habitat variables in twelve 20×20 m quadrats in both plantation and control forests to quantify vegetation structure and to determine foliage volume of different layers (Lee, 1995). In the TSI study, we sampled 45 habitat variables in five 10×10 m quadrats around each bird sampling point in both TSI and control forests, and measured vertical foliage distribution at 20 point locations in each quadrat (Fang, 1996).

3 Results

The Japanese cedar plantation had a sparser canopy, subcanopy, and shrub layer but a denser grass layer than the control natural forest (Fig. 1). Tree species richness, sapling and pole-timber densities, and the coverage of the subcanopy were all significantly lower in the plantation. For subsequent analysis, upperstory refers to the canopy and subcanopy, and understorey to shrub and grass strata (Lee, 1995). The TSI stand also had a sparser subcanopy and a denser grass layer than its control natural forest (Fig. 1). Tree species richness, sapling and pole-timber densities, and the coverage of the subcanopy were significantly lower in the TSI stand. Density of trees with larger trunk diameter at breast height (DBH), and the coverage of the grass layer, were significantly higher in the TSI stand than in the control (Fang, 1996).

We recorded 33 species of breeding birds in the plantation study and 30 species in the TSI study. Bird species richness, density, and total biomass were all lower in the plantation than in the control forest (Table 1). In the TSI study, bird species richness and density were again lower in the TSI stand, but total biomass was higher (Table 1). Bird biomasses in the canopy and ground layer were significantly lower in the plantation than in the control forest,

Table 1 Comparison of species richness, density, and biomass of bird communities in treatment forests and controls

Study index	Plantation		<i>P</i>	TSI		<i>P</i>
	Plantation	Control		TSI forest	Control	
Species Richness	17	33		25	29	
Density (birds/100 ha)	586	673	ns	267	325	ns
Total biomass (kg/100 ha)	18.4	27.1	*	99.9	89.8	*
Canopy	8.8	13.4	**	55.0	31.1	***
Subcanopy	4.9	4.8	ns	16.1	24.2	***
Shrub	0.9	1.3	ns	4.4	11.6	***
Grass	3.4	2.7	ns	20.1	11.1	**
Ground	0.4	4.9	***	4.1	11.9	ns

Mann-Whitney U test: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Large differences in bird density and biomass between the two studies resulted from different survey methods.

but were similar in subcanopy, shrub, and grass layers. Biomasses in the canopy and the grass layer in the TSI stand were significantly higher, but those in the subcanopy and shrub layer (10–0.6 m) much lower (Table 1).

We assigned bird species to different guilds according to their foraging strata, foraging methods, and food type. As a group, upperstory flycatching insectivores, upperstory gleaning insectivores, upperstory trunk-probing insectivores, and ground-feeding omnivores were all markedly sparser in the plantation, from which most guild members were absent (Table 2). In the TSI stand, the same guilds were also depauperate (Table 2), although some of their species favored the TSI stand. Upperstory trunk-probing insectivores and understory gleaning insectivores were also more frequent in the TSI stand.

Overall, bird densities in the plantation were 19%–100% lower across the guilds except for understory gleaning insectivores and upperstory gleaning omnivores. The densities in ground-feeding omnivores and upperstory flycatching insectivores in the plantation were significantly lower. Upperstory trunk-probing insectivores were absent from the plantation, but this difference was not statistically significant because of the low density of trunk probers in the control forest. The differences in relative abundance of different guilds demonstrated both quantitative and qualitative differences between the avian communities in the conifer plantation and control forest (Fig. 2). In the TSI stand, the numbers of upperstory trunk-probing insecti-

vores were significantly higher and of upperstory gleaning insectivores significantly lower. Ground-feeding omnivore density in the TSI stand was also lower, almost significantly so. The species that were absent, or less frequent, in managed stands tended to be endemic or forest-interior species, whereas those species more frequent were all edge species that are common in most wooded and disturbed areas.

4 Discussion

The two forestry practices studied involved structural fragmentation of forest habitat. In the TSI forest, gaps were opened in foliage structure, and the habitat shifted toward “edge” conditions, even though the dominant tree species were substantially unchanged. In the plantation, sparse canopy foliage permitted more light penetration, resulting in habitat similar to “edge” conditions. In both cases, an increase in “edge” bird species occurred concomitantly with a fall in forest-interior species; but the extent of the changes differed with species and guild. Basic species richness was lower generally; ground-feeding omnivores, upperstory gleaning insectivores, and upperstory flycatching insectivores were fewer; and upperstory gleaning omnivores and understory gleaning insectivores were more frequent in the managed stands. These results are consistent with those of other such studies conducted in tropical rain forests (Johns, 1988; Mason, 1996; Thiollay, 1997).

Reduction in diversity of plant species and vegetation structure in the upperstory reduced the nest sites for some upperstory bird species (cf. Powell and Steidl, 2000), and reduced the foraging habitat for arthropods (cf. Recher et al., 1996; Schowalter and Ganio, 1998), especially herbivorous insects that rely on the tender shoots and leaves of shade-tolerant tree species. Reduction of canopy foliage changed the microclimate within the entire canopy layer (Mason, 1996), which modified arthropod diversity and, in turn, affected upperstory gleaning and flycatching insectivores (cf. Karr and Freemark, 1983; Recher et al., 1996).

Reduced canopy foliage also changed microclimate in the understory, thus influencing composition and abundance in ground arthropods (Levings and Windsor, 1984; Karr et al., 1990). Sparse canopy and subcanopy allowed more sunlight to penetrate to the understory, resulting in denser growth of the grass layer. Such growth made foraging more difficult for some ground feeders (Severinghaus and Severinghaus, 1987). Moreover, managed forests accumulated less litter, so supporting fewer ground-dwelling arthropods (Liu and Kao, 1994). Increase in foraging difficulty and drops in prey density combined in a negative impact on ground-feeding omnivores. For understory gleaning insectivores, however, increased vegetation in the grass layer created more feeding habitat (Turchi et al., 1995), resulting in a rise in density.

During the past decade, forest coverage in southeast Asia has been reduced by around 10% (FAO, 2000), and forest coverage in most countries has declined significantly.

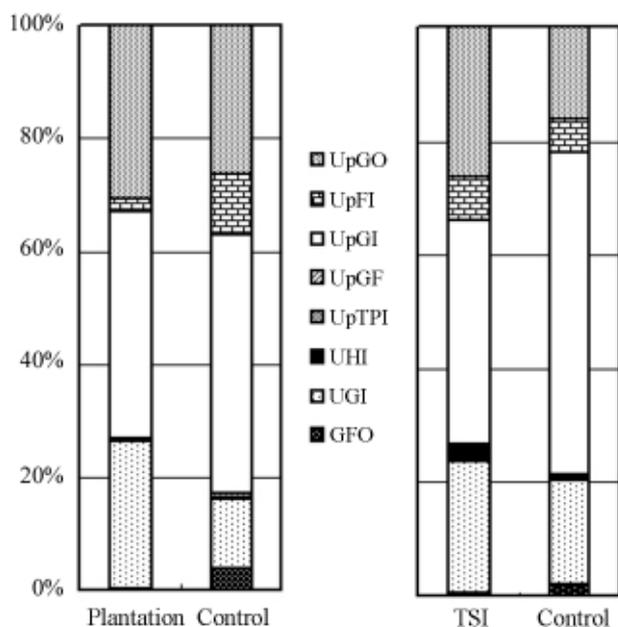


Fig. 2 Comparison of relative abundances of birds in different guilds between treatment forests and controls

UpGO = upperstory gleaning omnivores, UpFI = upperstory flycatching insectivores, UpGI = upperstory gleaning insectivores, UpGF = upperstory gleaning frugivores, UpTPI = upperstory trunk-probing insectivores, UHI = understory hovering insectivores, UGI = understory gleaning insectivores, GFO = ground-feeding omnivores.

Furthermore, an average of 9.5% of the forest has been converted to plantation in this region (FAO, 2000); the percentage is especially high for Thailand, Taiwan, and Vietnam. Logging of old-growth forest in Taiwan has been stopped by conservation efforts, but the TSI program continues. In southeast Asia, at least 59 endemic forest bird species are endangered, and 72 forest bird species are vulnerable (FAO, 2000). The survival of these species can be seriously affected by forest management practices. Even if the original cause of decline was not forest loss or degradation, further loss of habitat can only exacerbate the trend.

The results of our two studies should alert researchers in southeast Asian countries to monitor forest management practices closely. The impacts of various techniques need to be assessed carefully by research before they can be accepted as ecologically responsible.

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Table 2 Comparison of densities of guilds and birds in treatment and control forests (per 100 hectares)

Guild and Species	Plantation		P	TSI		P
	Plantation	Control		TSI forest	Control	
Ground-feeding omnivores (4 species)	1	26	**	18	63	
<i>Lophura swinhoii</i>	0	4	**	0	12	
<i>Cinclidium leucurum</i>	0	17	***	2	42	**
Understory gleaning insectivores (5 species)	154	82		608	588	
<i>Pomatorhinus erythrogeus</i>	7	7		69	20	**
<i>Pomatorhinus ruficollis</i>	2	2		73	25	***
<i>Stachyris ruficeps</i>	11	5	*	86	81	
<i>Garrulax poecilorhynchus</i>	0	5	*	87	71	
<i>Alcippe brunnea</i>	134	63	*	293	392	
Understory hovering insectivores (1 species)	2	3		0	0	
Upperstory trunk-probing insectivores (3 species)	0	4		83	15	**
<i>Dendrocopos canicapillus</i>	0	2		51	11	**
<i>Dendrocopos leucotos</i>	0	1		17	0	**
<i>Picus canus</i>	0	1		15	4	*
Upperstory gleaning frugivores (2 species)	1	1		3	15	
Upperstory gleaning insectivores (10 species)	237	307		1 044	1 824	**
<i>Cuculus sparverioides</i>	0	7	***	7	10	
<i>Alcippe morrisonia</i>	194	160		562	1 249	***
<i>Parus monticolus</i>	0	27	***	0	24	*
<i>Parus varius</i>	14	39	**	225	161	
<i>Parus holsti</i>	0	2		0	5	
Upperstory flycatching insectivores (4 species)	13	73	**	200	180	
<i>Pericrocotus solaris</i>	13	17		152	58	*
<i>Abroscopus albogularis</i>	0	49	***	49	83	
<i>Niltava vivida</i>	0	5		0	38	**
Upperstory gleaning omnivores (6 species)	179	176		692	516	
<i>Megalaima oorti</i>	25	58	*	168	127	**
<i>Hypsipetes leucocephalus</i>	122	77	*	231	195	
<i>Garrulus glandarius</i>	17	14		179	23	***
<i>Dendrocitta formosae</i>	10	12		25	11	**

Only species showing significant differences are tabulated. Mann-Whitney U test: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

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S39-2 The impact of herbivory by deer on forest bird communities in Japan

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Abstract Deer overabundance has become a worldwide phenomenon. Herbivory (browsing, grazing, and bark-stripping) by deer has had a great impact on forest bird communities by changing vegetation structure. My study in central Japan compared breeding-bird communities and vegetation characteristics along a gradient of deer densities. Reduction of the understory and forest midstage by deer decreased the number of species and abundance of birds nesting and foraging on these substrates but increased those of birds preferring open habitats. The increase in density of dead trees increased the number of tree-hole-nesting and bark-foraging birds. The results indicate that the responses of vegetation and bird species to deer pressure are nonlinear because of a combination of positive and negative effects from deer herbivory. Comparative studies across gradients of deer density can yield useful information for deer population management, but most studies have only compared grazed and ungrazed plots.

