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ENERGY EXPENDITURE AND JUVENILE FORAGING EFFICIENCY: A MAJOR CONSTRAINT ON PASSERINE REPRODUCTIVE SUCCESS

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ABSTRACT. We calculated the foraging efficiency (FE) of adult Yellow-eyed Juncos *Junco phaeonotus* and their offspring during the 1985 and 1986 breeding seasons from measurements of their metabolized energy (ME) intake (doubly labeled water technique), prey capture rates, and time spent foraging. FE (kJ ME acquired per h spent foraging) of adults ranged from 15.2 to 26.2, depending upon the stage of the breeding cycle. FE of juveniles was only 5.3 during their first week of parental independence: a period of marked juvenile mortality due to starvation. The FE of independent juveniles increased as they gained proficiency at foraging, but it was still only about half the adult level six weeks after they attained independence. The first few weeks of independence are a critical period in the life of a Yellow-eyed Junco. During this period an individual's foraging efficiency may determine whether it survives to reproduce or perishes as an adolescent.

Keywords: Energetics, foraging efficiency, doubly labeled water, survivorship, breeding.

INTRODUCTION

Yellow-eyed Juncos* *Junco phaeonotus* are small (ca. 19 g), monogamous passerines. They maintain all-purpose breeding territories and have bi-parental care of the young. At our study site in Arizona's Chiricahua Mountains, they begin nesting in late April and continue until late August, with pairs producing up to three successful clutches in a single season (for details, see Sullivan 1988a). Juncos conceal their nests on the ground, and females carry out all of the nest building, incubation, and brooding activities. Most nests contain three or four nestlings and both males and females feed the nestlings and fledglings, insects being the primary food source of both young and adult juncos during the breeding season.

After fledging, immature juncos spend 3-4 weeks with one or both parents in a family flock. During this period the parents supplement the foraging efforts of their young. At the end of the 3-4 week fledgling period, the young juncos are evicted from the family territory. They then join juvenile flocks, but remain in the general area for the rest of the breeding season.

In our prior studies (Sullivan 1988a,b, 1989, 1990, Weathers & Sullivan 1989a,b, 1991), we measured, among other things, the allocation of time and energy of adult juncos and their young (nestlings, fledglings, independent juveniles) throughout the breeding season using concurrent time-activity budgets and the doubly labeled water (DLW) technique. Our data indicated that energy constraints are a major selective

* *Footnote:* Common and scientific names follow American Ornithologist's Union (1983).

force in Yellow-eyed Juncos, operating not through food limitation among adults but rather through the inefficient foraging of young juncos. In this paper, we employ our previous data together with new data (Table 1) on prey capture rates and prey energy content to examine more fully the foraging efficiency of adults and their offspring.

METHODS

As our index of foraging efficiency (FE), we used the rate of metabolizable energy (ME) acquisition (kJ acquired/hour spent foraging). We equated ME of birds in energy balance (juveniles and incubation stage adults) with their field metabolic rate (FMR), which we measured using the doubly labeled water (DLW) technique (Weathers & Sullivan 1989a). For these birds, FE in kJ/h = FMR (kJ/day) divided by h/day spent foraging. Some birds were not in energy balance, despite being in mass balance, either because they obtained less ME through foraging than required to meet their FMR (i.e., nestlings and fledglings being fed by their parents), or because they acquired more ME by foraging than required to meet their FMR (i.e., adults feeding young). Calculating FE of these birds necessitates accounting for the supplemental ME. To calculate FE of an adult feeding dependent young, we added the ME provided to its young to the adult's ME (measured by DLW) to obtain the total ME that the adult acquired while foraging. Similarly, for a dependent fledgling we subtracted the ME supplied by its parents from the young's ME (as measured by DLW) in order to obtain the young's actual FE . We estimated the ME that dependent fledglings gained by foraging from the product of their feeding rate (insects captured per hour), mean insect energy content (kJ/insect), and hours spent foraging per day (Tables 1 and 2).

TABLE 1 - Prey capture rate and prey energy content (Sullivan, unpubl. data).

Age/Stage ^a	Capture rate ^b Insects/h	Energy content ^c J/insect
Adults		
INC	240 ± 29.6 (11)	68
1 wk	251 ± 35.7 (12)	63
2 wk	254 ± 20.3 (19)	76
3 wk	320 ± 19.2 (24)	46
Immatures		
1 wk	3 ± 3.8 (31)	—
2 wk	83 ± 8.2 (39)	11
3 wk	180 ± 19.3 (21)	12
4-5 wk	222 ± 25.5 (16)	24

^a For adults: INC = incubating females and males paired to incubating females; Nestling = adults feeding nestlings; 1 wk, 2 wk and 3 wk = adults feeding, respectively, 1 wk-old fledglings, 2-wk old fledglings, and 3-wk old fledglings. For immatures, 1 wk = fledglings during the first week out of the nest, etc.

^b Mean feeding rate ± SE; number of 5-min observation periods in parentheses.

^c Metabolized energy content of average sized insect eaten, determined by bomb calorimetry.

TABLE 2 - Foraging efficiency of adult and immature juncos.

Age/Stage ^a	Energy acquired kJ/d	Foraging	
		Time ^b h/d	Gain ^c kJ/h
Adults			
INC. male	71	4.7 (72)	15.2
INC. female	67	2.6 (18)	26.2
Nestling	166	8.0 (149)	20.8
1 wk	177	11.2 (89)	15.8
2 wk	211	10.9 (81)	19.4
3 wk	155	10.2 (69)	15.2
Fledglings			
1 wk	0.1	1.2 (70)	0.1
2 wk	8.5	7.2 (75)	0.9
3 wk	34	12.0 (84)	2.2
Juveniles			
4-5 wk	73	13.7 (73)	5.3
6-7 wk	93	13.9 (69)	6.7
10-12 wk	100	9.2 (70)	10.9

^a For explanation of symbols, see Table 1 footnote.
^b Hours foraging/d based on the number of 15-min observation periods indicated in parentheses (Sullivan 1990)
^c Energy acquired through foraging (kJ/d) divided by foraging time (h/d).

RESULTS

Adult foraging efficiency

Incubation stage females lack visible fat, are not fed by their mates, and do not lose mass during incubation (Sullivan, unpubl. obs.). Incubation stage males also are in energy balance (no net mass change, no ME allocated to young). Consequently, both sexes acquire enough energy while foraging to meet their FMR requirement. Although the FMR of male and female incubation stage adults was similar (71 v 67 kJ/day), the time that the sexes devoted to foraging was vastly different (4.7 v 2.6 h/day) (Table 2). As a consequence, females exhibited a much higher FE than males (26 v 15 kJ/h) (Table 2).

Nestling stage adults foraged to meet their own energy needs as well as those of their young. Because both sexes provision nestlings equally (Sullivan 1988a), the ME acquired by adults feeding nestlings is the sum of the adult's FMR and one half the total nestling ME. Nestling energy demand depends upon nestling size; increasing from about 2 kJ/d on the day of hatch to a plateau of 54 kJ/d by the time nestlings weigh about 17 g (day 9) (Weathers & Sullivan 1991). The nestling stage adults whose FMR we determined by DLW were feeding nestlings with an average mass of 14.5 ± 2.0 g (mean ± SD, n = 24). The ME of nestlings this size averages 51 kJ/day (Weathers & Sullivan 1991), which represents the sum of their FMR (about 38 kJ/d) and the energy accumulated as new tissue (growth). The adult pairs that we measured with

DLW fed broods which averaged 3.6 nestlings. Hence, parents had to acquire an amount of ME equal to the demand of 1.8 nestlings ($1.8 \times 51 \text{ kJ/day} = 92 \text{ kJ/d}$) plus their own FMR of 74 kJ/day, for a total of 166 kJ/day of acquired ME (Table 3). Adults feeding nestlings obtained this amount of energy while foraging for 8.0 h/d. Hence, their FE was 21 kJ/day (Table 2).

Whereas calculating the FE of adults feeding nestlings is relatively easy, because the adults supply all of the nestling's ME, determining how much energy adults supply to their fledglings is more complicated because fledglings obtain some energy through their own foraging efforts. Initially the amount of this energy is very small, but as fledglings age and become more proficient at foraging it increases. We estimated how much energy fledglings gathered per hour based on their observed prey capture rates and the prey's energy content (Table 1). This value multiplied by the number of hours spent foraging per day gave the total energy that fledglings obtained on their own. Subtracting the latter value from the fledglings FMR, as measured by DLW, gave the amount of energy that the adults supplied. This value multiplied by the number of young that each parent fed, gives the total ME that adults feeding different aged fledglings had to acquire (Table 3). From the total energy that adults acquired, we calculated their FE (Table 2). The FE of parents feeding fledglings varied somewhat, depending upon the fledgling's age, due to variation in brood size of the different age classes. Overall, FE of adults feeding fledglings averaged 16.8 kJ/h. This is roughly equivalent to that of incubation stage males foraging to meet only their own energy needs.

TABLE 3 - Energy requirements of adult juncos and their young for various stages of the breeding cycle. All energy values are kJ/day metabolized energy.

Stage	Adult FMR ^a	Immature FMR	Brood size ^b	Brood energy demand ^c	Energy brood supplies ^d	Energy adult supplies ^e	Total energy adult acquires ^f
Nestling	74 (13)	53 (13)	1.8	92	0	92	166
Fledgling							
1 wk	75 (11)	60 (11)	1.7	102	0.1	102	177
2 wk	76 (6)	68 (10)	2.2	150	14	136	211
3 wk	79 (8)	74 (11)	1.6	118	42	76	155

^a FMR = field metabolic rate as measured with doubly labelled water, sample size in parentheses (Weathers & Sullivan 1989a).
^b Number of young fed per adult.
^c Immature's FMR times brood size.
^d Energy brood gains due to the immature junco's own foraging efforts (see text).
^e Brood energy demand minus energy brood supplies.
^f Sum of adult's FMR and energy adult supplies to the brood.

Foraging efficiency of young juncos

The FE of fledglings during their first week out of the nest was nearly nil (Table 2). Fledglings this age captured an average of only 3 insects per hour spent foraging, and they foraged for only 1.2 h/day. Although FE increased as dependent fledglings aged, it still remained very low compared with that of adults (Table 2). When fledglings became independent of their parents (age 4-5 wk post fledging), their FE more than doubled to an average of 5.3 kJ/h, as compared with the FE of fledglings seven days

younger. Nevertheless, FE of 4-5 wk-old juveniles was still only about 1/3 to 1/5 that of adults. Juveniles this age forage for over 90% of the daylight hours and still often fail to maintain body mass (Sullivan 1988a, 1990).

The FE of juveniles improved markedly during their first month of parental independence, as they gained proficiency at handling prey, but even at two-months post-independence it was still only 72% of that of incubation stage males, the most comparable adult group (Table 2).

DISCUSSION

Among immature Yellow-eyed Juncos, foraging efficiency (FE) improves with age and appears to be a major factor in age-specific survivorship. The FE of recently independent juveniles (4-5 wk age) is only 1/3 to 1/5 that of their parents (Table 2). Although independent juveniles (4-5 wk) and adults capture nearly the same number of insects per unit time (Table 1), juveniles spend a greater proportion of their time searching for and handling food items than adults (Sullivan 1988b), and consume prey of lower energy content (Table 1).

The consequences of inefficient foraging are severe for recently independent juveniles. Whereas 8.4% of adult juncos die during the breeding season (daily mortality rate = 0.11%, Sullivan 1989), 46.3% of independent juveniles die during their first two weeks of independence (daily mortality rate = 3.85%, Sullivan 1989). During this period, all juveniles lose mass, and the extent of mass loss correlates significantly with survival to the end of the breeding season (Sullivan 1989).

During the first few weeks of independence, young juncos must quickly gain proficiency at foraging or die. Juveniles that survive their first month of independence experience substantially lower mortality (daily mortality rate = 0.55%, Sullivan 1989) and have double the FE of recently independent young (10.9 vs. 5.3 kJ/h, Table 2). The relatively low FE of 10-12 wk juveniles (compared with adults) reflects their more rudimentary foraging skills, rather than benign environmental conditions that might permit lower FE. Juveniles this age encounter late-season (late July-August) conditions of shorter daylength, cooler temperatures, and rainy weather which increase their energy demands (Weathers and Sullivan 1989).

The foraging efficiency of adults varied 1.7 fold over the breeding cycle (Table 2). Males paired to incubating females, and males and females feeding fledglings acquired energy at substantially lower rates (ca. 15 kJ/h) than incubating females (26 kJ/h) or males and females feeding nestlings (21 kJ/h). We discount the possibility that seasonal changes in prey availability account for these differences. Such was clearly not the case for incubation stage males and females, for whom DLW measurements were made at the same time of year. Although there was a significant correlation between the date that adult FMR was measured and stage of the breeding cycle in 1986 ($r = 0.838$, $P < 0.01$, $n = 20$), there was none in 1985 ($r = 0.100$, $P > 0.05$, $n = 31$). Furthermore, no correlation exists between FE and stage of the breeding cycle (Table 2), as would be expected if seasonal changes in insect availability had an effect on FE.

The relatively high foraging efficiency exhibited by incubating females reflects their time constraints. Female juncos carry out all of the incubation and brooding activities (males lack brood patches). Because male juncos rarely feed their mates, incubating females must periodically leave the nest to forage. In the juncos' montane environment, eggs cool rapidly during off-bouts and this factor effectively limits foraging bout length (Weathers & Sullivan 1989b). Presumably, incubating females increase their foraging efficiency in the face of intense time constraints through increases in prey capture rate and/or increases in prey energy content. We lack the data necessary to distinguish between these possibilities.

The FE of adults feeding nestlings was about 39% higher than that of adult males feeding only themselves and about 27% higher than that of adults feeding fledglings (Table 2). The behavioral responses underlying these shifts in FE are also uncertain.

INFERENCE

A basic tenet of optimal foraging theory holds that fitness is a function of foraging efficiency (Schoener 1971, Pyke et al. 1977, Krebs 1978). Animals that maximize their net energy gain when foraging should produce more surviving offspring on average than less efficient individuals, because less efficient individuals will either accumulate less energy for growth and reproduction or spend more time foraging. Implicit in this statement is the idea that animals should always forage as efficiently as possible given the constraints imposed upon them by the need to avoid predators (Holmes 1984, Lima 1987), meet nutritional demands (Belovsky 1981), defend territories and mates, and provide parental care. Adult Yellow-eyed Juncos adjust both the amount of time they spend foraging and their foraging efficiency to meet their changing energy demands and time constraints during the breeding cycle. From this, we infer that animals may reduce their foraging efficiency when energy demands and time constraints are relaxed, either because the costs of inefficient foraging are negligible during these periods or because there are stress or risk related costs associated with foraging more efficiently.

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ON THE IMPORTANCE OF ENERGY CONSIDERATIONS TO SMALL BIRDS WITH GYNELATERAL INTERMITTENT INCUBATION

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ABSTRACT. In some bird species, especially small passerines, the female receives no assistance from the male during incubation (gynelateral intermittant incubation, GII) requiring her to balance the regulation of egg temperature with fulfilling her own requirements for food and water. In this review, I argue that for GII systems, the incubation period is not necessarily a period of reduced energy demand, and that energy constraints during incubation can negatively influence reproductive success. Several factors seem to function synergistically to impact the energy balance of females with GII: not only does the steady state act of incubating eggs require added energy expenditure, but also rewarming eggs after periods of inattentiveness; females often incubate eggs when ambient temperatures are low and food supplies are diminished; and available foraging time is restricted during this time. For GII systems, the FMR of females during incubation equals their FMR when feeding nestlings. Calculations show that under some circumstances females that incubate 80% of each hour are likely to encounter problems of energy balance especially during periods of inclement weather when energy expenditure is high. In support of this idea, some small birds lose body mass during incubation when ambient temperatures are low. For small nectarivorous birds breeding in temperate environments, problems of energy balance have been indicated when incubating females became torpid or hypothermic.

Keywords: Gynelateral intermittent incubation, incubation, field metabolic rate, birds, Savannah Sparrow, energetics, attentiveness.

INTRODUCTION

Birds lay eggs which require exogenous heat for successful development (Lundy 1969). Because they nest in environments where ambient temperatures fall below optimum values for embryological development, parents face the challenge of supplying heat to their eggs while also providing for their own needs for self-maintenance. Partitioning of time and energy between these two mutually exclusive behaviors can affect reproductive performance (Lyon & Montgomerie 1987, Nilsson & Smith 1988).

Evolution has fashioned a number of incubation behaviors (Skutch 1976). In many species, parents share incubation duties, or males deliver food to the female while she alone incubates the eggs. In both situations, eggs are covered almost continuously. Within some orders, the incubating partner, usually the female, is unaided during this period requiring her to balance the regulation of egg temperature with fulfilling her own requirements for food and water.

For the unassisted female (gynelateral intermittent incubation, GII), particularly small passerines since they are not equipped with large metabolic reserves (Jones & Ward 1976), the incubation period may be challenging. Nest attendance of up to 50 min each hour markedly reduces foraging time (Skutch 1962) and eggs are often incubated when food availability is relatively low (Mertens 1987, Williams 1987). Moreover, incubating females elevate their energy expenditure while supplying heat to

eggs (Vleck 1981, Weathers 1985, Biebach 1986). Taken together these ideas suggest that under some circumstances incubating females may experience energy imbalance. In this review, I examine the importance of energy considerations to free-living incubating birds, especially small birds that incubate their eggs unaided by their mate. I argue that for GII systems, the incubation period is not necessarily a period of reduced energy demand compared to other phases of the reproductive cycle; that because of their restricted foraging time, incubating females may experience an energy deficit; and that energy constraints during incubation can influence reproductive success by increasing the incubation period and decreasing hatching success (Clark & Wilson 1981).

METHODS

Assessment of the metabolic rates of free-living birds by the standard two-sample DLW method during the incubation period has often proven difficult because females sometimes abandon their nests when held captive during the required initial isotope equilibration period (Williams 1987). A one-sample variant of the DLW is now available wherein the initial ratio of isotopes in the body water can be predicted from the ratio of isotopes in the injection solution or, more preferably, from the average ratio in a group of previously injected birds (Ricklefs & Williams 1984, Williams & Dwinell 1990). With this method, incubating birds can be captured, injected, and immediately released enhancing the likelihood that experimental subjects will quickly resume their incubation duties. The single-sample DLW method has been validated in the laboratory on Verdins *Auriparus flaviceps*: results based on one-sample calculations differed from gravimetric determinations of CO₂ production by less than 0.5% on average (Webster & Weathers 1989). This method will likely prove valuable in future studies on the energetics of free-ranging incubating birds.

RESULTS AND DISCUSSION

The thermal energy cost of incubation

During the last two decades several studies have examined facets of the energy cost of supplying heat to eggs (Mertens 1977, Walsberg & King 1978a, Biebach 1981, Vleck 1981, Grant & Wittow 1983, Haftorn & Reinertsen 1985, Weathers 1985). Although controversy remains (Walsberg 1983), the accumulating data suggests that energy expenditure of incubating birds is increased over that of non-incubating birds when they experience temperatures below their thermoneutral zone, and that energy expenditure of incubating females escalates as clutch size increases. Among passerines with 4-5 egg clutches, power consumption of incubating birds is elevated by 20-30% over non-incubating birds (Weathers 1985). For GII, the thermal requirements for incubation are further increased above these steady state costs because of an additional heat requirement to rewarm eggs after inattentive periods (Biebach 1986).

Field metabolism during the incubation period

The energy expenditure of females is thought to be relatively high during the egg laying and nestling periods, whereas during incubation, expenditure is considered to be low because of reduced activity levels (Walsberg 1983). To test this idea, I have

TABLE 1 - Field metabolism of females during the incubation and nestling period for birds in which males and females incubate, in which the female alone incubates but receives food from her mate, and in which the female incubates unaided by the male.

Species	Body mass	FMR ^a kJ/d	Nest ^b type	Body mass	FMR kJ/d	P	Source
	Incubation Period			Nestling Period			
Male and Female Incubate							
Sand Martin <i>Riparia riparia</i>	14.3	75.9	1	13.0	83.5	<0.05	Westerterp & Bryant 1984
House Martin <i>Delichon urbica</i>	18.7	74.9	1	18.4	95.8	<0.001	Westerterp & Bryant 1984
House Martin	18.9	69.2	1	18.2	73.1	NS	Bryant & Westerterp 1980b
Wilson's Storm-Petrel <i>Oceanites oceanicus</i>	42.3	119.0	3	42.2	157.0		Obst et al. 1987
European Starling <i>Sturnus vulgaris</i>	85.0	212.3	1	74.1	301.4	<0.001	Ricklefs & Williams 1984
Female Incubates - Male Provides Food							
Pied Flycatcher <i>Ficedula hypoleuca</i>	15.0	68.0	1	-	-	-	Moreno & Carlson 1989

Collard Flycatcher <i>Ficedula albicollis</i>	15.9	78.6	1	12.9	71.7	NS	Moreno, pers. comm.
Tree Swallow <i>Tachycineta bicolor</i>	22.6	118.9	1	19.4	136.4	<0.01	Williams 1988a
Dipper <i>Cinclus cinclus</i>	64.0	204.5	2	58.0	250.1	<0.01	Bryant & Tatner 1988
Female Incubates - No Assistance							
Savannah Sparrow <i>Passerculus sandwichensis</i>	18.7	73.8	2	17.0	67.7	NS	Williams & Dwinnel 1990
Savannah Sparrow	20.2	85.2	2	18.3	80.6	NS	Williams 1987, Williams, Bergstrom & Wheelwright unpubl.
Yellow-eyed Junco <i>Junco phaeonotus</i>	20.5	66.7	2	18.9	74.4	NS	Weathers & Sullivan 1989
Barn Swallow <i>Hirundo rustica</i>	20.5	112.2	2	19.2	101.5	NS	Westerterp & Bryant 1984

^a To convert units of CO₂ to units of energy, I used 24.6 J/ml CO₂ (Williams & Prints 1986).

^b Nest type 1 = tree cavity or nest box, 2 = open cup, 3 = cavity in ground.

compared the FMR of incubating females to their FMR when they were feeding nestlings (Table 1). Among species in which parents share incubation duties, or in which the male delivers food to the incubating female, females exhibit a reduced FMR during incubation. For species with GII, Savannah Sparrows, Yellow-eyed Juncos, and European Barn Swallows, FMRs are statistically indistinguishable between the two periods. Hence, for GII systems, there is no evidence that the FMR of incubating females is diminished relative to the ostensibly strenuous period when they are delivering food to nestlings. Further, absolute values of FMR must be evaluated relative to food availability and available foraging time. Even if the energy expenditure of females during incubation were relatively low, this would not obviate the possibility that they experience energy stress during this time because they have far less time available to find food.

Consequences of attentiveness on energy acquisition

The nestling period is presumed to be the most likely phase of reproduction during which energy expenditure exceeds acquisition and, as a result of depressed body condition, the probability of parental death increases or future reproduction is impaired (Stearns 1976, Freed 1981, Reyer 1984, Nur 1986, Williams 1988b). Despite the fact that a number of species with GII lose mass during incubation (Freed 1981, Mertens 1987, Johnson et al. 1990), this period is rarely considered to pose energy problems for breeding adults (King 1973, Walsberg & King 1978a, Walsberg 1983). Adhering to this latter idea, Freed (1981) rejected the notion that mass loss reflected physiological stress during breeding primarily because female Wrens *Troglodytes aedon* lost mass during incubation rather than the nestling period. He suggested that the observed reduction in mass of females during incubation reflected a genetically programmed anorexia which lowered power requirements necessary for flight during the forthcoming nestling period (see also Sherry et al. 1980, Norberg 1981). The alternative hypothesis, that incubating females were unable to procure enough food to meet their requirements, remains untested.

To explore the possibility that females of small body size with GII may at times encounter energy expenditures that exceed their rate of acquisition, I have estimated the rate of gross energy acquisition (kJ/h) for a 20 g passerine as 15.4 kJ/h, a value calculated from an equation generated from data taken on birds observed feeding in the wild (Bryant & Westerterp 1980a). Assuming a foraging period of 16 h and an assimilation efficiency of 75% (Ricklefs 1974), maximum metabolizable energy intake would be 184.8 kJ/d. According to Nagy (1987), the FMR of a comparably-sized bird belonging to the same order is 83.8 kJ/d. Females attending their eggs 60% or 80% of each hour (Skutch 1962) would have a metabolizable energy intake of 73.9 kJ/d or 37.0 kJ/d, respectively. Both values fall below the predicted FMR. Assimilation efficiencies for some birds that prey on insects are lower than 75% (Kacelnik 1984): this would further increase the difference between energy acquisition and FMR.

From the above, females with GII could experience energy shortfalls with a concomitant depletion of body reserves especially during periods of adverse weather. For example, in response to periods of low ambient temperature females must elevate their metabolic rate, and they may increase their attentiveness further reducing the time available for foraging (Jones 1987).

In support of these ideas, Great Tits *Parus major* often postpone incubation when nocturnal ambient temperatures remain below 8°C (Mertens 1980). However, if air

temperatures fall after incubation has begun, females continue incubating but apparently have difficulty in obtaining sufficient food as evidenced by a decline in their body reserves, primarily lipids (Mertens 1987). Moreover, during poor weather conditions incubating female Swallows *Hirundo rustica* increase their attentiveness and as a result lose body mass - one female lost 9% of her body mass in 6 h (Jones 1987).

Consequences of body size on attentive periods

For females with GII, two factors maximize attentive periods, thereby reducing the number of visits to the nest. First, after each recess, eggs must be rewarmed which requires added energy expenditure (Biebach 1986). Second, each visit to the nest increases the likelihood of detection by predators (Skutch 1962). Hence, females should remain at the nest as long as possible with food requirements dictating their departure schedule. With high mass-specific metabolic rates, relatively large clutch masses, and low energy reserves, it can be predicted that small birds should leave their nest to forage more often than should large birds. Though Skutch (1962) first mentioned this idea, he could find only broad qualitative trends in his analysis. Among 41 temperate species with uniparental intermittent incubation, attentive period is positively related to body mass (Figure 1). The slope of this line, 0.675, is similar to the slope of the line relating both basal and field energy expenditure to body size in birds (0.675, Aschoff & Pohl 1970; 0.64, Nagy 1987), suggesting that metabolism may have a strong influence on incubation behavior in this group of birds.

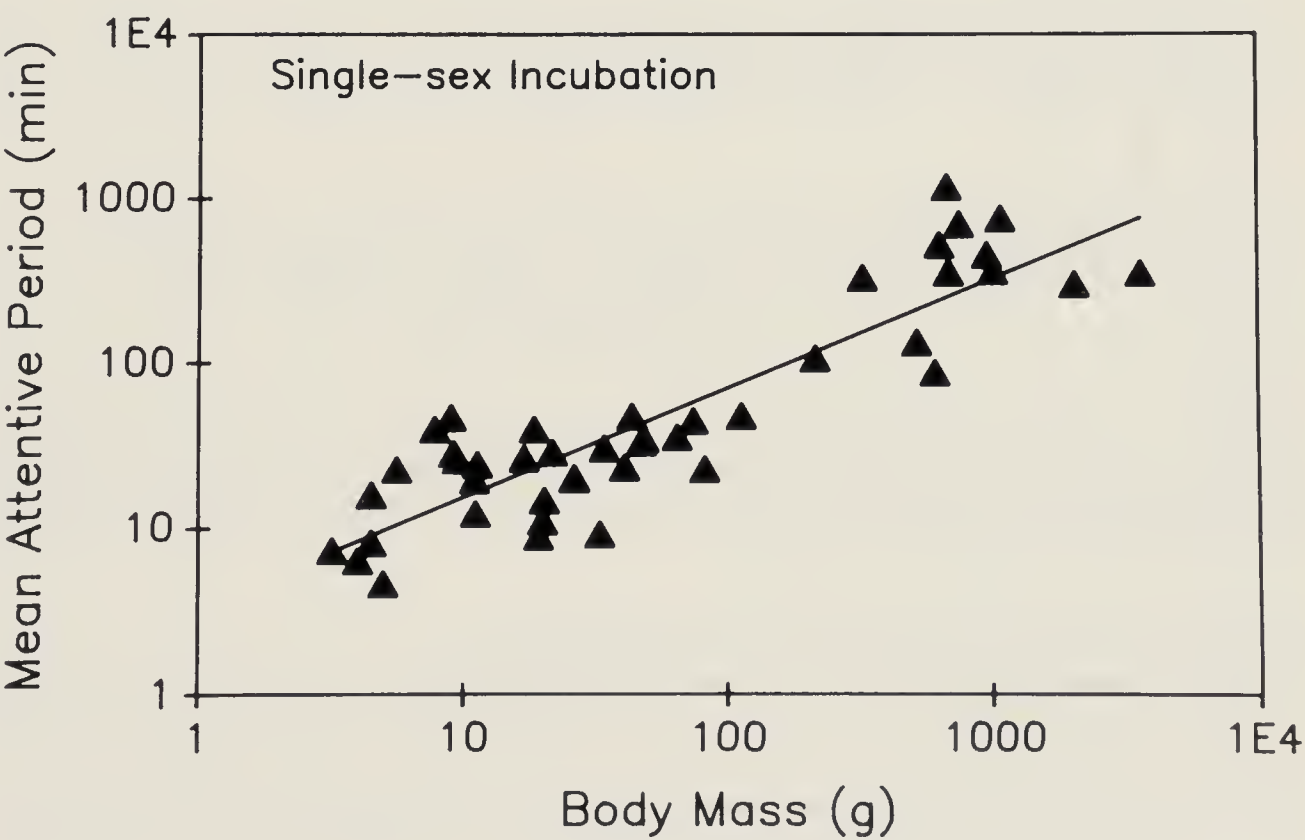


FIGURE 1 - Attentive period as a function of body mass for terrestrial birds from temperate regions in which the female incubates the eggs unaided by the male. Log attentive period (min) = 0.502 + 0.675 log body mass (g) ($r^2 = 0.78$, $F = 135.7$, $P < 0.0001$, $N = 41$). Most of the data comes from Kendeigh 1952; other sources available on request

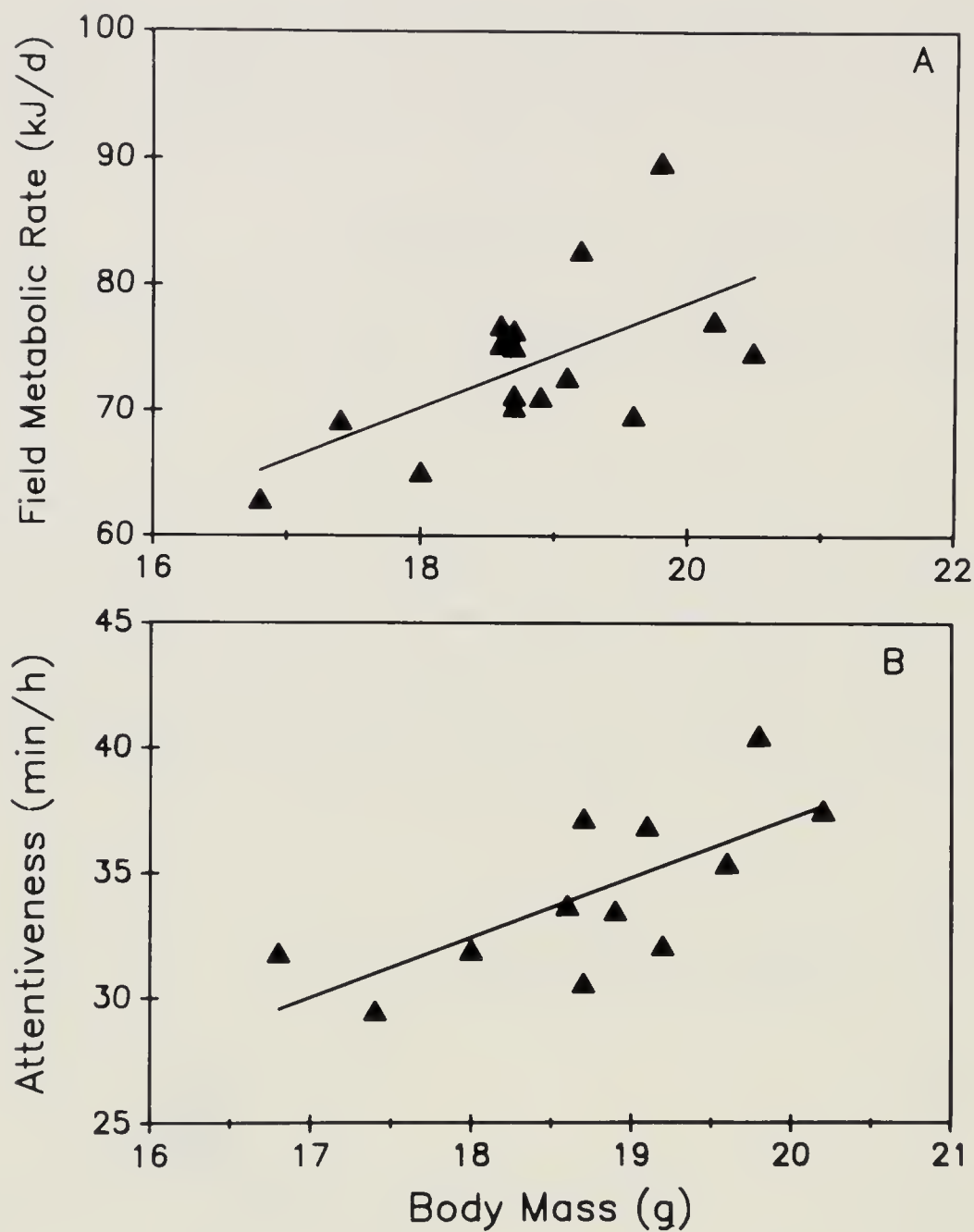


FIGURE 2 - (A) The relationship between FMR and body size for female Savannah Sparrows during incubation in a salt marsh near San Quintin, Mexico. (B) The relationship between attentiveness (min on the nest per h) and body size for female Savannah Sparrows in a salt marsh near San Quintin, Mexico.

Energetics of small passerines during incubation

Females of small body size with no food subsidy from their mate are the most likely to encounter periods of energy stress during incubation, which may result in decreased reproductive performance. In Marsh Tits (12.5 g; *Parus palustris*), females that were provided with supplementary food during incubation had shorter incubation periods and higher hatching success than birds without supplementary food (Nilsson & Smith 1988). Cold nest microclimates that require increased thermoregulation may have influenced the evolution of incubation feeding in the hole-nesting Snow Bunting (35.4 g, *Plectrophenax nivalis*; Lyon & Mongomerie 1987). In Pied Flycatchers *Ficedula hypoleuca* females of small body mass during incubation produced fledglings that were lighter and in poorer condition than heavy females (Lifjeld & Slagvold 1986).

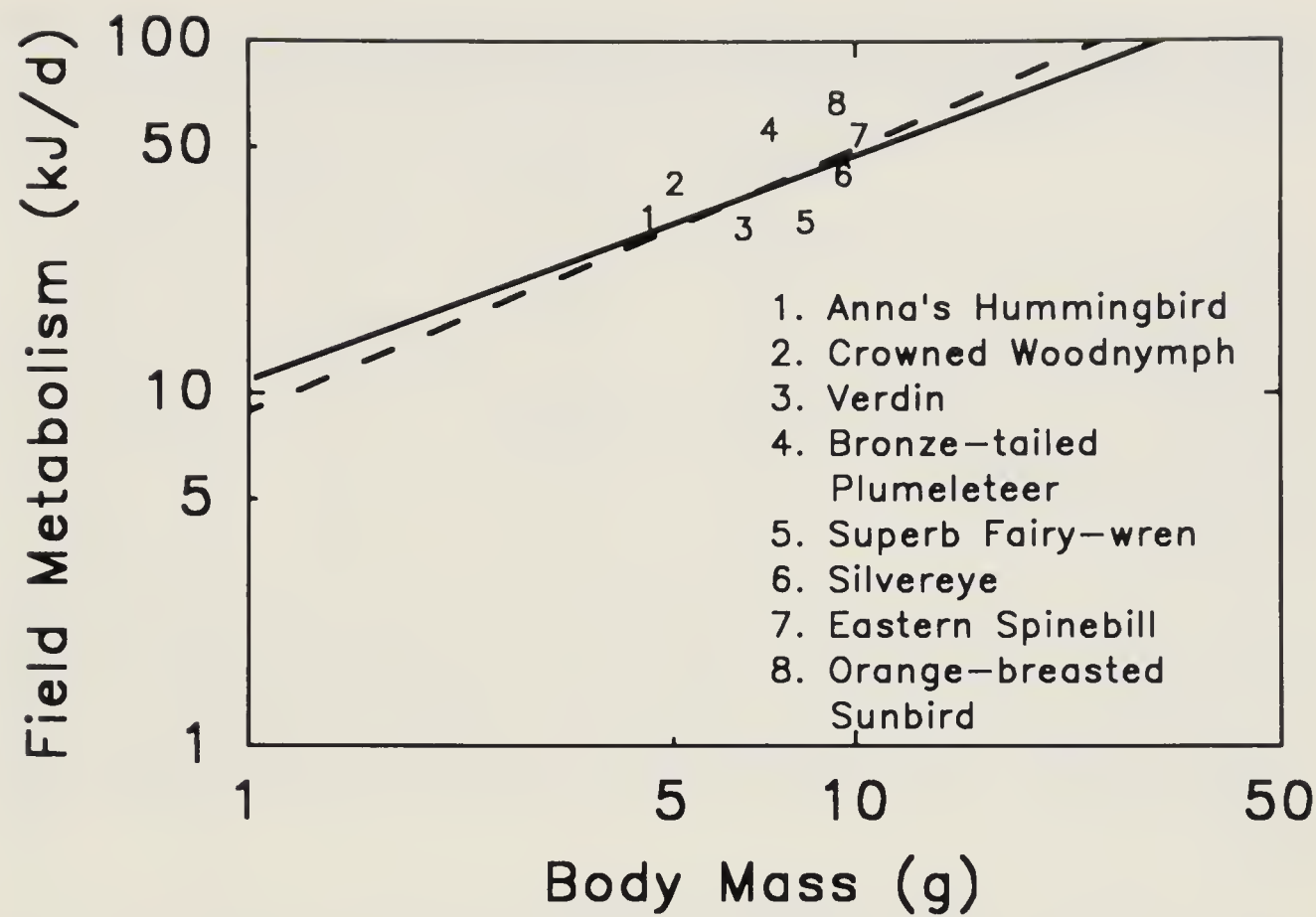


FIGURE 3 - The relationship between FMR (kJ/d) and body mass (g) for small birds. Scientific names and data for birds other than Orange-breasted Sunbirds from Weathers and Stiles (1989). The solid line represents the allometric prediction for all birds combined and the dashed line for passerine birds (Nagy 1987).

SAVANNAH SPARROWS. Savannah Sparrows (18-20 g) breed in a variety of habitats across North America, typically open grasslands but some races inhabit salt marshes along the southern Pacific coast (Van Rossen 1947, Rising 1987). Females construct an open-cup nest near ground level and incubate eggs unaided by the male. With several collaborators, and using the single-sample DLW technique, I studied the energetics of incubation in this species in two widely separated localities, a salt marsh near San Quintin, Mexico, and a grass field on Kent Island, New Brunswick, Canada (Williams & Dwinneel 1989, Williams, Bergstrom & Wheelwright, unpubl.). Salt-marsh sparrows are permanent residents, lay 3 eggs, and experience moderate temperatures during the incubation period (average = 15-25°C), whereas sparrows on Kent Island are migratory, lay 4 eggs, and cope with lower ambient temperatures which typically average around 8-15°C during the day and often fall to near freezing during the night. Additionally, fog periodically covers the island (Williams 1987).

On Kent Island, incubating females weighed more than females from Mexico, a consequence, in part, of the former depositing more fat prior to egg laying (Table 2). Though larger body size may have contributed to a higher FMR for Kent Island birds, they also had significantly higher thermoregulatory costs as evaluated by calculations of standard operative temperature for both populations (Bakken et al. 1985). In response to lower ambient temperatures on Kent Island, females stayed away from the nest for shorter periods and made more trips to the nest each hour. In both populations females lost mass during experimental periods.

TABLE 2 - A comparison of body mass, field metabolism, maintenance metabolism, and attentive periods for two populations of Savannah Sparrows.

	San Quintin	Kent Island	t value	P
Body mass (g)	18.8	20.2	4.7	<0.001
Field metabolic rate (kJ/d)	73.8	85.2	3.9	<0.001
Mass change/d (%)	-2.7	-2.4	0.7	NS
Maintenance metabolism (kJ/d)	40.7	44.5	3.2	<0.004
Maintance/FMR	0.56	0.53	1.1	NS
Mean attentive period (min)	12.8	12.6	0.2	NS
Mean inattentive period (min)	11.7	7.2	2.4	<0.03
Mean trips/h	4.1	6.1	2.5	<0.02

Among incubating females in the salt marsh population, body size varied widely with larger birds having a higher FMR ($r^2 = 0.59$, $P < 0.001$; Figure 2A). Interestingly, larger females tended to spend more time incubating eggs than did smaller birds ($r^2 = 0.51$, $P < 0.01$; Figure 2B). Larger females with more metabolic reserve sat on their eggs for longer periods ($r^2 = 0.32$, $p < 0.04$), perhaps shortening the overall length of incubation.

WHEATEARS *OENANTHE OENANTHE*. In this species with GII, female attentiveness may be constrained by their food requirements (Moreno 1989b). Augmentation of the food supply of incubating females showed that they spent significantly more time incubating eggs as food supply increased. Females with the largest food supplement shortened their incubation period by 1.5 days compared to controls. Hence, energy considerations may directly influence reproductive performance in this species mediated by changes in the length of incubation.

ORANGE-BREASTED SUNBIRDS *NECTARINIA VIOLACEA*. From the few studies available, nectarivorous birds have high energy expenditures compared to other birds of similar body size with FMR values exceeding allometric predictions by as much as 140% (Weathers & Stiles 1989). Sunbirds occupy the nectarivory niche in the Old World which hummingbirds occupy in the New World, but unlike hummingbirds, they feed while perched, not by hovering. Endemic to South Africa, Orange-breasted Sunbirds (9.5g) inhabit fynbos vegetation where they breed during the winter months when air temperatures are cool and frequent rains occur. During incubation, females of this species have the highest FMR so far recorded for any small bird including three species of hummingbirds (Williams unpubl., Figure 4). Inclement weather often impedes foraging, and under such circumstances, short-term energy problems may arise for incubating females. One female that for two previous nights had continuously maintained egg temperature near 35°C, apparently became hypothermic with the result that egg temperature fell to below 30°C (Figure 4). After feeding during her first morning recess, she rapidly rewarmed her eggs and maintained egg temperature at normal levels throughout the rest of the day. Whether this female voluntarily reduced her body temperature as an energy saving mechanism or simply lacked sufficient energy reserves, remains unanswered.

Short-term energy problems during incubation have also been indicated in female hummingbirds. After rainy days limited their foraging success, nocturnal egg

temperatures dropped to near ambient levels, presumably because females became torpid (Calder 1975, Vleck 1981). Torpor and hypothermia reduce daily energy requirements, but are also likely to lengthen the incubation period which ultimately may diminish reproductive success (Clark & Wilson 1981).

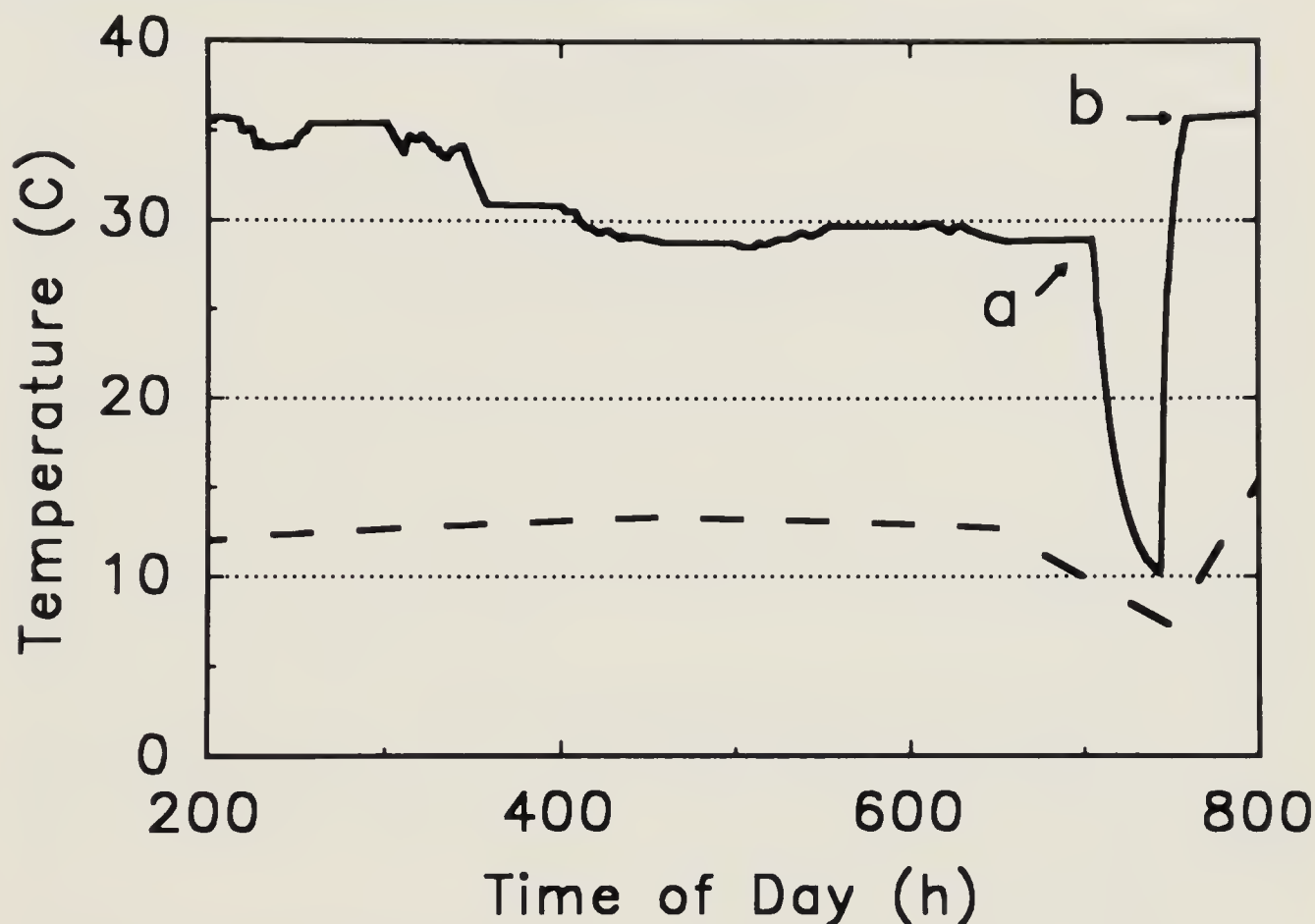


FIGURE 4 - Egg temperature ($^{\circ}\text{C}$) as a function of time of day for an incubating Orange-breasted Sunbird (solid line). Point a represents female departure from the nest, point b represents egg temperature after her return. The dashed line represents ambient temperature.

CONCLUSIONS

Adherents to the contemporary paradigm of avian life-history evolution often focus on the nestling period as the time when birds are most likely to experience problems in balancing their energy budget, and suggest that this is a key factor in limiting long-term reproductive success. There is some evidence that parents raising large broods suffer increased mortality. Adult feeding frequency during this time has even been proposed as a measure of reproductive effort (Nur 1988). In this review, I have attempted to show that energy considerations during incubation can be an important influence of reproductive success in some species. The array of circumstances in which energy stress in incubating females occurs, how often it occurs, and whether short-term energy stress during incubation translates into increased female mortality, are questions that await further study.

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DAILY ENERGY TURNOVER DURING REPRODUCTION IN BIRDS AND MAMMALS: ITS RELATIONSHIP TO BASAL METABOLIC RATE

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ABSTRACT. Basal Metabolic Rates (BMR) in birds are generally greater than those of mammals of the same size. We explore here the hypothesis that this difference reflects corresponding differences in daily energy expenditure during parental care (DEE_{par}). This is indeed the case: DEE_{par} in mammals is about 37% below that in birds of the same size. Furthermore, as found previously in birds, DEE_{par} in mammals, after accounting for body mass, is positively correlated with BMR. A recent explanation of this relationship in birds is based on the mass-independent association between BMR and the size of heart and kidney, which represent the metabolic machinery available to support DEE at its peak. We now report this same association in a comparison between birds and mammals. Five mammals investigated so far had significantly smaller heart and kidneys (fat free dry mass) than birds of the same body mass. By this association, heart and kidney mass turn out to be a better predictor of BMR, and thereby of DEE_{par} , than body mass, a predictor which seems independent of taxon.

Keywords: BMR, DEE, *Spermophilus saturatus*, *Falco tinnunculus*, parental investment, reproductive energetics, doubly labeled water.

INTRODUCTION

The balance between daily energy expenditure (DEE) and daily metabolizable energy intake (DME) is an important determinant of survival, and hence of fitness. Both DEE and DME are affected by behavioural and reproductive "decisions". Therefore, the study of energy balance is an important tool for understanding the relationship between behaviour and fitness. Energy balance is constrained between upper and lower limits. The lower limit of energy expenditure in endotherms is reached in the laboratory under post-absorptive, thermoneutral conditions in the rest phase of the daily cycle, and is referred to as the Basal Metabolic Rate (BMR, Aschoff & Pohl 1970). The daily energy expenditure of free-living endotherms during parental care, DEE_{par} , is probably close to the upper limit of sustained energy expenditure (Drent & Daan 1980). Whether DEE_{par} really constitutes an upper limit by constraint, or is optimised at a submaximal level can be determined only by experimental manipulation. In this paper we summarize the results from the first two studies in which this question has been experimentally addressed, in the European Kestrel *Falco tinnunculus* and the Golden-mantled Ground Squirrel *Spermophilus saturatus*.

During reproduction parents not only use energy for their own maintenance but also provide energy to the offspring (egg production, incubation, gestation, food provision and milk production). Mammals and birds differ fundamentally in the pathway of energy transfer from parents to offspring (Figure 1). Whereas mammals assimilate energy before it is transferred to the offspring, birds usually distribute food directly to the young rather than ingesting it. Mammals and birds of the same body mass further

differ systematically in BMR, and birds show a size-independent ratio of DEE_{par} to BMR (Daan et al 1990b). If the same ratio were valid also for mammals, one would predict a difference in DEE_{par} between mammals and birds. The first aim of the present paper is to test this prediction. We therefore analysed interspecific variation in DEE_{par} and BMR, after eliminating body size, for both birds and mammals. Secondly, based on a comparative analysis of associations between avian BMR, organ mass and DEE_{par} , Daan et al. (1990b) suggested that natural selection has led to an adjustment of the size of the organs (such as heart and kidney) involved in sustaining energy metabolism to the peak levels of DEE associated with avian parental care. Initial data on mammalian heart and kidney mass in relation to BMR allows us a preliminary evaluation of this concept for mammals.

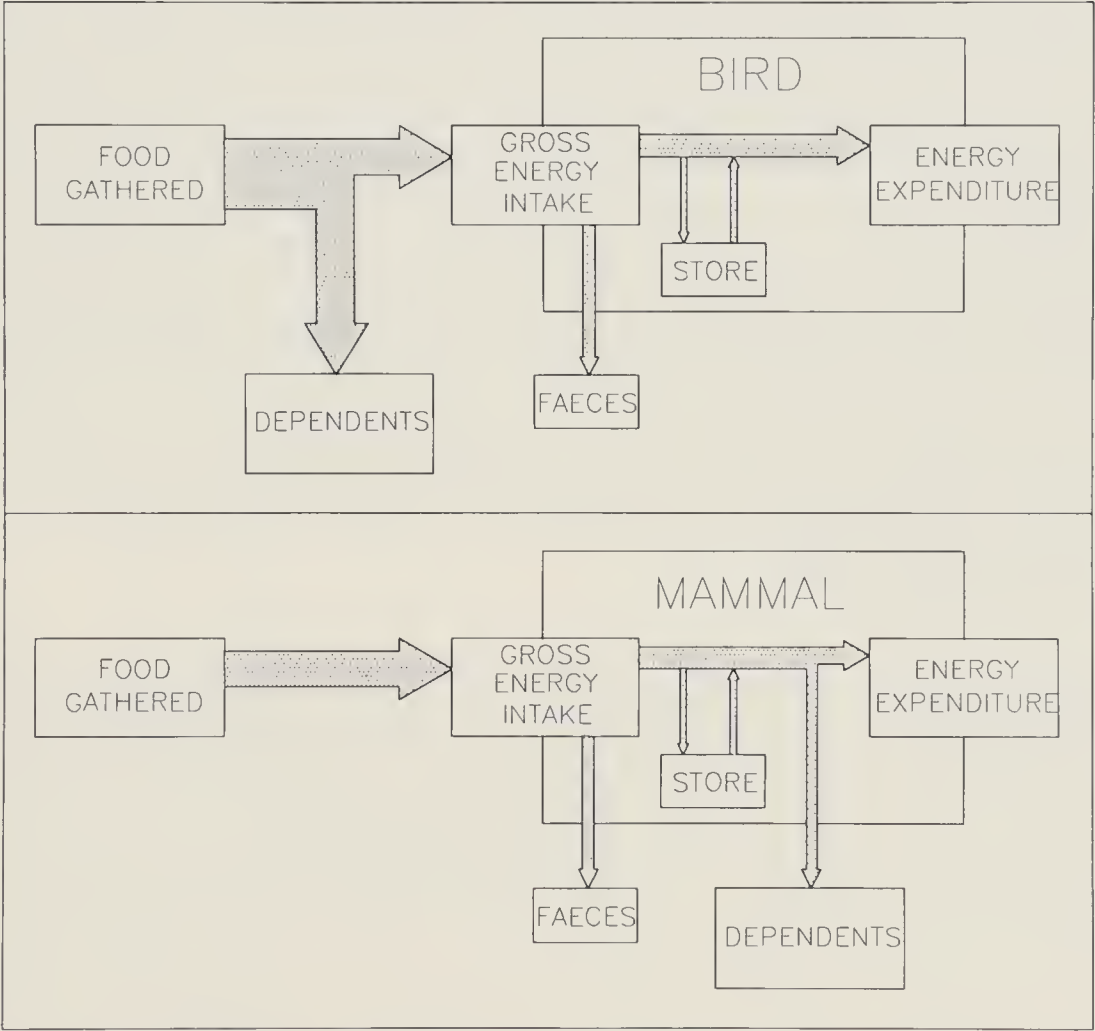


FIGURE 1 – Diagram of the energy flow during brood rearing in altricial birds and lactating mammals. Avian daily metabolizable energy (DME = Gross energy intake minus faeces) can completely be channeled into energy expenditure, while mammalian DME is shared between parent and dependents.

INTRASPECIFIC VARIATION IN DEE_{par}

We first address the question of whether a single level of parental energy expenditure can be representative for a particular species. Many avian and mammalian species show considerable variation in the number of offspring raised. Since energy allocation to the offspring varies with the number of offspring, one might presume that DEE_{par} is also highly variable within populations. Two detailed case studies of variation in DEE_{par} with number of offspring raised, combined with experimental manipulation of parental workload are currently available, the European Kestrel (Masman et

al. 1989) and the Golden-mantled Ground Squirrel (Kenagy et al. 1990). Neither species shows a substantial increase of DEE with increase in natural number of offspring (Figure 2). Recently Tatner (1990) demonstrated that the Wheatear *Oenanthe oenanthe* shows no association of DEE_{par} with the natural brood size. A functional explanation for this phenomenon can be addressed by evaluating the effects of experimental manipulation of offspring numbers.

In the kestrel we measured the energy budget of males (the sex taking the larger share in food provisioning for the offspring) and we manipulated food demands of the brood (Masman et al. 1989). In unmanipulated nests, males with larger broods were able to provide their broods with the same amount of food per chick as those with smaller broods. The daily effort exerted by males (DEE_{par}) was independent of brood size. The greater provisioning of larger broods was allowed by a larger hunting yield (voles obtained/hour flight hunting) of the male parent. Under experimental food shortage in the nest, males were able to increase their DEE in order to increase the daily rate of food delivery to the nest. In long-term experiments, where the food demand of the brood was manipulated by adding or removing chicks, Dijkstra et al. (1990) demonstrated that local survival was decreased in kestrel parents that had raised experimentally enlarged broods, and increased in parents of reduced broods. Thus, kestrel males are physiologically able to increase their daily workload, but this imposes a cost in future survival. By means of a quantitative model, including data on seasonal variations in hunting yield and survival parameters for parents and offspring, we have concluded that kestrel parents maximize their total reproductive output by individually optimizing clutch size and timing of reproduction (Daan et al. 1990a). Different optima are adaptive to different territory qualities (hunting yield) and lead to the same parental workload.

Kenagy et al. (1990) were the first to report on mammalian parental energy expenditure in relation to number of offspring. In the Golden-mantled Ground Squirrel, DEE_{par} of lactating females significantly increased with natural litter size. However, the average increase was small (Figure 2): only 10% over the typical range of three to five young. Body mass and age of individual young at emergence from the natal burrow were independent of litter size, indicating that offspring biomass production was directly proportional to the number of young raised. Kenagy et al. (1990) suggested that the extra heat increment of digestion, induced by the extra food intake to produce the extra milk, accounts for the major part of the observed increase of DEE with increasing litter size, and that the overall efficiency (energy transferred to the offspring/energy expended by the parent) increased with increasing litter size. Thus it is clear that the association between DEE_{par} and offspring number is less pronounced than expected.

To seek a functional explanation for this phenomenon, litter size was experimentally enlarged and the impact on DEE_{par} and pup mass of free-living ground squirrels was measured (G.J. Kenagy, S.M. Sharbaugh and D. Masman, unpublished data). Six mothers were studied at the peak of lactation (days 31-35), as they provided milk for litters of six young that successfully emerged from their natal burrows several days later. DEE_{par} of these mothers was not elevated above that of the unmanipulated con-

trol mothers shown in Figure 2, and in fact the mean value was only 88% that of the controls. Furthermore, average pup mass in the litters of six young was reduced to 69% that of controls. Michener (1984) suggests that juvenile ground squirrels in general delay their entry into hibernation, compared to adults, because of the need to continue growing and to accumulate energy reserves. This process would be even more critical to young that emerge with below-average body mass, and their survival chances would thus be reduced. Although free-living Golden-mantled Ground Squirrels can raise one more young than their usual natural maximum, the mother does not increase her DEE_{par} , rather she produces smaller young.

In both kestrels and ground squirrels parental energy expenditure does not vary substantially with brood/litter size under natural circumstances. Neither is offspring mass at independence associated with the number of young in these case studies, indicating that parental efficiency (energy transferred to offspring/energy expended by parents) increases with increase in number of offspring. This, as such, may be a reflection of variation in parental quality, home range quality or both, as also suggested by Tatner (1990). It seems that the level of DEE_{par} is largely independent of actual offspring numbers and is presumably optimized in terms of life-time reproductive success. While this proposition needs confirmation in other species, we use it tentatively as a starting point for a functional understanding of DEE_{par} and its interspecific variation.

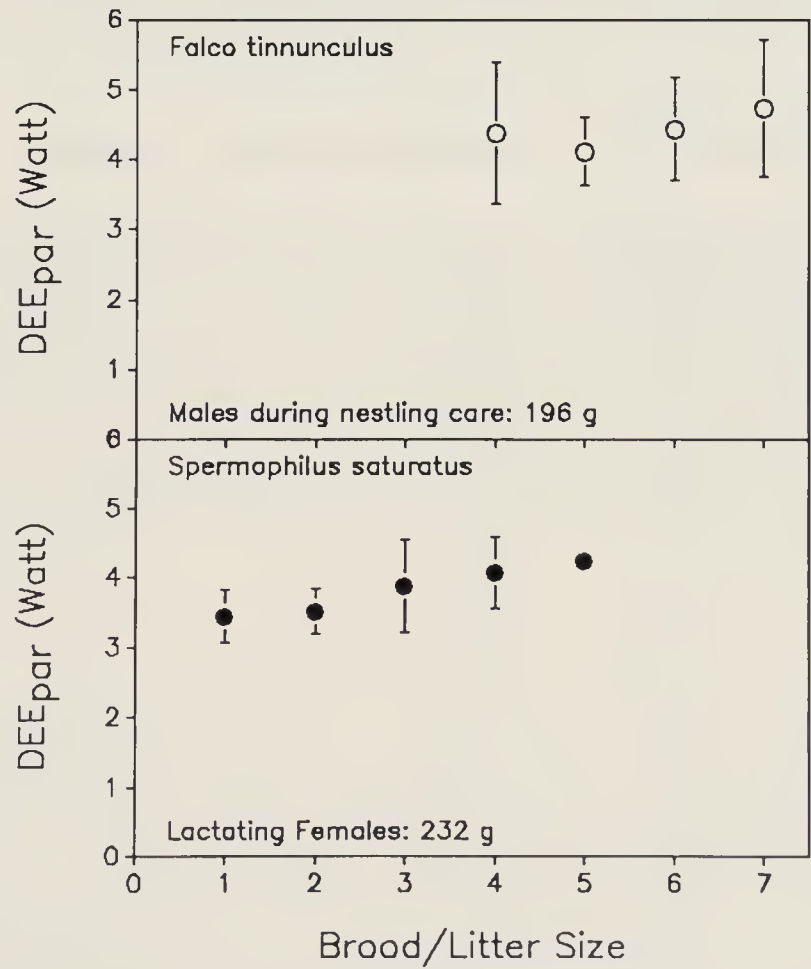


FIGURE 2 – Natural variation in DEE_{par} with brood/litter size in Kestrel (upper panel) and Ground squirrel (lower panel). See Masman et al. (1989) and Kenagy et al. (1990) for details. Vertical lines represent 1 SEM on both sides of the mean.

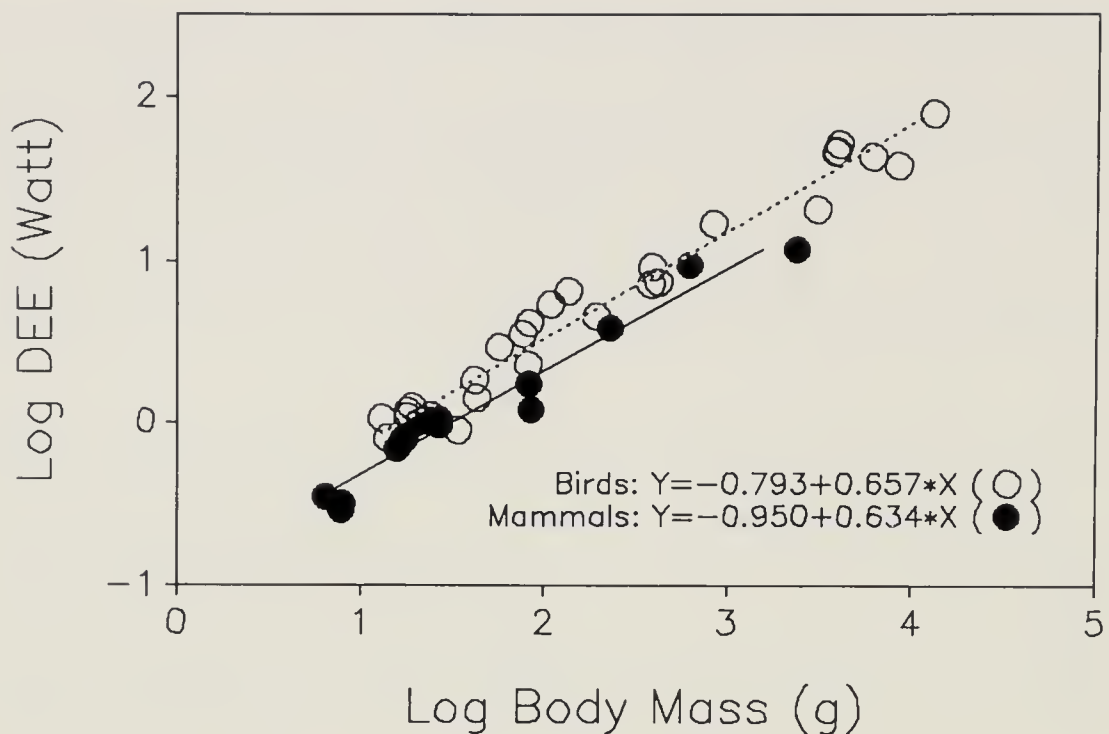


FIGURE 3 – Daily energy expenditure during avian and mammalian parental care (DEE_{par}). Altricial birds: 26 species from Daan et al. 1990 b; 2 species from Table 1. Lactating mammals: Table 1. For all 15 species represented, BMR data are available as well (see Figure 5).

INTERSPECIFIC VARIATION IN DEE_{par} and BMR

Estimates of natural daily energy expenditure during parental care (DEE_{par} , assessed by singly or doubly labeled water techniques, Nagy 1987) and basal metabolic rates (BMR) are currently available for 28 bird species and 15 mammalian species (Figure 3, Table 1). We restricted the data set to studies in which free-living DEE_{par} was estimated by means of the turnover of isotopes (Lifson & McClintock 1966, Nagy 1980, 1987). In Figure 3, DEE_{par} (Watt) is plotted as a function of body mass (g) on a double logarithmic scale. Birds and mammals show parallel allometric scaling:

$$\text{Birds: } \log DEE_{par} = -0.793 + 0.657 \log \text{mass} \quad (1)$$

$$\text{Mammals: } \log DEE_{par} = -0.950 + 0.634 \log \text{mass} \quad (2)$$

where $n = 28$ and $r^2 = 0.966$ in Eq. (1) and $n = 15$ and $r^2 = 0.955$ in Eq. (2). Entering the taxon (birds, mammals) as a factor in multiple regression of the whole data set significantly increased the explained variance ($P < 0.0001$), while the interaction factor (taxon * log mass) did not ($P > 0.05$). Hence the two regressions differ significantly in level, not in slope. For a 100 g animal DEE_{par} is estimated as 3.32 Watt using Eq. (1), and as 2.08 Watt using Eq. (2). This indicates that, on average, mammalian energy expenditure during lactation is about 37% below the expected level for birds of the same body mass rearing chicks.

For both birds and mammals a large data set exists for BMR measurements (Figure 4). For birds, Gavrilov and Dol'nik (1985) presented the most complete data set (BMR in Watt, mass in g) to date, yielding the regression:

Birds: $\text{Log BMR} = -1.407 + 0.677 \text{ Log mass}$ (3)

where $n = 263$ (Daan et al. 1990b). For eutherian mammals, Hayssen and Lacy (1985) published the most complete data set, from which we obtained the regression:

Mammals: $\text{Log BMR} = -1.606 + 0.696 \text{ Log mass}$ (4)

where $n = 248$. Entering the taxon as a factor in multiple regression of the whole data set significantly increased the explained variance ($P < 0.0001$), while the interaction factor (taxon * log mass) did not ($P > 0.05$). Hence the two regressions differ significantly in level, not in slope. For a 100 g animal BMR is estimated as 0.89 Watt using Eq. (3), and as 0.61 Watt using Eq. (4). This indicates that, on average, mammalian BMR is about 32 % below the expected level for birds of the same body mass. Thus, the concept that among avian species BMR is associated with DEE during parental care (Daan et al. 1990b) appears to hold also in the inter-class comparison between endotherms. The lower mammalian DEE during parental care is associated with a similarly lower BMR compared to that of birds.

TABLE 1 – DEE_{par} (Watt) and BMR (Watt) in birds and mammals of different body mass (g) as presented in Figure 3. Data for 26 bird species were presented by Daan et al. 1990 b. Here we present data approximations for 15 mammal species and 2 additional bird species. Body mass values for the BMR (Mass^a) and DEE_{par} (Mass^b) measurements were taken from the original references.

Species	Mass ^a	BMR	Mass ^b	DEE _{par}
Mammals				
1. <i>Pipistrellus pipistrellus</i>	6.5	0.090	6.5	0.353
2. <i>Myotis lucifugus</i>	7.4	0.066	7.9	0.294
3. <i>Plecotus auritus</i>	8.0	0.1	8.0	0.324
4. <i>Peromyscus maniculatus</i>	14.1	0.215	17.6	0.807
5. <i>Eptesicus fuscus</i>	16.9	0.113	17.4	0.786
6. <i>Microtus arvalis</i>	20.0	0.318	27.0	1.042
7. <i>Perognathus formosus</i>	20.5	0.258	20.5	0.995
8. <i>Clethrionomys glareolus</i>	23.4	0.352	25.0	1.019
9. <i>Microtus agrestis</i>	27.2	0.312	27.2	0.961
10. <i>Clethrionomys rutilus</i>	28.0	0.428	15.9	0.697
11. <i>Arvicola terrestris</i>	63.0	0.804	82.8	1.740
12. <i>Ammospermophilus leucurus</i>	95.7	0.522	85.5	1.204
13. <i>Spermophilus saturatus</i>	232.0	1.194	232.0	3.889
14. <i>Spermophilus parryi</i>	630.0	3.044	630.0	9.456
15. <i>Marmota flaviventris</i>	2400.0	5.716	2400.0	11.771
Birds				
16. <i>Cinclus cinclus</i>	56.9	0.765	56.9	2.890
17. <i>Melanerpes formicivorus</i>	82.0	0.828	82.0	2.260

References: 1. and 3. BMR: J.R.Speakman, unpublished data, DEE: Racey & Speakman 1987; 2. Kurta et al. 1989; 4. BMR: Hayssen & Lacy 1985, DEE: Hayes 1989; 5. BMR: Hayssen & Lacy 1985, DEE: A.Kurta, in press; 6.,8. and 9. P.Meerlo & D.Masman, unpublished data.; 7. BMR: Hayssen & Lacy 1985, DEE: Mullen & Chew 1973; 10. Holleman et al. 1982.; 11. Grenot et al. 1984; 12. BMR: Hayssen & Lacy 1985, DEE: Karasov 1981.; 13. Kenagy et al. 1990; 14. G.J.Kenagy, B.M.Barnes, M.C.Reed & D.Masman, unpublished data; 15. Melcher et al. 1989; 16. BMR: D.M.Bryant & P.Tatner, in press, DEE: Bryant & Tatner 1988.; 17. Weathers et al. 1990.

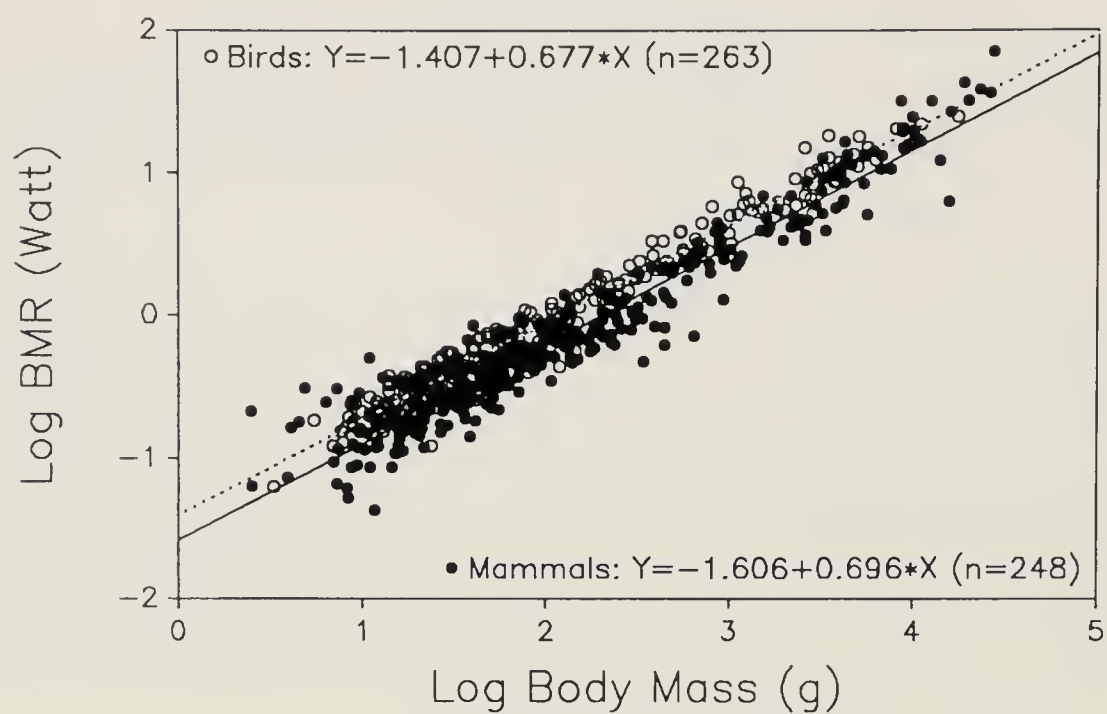


FIGURE 4 – Allometric relationship between basal metabolic rate (BMR) and body mass in 263 bird species (Gavrilov & Dol’nik 1985) and 248 mammalian species (Hayssen & Lacy 1985).

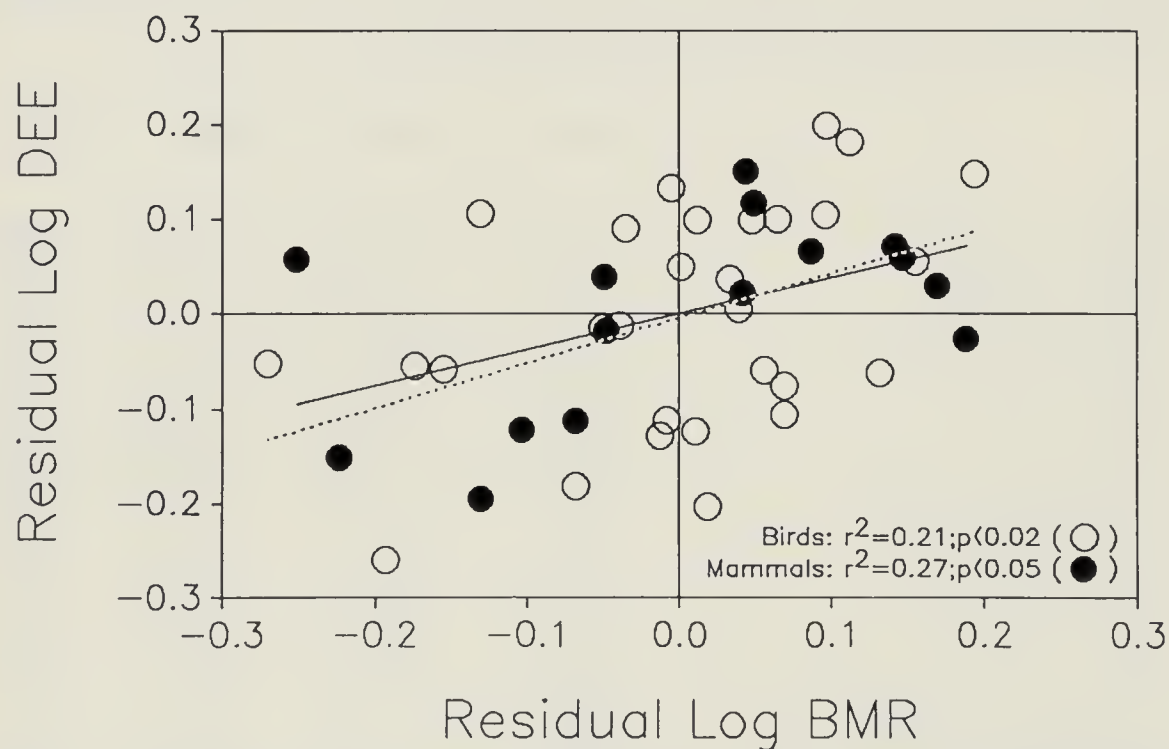


FIGURE 5 – Association between the deviation from allometrically predicted DEE_{par} (Residual Log DEE_{par}) and the deviation from allometrically predicted BMR (Residual Log BMR) for 28 bird species and 15 mammalian species (see Figure 3, Table 1).

We further analysed the mass-independent association of DEE_{par} and BMR among mammals (Figure 5). For this we regressed the deviation from the allometrically predicted species-specific level of DEE_{par} (residual Log DEE_{par} , based on regressions (1) and (2) in Figure 3) against the deviation from the allometrically predicted species-specific level of BMR (residual Log BMR, based solely on data for the species presented in Figure 3 and Table 1). For both birds and mammals these residuals are

significantly positively correlated with each other (birds: $r^2 = 0.21$; $n = 28$; $P < 0.02$; mammals: $r^2 = 0.27$; $n = 15$; $P < 0.05$). This means that within both classes, a species with a high DEE_{par} for its body mass is also characterized by a relatively high BMR and vice versa (Figure 5).

Daan et al. (1990b) suggested that the functional relationship of the observed association of avian DEE_{par} and BMR was due to an association between the relative size of metabolically highly active tissues (such as heart and kidney) with the level of DEE_{par} , reflected in the species-specific BMR. The available data to test this hypothesis for mammals are still scanty. Recent experiments in progress show that within the vole species *Microtus agrestis*, individuals with a high BMR for their body mass are characterized by proportionately larger liver, heart and kidneys (Meerlo & Masman, in prep). This is consistent with the hypothesis. On the assumption that variations in the level of BMR generally reflect variations in the lean dry mass of these tissues, we may expect a uniform allometric relationship between BMR and organ mass in a data set for mammals and birds. We have so far collected data for only five mammalian species that can be compared to the available 22 avian species (Daan et al. 1990b, Table 1). The BMR data are plotted against body mass and against lean dry heart and kidney mass in Figure 6. The variance remaining unexplained by body mass ($1-r^2 = 0.044$) considerably exceeds the variance remaining unexplained by heart + kidney mass ($1-r^2 = 0.026$). In multiple regression of log BMR on log body mass, including taxon as a factor significantly increased the explained variance ($P < 0.01$). In contrast, in multiple regression on log H + K, including taxon as a factor, did not increase the explained variance ($P > 0.1$). We take this to indicate that, unlike body mass, heart and kidney lean dry mass quantitatively predict BMR independently of taxonomic class.

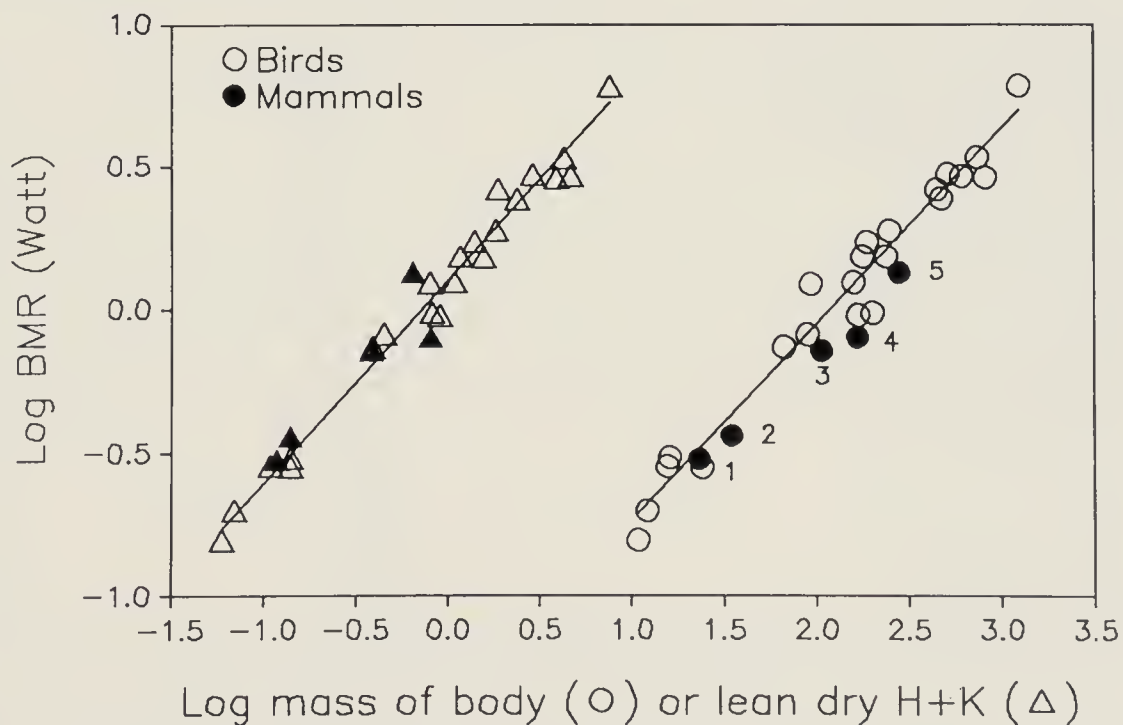


FIGURE 6 – Allometric relationship between BMR, body mass and dry lean heart and kidney mass, in a combined data set for mammals (closed symbols; unpublished data) and birds (open symbols; Daan et al. 1990b, Table 1). Circles: Log BMR as a function of Log body mass. Triangles: Log BMR as a function of Log dry lean heart and kidney mass. Mammal species: 1. *Microtus agrestis*, 2. *Microtus arvalis*, 3. *Eutamias sibiricus*, 4. *Tupaia belangeri*, 5. *Spermophilus citellus*.

BIRDS AND MAMMALS COMPARED

DEE_{par} of birds is higher than that of mammals (Figure 3); likewise avian BMR is higher (Figure 4). Daan et al. (1990b) suggested that birds with a relatively high DEE_{par} are characterized by a relatively high BMR (Figure 5). The analyses presented here suggest that this concept holds in both birds and mammals. Moreover, if we test the hypothesis among mammals, we continue to find that species with a relatively high DEE_{par} are characterized by a relatively high BMR (Figure 5).

The data for mammalian organ size and BMR further lend support for the idea we developed for birds, that the size of the metabolic machinery (reflected in heart and kidney mass) has been adjusted to a species' maximal or parental natural energy turnover and is reflected in its BMR. This implies that the size of heart and kidneys as such may be a better predictor for BMR than whole animal body mass. This hypothesis is supported by the homomorphic allometric relationship between BMR and dry lean mass of heart and kidney (Figure 6), where we found no indication of a fundamental difference between mammals and birds.

The functional question then is: why do birds have higher natural levels of energy turnover than mammals of the same size ? We propose two concepts.

TABLE 2 – Daily metabolizable energy intake (DME_{par}, Watt) of lactating mammals of different body mass (g). Data were collected under laboratory and free-living conditions, as presented in Figure 7.

Species	Mass	DME
Laboratory data:		
1. <i>Clethrionomys glareolus</i>	22.5	1.290
2. <i>Peromyscus maniculatus</i>	24.7	1.216
3. <i>Peromyscus leucopus</i>	25.6	1.133
4. <i>Microtus arvalis</i>	26.5	1.029
5. <i>Mus musculus</i>	26.6	2.099
6. <i>Clethrionomys gapperi</i>	26.8	1.576
7. <i>Microtus pennsylvanicus</i>	29.4	1.726
8. <i>Phodopus sungorus</i>	37.0	1.018
9. <i>Sigmodon hispidus</i>	136.3	2.317
10. <i>Oryctolagus cuniculus</i>	4390	49.31
11. <i>Erethizon dorsatum</i>	5767	23.2
12. <i>Callorhinus ursinus</i>	37000	574
13. <i>Odocoileus hemionus</i>	49750	312
14. <i>Sus scrofa dom.</i>	205000	794
15. <i>Bos taurus dom.</i>	550000	1661
Field data:		
16. <i>Myotis lucifugus</i>	7.9	0.478
17. <i>Spermophilus saturatus</i>	232	6.921
18. <i>Marmota flaviventris</i>	2400	38.00

References: 1.,4.,9. Mattingly & McClure, 1982; 2. Millar, 1979; 3. Millar, 1978; Mattingly & McClure 1982; 5. Konig, 1989; Studier, 1979.; 6.,7. Innes & Millar, 1980; 8. Weiner, 1987; 10. Partridge et al. 1986; 11. Farrel & Christian, 1987; 12. Anderson & Fedak, 1987; 13. Sadleir, 1980, 1982; 14.,15. Kirkwood, 1983; 16. Kurta el al. 1989; 17. Kenagy et al. 1990; 18. Melcher et al. 1989

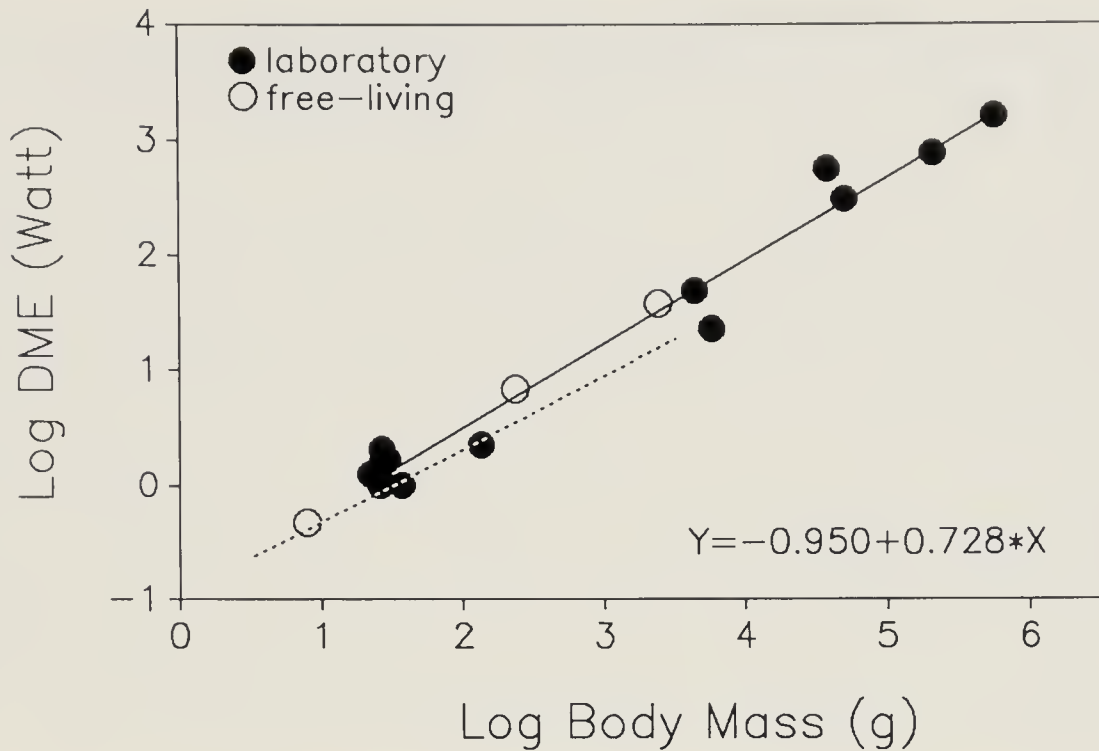


FIGURE 7 – Allometric relation between daily metabolizable energy intake (DME) and body mass in lactating mammals in the laboratory (closed symbols and solid line). Data for free-living lactating females are indicated as open symbols (Table 2). Dashed line: mammalian DEE_{par} during lactation (Equation 2).

First, the pathways of energy transfer from parent to offspring differ (Figure 1). We have no reason to suspect that natural selection has been basically different in setting the optimal rates of energy intake of equal sized mammals and birds during reproduction (Kirkwood 1983, Weiner 1989, Daan et al. 1990b). However, mammals channel a considerable part of this daily metabolizable energy intake (DME_{par}) into milk (Ofstedal 1984). In free-living mammals the peak exported milk on a daily basis has been reported to account for 69 % of DME_{par} in *Marmota flaviventris* (Melcher et al. 1989), 40 % in *Spermophilus saturatus* (Kenagy et al. 1990), and 32 % in *Myotis lucifugus* (Kurta et al. 1989). Thus, in mammals maximal DEE_{par} may well be reduced below sustainable maximum rates of DME, while in birds DEE_{par} may equal DME to maintain energy balance. We evaluated this hypothesis further by assembling the allometric relationship between DME_{par} (Watt) during lactation and body mass (g) in 15 mammals studied in the laboratory (Table 2; Figure 7, closed symbols):

$$\text{Log } DME_{par} = -0.950 + 0.728 \text{ Log mass} \quad (5)$$

where $n = 15$ and $r^2 = 0.98$. The three species studied in the field (Table 2; Figure 7, open symbols) closely follow this allometric relationship, suggesting that the level of daily energy intake during lactation in the laboratory may not be distinguishable from the level under free-living conditions. A comparison of Eq. (5) and Eq. (2) (Figure 7) indicates that DME_{par} of mammals normally exceeds DEE_{par} . In birds, which are normally not gaining mass and thus not in positive energy balance during the rearing stage of reproduction, DME_{par} probably never exceeds DEE_{par} . With the same energy intake, female mammals during lactation thus have a lower DEE_{par} than birds during parental care. This is therefore probably supported by a smaller metabolic machinery, reflected in a lower BMR.

A second and more general hypothesis can also be proposed. By the basic adaptation of birds for flight, natural selection has exerted a stronger selective pressure against added mass in birds than in mammals. Mammals for instance carry not only milk for the offspring, they also generally have more fat deposits than birds, a bladder containing urine, and a litter growing in utero instead of eggs in a nest. One might thus look at the general comparison of mammals and birds from a wholly different perspective: For a bird or mammal with the same rate of energy expenditure in the field, the same size heart and kidney to support this rate, and hence the same BMR, the bird should be usually more economical in the other, less metabolically active, tissues it carries. Hence the bird in this comparison should have a smaller total body mass than the mammal. In fact a bird with an energy turnover of 1 Watt has a mass of 59% that of the mammal on the basis of equations (3) and (4) for BMR (or 51% on the basis of equations (1) and (2) for DEE_{par}). In allometric analysis, body mass is usually taken to be the independent, and therefore determining, variable. Organ size analysis suggests that heart and kidney are much better predictors of energy turnover than the whole body. It might well be illuminating to rephrase functional questions concerning energetics, by not asking why do two species of the same size differ in energy turnover, but why do two species with the same DEE differ in body mass?

ACKNOWLEDGEMENTS

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SEASONAL AND GEOGRAPHICAL CORRELATES OF STANDARD METABOLIC RATES IN AUSTRALIAN ACANTHIZIDS

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ABSTRACT. Some species of small Australian scrubwrens and thornbills (Acanthizidae) inhabit a broad range of environments from hot, dry deserts and alpine forests to subtropical rainforests. Their sedentary habits allow physiologists to study the metabolic responses of small passerines (less than 15 g) to extremes of environmental conditions. Seasonal changes in climatic conditions in rainforests are predictable and insectivorous food is abundant throughout the year; here, acanthizids exhibit little seasonal variation in SMR. Some acanthizids in alpine environments raise their SMRs in winter to increase body heat, whereas others have much lowered SMRs and may become torpid for a few days in periods of inclement weather and/or acute food shortage. All alpine species increase body insulation during winter by growing more feather down and/or depositing subcutaneous fat in the neck and abdomen. Arid-zone acanthizids have much reduced SMRs in the summer and during the hottest parts of the day. Banding studies suggest that desert acanthizids live for 2-3 yrs, whereas those in sub-alpine and alpine environments survive for up to 14-15 yrs.

CONSTRAINTS ON ENERGY EXPENDITURE BY BIRDS

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ABSTRACT. Evidence of a ceiling or constraint on energy expenditure by small birds was sought. Data on energy expenditure by 553 free-living individuals were obtained using the doubly labelled water technique. At least 16% and perhaps up to 30% of individuals, and up to 48% of the 28 species examined had daily energy expenditures which exceeded a proposed maximum sustained energy expenditure of 4 times BMR. In the House Martin *Delichon urbica*, individuals which died had a significantly higher energy expenditure than those which survived. Lifetime reproductive success was greatest for an intermediate (optimal) energy expenditure during breeding. These data suggest mortality risks increase progressively with the energy allocated to breeding.

Keywords: Double labelled water, energy expenditure, breeding, *Delichon urbica*, lifetime reproductive success.

INTRODUCTION

We are increasingly aware of factors which have a direct effect on daily energy expenditure by free-living birds. This comes both from extrapolation of metabolic responses observed in the laboratory (Brody 1945, Mugaas & King 1981), and the application of techniques which allow energy expenditure to be measured directly under natural conditions (Bryant 1989, Bridges & Butler 1989). The functional significance of variation in energy expenditure, nevertheless, remains unclear.

An increased energy expenditure is often associated with short-term benefits. For example, provisioning of offspring, escape from predators, seeking food or moving to avoid adversity are, in different ways, likely to increase energy expenditure and at the same time enhance reproductive success or survival. Even so, unconstrained energy expenditure is clearly not the rule, because energy expenditure measured over periods of days is invariably below the theoretical maximum (Utter 1971, Drent & Daan 1980, Peterson et al. 1990). This could arise from a shortage of time in which to make profitable use of energy-costly activities. Seasonal and latitudinal differences in daylength, for example, account for some of the variation in energy expenditure by free-living birds (Mugaas & King 1981, Bryant et al. 1984, Bryant & Tatner 1988a). Yet, time constraints of this type do not alone appear to limit energy expenditures, because experimental manipulations of activity can induce greater expenditures than are normally observed, even when costs are already high, such as during breeding (Hails & Bryant 1979, Dijkstra et al. 1990). An alternative explanation is that energy expenditure may be constrained physiologically, due to processes operating at the cell, tissue, organ or individual level. Such physiological constraints could reflect one or more limiting factors, such as digestive capacities (Kirkwood 1983, Diamond et al. 1986), or trade-offs between factors which can have positive or negative effects on both energy expenditure and fitness (Williams 1966, Sibly & Calow 1988). If sustained energy expenditure is indeed limited by physiological constraints in these ways, two

outcomes are likely. Firstly, energy expenditure in the field may reach a ceiling. Secondly, when rates of energy expenditure approach such a ceiling, or a related threshold, a fitness cost may be incurred, such as reduced survival or subsequent fecundity.

Several studies have presented evidence for a ceiling in avian energy expenditure, ranging up to seven times the basal metabolic rate (Utter 1971, Drent & Daan 1980, Weathers & Sullivan 1989, Peterson et al. 1990), but none has found direct evidence of a fitness cost associated with high energy expenditures. Amongst insects, however, high rates of energy expenditure have been shown to reduce lifespan (Schmid-Hempel & Wolf 1988). Also, experimental diet studies with rodents show high energy intakes, which over a long period must correspond to high energy expenditures, lead to shorter lives (Holehan & Merry 1986). The mechanisms underlying these experiments appear quite different but allow that the expenditure of energy itself may have adverse effects on survival. Even so, the evidence is often tenuous: that from Honey Bees *Apis mellifera*, implies that only energy expenditures above normal shorten lifespans (Wolf & Schmid-Hempel 1989).

This paper examines data from studies of small wild birds for evidence of an upper limit or constraint on rates of energy expenditure. To do this three specific hypotheses are examined:

- I. Expenditure of energy is constrained by the assimilative capacity of the gut (Kirkwood 1983).
- II. There is a maximum sustainable work rate, of perhaps about four times the basal metabolic rate (Priede 1977, Drent & Daan 1980).
- III. High rates of energy expenditure reduce the chance of subsequent survival and hence affect lifetime reproductive success (Williams 1966, King 1974).

METHODS

Data on energy expenditure by small birds (10-150g) were available for 28 species. The sample was drawn from different environments and from species with contrasting habits. All estimates of energy expenditure for free-living birds were made with the doubly labelled water technique (Lifson & McClintock 1966, Nagy 1980, Tatner & Bryant 1989). Further details of the methods used in each study can be found in the original reports which are listed by Bryant & Tatner (1991).

To compare ADMR (average daily metabolic rate) and DEE (daily energy expenditure) with hypothetical metabolic constraints the following approaches were used. Maximum metabolizable energy intake (ME max) was calculated from Kirkwood (1983), where $ME_{max} = 1713 \text{ kJ/kg}^{0.72}$. Basal metabolic rate (BMR) is defined as occurring while an individual is confined within a darkened metabolism chamber in a quiescent, post-absorptive state, and in the thermoneutral zone. As given, this is not a fixed property of an individual or species, however, and may vary according to the plane of nutrition, acclimatization, body composition and other factors. Nevertheless it has proved useful for comparative studies. Alternatively, an estimate of BMR may be calculated from allometric equations, such as those of Aschoff & Pohl (1970), although this does not allow for possible interspecific differences unrelated to mass (Bennett & Harvey 1988). More satisfactorily, in some respects, it may be measured for the same species being

studied in the field. These data, however, are sometimes unreliable due to non-standard conditions. An ideal may be that free-living energy expenditure of individuals is compared with their own basal metabolic rate but this will usually be impractical in field studies and no relevant data were available for this study. In this analysis, free-living energy expenditure was compared with estimates of basal metabolism which were derived from allometric equations, from published studies of the same species and where basal metabolism was measured as part of a study.

RESULTS

Data on ADMR ($\text{cm}^3 \text{CO}_2 \text{g}^{-1} \text{h}^{-1}$) and DEE (kJ d^{-1}) were obtained for 553 individuals from 29 studies covering 28 species (Bryant & Tatner 1991). The full data set was used to examine hypotheses I and II. Data on House Martins *Delichon urbica* alone were suitable for evaluating hypothesis III.

Maximum metabolizable energy: hypothesis I

Kirkwood's (1983) equation (Table 1) was used to estimate the theoretical maximum daily energy assimilation (MEMax) for all individuals in the sample. Daily energy expenditure exceeded MEMax in 28% of individuals and 50% of species. The former were concentrated within 5 species, where over 50% of DEE estimates were greater than MEMax. These were Ringed Plover *Charadrius dubius*, Tree Swallow *Tachycineta bicolor*, Sand Martin *Riparia riparia*, Barn Swallow *Hirundo rustica* and Blue Tit *Parus caeruleus*. In House Martins, Dippers *Cinclus cinclus* and Savannah Sparrows *Passerculus sandwichensis* over 25% of individuals exceeded MEMax. While biased towards aerial feeding species (4/8), a wide range of foraging habits was nevertheless represented. Overall, 14 species (50%) showed cases of DEE greater than MEMax. Clearly, DEE rather commonly exceeds MEMax as predicted by Kirkwood's equation.

No species in Kirkwood's (1983) sample had an intake in excess of $2200 \text{ kJ/kg}^{0.72}$ (called MEMx). He considered this figure approached an absolute ceiling to ME in birds (and mammals), but it was derived from a single species and therefore lacked the more substantial empirical support available for calculating MEMax. In the sample of birds examined here, 7.4% of individuals exceeded MEMx (Table 1). Only Tree Swallows and Sand Martins, respectively, had more than 50% and 25% of individuals above this threshold. Overall, 10 species (36%) had cases of DEE greater than MEMx. Even under the more demanding criterion of this extreme value, therefore, a substantial proportion of small bird species had a daily energy expenditure which exceeded that predicted from Kirkwood's equations (1983).

Multiples of basal metabolism: hypothesis II

Basal metabolic rates were calculated for all species using Aschoff & Pohl's (1970) equation for the (night-time) resting phase of passerines and non-passerines (called BMR_{AP}). In ten of the studies considered, BMR was measured by the investigators (called BMR_{M}) in conjunction with their studies of energy expenditure in the wild. Published data on basal metabolic rate (called BMR_{p}) were available for 19 of the 28 species examined which, together with data from the same studies, meant that species- or taxon-specific BMR data were available for all but three species (Pied Kingfisher, Mockingbird *Mimus polyglottos*, and Purple Martin *Progne subis*).

TABLE 1 – Energy expenditure of free-living birds in relation to the maximum metabolizable energy intake, calculated from 1) Kirkwood (1983) (MEmax)^a and 2) estimated from an extreme value (MEmx)^b. See Table 2 for sources.

Species		> MEmax	> MEmx	n
Desert Quail	<i>Coturnix gambellii</i>	0	0	6
Ringed Plover	<i>Charadrius dubius</i>	4	1	5
Common Sandpiper	<i>Tringa actitis</i>	0	0	5
Pied Kingfisher	<i>Ceryle rudis</i>	0	0	32
Blue-throated Bee-eater	<i>Merops viridis</i>	0	0	27
Tree Swallow	<i>Tachycineta bicolor</i>	34	19	34
Purple Martin	<i>Progne subis</i>	1	0	4
Sand Martin	<i>Riparia riparia</i>	12	5	15
Barn Swallow	<i>Hirundo rustica</i>	10	3	16
Pacific Swallow	<i>Hirundo tahitica</i>	3	2	14
House Martin	<i>Delichon urbica</i>	19	2	87
Phainopepla	<i>Phainopepla nitens</i>	0	0	1
Dipper	<i>Cinclus cinclus</i>	28	8	77
Mockingbird	<i>Mimus polyglottos</i>	0	0	6
Dunnock	<i>Prunella modularis</i>	0	0	4
Blackbird	<i>Turdus merula</i>	0	0	1
Wheatear(1)	<i>Oenanthe oenanthe</i>	3	0	24
Wheatear(2)	<i>Oenanthe oenanthe</i>	0	0	19
Robin	<i>Erithacus rubecula</i>	4	1	42
Pied Flycatcher	<i>Ficedula hypoleuca</i>	0	0	1
Spotted Flycatcher	<i>Muscicapa striata</i>	0	0	1
Great Tit	<i>Parus major</i>	1	1	18
Blue Tit	<i>Parus caeruleus</i>	4	0	4
Willow Tit	<i>Parus montanus</i>	0	0	9
Crested Tit	<i>Parus cristatus</i>	0	0	7
Coal Tit	<i>Parus ater</i>	0	0	6
Savannah Sparrow	<i>Passerculus sandwichensis</i>	21	1	56
Bullfinch	<i>Pyrrhula pyrrhula</i>	0	0	4
Starling	<i>Sturnus vulgaris</i>	2	0	26
Total		156	41	553
%		28.2	7.4	100

^a MEmax = 1713 kJ/kg^{0.72}; ^b MEmx = 2200 kJ/kg^{0.72} (see text for explanation).

Energy expenditure of free-living birds (expressed as a multiple of BMR_{AP}, and termed M_{AP}) across all available stages of the annual cycle, ranged from 1+ to a maximum of 6+, with the modal category at 3+ times M_{AP} (Figure 1). Inevitably, the frequency distribution reflects both the selection of species and differences in sample sizes between studies (Table 2). Across all studies, 23% (n=128) of measurements exceeded 4 M_{AP} (Table 2). Values of M derived using the ‘best available’ BMR (called M_{ALL} and involving estimates taken in the order; first BMR_M, then BMR_P and finally BMR_{AP}), gave the following results. M_{ALL} ranged from 1+ up to 7+, (modal category = 2+), with 21% (B=115) of measurements exceeding 4 M_{ALL}. If only results for which corresponding BMR_M data were available are considered (n=303) the range remains as 1+ to 7+, with the mode at 2+ and 16% of M_M values exceeding 4.

TABLE 2 – Energy expenditure of free-living birds expressed as multiples of BMR calculated after Aschoff & Pohl (1970). All stages of the annual cycle are included.

Species	M (Multiple of BMR) ^b						Stages ^a involved	Sources ^c
	1+	2+	3+	4+	5+	6+		
Desert Quail	6						6	Goldstein & Nagy 1986
Ringed Plover		1	0	0	3	1	5	P R Evans et al.
Common Sandpiper		1	2	2			5	Bryant & Tatner 1991
Pied Kingfisher			10	19	3		32	Reyer & Westerterp 1985
Blue-throated Bee-eater		13	10	3	1		27	Bryant et al. 1984, Bryant & Tatner 1991
Tree Swallow			3	17	10	4	34	Williams 1988
Purple Martin		2	2				4	Utter 1971
Sand Martin			7	5	3		15	Westerterp & Bryant 1984
Barn Swallow		2	5	8	1		16	Westerterp & Bryant 1984
Pacific Swallow	3	7	2	1	1		14	Bryant et al. 1984, Bryant & Tatner 1991
House Martin	1	32	39	15			87	Bryant & Westerterp, 1983
Phainopepla			1				1	Weathers & Nagy 1989
Dipper		20	36	18	3		77	Bryant & Tatner 1988
Mockingbird	1	4	1				6	Utter 1971
Dunnoek		4					4	Bryant & Tatner 1991
Blackbird		1					1	Bryant & Tatner 1991
Wheatear(1)	2	11	10	1			24	Tatner 1990
Wheatear(2)			3				19	Moreno 1989
Robin	7	24	8	3			42	R Prys-Jones, Bryant & Tatner 1991
Pied Flycatcher			1				1	Bryant & Tatner 1991
Spotted Flycatcher		1					1	Bryant & Tatner 1991
Great Tit	1	9	7	1			18	R Prys-Jones, K Westerterp, Bryant & Tatner 1991
Blue Tit		2	4				6	R Prys-Jones, Bryant & Tatner 1991
Willow Tit	1	8					9	Moreno et al. 1988
Crested Tit	1	6					7	Moreno et al. 1988
Coal Tit		5	1				6	Moreno et al. 1988
Savannah Sparrow		11	40	5			56	Williams & Hansell 1981, Williams 1987
Bullfinch		4					4	P Greig-Smith, Bryant & Tatner 1991
Starling		14	12				26	Westerterp & Drent 1985
Totals	23	198	204	98	25	5	553	

^a N - non-breeding, I - incubation, R - rearing young, M - moulting. ^b All energy expenditures were calculated assuming $RQ=0.75$ and $1\text{ cm}^3\text{ CO}_2 = 26.44\text{ J}$ (Brody 1945). For passerines $BMR\text{ (kJd}^{-1}\text{)} = 0.1326\text{ W}^{0.726}$, non-passerines $= 15.026\text{ W}^{0.734}$, where W = mass in g (Aschoff & Pohl 1970). ^c Unpublished sources are listed without dates.

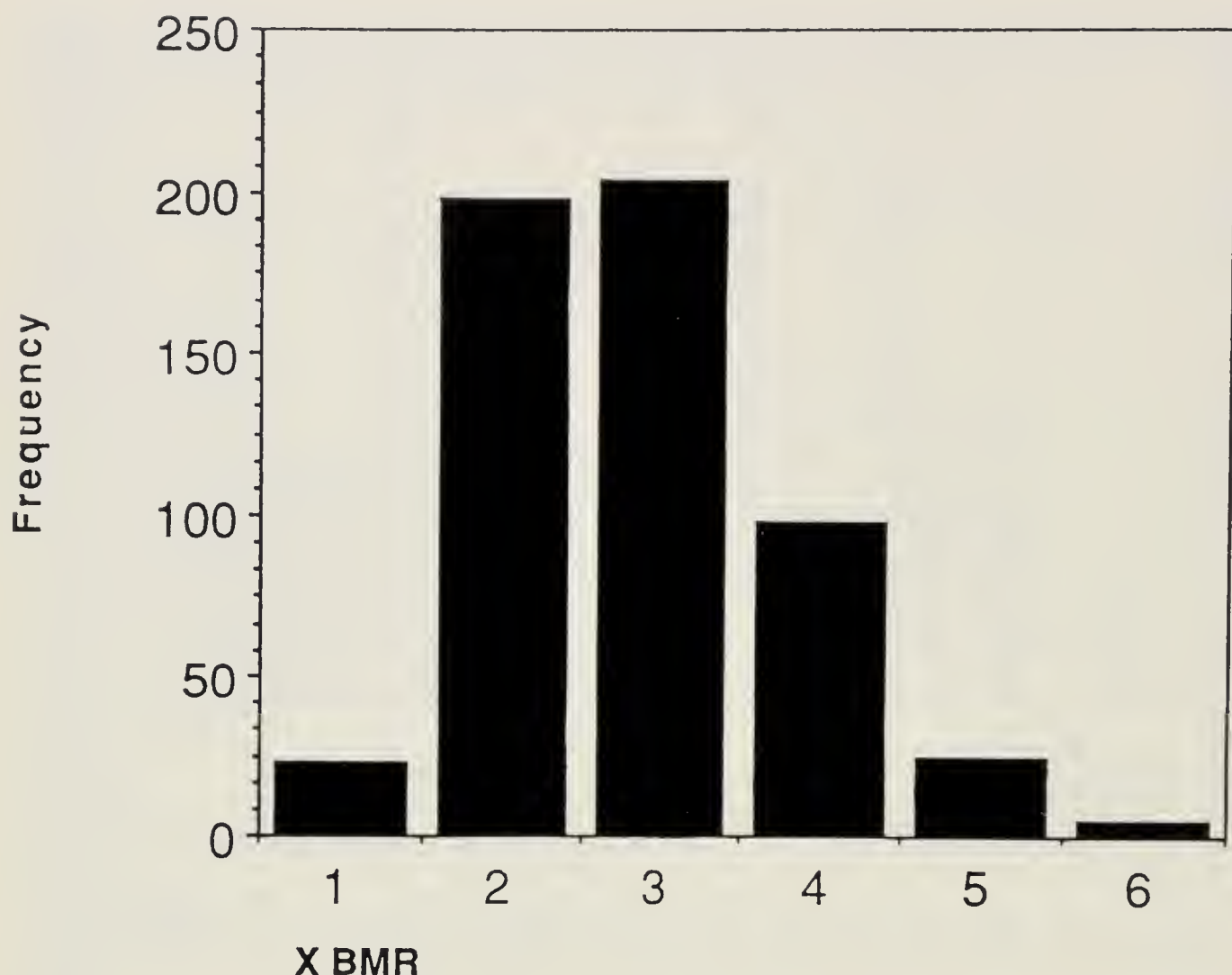


FIGURE 1 – Frequency distribution of energy expenditure expressed as multiples of BMR in a range of small bird species. The data are from 553 individuals of 28 species (see Table 2 for details).

Energy expenditure is generally at its highest during nestling rearing (Bryant & Tatner 1988b). It is therefore at this stage that any given threshold value of M is most likely to be exceeded. Data for parents rearing young were available for 323 individuals of 19 species (this excludes a single Common Sandpiper *Tringa actitis* with brood); M_{ALL} ranged from 1+ to 7+ with the mode at 3+. In 30% of cases ($n=98$), M_{ALL} exceeded 4. There was no correlation between sample sizes for each species and the frequency of energy expenditures above 4 times BMR, so further work with this sample is unlikely to alter the observed patterns substantially. Amongst those species for which BMR_M data were available, the mode stayed at 3+ and 24% exceeded $4M_M$. It is clear that energy expenditure by free-living birds, especially during breeding, commonly exceeds 4 M and that metabolic intensities of this order are not just a consequence of using unduly low or otherwise inappropriate estimates of BMR.

The species for which values of M_M , M_{ALL} or M_{AP} often exceeded 4 have in common their generally high cost method of feeding. For example all species with M -values of 5+ or more and raising young were either aerial-feeding species (swallows, bee-eater) or used an energy-expensive feeding method (Dipper, Bryant & Tatner 1988a; Pied Kingfisher, Reyer & Westerterp 1985). Therefore, the observation that small birds commonly exceed 4 M_M , should be qualified by stating that this pattern seems likely

to be relatively more frequent amongst species with habits which induce high levels of energy expenditure.

Within the samples considered, at least 16%, and perhaps up to 30% of individuals, and between 41% (M_{ALL}) and 48% (M_{AP}) of species, worked at levels which exceeded 4 times BMR. Only for one species (see below) were data available on survival of birds working at different rates. For most species, therefore, any fitness consequences of exceeding 4 times BMR or other thresholds cannot be evaluated directly.

Reproductive success, survival and energy expenditure: hypothesis III

Energy expenditure by breeding House Martins was measured using the DLW technique at a colony of around 20 pairs in central Scotland (Bryant & Westerterp 1983). Measurements were made over three seasons, so the results do not reflect conditions peculiar to any single year. Individual birds were monitored for 24 h while they raised broods aged 15 ± 2 d. The majority of nests contained four young (22 of 38), either naturally or as a result of manipulations involving transfer of young of the same age from or to other broods. Energy expenditure was not related to brood size in either an earlier analysis (Bryant 1989) or the present sample ($r_s = 0.01$, $n = 38$, NS). Nor was there an effect related to the manipulation treatment groups (young added, young removed, controls) on energy expenditure (ANOVA, $F = 0.19$, $P = 0.32$). Estimates of energy expenditure were therefore included in the present analysis irrespective of brood size and treatment group. Each bird was measured (mass, maximum chord, keel length) and throughout the study observations were made on many aspects of behaviour, prevailing weather and food supply (Table 3). The positive relationship observed between ADMR (average daily metabolic rate) and provisioning rate (energy value of food delivered per day) implied that a fitness benefit, in the form of additional or better nourished young, should arise from a greater energy expenditure during the rearing stage (Bryant 1989). Mortality was assumed if birds failed to appear at the study colony in the year following, nor were found in surveys at adjacent colonies. Previous work found no evidence of movements by established breeders between sites (Bryant 1979), so it is likely that all adults lost had indeed died.

House Martins which survived to the next breeding season differed in only one known respect from those which disappeared; they had a lower energy expenditure when rearing their young (Table 3). A number of factors which were correlated with energy expenditure in the full sample (Bryant & Westerterp 1983) did not differ significantly between survivors and others, nor were differences found for a range of additional factors (Table 3). It is concluded that a higher energy expenditure amongst breeding House Martins was associated with an increased subsequent mortality. The mechanism by which this mortality was induced remains unknown, but the result is consistent with models (Williams 1966, Calow 1979) which assume limited resources allocated to reproduction, in this case including energy used for gathering and transporting food to a centrally placed nest-site, are at the expense of somatic maintenance. The consequence of this was clearly not death in the short term, because all individuals measured with DLW survived until their broods had fledged. No losses to predators were recorded during the study, either within or outside the nest, so predation during breeding was not a significant cause of mortality. No information was available on parasites but were their presence to cause an increase in parental energy expenditure, then a positive association between parasite load and host energy expenditure would be feasible. Currently available evidence, however, points to an effect which

acts via a subtle impairment of body condition, which itself carries a survivorship penalty. This view takes some support from a discriminant analysis, using ADMR and % mass change as a measure of body condition change amongst breeding House Martins. The discriminant function correctly assigned 82% of House Martins to a 'live' and 'dead' categories (Bryant in prep). Alternative discriminant functions including ADMR and other measurements in a stepwise approach were all less successful. It appeared that martins which maintained a high energy expenditure were at the greatest risk of subsequent mortality, a risk exacerbated when they also lost body mass. More precise evaluation of body condition changes than is possible from mass data alone could further increase the accuracy of survival categorisation. These results suggest that reproductive costs incurred by House Martins are physiological in origin and are absorbed until the non-breeding period.