Key words Deer population management, Forest bird community, Forest ecosystem, Herbivory, Vegetation structure

1 Introduction

Overabundance of deer has become a worldwide phenomenon (McShea et al., 1997; Fuller and Gill, 2001). The increase in numbers has been attributed to several factors, according to region. Fuller and Gill (2001) listed six diverse reasons for deer increase in British woodlands. In North America, the recent explosion is thought to result partly from management intended to restore deer populations that had declined to near-extinction in the nineteenth century (Rooney, 2001). In Japan, one of the most important reasons for the abrupt increase in numbers is the increase in food resources from large-scale afforestation in the early 1960s (Takatsuki, 1996).

As a consequence, grazing, browsing, and bark-stripping by overabundant deer is having widespread impact on woodland vegetation (Putman et al., 1989; Gill, 1992; Yokoyama et al., 2001). Bird communities in woodlands and forests have often been correlated with vegetation structure associated with foraging and nesting sites (MacArthur and MacArthur, 1966; James and Wamer, 1982; Hino, 1985), so deer impacts should have an indirect effect on the diversity and abundance of forest birds through vegetation change. The present paper focuses on this effect and then considers the management of deer populations favorable not only for conservation of diverse avian communities but also for health in forest ecosystems.

2 Impact on Japanese forest bird communities

Three kinds of vegetational change can be expected from deer herbivory. The first is a depletion of the understory

due to direct grazing and browsing, reducing the height and density of the undergrowth. The second is a thinning of the forest midstage that results from cropping of seedlings and saplings to depress regeneration of woody plants. The third is an increase in dead trees resulting from bark-stripping. Changes develop fastest in the understory and slowest in the forest midstage, although that is advanced by bark-stripping.

These three types of change occurred in my study area in a natural mixed forest, dominated by *Fagus crenata*, *Acer shirasawanum* and *Abies homolepis*, in Ohdaigahara, central Japan (Hino, 2000, unpublished data). In my sampling, I distinguished among three groups of plots using cluster analysis of vegetational characteristics surveyed by belt-transect method on 12 study plots. The groups of plots differed in their densities of Sika deer (*Cervus nippon*) as a result of slope. Steep plots harbored few deer (7.3 ± 2.2 deer/km², $n = 6$), plots on gentle slopes held moderate densities (12.0 ± 3.3 deer/km², $n = 3$), and plots on flat ground supported the highest numbers (24.0 ± 8.2 deer/km², $n = 3$). As expected, dry mass and height of dwarf bamboo (*Sasa nipponica* and *Sasamorpha borealis*), which are predominant plants in the understory, were 10 and 8 times higher on the plots with few and moderate numbers of deer, and forest midstage cover was also twice as dense. In contrast, the basal area of dead trees was 7 times higher on the plots where deer were most abundant.

Censused by the point-count method, the composition of breeding birds on the study plots differed in accord with structural differences in the forest understory (Fig. 1). Species richness and abundance in birds that foraged or nested in the understory or on the ground, such as bush

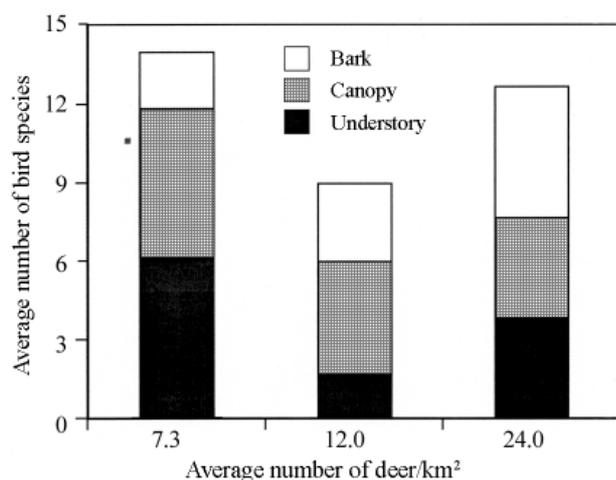


Fig. 1 Comparison of average number of bird species foraging in the understory, in the canopy, and on bark in plots with different deer densities

warblers (*Cettia diphone*) and robins, was highest on plots with fewest deer. Some bird species that foraged preferentially in the forest midstage, such as long-tailed tits (*Aegithalos caudatus*) and willow tits (*Parus montanus*), were found only these plots. In contrast, tree-hole-nesting and bark-foraging birds, such as woodpeckers, nuthatches, and creepers, were most diverse and abundant on the plots where deer were also most abundant. Moreover, birds preferring open habitats, such as pipits and large thrushes, were only observed on these plots. Overall, the number of bird species and individuals on plots where deer were least and most abundant differed little; and they were lowest on plots of intermediate deer density.

Table 1 summarizes the results of my study and four others in the USA that have examined the impacts of deer on forest bird communities. All these studies documented negative effects on understory- and forest midstage- birds. Yet, although paid less attention, positive effects were also found.

Casey and Hein (1983) reported that bark-foraging birds increased in response to abundant larger trees and dead standing timber in an area protected for deer. McShea and Rappole (2000) showed that some understory birds also benefited from deer grazing because of their preference for successional stages in understory vegetation. At sites where deer were abundant, however, DeCalesta (1994) attributed declines in both total bird species richness and abundance to the negative impact of deer herbivory on forest midstage birds.

Yet the other studies, including mine, did not find such clear effects. This result is explained by two factors. First, the negative and positive effects of deer herbivory offset one another. DeGraaf et al. (1991), who examined the effects of both deer browsing and thinning on avian communities, reported that thinning produced a high density of shrubs and seedlings despite the browsing. Secondly, thinning and selective felling aimed at stimulating natural regeneration often fail in areas of high deer pressure, leading to structurally impoverished stands (Fuller, 2001)

3 Management of deer populations for birds

What densities of deer are needed to maintain the most diverse avian community? Most studies have shown that total numbers of species and individuals are not affected by deer herbivory despite large shifts in species composition. Such results may nevertheless reflect simple comparisons between ungrazed and grazed plots (Table 1). Because the numerical response of birds to deer pressure can be nonlinear, the effects of different densities of deer need to be investigated (Fuller, 2001). In my study of the effects of three different deer densities, the number of bird species decreased between 7.3 and 12.0 deer/km² and increased between 12.0 and 24.0 deer/km² (Fig. 1). If I had studied only two plots with 7.3 and 24.0 deer/km², I might have concluded that deer had no effect. And had I selected two plots of densities each below or above 12.0 deer/km², moreover, I would have deduced nega-

Table 1 Summary of studies on the effects of deer herbivory on forest bird species diversity in forest understory, canopy, and on bark

References	Country	Deer/km ²	Changes in number of bird species			
			Understory	Canopy	Bark	Total
Casey and Hein, 1983	USA	10–20 83	↓	↓	↑	→
DeGraaf et al., 1991	USA	1–3 13–23	(↓)	(↓)	–	→
McShea and Rappole, 2000	USA	0 25 <	↓↑	↓	–	→
DeCalesta, 1994	USA	3.7	→	→	–	→
		7.9	→	↓	–	↓
		14.9	→	→	→	
		24.9	→	→	→	
Hino (unpublished)	Japan	7.3	↓	(↓)	→	↓
		12				

tive and positive impacts respectively.

The most valuable approach is one that takes account of how bird species are distributed and how deer affect the availability of resources or vegetation critical for birds across a gradient of deer densities within the same habitat type. DeCalesta (1994) studied four plots with different deer densities (3.7, 7.9, 14.9, 24.9 deer/km²). He showed that the number of bird species declined abruptly between 7.9 and 14.9 deer/km², but did not change between 3.7 and 7.9 deer/km² or between 14.9 and 24.9 deer/km² (Table 1). This result indicates that changes in the avian community may occur abruptly along a gradient of deer densities, corresponding to changes in vegetation.

Abrupt change was also found in my study. That is, the number of species of understory-nesting birds diminished with decreasing biomass of dwarf bamboo between 7.3 and 12.0 deer/km², and that of tree-hole-nesting birds increased in accord with increasing frequency of dead trees between 12.0 and 24.0 deer/km² (Fig.1). DeCalesta (1994) found no such correlations for bark-foraging and open-habitat birds (Table 1), perhaps because the forest area that he studied may comprise tree species not bark-stripped by deer (Sekine and Sato, 1992).

DeCalesta (1994) recommended a deer density of between 7.9 and 14.9 deer/km², at the threshold for change in the number of bird species. In my study, it is not easy to determine a recommended density because both species richness and abundance in birds were lowest at intermediate deer density (12 deer/km²). If the present high density of deer (24.0 deer/km²) were maintained, the number of dead trees would continue to increase rapidly in forest on the flat areas, breaking up the canopy and making the habitat unsuitable for forest birds. Moreover, overabundant deer might intrude on and reduce the biomass of understory vegetation even in the steep areas. This behavior has already been observed.

On the other hand, if deer numbers drop to a low density (7.3 deer/km²) in all areas, large woodpeckers, thrushes, and pipits would be lost. I would recommend a deer density that can produce dead trees constantly but much more slowly than at present. This density would be between 12 and 24 deer/km². At that density, the overall diversity of birds in Ohdaigahara, central Japan, would be maintained because those birds using the understory could survive on steep slopes and those using tree trunks would have ample habitat in flat terrain. Such a management plan would be applicable wherever deer densities are moderated by topographic features.