TABLE 3 – Comparison of energy expenditure and other factors in breeding House Martins between individuals which survived to the following year and those which died.

	Survived			Died			F	P
	Mean	± S.D.	n	Mean	± S.D.	n		
ADMR	7.96	1.16	17	8.79	1.31	21	7.32	0.010
DEE	88.9	16.1	17	101.6	14.9	21	6.39	0.016
DEE/M ^{0.73}	10.7	1.7	17	12.2	1.8	21	7.24	0.011
Feeds d ⁻¹	102.5	44.5	16	101.1	45.7	18	0.01	0.2
Provisioning rate	146.3	58.5	16	142.7	62.1	21	0.03	0.2
Brood size	4.1	1.4	17	4.2	1.4	21	(0.05)	0.2
Δ Mass%	94.8	5.4	17	92.2	5.6	21	2.06	0.1
Fat score	6.63	2.22	15	6.35	1.11	17	(0.13)	0.2

In addition, no significant differences were detected between survival categories for: Measurement date, body mass, initial fat score, winglength, keel length, brood mass, natural clutch size, first egg date, parental age, mean temperature and windspeed, rainfall, aerial insect abundance, % 24 h in flight, time in flapping flight, foraging distance from colony and occurrence of a second brood. ADMR (average daily metabolic rate, cm³ CO₂ g⁻¹ h⁻¹), DEE (daily energy expenditure, kJd⁻¹ ind⁻¹) and dee/m^{0.73} (dee/metabolic mass, kJd⁻¹/Mg^{0.73}) are measures of energy expenditure derived using the DLW technique. Feeds d⁻¹ is the number of feeding visits made per individual to the nest and provisioning rate the energy value of food delivered (kJd⁻¹), derived from: dry faecal mass d⁻¹ x 59.7, split between individual parents according to their share of feeds d⁻¹. Δ Mass % describes 24 h mass changes expressed as a % of initial mass. Fat score denotes visual fat score following DLW measurements (10 = maximum fat score 0 = minimum fat score. Significance of differences was tested by one-way ANOVA, except for brood sizes and fat scores (Mann-Whitney U-test) and occurrence of 2nd brood (χ²).

Mean energy expenditure of individuals measured in this study was compared with lifetime reproductive success (LRS) obtained by long-term monitoring at the same colony. About half (52%) of the sample was measured once with DLW and the remainder 2-5 times. Of the individuals with measurements of energy expenditure, LRS data were also available for 28. These data were best fitted by a quadratic equation (concave down), which by differentiation indicated an optimal ADMR of 7.3 cm³ CO₂/g/h (Figure 2).

DISCUSSION

Variation in energy expenditure

Small free-living birds often exceed the theoretical maximum metabolic rates predicted by Kirkwood's (1983) equation and Drent & Daan's (1980) multiplier (4 times BMR). This occurs more frequently amongst birds with energy demanding foraging habits and during breeding. It is concluded that neither of these theoretical values defines a ceiling to daily energy expenditure which is common to different bird species. Equally, other possible ceiling values, such as the 7 times resting metabolism suggested by Peterson et al. (1990), lie above the measured energy expenditures of most birds studied to date, so are unlikely to define a shared operational ceiling for avian energy expenditure. The marked difference between swallow species (Hirundinidae) studied using DLW (n=6, Tables 1 & 2), furthermore, suggests that even restricted taxonomic or ecological categories would not have the same ceiling value. It remains possible, however, that metabolic ceilings can be defined for species or individuals. This is suggested by the relationship between survival and energy expenditure in House Martins.

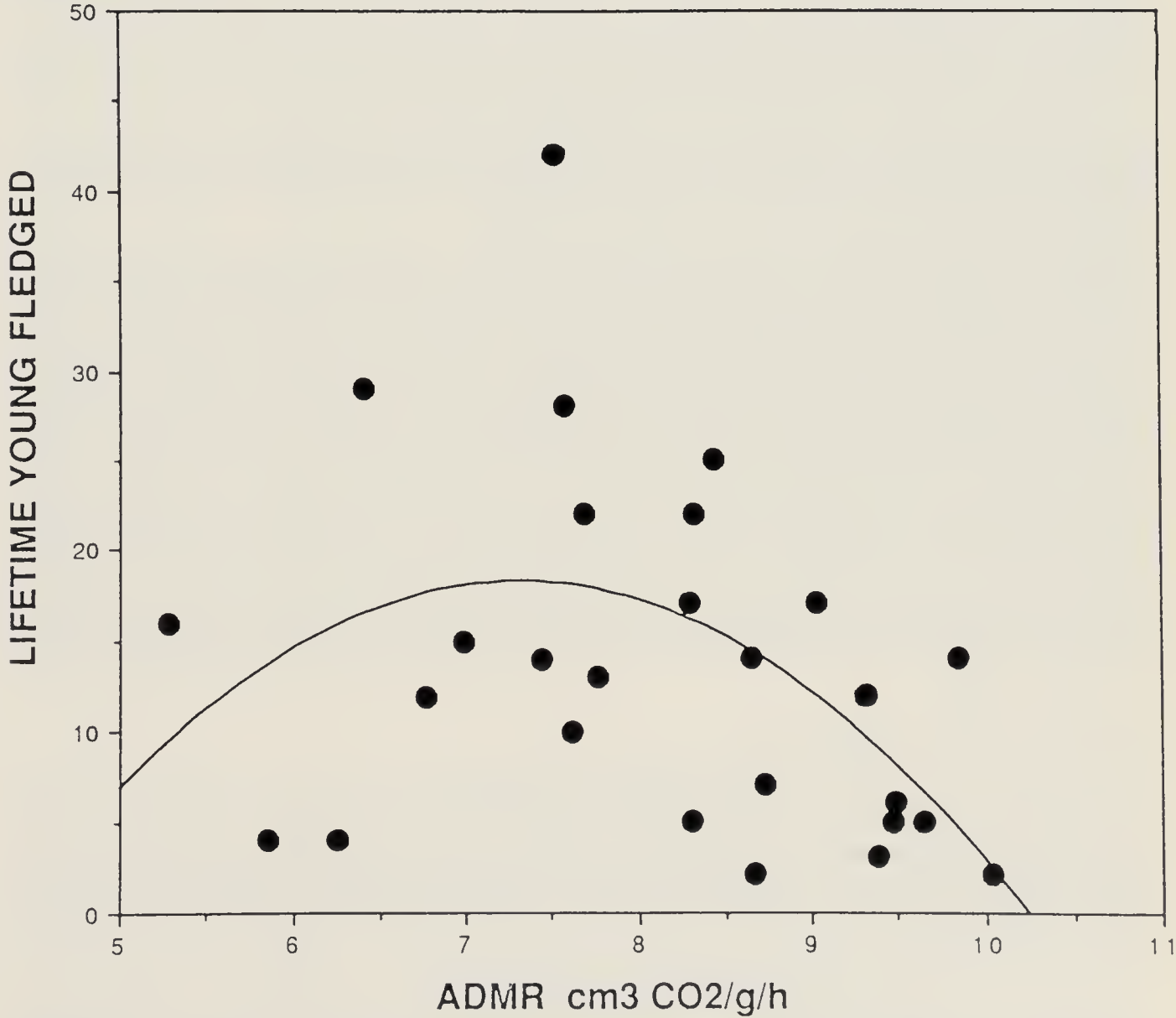


FIGURE 2 – Lifetime reproductive success (y) of House Martins in relation to energy expenditure (x) measured during the brood rearing stage. The equation for the fitted line is: $y = -95.4 (\pm 59.5) + 31.07 (\pm 15.42)x - 2.12 (\pm 0.98)x^2$ (\pm denotes standard error of partial regression coefficients. $F = 3.75$, $P = 0.04$, $df_2 = 25$, $r^2 = 23\%$).

Energy expenditure and lifetime reproductive success

Direct evidence of reduced survival or subsequent fecundity for individuals with a high energy expenditure is necessary for an adverse effect of high rates of energy expenditure to be established. Ideally, this should derive from individuals in which rates of energy expenditure have been manipulated over a sustained period, otherwise confounding factors may cause or compensate risks. Experimental manipulation of brood sizes has confirmed that raising large broods, itself likely to increase energy expenditure, may carry a survival cost (Linden & Moller 1989). In the absence of the experimental approach, however, data on lifetime reproductive success in relation to energy expenditure can demonstrate patterns which are consistent with an adverse effect of high rates of energy expenditure but cannot prove that energy is the causative agent or that selection acts directly on expenditure of energy.

Patterns of lifetime reproductive success (LRS) of House Martins revealed an optimum energy expenditure near the observed mean expenditure established over two studies (Hails & Bryant 1979, Bryant 1979, Bryant & Westerterp 1980). Individuals which raised their young in a way which entailed average rates of energy expenditure tended to live longer, and as a result had higher lifetime totals of eggs laid and young raised. So, while high rates of energy expenditure are of advantage in the short term for raising large broods, they apparently confer a disadvantage for survival. No effect of energy expenditure during first broods on the frequency of second broods (Table 3), or on clutch sizes in later years, was identified, but such effects are feasible given the results of brood manipulation studies in this and other species (Gustaffson & Sutherland 1988, Riley unpubl., Lessells unpubl.).

The relationship between lifetime success and daily energy expenditure logically demands an association between short term energy expenditure, measured over 1-2 days using DLW, and longer term energy expenditure, loss of body condition or other factors, which could be causative agents in survival patterns. Given the close link between body-size, in particular keel length, and energy expenditure in House Martins (Bryant & Westerterp 1982), this is entirely possible. Even so, it seems likely that measures of energy expenditure are also successfully integrating other crucial features of each individual. In which case the cause of variation in lifetime reproductive success is not variation in energy expenditure per se but involves a range of factors which moderate energy flow and balance at the individual level. These are likely to include morphological, physiological, environmental and behavioral attributes and experiences.

The form of the fitness cost

The existence of a fitness cost related to high levels of energy expenditure makes a case for its mode of action to be better understood. Drent & Daan's (1980) and other related hypotheses, when interpreted strictly, imply a precipitate threshold above which a cost is incurred. In contrast, Priede (1977) proposed a mechanism which involved a progressive increase in both energy expenditure and mortality risk, a pattern which is more obviously consistent with observed variation in short term costs such as mass or condition changes (Bryant 1989), survival costs related to experimental brood manipulation (Nur 1984, Gustaffson & Sutherland 1988) or much of life-history theory (Sibly & Calow 1988). Is it possible to distinguish between precipitate and progressive induction of fitness costs with the data presently available? The problems inherent in confirming a sharp increase in mortality risk make it unlikely. For example, differences in 'ability' or experience may modify the point at which a cost ceiling

is exceeded at the individual level, because energetic responses to circumstances or needs will differ. Only in the unlikely event that variation in BMR exactly matches variation in ability, could thresholds stay a constant ratio of BMR and so could operate as suggested by Drent & Daan (1980). In this case, however, a threshold could not be identified using an equation like that of Kirkwood (1983) which makes no allowance for individual differences in BMR. Also, fitness costs of energy expenditure may be dependent on body condition or circumstances. Hence, according to extrinsic factors such as habitat quality and environmental conditions, the survival penalty associated with a given level of energy expenditure seems likely to vary.

For these reasons a fitness cost tied to a particular level of energy expenditure is both difficult to identify and unlikely to occur. A progressive increase in risk as energy expenditure rises seems more tenable than assuming fitness costs will increase dramatically above a ceiling level. Given the marked differences in modal and ceiling energy expenditures in different species, and the absence of evidence that birds with more expensive foraging habits have high mortality rates (Saether 1988), it also seems likely that the point at which given risk levels are manifest will differ between species according to their habits and environments.

SUMMARY

Data on energy expenditure were available for 28 species of free-living birds spanning the mass range 10-150g. All estimates of energy expenditure were obtained using the double labelled water technique. These data were used to examine three hypotheses (I, II & III) concerned with the upper limit to sustained energy expenditure. I: Energy expenditures exceeding Kirkwood's (1983) theoretical maximum daily energy assimilation (ME_{max}) were found in 156 (28%) individuals and 50% of the species examined. II: Expressed as a multiple of basal metabolic rate (BMR), energy expenditure throughout the annual cycle ranged from 1+ to 6+ times BMR. At least 16% of individuals and 41% of species exceeded Drent & Daan's (1980) suggested maximum sustained working rate (MSWR) of 4 times BMR. III: Evidence of a survival cost related to high levels of energy expenditure was demonstrated for House Martins raising their broods. These data are consistent with life-history theories which propose that effort devoted to raising offspring may occur at the expense of self-maintenance. As a result, behaviours which induce high rates of sustained energy expenditure may reduce subsequent fecundity or survival.

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SYMPOSIUM 36

THE AVIAN PINEAL

Conveners E. GWINNER and C. BECH

SYMPOSIUM 36

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INTRODUCTORY REMARKS: THE AVIAN PINEAL

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Investigations on birds have played and still play an important role in pineal research. Extensive studies of pineal anatomy and cytobiology in a variety of avian species have provided us with significant insights into the complexity and diversity of pineal structures. Modern pharmacological and biochemical studies have revealed a similar diversity and complexity in pineal physiology. The demonstration in 1968 by Gaston and Menaker that the House Sparrow pineal contains a circadian pacemaker was a milestone in research on pineal function. It made circadian rhythms a “unifying theme” (Binkley 1988) of the field and set the stage for a host of subsequent discoveries. For example, the finding that the circadian clock in the pineal can be directly affected by light has stimulated investigations on pineal photoreception. Likewise, the suggestion that melatonin may be involved in conveying circadian information from the pineal to the rest of the system has led to intensive research on melatonin receptors and on extra-pineal sources of melatonin production.

This symposium reviews some recent developments in this field. H. Korf summarizes results on pineal photopigments and on the phototransduction and adrenoreceptor cascades both of which can be studied simultaneously in the pineal. The contributions by S. Ebihara and E. Gwinner are devoted to the role played by the avian pineal as a circadian clock. They emphasize the remarkable differences that exist between species in the relative significance of the pineal and other structures in generating circadian functions. A. Chandola-Saklani’s review of studies on pineal involvement in photoperiodic time measurement suggests that the avian pineal may be of greater significance in controlling annual cycles than had previously been thought. G. Heldmaier, finally, presents data about pineal effects on avian thermoregulation, an area that has been unduly neglected in the past.

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LOCALIZATION OF SIGNAL TRANSDUCTION PROTEINS IN THE CHICKEN PINEAL ORGAN

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ABSTRACT: Recent biochemical and physiological experiments with in vitro preparations of the chicken pineal organ have greatly contributed to our knowledge of the molecular mechanisms involved in generation and regulation of biorhythms. Immunocytochemistry allowing the identification of specific molecules in single cells appears as a valuable tool to complement biochemical and physiological data which may reflect not only the actions of a single cell type but also the interactions among multiple cell types presumably present in the chicken pineal organ. This contribution provided evidence for the presence of at least two different photopigments in the chicken pineal organ. A photopigment closely related to cone-opsin appears to predominate in the pineal photoreceptors. Furthermore, the chicken pineal organ was shown to contain immunoreactive transducin and other GTP-binding proteins. The present immunocytochemical results provide evidence that virtually all chicken pinealocytes contain epitopes highly characteristic of the alpha subunit of G_p . These immunocytochemical results conform to biochemical findings obtained with the chicken pineal organ.

Keywords: Pineal organ, chicken, photopigments, GTP-binding proteins, signal transduction, immunocytochemistry.

INTRODUCTION

In birds, like in other vertebrate classes, the pineal organ is an important component of photoneuroendocrine systems and, as such, of the biological clock. This organ plays an important role in generating locomotor and body temperature rhythms in passerine species (Gaston & Menaker 1968, Binkley et al. 1971, Zimmerman & Menaker 1975, 1979, Gwinner 1978). Although pinealectomy is without effect on circadian rhythms of gallinaceous birds (cf. Cassone & Menaker 1983), the chicken pineal organ was shown to produce and release its specific hormone, melatonin, in a rhythmic pattern (e.g., Kasal et al. 1979, Takahashi et al. 1980). The rhythmic production and release of melatonin strictly follow the rhythm of serotonin N-acetyltransferase activity (cf. Binkley 1981). Both, the melatonin rhythm and that of serotonin N-acetyltransferase activity persist in cultured chicken pineal organs or dissociated pineal cells for several cycles (Deguchi 1979a, Takahashi et al. 1980, Takahashi & Menaker 1984, Robertson & Takahashi 1988a, Zatz et al. 1988). These results show that the avian pineal organ contains circadian oscillators.

Furthermore, the pineal organ of birds functions as a photoreceptor. Light stimuli acutely suppress the melatonin biosynthesis in the isolated pineal organ (Veguchi 1981, Binkley et al. 1975, 1979, 1981, Wainwright & Wainwright 1980, Zatz & Mullen 1988c) and mediate also entrainment of the circadian oscillators (Robertson & Takahashi 1988b, Zatz & Mullen 1988c).

In addition to photic stimuli, pinealopetal sympathetic nerve fibers and their neurotransmitter, norepinephrine, are involved in the regulation of melatonin

production (Cassone & Menaker 1983, Cassone et al. 1986). The light-induced inhibition of the serotonin N-acetyltransferase activity is reduced by sympathetic denervation (Binkley et al. 1975); norepinephrine and its agonists inhibit the N-acetyltransferase activity of the cultured chicken pineal organ (Deguchi 1979b, Zatz & Mullen 1988a). The effects of norepinephrine in the avian pineal organ are obviously mediated by alpha-2 adrenergic receptors (Voisin & Collin 1986, Voisin et al. 1987, Pratt & Takahashi 1987).

The fact that three key components of the vertebrate biological clock, i.e., circadian oscillators, photoreceptors and adrenoreceptors, all reside within the chicken pineal makes this organ an ideal candidate to study the molecular basis of the generation and regulation of biological rhythms (see Robertson & Takahashi 1988a, b, Zatz & Mullen 1988a, b, c, Zatz et al. 1988). Furthermore, this organ appears as an excellent model to study the interactions of distinct signal transduction processes, because it comprises the phototransduction and the adrenoreceptor cascade. Both display the basic design of transmembrane signalling processes involving GTP binding proteins which act as transducers between receptors and the second messengers cyclic AMP and cyclic GMP and are now known to play a major role for activation and regulation of various sensory, neuronal and endocrine cells (Gilman 1987, Stryer & Bourne 1986, Spiegel 1987)

GENERAL DESIGN OF THE PHOTOTRANSDUCTION CASCADE

As established for retinal rods, the phototransduction cascade comprises a membrane-bound receptor protein, the visual pigment rhodopsin, a GTP-binding protein as signal transducer, cyclic GMP-phosphodiesterase, a specific kinase, arrestin (S-antigen) and cyclic GMP-gated cation channels (Chabre & Applebury 1986, Wilden et al. 1986, Pfister et al. 1985). As is characteristic for all vertebrate photopigments, rhodopsin is composed of a protein group, the apoprotein denominated as rod-opsin, and the prosthetic group 11-cis retinal covalently bound to the apoprotein. Light stimuli cause stereoisomerization of 11-cis retinal into all-trans retinal which is finally released from the apoprotein (Wald 1968). The stereoisomerization is accompanied by conformational changes of the apoprotein which activate the rod-specific GTP-binding protein, transducin. Like all GTP-binding proteins, transducin consists of three subunits called alpha, beta and gamma subunits. The alpha-subunit of each species of the GTP-binding protein family appears to be unique (Gilman 1987, Stryer & Bourne 1986, Spiegel 1987). Upon activation, transducin couples to the activated rod-opsin molecule, the GDP molecule bound to the alpha-subunit of transducin is exchanged by GTP, the alpha subunit is released from the beta and gamma subunits and stimulates the cyclic GMP-phosphodiesterase which hydrolyzes cyclic GMP. The decreasing concentration of intracellular cyclic GMP causes the closure of cyclic GMP-gated cation channels and the hyperpolarization of the photoreceptor membrane (Stryer & Bourne 1986). After exchange of GDP by GTP the affinity of alpha-transducin to the membrane-bound receptor protein is lowered and the latter is free to interact with other transducin molecules. Via this process, one stimulated membrane-bound receptor protein interacts with 500 transducin molecules .

The desensitization is mediated by (1) rhodopsin kinase, a rod specific enzyme, phosphorylating the activated rhodopsin and (2) arrestin (S-antigen) which binds to

the phosphorylated opsin and catalyzes the inhibition of the cyclic GMP phosphodiesterase (Pfister et al. 1985).

PHOTORECEPTIVE MECHANISMS IN THE AVIAN PINEAL ORGAN

There is some evidence that the molecular mechanisms of photoreception and phototransduction in the avian pineal organ are identical with – or at least closely related to – the rod phototransduction cascade. Thus, the light-induced inhibition of the serotonin N-acetyltransferase activity displays a rhodopsin-like spectral sensitivity in the chicken pineal organ (Deguchi 1981). Moreover, immunocytochemical studies with the use of highly specific antisera against bovine rod-opsin (Vigh et al. 1982, Korf & Vigh-Teichmann 1984, Foster et al. 1987, 1989), bovine alpha-transducin (van Veen et al. 1986, Foster et al. 1987) and bovine arrestin (S-antigen) (Korf et al. 1986, Foster et al. 1987) suggested that all these proteins of the rod phototransduction cascade are present in the avian pineal organ (see also Korf & Foster 1988).

ADRENORECEPTION IN THE AVIAN PINEAL ORGAN

As mentioned before, norepinephrine influences the biosynthesis and release of melatonin in the avian pineal organ. In contrast to mammals, where norepinephrine stimulates melatonin biosynthesis via elevated cyclic AMP levels (cf. Klein et al. 1987, for review and references), the avian pineal organ shows an inhibition of the melatonin synthetic pathway upon noradrenaline treatment (Deguchi 1979b). This conforms to the finding that the norepinephrine turnover in the chicken pineal organ is high during the day and low at night (Cassone et al. 1986) and, thus, 180 degrees out of phase with the rhythm of melatonin biosynthesis. The different responses to norepinephrine of the mammalian (rat) and chicken pineal organ can be readily attributed to different receptors and different GTP-binding proteins acting as signal transducers.

In the mammalian pineal organ norepinephrine couples to beta-1 adrenergic receptors, but alpha-2 adrenergic receptors mediate the norepinephrine response in the chicken pineal organ (Voisin & Collin 1986, Voisin et al. 1987, Pratt & Takahashi 1987). As is well established for other systems, beta-1 adrenergic receptors activate the GTP-binding protein G_s which stimulates the adenylate cyclase activity whereas alpha-2 adrenergic receptors couple to the GTP-binding protein G_i which inhibits the adenylate cyclase activity. Experiments with cultured chicken pineal organs suggest that, also in this system, the signal transduction via the alpha-2 adrenergic receptors involves G_i (Zatz & Mullen 1988a, Pratt & Takahashi 1988).

SOME UNSOLVED ASPECTS OF SIGNAL TRANSDUCTION IN THE AVIAN PINEAL ORGAN

Although a general idea on the molecular basis of the generation and regulation of biorhythmic processes in the avian pineal organ has evolved from the above-mentioned experimental data, several aspects remain to be resolved. The acute inhibitory effects of light stimuli on the melatonin biosynthesis appear to be processed by other molecular mechanisms than the light-dependent entrainment of the circadian oscillator

(Zatz & Mullen 1988c). This raises the possibility that the two effects are elicited by different types of pineal photoreceptors employing different photopigments (Zatz & Mullen 1988c). The finding in the Japanese Quail (Foster et al. 1989) that the molar ratio between the chromophore, 11-cis retinal, and the apoprotein rod-opsin is more than one would conform to this assumption. Finally, Wallingford and Zatz (1988) showed that in cultured chicken pineal cells retinal is bound to a membrane protein of 30 kDa which by its molecular weight differs from rhodopsin whose molecular weight is approximately 40 kDa as established by SDS-polyacrylamide gel electrophoresis.

It is also unknown whether phototransduction and adrenoreception occur within the same cell.

To address these issues the immunocytochemical technique appears as a valuable tool which allows identification of specific molecules in single cells and may thus help to complement functional and biochemical data from in vitro systems which may reflect not only the action of a single cell type but also the interactions between several distinct cell types present in the avian pineal organ.

As an initial attempt to correlate immunocytochemical findings with biochemical and functional results we have started a series of immunocytochemical investigations of the chicken pineal organ and some of these results will be presented in the following section.

IMMUNOCYTOCHEMICAL DEMONSTRATION OF MEMBRANE-BOUND RECEPTOR PROTEINS IN THE CHICKEN PINEAL ORGAN

Rod-opsin, the rod-specific membrane receptor protein was demonstrated by means of a highly specific antibody against bovine rod-opsin. This antibody has been kindly provided by Dr. W. J. de Grip, Nijmegen, The Netherlands, and is well characterized in previous studies (cf. Korf et al. 1985, Foster et al. 1987, 1989). Like in the Japanese Quail (Foster et al. 1987), the rod-opsin immunostaining was restricted to a limited number of pinealocytes in the chicken pineal organ. Many pineal follicles showed no rod-opsin immunoreactive pinealocytes at all and those that did were concentrated in the more distal portion of the gland. Immunostaining was distributed throughout all parts of the labelled pinealocytes and not restricted to the outer segments. Also basal processes terminating near the basal lamina of the pineal follicles were frequently immunolabelled. In previous studies employing another antibody against bovine rod-opsin the immunoreaction was exclusively located in the outer segments of the modified pineal photoreceptors (Vigh et al. 1982, Korf & Vigh-Teichmann 1984). It is likely that these differences can be attributed to a variation in the antigenic sites recognized by the different antibodies (cf. Foster et al. 1987).

In addition to the rod-opsin immunoreactive pinealocytes displaying the bipolar feature of modified photoreceptor cells, multipolar cells were immunolabeled which inhabited the more basal portion of the pineal follicles and apparently did not contact the lumen of the pineal follicles (see also Sato et al. 1990).

The intensity of the rod-opsin immunoreaction and the number of immunoreactive cells remained unchanged irrespective whether the animals were killed during the day

or at night under dim red light conditions. However, the number of rod-opsin immunoreactive pinealocytes decreased during posthatching development (Sato et al. 1990).

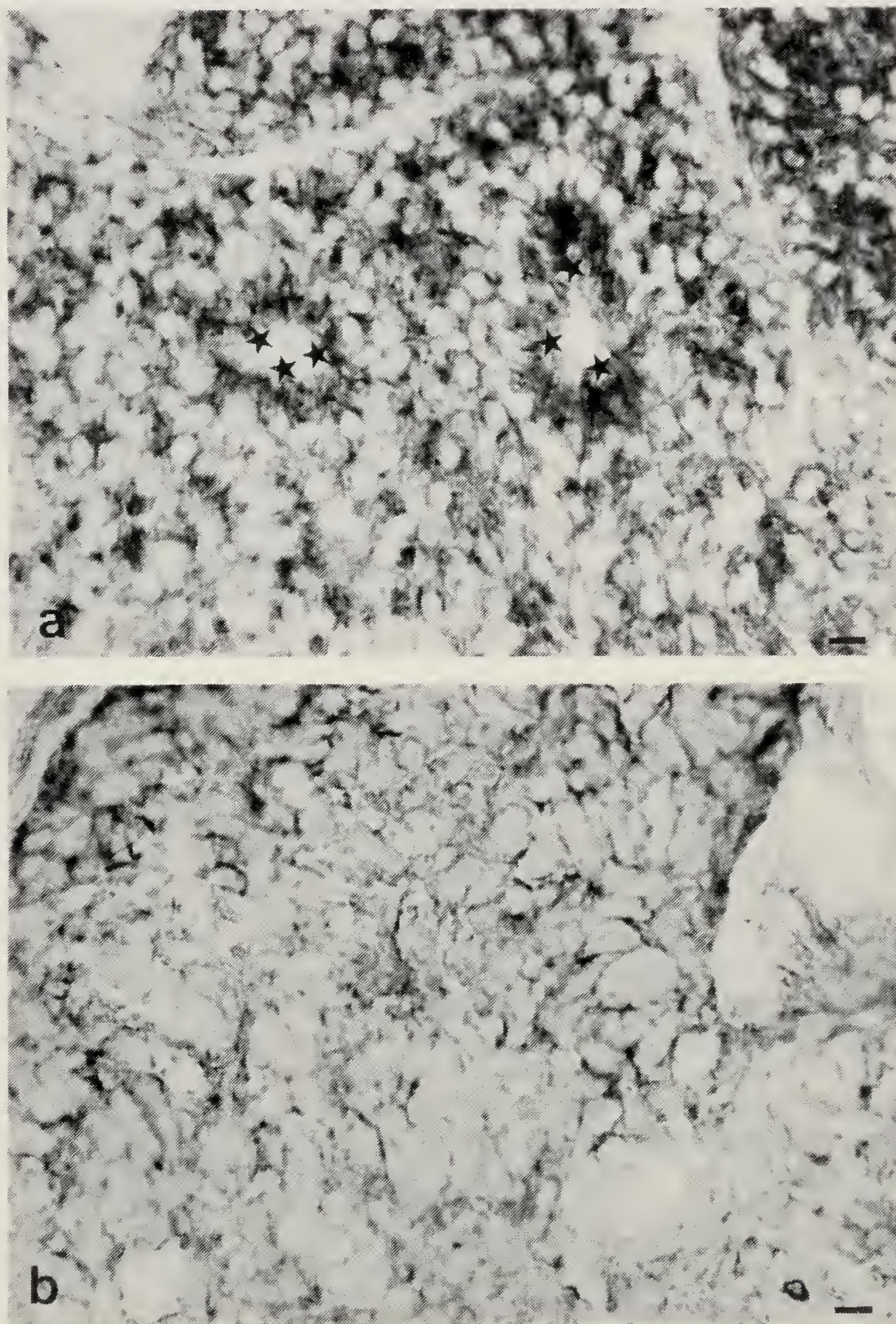


FIGURE 1 – Immunocytochemical demonstration of cone-opsin (a) and the alpha-subunit of G_i in the pineal organ of 10-day-old chicken. The cone-opsin immunoreaction is distributed throughout all parts of the cell, it appears very intense at the apical (luminal) pole of the modified pineal photoreceptors (asterisks). Cell nuclei are devoid of immunoreactivity. The labelling of the apical pole of the pinealocytes is less conspicuous after application of the antibody against alpha- G_i . Bar = 20 μm

At all developmental stages the rod-opsin immunoreactive pinealocytes were few when compared to the total amount of modified pineal photoreceptors shown to be present in the chicken pineal organ by means of electron microscopy (cf. Collin & Oksche 1981, Korf & Oksche 1986). This suggests that, in the chicken, the majority of these cells bear a photopigment which does not cross-react with the rod-opsin antibody and which is different from the rod visual pigment.

To test this assumption we investigated chicken pineal organs with the use of antibodies raised against cone-opsin isolated from the chicken retina (Kramm, Korf & de Grip, unpublished results, Foster & de Grip, unpublished results). This antibody was a generous gift of Dr. W. J. de Grip, Nijmegen, The Netherlands. Numerous chicken pinealocytes were shown to bind this antibody; they were evenly distributed throughout all follicles (Figure 1a). This immunocytochemical result provides further evidence for the presence of multiple photopigments in the chicken pineal organ. According to these results, a cone-like photopigment appears to be the predominant protein of the phototransduction cascade in the chicken pineal organ. It remains to be established whether the protein accounting for the cone-opsin immunoreaction is identical with the 30 kDa membrane protein shown to bind retinal in cultured chicken pinealocytes (Wallingford & Zatz 1988) .

IMMUNOCYTOCHEMICAL DEMONSTRATION OF GTP-BINDING PROTEINS IN THE CHICKEN PINEAL ORGAN

The rod-specific GTP-binding protein transducin was immunocytochemically demonstrated by means of a polyclonal antibody raised against the alpha-subunit of bovine transducin (cf. van Veen et al. 1986). This antibody was a generous gift from Dr. A. Spiegel, NIH, Bethesda, USA. In contrast to the rod-opsin immunoreaction, immunoreactive alpha-transducin was found in numerous pinealocytes in all follicles. Similar results have been reported previously for the Japanese Quail (Foster et al. 1987). The alpha-transducin immunoreaction was distributed throughout all parts of the pinealocyte, but a more intense reaction often marked the outer segment projecting into the lumen of the pineal follicles. Also the alpha transducin immunoreaction labelled round or oval cells located distant from the pineal lumen in the basal portions of the pineal follicles in addition to the bipolar modified photoreceptor cells.

Two explanations can be offered for the discrepant numbers of rod-opsin and alpha-transducin immunoreactive pinealocytes. The alpha-transducin immunoreactive pinealocytes contain rhodopsin in such a low concentration that this molecule escaped the immunocytochemical detection. On the other hand, the alpha-transducin antibody used may also bind to a GTP-binding protein acting upon a photopigment which is different from rhodopsin and may be the protein cross-reacting with the cone-opsin antibody.

The issue of whether GTP-binding proteins other than transducin were present in the chicken pineal organ was addressed by use of antibodies recognizing epitopes common to the alpha-subunit of all GTP-binding proteins known to date. These antibodies have been kindly provided by Dr. D. Palm, Wurzburg, Germany, and Dr. K. Hinsch, Giessen, Germany. Virtually all chicken pinealocytes were found to bind these antibodies.

In order to precisely characterize the GTP-binding proteins accounting for this immunoreaction, antibodies were tested in the chicken pineal organ which recognize epitopes specific of the alpha-subunit of G_i or G_s . These antibodies were a generous gift from Dr. K. Hinsch, Giessen, Germany. The staining obtained with the G_i antibody (Figure 1b) was very similar to the immunoreaction elicited by the antibodies against common epitopes of the alpha-subunit of all GTP-binding proteins. Virtually no immunostaining was found with the G_s antibody. To date it is not known whether this negative result actually reflects the absence of G_s from the chicken pineal organ or is due to methodological reasons. It also remains to be established whether all pinealocytes displaying G_i immunoreaction bear alpha-2 adrenergic receptors.

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THE ROLE OF PINEAL AND RETINAL MELATONIN IN THE CONTROL OF CIRCADIAN RHYTHMS OF THE PIGEON

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ABSTRACT. The circadian system of the Pigeon consists of at least three oscillatory components, the pineal gland, the eye and a hypothalamic oscillator. Melatonin synthesized in the pineal gland and the eye acts as a synchronizer in the circadian system. Neural inputs from the hypothalamic oscillator are supposed to be involved in the mechanism of interaction among these oscillators. In order to understand the interaction, the microdialysis technique has been applied to the pineal gland of the Pigeon and clear rhythmicity of melatonin has been obtained. Thus this technique may prove to be useful in the study to uncover the interaction among the circadian oscillators.

INTRODUCTION

A number of studies have shown that the pineal gland is involved in the avian circadian system. Menaker's group has found that pinealectomized (PX) sparrows lose their rhythmicity under constant conditions and transplantation of the pineal gland into the anterior chamber of the eye of an arrhythmic PX host restores the rhythmicity, and further, the phase of the donor's rhythm is imposed on the host (Menaker et al. 1981). Other evidence supporting the importance of the pineal gland in the circadian system includes the demonstration that the circadian rhythms of activity of N-acetyltransferase (NAT) which is required for melatonin synthesis and melatonin release in the chicken pineal persist in vitro (Binkley et al. 1978; Deguchi 1979, Kasal et al. 1979, Takahashi et al. 1980). Moreover, administration of melatonin affects the circadian system in several avian species (Gwinner 1989). Although these results have indicated that the pineal gland is important in the avian circadian system, evidence that other oscillators are also involved in the system has been accumulated. For example, in the Pigeon, pinealectomy has only minor effects on circadian rhythms of locomotor activity and body temperature under constant conditions. We have attempted to determine the circadian oscillators other than the pineal gland and found that the eye has the same function as the pineal gland (Ebihara et al. 1984, Ebihara et al. 1987, Oshima et al. 1989a). Because these organs produce melatonin with the circadian rhythm (Foa & Menaker 1988), we have tested the hypothesis that melatonin produced in the pineal and the eye controls the circadian system (Oshima et al. 1987, Oshima et al. 1989a,b). Although these data have suggested that both of the organs contain the circadian oscillator, the pineal oscillator may be affected by neural signals originating in the hypothalamic oscillator (the suprachiasmatic nucleus) (Cassone & Menaker 1983; Cassone et al. 1990). Thus, in order to know the interaction among these oscillators, we have applied the novel technique of microdialysis to the avian pineal by which direct measurement of pineal rhythmicity is possible.

PINEALECTOMY

PX pigeons entrain their circadian locomotor activity and body temperature rhythms to light-dark (LD) cycles without any considerable changes in the pattern of entrainment from the intact Pigeon, but in constant dim light (LLdim) the rhythms become unclear and lose the stability of circadian period. These results have indicated that the pineal gland is necessary for the stability of the circadian system, but it is not indispensable to generate the rhythmicity (Ebihara et al. 1984, Oshima et al. 1989a).

BLINDING

Effects of blinding (EX) on circadian rhythms of locomotor activity and body temperature are similar to those of PX. EX does not eliminate entrainment of the circadian rhythm to LD cycles and free-running rhythms in LLdim although clear separation between rest and activity phase in free-running rhythms is not observed in some pigeons. These results have suggested the existence of the extraretinal photoreceptor which couples to the circadian system and the eye has the same function as the pineal gland (Ebihara et al. 1984, Oshima et al. 1989a).

PINEALECTOMY + BLINDING

Although PX or EX alone can not abolish the circadian rhythm, combined treatments with PX and EX consistently abolish the free-running rhythms in these pigeons which are kept under prolonged LLdim. However, PX + EX pigeons still entrain to LD cycles and show a weak circadian rhythm which gradually decays after transfer from LD to LLdim. These results have suggested that both the pineal and the eye are involved in the pigeon's circadian system but other circadian oscillator(s) and photoreceptor(s) still remain in the system (Ebihara et al. 1984, Oshima et al. 1989a).

LESIONS OF THE HYPOTHALAMUS

As in mammals, the avian hypothalamus contains the circadian oscillator because lesions in the anterior hypothalamus disrupt circadian rhythms of locomotor activity in several avian species (Ebihara & Kawamura 1981, Simpson & Follett 1981, Takahashi & Menaker 1982). However, the site of the oscillator in the hypothalamus is not clearly determined. In the pigeon, lesions aimed at a medial site of the anterior hypothalamus sometimes induce arrhythmicity in the birds kept in LLdim, though complete arrhythmicity is not obtained (Ebihara et al. 1987). Thus it is possible that the oscillator responsible for entrainment to LD cycles and residual rhythmicity after transfer from LD to LLdim in PX+EX pigeons may reside in the anterior hypothalamus.

MELATONIN

As stated, circadian rhythms of locomotor activity and body temperature can not be eliminated by a single removal of either the pineal or the eye, but when both operations are combined the rhythmicity disappears in constant conditions. Plasma

melatonin rhythms also can not be eliminated by a single treatment, but disappear when both are combined. The peak level of plasma melatonin is reduced to about half of that of intact pigeons in either case of PX or EX, and its concentration is reduced to near the minimum level of melatonin detection throughout the day after both organs are removed (Ebihara et al. 1987, Oshima et al. 1989a). The similar state in circulating melatonin levels to that of PX + EX pigeons can be induced by exposing pigeons to constant bright light (LLbright). Under the bright light intensity (2000 lux), circulating melatonin is significantly suppressed and no rhythmicity is observed. Similarly, the rhythmicity of locomotor activity and food intake disappears under this light intensity (Yamada et al. 1988). On the other hand, free-running rhythms of locomotor activity and plasma melatonin levels persist in LLdim, retaining a phase relationship of 180° similar to that found in LD cycles (Oshima et al. 1987). These results have indicated that pineal and retinal melatonin may be an essential factor to control the pigeon's circadian system. However this idea must be supported at least by the flnding that melatonin has a function of entraining the circadian rhythm. Figure 1 demonstrates that daily injections of melatonin entrain the circadian rhythm of locomotor activity in an arrhythmic PX + EX pigeon kept in LLdim (Oshima et al. 1989a). In this bird, suppression of locomotor activity occurs before the injections and persistence of circadian rhythms is observed after discontinuation of the injections suggesting that melatonin does not directly suppress the activity level, but affects locomotor activity via circadian oscillators which may be responsible for residual rhythmicity after discontinuation of melatonin injections.

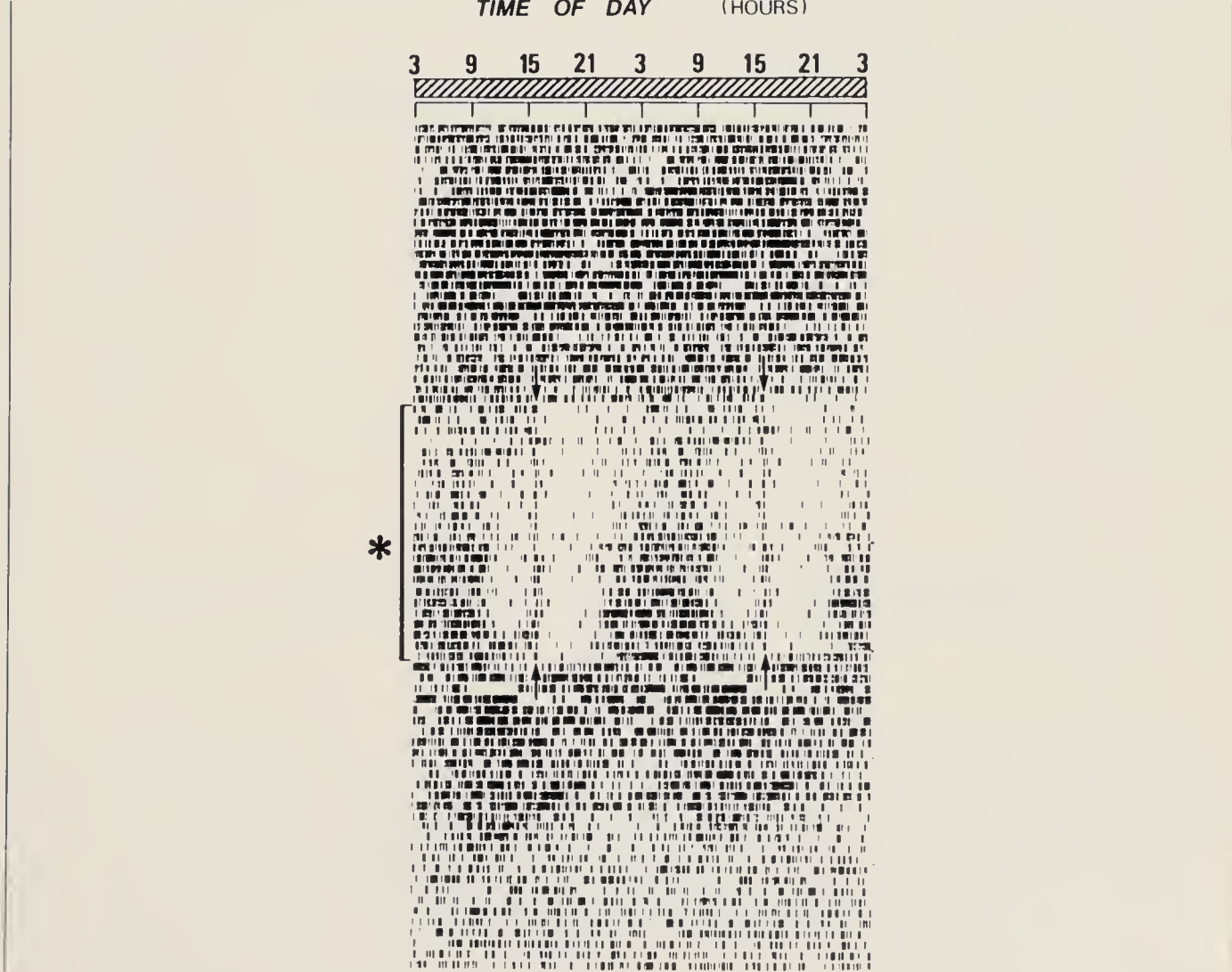


FIGURE 1 – Effects of daily melatonin injections (500 µg/kg) on locomotor activity of a PX + EX pigeon kept in LLdim. Arrows in actograms indicate time of injections, asterisk indicates period of melatonin injections.

IN VIVO MICRODIALYSIS

In order to understand the mechanism of the interaction among the circadian oscillators in the pigeon, it is necessary to develop a system with which direct measurement of the rhythmicity of each component is possible. In vivo microdialysis is an excellent technique for this purpose, because this technique provides a way of successive monitoring of extracellular chemical compounds in the local area of the brain together with the behavior of free-moving animals (Delgado et al. 1972, Ungerstedt & Pycock 1974, Nakahara et al. 1988, Azekawa et al. 1990). We have applied this technique to the pigeon's pineal gland and succeeded in obtaining pineal melatonin rhythmicity.

Figures 2 and 3 illustrate the diagram of the dialysis probe and the situation of collecting the dialysate from the pineal gland, respectively. The pigeon in this situation can move freely and no problems of taking food and water are observed. We have collected melatonin through the membrane of the probe (1.7 mm x 0.25 mm O.D., 10 μ m membrane thickness, 5000 mol. wt. cutoff) every 2 hours (240 μ l, 2 μ l / min.) and measured melatonin with a radioimmunoassay. Figure 4 shows pineal melatonin rhythmicity obtained by this technique. The level of melatonin increases during the dark and decreases during the light which is consistent with the data of melatonin content in the pineal tissue and concentration in the plasma.

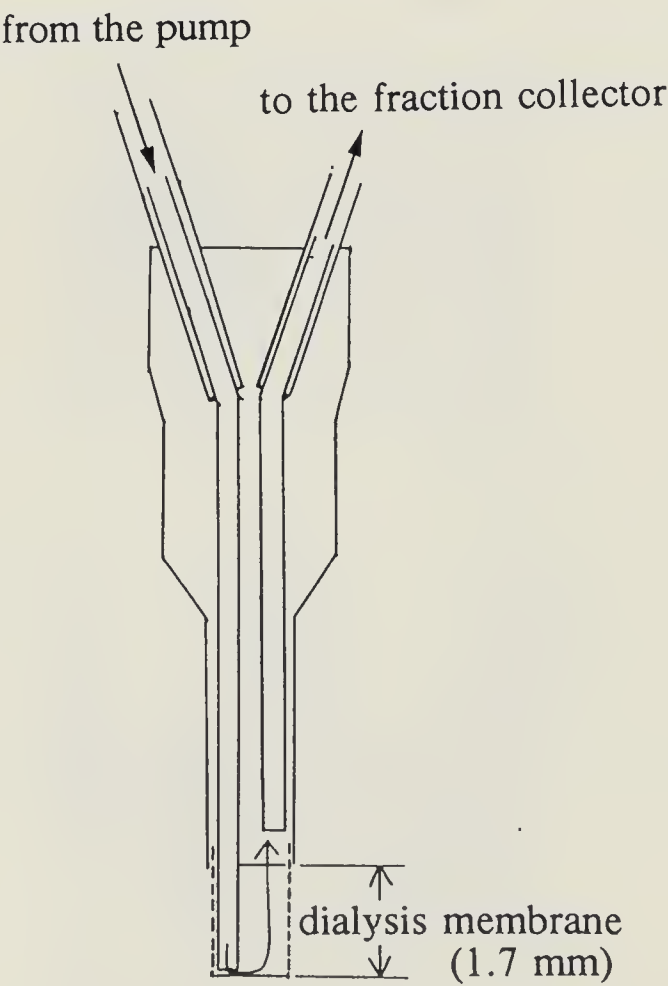


FIGURE 2 – Dialysis probe

FIGURE 3 – Diagram of recording situation

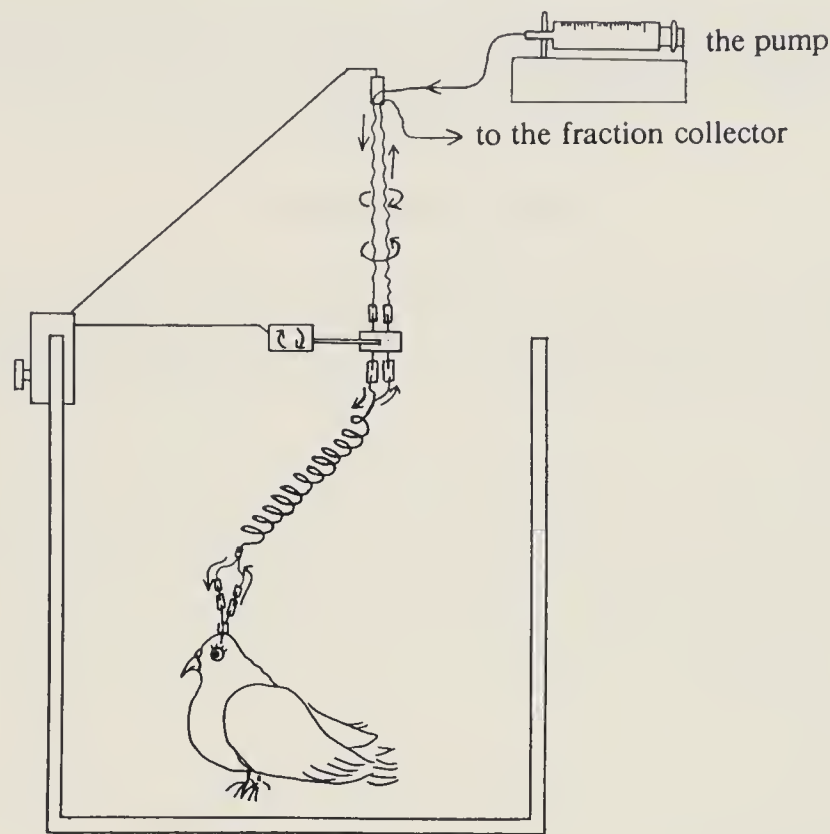
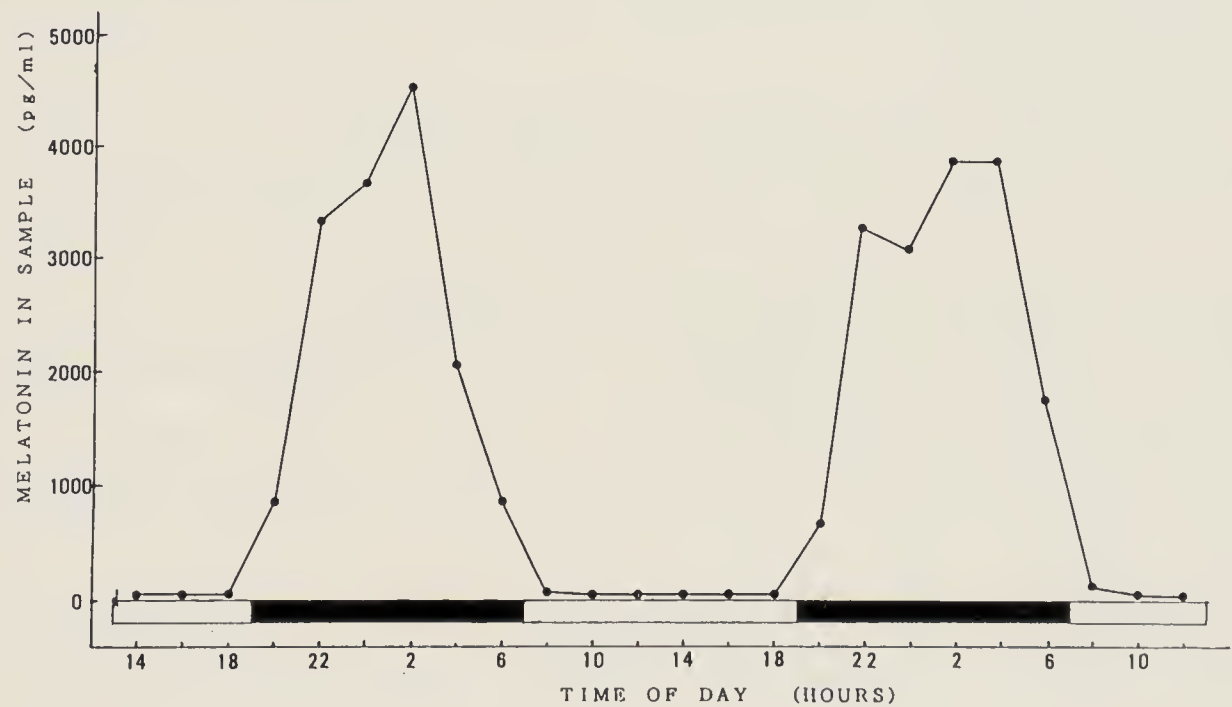


FIGURE 4 – Melatonin rhythm in the pineal gland of a pigeon kept under LD cycles obtained by the microdialysis method



It is supposed that the avian pineal melatonin rhythmicity is regulated by noradrenergic fibers from the superior cervical ganglion (Cassone & Menaker 1983). The microdialysis technique can measure not only melatonin but also other compounds including norepinephrine. Therefore it is possible to examine the relationship between melatonin production and noradrenergic activity by measuring both melatonin and norepinephrine simultaneously. We are currently conducting such experiments in both pigeons and chickens.

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SIGNIFICANCE OF MELATONIN AND THE PINEAL ORGAN IN THE CONTROL OF AVIAN CIRCADIAN SYSTEMS

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ABSTRACT. Comparative studies on several species of birds have demonstrated the significance of the pineal organ in the control of avian circadian systems. The pineal is the seat of a circadian pace-maker and all evidence indicates that it communicates with the rest of the system through the periodic synthesis and secretion of its hormone melatonin. However, other circadian pacemakers are involved as well, e.g. the eyes and hypothalamic structures possibly homologous to the mammalian SCN. The relative contribution of these oscillators to the overall circadian systems seems to vary among species in a manner that can be accommodated by the model of a "neuroendocrine loop" or that of "internal resonance".

Keywords: Melatonin, pineal, circadian rhythms.

INTRODUCTION

Numerous daily rhythms in plants and animals are controlled by endogenous oscillatory processes that persist even in the absence of 24 hours environmental cycles. Under constant conditions the period of these rhythms usually deviates slightly from 24 hours, the precise value depending on the individual, its internal state and the environmental conditions to which it is exposed. This attests to the truly endogenous nature of these rhythms and justifies their designation as circadian (circa = about, dies = day; e.g. Aschoff 1980, 1981 for reviews). Until the late sixties essentially nothing was known about the localization and concrete physiology of the mechanisms underlying circadian rhythms in any vertebrate species. In 1968, however, Gaston and Menaker discovered that the avian pineal represents an essential structure for the proper functioning of avian circadian rhythms: House Sparrows *Passer domesticus* held in continuous darkness (DD) lost their circadian rhythm of locomotor activity when the pineal was surgically removed. This result suggested that the pineal is a circadian oscillator, but further experiments revealed that other structures must be involved as well. For instance, it was found that pinealectomy did not abolish circadian rhythms of sparrows held in a 24 h light-dark (LD) cycle and that it took the rhythmicity several days to disappear when pinealectomized sparrows were transferred from LD to DD. These two sets of results suggesting (1) that the pineal is a circadian oscillator but (2) that it may not be the only one, have set the stage for a host of subsequent studies. In this paper some recent developments in this field will be reviewed and some ideas will be presented about the origin of the diversity found among various species.

THE PINEAL AS AN OSCILLATOR

The most striking initial result supporting the idea that the pineal contains an oscillator was obtained in a pineal transplantation experiment. Pineal organs implanted into the anterior chambers of the eyes of pinealectomized sparrows restored their previously

arrhythmic locomotor activity. Since the restored rhythms emerged with the phase of the rhythms of the donor birds, the results strongly suggested that the pineal is in effect an autonomous circadian oscillator (Zimmerman & Menaker 1979). The results also indicated that this oscillator exerts its effects on the subordinate system chemically. Melatonin was proposed as a possible agent. In all vertebrates yet studied melatonin is secreted periodically with high values at night and low values at daytime. The conclusion that the pineal contains an autonomous oscillator was further supported by the finding that pineal organs cultured in vitro continued to secrete melatonin in a rhythmic fashion, even in DD (Binkley et al. 1978, Deguchi 1979a,b, Kasal et al. 1979, Takahashi et al. 1980, Takahashi 1981, Robertson & Takahashi 1988 a,b). The hypothesis that it is the periodic melatonin output of the pineal that transmits circadian information to the rest of the system was supported by the finding that periodic injections (Gwinner & Benzinger 1978, Oshima et al. 1989) or infusions (Chabot & Menaker 1988) of melatonin into arrhythmic Starlings *Sturnus vulgaris*, Pigeons *Columba livia* or sparrows can restore and/or synchronize locomotor activity with the appropriate phase relationship. Synchronization can even be achieved with melatonin offered periodically in the drinking water (Klockner & Gwinner, unpublished). The implication derived from these results that there is a response curve of the circadian system to melatonin has not yet been rigorously tested in birds but evidence is available from a lizard (Underwood 1986) as well as from some mammals (Armstrong 1988). The finding that melatonin receptors are present in the SCN, and other putative circadian oscillators (see below) at least in the chicken and the Java Sparrow *Padda oryzivora* (Rivkees et al. 1989, Stehle 1990) is also consistent with the idea that melatonin is the substance that transduces circadian information to other components of the circadian system. Finally, it has been found that the period and other properties of free-running circadian rhythms in several avian species respond to chronically applied melatonin in a similar way as the rhythms respond to other environmental factors that have zeitgeber qualities (see Gwinner 1989 for review).

EXTRA-PINEAL OSCILLATORS

Although in the initial studies on House Sparrows pinealectomy abolished free-running circadian activity rhythms in constant conditions, a clear rhythm was present in birds held in 24 h LD-cycles (Gaston & Menaker 1968). Activity onset usually preceded lights on, indicating that activity was not just the passive response to light and suggesting that the activity/rest cycle was still controlled by an oscillatory system activated and synchronized by the environmental LD-cycle (Gaston 1971). This idea was further supported by the observation that after transfer from LD to DD the rhythm in activity was not abolished instantaneously; rather it took about a week for the rhythm to fade away. These observations, which were confirmed in several other studies with other species (e.g. Gwinner 1989 for review), are consistent with the idea that activity in pinealectomized sparrows is controlled by a damped oscillator. However, there are also observations indicating that, at least occasionally, pinealectomized sparrows may even sustain continuing (though relatively labile) circadian rhythms (Gwinner 1989). The same seems to be true for other extensively studied species which usually become arrhythmic after pinealectomy, e.g. the House Finch *Carpodacus mexicanus* (Fuchs 1983) and the White-throated Sparrow *Zonotrichia albicollis* (McMillan 1972). Moreover, there are species in which pinealectomy is generally much less effective than in these seed-eating passerines. In the European Starling free-running circadian activity rhythms were only occasionally abolished by

pinealectomy and in those individuals in which rhythmicity initially disappeared it often spontaneously recovered after some weeks or months (Gwinner 1978). As in sparrows the remaining rhythmicity was unstable and labile and the separation between the activity phase and the rest phase was not as clear as in pineal-intact starlings. Finally, there are at least three avian species: the chicken, the quail *Coturnix coturnix japonica* and the pigeon in which pinealectomy is essentially ineffective (MacBride 1973, Simpson & Follett 1981, Underwood & Siopes 1984, Ebihara et al. 1984).

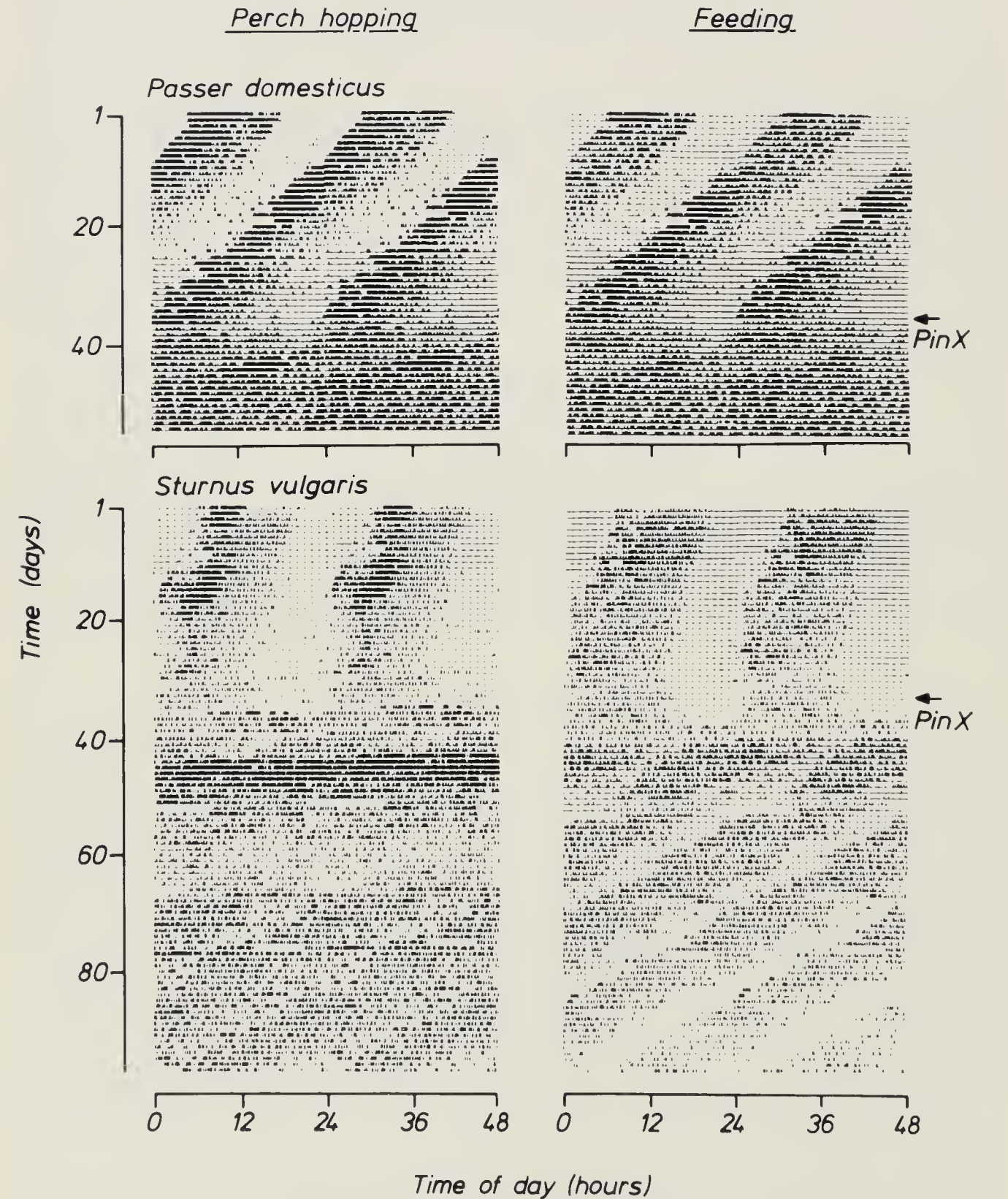


FIGURE 1 - Circadian rhythms of perch-hopping (left) and feeding (right) of a House Sparrow (upper diagram) and a European Starling (lower diagram) held in constant darkness (sparrow) or dim light of 0.2 lux (starling). At the time indicated by the arrows, the birds were pinealectomized (PinX) (after Beldhuis et al. 1988 and Gwinner 1989).

Pinealectomy may not only have different effects on different species but also on different circadian functions within the same individual. This is the case in the European Starling in which the circadian rhythm of food uptake always survived pinealectomy, even in those individuals in which the circadian rhythm of locomotor activity was abolished (Gwinner et al. 1987). In the House Sparrow, in contrast, feeding activity always disappeared together with the locomotor activity rhythm (Gwinner 1989). The same is true in this species for the rhythm in body temperature (Binkley et al. 1971).

POSSIBLE NATURE OF EXTRA-PINEAL OSCILLATORS

Above, evidence has been presented that melatonin is a transducer of circadian information from the pineal to the rest of the circadian system. It must be asked, therefore, whether melatonin is produced only by the pineal or whether there are extra-pineal sources of periodic melatonin secretion that may account for the continuation of circadian rhythms after pinealectomy in some species. Results obtained from pigeons (in which pinealectomy does not abolish circadian rhythms) have shown that indeed a rhythm of plasma melatonin was still present in pinealectomized birds. It was due to periodic melatonin production and secretion in the retina as shown by the fact that binocular enucleation of pinealectomized pigeons abolished the plasma melatonin rhythm (Ebihara et al. 1987). Simultaneously, the rhythm in locomotor activity also disappeared. These results as well as several other observations indicating an almost complete parallelism in the behaviour of the circadian rhythms of plasma melatonin and locomotor activity are indeed consistent with the hypothesis that the activity rhythm is a result of the rhythm in plasma melatonin, although other mechanisms are also possible (see below).

It must be emphasized that most of the evidence available for a direct and exclusive control of activity rhythms by the rhythm in plasma melatonin is based only on correlations. The results obtained in studies by Underwood and Siopes on quail indicate that this kind of correlational evidence must be treated with extreme caution. Like pigeons, quail sustained a circadian rhythm in locomotor activity after pinealectomy and a plasma melatonin rhythm also persisted (albeit with a decreased amplitude). If pinealectomized quail were blinded, both the rhythms in plasma melatonin and activity disappeared, consistent with the findings in pigeons (Underwood & Siopes 1984, Underwood et al. 1984, Underwood & Goldman 1987). Still it is not the periodic melatonin secretion from the eyes and the pineal that is important in this species because sectioning of both optic tracts sufficed to abolish locomotor activity rhythms, in spite of the fact that the plasma melatonin rhythm remained entirely intact in these birds (Underwood & Siopes 1985, Underwood et al. 1990). Further evidence suggested that each of the quail's eyes contains a circadian clock that transmits its circadian information directly and presumably neuronally to the brain (Underwood et al. 1990).

Extra-pineal periodic melatonin secretion is also excluded as an explanation for persisting behavioural rhythms in pinealectomized starlings. First, measurements of plasma melatonin levels have shown that pinealectomy in this species (in contrast to the pigeon and the quail) rendered plasma melatonin levels basal and arrhythmic both in LD and in DD (Janik et al., unpublished). There is also no evidence for a resumption of the plasma melatonin rhythm some time after pinealectomy that might explain the

improvement of circadian patterns often observed in pinealectomized starlings six to eight weeks after pinealectomy (Gwinner 1978). Even one month and three months after pinealectomy melatonin levels were consistently basal in pinealectomized starlings showing rhythms in feeding and hopping (Janik et al. unpublished). Secondly, persisting free-running circadian rhythms of locomotor activity and feeding could be observed in intact starlings that were chronically treated with melatonin, applied subcutaneously through silastic tubes. This treatment lead to an almost one hundred fold increase in plasma melatonin levels above the average levels and completely abolished or masked the endogenous melatonin rhythm (Beldhuis et al. 1988). A role of periodic melatonin for the persisting rhythm of locomotor activity is also excluded for the chicken in which pinealectomy abolished the rhythm in plasma melatonin (Pang et al. 1974, Pelham 1975) but not that of activity (MacBride 1973).

In conclusion then these results indicate considerable differences among species, both in the extent to which nonpineal melatonin is secreted into the bloodstream and in the extent to which periodic extra-pineal melatonin secretion may play a role in sustaining circadian rhythmicity. In a few species (e.g. the quail, the starling) all evidence suggests that those circadian rhythms that persist after pinealectomy are not due to periodic melatonin secretion.

Extensive investigations in mammals have revealed that the suprachiasmatic nuclei (SCN) in the hypothalamus contain a major circadian pacemaker (Rusak 1989 for review) and some investigations suggest that homologous brain areas may play a role as oscillators in birds as well. Lesions in the medial hypothalamus of House Sparrows, Java Sparrows and quail sometimes resulted in the abolition of free-running circadian activity rhythms similar to (but not entirely identical with) the effects of SCN lesions in mammals (Takahashi & Menaker 1979a,b, 1982, Takahashi 1981, Ebihara & Kawamura 1981, Simpson & Follett 1981). However, the data-base in these studies is small and the identity of the hypothalamic structures involved is still a matter of debate. In fact, either of two nuclei, one in the medial and another one in the lateral hypothalamus, may be homologous to the mammalian SCN (for discussions see e.g. Ebihara et al. 1987, Cassone & Moore 1987, Norgren 1990). The distribution of neurotransmitters and neuropeptides in these two nuclei does not allow an unequivocal answer to this question (Norgren & Silver 1989). However, the fact that it is the lateral nucleus which receives direct retinal input, just like the mammalian SCN (e.g. Cassone & Menaker 1984, Cassone & Moore 1987), that this nucleus contains melatonin receptors (Rivkees et al. 1989, Stehle 1990) and that its metabolic activity shows a daily rhythm, argues in favor of this structure as being homologous to the mammalian SCN (Cassone 1988). Unfortunately, in the lesion studies carried out so far on birds the lesions were so large that structures other than the medial hypothalamus were presumably affected as well.

SYNTHESIS AND CONCLUSION

The data reviewed in the previous sections have revealed a remarkable diversity in the relative contribution of at least three structures to avian circadian systems: the pineal, the eyes and hypothalamic structures that may be homologous to the mammalian SCN (subsequently: "SCN"). There is good evidence that these three structures are normally interconnected: The SCN contains melatonin receptors, at least in

the chicken and the Java Sparrow (Rivkees et al. 1989, Stehle 1990) and hence is presumably affected by the periodic output of melatonin from the pineal and the eyes. It also receives input from the retina via a direct retino-hypothalamic projection (Cassone & Menaker 1984, Cassone & Moore 1987). The pineal is connected with the SCN through a multisynaptic pathway via the superior cervical ganglion (SCG; Oksche 1980) but possibly also by an additional pathway that is not mediated by the SCG (Herbute & Bayle 1970). The melatonin content of the retinae, finally, is affected by light impinging upon the head, suggesting that encephalic and/or pineal photoreceptors convey information to the eyes (Max et al. 1986).

On the basis of these findings it was proposed that the avian circadian system is a "neuro-endocrine loop" and that the overt rhythms normally result from the mutual interactions of oscillators residing in the pineal, the SCN and, at least in some cases, the eyes (Cassone & Menaker 1984). Details about the way in which these components interact are unknown but at least hypothetically most of the above mentioned species' differences might be explained as resulting from differences in the relative contribution of the various components of the system. Based on the general concept of a neuro-endocrine loop, the more specific "internal resonance model" was proposed (Gwinner 1989). It assumes that the oscillators in the pineal and those in the SCN (and/or the eyes) amplify each other through resonance. On the assumption that the SCN-oscillator is more directly involved in the control of overt rhythms than the pineal, the variable effect of pinealectomy on circadian rhythms in different species can be explained as a consequence of differences in the strength of the SCN-oscillator, i.e., its dependence on periodic melatonin input.

The question remains of why the relative contribution to the overall circadian system of the various structures discussed above shows such a high species specificity in birds. With the few species yet studied it is obviously difficult to draw generalizations about possible ecological or taxonomic relationships. Still, the available data suggest that the pineal and its hormone melatonin may play a dominant role only in passerines. But even in passerines there are considerable and as yet unexplained differences between species. Why is the starling circadian system so much less dependent on the pineal than that of the other species and why is the starling's rhythm in food-uptake so much less dependent on the pineal than the rhythm in locomotor activity? Since the starling is a primarily insectivorous and frugivorous species, whereas all the other passerines studied are primarily granivorous, different dietary adaptations may play a role, but with the few species studied such conclusions are obviously premature. What is needed is an extension of the comparative studies to other carefully selected taxonomic and ecological groups. When designing these comparative studies, it might be useful to also consider the situation among reptiles, particularly lizards in which there seems to be a similar diversity as in birds (Underwood & Goldman 1987).

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INVOLVEMENT OF THE PINEAL GLAND IN AVIAN REPRODUCTIVE AND OTHER SEASONAL RHYTHMS

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ABSTRACT. The pineal gland is known to be a pacemaker of circadian rhythms in birds but its involvement in the annual rhythms is not clear. In the present paper the role of the pineal has been reassessed and reinterpreted in the light of recent findings in tropical birds. It is fairly certain that the pineal may have a role, marginal or strong, in the regulation/modulation of avian reproductive cycle, most likely as a transducer of photoperiodic information. An intact pineal seems to be necessary for coping with the daily/seasonal fluctuations in environmental temperature and with environmental stress. An intact pineal also appears to be required for the expression of circannual rhythms (in the absence of external L:D synchronisation) especially the neurally regulated behavioral rhythms like feeding. Obviously the pineal gland is involved to a much greater extent in the adaptive physiology of birds than hitherto believed.

INTRODUCTION

The phenomenon of seasonality observed in various behavioral and physiological attributes of organisms constitutes an adaptive measure to cope with the seasonally fluctuating environment which derives from the rotation of the earth around the sun. Thus successful propagation of species depends on adequate timing of reproduction with the environmental factors most conducive for the upbringing of the offspring e.g. availability of food. And the other characteristic seasonal events like migration, fattening, molting etc. are adjusted, in accordance with the annual energy budget, to the demands of their seasonally changing environment, tropical or temperate.

Among the abiotic factors in the environment the importance of daylength as a stimulus for the initiation of breeding and other seasonal phenomena in birds of middle and high latitudes is well documented (reviews, Farner 1970, Farner & Follett 1980, Murton & Westwood 1977). But in the tropics the role of photoperiod as an environmental cue was totally ruled out by earlier researchers and rainfall was believed to be the environmental factor regulating sexual cycles (Baker 1938, Misra 1948, Marshall 1961, Immelman 1971, Thapliyal 1978). However, in the last several years extensive and intensive experimental studies on some excellent Indian models have clearly established that birds at relatively low latitudes are capable of very fine discrimination of photoperiodic information and that the annual photocycle may indeed time the breeding season to coincide with periods of ample food availability e.g. monsoon (June to September) (reviews, Chandola et al. 1982a, 1983, 1985a, b; Chandola-Saklani et al. 1988a, 1990; Chakravorty et al. 1985.).

The photoperiodic information in birds, as in other vertebrates, perceived through photoreceptors, is translated into physiological terms through the mediation of the

neuroendocrine system. The pineal gland constitutes an integral component of this photoneuroendocrine system governing reproduction in mammals (Reiter 1980, Hoffman 1981). The results obtained on the significance of the pineal in avian photic responses and sexual cycles, however, are discrepant (progonadal, antigonadal, no effect) and generally considered somewhat controversial (Gwinner et al. 1981, Ralph 1981). Considering that the pineal serves as a pacemaker in circadian systems of passerines and that a circadian system is implicated in the culmination of seasonal cycles in photoperiodic birds one would assume participation of this gland, at some level, in control of seasonal rhythms. Also, considering that birds with the invasion of diverse ecosystems have evolved diverse adaptive mechanisms several times, we do not find the varied effects of the pineal in birds astonishing. Castration effects, for example, may produce varied responses in the same bird (Singh & Chandola 1981). The avian thyroid also is known to have differential effects not only in different species but between sexes of the same species (Kar & Chandola-Saklani 1985, Lal & Thapliyal 1985). In our opinion the involvement of the pineal gland in the phenomenon of seasonality in birds needs to be re-examined and reinterpreted especially in the light of some recent findings in tropical birds. The present review serves such a purpose.

EFFECT OF PINEALECTOMY ON SEASONAL CYCLES OF PASSERINES

So far ten species of birds have been investigated for the effects of pinealectomy on seasonal cycles and/or photogonadal response, nine among them passeriforms. The reader is referred to Gwinner et al. (1981) and Ralph (1981) for details. Surprisingly very few studies have been made on the effect of pinealectomy under natural conditions. Most of the experiments were performed under drastically abnormal lighting conditions which birds never experience in their life. Effects on complete reproductive cycles have been studied in detail only in four passerines viz., migratory Starling *Sturnus vulgaris* and bunting *Emberiza bruniceps*, and nonmigratory subtropical populations of Baya Weaver *Ploceus philippinus* and Spotted Munia *Lonchura punctulata* with information on effects on seasonal fattening being available in the bunting and Spotted Munia. Data on pinealectomy effects on seasonal food intake and molting have been provided in Spotted Munia and Starling, respectively.

Baya Weaver (Ploceidae)

The baya is an early monsoon breeder. Irrespective of latitudinal distribution, from 10°N to 30°N, the characteristic gonadotrophin-dependent nuptial plumage makes its appearance in April with increasing daylength associated with a slow increase in hypothalamic LH-releasing hormone (Malhotra et al. 1979), plasma LH, testosterone and gonadal development (Acharya et al. 1988, Pavgi & Chandola 1981, Chandola-Saklani et al. 1990). Gonads reach peak by June and regression ensues thereafter depending on the latitude (Chandola-Saklani et al. 1990). Experimental results indicate that long photoperiod is a prerequisite for gonadal development in this bird. It is clear now that increasing daylength (through direct stimulation of hypothalamo-hypophysial system) prepares the bird physiologically for reproduction i.e. completion of development of gonads, accessory and secondary sex characters, and the monsoon rainfall may provide the final trigger for overt activities like frenzied nest-building and egg laying. (Chandola et al. 1985a, b; Chandola-Saklani et al. 1988a, 1990; Chakravorty et al. 1985, Pavgi & Chandola 1981, Sharma 1987). Increasing daylength also programmes the post reproductive refractory phase in this bird (Chandola & Chakravorty 1982, Chandola-Saklani et al. 1990, Chakravorty & Chandola-Saklani 1985, Bisht 1987).

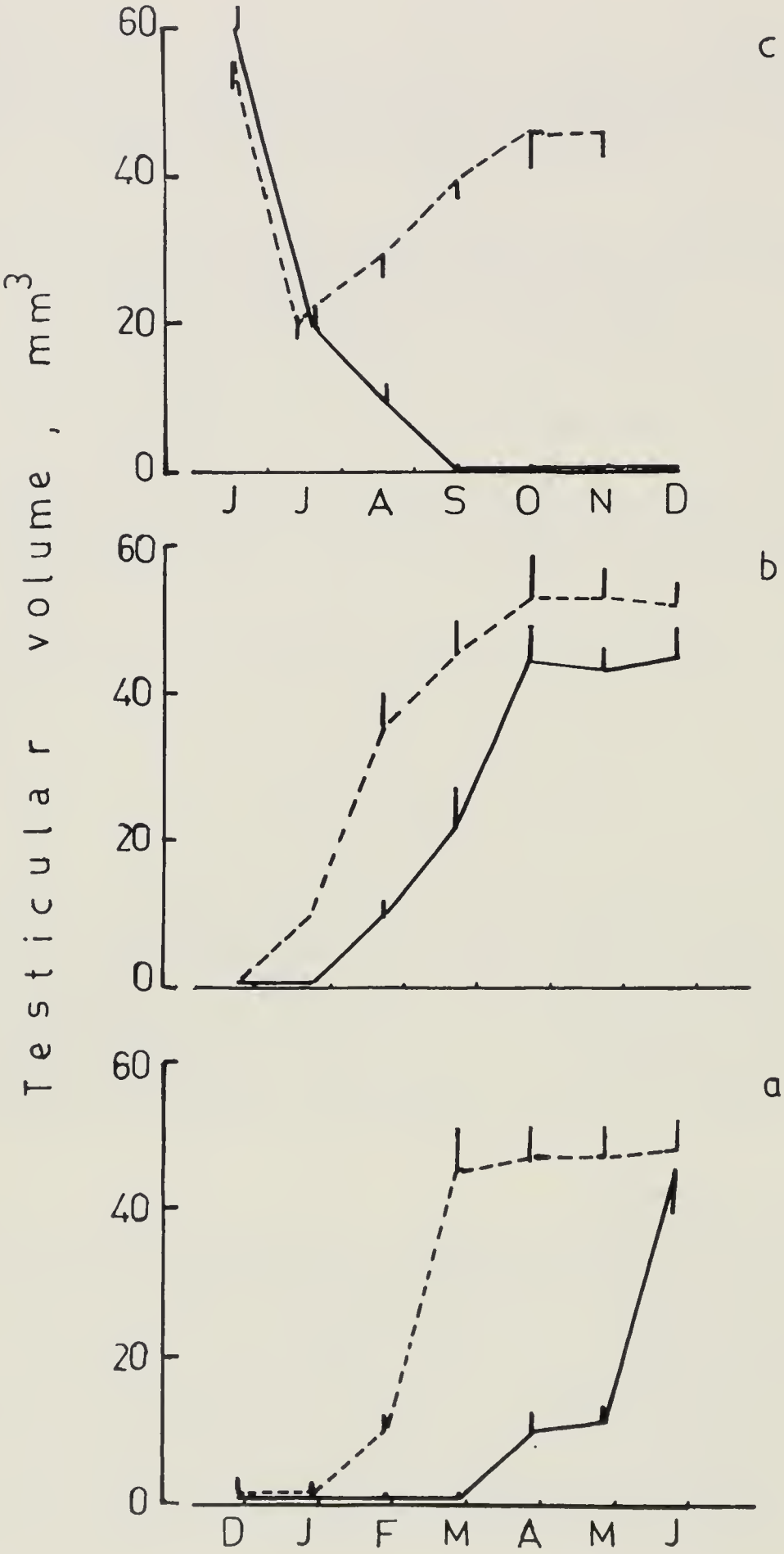


FIGURE 1 – Effect of pinealectomy on the testicular cycle of Baya Weaver in natural daylength (NDL), long (18L:6D)) and short days (9L:15D). Vertical bars indicate SE of means. --o Pinealectomised, o—o sham-operated controls. After Balasubramanium & Saxena 1973.

Long-term experiments to study the role of the pineal were carried out in the Baya Weaver by Saxena's group (Balasubramaniam & Saxena 1973, Balasubramaniam 1977, Saxena 1977, Saxena et al. 1979). Pineal removal during non-breeding phase caused early recrudescence of gonads in birds held on natural daylength or stimulatory long photoperiods. When birds were pinealectomised during breeding the period and held on non-stimulatory short days gonads initially regressed as in controls but redeveloped later to almost full size (Figure 1 a, b, c). This is identical to the long-day response of bayas during this period when refractoriness has set in but the regressing gonads can still be stimulated by long days after an initial delay (Singh & Chandola 1982). Subsequently pinealectomy effects in bayas were shown to be mediated via hypothalamic LHRH and pituitary LH (and possibly FSH) (Saxena et al. 1979). Obviously the pineal gland seems to have a strong antigonadotrophic effect in Baya Weaver, the reproductive cycle of which is directly driven by the photoperiod. Also pinealectomy seems to produce the same response as that of long days.

Bunting (Emberizidae)

The Red-headed Bunting is a migratory species which winters in India departing for the breeding grounds by mid April. They breed over a vast area ranging from west Asia to east Europe (Ali 1964). The gonads begin to develop in spring while still in the wintering grounds and in captive birds, not allowed to migrate, reach peak in June followed by regression. These birds are primarily photoperiodic exhibiting the typical long and short day responses and a photorefractory phase (Thapliyal et al. 1983, Lal & Thapliyal 1985).

Pinealectomy effects on seasonal gonadal and fattening cycles have been studied most extensively in buntings by Lal (1987). When pinealectomy was performed during the non-breeding phase (November or January) in birds held on natural daylength, gonadal growth in spring was significantly accelerated. Gonadal regression was not significantly different from that in controls (Figure 2a,b) and birds entered the next cycle at the same time as the intact controls. The body weight cycle was significantly influenced in that the pinealectomised birds were heavier in general.

Pinealectomy had no effect on testicular size if performed during progressive, peak and regression phases of the gonadal cycle under ambient conditions, although gonads of birds pinealectomised in May (when maximal size had been attained) regressed earlier most likely indicative of an early onset of photo-refractoriness (Figure 2c). Pineal ablation failed to exert any influence on gonadal cycle of birds maintained in either stimulatory long or inhibitory short day-lengths (Figure 2d). The body weight cycles of these birds, however, showed differences as compared to the controls.

It is obvious that in Red-headed Bunting, which is strongly photoperiodic, the pineal gland exerts marginally anti- or pro- gonadal or no effects, all in one bird. It is clear from Lal's findings that the effects of pineal ablation may be expressed depending on the seasonally varying physiological status of the bird. This may explain the failure of response in some earlier studies. Further, the effects of pinealectomy mimic the effects of long days (gonadal recrudescence and onset of refractoriness) in ambient conditions which may be masked in artificial long days. Effects of pineal ablation on fattening are quite significant like in Spotted Munia.

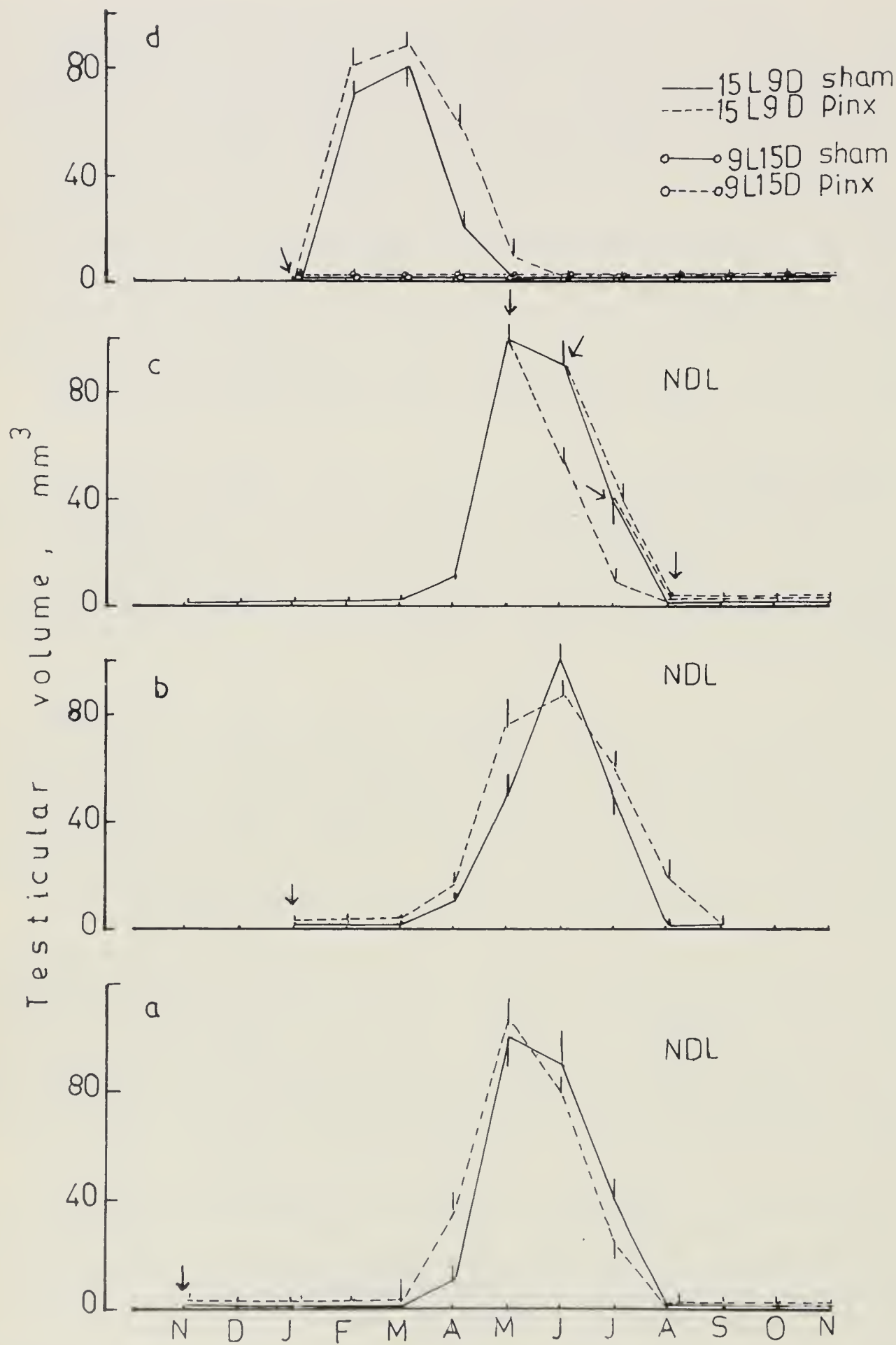


FIGURE 2 – Effect of pinealectomy on testicular cycle of buntings held in ambient daylength (a, b, c, NDL) and constant long (15L:9D, d) or short (9L:15D, d) days. Arrows indicate time of pinealectomy. o-o pinealectomised, o—o sham-operated controls. After Lal 1987.

Starling (*Sturnidae*)

Gonadal development in these birds begins in early spring marked by increased plasma LH levels and is complete by April followed by a state of photorefractoriness (Dawson & Goldsmith, 1982). The reproductive cycle of Starlings is controlled by annual photoperiod.

Effects of pinealectomy in this bird have been most extensively studied by Gwinner's group (Gwinner & Dittami 1980, 1982, Gwinner et al. 1981). In birds held on 12L:12D over 16 months pineal ablation during progressive phase did not affect gonadal growth but led to a somewhat earlier regression accompanied by an earlier molt. Interestingly these birds failed to undergo a second testicular cycle as in controls (Gwinner & Dittami 1980).

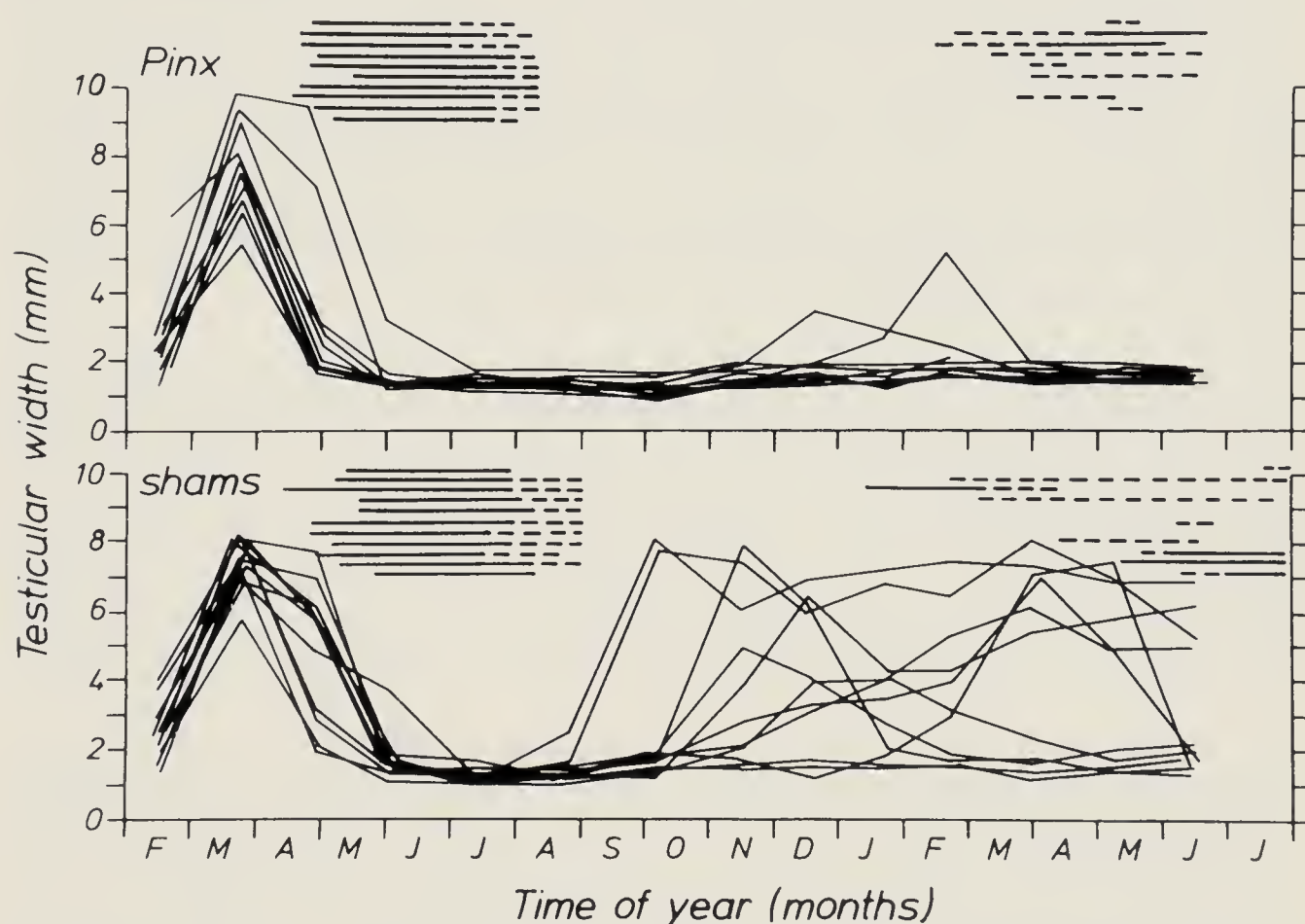


FIGURE 3 – Effect of pinealectomy on the testicular cycle of individual Starlings held in 12L:12D. After Gwinner & Dittami 1980.

Gonads of birds pinealectomised during peak of gonadal development and exposed to simulated annual photocycle, with a periodicity of three months, did not differ in any way from the controls in the same regime. Similarly pinealectomy when performed in post-reproductive refractory birds exposed to a photoperiodic regime described above but with six and nine month periodicity had no effects on the gonadal cycle. In another set of experiments pineal removal failed to influence the normal long-day induced testicular growth except in continuous low intensity illumination of 0.2 lux where gonadal growth was considerably slowed in pinealectomised birds (Gwinner et al. 1981).

The above results when considered overall may appear rather insignificant suggesting an apparently marginal role, if any, but in our opinion the early regression of gonads in 12L:12D accompanied by the failure of gonads to show another cycle are actually

quite drastic in that the process of onset of photorefractoriness was accelerated in pinealectomised birds and they failed to break it subsequently.

Spotted Munia (*Estrildidae*)

These munias are sedentary species distributed from 8° to 30°N in the Indian sub-continent, are late monsoon breeders and, in captivity, exhibit parallel gonadal and fattening cycles which are inversely related to the cycle of food intake (Chandola et al. 1980, Bhatt & Chandola 1985). Gonads begin to develop in May/June reaching peak by September followed by regression in October/November attaining minimal values by December. Customary long and short days have no effect on the gonads but in conditions of continuous dark or illumination (LL) birds become desynchronised and show distinct free-running circannual rhythms with a periodicity of about 10 months indicating that the reproductive cycle is an endogenous autonomous rhythm which requires daily alternation of light and dark periods for synchronisation with the calendar year (Bhatt & Chandola 1985, Chandola et al. 1975, 1982b, 1983). Subsequent investigations revealed that the circannual rhythm may actually be synchronised by daylength (Chandola et al. 1985, Bhatt et al. 1986). It must be emphasised that in this bird photoperiod is not a prerequisite for generating the rhythm (as e.g. in baya, bunting, starling and many other photoperiodic birds) but merely adjusts (entrains) the underlying free running rhythm with the environmental cycle.

Considering that effects of pinealectomy on circadian rhythms become evident only in LL or DD conditions with the availability of a bird model (Spotted Munia) showing clear-cut circannual rhythm in LL it now became possible to examine whether the discrepant results obtained in studies of pinealectomy effects on avian reproduction so far (viz., progonadal, antigonadal, no effect) may be attributable to the masking effects of different LD conditions used. Effects of pinealectomy were, therefore, studied in Spotted Munia in free running (LL 300 lux; constant temp. $27 \pm 2^\circ\text{C}$) as well as ambient conditions over 18 months (Chandola-Saklani et al. 1988b, Pant et al. 1990).

Surprisingly pinealectomy had no effect on reproductive and fattening rhythm (apart from a lowering of amplitude in the latter, Figure 4a,b) in LL but had marginal effects on reproductive cycle (accelerated slightly but significantly gonadal growth and delayed complete regression) and drastic effects on fattening cycle (arrhythmia with higher minima, Figure 4b) in entrained NDL condition. Birds which showed pinealectomy effects in the first cycle (NDL) entered the next testicular cycle simultaneously with the intact controls. Also effects on gonadal cycle in NDL were not evident if pinealectomy was performed during peak breeding condition (Figure 4a). Pinealectomised birds in LL did not show the characteristic hyper- or hypophagia, the rhythmicity in food intake becoming abolished (with lowered maxima). There was no difference in the food intake cycles of sham operated and pinealectomised birds in NDL (Figure 4c).

The fact that pineal removal exerts its antigonadal influence on the reproductive cycle, however little, in entrained condition only and not in LL indicates that the effects on the overt reproductive cycle in entrained NDL conditions may not be through the circannual oscillator. In other words, the pineal may play a role, if any, only in photoperiodic synchronisation of the circannual rhythm and not in its production. Also the pinealectomy effect on gonads, like in buntings, indicates a seasonal variation in response.

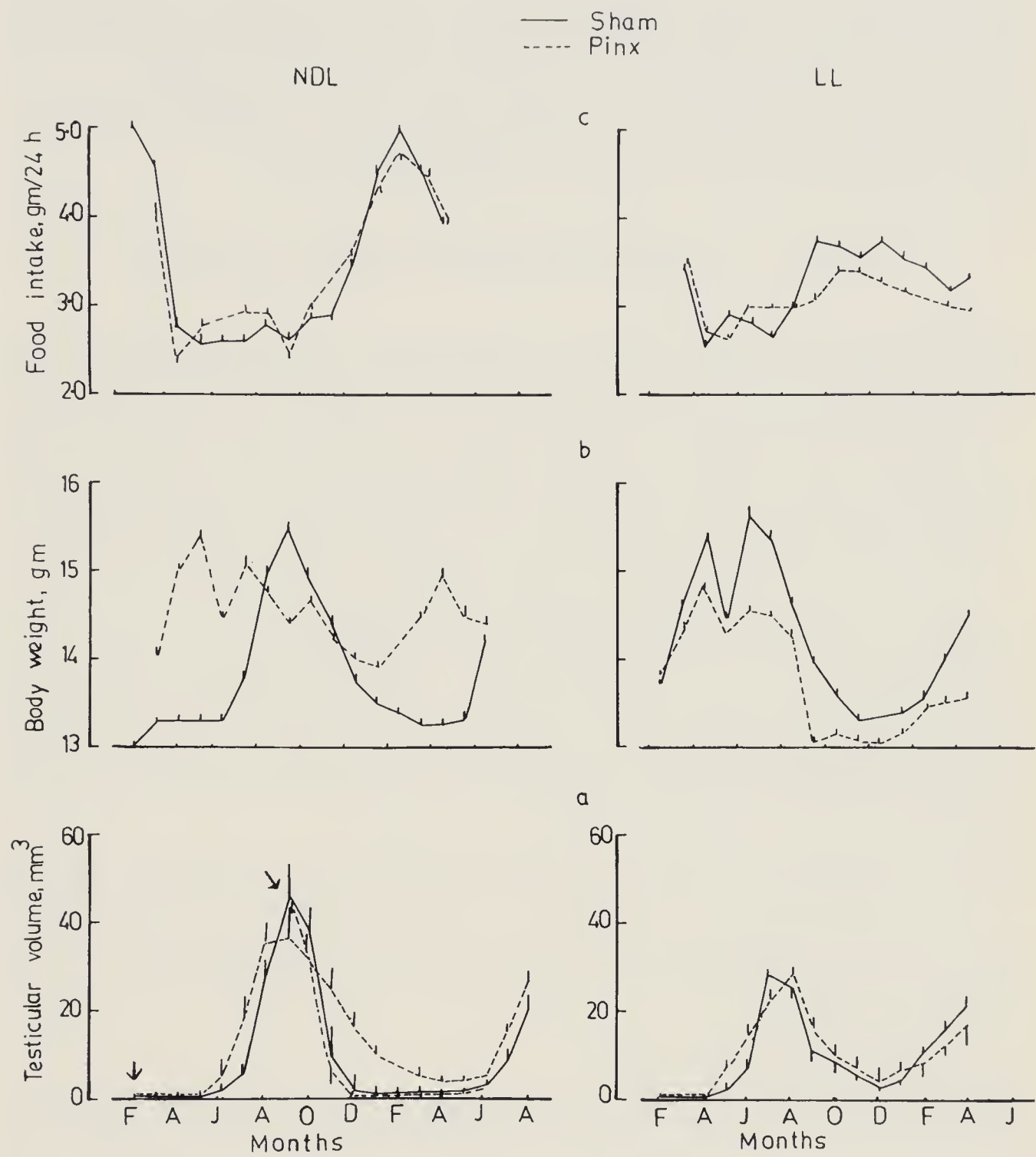


FIGURE 4 – Effect of pinealectomy on seasonal testicular (a), body weight (b) and feeding (c) rhythms of Spotted Munia in entrained natural daylength (NDL) and free running conditions of continuous illumination (L:L 300 lux,; 27 ±2°C). Arrows indicate time of pinealectomy. o--o pinealectomised, o—o sham-operated controls. After Bhatt et al. 1988; Pant et al. 1990 and unpublished.

The rather drastic disturbances in body weight of pinealectomised birds in NDL exposed to the extremes of annual temperature (Figure 4b), however, suggest that the presence of pineal may be crucial for physiological adaptations to daily fluctuations in certain environmental factors e.g. temperature. Similarly from effects on food intake it can be concluded that the stressful effect of LL treatment (as evident from lowered food intake) is exaggerated in the absence of pineal (Figure 4c). Overall effects of pinealectomy on seasonal rhythms of Spotted Munia indicate an alteration in the

phase relationships of various rhythms in entrained as well as free running conditions (Bhatt & Chandola 1985, Chandola-Saklani et al. 1988b). This may be interpreted as the pineal gland being important in the temporal spacing of various cycles along the annual scale via so-called circannual oscillators or through peripheral effects, or, more likely, may merely reflect inability to handle stressful situations like constant illumination or temperature fluctuations in the absence of the pineal.

A ROLE FOR THE PINEAL IN AVIAN SEASONAL CYCLES

Findings described in the preceding section can be summarised as follows:

- 1) Pineal removal may have marginal or drastic effects on seasonal reproduction depending on the species. Pro- or antigonadal or no effects may be obtained in the same bird depending on the time of surgery in the year. This may explain failure of response in several earlier studies. There are also indications that pinealectomy may advance or cause photo-refractoriness. Pinealectomy effects observed in the first reproductive cycle are compensated in the next cycle indicating the pineal may only be indirectly involved. That the pineal does not influence the circannual oscillator governing reproductive cycle is clear but it may be involved in the process of photoperiodic synchronisation.
- 2) Pinealectomy drastically affects seasonal body weight cycle in L:D conditions and food intake in L:L in birds examined so far. It seems the absence of the pineal renders the birds more sensitive to strong fluctuations in environmental temperature or to stress of abnormal light conditions. Pineal ablation also results in alteration in the phase relationship of annual gonadal fattening and feeding rhythms in entrained or free running conditions.

It is fairly obvious from above that a) the pineal may have a role, marginal or strong, in the regulation/modulation of reproductive cycle - most likely as a transducer of photoperiodic information; b) an intact pineal is required for coping with the daily/seasonal fluctuations in other environmental factors (e.g. temperature) as well as environmental stress.

Pineal versus photoperiodic effects

From the detailed discussions on the effects of pinealectomy and those of photoperiod in birds described in the preceding section it appears that pinealectomy mimics long day response e.g. like long days it shows seasonal response depending on the physiological status of the bird, it causes gonadal recrudescence (baya, bunting, Spotted Munia, and even White-crowned Sparrow (Kobayashi 1969, Oksche et al. 1972) and to some extent accelerates onset of refractoriness (Starling, bunting, even duck in the first cycle, Cardinali et al. 1971) the two typically photo-dependent events. An inhibitory action of light on the pineal gland, similar to that observed in mammals, could explain these effects. This assumption must, of course, be tested before drawing final conclusions. In the present context it is indeed remarkable that pinealectomy should similarly mimic the effects of strong light on the circadian rhythms of motor activity in birds - both treatments leading to arrhythmia or lengthening of activity period. Obviously for an explanation we must await information on the mechanisms and modes of interaction of light reception and the neural components of the photoperiodic clock.

There are several possibilities through which the pineal may exert its effects on the reproductive cycle. Photoperiodic control of seasonal cycles in birds through interaction with circadian components is well known (Hamner 1964, Follett et al. 1981) and has been demonstrated in baya and buntings also (Singh & Chandola 1983, Tewary et al. 1982). Although no data are available on the effects of pinealectomy on the circadian photoperiodic time-measurement system the photoperiodic responses and effects of pinealectomy observed in these two birds (and Starlings) are compatible with the possibility that the pineal may affect annual cycles via the circadian system. This attractive possibility, thoroughly discussed by Gwinner et al. (1981), however, remains only hypothetical until direct evidence is available.

The other possibility, not mutually exclusive, may be through a direct inhibitory effect of the pineal on the reproductive cycle. Especially in tropical birds like the Spotted Munia in which the reproductive cycle is relatively independent of photoperiod (yet governed by it !), the underlying rhythm running with a periodicity of ten months in LL, a marginal stimulus so as to bring about a phase-shift of one to two months may be sufficient to entrain the entire cycle with the environment. It remains to be seen whether the pineal under the influence of daylength could provide such a stimulus.

Pineal and daily/seasonal environmental fluctuations

Our findings, in harmony with those of Lal (1987) on the effect of pineal ablation on seasonal fattening in birds held in ambient conditions (not in those held in constant LL and temperature, Figure 4b), suggest that the pineal may somehow render the organism more capable of handling daily/seasonal environmental fluctuations in temperature. Not only that, the data on food intake in the birds held on LL (Figure 4c) clearly show that in the absence of pineal birds are more vulnerable to the stressful effect of the abnormal photo-regime on this parameter. Some of the apparent effects of pinealectomy on uncoupling of various circannual/annual rhythms e.g. in gonadal function, fattening and feeding, may be explained on this simple basis.

Alternatively an intact pineal, in the absence of external L:D synchronisation, may be a prerequisite for the expression of behavioral rhythms like feeding but not for other rhythms like in body weight which is a nonspecific general parameter. In other words pineal may be involved to a greater extent in rhythms which are neurally regulated (feeding) than those (body weight) regulated by various metabolic factors peripherally. This would be understandable considering the nervous nature of the pineal. It has become clear from this review that the pineal gland may have a much greater role in the adaptive physiology of birds than hitherto believed.

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PINEAL INVOLVEMENT IN AVIAN THERMOREGULATION

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ABSTRACT. The pineal affects avian thermoregulation in at least two different ways. It directly influences the circadian variation of body temperature suggesting that the pineal and its compound melatonin may interact with the 'set-point' mechanism for thermoregulation in birds and may thus be essential for the expression of diurnal variations in body temperature. Besides these rather acute effects of the pineal on avian thermoregulation there is also recent evidence that the pineal gland and melatonin are involved in photoperiod-induced seasonal improvements of thermoregulatory properties in birds. This dual role of the pineal for thermoregulation indicates that the pineal serves as an endocrine interface for birds to adjust thermoregulation and energy requirements according to seasonal changes in the photoperiod.

Keywords: Circadian rhythms, body temperature, metabolic rate, heat production, cold tolerance, adaptation, seasonal acclimatization, shivering, nonshivering thermogenesis.

PINEAL AND MELATONIN CIRCADIAN RHYTHMS

The pineal gland of birds acts as a major neuroendocrine interface for circadian rhythms. It produces and releases melatonin during the night and this endocrine signal is largely responsible for circadian entrainment to a light dark cycle. Depending upon the species studied, pineal melatonin is also involved in the maintenance of free running circadian rhythms in constant conditions (Underwood 1978 for review). The pineal gland is not the only source for systemic levels of melatonin, since at least the retina and the Harderian glands can also synthesize melatonin. In pinealectomized Pigeons the nocturnal rise of melatonin was reduced by 60% and in Chicken it was abolished completely following pinealectomy (Vakkuri et al. 1985, Osol et al. 1985, Coghburn et al. 1987). However, within six weeks following pinealectomy retinal melatonin synthesis increased and compensated partly for the lack of pineal melatonin (Vakkuri et al. 1985, Osol et al. 1985). This indicates that the pineal is the major source of melatonin but other oscillating sources of melatonin like the retina may also contribute to the circadian pattern of melatonin (Underwood & Siopes 1985).

It is still an open question how melatonin exerts its effects on the circadian system. Melatonin is secreted into the blood but it is unlikely that it acts as a peripheral hormone. It affects physiology and behaviour of the entire organism and this multifactorial nature of responses indicates a mediatory action on the brain and for other endocrine glands. Recently, a large number of binding sites for melatonin have been located in the avian brain, predominantly in visual and auditory areas (Rivkees et al. 1989). This is different from the situation in mammals where melatonin receptors could only be located in the median eminence and the suprachiasmatic nuclei (Vanecek et al. 1987). The reason for this discrepancy is not known. But it is coincident with the observation that pinealectomy or melatonin treatment generally causes much larger effects on the circadian system of birds than in mammals. In the latter mainly photoperiodic responses are affected by removal of the pineal treatment with melatonin (Heldmaier & Lynch 1986).

Most evidence on the pineal involvement in circadian rhythms was obtained from the effect of pinealectomy on locomotor activity rhythms. Pinealectomy or chronic implants with melatonin caused arrhythmicity or period changes of free running locomotor activity rhythms in several species of sparrows, Pigeons and Starlings (Takahashi & Menaker 1979, Ebihara & Kawamura 1981, Ebihara et al. 1984, Gwinner et al. 1987). Daily injections of melatonin could entrain the free running activity rhythms of Starlings (Gwinner & Benzinger 1978), and transplantations of pineals into the eye of pinealectomized arrhythmic House Sparrows initiated locomotor activity rhythms which coincided with the phase of the donor birds' rhythms (Zimmermann & Menaker 1978). However, the pineal is not the only site of the circadian clock, since destruction of the avian SCN could abolish free running rhythms in the Java Sparrow (Ebihara & Kawamura 1981). In Quails blinding abolished circadian rhythms of locomotion whereas pinealectomy had only little effect suggesting that in this species the eyes are involved in circadian organization much more than being merely a photosensor (Underwood & Siopes 1985). These findings suggest that the circadian organisation of locomotor activity rhythms is based on the interaction of several endocrines and brain areas, including the pineal, the avian SCN, the retina and some unknown extraretinal photoreceptors, and this interaction may vary between different species. Locomotor activity rhythms are used for this analysis because their circadian pattern can be easily monitored over prolonged periods of time. However, circadian changes govern the entire physiological and behavioural organisation of birds, including circadian changes of body temperature, metabolic rate, feeding, and endocrines.

Circadian rhythms of body temperature

Birds show rather large diurnal changes in body temperature with an amplitude of about 3°C. This is greater than in mammals which usually change their body temperature only by about 0.5 - 1°C (Aschoff 1982). The large circadian changes in body temperature of birds require considerable thermoregulatory efforts, involving circadian changes in heat production as well as heat loss. During the activity time of birds their resting metabolic rate at thermoneutrality is about 30% above rest time values and this difference is further enhanced during cold exposure (Aschoff & Pohl 1970). Diurnal changes in body temperature are further accompanied by an increase in total thermal conductance during activity time and lower conductance values in resting birds (Aschoff 1982).

The elevated body temperature during the activity period is not simply a byproduct of heat generated by locomotor activity, but is based on changes in the central "set-point" for temperature regulation. In Pigeons the thresholds for shivering and panting change as function of time of day. The spinal cord thermosensitivity for onset of shivering was reduced or largely abolished during the resting period, and also the interaction of autonomic and behavioural thermoregulatory responses varied between day and night (Schmidt et al. 1978, Graf 1980a, 1980b). These diurnal changes in physiological properties of thermoregulation can be explained on the basis of circadian changes in the "set-point" for thermoregulation.

In House Sparrows pinealectomy abolished free-running circadian rhythms of body temperature in constant darkness (Binkley et al. 1971). In this species pinealectomy also abolishes circadian locomotor activity in constant darkness, suggesting that the pineal is an essential part of the circadian organisation of locomotor activity as well as body temperature rhythms. In a light dark cycle the rhythms of body temperature and activity could be entrained. However, pinealectomy caused an increase in

nocturnal minimum body temperature (Figure 1). A similar effect was observed in pinealectomized Pigeons (John et al. 1978) as well as in Chicken (Cogburn et al. 1976). In the latter species the effects were very small and were only significant when several treatment groups were pooled, therefore data are not contained in Figure 1. The high body temperatures during the day were only slightly affected by pinealectomy, consequently the amplitude of circadian changes in body temperature was reduced following pinealectomy. Treatment with melatonin had the reverse effect, it lowered body temperature in Quails and compensated for the effect of pinealectomy in Pigeons (John et al. 1978, Saarela & Heldmaier 1987). In Quail this response to melatonin was only found in short photoperiod whereas in long photoperiod melatonin had no effect on the level of body temperature.