4 Management of deer populations for the forest ecosystem

Deer are a keystone species in the forest ecosystem. Research has examined the striking impacts of deer herbivory not only on birds but also on many other animals and plants in forests (McShea et al., 1997; Flowerdew and Ellwood, 2001; Rooney, 2001; Stewart, 2001). Deer may affect forest birds

through the interactive network among organisms in general. For example, McShea (2000) demonstrated that deer decreased the survival of rodents by eating acorns, thereby increasing the number of birds as a result of a drop in nest predation by rodents. Therefore, deer herbivory has both positive and negative effects on forest ecosystems, just as it has on forest bird communities. Determining the number of deer that would maintain the most diverse forest ecosystem is a complicated but challenging problem.

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S39-3 Building a bird-friendly forest: lessons from the boreal forest of Canada

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Abstract Many parts of the boreal forest of Canada are being harvested for the first time. Research on the effects of forestry, primarily clearcutting, on birds has focused mainly on (1) documenting impacts of forest fragmentation (edge creation, isolation, patch size effects) and their mitigation (reserve design, provision of corridors), (2) investigating the natural disturbance model as a guide to forest harvesting at several spatial scales, (3) searching for critical thresholds in landscape and cutblock forest cover, (4) assessing the cumulative effects of several land uses, such as forestry, oil and gas extraction, agriculture, roading, and (5) attempting to construct indices of “ecological integrity” at stand and landscape scales that can be used in monitoring for forestry impacts. I review the studies conducted to date in the boreal mixedwood forest of Alberta, and evaluate whether this research has helped forest managers in landscape planning and monitoring. The major research needs for bird conservation in a working forestry landscape are addressed.

Key words Forest bird communities, Edge effects, Fragmentation, Clearcutting, Corridors, Monitoring

1 Introduction

The boreal forest is the most extensive ecosystem in North America, and until recently, human impacts have been relatively few. Avian species richness is high in this ecosystem compared to that in other systems in North America (Robbins et al., 1986), particularly in the boreal mixedwood. However, the rate of development of forestry has increased in the last 20 years and, in concert with other human disturbances, has led to an increase in forest fragmentation and a decrease in older seral stages (Schmiegelow et al., 1997). Determining the impact of these changes on boreal bird populations is crucial, especially if these areas serve as source populations for other more severely affected ecosystems (Robinson et al., 1995).

The boreal mixedwood forest region is situated south of the northern coniferous forest and north of the aspen parkland in Alberta and Saskatchewan, Canada. This region has been affected increasingly by human disturbance. Clearing for agriculture is prevalent along the southern fringe and in the Peace River area. Transportation routes, pipelines, and seismic lines have bisected many areas. Small-scale harvesting of white spruce (*Picea glauca*) for saw logs is common, and large-scale harvest of aspen (*Populus tremuloides*) for pulp and paper began in 1992. The pure aspen and aspen-dominated mixedwood forests are coming under increasing pressure from logging companies.

The province of Alberta contains over half of the Mixedwood Ecoregion in Canada, and the government has leased over 75% of its mixedwood area to forestry companies under Forestry Management Agreements. Mature (50–

100 yr) and old (>100 yr) aspen forests are slated to be cut first. The rotation period will be 40–70 years, so few stands of aspen will reach old-growth stage. Most stands are clearcut in a checkerboard pattern, and average cutblock size is 40 ha (maximum 60 ha). The intervening uncut blocks are harvested when trees on the original cutblocks are about 3 m tall. If the pattern continues, it will result in high fragmentation of the forest, high edge-to-area ratios in the remaining uncut portions, and a lack of large continuous stands of older aspen and mixedwood. Old aspen and mixedwood forests are structurally distinct from younger stands and have higher avian species richness (Schieck et al., 1995). In addition, salvage logging, common after fires, reduces the amount of natural early-seral-stage forest.

Studies aimed at evaluating the effects on forest songbirds of forest fragmentation by clearcutting have been ongoing in the boreal mixedwood forest of north central Alberta since 1993 (Fig. 1). This forest is a mosaic of trembling aspen, white spruce, and jack pine (*Pinus banksiana*) stands in upland sites and of black spruce (*Picea mariana*), balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), and tamarack (*Larix laricina*) in lowland sites. Peatlands, other wetlands, and lakes generally occur in areas of low relief. Forest stands had not been harvested previously, and natural disturbances are primarily fire, insect outbreaks, and wind throw.

The purpose of the present paper is to outline the foci of research activities on forestry impacts on birds in this region and to provide an overview of results to date. In addition I will evaluate whether these studies have provided concrete information that will help forest managers to

conserve birds. I end with a set of research questions, listed in order of priority, that should be addressed for the long-term conservation of birds in this managed forest system.

2 What research questions have scientists asked?

Avian research in the boreal mixedwood has focused on the following questions:

1. What are the impacts of forest fragmentation on bird communities and populations?
2. Are the effects of logging similar to those of fire?
3. Are there critical thresholds in forest cover below which species loss and/or population decline is accelerated?
4. What are the impacts of cumulative effects of different land uses on bird biodiversity?

2.1 Forest fragmentation

The bulk of research to date has focused on the impacts of forest patch size, edge effects, and the influence of isolation on bird communities and populations. Overall, these impacts have not been large and can be summarized as follows. The larger the patch, the higher the species richness; and patches surrounded by clearcutting do not differ in richness from those embedded in continuous forest (Schmiegelow et al., 1997). Species turnover is higher in the smallest fragments and species composition dominated by edge species (1–10 ha). Abundances of resident species and neotropical migrants are lower in isolated fragments. Some bird species compensate for fragmentation effects by using adjacent habitats (Norton et al., 2000).

Most of the work on edge effects is concerned with reproductive output and density of songbirds at edges com-

pared with those in the forest interior. Nest-predation rates on artificial nests are not higher at edges than in interior forest (Cotterill and Hannon, 1999; Song and Hannon, 1999; Tittler and Hannon, 2000), nor are predation rates higher in forest fragments than in continuous forest (Cotterill and Hannon, 1999). Songbird density is not greater at forest-clearcut edges but rather is related positively to structural heterogeneity of the stand and stand age (Song, 1995). Of 16 common species, none avoided edges, 3 were attracted to them, and 13 were neutral with respect to territory location and edge (Song, 1995). In another study, abundance of forest-dependent bird species declined in linear strips as they narrowed from 200 to 20 m wide (Hannon et al., 2002).

Patch isolation does not appear to deter movement to or colonization of patches isolated by clearcutting. Although large gaps in forest cover were avoided by some species (Desrochers and Hannon, 1997; St. Clair et al., 1998) which used corridors when provided (Machtans et al., 1996), gap permeability to bird movement increased as clearcuts regenerated (Robichaud et al., 2002). An analysis of species abundances in isolated, connected, and control reserves up to 5 years after harvesting indicates that provision of corridors does not increase abundance for most species (Hannon and Schmiegelow, 2002), although resident species appear to be more sensitive to isolation than other groups.

Overall, the impacts of fragmentation appear to be low in this system, perhaps because the forest has a high frequency of natural disturbances such as fire. Boreal bird species may therefore be adapted to dealing with gaps. Given the rapid regeneration in clearcuts, moreover, any fragmentation effects are short-lived, and changes in predator communities or invasions by cowbirds do not occur (Schmiegelow et al., 1997; Cotterill and Hannon, 1999). Most of the population-level work has focused on common species, however; rare species could not be analyzed statistically.

2.2 Comparative effects of logging and fire

Increasingly, the forest industry is embracing the concept of “ecosystem management” to ensure that harvesting is conducted in an ecologically sustainable manner. A recent focus has centered on attempts to pattern forest harvesting to resemble that created by natural disturbance, predominantly fire (Hunter, 1993). A critical prerequisite for implementing such a management scheme is a thorough understanding, at stand and landscape scales, of the effects of natural disturbances on wildlife communities and how they compare with the effects of logging.

In the mixedwood, bird community composition in early postdisturbance burned and logged stands differs markedly. In burns, the community is dominated by cavity nesters and species that forage on beetle infestations in the dead trees, whereas clearcuts are dominated by open-country species (Hobson and Schieck, 1999). Between 12 and 25 years after disturbance, the vegetation structure and com-

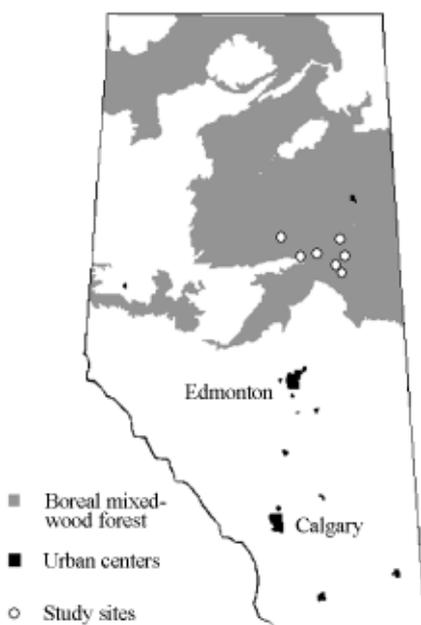


Fig. 1 The province of Alberta, Canada, with boreal mixedwood forest shaded and study sites indicated by circles

position of burns and clearcuts converge, as does bird community composition (Hobson and Schieck, 1999; Schieck and Song, 2002). Some species, such as black-backed woodpeckers (*Picoides arcticus*) and three-toed woodpeckers (*P. tridactylus*), appear to reach their highest densities in recent burns, exploiting wood-boring insect larvae (Cerambycidae, Buprestidae) and bark-beetle larvae (Scolytidae). Both species are otherwise absent from mature forests but re-appear in older forest at low density (Hoyt and Hannon, 2002). Over the long term, burns may be temporal sources for fire specialists (Hutto, 1995; Hoyt and Hannon, 2002).

The most important current threat to biodiversity and birds associated with recently burned forest is salvage logging. Salvaged trees are in the same diameter classes that woodpeckers use for foraging and nesting (Hoyt, 2000), and densities of three-toed woodpeckers, black-backed woodpeckers, downy woodpeckers (*Picoides pubescens*), and hairy woodpeckers (*P. villosus*) are lower in salvage-logged than unsalvaged burns (Schmiegelow et al., 2001). In addition, secondary cavity nesters such as house wrens (*Troglodytes aedon*), American kestrels (*Falco sparverius*), and brown creepers (*Certhia americana*) are also more abundant in unsalvaged burns (Schmiegelow et al., 2001).

Colonization of forest tracts that are surrounded by burns or clearcuts may be influenced by such landscape-level loss of forest cover. In a recent study I examined the influence of burns or clearcut logging in the landscape (within 1 km of the sampling location) on the probability of detecting a species in an intact stand of aspen-mixedwood (Hannon, 1999). Some species responded positively to burning in the landscape, some responded positively to logging, some responded negatively to logging, and others responded positively to both burning and logging. The presence of other species was not related to disturbance at the landscape scale.