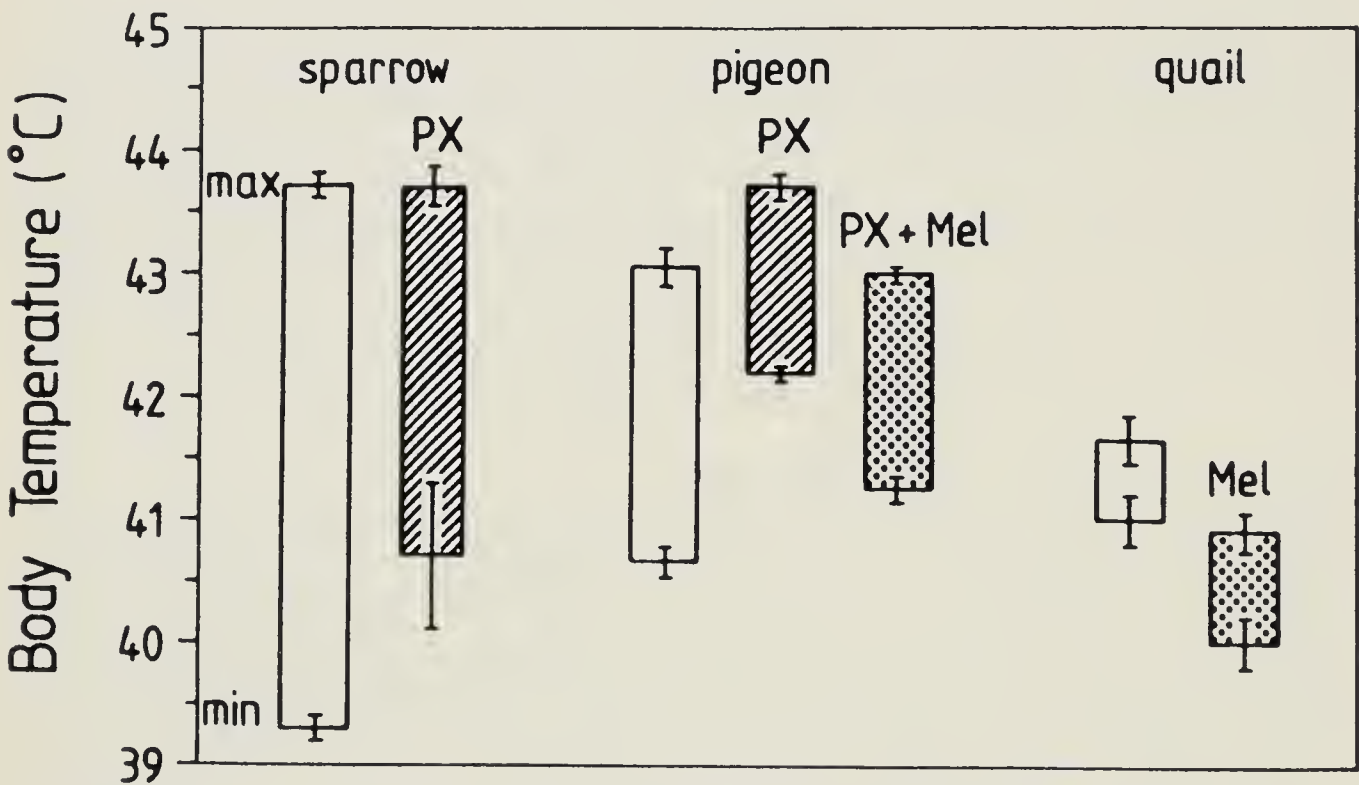


FIGURE 1 – Effect of pinealectomy (PX) and chronic treatment with melatonin (Mel) on circadian changes of body temperature of birds kept in a light dark cycle. The upper and lower end of the columns represent daytime (max) and night-time (min) body temperature. Sparrow data are from Binkley et al. 1972, Pigeon from John et al. 1978, and Quail from Saarela & Heldmaier 1987.

These responses to pinealectomy and chronic melatonin can only be explained by interference with circadian body temperature regulation, and are not simply the result of a hypothermic action of melatonin. In addition to these circadian effects on body temperature there is also evidence for a direct hypothermic action of melatonin. In Sparrows a single injection of 1 - 2.5 mg of melatonin caused a 4.7°C drop of body temperature within 30 min (Binkley 1986). Pinealectomized Chickens showed no major changes in body temperature; however, their heat tolerance was impaired especially during the scotophase (Cogburn et al. 1976, 1980). These findings suggest that melatonin may not only affect central thermoregulatory control but may further interfere with effector mechanisms of thermoregulation.

SEASONAL ACCLIMATIZATION

Cold tolerance

Winter acclimatized birds from temperate or higher latitudes can tolerate cold much better than during summer. This has been observed in House Sparrows, Evening Grosbeaks, Starlings and Pigeons (Hart 1962, Barnett 1970, Lustick & Adams 1977), American Goldfinches (Dawson & Carey 1976), Quails (Saarela & Heldmaier 1987), Greenfinches and Siskins (Saarela et al. 1989). Winter acclimatized birds could either tolerate much greater cold load (Hart 1962, Saarela & Heldmaier 1987, Saarela et al. 1989) or they showed prolonged survival time in the cold (Hart 1962, Dawson & Carey 1976).

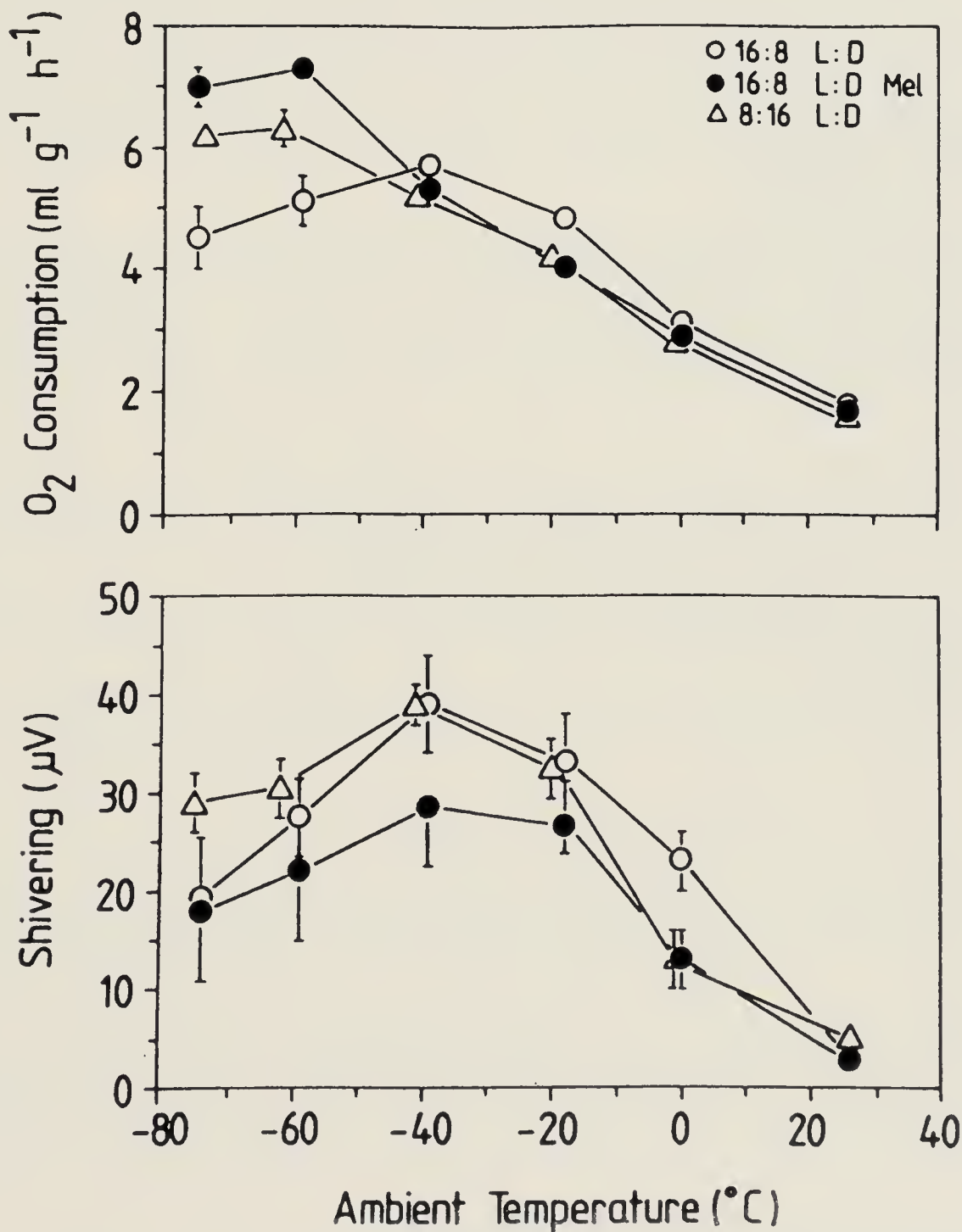


FIGURE 2 – Thermoregulatory responses of Quails acclimated for eight weeks to short photoperiod (L:D 8:16), long photoperiod (L:D 16:8) and implanted with melatonin in silastic capsules in long photoperiod. Data from Saarela & Heldmaier 1987, modified.

Small-sized birds have little capacity for thermal insulation and will therefore depend mainly on their metabolic capacity for heat production; hence seasonal acclimatization will primarily be a metabolic process. The maximum capacity for thermoregulatory heat production can be measured by exposing birds to a gradually lowered ambient temperature and simultaneously recording metabolic rate and body temperature. The lowest ambient temperature at which the birds can just maintain their body temperature is defined as the cold limit. The metabolic rate measured at this point will be the maximum capacity for thermoregulatory heat production. Using this procedure the cold limit of Siskins was found at -46.9°C in summer and improved to -61.2°C in winter. Corresponding values in Greenfinches were -32.6°C and -41.3°C , and in Quails -48°C and below -75°C , which was the lowest temperature of our equipment (Saarela & Heldmaier 1987, Saarela et al. 1989). With a similar setup the cold limit of American Goldfinches was found at about -30°C in summer and improved to $<-70^{\circ}\text{C}$ in winter (Dawson & Carey 1976). Three of these four species had a greater thermogenic capacity in winter. In the Goldfinch it was 1426 mW in summer and 1866 mW in winter. Corresponding values for Siskins were 1395 and 1518 mW, and for Quails 5134 and >7550 mW, respectively.

Winter acclimatized Goldfinches, Sparrows, and Evening Grosbeaks did not only show greater thermogenic capacities but they could maintain this elevated metabolic rate for a longer period of time. This indicates that in addition to capacity adaptation metabolic pathways were activated which enabled substrate supply and respiratory properties for sustained maximum metabolic rates (Hart 1962, Carey et al. 1978).

Seasonal acclimation requires that thermoregulation can be modified under the influence of environmental cues. Potential cues like temperature, photoperiod or food could either be responded to directly or they could act as a Zeitgeber for seasonal entrainment of endogenous circannual rhythms. The entrainment of seasonal changes in reproduction, migration or molt by the photoperiod is well documented (Gwinner 1989), but effects on temperature regulation have rarely been studied. In the Pigeon short photoperiod exposure caused an elevation in resting metabolic rate (Haim et al. 1979). This is similar to the response during cold adaptation, but is contrary to seasonal acclimation since winter acclimatized Pigeons had lowered metabolic rates (Hart 1962). In Quails no significant effects of photoperiod on resting metabolic rate at thermoneutrality were observed. But maximum metabolic rate in the cold as well as cold tolerance was improved following exposure to short photoperiod. A similar response was obtained in Quails treated with melatonin in long photoperiod (Figure 2). These results show that the photoperiod may act as a cue for seasonal acclimatization in birds and that pineal melatonin may be involved in the transduction of photoperiod i.e. information for seasonal adjustments of the thermoregulatory system. It can further be noticed in Figure 2 that thermal insulation of Quails did not change during acclimation, since slopes of cold induced metabolic rates were similar in all groups. This indicates that seasonal acclimatization of Quails is based entirely on thermogenesis.

Shivering versus nonshivering thermogenesis

The physiological background for this elevated capacity for thermogenesis is not known. In mammals brown fat has been found as a major organ site for seasonal thermogenic acclimation. Its mitochondria contain a unique uncoupling protein which allows maximum respiration without the formation of ATP and metabolic energy is

released as heat instead (Heldmaier et al. 1989). Birds do not possess brown fat and electromyography [EMG] does not show the mammalian type of nonshivering thermogenesis, i.e. an increase in heat production prior to the onset of shivering thermogenesis. In birds there is a close correlation between EMG and heat production at moderate cold (Figure 2 and 3). However, at temperatures below -20°C this clear proportionality is lost, indicating that an increasing amount of heat is produced without the electromechanical coupling to muscle fiber movements. This in turn suggests an alternative pathway for nonshivering thermogenesis in birds (Saarela & Heldmaier 1987). The EMG of melatonin treated Quails was less than the EMG of control birds at each temperature studied which is most obvious when heat production per unit electrical activity is compared (Figure 3). This indicates that the amount of heat generated per unit EMG-activity was improved by treatment with melatonin.

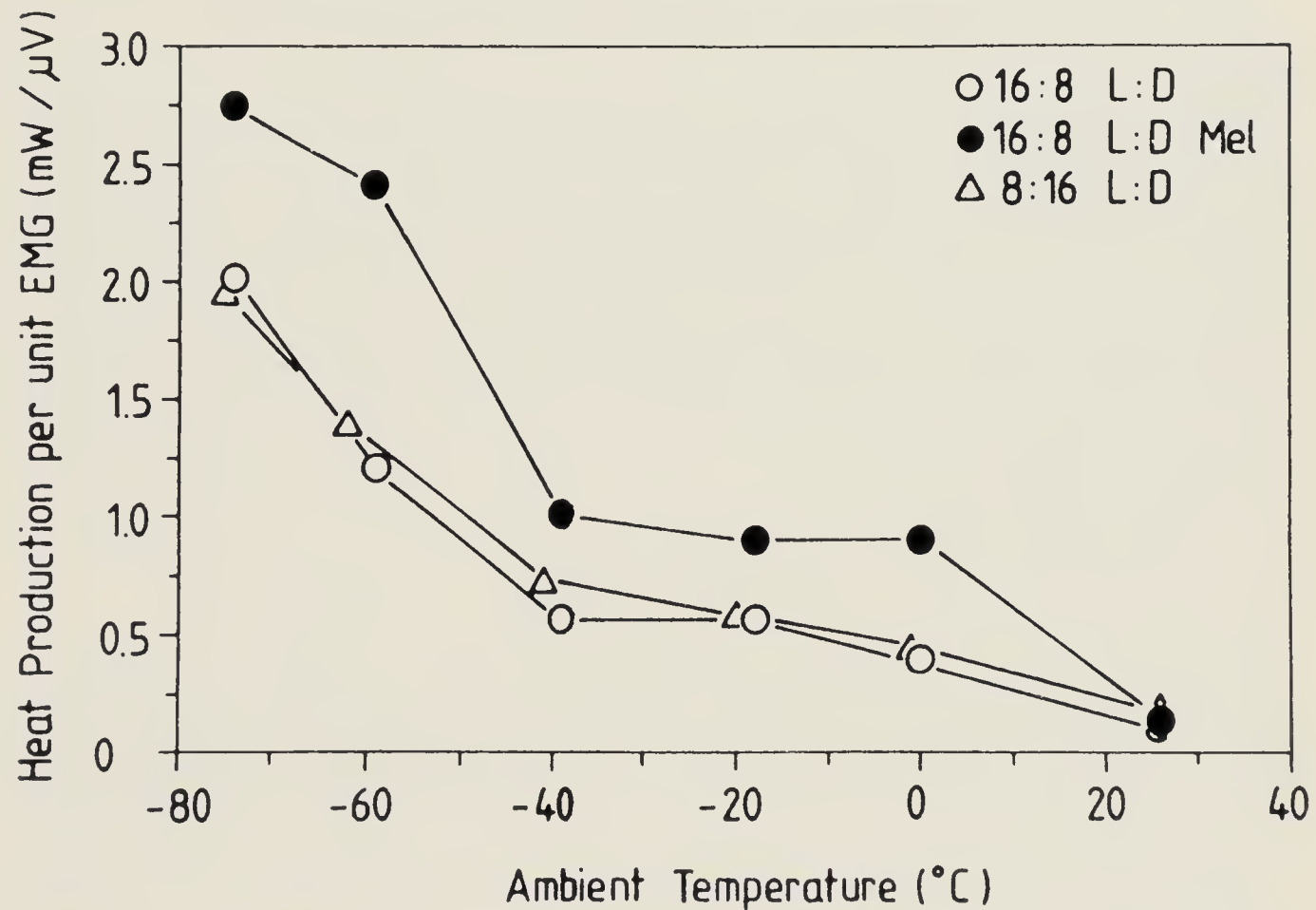


FIGURE 3 – Thermoregulatory heat production per unit electrical activity of the pectoralis muscle. Calculations are based on data shown in Figure 2, and basal metabolic rate was subtracted from total metabolic rate (Saarela & Heldmaier 1987).

The physiological and biochemical nature of this functional nonshivering thermogenesis is not known. In liver mitochondria from ducklings respiration could be uncoupled from ATP synthesis by small amounts of fatty acids (0.1 mMol) (Barre et al. 1986). This generates heat from respiration without the formation of ATP and the subsequent dissipation of ATP by myofibrillar movements (Heldmaier et al. 1989). Such a nonshivering pathway of heat generation in birds would have the advantage that high metabolic rates for heat production in severe cold could be maintained without shivering. Vigorous shivering will disturb the insulative layer of air trapped in the plumage and cause additional heat loss. This could be prevented by nonshivering thermogenesis under severe cold load.

An uncoupling of mitochondria would require an increase of plasma and intracellular levels of fatty acids in the cold. American Goldfinches had constant plasma fatty acid levels of about 1.4 mMol at 30 and -15°C, but in a Helium atmosphere at 0°C, which corresponds to about -70°C in air, the fatty acid levels were almost doubled (Marsh & Dawson 1982). In Pigeons, injections of melatonin also increased fatty acid levels in plasma and muscle tissue by almost 100% (John & George 1976). This suggests that melatonin can interact with the substrate supply for respiration and mitochondrial uncoupling. It is in accordance with our observation that melatonin treated Quails had an elevated level of heat production per unit electrical activity and this effect was enhanced at severe cold load (Figure 2).

PINEAL EFFECTS ON ENDOCRINES AND METABOLITES

Thyroid

In addition to circadian and seasonal changes in thermoregulation the pineal also affects endocrines and metabolites which are involved in the control of energy balance. The circadian rhythm in body temperature and metabolic rate is closely correlated with thyroid activity. Plasma levels of T_3 are high during the day and low during the night, and T_4 levels show an inverse pattern (Newcomer 1974, Sharp et al. 1984). Removal of the thyroid lowered the level of the circadian metabolic rate by about 17% (% calculations based on nocturnal minimum), but the amplitude and shape of circadian rhythm remained intact (Klandorf et al. 1981). Starvation had a similar effect and reduced the level of metabolic rate by 26%, and starvation in thyroidectomized Chicken decreased metabolic rate even further by 35% as compared to starved intact birds. These examples show that the level of metabolic rate is closely linked to the activity of thyroid hormones, but these hormones cannot be held responsible for the generation of the circadian rhythm of body temperature and metabolic rate.

This conclusion is further supported by the observation that pinealectomy does not produce major changes in the circadian pattern of plasma thyroid hormone levels (Cogburn & Harrison 1980). On the basis of these results it is even unlikely that thyroid hormones are involved as secondary mediators of pineal endocrine activities. The circadian variation of metabolic rate and body temperature is generated independently from thyroid activities, but thyroid hormones may alter the level at which these circadian changes take place.

Energy uptake, glucose and fatty acids

Maintenance of a constant and desired body weight is one of the most obvious results of the control of energy balance in the body. In Chicken the pineal does play a significant role for the development of body mass. Pinealectomized Chicken grow at a slower rate (Cogburn & Harrison 1980, Osei et al. 1989). Treatment with melatonin (added to the food) has the reverse effect. It increased body weight, food uptake and energy retention. These responses were accompanied by an increase in liver lipogenesis, jejunal glucose uptake as well as by an increase in plasma levels of T_3 and T_4 . The responses were rather small in intact Chickens but larger in pinealectomized Chicken thus compensating for the reduced levels observed following pinealectomy (Osei et al. 1989). This indicates that the pineal does interact with the control of energy flow in Chicken but the nature of this interaction and its biological significance are unknown.

In Pigeons pinealectomy caused a decrease of blood glucose levels from 250 mg% to about 170 mg% which is more pronounced than the effect of pinealectomy in rats (Csaba & Barath 1971, Patel & Ramachandran 1989). Injections of adrenalin or glucagon raised the blood glucose level to about the same extent (Patel & Ramachandran 1989). Glucose tolerance and insulin sensitivity were increased in pinealectomized Pigeons during the breeding season (March to May). In the nonbreeding season (July to September) pinealectomy had no effect on glucose tolerance and sensitivity to insulin (Ramachandran & Patel 1989), suggesting that the glycaemic action of the pineal is part of seasonal acclimation. In Pigeons a single injection of melatonin (1.25 mg/kg) does elevate plasma free fatty acid levels by about 80%. A higher dose of 5 mg/kg additionally elevated fatty acids levels in muscle.

These changes in the level of metabolites are most probably due to the interaction of the pineal with other endocrine and neuroendocrine responses. In the Pigeon melatonin injections caused an increase in GH levels and pinealectomy lowered GH levels (McKeown et al. 1975, Rintamaki et al. 1984). The lipolytic action of this hormone may at least partly explain the pineal effects on plasma level of metabolites. However, GH is certainly not the only pathway for the metabolic effects of melatonin. Pinealectomy and melatonin treatment changed the plasma level of various other hormones which can alter metabolite levels like those of TSH, AVT, LH, FSH, etc. (Panda & Turner 1968, John et al. 1973, Rintamaki et al. 1984). The entire pattern of endocrine interactions with the pineal gland is not known in all details, but the available evidence shows that via these interactions the pineal exerts profound effects on energy balance and metabolite levels in birds.

CONCLUSIONS

In addition to its major role for circadian rhythms of locomotor activity the pineal gland is involved in thermoregulation and the control of energy balance in birds. Pinealectomy increases the nocturnal body temperature minima, whereas treatment with melatonin decreases body temperature and metabolic rates. During winter small birds improve their cold tolerance by an extension of the thermogenic capacity. In Quails this thermogenic acclimatization is cued by short photoperiod, and treatment with melatonin in long photoperiod did provoke similar thermogenic improvements.

These examples show that the thermoregulatory involvement of the pineal is closely linked to its circadian and photoperiodic properties. The pineal acts as a central neuroendocrine interface for the control of circadian rhythms, and based on this circadian property also as a neuroendocrine interface for mediation of seasonal adjustments of thermoregulation and energy balance.

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SYMPOSIUM 37

**ENDOCRINOLOGY OF AVIAN
BREEDING SYSTEMS**

Conveners L. W. ORING and J. F. COCKREM

SYMPOSIUM 37

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MATING SYSTEMS AND HORMONE-BEHAVIOR INTERACTIONS

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ABSTRACT. Experiments on the relationship of social interactions and secretion of testosterone (T) in male birds have revealed conflicting results. In those species in which males provide substantial parental care (e.g. *Zonotrichia*, *Passer*), T inhibits expression of parental behavior. Thus circulating levels of T are low throughout the parental phase. However, if males are challenged, or when females once again become receptive, then the subsequent behavioral interactions result in an increase in T secretion to regulate territorial aggression and mate guarding. In contrast, those species tending toward polygyny and/or little male parental care (e.g. *Agelaius*, *Lagopus*), do not appear to respond to male-male interactions or exposure to receptive females with a rise in circulating T. Others (e.g. *Molothrus*), show intermediate responses. It is proposed that endocrine responsiveness to behavioral interactions is related to mating system and breeding strategy. Greatest responsiveness appears in males with most parental care and, perhaps paradoxically, least in males showing low parental care but high male-male aggression.

Keywords: Testosterone, mating systems, breeding strategies, aggression, parental care, breeding.

INTRODUCTION

It is well established that the steroid hormone testosterone (T) has profound influences on sexual and aggressive behavior in vertebrates (see Wingfield & Marler 1988). Nevertheless, the precise interrelationship of T and aggression, i.e. whether it acts during development ("organizational effect") or on a seasonal basis ("activational effect") or both, has been a matter of debate for decades (Arnold & Breedlove 1985). The relation of circulating levels of T to frequency of aggression is even more controversial. Approximately 50% of published investigations found a positive correlation of T level and frequency of aggression and 50% found no relationship (see Wingfield & Ramenofsky 1985 for review). It has been suggested that blood levels of T are correlated with reproductive aggression only when breeding territories are established, when dominance hierarchies (determining access to females) are disrupted or formed, or when mates are receptive (Sapolsky 1987, Wingfield et al. 1987). At other times frequency of aggression is low and not correlated with T concentrations. However, there remain unexplained anomalies in the diverse relationships of T and aggression. For example, some avian species not only reveal no relationship of T level to aggression, but also show no increase in T secretion when challenged or presented with a sexually receptive female (Delville et al. 1984, Dufty & Wingfield 1986, Harding & Follett 1979, Ramenofsky 1984, Stokkan & Sharp 1980). More recently, it has been suggested that in birds the relationship of T to reproductive aggression, and responsiveness of T secretion to social cues, may be dependent upon mating systems and breeding strategies (Wingfield et al. 1990). Here, experimental evidence for this idea is presented and the implications for further investigations at both the organismal and reductionist levels are discussed.

TESTOSTERONE, MATING SYSTEMS AND BREEDING STRATEGIES IN BIRDS

Testosterone and aggression

The steroid hormone T has several biological actions that include promotion of spermatogenesis, growth of some secondary sex characters (e.g. wattles, nuptial plumages, vas deferens), and activation and organization of reproductive behaviors (e.g. Arnold & Breedlove 1985; Wingfield et al. 1990). It has been suggested that an increase of T levels from a non-breeding baseline (level a) to a breeding baseline (level b) is sufficient for complete spermatogenesis, all androgen-sensitive secondary sex characters develop normally, and the full spectrum of reproductive behaviors can be expressed (Wingfield & Moore 1987, Wingfield et al. 1990). However, during the breeding season, plasma levels of T may show complex patterns with elevations above the breeding baseline (to level c). Since reproductive function appears to be complete with plasma levels of T at the breeding baseline (level b), then why are there such complex patterns of T among populations and species, and what is the function of increased T above level b? Wingfield et al. (1990) suggested that increases of T concentrations from level b to c are solely involved with increased frequency and intensity of male-male aggression in territorial and mate-guarding contexts. Although the full repertoire of aggressive behaviors can be expressed with T concentrations at level b, further increases in T to level c may be required to support very high levels of aggression. Thus variations in the patterns of T levels in the blood of individuals may reflect parallel changes in male-male competition over territories and/or mates. But what regulates these increases of T secretion above level b?

THE "CHALLENGE HYPOTHESIS"

There is now extensive evidence that elevations of male-male aggression during periods of social instability, or when females are receptive, are often accompanied by increased secretion of T in males (Sapolsky 1987, Wingfield et al. 1987). The "Challenge Hypothesis" claims that these changes in secretion of T may be induced by behavioral cues emanating from a challenging male, or the sexual behavior of a female (e.g. Wingfield 1985, Wingfield & Moore 1987, Wingfield et al. 1987). For example, if male Song Sparrows, *Zonotrichia melodia*, were challenged by placing a decoy male on the territory and playing back tape-recorded songs through a speaker placed alongside, the resident male attacked the intruder and the interaction resulted in an increase of circulating T level (Wingfield 1985). Similarly in the White-crowned Sparrow, *Z. leucophrys gambelii*, if a male was paired with a sexually receptive female, his T levels increased significantly over those of males paired with non-receptive females or males caged alone (Moore 1983). Rises in plasma T levels may then support a period of heightened aggression as the territory is established or defended, or during mate-guarding (see Wingfield et al. 1987). Once the stimulus is removed, T levels decline rapidly (to level b).

Patterns of T level, mating systems and breeding strategies

Since the advent of "field endocrinology", a number of investigations have shown that the seasonal patterns of T concentrations in the blood of over 25 free-living avian taxa are highly variable. In those species in which males provide parental care, the level of testosterone remained at level b or lower when attending eggs or young. However, these males usually retained the ability to increase T to level c if challenged by

another male (see Wingfield 1985, Wingfield & Moore 1987, Wingfield et al. 1987). A lower level of T, at or below the breeding baseline b, appeared to be critical for expression of male parental behavior. If male Pied Flycatchers, *Ficedula hypoleuca*, House Sparrows, *Passer domesticus*, Spotted Sandpipers, *Actitis macularia*, and Song Sparrows were given implants of T that maintained plasma concentrations at the seasonal maximum (i.e. level c), parental behavior was significantly lowered resulting in reduced reproductive success (Hegner & Wingfield 1987, Oring et al. 1989, Silverin 1980, Wingfield et al. 1989). These data suggest strongly that high levels of T above level b are incompatible with male parental behavior. Thus the temporal pattern of T in these species may be regulated by the degree of male-male interaction (that would elevate T) and the extent to which the male provides parental care (that would tend to depress circulating T). In contrast, those males that show no parental care would have no such restrictions on high levels of T, and maximum responses to male-male aggression would be expected.

On reviewing the literature, Wingfield et al. (1987) found that, indeed, circulating T levels in males of polygynous species tended to be higher for longer periods during the breeding season than in males of monogamous species. This relationship was supported by observations that, if normally monogamous male Song and White-crowned Sparrows were given implants of T to maintain high levels similar to the pattern seen in polygynous species, these males also became polygynous (Wingfield 1984). However, the "costs" of such prolonged high levels of T resulted in reduced reproductive success despite some males having up to three mates (see also Wingfield 1990).

A simple correlation of mating system (monogamy versus polygyny) and the temporal pattern of T level in blood may be misleading because some monogamous males show little or no parental care, and some polygynous males feed young extensively. Thus correlations of breeding strategy and T secretion may be more meaningful. This led Wingfield et al. (1990) to propose that the interrelationship of male-male aggression (that tends to elevate T) and the degree of male parental care (that tends to depress T) may be the major determinant of the temporal pattern of T secretion throughout a breeding season. In populations with males that show high male-male aggression and low parental care, T levels would tend to be high for long periods throughout the breeding season.

Alternatively, those males in populations that have low male-male aggression and high parental care would tend to have much lower levels of T. By varying the degrees of male-male competition and parental care it is possible to generate many intermediate theoretical patterns of T secretion during a breeding season (Wingfield et al. 1990). It was also found that the temporal patterns of T measured in males of all free-living species studied to date fit the pattern predicted by the degrees of male-male aggression and male parental care expressed by each species (Wingfield et al. 1990). Thus, it is possible to suggest this theoretical relationship as a hypothesis for the hormonal basis of breeding strategies in birds.

Some further predictions can be made from this hypothesis. Since males that show little or no parental care have no behavioral inhibitions on high levels of T, the temporal patterns that have elevated T levels for prolonged periods may represent high responsiveness to social cues such as challenges from conspecific males, and sexual

behavior of females. Alternatively, lower levels, or very transient peaks, of T in males that do show parental care may be a result of reduced sensitivity to social cues, including possible suppression of T secretion by stimuli from the nest, eggs and young. To test this requires a comparison of T levels in males of species showing different degrees of aggression and parental behavior. However, absolute levels of T can be misleading because of species differences in T receptor levels. To circumvent this Wingfield et al. (1990) compared the ratio of the seasonal peak of T corrected for the non-breeding baseline (level c - level a) to the breeding baseline (level b - level a) with the ratio of male-male aggression to male parental care. The T level ratio was estimated in those species for which appropriate data were available (i.e. at least a complete cycle of T levels through all stages of the reproductive cycle). The behavioral ratio was obtained by assigning numbers to the degree of male-male aggression (low aggression = 1, moderate aggression = 2, high aggression = 3), and male parental care (low parental care = 1, high parental care = 2). Thus when the ratio is high (e.g. 3) for a species or population under investigation, male-male aggression is high and male parental care is low. If the ratio is low (e.g. 0.5), male-male aggression is low and male parental care is high.

Using these ratios, it was predicted that males showing no parental care would have a higher T level ratio than males showing high parental care. This would indicate that the parental males are less responsive to social cues in terms of stimulation of testosterone secretion. Wingfield et al. (1990) found that the opposite was true! There was a very tight relationship of T level ratio and behavior ratio, but the males with high parental care had the highest T level ratio and thus appeared most sensitive to social cues that modulate endocrine function. Thus the high levels of T seen in males with low parental care are possibly genetically determined (i.e. T secretion is stimulated at the onset of the breeding season and remains at full capacity throughout) and much less responsive to social cues.

EXPERIMENTAL INVESTIGATIONS OF ENDOCRINE RESPONSIVENESS TO SOCIAL CUES AND BREEDING STRATEGY

From the theoretical relationships generated by Wingfield et al. (1990) it is possible to predict the ability of males from a population of known breeding strategy to increase T concentrations from level b to c. This should be greatest in males that show high parental care ($b < c$), and least ($b = c$) in males with low parental care. These predictions can be tested by laboratory experimentation, or natural experiments in free-living populations (e.g. the responsiveness of T secretion to male-male competition and behavior of sexually receptive females).

Responsiveness of T secretion to male-male aggression

Changes in plasma levels of T in response to increased male-male aggression or experimentally induced challenges from conspecific males have been measured in about seven species to date. Four species that show high parental care (Song Sparrow; White-crowned Sparrow; Western Gull *Larus occidentalis wymani*; and European Starling *Sturnus vulgaris*) had significantly elevated T levels when challenged or during increased male-male aggression (from Ball & Wingfield 1987, Wingfield 1985, 1990 and unpublished). In contrast three species with low or no parental care gave mixed results. Male challenges in Red-winged Blackbirds *Agelaius phoeniceus*, and

Japanese Quail *Coturnix coturnix*, resulted in no increase in T levels above those of controls (Harding & Follett 1979, Ramenofsky 1984). In contrast, the Brown-headed Cowbird *Molothrus ater*, did show an elevation of T level when males were exposed to conspecifics. Controls held in isolation had lower plasma levels of T (Dufty & Wingfield 1990). The relationship between T level ratio and the estimated behavior ratio is presented in Figure 1. With the exception of the cowbird the trend is clearly for males with parental care to show greater responsiveness to challenges from other males. Why is the cowbird an exception? This species is a brood parasite and neither males nor females provide any parental care. Males are highly social and form hierarchies and compete aggressively for access to females. Thus it is possible that isolation may have resulted in a reduction of T level. Further investigation may clarify this fascinating exception.

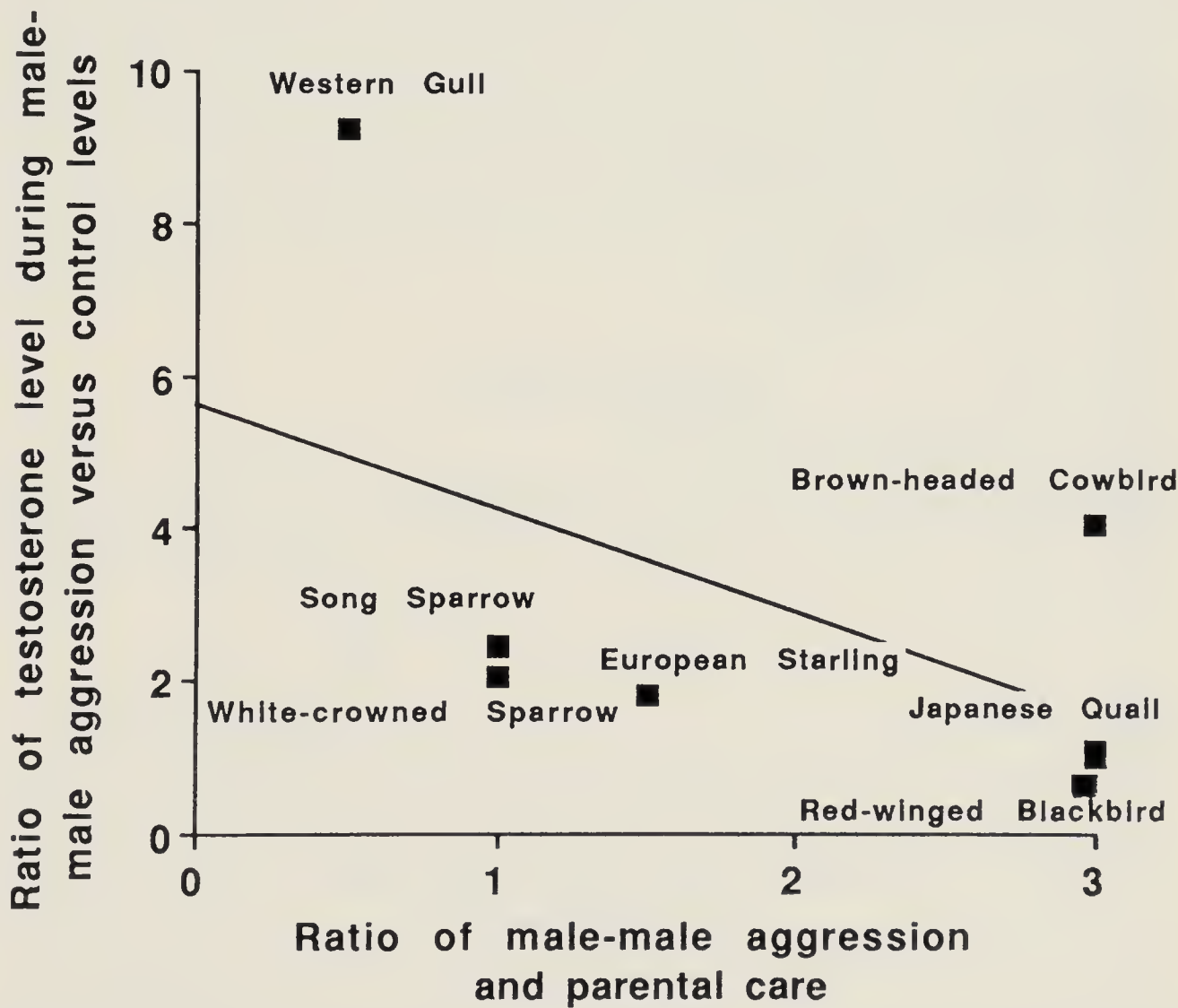


FIGURE 1 - The relationship of testosterone level ratio (i.e. testosterone level in experimentals versus controls) to the behavior ratio (degree of male-male aggression versus degree of male parental care) during increased male-male competition.
 $y = 5.6207 - 1.3581x$, $R^2 = 0.270$, $p > 0.3$.

Responsiveness of T secretion to sexual behavior of females

It is well known that males of many vertebrate taxa show increased levels of T when exposed to sexually receptive females (Wingfield & Marler 1988). Ten avian species have been studied and five that show extensive male parental care (Song Sparrow; White-crowned Sparrow; European Kestrel, *Falco tinnunculus*; and Ring Dove, *Streptopelia risoria*) show significant elevations of plasma T level when exposed to

receptive females (Feder et al. 1977, Moore 1983, Ball & Wingfield 1987, Meijer & Schwabl 1989, Wingfield et al. 1989). The European Starling, however, responded less dramatically to females and more to presence of a nest box (Dittami et al. 1986). Four species that show little or no parental care (Brown-headed Cowbird; Willow Ptarmigan, *Lagopus lagopus*; Canada Goose, *Branta canadensis* and Japanese Quail) did not have elevated T levels when exposed to receptive females (Stokkan & Sharp 1980, Akesson & Raveling 1981, Delville et al. 1984, Dufty & Wingfield 1986). An exception is the Mallard, *Anas platyrhynchos*, that did show a significant elevation of T when exposed to receptive females although not as marked as in males of some species with greater parental care (Klint et al. 1989). The relationship of T level ratio and behavior ratio in these species is presented in Figure 2. These data show a strong trend for those species with parental care to be more responsive to social cues that elevate T secretion.

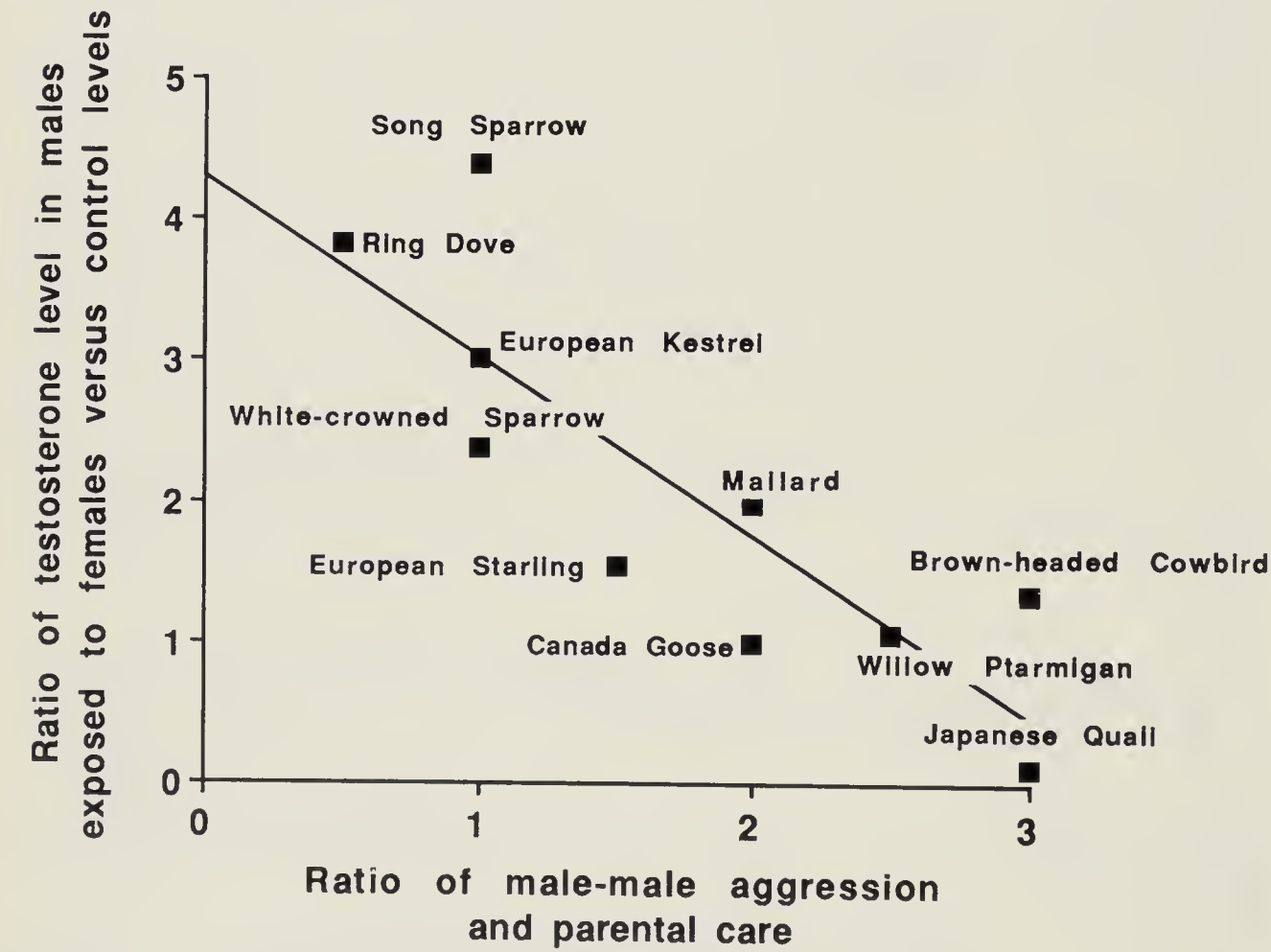


FIGURE 2 - The relationship of testosterone level ratio (i.e. testosterone level in experimentals versus controls) to the behavior ratio (degree of male-male aggression versus degree of male parental care) during exposure to sexually receptive females. $y = 4.3041 - 1.2825x$, R squared = 0.723, $p < 0.02$.

CONCLUSIONS

Experimental evidence supports the hypothesis that endocrine responsiveness of the testis to social cues is related to breeding strategy. With one exception, males with low or no parental care, but with moderate to high male-male aggression, show greatly reduced responsiveness to male-male aggression and sexually receptive females. In these species it is possible that T secretion proceeds at a maximal rate as

the gonadal cycle proceeds. In contrast, species with high parental care must reduce T levels because T-induced aggression is incompatible with parental behavior. However, if a male is challenged, or when the female is sexually receptive, males of these species have evolved the capacity to increase secretion of T and adjust expression of aggression accordingly. This endocrine responsiveness may be highly adaptive in regulating the fine balance of aggression and parental care in highly complex social situations. It would be of particular interest to test the hypothesis further by testing more extreme examples of breeding strategy. For example, we can predict that lekking species such as grouse and manakins would show no hormonal response to social cues. On the other hand, species in which males provide all parental care, e.g. phalaropes, button quails, kiwis, would be highly responsive.

The concept also suggests that the hormonal basis for breeding strategies in birds can be manipulated easily by implants of T or its antagonists. Furthermore the data point to considerable neural plasticity in transducing information from the social environment into neuroendocrine and endocrine cascades that make up the hypothalamo-pituitary-gonadal axis. Although more species need to be studied to further support or modify these concepts, it does seem clear that a comparison of species that show high and low endocrine responsiveness may be useful for elucidating the neural pathways involved.

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PROLACTIN AND AVIAN REPRODUCTIVE STRATEGIES

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ABSTRACT. High circulating levels of prolactin (Prl) are associated with incubation and brooding in free-living and captive individuals of many avian species. Sex differences in Prl concentrations are generally consistent with parental contributions, i.e. where one sex contributes most parental care, they have relatively high Prl levels. In most multibrooded birds there is an increase in Prl during the parental phase of each subsequent cycle, while non-breeding birds, or birds experiencing experimental disruption of exposure to eggs or nestlings, have reduced Prl levels. Outside of the context of parental behaviour, Prl may be stimulated by photoperiodic change, with pronounced seasonal variation observed in non-breeding individuals of several species and in non-parental nest parasites. While the parental behaviour-Prl interaction appears to be a fundamental element of avian breeding systems, it has been modified by various ecological and physiological constraints.

Keywords: Prolactin, breeding, parental behaviour, incubation, brooding, reproductive strategy, nesting stimuli.

INTRODUCTION

This paper focuses upon the pituitary hormone prolactin (Prl) in different strategies of parental care. Parental behaviour includes incubating eggs, brooding and feeding young, and defending the family, nest site and territory from predators and other conspecifics. Whilst most birds exhibit biparental care, relative contributions of males and females vary, including extremes of female-only and male-only parental behaviour. The parental strategy of course leads to considerable consequences for other aspects of the mating system (e.g. Silver et al. 1985). Data on Prl are now described for some 33 species including cases of no parental care (nest parasites) and parental care by non-breeding 'helpers'. Literature on Prl in Galliformes and Columbiformes has been reviewed recently (Buntin 1986, Lea 1987, El Halawani et al. 1988) but it is now timely to reassess the value of comparative analysis (Goldsmith 1983) and in particular to review studies in free-living birds. Experimental work is especially valuable in distinguishing hormonal and environmental contributions to parental behaviour, yet also challenging in controlling for the many potential influences in the natural breeding situation.

PROLACTIN AND INCUBATION

Temporal correlations and initiation of incubation

In free-living birds, plasma Prl concentrations are low before breeding, increase at the start of the breeding season and during egg laying, reach maximal levels during incubation and are high throughout the incubation period (Dawson & Goldsmith 1981, Silverin & Goldsmith 1983, Hector & Goldsmith 1985, Hall 1986, Hiatt et al. 1987, Wingfield & Goldsmith 1990). The initial increase in Prl may be facilitated by photoperiod or other environmental factors, but development of maximal levels depends upon full incubation behaviour. The temporal correlation between Prl and

incubation holds in laboratory studies, and the only case where Prl is not increasing at the start of incubation is in Ring Doves *Streptopelia risoria* where the delay might have arisen to avoid premature crop milk production (Lea 1987).

The onset of incubation has been extensively studied in captive Mallards *Anas platyrhynchos* and in domesticated chickens and turkeys, in which daily nest occupation time and plasma Prl both increase steadily during laying of the large clutch of eggs (Bluhm et al. 1983, Hall 1987, Lea 1987, El Halawani et al. 1988). Whilst exogenous Prl is reported to cause incubation in some studies (see Buntin 1986), there is evidence in female turkeys and doves that gonadal steroids, in particular oestradiol and progesterone, are more important hormonal agents in the induction of this behaviour though there may be a role for Prl in establishment of full incubation (Lea 1987, El Halawani et al. 1988). Control of incubation in male birds is less clear, especially in sex-role reversal where gender-typical steroid concentrations are not reversed (Fivizzani et al. 1986). Incubation does not depend upon endocrine events alone, however, and visual and tactile cues are crucial in the development of both incubation and high Prl (Goldsmith 1983, Lea 1987, El Halawani et al. 1988).

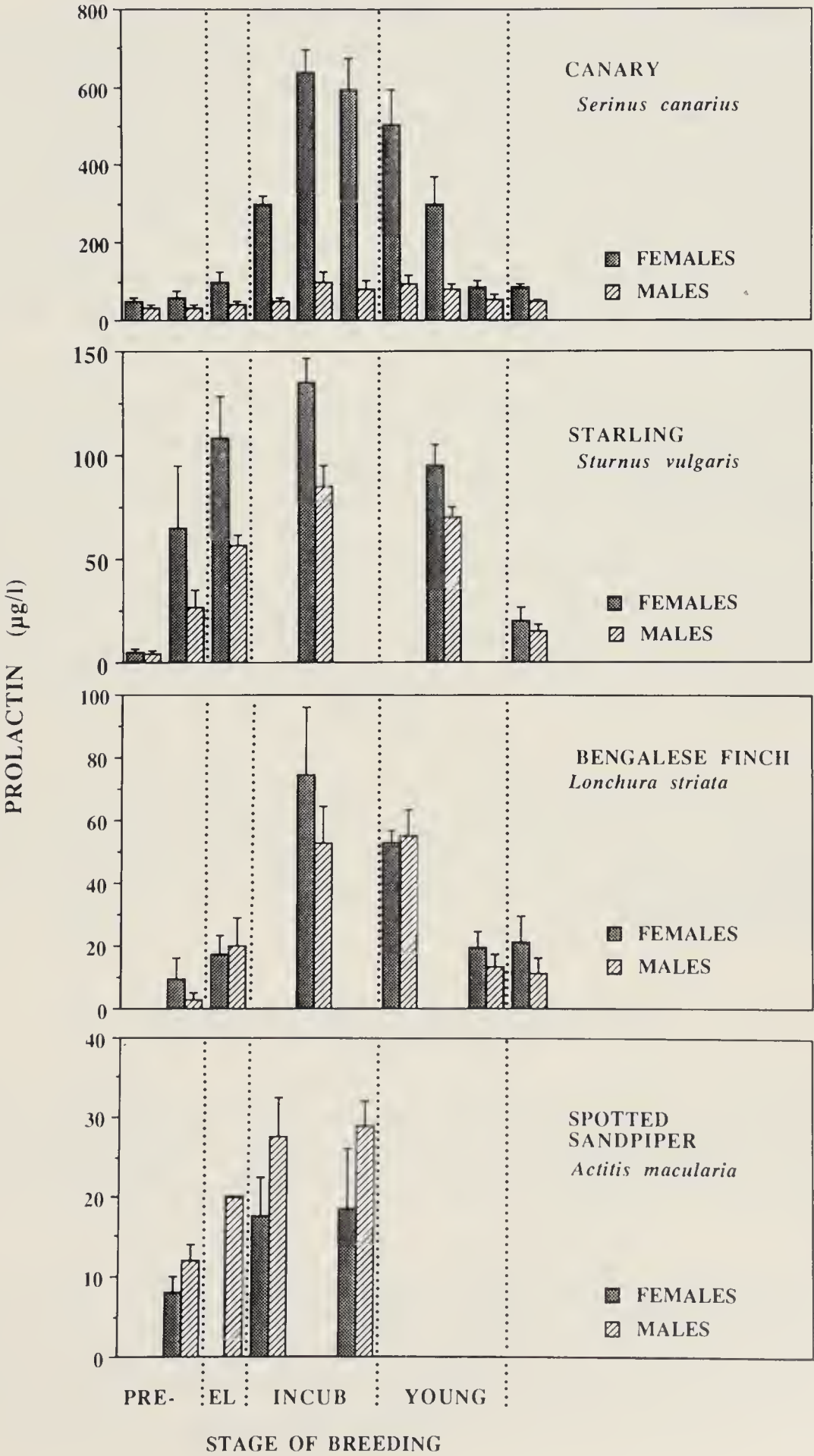
Gender differences in prolactin and incubation

In Mallards and Bar-headed Geese *Anser indicus*, in which only females incubate, Prl is much higher in females than in males, whilst shared incubation in Black Swans *Cygnus atratus*, Gannets *Sula capensis* and in three species of *Diomedea* albatrosses is characterised by high Prl in both sexes (Goldsmith 1983, Hector & Goldsmith 1985, Hall 1986). Laboratory studies of Ring Doves, Cockatiels *Nymphicus hollandicus* and Bengalese Finches *Lonchura striata* also indicate high Prl in incubating birds of both sexes (Goldsmith 1983, Myers et al. 1989, M. Gahr & A. R. Goldsmith unpublished). Where males contribute to parental care of the young but perform little or no incubation, gender differences in Prl are variable. Concentrations are generally higher in females than in males, the difference being substantial in Canaries *Serinus canarius*, moderate in Pied Flycatchers *Ficedula hypoleuca* and Starlings *Sturnus vulgaris* but less pronounced in White-crowned Sparrows *Zonotrichia leucophrys* and in Song Sparrows *Melospiza melodia* (Goldsmith 1983, Silverin & Goldsmith 1983, Hiatt et al. 1987, Wingfield & Goldsmith 1990). Finally, where males contribute most or all of incubation (Spotted Sandpiper *Actitis macularia* and Wilson's Phalarope *Phalaropus tricolor*), Prl tends to be higher in males than in females (Oring et al. 1986, 1988). Some of these examples are illustrated in Figure 1. Thus, gender differences across species in Prl correlate broadly with relative contributions to incubation, but non-incubating partners also show increased Prl to some degree; clearly other factors need to be considered in explaining the production of this hormone during the breeding season.

Prolactin and the maintenance of incubation behaviour

Evidence from several species indicates that stimuli associated with incubation maintain high Prl. Removal of the nest/eggs from incubating Ruffed Grouse *Bonasa umbellus*, Mallards, chickens, turkeys, Ring Doves, Canaries and free-living Gannets causes a rapid decline in plasma Prl (Goldsmith 1983, Bluhm et al. 1983, Hall 1986, Lea 1987, El Halawani et al. 1988). Partial clutch loss may not, however, result in suppression of Prl (Silverin & Goldsmith 1983, Hall 1987). Tactile contact with eggs is necessary to maintain Prl in incubating Mallards as shown by experimental desensitisation of the brood patch by denervation or by local anaesthesia (Hall 1987). Experimentally cooling the eggs under incubating birds also reduces plasma Prl in this

FIGURE 1 - Plasma prolactin concentration in female and male birds of four species sampled during a pre-breeding period (PRE-), egg laying (EL), incubation (INCUB) and with young (YOUNG). Plasma concentrations are also indicated, for the first three species, in samples taken from parents after their young had fledged. Modified from Goldsmith (1983), Dawson & Goldsmith (1981), M. Gahr & A. R. Goldsmith (unpublished) and Oring et al. (1986).



species (Hall 1987). In other birds visual cues from the nest and, in dual-incubating Ring Doves, from the partner, are involved (as well as tactile stimuli) in maintaining Prl (Lea 1987). With shared incubation, high Prl can be maintained in non-incubating birds during periods off the nest for hours (Lea 1987) or several days (Hector & Goldsmith 1985, Hall 1986) where this is the normal incubation pattern.

Experiments prolonging incubation by delaying hatching of eggs in free-living Pied Flycatchers and Grey-headed Albatrosses *Diomedea chrysostoma* (Silverin & Goldsmith 1984, Hector & Goldsmith 1985) show that the duration of high Prl is not prolonged compared with control birds whose eggs hatch at the normal time. The time "window" for incubation-stimulated Prl appears to be limited endogenously once incubation has begun as it is in doves (Lea 1987). Greater flexibility is seen in (male) incubating Wilson's Phalaropes, however, where extending incubation does prolong high Prl (Oring et al. 1988). The adaptive significance of these differences has been considered (Oring et al. 1988, Silverin & Goldsmith 1990), but clearly information is required on endogenous/environmental control of Prl in other naturally breeding birds.

Suppression of Prl by brood patch denervation or by injection of anti-Prl antiserum, and by nest removal, results in continued incubation and in readiness to resume incubation on nest return, respectively, so the behaviour is maintained for some days without high Prl (Goldsmith 1983, Lea 1987, Hall 1987). It has, however, been argued that incubation-stimulated Prl functions to maintain incubation behaviour over a longer time scale. Thus injections of Prl extend incubation duration in doves and prolong readiness to incubate in nest-deprived hens (Lea 1987, Sharp et al. 1988). This could explain why doves and flycatchers, for instance, abandon unhatched eggs a few days after Prl levels decline (Silverin & Goldsmith 1984, Lea 1987). Overall, however, evidence for a behavioural function of Prl in maintaining incubation is patchy and inconclusive, especially in view of poor results of intracerebrally applied Prl (see Buntin 1986).

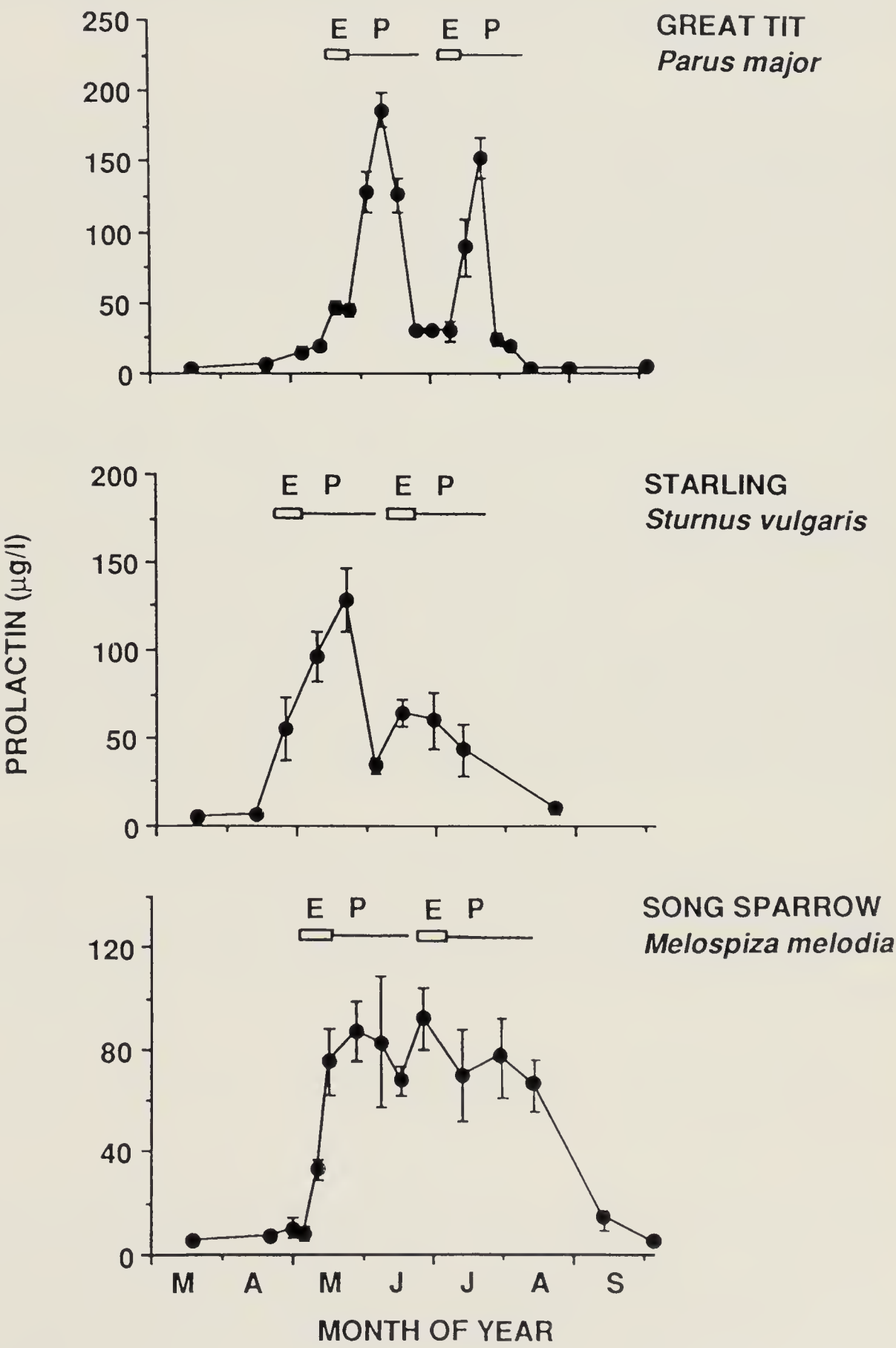
In contrast to the studies quoted above, plasma Prl does not decline after loss of clutch in incubating Song Sparrows (Wingfield & Goldsmith 1990). Clearly other factors are involved in maintaining high Prl during breeding in this species. Again, more work is needed on the interrelationships of stimulus factors, Prl and breeding behaviour in the natural breeding situation.

PROLACTIN AND CARE OF THE YOUNG

An earlier proposal that a distinction between altricial and precocial development could largely explain interspecific differences in parental Prl production (Goldsmith 1983) should now be re-evaluated. Data are available on species exhibiting a wide range of parental behaviour, and field studies reveal complexity in Prl-behaviour relationships.

Female Mallards, Bar-headed Geese, Black Swans, chickens and turkeys show a precipitous decline in Prl as the eggs hatch. There is no difference in post-hatching Prl in female Mallards with or without offspring (Hall 1987), but similar comparisons in Bar-headed Geese and bantam hens reveal a slight stimulatory effect of the young in slowing the decline in maternal Prl (Dittami 1981, Sharp et al. 1988). At the other

FIGURE 2 - Plasma prolactin concentration in female birds of three species during the breeding season. Periods of egg laying (E) and incubation/parental care (P) are indicated for the two broods raised in each case. Modified from Silverin & Goldsmith (1991), G. F. Ball & A. R. Goldsmith (unpublished) and Wingfield & Goldsmith (1990).



extreme, seabirds with prolonged brooding of vulnerable altricial young show undiminished Prl in both parents many weeks into the brooding period (Hector & Goldsmith 1985, Hall 1986). In Grey-headed Albatrosses, as noted above, the period of high Prl is limited endogenously (or seasonally) such that parents with late-hatching eggs show a decline in Prl and nest desertion before the young are old enough to survive predation (Hector & Goldsmith 1985).

In female Canaries and both sexes of Bengalese Finch, Cockatiel and Ring Dove, Prl declines 'gradually' (within limits of sampling frequency) during the care of the altricial nestlings (Goldsmith 1983, Myers et al. 1989, M. Gahr & A. R. Goldsmith unpublished). Parental male Canaries have much lower Prl than females but levels are higher than in unpaired males kept in otherwise similar conditions (A. R. Goldsmith unpublished). Stimuli maintaining Prl have been investigated in some detail in doves (see Lea 1987). In these four species, studied under laboratory conditions, repeated breeding generates marked cycles in Prl with high levels recurring during each incubation/parental phase (e.g. Goldsmith 1982).

Studies of wild birds exhibiting parental care reveal Prl profiles with changing levels sometimes but not always closely linked to breeding behaviour. Female Great Tits *Parus major* and both sexes of Pied Flycatcher show a decline in Prl during the parental period, low levels occurring at the end of the nestling phase (Silverin & Goldsmith 1990, 1991). Exchanging nestlings between flycatcher nests showed that exposure to newly hatched offspring could delay the Prl decline in female (though not in male) parents. The stimulatory effect of nestlings on maternal Prl was present for a limited period after normal hatching time, however, again evidence for limitation on receptivity to stimulus factors (Silverin & Goldsmith 1990). Flycatchers are naturally single brooded but in Great Tits two broods are raised, with a double cycle in Prl clearly demonstrated (Figure 2). Interestingly Prl declined more rapidly during the second brood indicating a probable seasonal influence combining with effects of breeding stimuli.

In other field studies, male Spotted Sandpipers and Wilson's Phalaropes show high Prl after the eggs hatch with a subsequent decline, possibly associated with diminishing frequency of parental (brooding) activity (Oring et al. 1986, 1988). However in two passerine birds there is a broad seasonal Prl profile with concentrations not so closely modulated by breeding activity. In double brooded Starlings (G. F. Ball & A. R. Goldsmith unpublished) there is a marked decline in Prl after the first brood leave the nest, but only a partial increase in levels for the second incubation-nestling phase (Figure 2). Also illustrated in Figure 2 are Prl concentrations in double-brooded female Song Sparrows (Wingfield & Goldsmith 1990); levels are high during parental phases but do not decline in between (even in individuals losing their first clutch to predators).

Setting interspecific comparisons aside, the association between Prl and parenting can be examined in individuals engaged in different amounts of parental activity. In Pied Flycatchers and Dark-eyed Juncos *Junco hyemalis* some females are assisted by males in feeding the young whilst others are unassisted and consequently spend more time brooding and feeding nestlings. In both studies, however, Prl did not differ significantly in assisted and unassisted female parents (Silverin & Goldsmith 1984, Ketterson et al. 1991). Levels of Prl are higher in male juncos feeding young than in males newly pairing with females whose mates have been removed, but Prl does not

differ between males which assist in feeding young and those which do not (Ketterson et al. 1991). Support for an association between Prl and male parental behaviour derives from a field study of cooperatively breeding Harris' Hawks *Parabuteo unicinctus*, in which levels increase significantly in non-breeding male "auxillaries" when they begin to assist a breeding pair in feeding nestlings (Vleck et al. 1991).

CONCLUDING REMARKS

Whilst much evidence links Prl to the parental phase of reproduction (incubation and, to an extent, care of the young) in many birds, it is clear that the correlation cannot explain all of the variance in Prl concentration with regard to stage of breeding, gender roles and interspecific differences. Secretion of Prl is known to be influenced by environmental factors including especially daylength. Photostimulated increases in Prl have been described in many birds, though levels are generally much lower than during the parental phase in breeding individuals of the same species. Repeated seasonal cycles in plasma Prl are seen in White Storks *Ciconia ciconia* during their pre-breeding years and, strikingly, in nest parasitic Brown-headed Cowbirds *Molothrus ater* (Hall et al. 1987, Dufty et al. 1987).

To return to the theme expressed in the Introduction, plasma Prl concentration appears to be a better predictor of avian parental strategy in some birds than in others! This is perhaps not surprising, since the hormone is known to have many physiological and behavioural effects only some of which are specific to the parental period. Functions include stimulation of incubation patches and of crop milk (in Columbiformes) and effects on food and water intake, on the gonads and liver and various aspects of metabolism; some of these effects include Prl acting in the brain (see Buntin 1986). However, the complexities of incubation and parental behaviour undoubtedly involve many internal and environmental factors of which Prl is just one. Furthermore, temporal changes in sensitivity to Prl might also occur; thus plasma concentrations might not correlate very closely with breeding events. To end on a more specific and positive note, however, two reports indicate striking effects of (exogenous) Prl in promoting maternal behaviour leading to protection of the young from predators (Lea 1987, Pedersen 1989). Current research now focuses particularly in the central nervous system, investigating brain sites for Prl action (see Ball 1991) and changes in activity of hypothalamic releasing mechanisms (e.g. Sharp et al. 1989, Cloues et al. 1990).

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REPRODUCTIVE ENDOCRINOLOGY OF SEX-ROLE REVERSAL

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ABSTRACT. In most avian species, males are socially dominant and females share equally, or perform most, parental care. These typical birds are characterized by high prolactin (Prl) levels in females and high testosterone (T) levels in males. In those shorebirds where males perform most (Spotted Sandpiper *Actitis macularia*) or all (Wilson's Phalarope *Phalaropus tricolor*; Red-necked Phalarope *P. lobatus*) parental care, Prl levels are higher in males than females. Prolactin rises in males with laying of the first egg, though incubation does not begin until three eggs of the four-egg clutch have been laid. Prolactin declines as chicks become thermally independent. Although circulating levels of Prl are "reversed," gonadal steroids are not. Males of these three species have T levels 3-20 times those of females, and females have higher estradiol and progesterone levels than males. Male T values decline dramatically at the onset of incubation, probably because T inhibits the expression of parental behavior. Testosterone implants reduce or eliminate male incubation, and implants of flutamide, an androgen blocker, disrupts the incubation-inhibiting effect of high T levels. The basis of female social dominance is not due to high levels of gonadal steroids in adults, but may lie in enhanced sensitivity to adult steroid hormones or in atypical differentiation of neural centers during development.

Keywords: Testosterone; prolactin; sex-role reversal; polyandry; parental care; incubation.

INTRODUCTION

In the vast majority of avian species, males are socially dominant to females, and parental care either is shared equally or females provide more care than males. In these typical species, testosterone (T) levels of males exceed those of females, whereas prolactin (Prl) levels during incubation are higher in females (Goldsmith 1983, Lea 1987). In a small proportion of avian species, males provide most or all parental care and females are socially dominant to males. The endocrinology of "sex-role reversal" was studied in the Spotted Sandpiper *Actitis macularia*, Wilson's Phalarope *Phalaropus tricolor* and Red-necked Phalarope *P. lobatus*. The goals of this paper are: (1) to examine the degree to which sex-role reversed shorebirds express reversed male-female hormone profiles of sex steroids and Prl, and (2) to examine the relationship between Prl and T in governing reproduction of these birds.

Testosterone in birds has been linked to a number of basic reproductive functions including gamete maturation, development of secondary sexual characteristics, growth of song nuclei, and both the performance of and preparation for aggressive behavior (reviewed in Wingfield et al. 1987). There is a growing body of evidence that high T levels are incompatible with the performance of normal parental behaviors, thus explaining the basal T levels witnessed during parental phases of reproduction (Silverin 1980, Hegner & Wingfield 1987, Oring et al. 1989). In Pied Flycatchers *Ficedula hypoleuca* (Silverin 1980) and House Sparrows *Passer domesticus* (Hegner & Wingfield 1987), experimentally elevated T levels resulted in reduced feeding of young by males, and in Spotted Sandpipers *Actitis macularia*, elevated T levels resulted in a significant reduction in male incubation (Oring et al. 1989).

The function of avian Prl in parental care has been widely debated (e.g. Lehrman 1963, Riddle 1963, Buntin 1986, Lea 1987). While high levels of the hormone are correlated with such reproductive events as brood patch formation, incubation, and brooding of young, there is little experimental evidence that Prl alone induces incubation or brooding (reviewed in Lea 1987). Prolactin is known to have an antigonadal effect, but the mechanism of this effect is not well known. In the domestic chicken and turkey Prl appears to inhibit production of LHRH by the hypothalamus (Sharp & Lea 1981, El Halawani et al. 1986). In addition, Prl may inhibit steroid production at the level of the gonad or luteinizing hormone at the pituitary level, i.e. it may act at any of several levels (Camper & Burke 1977). To date, studies of Prl inhibition of steroid production have concentrated on estradiol or progesterone production in gallinaceous birds. The potential of Prl to inhibit steroid production is especially interesting considering the influence of exogenous T in blocking parental care.

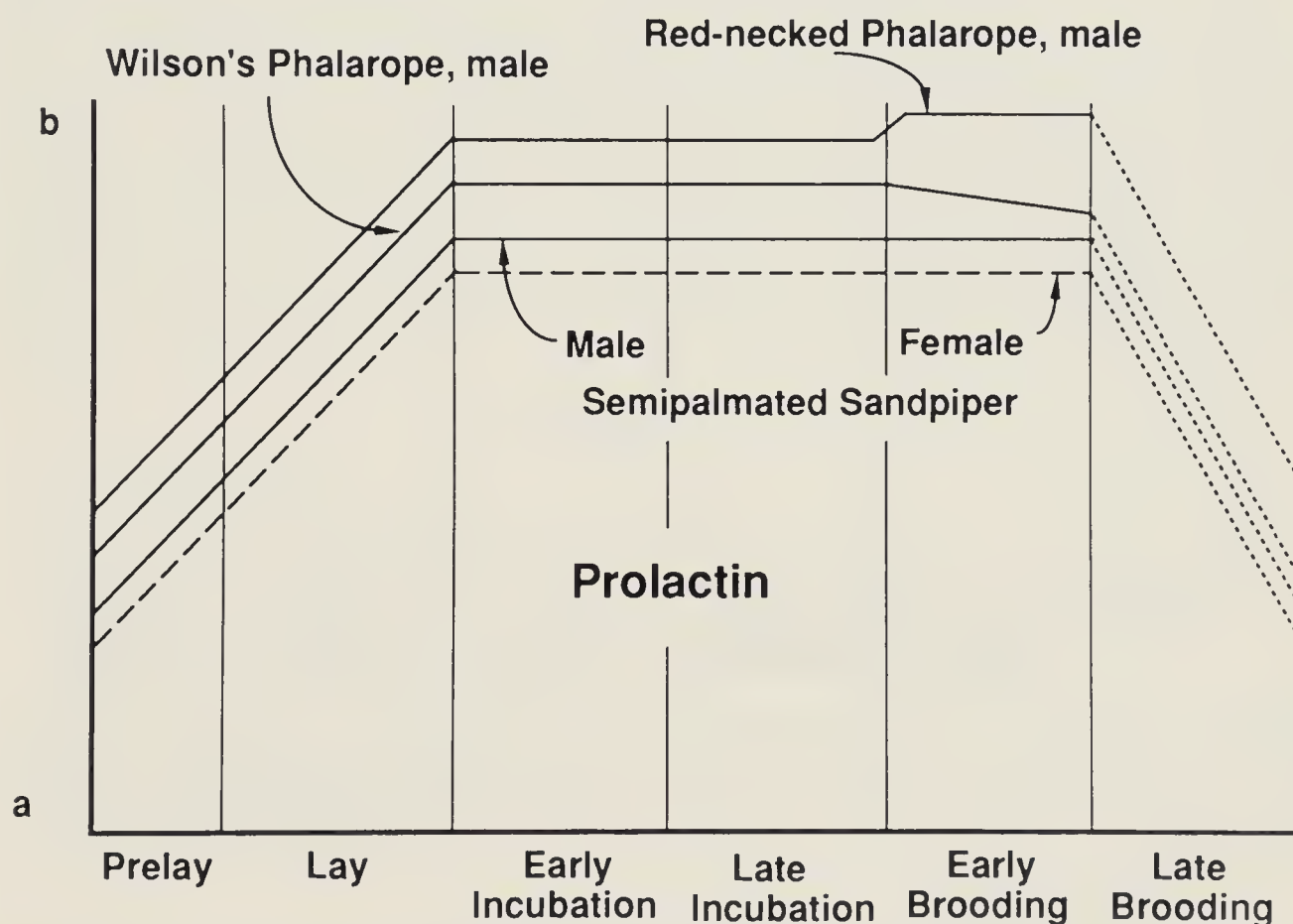


FIGURE 1 – Seasonal changes in circulating prolactin levels of male Wilson's and Red-necked Phalaropes and male and female Semipalmated Sandpipers. High levels during incubation and early brooding are evident. Dotted lines in late brooding period are hypothetical.

Hormone profiles of a monogamous shorebird

To be certain that any reversal of normal avian hormone patterns found among sex-role reversed shorebirds was related to behavioral reversals and not to the unique phylogenetic history of shorebirds, a monogamous biparental caring species, the Semipalmated Sandpiper *Calidris pusilla* was studied (Gratto-Trevor et al. in press). Mean T values of males were two to four times those of females at each reproductive stage, and males had significantly greater T levels than their mates. Both sexes had basal T levels during incubation. Males had more variable T levels during incubation than did females, perhaps related to the greater likelihood of males being involved in territorial defense at that time (Gratto-Trevor et al. in press).

There were no significant differences in Prl levels of male and female Semipalmated Sandpipers, a situation paralleling the fact that incubation is shared equally by the sexes (Figure 1). Prolactin levels rose markedly at the start of incubation in both sexes, and remained high throughout incubation. Brooding birds tended to have even higher Prl levels than those incubating — of 19 serially sampled individuals, 15 experienced increased Prl levels from incubation to brooding while four declined ($p = .10$) (Gratto-Trevor et al. 1990). Prolactin levels of both males and females remained high for at least the first week of the brooding period.

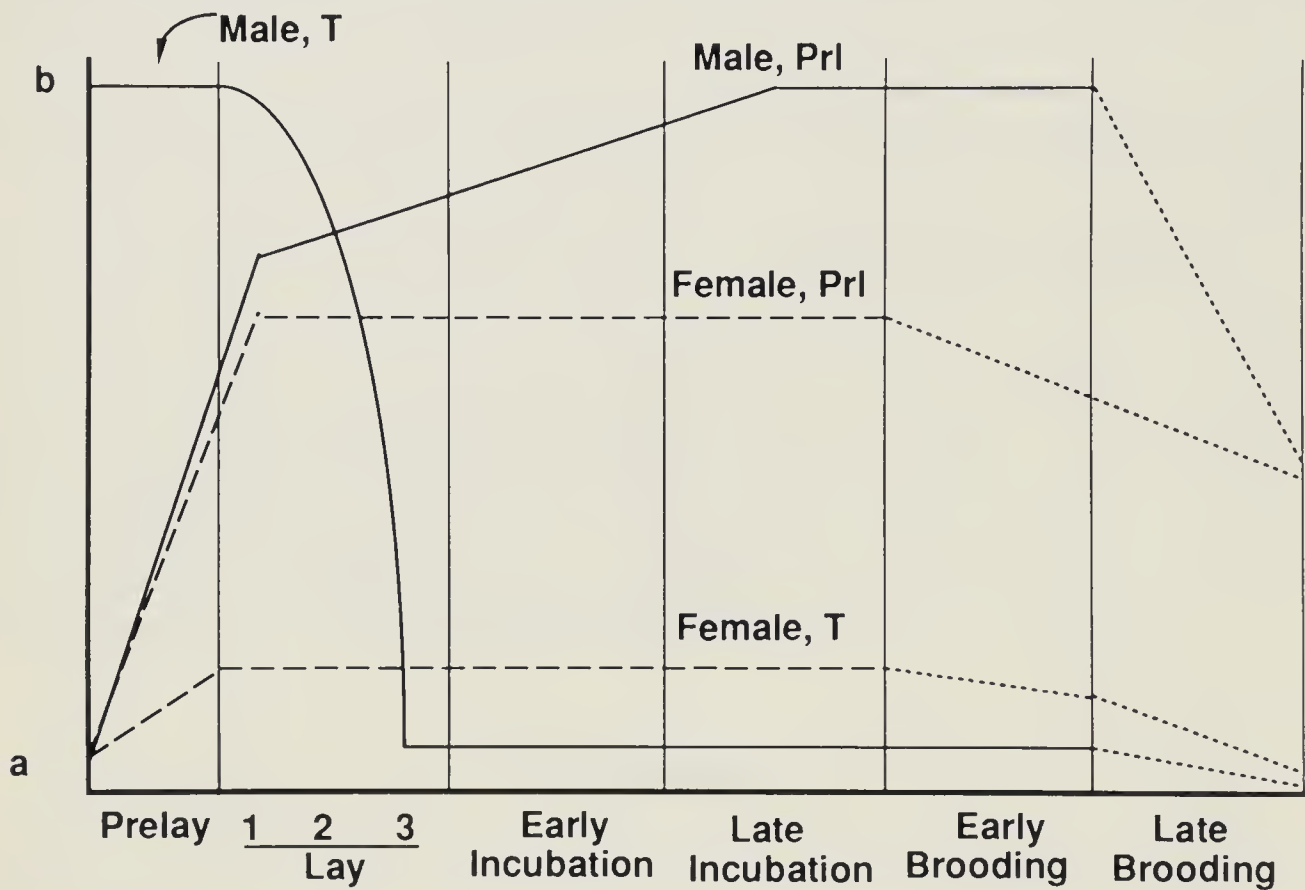


FIGURE 2 – Seasonal changes in prolactin and testosterone levels associated with breeding in Spotted Sandpipers. In the male, a rise in prolactin following the laying of the first egg is followed by low testosterone at the 3-egg stage. Dotted lines during late season are hypothetical.

A territorial, sex-role reversed species, the Spotted Sandpiper

Male Spotted Sandpipers had blood levels of T 10 times those of females (Fivizzani & Oring 1986). Testosterone concentrations declined dramatically, from high values witnessed at the 1- and 2-egg stage of laying, to low values found at the 3-egg stage (Figure 2). Spotted Sandpipers normally commence incubation with the laying of the third egg. The seasonal T profile of males was similar to that typical of males in monogamous passerines. Females experienced a 7-fold rise in T from the early-season, unpaired stage, to the “paired” stage, indicating that despite low absolute levels, T may play a role in mate and territory defense by females (Fivizzani & Oring 1986). Thus, while T levels are not “reversed,” females do show a seasonal profile of T that parallels that found in males of polygynous passerines.

Male Spotted Sandpipers had higher plasma levels of Prl than females at all stages of the breeding season, though the differences were only significant during incubation (Figure 2) (Oring et al. 1986a). Clearly, Prl levels are “role-reversed,” a situation

essentially unique among birds (Goldsmith 1983, Lea 1987). Prolactin in males doubled from prelaying to the 1-egg stage and remained high at least to three days post-hatch (Oring et al. 1986b). This is especially interesting relative to arguments on the function of Prl since incubation normally does not commence until the 3-egg stage. In males there was a significant negative correlation between Prl and both T and dihydrotestosterone (DHT) ($p < 0.001$, $r = -0.59$ and -0.58 respectively, Fivizzani & Oring 1986). Whereas T levels remained high until incubation commenced at the 3-egg stage, Prl was elevated beginning with the laying of the first egg. Perhaps T interferes with the incubation-promoting activity of Prl; and the preincubation rise of Prl may be responsible for the decline of T before incubation onset.

Sex-role reversed, non-territorial species: phalaropes

In both Red-necked and Wilson's Phalaropes, males perform all incubation and brooding and males have higher blood Prl levels than females. Prolactin rises sharply by the onset of incubation in Wilson's Phalarope whereas the rise in Prl in Red-necked Phalaropes is highly variable among years. In neither species are there sufficient data from the 1- and 2-egg stages to allow comparisons with the Spotted Sandpiper where Prl rises at the 1-egg stage (Oring et al. 1986). In Wilson's Phalarope ($r = 0.59$, $p < 0.05$) (Oring et al. 1988) and in the Red-necked Phalarope in one of two years ($r = -0.70$, $p < 0.05$) (Gratto-Trevor et al. 1990), there was a significant negative relationship between post-hatch Prl values and brood age (Figure 1). In Wilson's Phalarope, Prl concentrations were low by about nine days post-hatch when chicks were thermally independent.

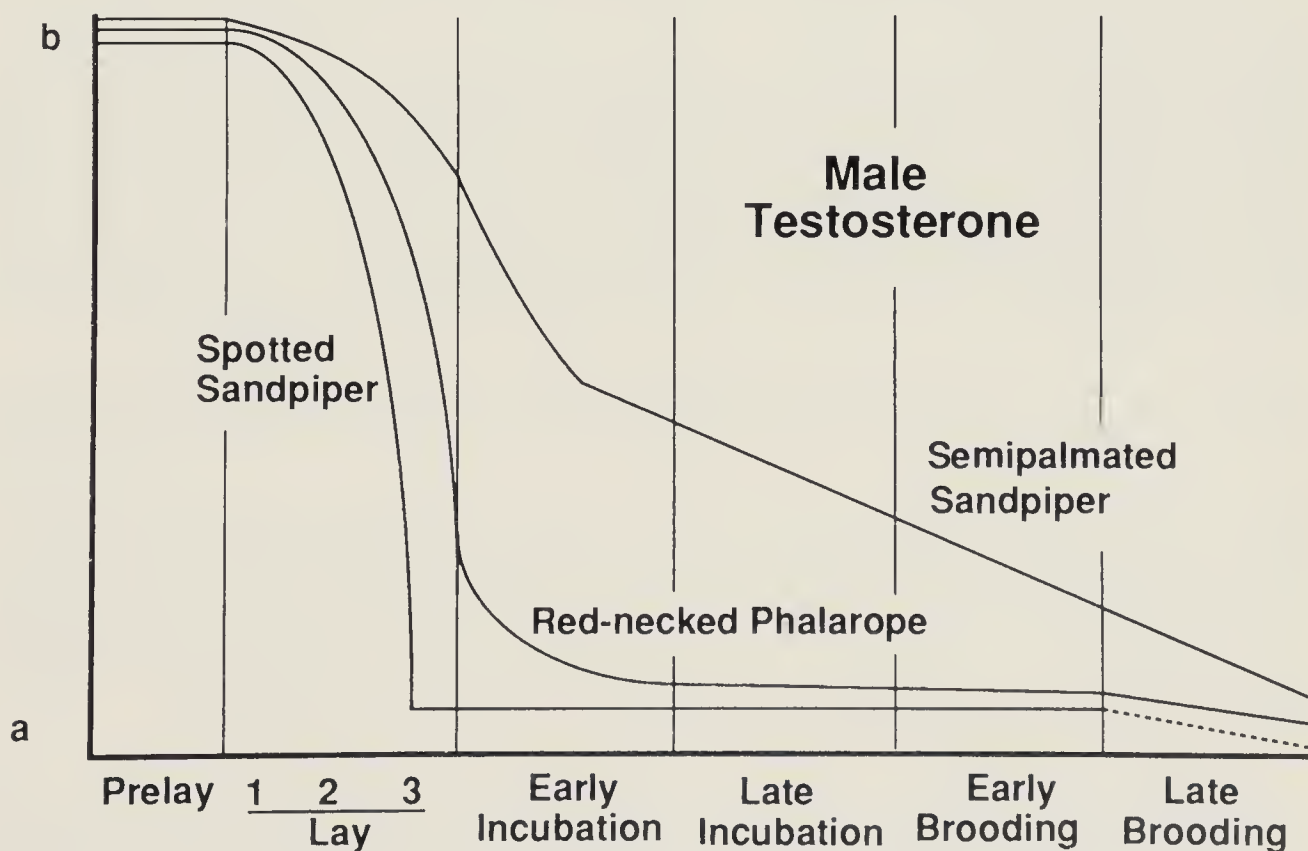


FIGURE 3 – Seasonal changes in circulating testosterone levels of male Spotted Sandpipers, Red-necked Phalaropes and Semipalmated Sandpipers. In the first two species, where males perform all or most parental care, testosterone levels drop drastically by incubation onset. In Semipalmated Sandpipers, where incubation is shared, testosterone levels decline gradually throughout the parental care period.

Experiments in which clutches of eggs that had been incubated for five days were exchanged with those that had been incubated for 15 days created situations in which males sat for 10 days (shortened incubation), 20 days (normal incubation), and 30 days (extended incubation) (Oring et al. 1988). Thus, by sampling males at specific times beyond when they started incubation it was possible to differentiate between competing hypotheses dealing with factors regulating changes in Prl values: namely, whether these changes were due to endogenous timing rhythms or to changing environmental cues. It was found that males responded to changing cues such that Prl dropped after chicks hatched, not in accord with the appropriate number of days since the beginning of incubation. Incubation could be maintained far beyond the natural incubation period. Hence, in Wilson's Phalarope, Prl levels appear to be primarily regulated by environmental events as opposed to endogenous factors, a situation well adapted for occupying highly variable environments.

SEX-ROLE REVERSAL AND HORMONES: AN OVERVIEW

In all three sex-role reversed species described above, T levels of males greatly exceeded those of females before incubation, and males exhibited seasonal T profiles characteristic of monogamous passerine birds (Figure 3). However, in Spotted Sandpiper and Red-necked Phalarope, where males do all or most incubating, the decline of T was precipitous at or just before the onset of incubation, whereas in the Semipalmated Sandpiper, where males and females share incubation equally, male T levels decline gradually throughout incubation and brooding. Limited data from female Spotted Sandpipers revealed a seasonal profile characteristic of males of polygynous passerines, i.e. T levels remained high during incubation (Figure 2). On the other hand, female Semipalmated Sandpipers exhibited a profile similar to their mates, with whom they share incubation, declining gradually throughout the parental care period (Gratto-Trevor et al. in press). The lack of reversal in T, as well as other sex steroids (Rissman & Wingfield 1984, Fivizzani & Oring 1986, Fivizzani et al. 1986), perhaps stems from the fact that these steroids have primary reproductive functions in development and maturation of germ cells and reproductive tracts.

The action of T on the brain and peripheral receptive tissue is indirect, requiring conversion to either estradiol via the enzyme aromatase or conversion to 5α -dihydrotestosterone via the enzyme 5α -reductase. Brain aromatase and reductase activity was studied in Wilson's Phalarope in order to ascertain whether or not a reversal of normal levels of these enzymes could explain behavioral sex-role reversal. Enzyme patterns in the brain did not differ from the normal avian pattern (Schlinger et al. 1989). In both the anterior hypothalamic-preoptic area and the posterior hypothalamus, aromatase levels were greater in males than in females.

The physiological basis for female aggression in shorebirds is unknown. It may be expressed independent of hormonal variation, or there may be non-gonadal endocrine influences. Alternatively, female aggressiveness may be due to enhanced neural sensitivity to normal female levels of gonadal steroids. This enhanced sensitivity could result from increased density of steroid receptors in neural cells, or by neural differences established during a critical period of embryonic development. In domestic chickens and Japanese Quail *Coturnix coturnix* the capacity of the brain to respond to gonadal steroid hormones is dependent upon exposure to elevated estrogens

during a critical period in which the steroid plays an organizational role, thereby allowing for appropriate responsiveness to specific steroids as an adult. Because of the aggressive behavior of female phalaropes and Spotted Sandpipers, it would be particularly enlightening to determine whether their hormonal profiles during development differ from chickens, quail, and monogamous birds in general. The behavioral repertoire of these role reversed females may result from brain response patterns hormonally established during development, and are not dependent upon exposure to atypical plasma steroid levels as adults.

In contrast to gonadal steroids, Prl levels of each of the three studied sex-role reversed species is reversed (Oring et al. 1986a,b, Oring et al. 1988, Gratto-Trevor et al. 1990). An important function of Prl in this group of shorebirds appears related to parental behavior and, therefore, tracks both evolutionary reversal and proximate variation in parental behavior. Indeed, it tracks behavior so closely that in the Spotted Sandpiper, where males incubate progressively more as incubation proceeds, Prl rises later in incubation, whereas in phalaropes, where males perform all incubation, there is no rise beyond levels during early incubation. Furthermore, when phalaropes reduce incubation constancy due to extreme environmental conditions, Prl levels decline. Thus it appears that while Prl promotes incubation, the hormone and behavior are on a double feedback loop such that a change in either promotes a change in the other.

TESTOSTERONE INHIBITS INCUBATION: EXPERIMENTAL EVIDENCE

In Spotted Sandpipers, the suggestion that T interferes with male parental care was made following the discovery that T plummeted at the onset of incubation (3-egg stage) (Fivizzani & Oring 1986), two days after a substantial rise in Prl (Oring et al. 1986a,b). In other words, Prl rose to incubation levels two days before the onset of incubation, while incubation did not begin until two days later when T levels dropped (Figure 2). Subsequently it was discovered that T filled silastic tubes (Dow Corning, i.d. = 1.47 mm, o.d. = 1.96 mm) caused desertion of clutches in 30% of the cases, and reduced incubation constancy in 50% of experimental males. These results strongly indicate that high levels of T are incompatible with the normal expression of parental behavior.

If T interferes with the performance of parental behavior, and if such behavior is Prl promoted, blockage of T action at times when Prl levels are high, e.g., during the 1- and 2-egg stages, should result in the early onset of incubation. To test the effect of T in blocking parental behavior in Spotted Sandpipers, males were implanted before the onset of egg laying with 20 mm silicone sealed silastic tubes filled with flutamide, an anti-androgen that binds T receptors. Controls were implanted with empty, silicone sealed silastic tubes. The parental behavior of experimental and control birds was monitored by direct observation for five hours per day during the laying period, three hours in early morning and two hours in the evening. Subsequently, birds were caught and tubes removed, thus assuring that the tubes had remained in place. Flutamide implantation resulted in an increase in the number of males incubating at both the 1- and 2-egg stages ($P = 0.19$ and $P = 0.03$). However, probably due to the small number of controls, the increase was significant only at the 2-egg stage (Figure 4). This experiment further verifies that elevated levels of T act as a delaying agent as far as parental behavior is concerned.

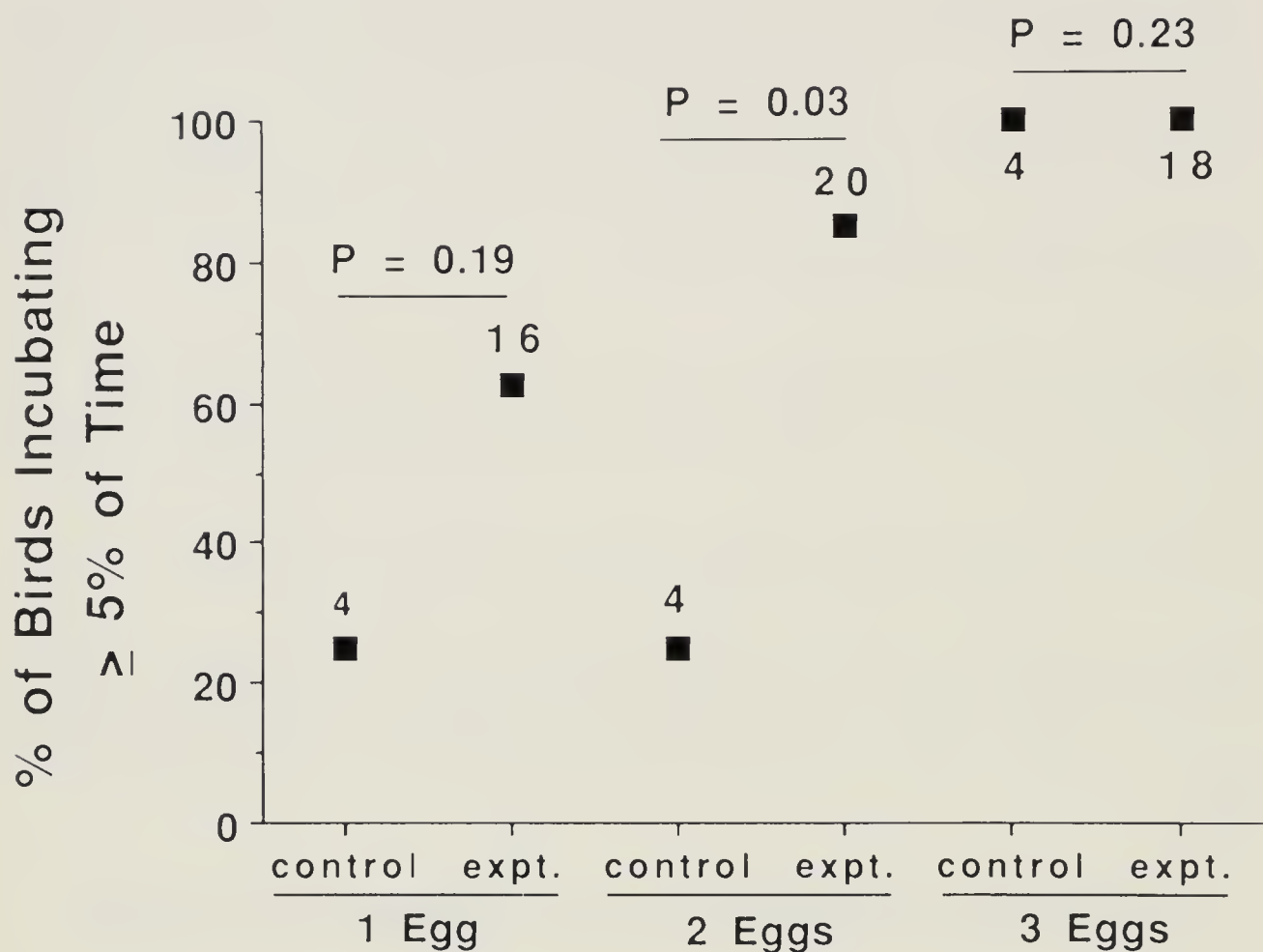


FIGURE 4 – Flutamide implants block the inhibiting effect of high testosterone levels on parental care, resulting in an increase in the percent of birds incubating during the egg laying period. Sample size is indicated above each data point. P values determined by Fisher’s exact test.

CONCLUSION

In male Spotted Sandpipers, T-levels appear to influence the performance of incubation. When T drops at the 3-egg stage, incubation constancy rises rapidly under the promoting influence of Prl. Blockage of T action with the anti-androgen flutamide removes the inhibiting effect of T without reducing fertility or the propensity of males to defend their territories. Thus, one function of high T levels may be in the regulation of parental care onset. This function may be widespread among precocial birds.

Prolactin rises before the onset of incubation and remains high throughout incubation, gradually dropping as chicks become thermally independent. Our observations support the notion that Prl promotes and helps sustain parental care in sandpipers. The fact that Prl rises in accord with environmental change, namely presence of one or more eggs, and declines when thermal independence of chicks is attained, suggests that this hormone’s secretion in these shorebirds is regulated more by environmental cues than endogenous rhythms as has been found important in some species (e.g. Pied Flycatcher, Silverin & Goldsmith 1984). This was corroborated by experimental manipulation of clutches (Oring et al. 1988). Environmental regulation of Prl secretion is consistent with the fact that Spotted Sandpipers and phalaropes occupy early suc-

cessional environments varying widely within and among seasons in suitability for breeding. A physiological explanation of the high levels of female aggression in these birds awaits further investigation.

FUTURE ENDEAVOUR

Evidence has continued to mount that Prl is integrally involved in the performance of parental behavior by birds. However, knowledge of factors regulating the onset, maintenance and cessation of seasonal elevations in Prl, and of parental behavior, has lagged behind. Recent experimental evidence indicates that in some species endogenous rhythms are extant, but that these may be modified by environment (Silverin & Goldsmith 1990). In others, annual rhythms appear to be largely determined by environmental factors (Oring et al. 1988). The antigonadal effect of Prl may be widespread and yet there is evidence from an experimental study (Wingfield & Goldsmith 1990) indicating independence of seasonal variation in Prl and T. Thus, there is a great need for expanded experimental studies exploring the interaction of Prl and T in regulating parental behavior. Such studies should include non-passerines and should be expanded to taxa representing the great variety of avian parental care patterns. Especially illuminating would be comparative studies of other avian groups that have evolved exclusive or predominant male parental care, e.g. kiwis, tinamous, jacanas, painted snipe, and button quail.

The experimental analysis of avian reproductive behavior and its regulation will be augmented by further development of osmotic minipumps, allowing for experimental addition of Prl over prolonged periods without repeated handling. Similarly, additional implant experiments employing gonadal steroids and antisteroids will continue to paint the picture of Prl involvement with parental care. Birds are unique among vertebrates in the degree to which incubation and brooding of young occur. Future experiments will greatly augment our knowledge of how these fascinating behaviors are regulated.

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SOME ASPECTS ON THE SEASONAL CHANGES IN CIRCULATING LEVELS OF LH AND TESTOSTERONE IN WILLOW TITS *PARUS MONTANUS* AND GREAT TITS *P. MAJOR*

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ABSTRACT. This paper reviews endocrine studies on Willow Tits *Parus montanus* and Great Tits *P. major*. The paper is concentrated on three periods with increasing plasma levels of luteinizing hormone (LH): early spring, early autumn, and early winter. It is shown that field data and laboratory data are not always identical, but that environmental factors, such as population density can effect e.g. the time of increasing LH levels in the spring. During early autumn some juvenile tits show very high testosterone (T) levels, and it is concluded that high T levels do not facilitate a juvenile tit to become a permanent member of a winter flock. The cause of the increasing LH levels in August/September is discussed. The winter increase in circulating LH levels is not followed by increasing T levels. The cause of this increase is unknown. Correlations to a gonadal winter growth, to an "endogenous" LH cycle, and to seasonal changes in the photoperiodic response are indicated.

INTRODUCTION

The Willow Tit *Parus montanus* and the Great Tit *P. major* are common forest birds in Sweden. The two species have several ecological features in common, but there are also important differences in their ecology. My objectives in this paper are to present some data from different field and laboratory studies and experiments on males of these species.

LH AND TESTOSTERONE CYCLES

With the exception of the breeding season the annual cycles of plasma levels of testosterone (T) and luteinizing hormone (LH) are basically identical in male Great Tits and male Willow Tits. Figure 1 illustrates these cycles in the male Great Tit. Corresponding cycles in male Willow Tits differ in that LH and T levels peak during early May and not during March as in the Great Tit. In addition, Willow Tits do not show a second LH peak in June (Röhss & Silverin 1983, Silverin et al. 1986). This paper concentrates on the three stages indicated by A, B and C in Figure 1. Each is characterised by a period of increasing plasma hormone levels, and all occur in both species.

AUTUMN AND WINTER ECOLOGY

To understand the following discussion it is necessary to understand the major behavioural events in the annual cycle. For more detailed descriptions see e.g. Saitou 1978, 1979a,b,c., Ekman 1979, 1989, Jansson 1982, Drent 1983, Ekman & Askenmo 1984, Hogstad 1987, 1988.

The non-breeding season of the parids is characterised by flocking behaviour. Winter flocks are dominance-structured, and generally males dominate females, and adults dominate juveniles (Hogstad 1987). For both species a winter group is usually formed around the adult pair that previously bred in the area. The permanent group consists of this pair and non-genetically related juveniles (Saitou 1978, Ekman 1979).

The Willow Tit flock is a discrete territorial non-kin group with high coherence among members. In southwest Sweden the group normally contains four members. Different flocks do not intermingle, and each flock resides within a non-overlapping territory (0.20-0.25 km² large). Willow Tits improve the value of their winter territory by hoarding large amounts of food in summer and autumn. No matter how hard the winter may be, the Willow Tit flock never abandons its territory (Haftorn 1956, Ekman 1979, 1989).

Great Tit winter flocks are organised in a looser system than winter flocks of Willow Tits. During autumn Great Tits belong to "basic flocks" consisting of 2-15 members. Great Tits do not hoard food, and the basic flock does not defend a territory. Rather, the foraging area is more like a home range. When different basic flocks meet they may intermingle and form "compound flocks", utilising a communal area for foraging. Compound flocks may break up and re-unite repeatedly during winter. If winter conditions get too harsh the home range may be abandoned for long periods of time, or for the entire winter (Saitou 1978, Drent 1983, Silverin unpubl. data).

After having left the nest, fledglings of both species live together with their parents in a family flock. The breaking of family flocks and onset of juvenile dispersal start about one month after fledging in both Great Tits and Willow Tits, i.e. in July-August. The adult birds do not move much during summer. When the juveniles start to disperse, adult tits usually stay on, or near, their previous breeding territory. The dispersal phase, i.e. the time between leaving the parental territory and becoming established as a permanent member of a winter flock varies from a couple of days up to several weeks. Not all juveniles succeed in becoming a permanent member of a flock, and some remain as floaters in the area. In Sweden juvenile Great Tits seem to have two periods of dispersal, an initial period in late July and a second period in September. On the other hand, juvenile Willow Tits seem to disperse more regularly from late July to September. However, most juvenile Willow Tits that succeed in becoming a permanent member of a winter flock have done so by August. After September there are no longer any cohorts of floaters in the Willow Tit population, whereas floating young Great Tits may be found throughout the winter (e.g. Dhondt 1979, Källander 1983, Ekman 1989). As Willow Tits are strictly territorial during winter, and as winter resources are limited, it is crucial for young Willow Tits to become established in a winter group. Without joining a group, Willow Tits stand little chance of surviving the winter (Ekman et al. 1981).

The difference in autumn/winter behaviour between Willow Tits and Great Tits results in some differences when it comes to the establishment of breeding territories. Willow Tit pairs are formed before winter, and in March the male establishes a small breeding territory somewhere within the borders of the winter territory. As there are no immigrants entering the forest in spring, male Willow Tits do not have to compete with other males over a breeding territory. The population density of Willow Tits in spring normally is quite low as usually less than two members of the winter flock survive the winter. In almost all cases where only one flock member survives it is a male.

This single male is now faced with the problem of not having a female. Unpaired female Willow Tits are extremely rare at this time of the year, and in almost all cases single males fail to breed (Ekman 1979). In Great Tits, pair formation takes place after the basic flocks break up in spring. As a consequence of having left the forest during winter the males have to reoccupy the breeding area in spring and establish new breeding territories (Saitou 1979c). This is done sometime in March in Sweden. Great Tits breed at a higher density than Willow Tits.

On average, Willow Tits in southwest Sweden lay their first eggs around 7 May, whereas Great Tits start laying about one week later (Silverin et al. 1989a).

Vernal increase in plasma levels of LH and testosterone

The fast vernal increase (stage A in Figure 1) in circulating levels of LH in Great Tits and Willow Tits is caused by photoperiodic stimuli (Silverin unpubl. data). Despite differences in winter ecology both species establish breeding territories around mid-March and start egg-laying at about the same time. One could therefore expect both species to have about the same photoperiodic threshold value, i.e. Great Tit and Willow Tits should need about the same number of light hours in spring to increase their gonadotrophin secretion.

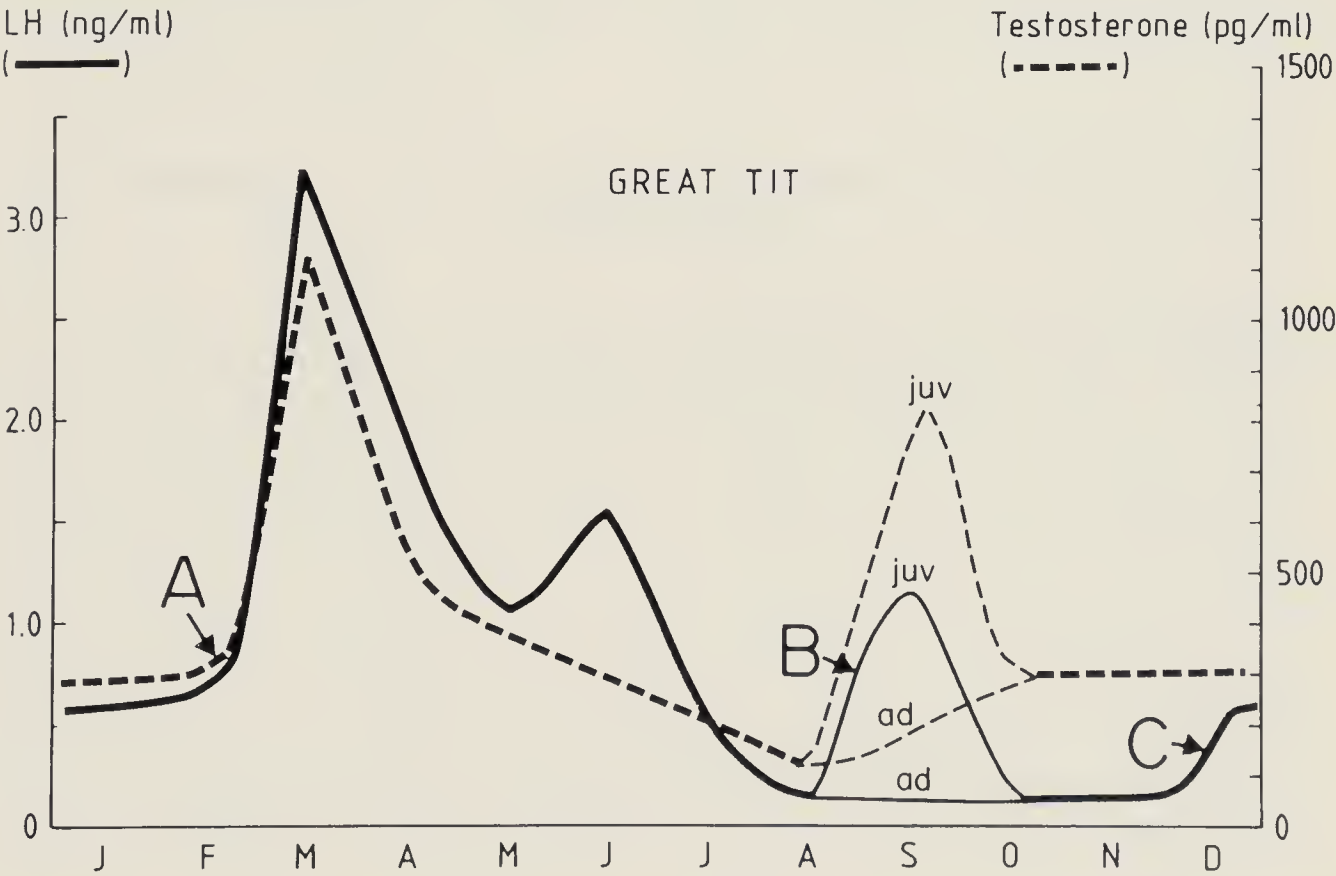


FIGURE 1 – Seasonal changes in plasma levels of LH and testosterone in male great tits from south-west Sweden (data from Röhss & Silverin 1983). A, B, and C points to the three stages discussed in the present paper.

This hypothesis was tested by bringing fully photosensitive birds into the laboratory and artificially simulating the increasing day lengths of spring. Figure 2 summarises results from an experiment that started in December, and where light was increased with 1/2 hour per week (Silverin et al. 1989a). Results were not as expected. In Great Tits, LH levels started to increase dramatically when days reached a length of 11 hours. In Willow Tits there was no change in LH levels until the birds were exposed

to 14 hour day lengths. Testicular growth patterns showed a similar response to light. In the south of Sweden, 11 hours of light corresponds to day lengths in early March, and 14 hours of light to day lengths in early April.

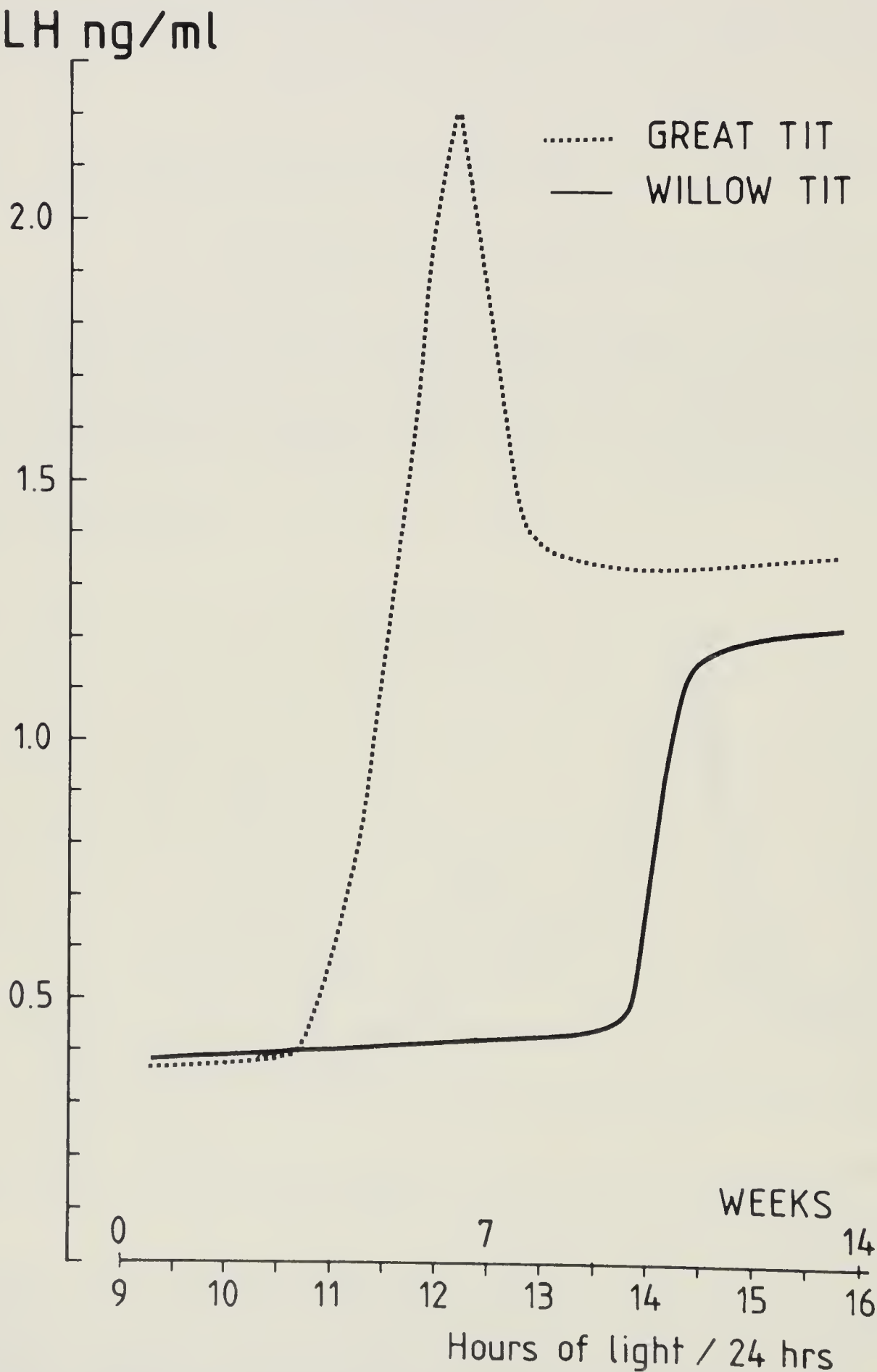


FIGURE 2 – LH data from a study where male great tits and male willow tits were captured in December and exposed to a simulatory vernal increase of day lengths. Weekly increase in day length was 1/2 hour/week (Silverin et al. 1989a).

However, in free-living male Great Tits and Willow Tits plasma levels of LH and T may increase in early March in both species, i.e. when day length is about 11 hours. The beginning of March is also the time when the slow vernal growth of the testes starts in free-living birds of both species (Silverin 1978, Röhss & Silverin 1983, Silverin et al. 1986, Viebke pers. comm.). The laboratory data thus agree with the field data for the Great Tit, but not the Willow Tit. However, in another study of free-living Willow Tits, LH levels did not rise in March (Silverin et al. 1989a - see below). The testes, however, showed a similar growth pattern between February and March in both Willow Tit studies.