2.3 Critical thresholds in forest cover

Critical thresholds are levels of a resource below which small changes in the configuration of that resource will pro-

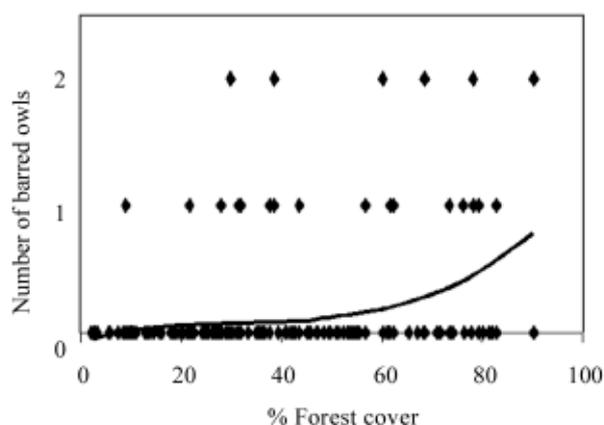


Fig. 2 Number of barred owls detected in 15-km² landscapes that differed in extent of forest cover

duce abrupt shifts in ecological response (With and Crist, 1995; With and King, 1999). Critical thresholds in forest cover leading to species losses or dramatic declines in abundance have been theoretically (With and Crist, 1995; Fahrig, 1997) and empirically (Andren, 1994) predicted to be ~20%–40%. In the boreal mixedwood, we are currently testing for critical thresholds of landscape forest cover on resident owls, passerines, grouse, and woodpeckers by sampling these species at landscape level across a range of forest covers and configurations in different regions. Data collection is ongoing, but preliminary results indicate that, of six owl species sampled, only the barred owl (*Strix varia*) showed a threshold response to amount of forest cover (Grossman and Hannon, unpublished data; Fig. 2).

2.4 Cumulative effects of different land use

Research has recently been initiated to examine the cumulative effects on bird community composition of forest loss due to logging, oil and gas development, agriculture and linear development such as roads, pipelines and seismic lines. These studies are being conducted at fine scales within a single landscape (S. Hannon, unpublished data) and at large scales across an ecoregion (F. Schmiegelow, unpublished data). Studies on forest cover thresholds and cumulative effects should contribute to identifying species that are particularly sensitive to forest loss and human disturbance. The Biodiversity Group of the Network of Centres of Excellence in Sustainable Forest Management (NCE/SFM) is working to develop a multispecies index of ecological integrity to be used in biodiversity monitoring for the boreal forest.

3 Preliminary conclusions and relevance to management

Most forestry companies in Alberta have embraced the concept of ecologically sustainable forest management and look to researchers to provide recommendations for maintaining biodiversity in managed forests. Foresters want answers to three simple questions: (1) What forest type should be maintained on the landscape (e.g., composition, seral stage)? (2) Where should this forest type be located on the landscape? (3) How much of this forest type should be left? Although these questions sound simple, they are challenging to answer. To date, research conducted in Alberta's boreal mixedwood has provided answers to question 1 but not to questions 2 and 3. We know that intact burned forest and old-growth forest must be present, but we cannot say how much of this forest should be maintained or where it should be located. In a recent review of studies on focal species conducted by NCE/SFM researchers, I found that very few studies provided quantitative recommendations for forestry cutblock or landscape planning (Hannon and McCallum, 2002). The result has been increasing frustration among forest managers with researchers.

Tackling applied ecological research projects is diffi-

cult because of the spatial and temporal complexity of ecosystems, the problems of finding the appropriate spatial scale, and the species specificity of many biotic responses to forestry techniques. Obviously, impacts cannot be tested on every species. The common approach of testing null-hypotheses, moreover, may allow us to determine whether a particular treatment has an effect but it does not enable us to tell managers how much edge is too much. Focusing on testing a range of conditions experimentally will provide more insight and allow quantitative prediction of the effects of different levels of perturbation (also O'Connor, 2000).

4 How researchers can help management build a bird-friendly forest

1. Before beginning a study, try to identify the species most likely to be sensitive to changes in forest cover, structure, and composition, such as seral-stage specialists and species with large home ranges.
2. Focus studies on habitats that are most likely to be adversely affected by forestry activities, such as early and late seral stages.
3. Design research to search for thresholds in species response across a range of conditions in order to answer the question "how much?"
4. Consider the influence of the matrix surrounding forest patches on the responses of birds to forestry.
5. Evaluate the impacts of forestry in the context of other land uses in the area, which contribute to cumulative effects.
6. Develop methods for study and evaluation of impacts on rare species.
7. Use this information to help design monitoring programs for forestry companies.

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S39-4 Human impacts on forest bird communities in the Western Ghats, India

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Abstract We studied bird communities along a gradient of disturbance levels in five major habitats in the Western Ghats during 1994–1997: the montane (shola) forests and grasslands, and wet evergreen, moist deciduous, dry deciduous, and thorn forests. Species richness of birds was higher with moderate disturbance, but species richness and abundance were very low in the most highly disturbed areas (plantations). Abundance was 35% lower in disturbed evergreen forest, and 23% lower in the montane (shola) forest, whereas abundance was higher in the moist deciduous forest, mainly due to more habitat specialists and endemics in the wet forests. The populations of the threatened endemic Nilgiri laughing thrush of the shola forest and the Nilgiri pipit, a grassland specialist and endemic, were discernibly lower in disturbed habitat. Breeding bird species and their nests were much less abundant in disturbed dry deciduous and thorn forests, particularly nests, demonstrating a negative correlation with intensity of grazing and firewood collection: the tree species most used for firewood are also those preferred for nesting. Some of the habitat specialists, such as the paradise flycatcher, white-browed fantail flycatcher, spotted munia and crested hawk-eagle, were affected by disturbance at nest sites.

Key words Forest birds, Habitat specialists, Human impacts, Western Ghats, India

1 Introduction

The Western Ghats in India, one of the Global Hotspots of Biodiversity and Endemic Bird Areas (Stattersfield et al., 1998), has experienced significant land-use change as a result of development programs. In Kerala in 1987, the National Remote Sensing Agency documented a 0.3% loss of forest during 1972–1985, and Prasad (1998) reported the same fall during 1961–1988. Menon and Bawa (1997) found a 0.5% loss between 1920 and 1990 over a larger area (Kerala, Karnataka and Maharashtra states); and Jha et al. (2000) reported a 1.16% loss for Kerala and Tamil Nadu between 1973 and 1995. Also notable is the 47% decline in evergreen forest in the southern Western Ghats (Prasad, 1998), which is the habitat for most of the regional habitat specialists and endemics (Vijayan and Gokula, 1999). Although some studies have been conducted on the bird communities in this region, they are mainly short-term surveys carried out in a limited area (Gokula and Vijayan, 1996; Daniels, 1996; Pramod et al., 1997; Prasad et al., 1998). Accordingly, we took up the study reported here to assess the impact of habitat changes on the bird communities in the major forest types in the Western Ghats.

2 Materials and methods

2.1 Study areas

The study areas were sited in the Nilgiri Hills in the Nilgiri Biosphere Reserve (10°45'–12°15'N and 76°–77°15'E)

in the Western Ghats, south India, and show remarkable topographic, climatic, and vegetational diversity (Vijayan et al., 1998). The habitats that we assessed were: (1) thorn forests on lowland plains, (2) dry deciduous forest on lower slopes, (3) moist deciduous forest in Mudumalai, at over 1 000 m altitude, (4) montane (shola) forest and grassland in and around Upper Bhavani at >2 000 m altitude in Tamil Nadu, and (5) wet evergreen forest in and around Silent Valley at 900–1 100 m altitude in Kerala State. Our approach was to study a gradient of disturbance levels in areas adjacent to intact stands of each of the habitats. Categories of disturbance level were (1) undisturbed (or least disturbed), disturbed, and highly disturbed (completely altered plantation habitat). For each habitat, study sites representing the three disturbance levels were chosen with the same physiognomic settings and altitudes as sites of intact habitat to reduce bias.

2.2 Methods

Disturbance factors such as distance from human settlement, movement of people, presence of cattle and their tracks, signs of grazing, and dung in 2-ha sampling areas were documented. Signs of tree cutting and pruning were also recorded to assess timber preferences in relation to impacts on nesting of birds in the dry deciduous and thorn forests, where human pressure was greater. We recorded the intensity of firewood collection, and the plant species and size class of stems within the bundles of collected wood. We interviewed 100 people to learn their preferred firewood

species.

We studied bird communities by the variable circular plot method (Reynolds et al., 1980), sampling 10 ha in each habitat. Censusing began half an hour after sunrise and lasted 10 minutes in each plot. We repeated the sampling over three seasons, namely the dry (December–March), first wet (June–August), and second wet (September–November) periods during 1994–1996. We analyzed populations of the two rare endemics in the montane shola forest and grassland to assess the impact of habitat changes on them.

We also laid one 5-ha plot each in undisturbed and disturbed dry deciduous and thorn forest during 1995 to study the impact of disturbance on nesting birds; in 1996–1997, we laid two 5-ha plots for detailed studies on nest-site selection by several habitat specialists (Martin and Roper, 1988). We observed nest-tree or substrate variables and nest-patch variables within a 0.07-ha circular plot centered on the nest tree. Variables included nest height, vegetation cover (canopy, shrub, and ground), and cover over the nest, and we compared these with those of randomly selected sites to test for selection. The SPSS software (Norusis, 1994) was used for analyzing the data.

3 Results

3.1 Human disturbance of habitat

Table 1 Disturbances in different habitats

Habitat	Number of cattle	No. of dung piles	Cattle tracks	% trees logged	% area burned
Undisturbed dry deciduous	-	-	-	0.7	1
Disturbed dry deciduous	21	36	9	3.7	3
Teak plantation	12	6	3	4.6	-
Undisturbed moist deciduous	-	-	-	1.2	1
Disturbed moist deciduous	11	6	6	3.5	-
Coffee and tea plantation	-	-	-	8.4	-
Undisturbed thorn	-	-	-	1.7	-
Disturbed thorn	137	89	12	21.2	1
Eucalyptus plantation	63	71	7	35.5	-
Undisturbed evergreen	-	-	-	-	-
Disturbed evergreen	-	-	-	3.8	-
Coffee plantation	-	-	-	7.5	-
Undisturbed shola	-	-	-	-	-
Disturbed shola and grasslands	-	-	-	4.0	3.5
Wattle plantation	-	-	-	3.8	3

Sample plots 2 ha each. Unless specified, all habitats are forest.