From the above experiments it could be concluded that 11 hours of light is a threshold value for photoperiodic stimulation of testicular growth and LH secretion in Great Tits. However, if photosensitive male Great Tits are placed on photoregimes close to 11 hours (10.5L:13.5D; 11L:13D and 11.5L:12.5D) LH levels never rise during a period of 160 days, whereas the testes show a slow but continuous growth under all photo regimes. For birds held on 11.5 hours of light, but in none of the other groups, testes (after having reached about half the maximum size obtained in birds kept on 20L:4D) start to regress after about 80 days (Silverin unpubl. data). Thus, one cannot simply say that 11 hours of light increases gonadotrophin secretion in male Great Tits. Yet unknown factors must also be involved in regulation of the vernal increase of gonadotrophin secretion.

ENVIRONMENTAL FACTORS AFFECT THE VERNAL INCREASE IN LH AND TESTOSTERONE

When winter starts the Willow Tit flock normally contains four members. On average, only 1.4 birds are left in the winter territory after winter. However, winter survival can easily be increased with artificial feeding stations (Jansson et al. 1981). Under such circumstances about three birds per territory survive the winter. The density of breeding birds is therefore about twice as high in a fed as in an unfed population. When more than one male from the winter flock survives the winter there is competition for good breeding territories in spring. This circumstance is reflected in the time for the onset of the vernal increase in LH levels in males. Figure 3 summarises the results from a study made by Silverin et al. (1989a) where one population was given extra food during the entire winter, and one was left undisturbed. Population densities were carefully examined. In the low density population - where there was little or no competition for breeding territories - there was no increase in LH levels between mid-February and mid-March, i.e. between periods when day length increases from about 9.5 hours to 12.5 hours. This result therefore agrees with laboratory data discussed above, but contrasts with results from our earlier study (Silverin et al. 1986). where LH levels started to increase slowly in March. However, the density of that population was unknown. In the fed population, with the high density, male LH levels, as well as male T levels, started to increase significantly at the time of territorial establishment. Thus, laboratory data discussed above (on "threshold levels" for photoperiodic induction of LH secretion in Willow Tits) seem to mirror a situation in the field when there is no competition for a resource. It must be concluded that the vernal increase in LH secretion in Willow Tits can, in response to environmental conditions, occur earlier than laboratory data indicate. Although the ecological implications of this early rise in LH and T are self evident, it is not known what causes the discrepancy between laboratory and field data.

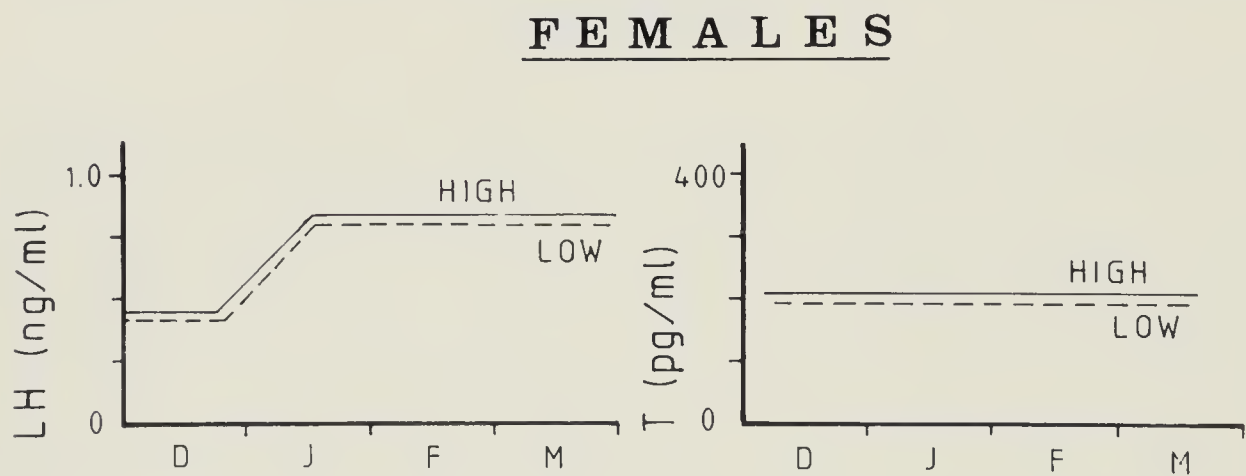
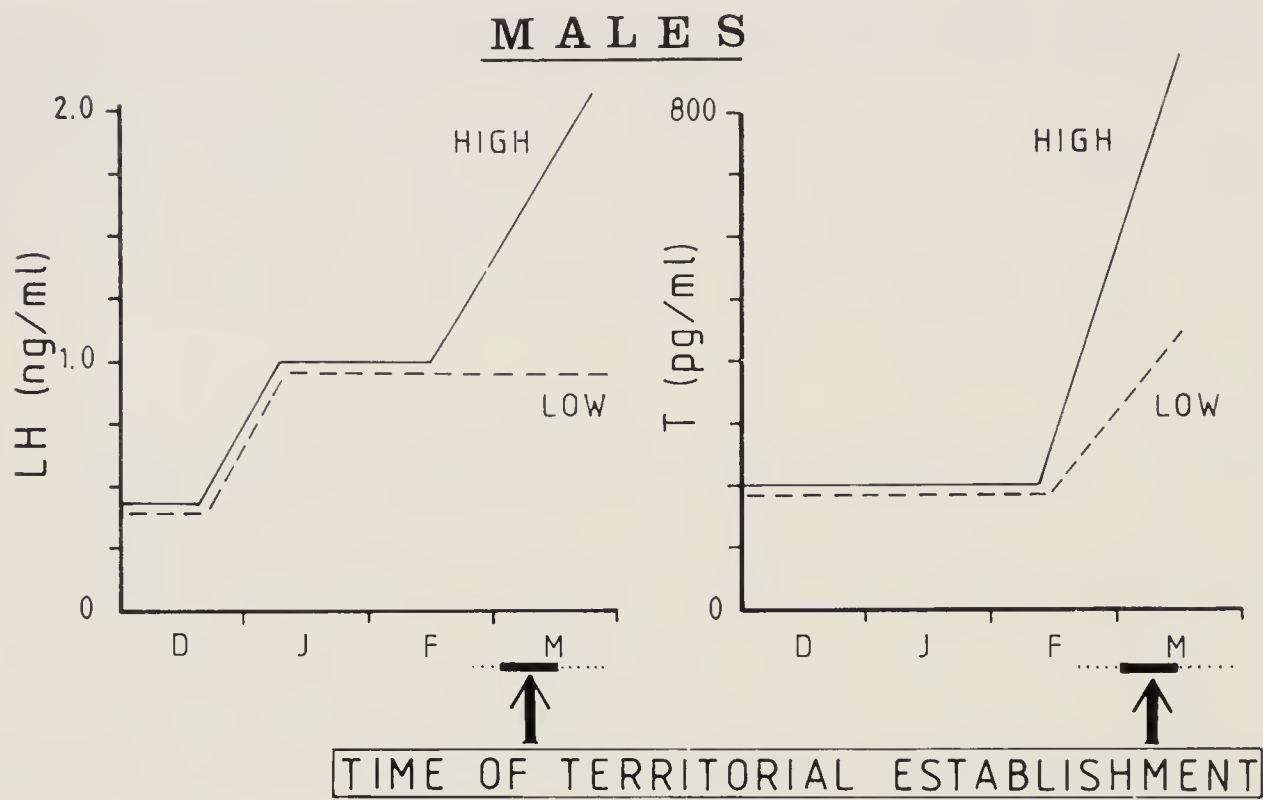


FIGURE 3 – If a territorial willow tit winter flock is provided with extra food the entire winter, winter survival increases from about 1.4 to 3.0 individuals per flock. The increased population density in spring causes male LH levels to rise earlier than in the low density population, and earlier than expected from laboratory data (see Figure 2). Also testosterone levels increase faster in the high density population. LH and testosterone levels in female willow tits are not affected by changes in the population density. (Data from Silverin et al. 1989a.)

However, one cannot simply say that LH levels increase earlier in the males if there is territorial competition. Laboratory data indicate that the presence or absence of a female in the territory also might influence LH secretion in free-living males. If a male Willow Tit is kept alone in a cage and exposed to long days, LH levels increase much slower than if a male has a female in his cage (Westin 1989).

It seems reasonable that the vernal LH secretion pattern observed in Great Tits, and in Willow Tits from a high density population, reflect the ancient parid pattern and that the "delayed" vernal LH rise, as seen in Willow Tits from a low density population, is a physiological response to the normally ecologically prevailing situation for Willow Tits.

Figure 3 also shows that hormonal secretion in female Willow Tits was not affected by the increased population density, but plasma levels of LH and estradiol (not shown in the figure) did not start to increase until the end of March. Contrary to the situation in female Willow Tits, LH levels rise quite drastically in female Great Tits in March (Silverin 1990).

THE LH AND TESTOSTERONE AUTUMN PEAKS

Autumn peaks are shown as stage B in Figure 1. In both Willow Tits and Great Tits, and in males as well as in females, there is an early autumn peak in plasma levels of LH and T. In Willow Tits these high LH and T values are found both in August and September (Silverin et al. 1986); and in a study on female Great Tits this LH peak was observed in August (Silverin 1990). For Great Tits – as indicated in the figure by the splitting of the curves into one adult and one juvenile part during September - these high LH and T values are only found in juveniles and never in adults. Adult Great Tits all the time have basal levels of LH and testosterone. The situation is not exactly the same in Willow Tits. Here high LH levels are also found among adults, but, as in the Great Tit, at this time of the year high T levels are only found in juveniles. However, only about 30% of these juveniles have high T levels, whereas the remaining 70% have levels as low as those of adult birds, i.e. basal levels. Juveniles having high T levels, on the other hand, are as high as those found in breeding birds. Most juveniles have slightly elevated LH levels in September.

As discussed above, juvenile tits attempt to become established in winter flocks. For the juvenile Willow Tit this is essential if a male is to breed in his natal area. During 10 years of intensive ecological studies of the Willow Tit Ekman (1979) never found one individual from outside his study area breeding within it. As 30% approximately equals the number of juvenile Willow Tits that manage to become permanent members of the territorial winter groups (Ekman 1979), and considering the importance of T in establishment of breeding territories, it is not unreasonable to conclude that high T levels would be an advantage for juveniles at this time of the year. To test this hypothesis an experiment was performed where all juvenile Willow Tits within an area (2 km² large) were implanted (during late July - early August) with either T or empty silastic tubes (Silverin et al. 1989b). Results from this study are summarised in Figure 4. Less than half of the T implanted birds, as well as controls, remained in the area in November, and only four of the remaining birds were observed in the same flocks; in August and November. It can therefore be concluded that having a high T level during early autumn does not facilitate a juvenile's becoming a permanent member of a winter group.

But why then do only some juvenile tits have high T levels during early autumn? Individuals with high T levels are also found among migratory juvenile Willow Tits in September (Silverin et al. 1989b). It is possible that high T levels are the result of

social interactions, or some birds may have become photosensitive when day lengths were still stimulatory (see below).

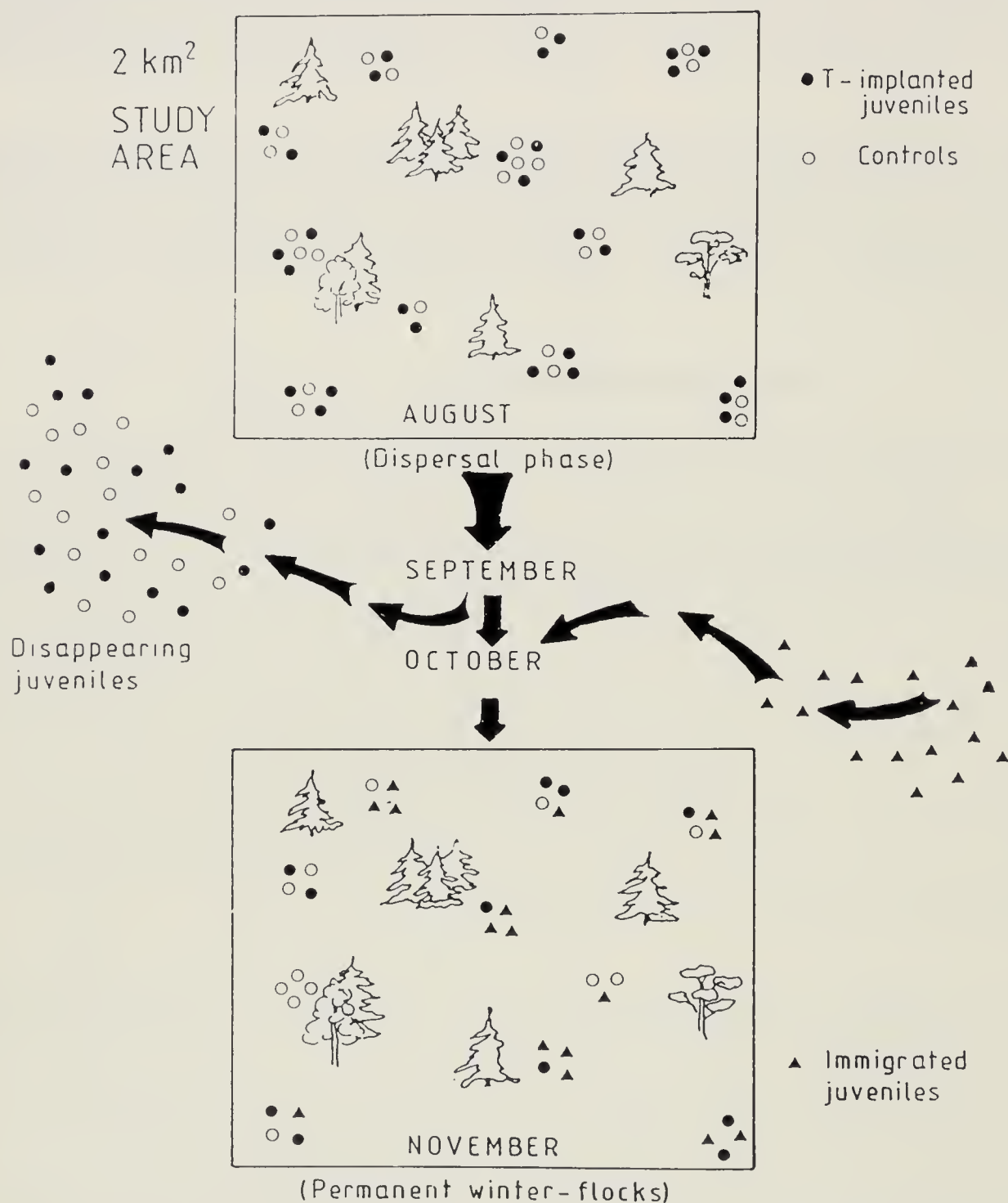


FIGURE 4 – Results from an experiment by Silverin et al. (1989b). In early August all juvenile willow tits within a study area were given either a testosterone implant or an empty silastic tube. By the time the permanent winter flock had been established only about half of the juvenile population from August was still present in the area, and in only a few cases were the birds observed in the same flock in August and November. The conclusion is: having high testosterone levels in early autumn does not facilitate a juvenile willow tit becoming a permanent member of a winter flock.

With few exceptions all birds breeding in the northern hemisphere become photorefractory at the end of the breeding period. Photorefractoriness is normally associated with low plasma levels of LH and T. Therefore it is natural to ask: are the tits photorefractory in August September? As discussed above, the tits seem to re-

quire a day length of about 11 hours before experiencing an increase in LH secretion. By mid-September day lengths are still a little bit longer than 12 hours, and 11 hours is not reached until early October (i.e. day lengths are still photostimulatory in mid-September). If the birds have broken their refractoriness in August/September, castrated birds put on long days should increase LH secretion. Studies on castrated male Great Tits found both adults and juveniles to be photorefractory at the end of August. However, two weeks later the birds could be divided into two categories. Some of the castrated birds responded to the experimental conditions (20L:4D) by rapidly increasing LH secretion. These birds therefore were photosensitive. Other birds did not increase LH secretion. When the experiments were repeated in early October, all castrated birds increased LH secretion (Silverin unpubl. data). Therefore it seems as if Great Tits break photorefractoriness not later than some time between mid-September and late September. Obviously there is a difference among individuals in the time of breaking photorefractoriness. What causes this flexibility is not known. Similar studies have not yet been performed on Willow Tits. The question remains, are Willow Tits breaking photorefractoriness earlier than Great Tits since Willow Tits show high LH levels in August? Further, why did the female Great Tits show high LH levels in August and not in September?

THE WINTER INCREASE IN PLASMA LEVELS OF LH

The winter increase is shown as stage C in Figure 1. It occurs in both sexes and in both age groups of Willow Tits and Great Tits, and it happens at a time of the year when day lengths are not longer than about 6 hours, and temperatures can be very low. However, only LH levels rise. T levels remain basal until spring.

If photosensitive male Great Tits are captured at different times of the year and put on long days they respond by increasing LH secretion. However, their response to the photo stimuli increases with season. In October, for example, there is only a low LH peak. In November there is a medium sized peak, and not until early January is the maximum LH response reached (Silverin unpubl data), i.e. at about the same time as there is an increase in circulating levels of LH in free-living tits. Castrated Great Tits also show a seasonal change in the castration response. For castrated males held on long days (20L:4D) at different times of the year, maximum response in increased LH levels is reached in birds captured in early January. The same seasonal pattern is observed if castrated males are kept on short days (8L:16D) (Silverin unpub. data).

If photorefractory Great Tits are caught in August one year and kept on short days (8L: 16D) for a year, LH levels start to increase during early January despite day lengths not long enough to be stimulatory. This increase levels off during early March (Silverin unpubl. data). Again, this increase starts when a corresponding increase occurs in free-living tits.

Obviously there is something happening to the mechanism(s) regulating plasma levels of LH during December/January. The cause of this winter increase in plasma levels of LH in free-living birds is unknown. Nor is the functional significance of this rise obvious. Today I can only point to some correlations that might be of interest. Figure 5 shows the testicular growth curve for adult and juvenile Willow Tits during autumn and winter. The curves for Great Tits look basically the same. During autumn there

is no growth of the testes. On the contrary, testes from both adult and juvenile males are decreasing in size. By late December - early January this trend is broken and the testes start to grow slowly, faster in adults than in juveniles. This slow testicular growth continues through January, February and early March. Once day length exceeds 11 hours, the testicular growth rate changes, and the testes start to grow very fast. By early April testes have reached full size (Silverin 1978 and unpubl. data). What causes this winter growth of the gonads, and what causes the winter rise in LH and what are the functional significance of these changes? These are questions that remain to be solved.

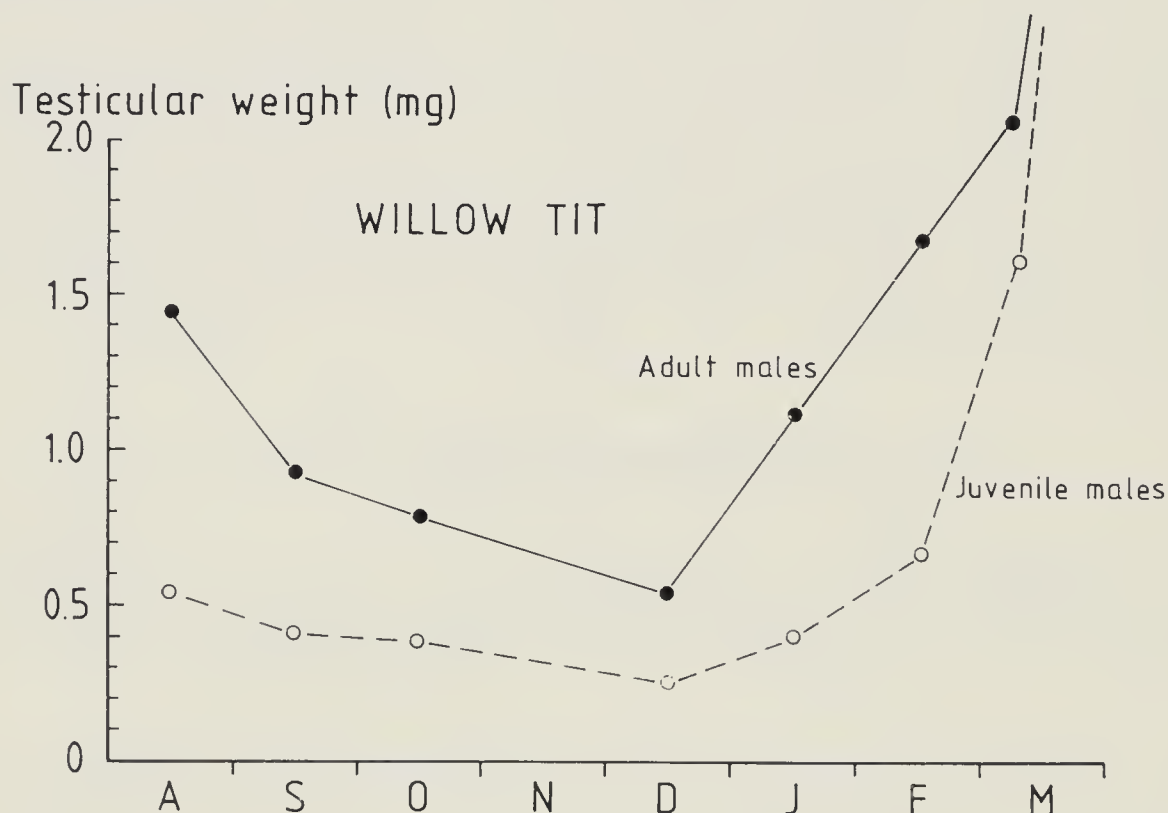


FIGURE 5 – Testicular growth pattern in adult and juvenile willow tits during autumn and winter (Viebke, pers. comm.).

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REPRODUCTIVE ENDOCRINOLOGY OF THE NORTH ISLAND BROWN KIWI *APTERYX AUSTRALIS MANTELLI*

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ABSTRACT. The breeding season of the North Island Brown Kiwi *Apteryx australis mantelli* extends from June to February, with a peak of egg-laying in late winter. Incubation of eggs takes 70-90 days and is performed entirely by the male. A recent study found an annual cycle of plasma levels of estradiol in both sexes. Estradiol levels were low from January to March, rising in April to high levels (>1000 pg/ml) that were maintained over 2-3 months before declining during egg laying. There was an annual cycle of testosterone levels in males, with a large rise in April and May to a peak 1-2 months before egg laying started. Levels declined towards the onset of incubation and were low in brooding birds. The annual cycles of plasma steroid hormones in Brown Kiwi reflect the stages of breeding during the long egg-laying season, and may be correlated with the pattern of male parental care.

Keywords: Kiwi, Brown Kiwi, estradiol, testosterone, incubation, endocrinology, seasonal breeding, sex-role reversal, New Zealand, ratite.

INTRODUCTION

Kiwi are distinctive New Zealand members of the group of flightless birds known as ratites. This group also includes rheas, Ostrich, Emu, and cassowaries. There are 3 species of kiwi, with the Brown Kiwi comprising 3 subspecies. The North Island Brown Kiwi *Apteryx australis mantelli* is now found in inland Taranaki, the Rotorua/Urewera district and Northland (Bull et al. 1985). The South Island Brown Kiwi *Apteryx australis australis* is found on the southern West Coast and in Fiordland (Bull et al. 1985). The Little Spotted Kiwi *Apteryx owenii* is found on Kapiti Island (with recent transfers to islands in the Hauraki Gulf), and the Great Spotted Kiwi *Apteryx haastii* only in North-West Nelson and the northern West Coast of the South Island (Bull et al. 1985).

The reproductive cycle of kiwi is characterised by a seasonal pattern of egg laying with a peak in late winter, a very large egg in relation to the size of the female, and a long incubation period. Parental care in kiwi comprises an incubation period of 70-90 days and brooding of the chicks for about 7 days (Cockrem in prep.). The chicks are precocial, and are not fed by the parents. It had previously been thought that incubation in kiwi was performed exclusively by the male (Reid & Williams 1975), but recently observations of incubation by female kiwi have been made in the Stewart Island Brown Kiwi (Sturmer & Grant 1988) and the Great Spotted Kiwi (McLennan & McCann 1989).

Winter breeding is unusual in birds (Follett 1984), and sex-role reversal, where the male is predominantly or solely responsible for incubation and brood care, occurs in less than 1% of bird species (Oring 1982). The endocrinology of reproduction has not previously been studied in a winter-breeding bird, and has been investigated in only three sex-role reversed species, the Spotted Sandpiper *Actitis macularia*, Wilson's Phalarope *Phalaropus tricolor* and Red-necked Phalarope *P. lobatus*. In this paper the

breeding season, reproductive behaviour and incubation pattern of the North Island Brown Kiwi are discussed, together with results from a recent study of reproductive endocrinology.

BREEDING SEASON

The breeding season of the North Island Brown Kiwi has been stated as being July-February (Reid & Williams 1975), but it is only recently that detailed field studies have confirmed this. In Hawkes Bay eggs were laid from June to February (McLennan 1988), with peak laying in August and September. A very similar pattern was found in Northland by Potter (1989). In contrast to free-living kiwi, North Island Brown Kiwi held in captivity under natural photoperiods can lay eggs in every month of the year (Cockrem et al. in prep.). However, a clear annual breeding season is maintained, with the majority of eggs laid from June to February. No detailed information is available on the timing of breeding in the South Island or Stewart Island Brown Kiwi.

REPRODUCTIVE BEHAVIOUR AND INCUBATION

Reproductive behaviour

In Hawkes Bay the home ranges of four pairs were estimated as 19.1-42.3 ha (McLennan et al. 1987). Birds very rarely moved into the home range of another pair, and there were apparent "boundaries" between the ranges of adjacent pairs. At Tangiteroria in Northland, a larger population had a density of kiwis about 10 times that in Hawkes Bay (Potter 1989). The home ranges of these birds were of similar size to those in Hawkes Bay (average of about 30 ha per bird), but there was extensive overlap of the home ranges. Colbourne & Kleinpaste (1983) observed male birds in Waitangi forest in Northland fighting and, on occasion, calling repeatedly at each other. However, no evidence was found of fighting or of birds calling repeatedly at each other in either of the other two studies (McLennan et al. 1987, Potter 1989).

The monthly frequency with which members of a pair roosted together was calculated from observations of birds in daytime roosts in Hawkes Bay and Northland by McLennan et al. (1987) and Potter (1989). Members of pairs in Hawkes Bay roosted together on only 8% of all days, with a rise in the frequency of roosting to a maximum of 14% in late May, June and July before breeding started. In Northland members of a pair roosted together on 22% of all days. There was an increase from a low frequency in December-January to a maximum in April-July, with a large rise from March to April (7-35%).

In Hawkes Bay pair bonds were stable over 2 years (McLennan 1988), whereas in Northland up to 50% of pairs changed mates between breeding seasons (Potter 1989). In both localities the birds were monogamous. The splitting and reforming of pairs in Northland occurred from January to April and was apparently not related to the breeding success of the birds in the previous season.

Incubation

In the North Island Brown Kiwi the female may spend one or two days in the nest after laying, after which all incubation is performed by the male (McLennan 1988, Potter 1989). Incubation may be sporadic for some time after egg laying. Incubating males

leave the nest each night to feed, emerging later each night and spending a shorter period active than either females or non-incubating males (McLennan 1988, Potter 1989). In the Stewart Island Brown Kiwi, in contrast to the North Island Brown Kiwi, females have been reported as incubating eggs on two occasions during the day (Sturmer & Grant 1988). As no systematic study of the Stewart Island Brown Kiwi has been undertaken, it is not known to what extent females normally participate in incubation.

In the Little Spotted Kiwi, incubation was performed only by the male (Jolly 1989), whereas incubation by the female has been found in Great Spotted Kiwi in North-west Nelson (McLennan & McCann 1989). Furthermore, a female Great Spotted Kiwi incubated an egg for at least one month after her mate died, and there were signs that a chick was produced from the egg. Female kiwi are therefore quite capable of incubating eggs.

MALE ENDOCRINOLOGY

The first study of the reproductive endocrinology of kiwi has recently been made at Tangiteroria, Northland, by Potter & Cockrem (submitted). A population of free-living North Island Brown Kiwi was studied for 2 years in conjunction with a radiotelemetry study of the movements, pair bonding and reproductive biology of the birds (Potter 1989). Blood samples were collected from kiwi and plasma hormone levels subsequently measured by radioimmunoassay. Varying numbers of serial samples were obtained from individual birds, with the breeding status of some birds known at the time of sample collection.

Testosterone

There was a clear annual cycle of mean plasma levels of testosterone (Figure 1). Mean levels were low (<0.18 ng/ml) from February-April, then rose to peak in May (1.90 ± 0.76 ng/ml). High levels were maintained until August, with a subsequent decline to low levels in February. A similar pattern was seen in each of the 2 years, and was seen (with individual variations) in males that were sampled in both years. Testosterone (T) levels were also expressed in relation to stages of breeding (Figure 2). Mean levels were low (0.38 ± 0.13 ng/ml) in the non-breeding period (after the last breeding attempt of the season, and at least 4 months before the next attempt). Elevated levels (1.60 ± 0.78 - 2.39 ± 0.97 ng/ml) occurred during the 16-4 weeks before the female laid the first egg. Testosterone levels declined towards the start of incubation, with a further decline during incubation to very low levels (0.06 ± 0.00 ng/ml) when brooding chicks. In some birds T had reached low levels before incubation started, whereas in others levels were still greater than 1 ng/ml as incubation started.

The pattern of T levels corresponds generally to the timing of the events of the reproductive cycle. Testosterone levels rose in autumn at a time when calling rates were increasing and when members of a pair spent more time together. Testosterone in birds is generally thought to be associated with aggressive behaviour. This association has been described by the "challenge" hypothesis, which asserts that T and aggression correlate only during periods of heightened aggression between males (Wingfield et al. 1987). Testosterone in male Brown Kiwi is elevated for 3 months or more before declining towards the start of incubation, suggesting that there might be interactions between males and/or interactions with females throughout this period. It has been suggested that high T levels are incompatible with parental care in birds

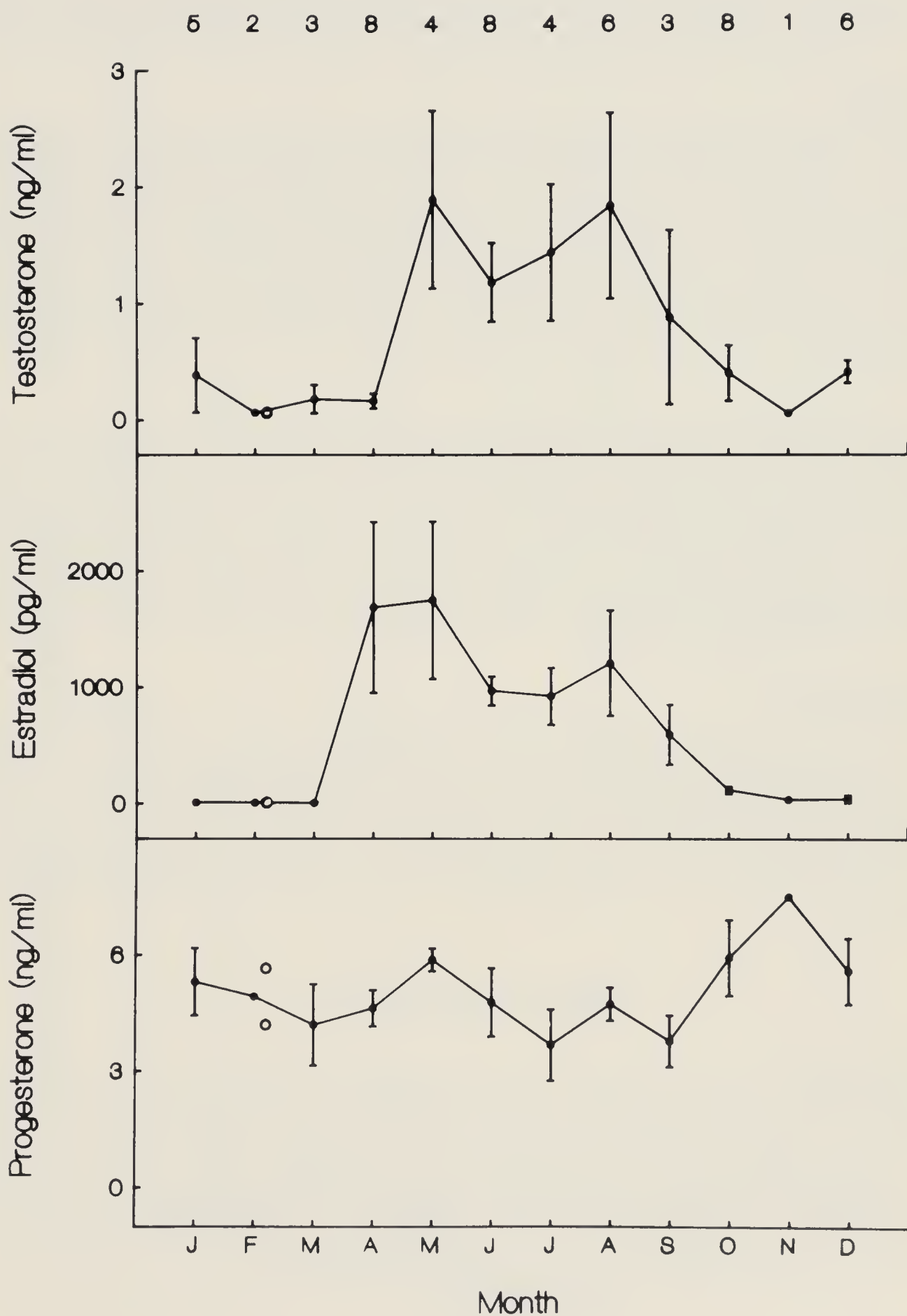


FIGURE 1 - Plasma levels of testosterone, estradiol and progesterone in free-living male North Island Brown Kiwi in Northland (after Potter & Cockrem submitted). Values are mean \pm S.E. Sample sizes are given at the top of the figure. Where the sample size was <3 individual values are shown.

e.g. Spotted Sandpiper (Oring et al. 1989). The results from the Brown Kiwi are consistent with this idea. Also, as for other birds irrespective of sex-role patterns, there was no reversal of the normal pattern of higher T levels in male than female birds.

Estradiol

Plasma levels of estradiol (E) had an annual cycle of mean levels, as found for T (Figure 1). Low (<50 pg/ml) mean levels occurred from November to March, with a rise in April to maximum levels in May (1702 ± 274 pg/ml). High levels (>900 pg/ml) were maintained until July, followed by a steady decline until November. This pattern was repeated in each of the 2 years, and was seen in males that were sampled in both years. The pattern of E levels in relation to breeding stage was very similar to that of T (Figure 2). Estradiol levels were very low in the non-breeding period, rising in the months preceding egg laying, then declining towards the start of incubation in a similar way to T.

Sex-role reversal in the Kiwi is accompanied by a change in the normal pattern of higher E levels in female than male birds, with similar levels in male and female kiwi. Estradiol levels in North Island Brown Kiwi were higher than the normal range for male birds, and might be associated with incubation behaviour. High levels of plasma E have been found in castrated male Song and Swamp Sparrows *Melospiza melodia* and *M. georgiana* (Marler et al. 1988), indicating that the adrenal gland may be a source of plasma E in male birds. However, both the source and function of estradiol in male kiwi remains unknown.

Progesterone

There was no pattern in monthly levels of progesterone (P) or in P levels in relation to stages of breeding (Figures 1 and 2). Progesterone levels in some other male birds also do not change markedly during the year, e.g. Starling, *Sturnus vulgaris* (Ball & Wingfield 1987). McCreery & Farner (1979) found similar levels of P in intact and castrated White-crowned Sparrows *Zonotrichia leucophrys gambelli*, indicating an extragonadal source of P. For the male Brown Kiwi, the source and function of P are unknown.

FEMALE ENDOCRINOLOGY

Testosterone

Mean levels of T were low (<0.10 ng/ml) throughout the year (Figure 3). When considered in relation to stages of breeding, there was a small rise over about 8 weeks before egg laying from basal levels (0.06 ng/ml) to a peak in the 2 weeks before the first egg of a clutch (Figure 4). The production of androgens by the ovary increases during sexual maturation in the chicken (Robinson & Etches 1986), and the rise in plasma T in the female Brown Kiwi approaching egg laying probably represents secretion from the follicle(s) that are growing towards ovulation.

Estradiol

In females there was an annual cycle of mean levels of E that was similar in timing and amplitude to the cycle in males (Figure 3). Mean levels were low (<60 pg/ml) from December to March, then rose to a peak in April (2676 ± 634 pg/ml). High levels were maintained until August, followed by a steady decline to December. Individual birds sampled over 2 years had annual peaks in both years. In relation to the stages of

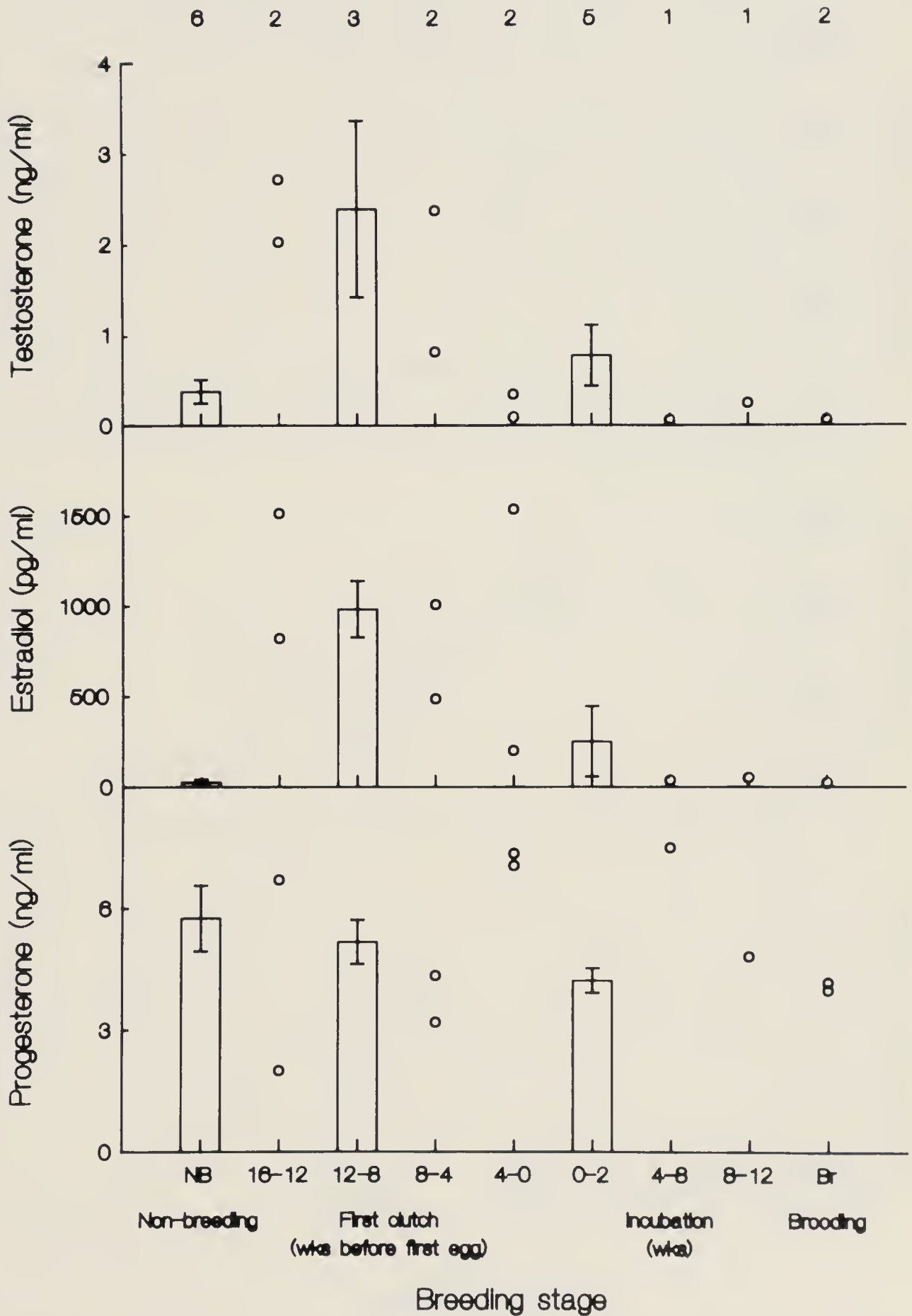


FIGURE 2 - Plasma levels of testosterone, estradiol and progesterone according to stages of breeding in free-living male North Island Brown Kiwi in Northland (after Potter & Cockrem submitted). Values are mean \pm S.E. Sample sizes are given at the top of the figure. Where the sample size was <3 individual values are shown.

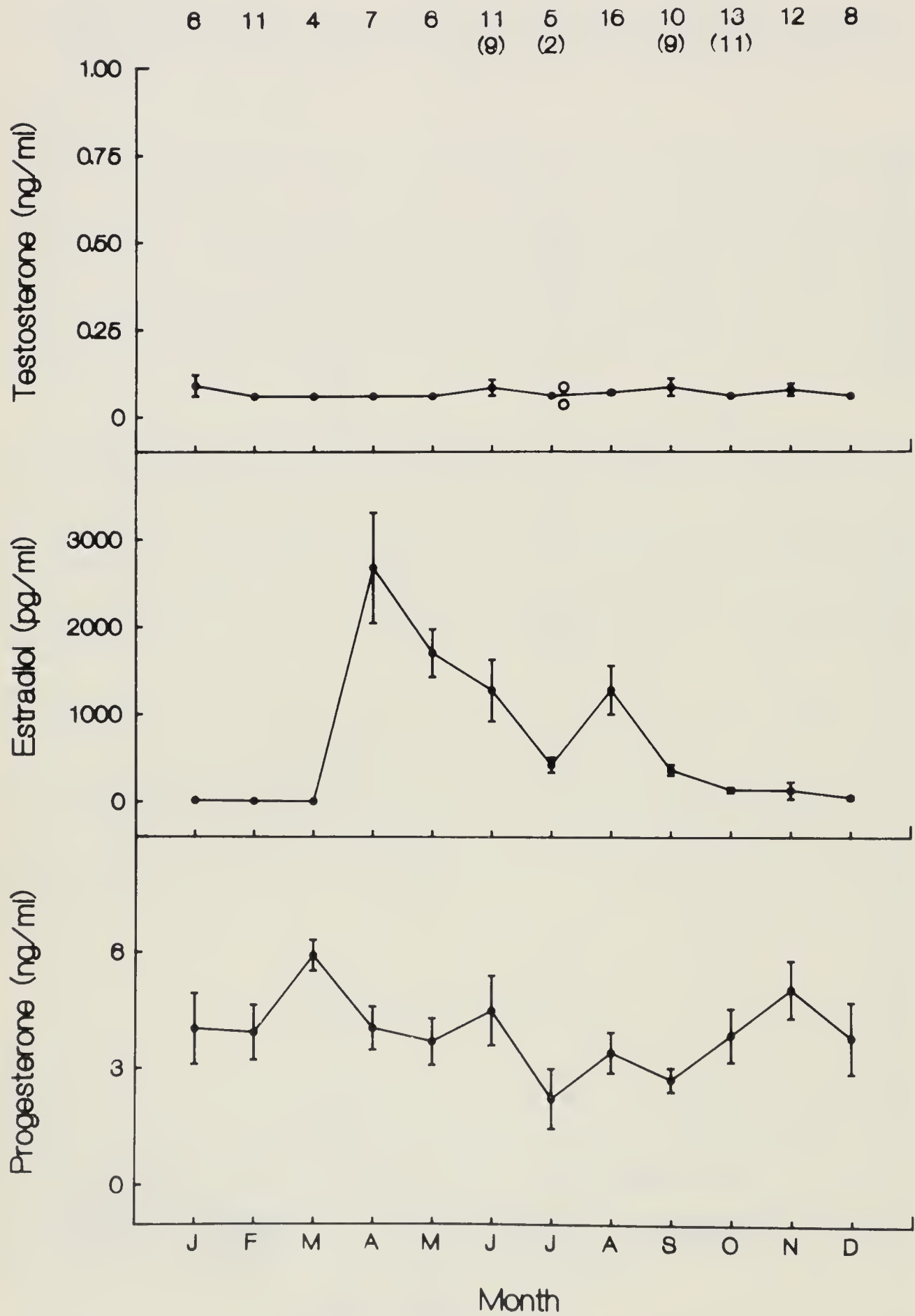


FIGURE 3 - Plasma levels of testosterone, estradiol and progesterone in free-living female North Island Brown Kiwi in Northland (after Potter & Cockrem submitted). Values are mean \pm S.E. Sample sizes are given at the top of the figure. Sample sizes for testosterone are given in brackets where they differ from those for other hormones. Where the sample size was <3 individual values are shown.

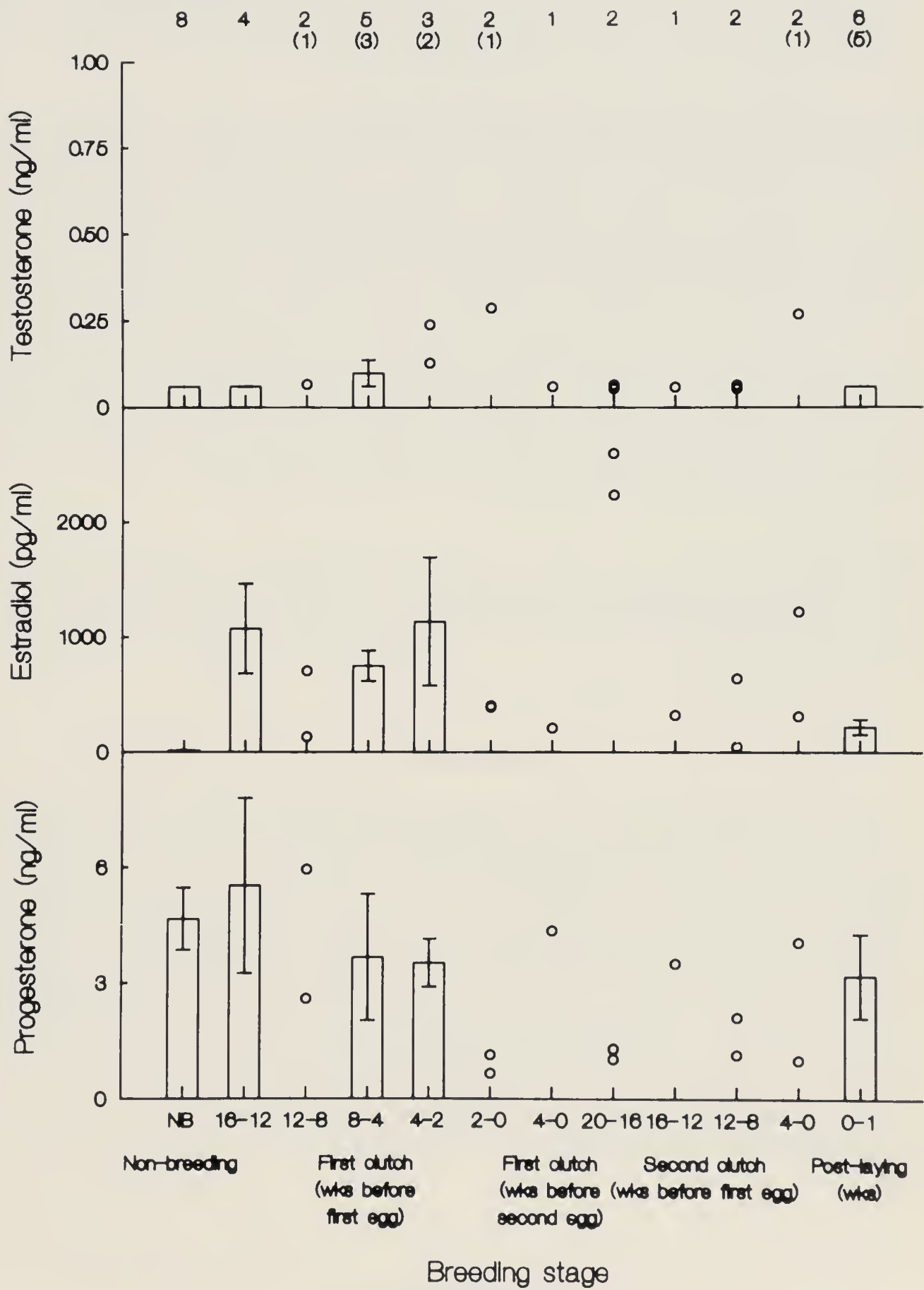


FIGURE 4 - Plasma levels of testosterone, estradiol and progesterone according to stages of breeding in free-living female North Island Brown Kiwi in Northland (after Potter & Cockrem submitted). Values are mean \pm S.E. Sample sizes are given at the top of the figure. Sample sizes for testosterone are given in brackets where they differ from those for other hormones. Where the sample size was <3 individual values are shown.

breeding, there was a general trend for a gradual rise in mean E levels from basal in the non-breeding period to high levels up until 2 weeks before laying (Figure 4). This was followed by a decline to low levels once incubation started. This trend was also apparent in limited data for the second egg of a clutch.

Estrogens in female birds stimulate vitellogenesis in the liver (Johnson 1986), and E levels have been reported to rise as follicles grow before egg laying in free-living birds (e.g. White-crowned Sparrow, Wingfield & Farner 1978, Song Sparrow, Wingfield 1984, House Sparrow, *Passer domesticus*, Hegner & Wingfield 1986). The several month period of elevated E in the Kiwi presumably reflects a similar period of ovarian activity, and implies that the Kiwi undergoes a seasonal pattern of ovarian growth and regression as do other seasonally breeding birds. This is consistent with the observations of Kinsky (1971) on Kiwi specimens, who found large variations between birds in ovarian size. The female Brown Kiwi has two functional ovaries. When developing follicles are present there are approximately equal numbers in each ovary (Kinsky 1971), and presumably both ovaries secrete E and contribute to plasma levels of E. The field study data do not allow any detailed analysis of estradiol secretion in relation to ovarian growth, yolk formation and ovulation in kiwi.

Progesterone

There was no annual pattern or relation of plasma levels of P to breeding stages (Figures 3 and 4). In the chicken a P surge before ovulation is largely responsible for initiating ovulation (Follett 1984), and P in the female Brown Kiwi might have a role in the initiation of ovulation.

CONCLUSION

Sex-role reversal of parental care in the North Island Brown Kiwi is not accompanied by a reversal of relative male/female androgen levels, but males do have similar E levels to females. There are differences between subspecies and species of the Kiwi in the pattern of parental care, with females undertaking incubation in the Stewart Island Brown Kiwi and Great Spotted Kiwi. These differences provide opportunities for interesting comparisons of the endocrinology of incubation between species. For the Brown Kiwi, the rise in autumn of T in males and of E in males and females probably reflects the activation of the hypothalamic-pituitary-gonadal axis at this time. The proximate factor(s) causing this activation are unknown, but it is suggested that daylength is an important proximate factor timing seasonal breeding in the Kiwi, with the possibility that the annual cycle of daylength entrains an endogenous circannual reproductive rhythm. Kiwi promise to be valuable subjects for future endocrine research.

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SYMPOSIUM 38

**INTEGRATIVE ASPECTS OF
OSMOREGULATION IN BIRDS**

Conveners E. J. BRAUN and D. H. THOMAS

SYMPOSIUM 38

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INTAKE OF FLUID AND ELECTROLYTES

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ABSTRACT. In body fluid homeostasis, changes in volume and osmotic pressure in the extracellular compartment give rise to tonicity-related and volume-related, neuronal and hormonal signals to induce thirst and ingestion of water and salt. Drinking may be considered as the behavioural component in a multiple-loop control system involving also reabsorptive and excretory effector mechanisms. Nervous control is established by receptors in the brain and in the periphery by which volume-related parameters and osmotic pressure are sensed to provide afferent information for the regulation of thirst, antidiuretic hormone and the autonomic innervation of effector organs like the salt secreting glands. Hormonal control by the renin-angiotensin-aldosterone system and the atrial natriuretic factor is mainly volume-dependent. Most important for the regulation of salt and fluid intake is coordination of hormonal with central nervous control by brain structures, like the subfornical organ, which serve as receptors for circulating angiotensin II and possibly also atrial natriuretic factor.

Keywords: Avian osmoregulation, thirst, osmoreception, volume reception, antidiuretic hormone, angiotensin II, atrial natriuretic factor, subfornical organ, paraventricular nucleus.

INTRODUCTION

In maintaining fluid and electrolyte balance birds face the same challenges and make use of the same repertoire of neurally and hormonally controlled regulatory activities as mammals do. Inasmuch as reabsorptive and excretory organs are common to both classes, all relevant cellular mechanisms of water and electrolyte transport across epithelia seem to be basically identical. However, birds utilize two additional modes of salt and fluid handling: first, urinary discharge of nitrous waste as barely soluble uric acid compounds into the cloaca, which permits recovery of the bulk of water and salt from the urine by post-renal modification; second, salt secreting glands as an auxiliary output system in a number of marine and estuarine birds (Skadhauge 1981). Ingestion of salt and water is a prerequisite for controlled reabsorption in the intestine and, as an essentially behavioural activity, is exclusively under the control of the central nervous system. Water intake is indispensable for fluid balance in most mammals and birds, not least because they share, as homeotherms, the thermoregulatory challenge imposed by water evaporation on fluid balance. Exceptions are a few desert species in each class for which supply with metabolic water seems to be sufficient. In both mammals and birds thirst is stimulated by the two fundamental disturbances of body fluid balance: dehydration and body fluid hypertonicity (Takei et al. 1989). Salt appetite as a special behavioural drive has received attention in herbivorous mammals which are constantly on the verge of a sodium deficit, and has also been demonstrated in granivorous birds (Cade 1964).

PRINCIPLES OF CONTROL

Ingestion of salt and water requires that the central nervous system receives adequate information about body fluid and electrolyte content to induce the appropriate

behavioural activity. As an intensive physical property, body fluid tonicity, i.e. the concentration of solutes confined to the extracellular compartment, may be perceived by receptive elements monitoring, in one or the other way, concentration differences. Osmoreception was first localized in the brain of mammals (Verney 1947). Evidence is now overwhelming that the rostral brain stem is, indeed, the main site for osmoreception in both mammals and birds (Andersson 1978, Gerstberger et al. 1984c). Osmoreceptors outside the brain in mammals (Haberich 1968, Chwalbinska-Moneta 1979) and birds (Hanwell et al. 1972) have remained elusive. More difficult to define are the modes by which volume derived signals contribute to the control of salt and fluid balance. While it is clear that the amounts of fluid present in the vascular, interstitial and intracellular compartments must be tightly controlled, no mode of direct biological monitoring can be conceived for fluid volume or mass as an extensive property. Current concepts postulate that intensive parameters that are correlated with the amount of fluid in a given compartment, such as interstitial or intravascular pressure, are transduced at certain strategical sites into nervous or hormonal signals which, apart from their effects on excretory and reabsorptive mechanisms, must be transmitted to the brain to control the behavioural activities associated with drinking. Even less well defined is additional information shown to be relevant in the control of cessation of drinking. For thirsty mammals it has been repeatedly demonstrated that water intake was adequately stopped at times before a decrease in body fluid osmolality or an increased central blood volume due to reabsorbed fluid could possibly have provided inhibitory signals to the brain. Oesophageal or gastric mechanoreceptors "metering" the amount of ingested fluid have been postulated (Thrasher et al. 1981) to provide preabsorptive inhibition of drinking upon which fine control by osmoreceptors and volume receptors is superimposed. While corresponding mechanisms have not been demonstrated in birds, they might also be important for species from habitats which necessitate infrequent drinking of large amounts of water.

Osmoreceptor signals in the control of thirst

It is common experience that conditions which increase body fluid osmolality in birds also stimulate drinking (Takei et al. 1988) and antidiuretic activity (Stallone & Braun 1986, Gray & Erasmus 1988). Studies in birds in which hypertonic solutions were injected intracerebroventricularly (icv.) or into the hypothalamic tissue have demonstrated osmosensitivity in close proximity to the third cerebral ventricle. This conclusion was derived from the observed stimulation of drinking (Fitzsimons et al. 1982, Thornton 1986) and/or salt gland activation and release of antidiuretic hormone to enhance renal water conservation (Gerstberger et al. 1984b). Conflicting data in mammals with regard to the relative efficiency of electrolytes v non-electrolytes in hypertonic stimulation of thirst and antidiuresis have been interpreted as indicative of the existence of both true osmoreceptors and sodium receptors (Thrasher et al. 1980, Thornton 1984, Rundgren et al. 1986). The same problem seems to exist in birds: while general osmosensitivity cannot be excluded, sodium sensitive receptors seem to exist in close proximity to the third cerebral ventricle (Fitzsimons et al. 1982, Simon-Oppermann et al. 1989). According to studies on mammals, osmoreceptive structures may be localized on both the brain and blood side of the blood brain barrier (Thrasher 1989). For birds as well, results of injection studies seem to suggest, at least, that hypothalamic osmoreceptive structures are not confined to a single nucleus (Fitzsimons et al. 1982, Thornton 1986). At the current state of analysis, evidence for preferential control of drinking and antidiuresis by receptors of one or the other type

and one or the other location appear still inconclusive in mammals (Thrasher 1989) and birds (Thornton 1986). On the other hand, it is clear that the receptors stimulating drinking and antidiuresis, if not identical, must be closely co-localized and that osmo- and sodium receptors should be similarly involved in the control of both drinking and antidiuresis.