Pruning and cutting of trees, and cattle grazing, were the major disturbance factors other than seasonal fire. Greatest disturbance occurred in the thorn forest, followed by dry deciduous forest (Table 1). Detailed studies in thorn and dry deciduous forests showed that rates of exploitation were highest in thorn forest. Interviews revealed human preferences for seven species for firewood and a few for other purposes. Wood bundles comprised eleven species (Table 2).

3.2 Impact of disturbance on the bird communities in different habitats

Montane (shola) forest and grassland Bird species richness and abundance were greater in shola forest than in the grassland or an adjacent wattle plantation (Table 3). Although similar numbers of species were found in undisturbed and disturbed habitats, the abundance of birds was on average 23% lower in disturbed sites, and species richness was 38% lower, and abundance 59% lower, in the wattle plantation. Of all habitats studied, shola forest is richest in endemic species, namely the Nilgiri wood pigeon (*Columba elphinstonii*), Nilgiri laughing thrush (*Garrulax cachinnans*), rufous-bellied shortwing (*Brachypteryx major*), Nilgiri flycatcher (*Muscicapa (Eumyias) albicaudata*), and black-and-orange flycatcher (*Muscicapa nigrorufa*) (Ali and Ripley, 1987). The first three are globally threatened (BirdLife International, 2001). Of the 16 bird

Table 2 Plant species used by birds for nesting and by people for firewood

Species	Dry deciduous	Thorn forest	% used by people
	Percentage of nests		
<i>Acacia chundra</i>	13.3	6.5	17
<i>Tectona grandis</i> (A)	7.8	0.0	-
<i>Anogeissus latifolia</i> (A)	27.8	10.5	23
<i>Anogeissus latifolia</i> (S)	6.7	0.0	-
<i>Lantana camara</i>	14.4	8.5	-
<i>Randia dumetorum</i>	5.6	3.5	-
<i>Acacia catechu</i>	2.2	1.0	-
<i>Phyllanthus emblica</i>	3.3	0.5	1
<i>Pterocarpus marsupium</i>	1.1	0.0	4
<i>Elaeodendron glaucum</i>	2.2	2.0	-
<i>Erythroxylum monogynum</i>	-	8.5	16
<i>Toddalia asiatica</i>	-	25.0	-
<i>Gymnosporia montana</i>	-	11.0	-
<i>Eucalyptus</i> sp.	-	1.5	10
<i>Zyziphus mauritiana</i>	-	6.0	-
Others	-	2.0	-
Unidentified species	-	-	13
Unidentified snag	7.8	1.5	16
Total number of nests	90	200	

A = alive, S = snag, - = not recorded

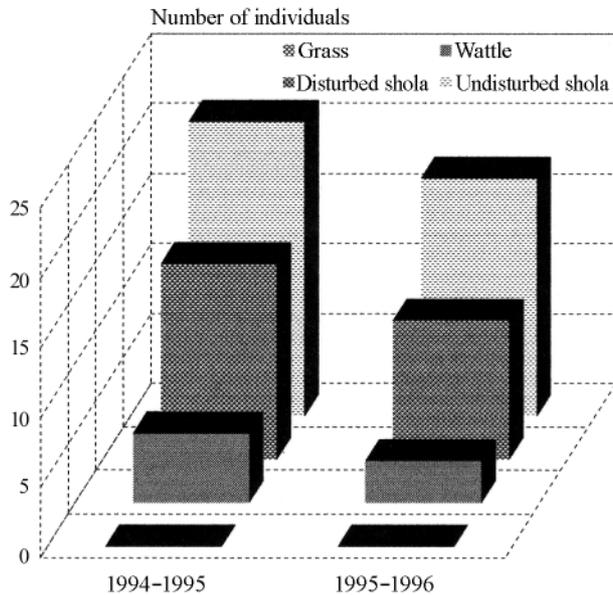


Fig. 1 Status of the Nilgiri laughing thrush in different habitats

species endemic to the Western Ghats, the Nilgiri laughing thrush is the only one that prefers shola forests > 2 000 m in altitude (Vijayan et al., 2001). The population density of this species was one pair/ha in undisturbed areas, and was 37% lower in disturbed forest and 79% lower in the wattle plantation (Fig. 1).

Grassland harbored a few species of birds: pipits, bulbuls, and chats. On grassland that had been converted to wattle plantation, the numbers of species and individuals were higher, but those of grassland specialists were lower. The Nilgiri pipit (*Anthus nilghiriensis*), endemic to the Western Ghats and globally near-threatened, is one such grassland specialist (BirdLife International, 2001). Its numbers were about 60% lower in the wattle plantation than on grassland (Fig. 2).

Evergreen forest Species richness was higher in disturbed forest, whereas abundance of birds was greater in the undisturbed forest (Table 3). In moderately disturbed areas, the number of species was 19% higher and the number of birds was 35% lower. A highly disturbed coffee plantation nearby supported 59% fewer species and 72% fewer individuals than did the undisturbed area. Even in disturbed forest, the abundance of habitat specialists and endemics, such as the white-bellied blue flycatcher (*Muscicapa (Ficedula) pallipes*) and Nilgiri flycatcher, was much lower.

Moist deciduous forest Bird species richness and abundance were both higher in disturbed than undisturbed forest, which in turn supported higher numbers than an adjacent tea and coffee plantation (Table 3). The average number of species in the disturbed area was 29% higher than in undisturbed forest (Mann-Whitney U-test, $U = 3$, $P = 0.01$), whereas in the plantation it was 41% lower ($U = 0$, $P = 0.002$). Numbers of individuals were also about 30% higher in disturbed than undisturbed forest ($U = 6$, $P = 0.05$), and

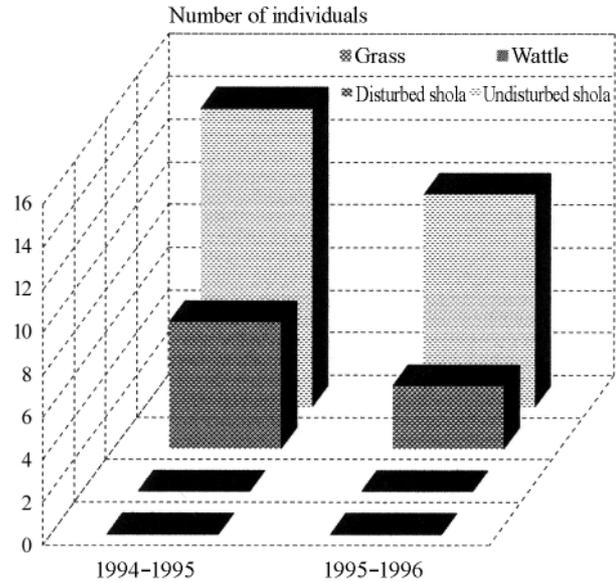


Fig. 2 Status of the Nilgiri pipit in different habitats

again lower by 46% in the plantation ($U = 1$, $P = 0.004$).

Dry deciduous forest Species richness and abundance were again both higher in disturbed than undisturbed forest (Table 3), species richness significantly so ($U = 0.0$, $P = 0.002$). The average number of species in an adjacent highly disturbed teak plantation was almost equal to that in the disturbed area, but abundance was lower ($U = 4.0$, $P = 0.02$). In general, however, dry deciduous forest is structurally simple and near-monospecific in tree species, being dominated naturally by teak (*Tectona grandis*) much as in the plantation.

Thorn forest In the thorn forest in and around Mudumalai, bird species richness and abundance was highest in undisturbed forest (Table 3). The number of species of birds was on average 13% lower in moderately disturbed and 22% lower in highly disturbed habitat. Individual numbers were slightly higher in moderately disturbed forest but 44% lower in a highly disturbed eucalypt plantation.

3.3 Impact of disturbance on breeding birds

Monitoring of breeding in the dry deciduous and thorn forests showed that birds use mainly 17 species of trees and shrubs for nest sites (Table 2), many of which are also preferred for firewood. Thus the collection of firewood impacts on the breeding bird community. In comparisons of both the disturbed and undisturbed (or, rather, less disturbed) 5 ha plots in these forests, we found a higher number of species and nests in less-disturbed areas. In the thorn forest, 19 nests of 10 species were recorded in the undisturbed site, as opposed to 12 nests of 6 species in the disturbed. Coordinate comparisons in dry deciduous forest were 9 nests of 4 species to 6 nests of 4 species. Nest-site-selection studies of several habitat specialists (paradise flycatcher, *Terpsiphone paradisi*; white-browed fantail,

Rhipidura aureola; spotted munia, *Lonchura punctulata*; crested hawk eagle, *Spizaetus cirrhatus*), showed that disturbance at the nest site had a significantly negative impact (PCA and stepwise DCA). The paradise flycatcher nested in shrubs in thorn forest of high shrub density; the white-browed fantail used small trees at sites with high tree density and ground cover; the spotted munia preferred thorny and straggler species, constructing nests in the lower canopy with more shade for concealment; and the crested hawk eagle preferred larger trees in undisturbed dry deciduous forest at least 3–4 km from human settlement, reflecting sensitivity to human disturbance.

4 Discussion

Habitat changes in the Western Ghats (Prasad, 1998; Menon and Bawa, 1997; Jha et al., 2000), particularly the 47% reduction in evergreen forests in the southern Nilgiri sectors, have caused great concern for biodiversity conservation (Prasad et al., 1998). Logging, firewood collection and grazing are the major disturbances (Desai and Baskaran, 1996; Ramakrishnan and Sivaganesan, 1997). The changes have contributed to the decline of many forest birds, especially endemic species (Stattersfield et al., 1998; BirdLife International, 2001).

Birds reach their maximum abundance in undisturbed evergreen forest, as expected, because of the complexity of the habitat and its structure (Jayson and Mathew, 2000).

Table 3 Number of species and individuals of birds in different habitats

Habitat	Species	Individuals
Shola, wattle plantation, and grassland		
Undisturbed forest	16.3±4.0	105.3±12.3
Disturbed forest	16.8±2.4	90.5±48.1
Plantation	10.3±1.1	43.00±7.7
Grassland	7.3±5.4	18.67±7.4
Evergreen forest, and coffee plantation		
Undisturbed forest	21.3±4.4	162.8±34.8
Disturbed forest	25.0±4.1	106.3±50.0
Plantation	13.5±3.0	45.5±4.7
Moist deciduous, and coffee and tea plantations		
Undisturbed forest	16.7±2.1	73.7±20.2
Disturbed forest	21.2±2.0	95.7±16.5
Plantation	9.8±2.8	840.0±11.9
Dry deciduous, and teak plantation		
Undisturbed forest	11.5±1.4	70.2±8.8
Disturbed forest	17.5±2.1	90.2±17.9
Plantation	11.7±1.7	48.7±21.9
Thorn forest, and eucalyptus plantation		
Undisturbed forest	30.7±4.6	154.3±28.3
Disturbed forest	26.7±3.4	158.7±33.5
Plantation	23.8±4.8	86.8±23.2

Figures are means and standard deviations.

Species richness too is highest in undisturbed forest. The difference between undisturbed and disturbed areas in species richness and abundance increased with the species richness of the habitat, mainly because habitat specialists or forest interior species are more sensitive to disturbance (Canterbury et al., 2000; Pattanavibool and Dearden, 2002; Riley, 2002). In most other drier forest, habitats, species richness increased with moderate disturbance. This increase is due to the increase in generalists, as found also in the Eastern Ghats (Beehler et al., 1987) and elsewhere (Daniels et al., 1989).

In general, the bird communities of the plantations were impoverished. Khan (1978) concluded that few species can adapt to such habitats in the Nilgiris. In any case, the bird fauna of plantations is largely derived from natural forest sources in the vicinity (Daniels et al., 1989; Estades and Temple, 1999). Teak plantations probably support more birds than other plantations because of foliage layers and the presence of leaf- and wood-feeding insects, as in *Albizia* plantations in Malaysia (Mitra and Sheldon, 1993).

The montane shola forest and grassland habitat is a major center of endemism in the Western Ghats and therefore requires immediate conservation action (Sukumar et al., 1995; Pramod et al., 1997; Vijayan and Gokula, 1999; Robin and Sukumar, 2002). The Nilgiri laughing thrush, a rare endemic and specialist of shola forest (Islam, 1994; Vijayan and Gokula, 1999), is affected by habitat alteration (Vijayan et al., 2001), as is the Nilgiri pipit, a specialist of short grasslands at high altitudes. The earlier concept of grassland as wasteland has created problems for it (Vijayan et al., 1998).

Breeding in the thorn forest is affected by logging, firewood collection, and grazing. Sensitive to disturbance, species there build nests in the lower canopy and select sites with more shade for concealment (Gokula, 2001; Gokula and Vijayan, 2001). The crested hawk eagle prefers larger trees in undisturbed dry deciduous forest, thus demonstrating the importance of densely wooded areas especially along rivers and streams.

Recommendations have already been made to stop the expansion of monoculture plantations, to restore the shola forests and grasslands with the involvement of local communities, and to reduce human pressure by providing alternative sources of income (Vijayan et al., 1998; Vijayan and Gokula, 1999). A proper in-depth study of the endemics and habitat specialists is needed to elucidate their ecology and monitor population changes.

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S39-5 Ecological forestry, old growth, and birds in the longleaf pine (*Pinus palustris*) ecosystem

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Abstract Renewed awareness of the longleaf-pine ecosystem and a legal mandate to provide suitable habitat for the endangered red-cockaded woodpecker (*Picoides borealis*) have generated interest in alternative forms of silviculture in the southeastern United States. Of 110–120 species of birds that occur in longleaf pine woodlands, 26 species (including three that are federally ranked) require special management attention. Over 80% of the extant ecosystem occurs on government-owned or privately-owned nonindustrial property, and constitutes potential sites for ecological forestry. Intensive forest management eliminates much of the structural complexity of old-growth longleaf pine woodlands that supports high avian community species richness. Two silvicultural systems that are candidates for a more ecological approach — irregular shelterwood and uneven-aged management — retain structural characteristics of old-growth forests, but more research is needed to contrast their relative effects on bird populations. Retention or development of old-growth characteristics — old trees, horizontal heterogeneity and openness, ground-cover integrity, sparse distribution of hardwoods, and coarse woody debris, including snags — would reintroduce valuable complexity within the longleaf pine ecosystem for supporting avian communities of higher species richness.

Key words Ecological forestry, Fire, Forest birds, Old-growth, Southeast United States

1 Introduction

Forestry in the United States has largely diverged into two approaches, one emphasizing increasing production of wood fiber and the other stressing maintenance of forest complexity, function, and biological diversity (Perry, 1998). Development of a more ecologically sensitive approach in the southeastern United States has been slow, in part because commercial models of timber production are deeply entrenched and old-growth forests that provide examples of high diversity and natural function are now very rare. Concerns over biological diversity, endangered species, particularly the red-cockaded woodpecker (*Picoides borealis*), and perpetuation of fire as a disturbance (Conner, 1988) have led to increasing interest in ecological forestry for longleaf pine forests (Means and Grow, 1985).

Ecological forestry, with emphasis on protecting natural function and native biological diversity, could have broad application on federal lands (National Forests, National Wildlife Refuges, military bases), state forests, and private forests where hunting, aesthetics, conservation, and production of high-quality wood are objectives. We assess how avian communities would be affected by application of ecological forestry, particularly retention of old-growth characteristics, in the longleaf pine ecosystem.

2 The longleaf pine ecosystem

Longleaf pine dominated forests occurred on 22.9 million ha pre-settlement in the southeastern United States, and extended over an additional 14.6 million ha in mixed forests (Frost, 1993). A combination of factors contributed to a 97% decline over a 150-year period (Frost, 1993), to approximately 1.3 million ha in 1993 (Outcalt and Sheffield, 1996). Contemporary longleaf pine forests are owned by the forest industry (18%), government (31%), and private landowners (51%), according to Outcalt and Sheffield (1996).

Longleaf pine woodlands contain some of the most species-rich ground-cover communities in North America (Peet and Allard, 1993). Relative dominance of grasses, shrubs, and mid-story trees within community types affects the resources and structure that determine patterns of avian abundance. An essential factor that affects the structure and composition of forest types throughout the entire ecosystem is fire (Harper, 1911), but very few of the remaining stands are still fire maintained (Frost, 1993). Development of shrub and mid-story levels and eventual truncation of pine regeneration are the consequences of extended intervals between fires or fire exclusion (Christensen, 1981). Vegetation changes in response to fire exclusion have dramatic effects on the avian community (Engstrom et al., 1984).

Old-growth longleaf pine woodlands that have a structure and composition similar to those in the earliest descriptions are extremely rare. Means (1996) estimated that only 3902 ha of old-growth forest remains; and according to a 1993 inventory, most of the extant stands are only 21 to 60 years old (Outcalt and Sheffield, 1996). Overstory composition of many original forests were typically dominated by longleaf pine itself, which made up over 75% of individual trees (Wahlenberg, 1946).

A focus on attributes and dynamics of old-growth forests provides a guide for development of ecological forestry. Landers and Boyer (1999) estimate that old-growth characteristics begin to develop in longleaf pine after 112 years, but old-growth forests are not composed exclusively of older trees. More typically, all age classes are represented. Old-growth forest characteristics (large old pine trees, old persistent snags, coarse woody debris on the ground, tree age-class diversity, horizontal and vertical heterogeneity, diverse ground cover, a mixing of hardwoods, and tip-up mounds) should be considered when developing an architecture to manage for biological diversity (Landers and Boyer, 1999).

3 Birds of the longleaf pine ecosystem

Apart from migrants passing through, approximately 120 species of birds occur in the longleaf pine ecosystem (Engstrom, 1993; Hunter et al., 2001). This total comprises species that are resident (42%), breed and migrate (28%), or overwinter and migrate (30%). Standardized censuses (Breeding Bird Censuses) of 11 longleaf pine sites in four states showed a fivefold variation in bird density (8 to 41 territories per 8.1 ha), and species richness that ranged from 6 to 22 per 8.1 ha (R.T. Engstrom, unpublished data). Three of its species — the bald eagle (*Haliaeetus leucocephalus*), Mississippi sandhill crane (*Grus canadensis pulla*), and red-cockaded woodpecker — are federally listed as threatened. Moreover, twenty-six species that occur in fire-dependent habitats are in need of management attention (Hunter et al., 2001).

4 Silvicultural effects on birds in longleaf pine forests

4.1 General issues

From 1880 to 1930, when most of the original forest was harvested (Williams, 1989), little thought was given to its maintenance (Frost, 1993). Many forests were converted to other land uses then, but residual flowering in some was sufficient for regeneration. An intensive, commercially-oriented silvicultural approach that included clearcutting, debris raking, and soil disking developed in the latter part of the 20th century (Croker, 1987). It eliminated many native plants from the ground cover, including native grasses that provide the fuel for the frequent fires needed to maintain the ecosystem and are important for species such as Bachman's (*Aimophila aestivalis*) and Henslows'

(*Ammodramus henslowii*) sparrows. Industrial pine forests typically are young, have a uniform structure of dense canopy, sparse ground cover, and few snags. Avian response to intensive silviculture is low species richness that increases as the forest matures (Repenning and Labisky, 1985; Dickson et al., 1995).

Fire, wind, lightning, and bark beetles are common disturbances that shape the structure and composition of longleaf forests. Wind and lightning are small-scale disturbances, killing trees, creating gaps in the canopy of variable size and providing coarse woody debris for birds. Two silvicultural approaches that imitate natural disturbances — irregular shelterwood and uneven-aged management — have been proposed to produce red-cockaded woodpecker habitat (Conner et al., 1991; Rudolph and Conner, 1996; Engstrom et al., 1996). In an irregular shelterwood, most overstory trees are harvested on long return intervals (120 years), but a low basal area of mature trees is permanently retained for structural reasons and as a source of seed and shelter for young pines (Smith, 1986). In uneven-aged management, all ages of trees can be thinned throughout a stand, but natural gaps may be enlarged and employed for regeneration. These techniques are at nearly opposite ends of the spectrum of overstory retention and have different implications for producing the structural elements needed to maintain biological diversity. We discuss below how characteristics of old-growth longleaf-pine forest within the context of uneven-aged management and irregular shelterwood influence populations of birds (Table 1).

4.2 Canopy tree age

Although longleaf pine trees can live to 500 years, noticeable old-growth features (large boles, contorted limbs, flat-topped crowns, and decay within living trees) start to appear at about age 112 (Landers and Boyer, 1999). These features are especially important for species like red-cockaded woodpeckers (amount of heartwood and fungal infection) and bald eagles (large limbs). Old trees probably tend to support primary (e.g., woodpeckers) and secondary (e.g., wood duck, *Aix sponsa*) cavity nesters in greater numbers because cavities may be more easily excavated in decayed crannies.

Harvest rotations in industrial forestry tend to be less than 50 years, but both irregular shelterwood and uneven-aged harvesting have the potential to produce old pines. In irregular shelterwood, mature pines are retained after harvest (basal area of approximately 9 m²/ha). If some of the oldest pines remain through two or more harvest cycles (120 year rotation), pines may grow to 240 years old or more. When high basal areas of residual pines are left as shelterwood, and the forest is burned regularly, the resulting forest will develop through time the appearance of an uneven-aged forest as the second generation of trees matures. If the number of residual pines left is too low and wind-caused mortality is high, the resulting stand will re-

semble a clearcut more than a forest of mature pines, and suitable densities of old-growth pines will not result.

High densities of old pines can be achieved by uneven-aged harvesting, but the occurrence and survival of pine reproduction is inversely related to the density of old-growth pines. Uneven-aged silvicultural systems are controlled by the number of pines harvested in each size (diameter) class. Typically, all pines are harvested beyond some maximum diameter (Farrar and Boyer, 1991), so it is critically important that the maximum diameter limit be set high enough to permit pines to grow to the desired maximum age. For uneven-aged silviculture to provide old-growth pines, the manager must know the ages of pines in all diameter classes, particularly the larger and presumably older diameter classes. If the maximum diameter of pines is set too low in such harvesting, old-growth pines will not result.

4.3 Horizontal heterogeneity

All forests develop heterogeneous spacing, no matter how uniform the initial regeneration; and different silvicultural techniques have large effects on tree spacing. Disturbances, such as lightning, wind, and fire, create small and large gaps in the canopy over time. The spacing of individual trees and clumps of trees is important for bird species that forage in open spaces within forests, such as flycatchers (e.g., eastern kingbird, *Tyrannus tyrannus*), com-

mon nighthawks (*Chordeiles minor*), and loggerhead shrikes (*Lanius ludovicianus*), as well as for the development of ground cover. In wetter areas, open woodlands interspersed with savannas are important habitat for sandhill cranes (*Grus canadensis*).

Irregular shelterwood harvesting and uneven-aged management will have different effects on horizontal heterogeneity. Irregular shelterwood will tend to produce stands that are horizontally homogeneous for 50 years or so after harvesting but will increase in heterogeneity as they approach harvest rotation age. In contrast, uneven-aged stands will be patchy as a result of the regular removal (every 7–10 years) of single and small groups of trees. In general, uneven-aged stands will have higher horizontal heterogeneity than stands produced by shelterwood harvesting.

4.4 Ground cover

Ground cover is strongly influenced by methods of tree harvest and regeneration within a silvicultural approach. To eliminate competition for young pine trees, industrial forestry frequently employs disking, chopping, and application of herbicides, which have detrimental effects on many of the native perennial ground plants that dominate undisturbed sites. Although intensive site-preparation techniques are not used in ecological forestry, harvesting procedures may still compact the soil and affect ground cover when

Table 1 Structural characteristics of old-growth longleaf pine forest of value to bird species

Structural components	Importance to birds	Bird species affected
Old trees	Large limbs, flat crowns; abundant heartwood; susceptibility to fungal infection that provides easy excavation of heartwood	<i>Aix sponsa</i> <i>Elanoides forficatus</i> <i>Haliaeetus leucocephalus</i> <i>Picoides borealis</i> <i>Sitta carolinensis</i>
Ground-cover integrity	Abundance of grasses (e.g., <i>Aristida beyrichiana</i>) for nesting material; functional role in providing fuel for fires	<i>Colinus virginianus</i> <i>Cistothorus platensis</i> <i>Aimophila aestivalis</i> <i>Passerculus sandwichensis</i> <i>Ammodramus savannarum</i> <i>A. henslowii</i> , <i>A. leconteii</i> <i>Sturnella magna</i>
Coarse woody debris	Large old snags that provide nesting and foraging substrate; tip-up mounds that provide escape cover	<i>Melanerpes erythrocephalus</i> <i>Colaptes auratus</i> <i>Dryocopus pileatus</i> <i>Sitta pusilla</i> <i>Sialia sialis</i>
Horizontal heterogeneity and habitat openness	Juxtaposition of foraging space and perches	<i>Grus canadensis</i> <i>Chordeiles minor</i> <i>Tyrannus tyrannus</i> <i>Lanius ludovicianus</i>
Hardwood distribution and abundance	Nesting and foraging substrate within an open-structured habitat	<i>Poliophtila caerulea</i> <i>Piranga rubra</i> <i>Icterus spurius</i>

Based on Breeding Bird Censuses (Engstrom, 1993; Hunter et al., 2001). The structural components are not necessarily independent, and bird species may respond to more than one aspect of habitat structure.

tree trunks are removed. The grasses that provide nest material and cover, and shrubs that act as nesting substrate, are likely to be different in old-field and undisturbed sites. 30% to 40% of the species and 35% to 60% of the territorial individuals in the breeding bird community in one old-growth forest are ground nesters and forage primarily on the ground (Engstrom, unpublished data). Northern bobwhite (*Colinus virginianus*), the resident Bachman's sparrow, a wide array of wintering sparrows, the sedge wren (*Cistothorus plantensis*), and the eastern meadowlark (*Sturnella magna*) are sensitive to composition and structure of the ground cover.

The ground cover in pine stands depends more on the fire regime than on the silvicultural system used to regenerate the pine canopy. Therefore, both irregular-shelterwood harvesting and uneven-aged management are compatible with maintaining a diverse flora in the herbaceous layer as long as frequent prescribed fire and natural pine regeneration are part of the overall management program. If managers use mechanical site preparation in conjunction with irregular-shelterwood harvesting, the floral diversity of the ground cover will decline.

4.5 Coarse woody debris

Snags are highly important to the diverse community of cavity nesters in longleaf pine forests, and woody debris on the ground, especially tip-up mounds, provides refugia for wrens and species such as Bachman's sparrow. Tree age and cause of death have an important effect on the persistence and rate of decay of standing snags because of the amount and density of heartwood needed to support dead trees. If high basal areas of residual pines are left during irregular shelterwood harvesting, natural mortality of residual pines and competitive mortality among growing younger pines will probably produce a continuous supply of snags. Snag production is not as certain in uneven-aged systems because regular tree removal during frequent harvests decreases competition among growing pines and can remove many of the older pines because of the maximum diameter limit. However, the length of time between harvest cycles and the maximum diameter limit can be increased to increase snag production. The density of snags and logs is also affected by the frequency and intensity of fire: hot, frequent fires will burn up most logs and snags yet may also kill some live pines to create new snags (Conner, 1981).

4.6 Hardwoods

The distribution and species of hardwoods within longleaf pine forests has a major effect on the bird communities. In old-growth forests that are burned frequently, scattered oaks (*Quercus* spp.) and hickory (*Carya* sp.) were probably normal. This small hardwood component in well-maintained forests is important for bird species such as the blue-gray gnatcatcher (*Poliophtila caerulea*), summer tanager (*Piranga rubra*), and orchard oriole (*Icterus spurius*). As hardwoods increase in abundance, additional bird species may appear (e.g., red-

eyed vireo, *Vireo olivaceus*); but others, such as the red-cockaded woodpecker, may disappear (Hunter et al., 1994). Increasing abundance of hardwoods also strongly affects the flammability of sites, as grasses and forbs are reduced or die from shading. Maintaining hardwoods within a longleaf pine forest is a balancing act: too much fire can eliminate hardwoods, and too little can provide the hardwoods with a competitive edge and cause a shift in species dominance and composition. If hardwoods are not intentionally removed during harvesting operations, the occurrence of hardwoods in longleaf pine forests will become more a function of the fire regime than of the silvicultural system used to regenerate pines.

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Symposium 40 Periodic environmental changes: understanding the physiological basis of life history adaptations

Introduction

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Most organisms adjust their phenotype to different environmental conditions, for example by thermal acclimation, organ remodeling or changes in body mass. Such seasonal changes have obvious selective advantages, yet it is often unclear how birds change from one phenotypic condition to another. For it to be effective, individuals must perceive and integrate environmental cues, transfer the cues into endocrine signals and undergo the morphological changes that are the basis of specific life history adaptations. Analyzing this cascade of events is one of the challenging tasks of avian ecology.

This symposium highlights common phenotypic alterations for breeding, migration, molt and wintering, and analyzes in some detail the physiological mechanisms underlying them. Its aim: to contribute to a better understanding of mechanisms underlying life history adaptations. Thomas Hahn related neuro-endocrinological mechanisms to a

specific reproductive adaptation: opportunistic breeding. Simone Meddle and John Wingfield presented an in-depth analysis of brain function in relation to seasonal reproduction, highlighting the use of seasonal environmental information at neural level. George Noskov and colleagues addressed the photoperiodic control of molt, and Martin Wikelski summarized current understanding of how different physiological systems interact to shape diverse phenotypes. All of these papers were presented as orals only, the abstracts of which are published in the Abstract volume for the Congress.

In the only paper submitted for the Proceedings, Barbara Helm and Eberhard Gwinner link constraints in the molt process to environmental seasonality, breeding and migration, using as their exemplars three subspecies of the stonechat (*Saxicola torquata*).

S40-2 Timing of molt as a buffer in the avian annual cycle

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Abstract Birds in seasonal environments must time stages in their annual life cycles precisely. While the fitness costs of mistimed reproduction and migration are widely recognized, molt has been viewed as a more flexible element. Birds modify the timing of molt in various ways to keep to overall timetables, but recent studies provide evidence for considerable attendant costs in fitness. Selective pressure, therefore, affects the timing of molt and its flexibility, favoring timing mechanisms that are finely tuned to local conditions. We illustrate such timing mechanisms for post-juvenile molt in stonechats (*Saxicola torquata*). These widely distributed passerines differ in life history traits such as length of breeding season, number of clutches and migratory behavior. To understand adjustments to temporal environments, we compared the temporal plasticity of captive African, European, and Siberian stonechats. The subspecies from these regions differed from each other in their reaction norms to photoperiod, in temporal patterns related to the timing requirements of their native habitats. Their circannual rhythms thus encode characteristic features of seasonal activities in a population-specific manner. High heritability in post-juvenile molt corroborates the interpretation of molt timing as adaptive. We conclude that stonechat populations adapt to temporal environments not by switching between distinct and rigid programs but by adjusting reaction norms to relevant time cues.

Key words Molt, Annual cycle, Photoperiod, Stonechat

1 Molt as a timing buffer in the annual cycle

In variable habitats, stages in life cycles must be timed precisely to match periodic environmental change. In general, birds attempt to reproduce, change their plumage, and acclimate to unfavorable conditions or migrate within the annual cycle. These activities impose competing demands such that the timing of the activities involves compromises and trade-offs. Timing of migration and reproduction is thought to be closely regulated by selection. Mistimed migration imposes fitness costs if birds encounter severe weather conditions, and the timing of migration thus responds to weather-mediated selection (Brown and Brown, 2000). Timing of reproduction is closely related to maximal food abundance, and mismatching reduces fitness (Visser and Lambrechts, 1999; Thomas et al., 2001). Because of the fitness correlates of reproductive and migratory timing, it has been suggested that molt functions as a buffer in annual cycles (Noskov et al., 1999).

If environmental conditions allow, passerines molt at relaxed rates and either avoid major overlaps with other costly activities or molt so slowly that the costs are small (Jenni and Winkler, 1994; Kjellen, 1994; Berthold, 2001). But often birds run out of time for it, as in populations with long migratory journeys and short breeding seasons. Another source of time stress is late breeding. Although the value of eggs generally declines over the breeding season, late clutches contribute markedly to recruitment in some years

(Van Noordwijk et al., 1981). Hence, birds often attempt late breeding. Under such time constraints, birds modify molt to catch up in several mutually nonexclusive ways. Molt is a flexible system that allows birds to keep to their timetable, particularly in northern hemisphere passerines (Hahn et al., 1992; Jenni and Winkler, 1994; Kjellen, 1994; Noskov et al., 1999).

2 Fitness implications of molt as a timing buffer

Evidence is growing that modifications of molt schedules are costly. Late breeding birds often start molt while still tending young (Jenni and Winkler, 1994; Kjellen, 1994) and thereby risk trading off current reproduction against future reproductive opportunities. Experimental simulation of molt by wing clipping reduced the body condition and fitness of feeding parents (Hedenström, 1999). Sexual differences in the overlap of molt and breeding are indicative of trade-offs between the two activities late in the breeding season. Males are more likely than females to initiate molt during chick-rearing, thereby reducing offspring provisioning or abandoning young. Reduced paternal investment often leads to poorer condition and lower recruitment of young. Presumably, the benefits of a timely molt for males outweigh additional fitness gains of breeding late. Females are more likely to delay molt during breeding than males, and sometimes the delay increases with clutch size (Slagsvold, 1999). They may compensate for reduced paternal provisioning at the cost of their own condition and sur-

vival chances (Hemborg and Merilä, 1998). Such costs in late-breeding females may be attributable in part to delayed molt.

Offspring from late clutches experience similar time-pressures when undergoing post-juvinal molt. Their molt is advanced compared to that in siblings from early clutches and may overlap with final growth stages and juvinal establishment (Jenni and Winkler, 1994). To our knowledge, there is no direct evidence of the cost of overlapping molt and post-fledging establishment, but disadvantages, such as a low social rank, are likely (König, 1996).

To avoid such costs, birds may delay the onset of molt at the cost of reduced survival. Molt is then either greatly accelerated or overlaps with subsequent life cycle phases. In residents, late molt can impair preparations for overwintering, such as territorial establishment or food hoarding; and thermoregulatory costs rise under inclement conditions (Kjellen, 1994; Jenni and Winkler, 1994). Migratory birds may delay fall departure briefly or extend overlap between molt and migration. Data from captive passerines reveal a close correlation between the completion of molt and the onset of migratory restlessness (Helm and Gwinner, unpubl. data; Pulido and Coppack, pers. comm.), suggesting that migration may be delayed until peak molt has passed. Some studies show that late breeders and young from late clutches migrate while still in molt (Flinks, 1999). Flight theory predicts high costs if wing molt overlaps migration, but experimental evidence is still inconclusive (Hedenström, 1999).

Instead of or in addition to overlaps with other seasonal activities, birds can control the time taken for molt by accelerating it, limiting its extent, or even suspending it temporarily. Costs of molt, such as elevated metabolism, are likely to increase with molt rate (Lindström et al., 1993). Fast molt may also impair flight, increasing wing gaps (Hedenström, 1999). Moreover, it can have long-term consequences due to reduced feather quality, as the following data show. Thermoregulatory costs after rapid molt rose by 15% (Nilson and Svenson, 1996). In a comparison of wader populations, speed of molt correlated with plumage abrasion (Serra, 2001). Captive passerines that molted faster than controls grew less symmetrical and less rigidly built flight feathers that subsequently suffered greater damage and abrasion (Dawson et al., 2000). Feathers grown under time constraints can also be significantly shorter in both adult and young birds (Hall and Fransson, 2000; Albrecht, Helm and Gwinner, unpubl. data). In birds that lack a prenuptial molt, greater feather wear is correlated with reduced fitness during the next breeding season, especially in species subject to sexual selection (Fitzpatrick and Price, 1997).

Many passerines reduce the extent of molt under time constraints. Some renew only part of the plumage and then resume molt under favorable conditions. Suspension of molt ranges from arresting flight feather renewal to completely delaying molt (Jenni and Winkler, 1994; Kjellen, 1994; Berthold, 2002). Hall and Fransson (2001) report that, by

suspending molt, passerines which had initiated it late were able to finish it simultaneously with conspecifics. These birds had less symmetrical flight feathers than those that had undergone complete molt, indicating that incompletely molted birds suffer disadvantages from partly worn plumage.

3 Precisely timed post-juvinal molt in captive stonechats

3.1 Cues for the timing of molt

The various strategies by which time-constrained birds modify molt schedules are costly and hence subject to selection. As a consequence, the extent and mechanism of molt-timing can be expected to be adjusted by selection to best match local conditions. The physiological basis of precise timing in birds relies on circannual programs, such as photoperiod (Gwinner, 1986; Wingfield et al., 1992; Gwinner, 1999). In keeping with costs of molt schedules, the timing of responses to environmental cues often differ regionally and can be described by population reaction norms (van Noordwijk, 1990). Timing programs also meet a genetic precondition for evolutionary adjustment: a sufficient amount of additive genetic variance within populations. Evolvable timing has been shown in wild and captive birds for migration, reproduction, and molt (van Noordwijk et al., 1981; Larsson, 1996; Helm and Gwinner, 1999, 2001; Brown and Brown, 2000; Pulido et al., 2002). We illustrate a flexible molt-timing mechanism that is fine-tuned to local conditions by summarizing research on post-juvinal molt in stonechats (*Saxicola torquata*).

3.2 The stonechat case study

To study adaptations to conditions in their native areas, we compared timing of molt in several subspecies of the stonechat, a passerine with a wide north-south breeding range (Helm and Gwinner, 1999, 2001). Concordant with the seasonal cycles in their native regions, African stonechats (*S. t. axillaris*), Siberian stonechats (*S. t. maura*) and European stonechats (*S. t. rubicola*) differ in migratory behavior and the time-pressures encountered during post-juvinal molt. African stonechats are single-brooded residents that tolerate young for several months in their year-round territories. Siberian stonechats are long-distance migrants that leave their breeding grounds shortly after raising a single brood. European stonechats are multi-clutched, and the young from the last brood have to prepare rapidly for migration. Because of these different schedules, we expected overall differences not only in the timing and duration of molt, but also in the mechanisms by which the populations respond to seasonal information conveyed by photoperiod.

We studied post-juvinal timing of molt in each population under a range of day-lengths. Short day-lengths simulated molting late in the year and long day-lengths the situation in summer. Fig. 1A plots the age at which young birds under different day-lengths reached peak molt intensity (Helm and Gwinner, 1999). Each data point represents a

group of birds, and regression lines estimate population reaction norms. African stonechats molted relatively late, European stonechats at intermediate ages, and Siberian stonechats at the youngest. This sequence of mean molting ages was expected on the basis of the different time-pressures in their life-cycles.

All subspecies tended to molt earlier under short day-length but only in European stonechats was the response to photoperiod pronounced. Fig. 1B shows the times of laying and molting against day length in the three populations. For African stonechats, day-length is continuously short, and a strong photoperiodic response is unlikely to have been selected for. Siberian stonechats breed and molt over a short time interval during midsummer. Day-length changes at the peak intensity of molt are small but later increase quickly. European stonechats, in contrast, are multi-clutched, and the young hatch and molt under very different day-lengths. A strong photoperiodic response allows young from early clutches to delay molt, in contrast to young from late clutches which molt early to prepare for migration. Here the range of correlations between molt peak and photoperiodic pattern highlight the importance of photoperiod as a timing cue for the European population in particular.

Duration of molt was longest in African, intermediate in European, and shortest in Siberian stonechats, as expected from relative time constraints. Under such constraints, adjustments of molt duration were very different from those of molt peak. Molt duration was most flexible in Siberian stonechats. Whereas neither African nor European stonechats shortened their molting under pressure of time, Siberian stonechats reduced its duration to less than half the time taken under long day-length. These birds evidently start to molt early at a fixed time, and then adjust its rate under time constraints (Helm and Gwinner, 2001).

Stonechats from all three populations thus had dif-

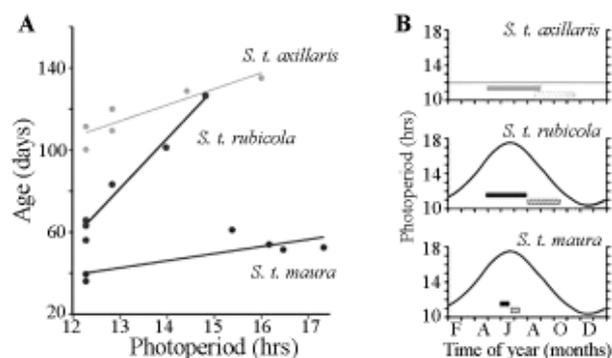


Fig. 1 Timing of post-juvénal molt in stonechats

A: mean population reaction norms for African (*Saxicola torquata axillaris*), European (*S. t. rubicola*), and Siberian stonechats (*S. t. maura*); the x-axis shows the day-length under which the birds were kept, and the y-axis shows the age at which the birds underwent peak molt. B: native photoperiodic conditions (curves), laying dates (solid bars), and dates of peak molt (hatched bars) for the three populations of stonechats.

ferent strategies for buffering time stress by molt schedules. Siberian stonechats accelerated molt while the other two subspecies shifted the timing of molt onset and peak. Circannual rhythms of stonechats thus encode characteristic features of seasonal activities in a population-specific manner. The differences in plasticity were paralleled by differences in heritabilities (Helm and Gwinner, 2001). In Siberian stonechats, additive genetic variance was high for molt duration, implying a facility for quick adjustments, but onset of molt did not differ between families. In European and African stonechats, heritabilities of molt onset were high, indicating that selection could lead to fast adjustments in the timing of molt; yet families did not differ in duration of molt. The high heritability of these conditions suggests that fitness consequences of molt schedules, as summarized above, can lead quickly to adjustments in the timing of molt to local conditions.

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