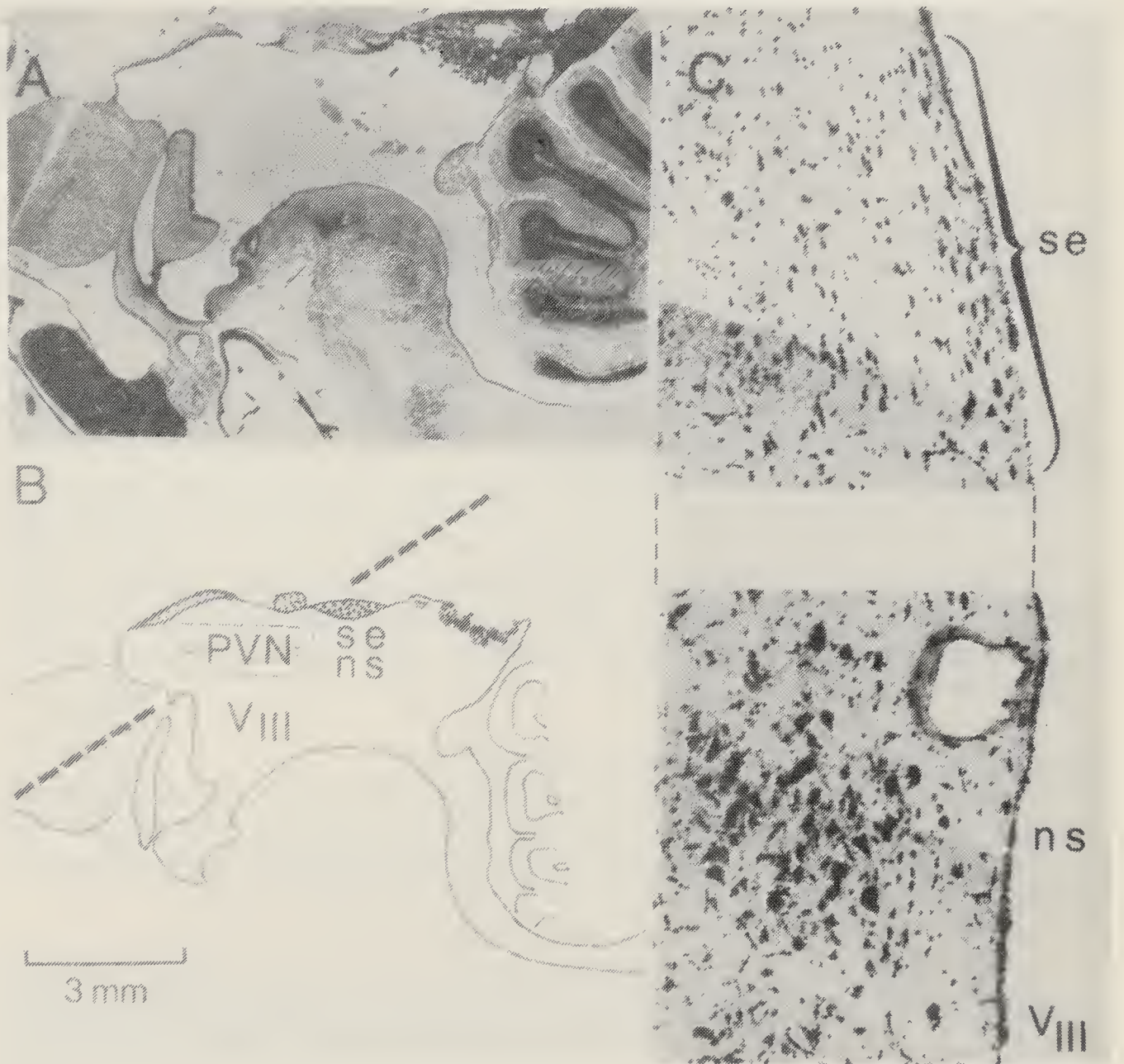


FIGURE 1 - Location of neurons exhibiting sodium sensitivity in the duck's rostro-dorsal hypothalamus. A: midsagittal section showing the structures surrounding the third ventricle. B: schematic drawing of A indicating the approximate location of the subependymal (se) neurons dorsal and parallel to the more laterally located neurosecretory (ns) cell somata of the paraventricular hypothalamo-neurohypophyseal system. C: frontal section (direction indicated in B by the interrupted line) showing in its upper part the subependymal neurons among which the majority were sodium sensitive, and in its lower part the magnocellular neurosecretory cells of the paraventricular nucleus.

Morphological studies in ducks have suggested that a group of subependymally located neurons in the periventricular region of the duck's hypothalamus might qualify as osmoreceptors because of their monosynaptic projections to the neurosecretory, magnocellular portion of the paraventricular nucleus (PVN) from which the antidiuretic

hypothalamo-neurohypophysial system of birds mainly originates (Korf 1984). As illustrated by Figure 1 these neurons are arranged medial and dorsal to the magnocellular PVN neurons in the rostro-dorsal extension of the third ventricle. Probing this region with microelectrodes revealed that a majority of the subependymally located neurons could be excited by adding NaCl to artificial cerebrospinal fluid (CSF) to increase local tonicity, whereas no sensitivity was found in the neurosecretory portion of the PVN (Kanosue et al. 1990). In agreement with the differential antidiuretic effects elicited in ducks by icv. hypertonic perfusion with electrolytes and non-electrolytes (Simon-Oppermann et al. 1989) single unit excitability was restricted to electrolytes, indicating a sodium-sensitive mechanism of transduction.

Neuronal signals in volume control of thirst

Commonly assumed as receptors monitoring intravascular volume in mammals and birds are the stretch receptors in the walls of the large intrathoracic veins and in the atria of the heart (Gauer et al. 1970, Hanwell et al. 1972). The immediate responses seen after acute hemorrhage – stimulation of drinking in the quail (Kobayashi & Takei 1982) and, in ducks, inhibition of salt gland secretion (Hammel et al. 1980) and enhanced release of antidiuretic hormone (Simon-Oppermann et al. 1984) – are ascribed to the reduced activity of vagal stretch receptors. Studies in birds have suggested that, in addition to intravascular volume (Zucker et al. 1977), interstitial volume might be monitored as well (Hammel et al. 1980), although at sites and in ways that are hitherto unknown. Renal and salt gland responses to changes in interstitial volume were observed without apparent relationships to changes in concentration of the osmoregulatory hormones (Keil et al. 1991) and, consequently, support the idea of a mainly neural mechanism of interstitial volume perception which might also contribute to the control of drinking.

Hormonal signals in volume control of thirst

Information relevant for body fluid homeostasis in general, and for the control of drinking in particular, may be provided by hormones acting on specific brain targets. With regard to volume monitoring, the role of those hormones has to be considered for which volume dependence of their release has been demonstrated.

ANGIOTENSIN II (ANGII). Among the osmoregulatory hormones, this peptide is the most likely candidate to act as a physiological messenger to the brain in states of volume deprivation. In birds, its importance as a regulating hormone in aldosterone release (Gray et al. 1989) and its direct interference with renal sodium excretion, as well as its action on brain targets to inhibit salt gland secretion (Gray & Erasmus 1989) are well established. In particular, however, ANGII has been shown to be a similarly strong dipsogen in birds and in mammals (Fitzsimons 1980). As in mammals ANGII formation from circulating angiotensinogen is regulated in birds mainly by the enzyme renin. Volume influences on its activity are transduced in the macula densa and, thus, cannot be accurately classified as due to changes in either the interstitial or the intravascular compartment. However, according to studies in ducks under chronic salt stress, changes in ANGII plasma concentration seem to be correlated more closely with the interstitial than the intravascular volume (Brummermann & Simon 1990).

Both systemic and intrahypothalamic or icv. injections of ANGII were shown to have dipsogenic effects in the pigeon (Evered & Fitzsimons 1981) and quail (Kobayashi & Takei 1982). The assumption that the central ANGII effects are mediated by the

subfornical organ (SFO), which is devoid of a blood brain barrier, has received support by the demonstration of high-affinity binding sites for ANGII. In an autoradiographic and kinetic study of high-affinity binding of ANGII in the rostral brain stem of ducks, the distribution of binding sites was found to be homologous to that in rats, with the SFO as the most densely labelled periventricular structure (Gerstberger et al. 1987). Supportive electrophysiological evidence for the SFO as an interface mediating central effects of circulating ANGII was recently obtained by demonstrating in ducks a high fraction of ANGII-sensitive SFO neurons which exhibited a clear dose-response relationship between ANGII-concentration and the degree of neuronal excitation (Matsumura & Simon 1990a).

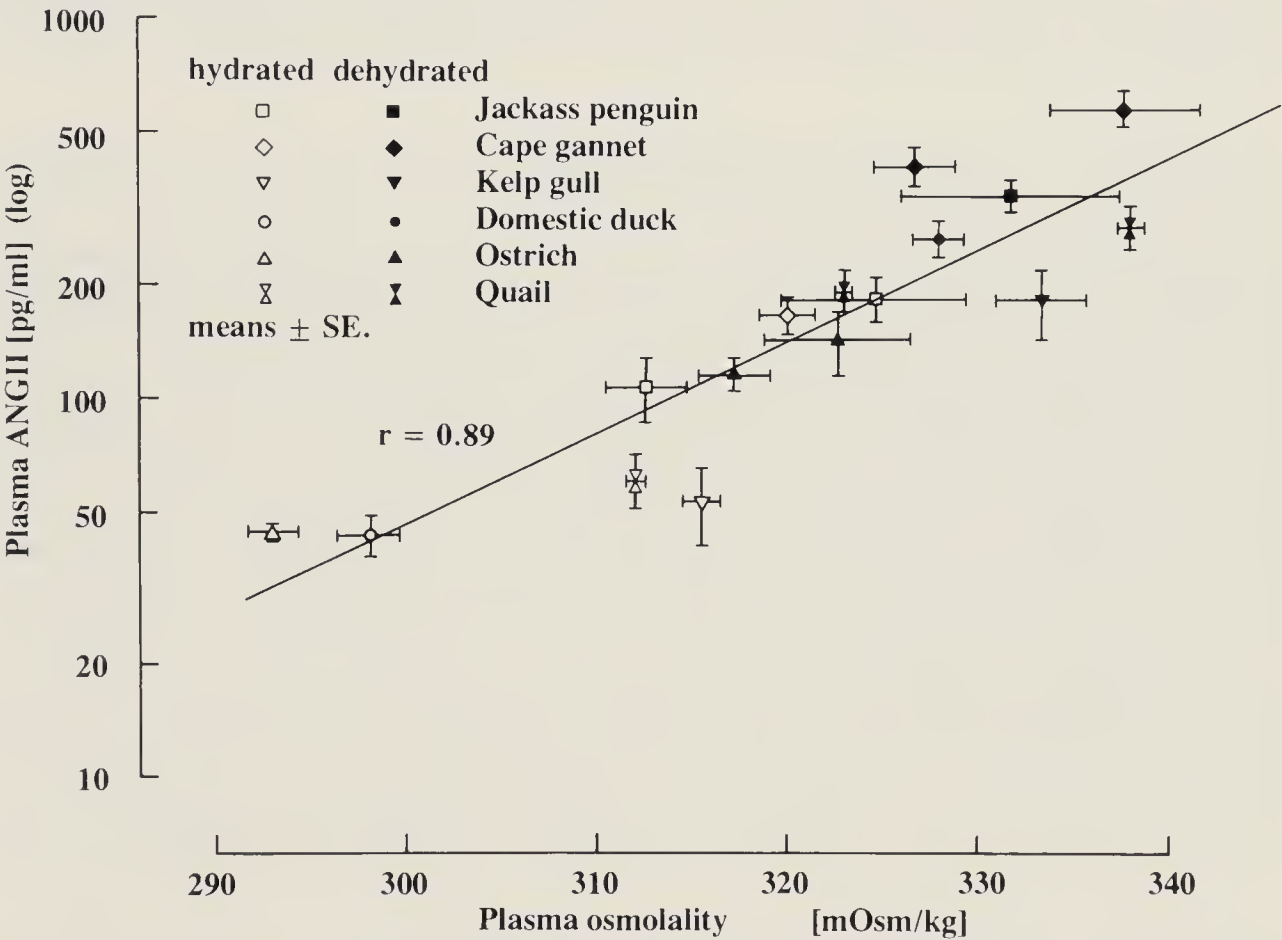


FIGURE 2 - Relationship between plasma osmolality as an indicator of dehydration and ANGII plasma concentration (on a logarithmic scale) existing in various birds when compared at normal hydration and after 1-3 days of water deprivation. A highly significant log-linear correlation was found. References in the text.

The role of circulating ANGII as a natural dipsogenic messenger to the brain requires that its volume dependence reflects water deprivation. As illustrated by Figure 2, this could, indeed, be demonstrated in several avian species (Takei et al. 1988, Gray & Erasmus 1988, Gray et al. 1988, Gray & Simon 1987). For the effects observed in birds in response to icv. ANGII injections (Evered & Fitzsimons 1981, Gerstberger et al. 1984a) a natural correlate has been provided by the increase in ANGII levels found in the CSF of ducks during chronic as well as acute dehydration (Gray & Simon 1987) and by the rapid selective decline of ANGII levels in the CSF at a time when plasma ANGII was still elevated. Taken together, these studies in birds support the idea of brain-intrinsic ANGII as a coordinating messenger for the stimulation of volume conserving activities involving not only thirst but also appropriate adjustments of antidiuresis, salt gland activity and cardiovascular functions (Simon et al. 1989).

For many birds with salt glands, especially marine species, the availability of only hypertonic saline for drinking in their natural habitat poses the problem of the role of salt taste as a supportive or apprehensive stimulus. It is clear that these birds, when given the opportunity in the laboratory, will prefer fresh water to salt water. On the other hand, when ducks were adapted to saline of increasing concentrations they were thereby forced to drink increasing amounts of salt water to ensure adequate supply with free water for, e.g., evaporation. It would be interesting to speculate whether the rise in both circulating and central ANGII might have dampened the adversity to ingest excessive amounts of salt. In this way the birds could be motivated to drink salt containing fluids of a composition that would otherwise impede the drive for drinking. This would imply that, in birds, ANGII produces some degree of salt appetite, which is considered to be the case in mammals (Blair-West et al. 1988, Tarjan et al. 1988).

The assumption of a physiological role of circulating ANGII in the control of thirst has been put forward on the basis of injection studies, which usually demonstrate effects at hormone concentrations higher than those naturally encountered. Supportive evidence comes from the observation of a natural, circadian correlation between ANGII plasma levels and drinking activity in the quail (Okawara et al. 1985). Similarly supportive with respect to the central target involved is the clear up-regulation of ANGII-receptor density observed in the SFO of ducks that were chronically exposed to hypertonic saline as their only water supply (Gerstberger et al. 1987). Enhanced receptor density may be interpreted as a molecular correlate of central nervous adaptation to a degree of salt stress that implies extracellular dehydration. The functional significance of this adaptation at the molecular level was confirmed in electrophysiological studies on the SFO of ducks which had been chronically salt stressed and in which ANGII receptor density was presumably enhanced. ANGII sensitivity of SFO neurons in these animals was consistently enhanced by a factor of 10 in comparison to SFO neurons recorded in ducks on fresh water (Matsumura & Simon 1990b). Taken together, correlation in time between ANGII levels and drinking activity, elevation of ANGII levels in both the blood and the CSF by dehydration, and enhanced ANGII receptor density in the SFO in association with increased ANGII sensitivity of SFO neurons in the state of chronic dehydration provide a consistent morphological and functional line of evidence for a physiological role of circulating and brain-intrinsic ANGII as central dipsogenic and osmoregulatory mediators.

ATRIAL NATRIURETIC FACTOR (ANF). For this peptide, synthesis in atrial myocytes and its release upon stretch both suggest that its plasma level should reflect intrathoracic vascular filling. This has recently been confirmed also for birds in studies on the duck (Keil et al. 1991). In mammals, an inhibitory action of centrally administered ANF on water intake has been recently demonstrated (Tarjan et al. 1988, Thornton & Baldwin 1988) besides its well-known systemic natriuretic and hypotensive effects. In birds, the involvement of ANF in salt and fluid balance has been documented, so far, by demonstrating natriuresis and salt gland stimulation as effects of ANF (Schütz & Gerstberger 1990) in ducks and by its interference with the control of aldosterone (Gray et al. 1990). The demonstration of ANF-receptors in ducks not only in the kidneys and salt glands (Schütz & Gerstberger 1990) but also in the SFO (Gerstberger this symposium) would suggest a central component in the antagonistic osmoregulatory actions of ANF and ANGII which might not be restricted to their opposing effects on salt gland activity but might also apply to the control of drinking.

ANTIDIURETIC HORMONE (ADH). As with arginine vasopressin in mammals, the release of arginine vasotocin in birds exhibits some degree of volume dependence (Simon-Oppermann et al. 1984) which is ascribed to the signals transmitted by vagal volume receptors. In mammals, injection studies have not conclusively demonstrated that ADH acts as a central mediator of thirst. However, ADH was found in the CSF of both mammals (dogs) and birds (ducks) in about 10-fold higher concentrations than in the plasma and was shown to exhibit parallel changes with peripheral hormone concentrations in conditions of acute and chronic dehydration as well as rehydration (Simon-Oppermann et al. 1988). Further analysis is required to substantiate the suggestion that brain-intrinsic ADH is involved in the control of salt and fluid balance in both mammals and birds.

CONCLUSION

According to the experimental evidence discussed in this review, intake of salt and water represents the behavioural effectors in a highly complex control system which involves, in addition, intestinal reabsorption, renal excretion and salt gland secretion as hormonally and/or neuronally controlled autonomic effectors. Neuronal regulatory activities are coordinated by hypothalamic structures according to signals from specific intracerebral and peripheral receptors providing information about osmotic pressure and fluid volume in the extracellular and possibly also interstitial compartments of the body. Hormonal control by the renin-angiotensin-aldosterone system and by the atrial natriuretic peptide are mainly volume related and, in principle, independent from central nervous control. However, it is established for angiotensin II and likely for atrial natriuretic factor that they serve an afferent function - apart from efferent control of aldosterone release and renal excretory parameters - by acting on specific brain targets. Both functional and morphological evidence suggests that the subfornical organ links the systemic hormonal control systems to hypothalamic control of salt and fluid balance, especially in the control of salt and fluid intake.

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REGULATION OF SALT GLAND FUNCTION

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ABSTRACT. The salt secreting glands of marine birds represent a highly vascularized osmoregulatory target organ specialized in the elimination of hypertonic sodium chloride from the extracellular space. Increases in extracellular fluid volume and tonicity represent the physiological stimuli, and are perceived by systemic volume and osmosensitive structures. Cation-sensitive neurons in the periventricular region of the hypothalamus and neuronal structures using angiotensin II (ANGII) as the putative neuromodulator appear to be involved in hypothalamic signal perception and integration. Released from the secretory nerve, acetylcholine and vasoactive intestinal peptide elicit salt gland secretion at elevated organ blood flow through interaction with discrete sets of receptor proteins, using inositol phosphate and cAMP as second messengers. Blood flow is additionally regulated through putative adrenergic innervation. With regard to circulating hormones, neither the antidiuretic hormone AVT, nor prolactin or corticosteroids influence salt gland secretion, while ANGII markedly inhibits blood flow and secretion via interaction with specific receptors in hypothalamic regions lacking a blood-brain-barrier. Avian atrial natriuretic factor (ANF) stimulates secretion through direct receptor-mediated processes, possibly using cGMP as second messenger, with additional putative interaction at the hypothalamic level.

Keywords: Salt glands, blood supply, osmoreceptors, volume sensitivity, hypothalamus, cholinergic, vasoactive intestinal peptide (VIP), angiotensin II (ANGII), atrial natriuretic factor (ANF), adrenergic.

INTRODUCTION

To maintain body fluid homeostasis even under conditions of severe osmotic stress, birds of marine or brackish water origin possess salt secreting glands ("salt glands") as accessory osmoregulatory organs. These supraorbitally located glands are able to secrete a strongly hypertonic fluid containing sodium chloride mainly, and enable the animals to gain free water from their food and drinking water supply, despite the limited concentrating capacity of the avian kidney due to the existence of mammalian- and reptilian-type nephrons (Schmidt-Nielsen 1960; Peaker & Linzell 1975; Dantzler 1988). With regard to their physiological function including the afferent and efferent control mechanisms involved, the salt glands of the saltwater acclimated Pekin Duck *Anas platyrhynchos*, some gull and penguin species *Larus dominicanus*, *Larus glaucescens*, *Pygoscelis adeliae*, *Spheniscus demersus* and the goose *Anser anser* have been studied most extensively. Ontogenetic development or gradual acclimation to salt yields active salt glands that can secrete up to 0.8 ml/min/g tissue of fluid containing NaCl at 1600 (gull) and 1100 (duck) mOsm/kg, respectively (Hanwell et al. 1971, Hammel et al. 1977, Gerstberger et al. 1984a, Hughes 1987, Gray & Erasmus 1989, Simon & Gray 1989).

SALT GLAND STRUCTURE AND FUNCTION

Salt glands represent compound tubular glands whose ducts open into the nasal cavity. Secretory lobes running in parallel along the rostrocaudal axis are composed of

numerous secretory tubules radially arranged around a central canal. These secretory tubules comprise principal secretory cells with five to eight cells connected by apical 'leaky' tight junctions surrounding the narrow lumen of the secretory tubule (Komnick 1963, Ernst & Ellis 1969, Riddle & Ernst 1979). A high degree of cellular metabolism is indicated by the dense packaging of mitochondria at the bases of the principal secretory cells, and acclimation to salt results in increased basolateral plasma membrane synthesis with subsequent cellular hypertrophy. Enhanced rates of mRNA synthesis and the incorporation of radiolabelled leucine and fucose into membrane-intrinsic glycoproteins can be detected two hours after feeding one percent saline to ducklings. A four-fold stimulated level of sodium-potassium ATPase is described after eight hours of adaptation, with distribution of the sodium-potassium pump throughout the basolateral, but also apical cell membranes (Martin & Philpott 1973, Sarras et al. 1985, Russo et al. 1987). In addition to the development of active secretory tissue, adaptation to salt stress is characterized by increased plasma tonicity in ducks and penguins with a concomitant reduction in extracellular fluid (ECF) volume, while Kelp Gulls keep their plasma osmolality rather constant (Simon & Gray 1989, Gray & Erasmus 1989).

High arteriolar blood supply represents the prerequisite for active salt gland secretion. A dense network of inter- and intralobular arteries originating from the ophthalmic artery (gull) or both the ethmoidal and supraorbital arteries (duck) feeds into an expanded system of capillaries aligned in a counter-current way to the secretory tubules (Fänge et al. 1958, Hossler & Olson 1990). During ongoing secretion, specific salt gland blood flow can increase more than ten-fold to values of 30 ml/min/g tissue with blood perfusion and salt gland secretion being linearly correlated (Hanwell et al. 1972, Kaul et al. 1983). Almost 20 percent of both sodium and chloride are extracted from the perfusing blood stream of the duck salt glands against a marked transtubular concentration gradient, and numerous models have been proposed to explain the trans- or paracellular transport of sodium and chloride, most of them favouring the hypothesis of a chloride secretory epithelium (Holmes & Phillips 1985, Lowy et al. 1989).

AFFERENT CONTROL OF SALT GLAND FUNCTION

A rise in ECF tonicity represents the major driving force for salt gland secretion in conditions of high salt intake or lack of water. Thus, oral seawater intake or the systemic application of hypertonic saline, but also mannitol or sucrose enhance salt gland secretion at augmented blood perfusion despite a reduced ECF sodium concentration in the case of sucrose and mannitol application, suggestive of an osmo- rather than sodium sensitive perceptive mechanism. Since an increase in ECF tonicity is always linked to directed fluid shifts from the intracellular to the ECF compartment, the contribution of ECF volume as the second property of body fluids influencing salt gland function is indicated (Figure 1). Glandular responsiveness to isotonic alterations of the ECF volume due to blood withdrawal and reinfusion or isotonic saline loading, however, appears more pronounced in the duck than the gull or goose (Hanwell et al. 1972, Deutsch et al. 1979, Hammel et al. 1980, Simon-Oppermann et al. 1984, Hughes 1987). ECF volume expansion with concomitant reduction in ECF sodium concentration reduces the threshold for salt gland secretion and vice versa. This inverse relationship between volume and tonicity of the ECF in establishing the

threshold conditions for salt gland activity indicates the involvement of a volume factor in the control of salt gland function (Kaul & Hammel 1979, Hammel et al. 1980, Simon & Gray 1989). Systemic volume perception with regard to afferent salt gland control is concluded from the observation of suppressed salt gland secretion after blockade of vagal nerve traffic in geese and ducks (Hanwell et al. 1972, Simon-Oppermann et al. 1980). It can, however, not be decided whether ECF volume or tonicity is the modality monitored, and where in the body the postulated sensors would be located. The role of interstitial volume sensitive elements can be derived from studies with intravascular volume expansion due to the infusion of hyperoncotic dextran-70 in hyper- or isotonic saline. The concomitant reduction of the interstitial space results in diminished salt gland secretion and also renal water elimination at unchanged plasma concentrations of important osmoregulatory hormones such as angiotensin II (ANGII) or vasotocin (AVT) (Simon 1982, Keil et al. 1991).

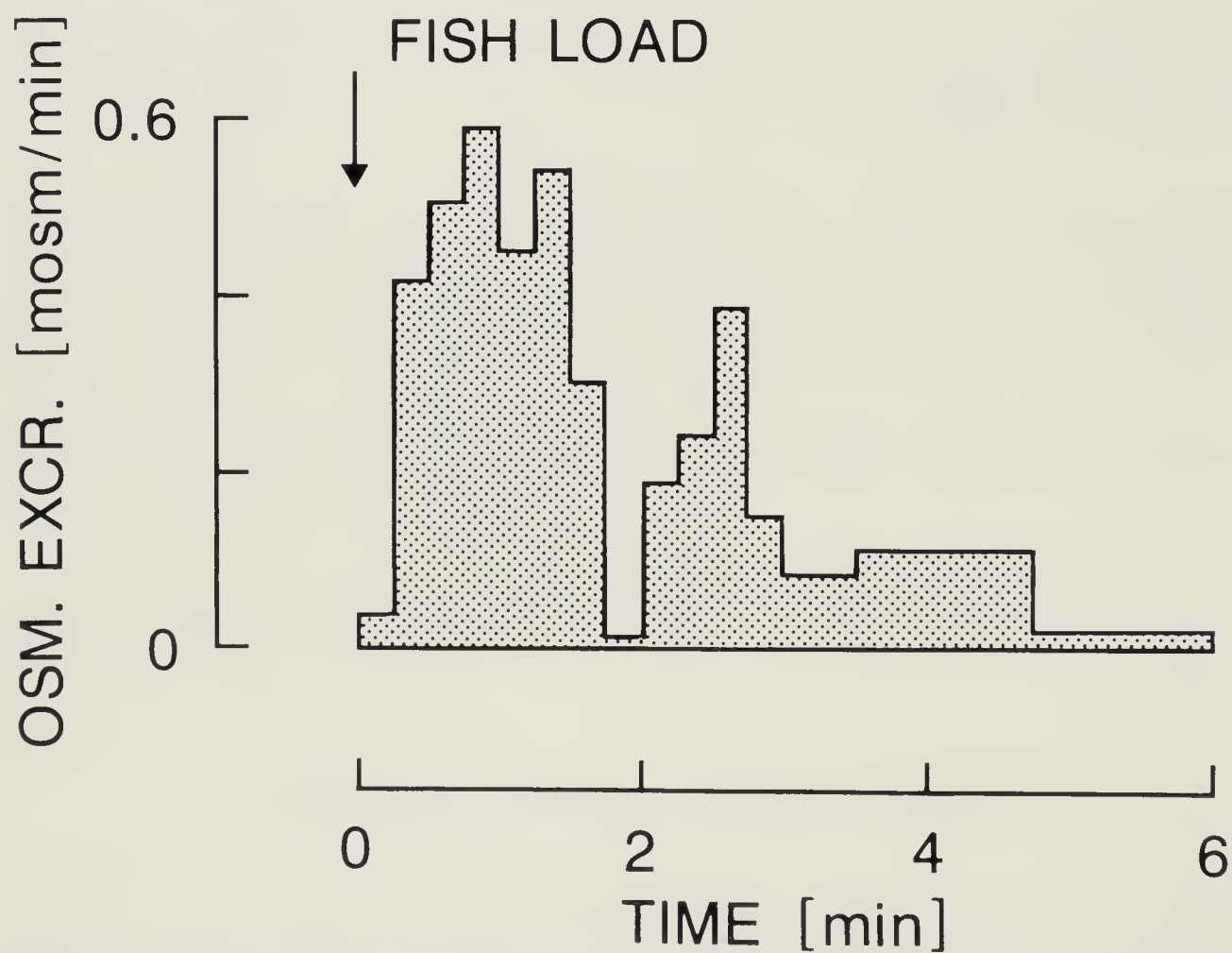


FIGURE 1 – Osmolal salt gland excretion [mOsm/min] of a Kelp Gull after an oral fish load. (Courtesy of Dr D.A. Gray, Bad Nauheim, Germany)

The central nervous localization of putative osmo- or sodium sensitive elements (Schmidt-Nielsen 1960) and the cellular mechanisms of transduction involved have been under investigation in the saltwater-acclimated duck mainly. Alternate administration of hyper- and hypotonic stimuli to the cephalic circulation of ducks at constant whole body salt and water loading causes stimulation and inhibition of steady-state salt gland secretion, respectively. The less pronounced activation of salt gland secretion after replacement of the hypertonic saline stimulus by equiosmolal sucrose is indicative of a central sodium-sensory mechanism (Gerstberger et al. 1984a). The parallel demonstration of alterations in salt gland function induced by local cooling or warming of the diencephalon in ducks as well as Adélie Penguins points to the

hypothalamus as the osmoreceptive and integrative central structure in the control of salt gland function (Hammel et al. 1977, Hori et al. 1986). Therefore, close-target stimulation of putative osmoreceptive periventricular sites in the hypothalamus has been performed by local perfusion of the third cerebral ventricle with artificial cerebrospinal fluid (aCSF) in the conscious duck. A reduction in aCSF sodium concentration (-70 mOsm/min) causes inhibition of glandular activity, while elevated aCSF sodium concentration (+30 mOsm/kg) results in an enhanced stimulation of steady-state salt gland secretion with strongest actions in the rostradorsal section of the third ventricular region (Figure 2). Replacement of sodium by lithium or cholin and of chloride by iodide or nitrate in hypertonic stimulations reveals physiological responses of comparable magnitude, while hypertonicity in the aCSF due to sucrose or mannitol is without effect (Gerstberger et al. 1984b, Kanosue et al. 1987, unpublished). Extracellular recordings in hypothalamic slice preparations strengthen these observations with excitatory actions of sodium-dependent hypertonic aCFS and vice versa (Figure 2), but unchanged neuronal discharge rate and pattern in response to hypertonic sucrose stimulation, indicative of a 'non-specific cation-channel involved (Kanosue et al. 1990). In search for putative neuro-modulators playing a major role in neuronal mechanisms of perception and/or signal transduction, centrally applied ANGII markedly inhibits salt gland secretion, possibly by interacting with ANGII receptive sites localized in hypothalamic areas within the blood-brain-barrier (BBB) such as the AV3V region, or the paraventricular and supraoptic nuclei (Gerstberger et al. 1984c,1987).

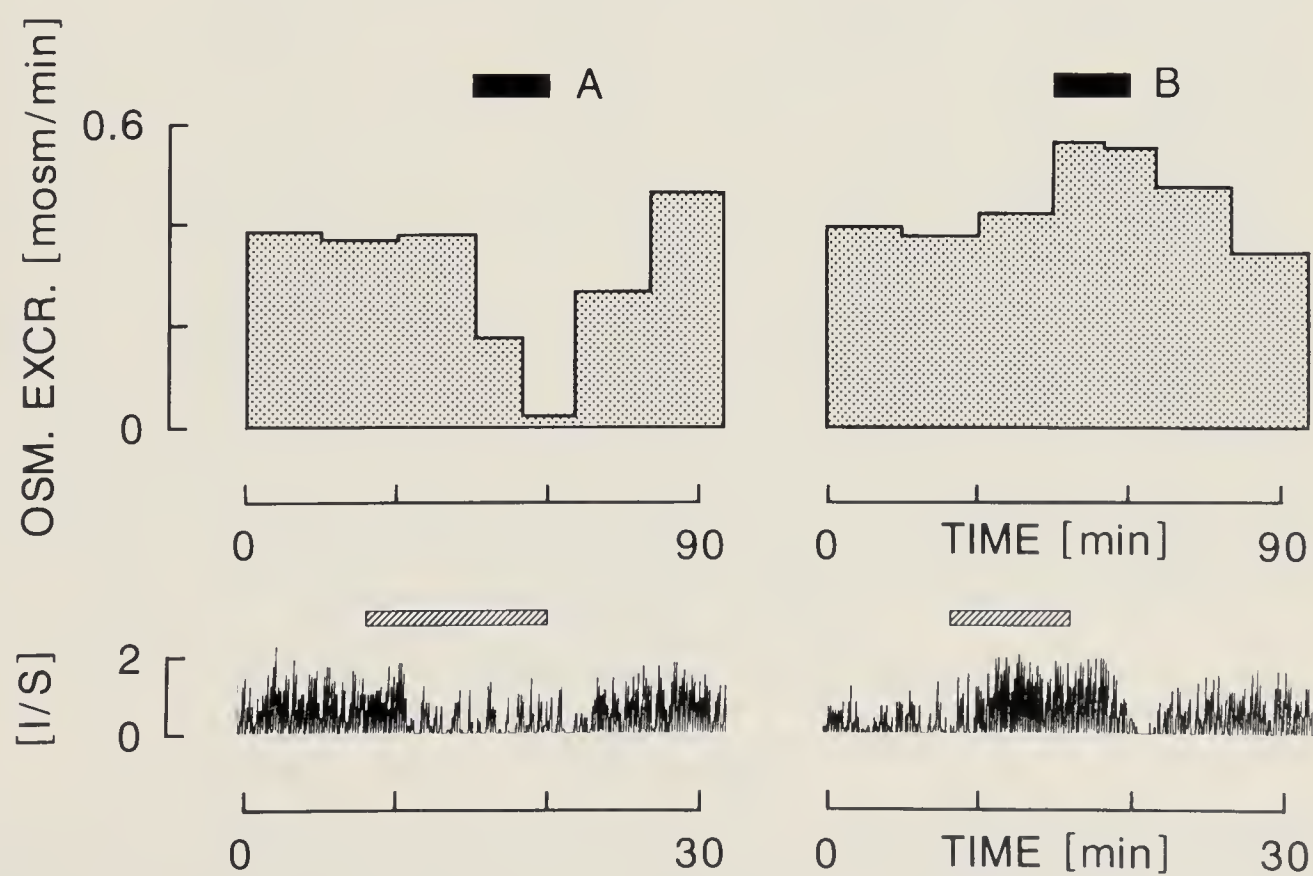


FIGURE 2 – Top: Osmolal salt gland excretion [mOsm/min] of saltwater-acclimated ducks systemically loaded with 0.4 ml/min of 1000 mOsm/kg saline during intracerebroventricular perfusion with hypotonic (A) or hypertonic (B) aCSF. Mean values of n= 5 each. Bottom: Extracellular recording of an osmosensitive periventricular neuron in a duck hypothalamic slice preparation during superfusion with hypotonic (-10 mOsm/kg, left) or hypertonic (+20 mOsm/kg, right) aCSF.

EFFERENT CONTROL OF SALT GLAND FUNCTION

Integration in the avian hypothalamus of afferent signals originating from peripheral osmo- and volume sensitive elements, and from brain-intrinsic tonicity sensitive neuronal structures is poorly understood, as is the final signal transfer from the hypothalamic regions to the ‘secretory nuclei’ of the brainstem. Supplied by a branch of the VIIth cranial nerve, cholinergic nerve fibers leaving the ethmoidal ganglion ramify throughout the salt gland parenchyma (Ash et al. 1969). Vasoactive intestinal peptide (VIP) can be co-localized in nerve terminals innervating both secretory cells and arterioles. Both neuromodulators stimulate salt gland secretion and blood flow, possibly through interaction with high-affinity receptors, when administered to the cephalic circulation, in a non-additive, independent mode as proven by atropin-resistant VIPergic vasodilation (Figure 3) (Hootman & Ernst 1982, Gerstberger 1988, Gerstberger et al. 1988). In vitro studies indicate stimulation of salt gland function with active chloride secretion via (1) rapid breakdown of inositol phosphates and increased intracellular free calcium due to the activation of cholinergic receptors and (2) stimulated cyclic AMP levels due to VIP receptor interaction (Shuttleworth & Thompson 1987, Lowy et al. 1989). An additional sympathetic innervation of the salt glands is supported by the presence of catecholaminergic nerve fibers, the autoradiographic localization of α_2 -adrenergic receptors in the glandular tissue, adrenergic modulation of short-circuit current in primary cell cultures, and the inhibitory effect of norepinephrine on salt gland secretion through inhibition of glandular blood flow (Figure 3) (Peaker & Linzell 1975, Lowy & Ernst 1987, Gerstberger 1991).

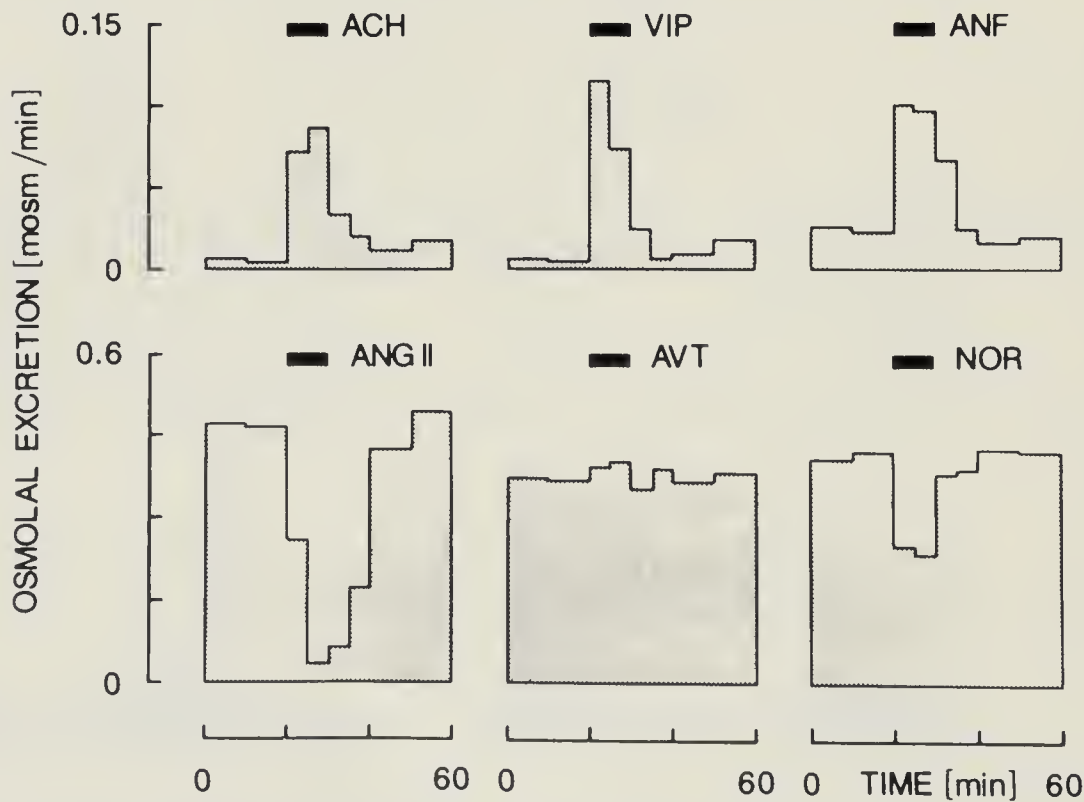


FIGURE 3 – Top: Stimulatory effect on duck osmolal salt gland excretion [mOsm/min] at threshold by acetylcholine (ACH; 5 nmol/min/kg), vasoactive intestinal peptide (VIP; 240 pmol/min/kg) and atrial natriuretic factor (ANF; 15 pmol/min/kg) infused intracarotideally. Bottom: Inhibitory or neutral effect on duck osmolal salt gland excretion [mOsm/min] during systemic infusion of 0.4 ml/min of 1000 mOsm/kg saline by angiotensin II (ANGII; 80 pmoles/min/kg), vasotocin (AVT; 20 pmoles/min/kg) and norepinephrine (NOR; 20 nmoles/min/kg) infused intracarotideally. Mean values of n= 6-12.

Among circulating hormones with possible impact on salt gland function, the corticosteroids, thyroid hormones and prolactin (PRL) have been investigated extensively in the past, but there is no compelling evidence for a direct relation between PRL or thyroid hormones and glandular hypertrophy or an increased rate of secretion. Due to the stimulatory effect on food and water intake, or uptake of electrolytes from the gut, however, PRL and thyroid hormones may be indirectly involved in the control of salt gland function (Holmes & Phillips 1985, Butler et al. 1989). Studies employing the administration of corticosteroids or adrenalectomy suggested that corticosterone - after transformation to 11-dehydrocorticosterone and binding to intracellular receptors - regulates transcriptional events leading to the regulation of active Na^+Cl^- transport (Sandor et al. 1977). Recent experiments, however, clearly demonstrate that the marked inhibition of salt gland activity often observed after adrenalectomy was due to cardiovascular side-effects of the surgical procedure and that "NaCl secretion by the nasal glands is not steroid-dependent" (Butler et al. 1989). The avian antidiuretic hormone vasotocin (AVT) circulating at chronically elevated plasma concentrations in saltwater-acclimated birds (Simon & Gray 1989), because of its tonicity-controlled release from the hypothalamo-neurohypophyseal system, does not appear to regulate salt gland activity (Figure 3) (Holmes & Phillips 1985).

The volume-regulated renin-angiotensin II system with ANGII as the active systemic principle induces a dose-dependent inhibition of salt gland secretion in both the duck and gull at slightly diminished glandular blood flow (Figure 3) (Gray et al. 1986, Gray & Erasmus 1989, Wilson 1989, Gerstberger 1991). Receptor binding studies, however, did not reveal high-affinity binding sites for ANGII in the salt glands, while regions of the central nervous system outside the BBB, and therefore accessible to blood-borne ANGII, are densely endowed with ANGII-specific receptors. These binding sites undergo up-regulation during salt-adaptation as proven by physiological studies, receptor autoradiography and electrophysiological preparations. Additional evidence for the centrally mediated effect of ANGII on salt gland function is provided by the ineffectiveness of ANGII to inhibit secretion induced by cholinergic stimulation in glands lacking functional neuronal input (Gerstberger et al. 1987, Butler et al. 1989, Matsumura & Simon 1990). The only true hormone described so far to directly influence avian salt gland function, the atrial natriuretic factor (ANF) synthesized in atrial myocytes, stimulates salt gland osmolal excretion under conditions of both threshold and ongoing secretion (Figure 3). High-affinity receptors are distributed equally throughout the secretory parenchyma, possibly using cGMP as second messenger system (Stewart et al. 1979, Schütz & Gerstberger 1990). The demonstration of ANF binding sites in hypothalamic structures without a BBB suggests additional control of salt gland function at the central nervous level.

CONCLUSION

Despite its morphologically simple structure and its straightforward physiological function, the avian salt gland represents an osmoregulatory target organ controlled by a multitude of efferent modulators after systemic and central perception and integration of afferent information concerning the osmotic and volume status of the extracellular body fluid.

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THE ROLE OF THE INTESTINE IN AVIAN OSMOREGULATION

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ABSTRACT. Intestinal transport of water and electrolytes has been studied in rather few bird species. Interspecific variation is considerable so the current generalisations may have to be revised. The small intestine (SI) appears to have osmoregulatory function only in species with salt glands (*Anas platyrhynchos*), in which Na-linked water absorption is enhanced on adaptation to saline conditions. Otherwise, the SI recycles daily a large proportion of body water and Na^+ , but is generally not involved with nett absorption to counteract excretory and evaporative losses. The lower intestine (LI = coprodeum + rectum + caeca if present) has important osmoregulatory functions: primary active Na^+ absorption responds homeostatically to altered Na^+ - and water-status via hormonal control, and drives absorption (of water, Cl^- and NH_4^+) and some secretion of K^+ . There is large interspecific variation in LI transporting capacity (per body mass or serosal area) largely independent of LI size; coupling ratio (J_v/JN_a) of Na-linked water absorption is higher in species from arid habitats than in those from moister ones.

Keywords: Osmoregulation, gastro-intestinal tract, small intestine, large intestine, duodenum, jejunum, ileum, caecum, rectum, colon, coprodeum, cloaca, Na, K, Cl, active transport, solute-linked water transport, aldosterone, AVT, salt glands, urine.

INTRODUCTION

Paradoxically, an understanding of the gastro-intestinal (GI) tract's osmoregulatory importance developed latest for the most thoroughly adapted terrestrial groups (birds, mammals, reptiles and insects) in which it had evolved to become the exclusive site of uptake for water and solutes. (By contrast, the osmoregulatory role of the intestine is probably most widely appreciated in fishes, in which other body surfaces (gills) also have a major role for both uptake and excretion).

In fact, for many species in all of these terrestrial groups (except mammals) the GI tract is doubly important: it is not only the sole site of uptake, but the lower GI tract can also have substantial effects on post-renal urine composition, after the ureteral urine has refluxed from the cloaca (birds and reptiles) or flowed down from the Malpighian tubules (insects).

OVERVIEW OF AVIAN INTESTINAL TRANSPORT OF SALTS AND WATER

It is useful to consider the scale of water and solute transport to get a proper perspective of the importance of the GI tract in osmoregulation. Transport rates of individual segments can be misleading, as (osmo)regulation results from the nett balance of absorptive and secretory processes as material flows serially down the tract. Soluble markers (of the GI luminal space) consumed by unrestrained conscious animals reveal this balance of unidirectional transport processes. Changes in solute: marker or water:marker ratios between successive GI segments reveal nett absorption or secretion in the interim (ratios decrease or increase respectively), and show the

cumulative effect of intestinal function. Figures 1 and 2 show Na⁺, K⁺ and water transport from such data for three species.

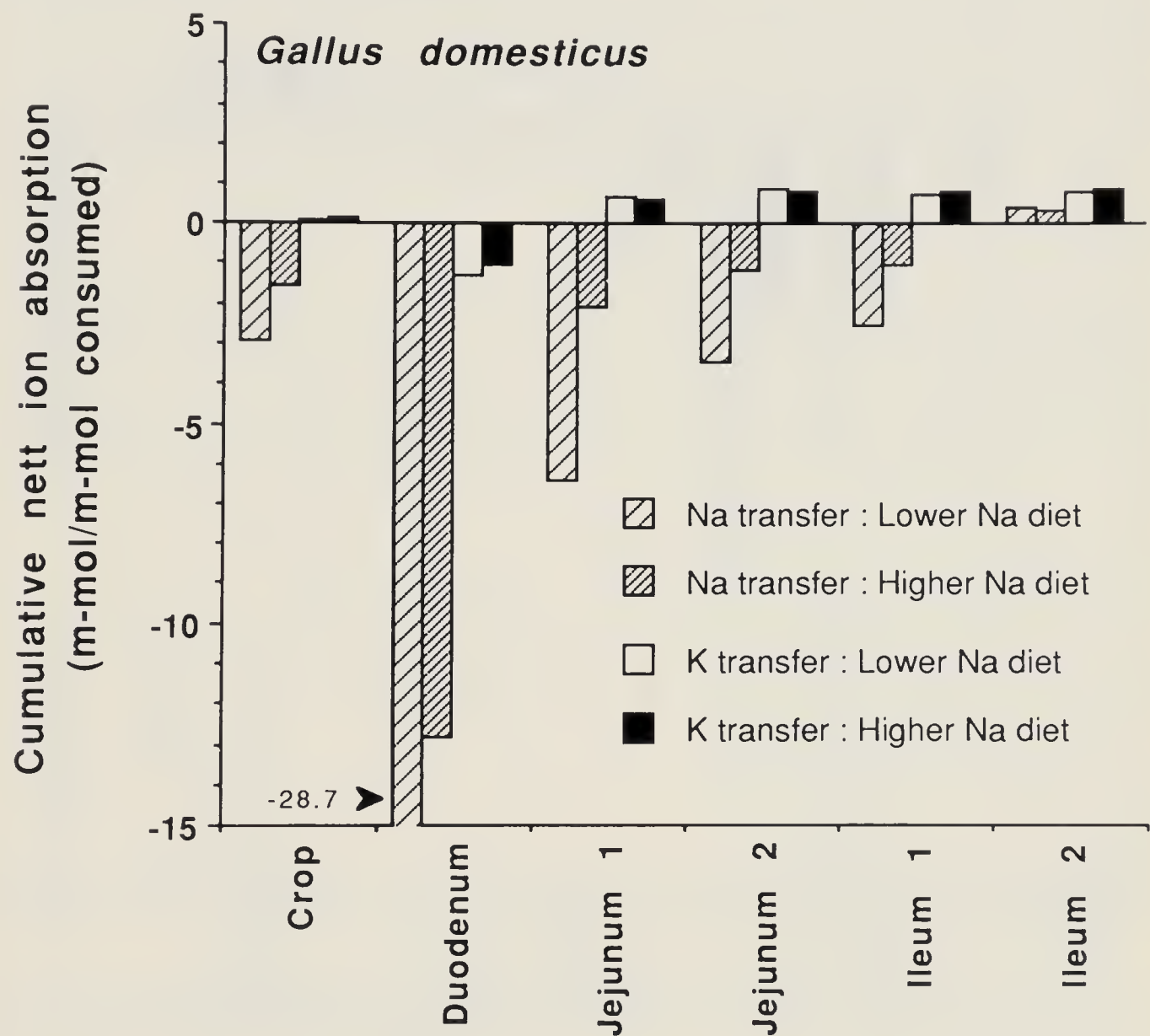


FIGURE 1 – Cumulative nett absorption or secretion (negative values) of Na⁺ and K⁺ in domestic fowls maintained on different dietary Na⁺ levels. Apparent differences in Na handling between treatments are almost entirely due to differences in Na⁺ concentration between diets: lower Na (3 Na⁺ + 23 K⁺) or higher Na (6.6 Na⁺ + 23 K⁺ m-mol/100g food). Compiled from data of Hurwitz et al.(1970).

The general picture which emerges is that the osmoregulatory functions of the avian intestine take place largely in the posterior segments. Several lines of evidence support this view, but in principle we are looking for the portions of the GI tract capable of regulated cumulative nett absorption at rates sufficient to match the bird's losses via other routes. Although much of the anterior GI tract is concerned with copious secretion and reabsorption of Na⁺ and water at high rates this has little or nothing to do with osmoregulation as such.

Thus Figures 1 and 2 show an enormous turnover of Na⁺ and water between the crop and posterior small intestine. Domestic fowls recycle virtually their whole body Na⁺ pool daily (Thomas 1982), while about 20-60% of body water pools are intestinally recycled by species in Figure 2. Eurasian Quails *C. coturnix* and Australian Wood Ducks *Chenonetta jubata* show similar patterns (Thomas 1982, Dawson et al.1989).

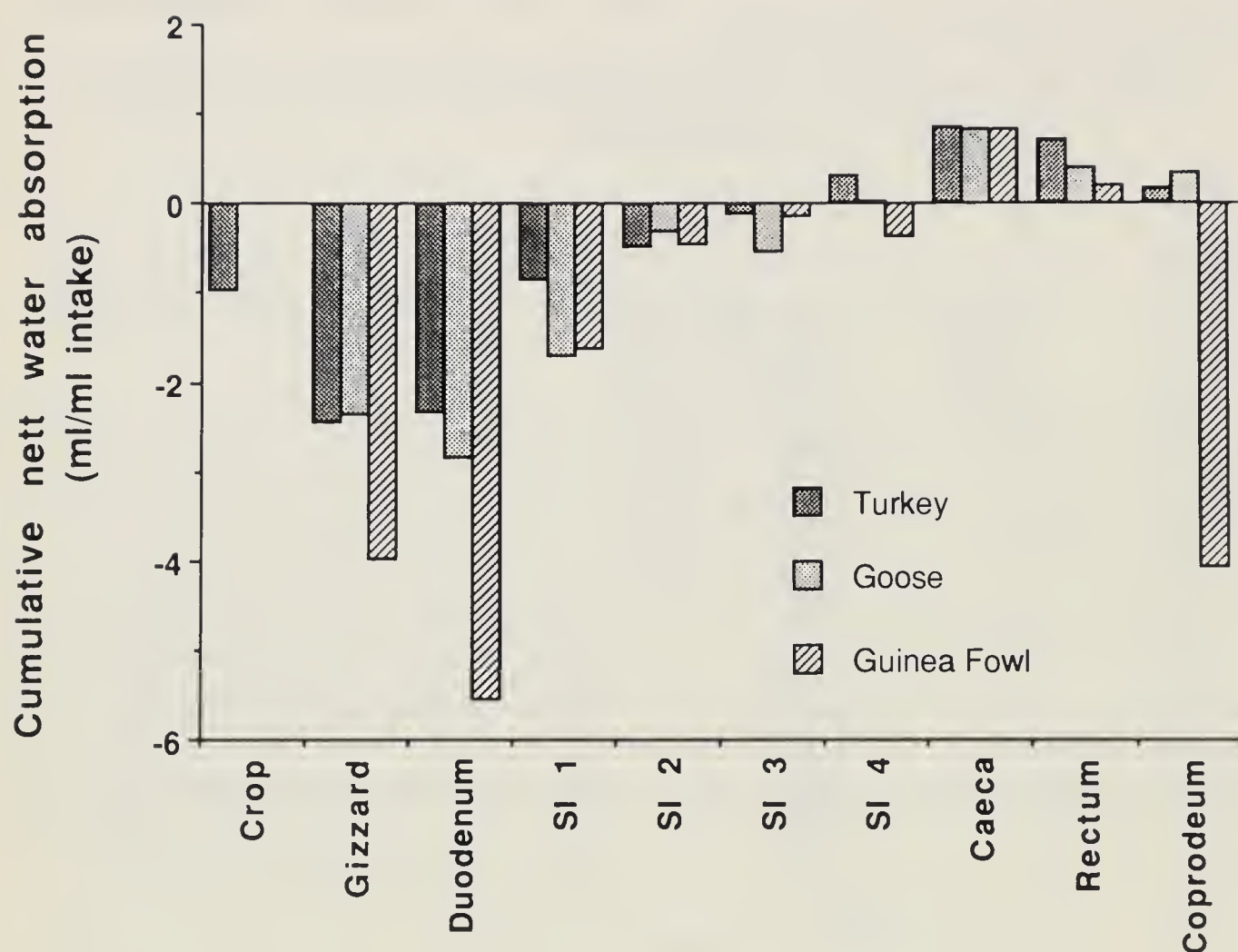


FIGURE 2 – Cumulative nett absorption or secretion of water in domestic turkeys, geese and Guinea fowls. Compiled from data of Bjornhag & Sperber (1977).

Despite this, there is no nett accumulation (necessary to offset inevitable excretory and evaporative losses) of Na^+ or water until the final quarter of the ileum or the lower intestine. It is therefore in these latter segments that these species must exert osmoregulatory control. Although domestic geese do have salt glands, it is not surprising that handling of water (at least) is similar in turkeys and geese on low- Na^+ and fresh water intake (Figure 2), since salt glands would be inactive under these conditions.

On the other hand, when domestic ducks *Anas platyrhynchos* were adapted to hyperosmotic intake (60% seawater) sufficient to activate salt gland function, the transporting capacity of the small intestine (water and Na^+ *in vitro*) was increased (Crocker & Holmes 1971). *In vivo*, a high- NaCl intake stimulated solute-linked water absorption by duck small intestine despite reduced Na^+ absorption, since the coupling ratio (J_v/J_{Na}) almost doubled (from 2.3 to 4.4 $\mu\text{l water}/\mu\text{Eq Na}^+$; Skadhauge et al. 1984). This effect is apparently steroid-mediated, since corticosterone induced the same effect in fresh-water maintained ducks, while spironolactone (competitive inhibitor of corticosterone) or metyrapone (blocker of corticosterone synthesis) prevented the effect (Crocker & Holmes 1976). Unfortunately, no study of GI function has been made using non-absorbed luminal markers in birds with active salt glands, so we can not be sure whether the increased small intestinal absorption just described represents nett absorption or merely active recovery of prior secretion.

THE OSMOREGULATORY ROLE OF THE LOWER INTESTINE

The major osmoregulatory function of the avian GI tract is in the lower intestine (Figures 1 and 2), although the small intestine may also be important in species with active salt glands. It is not just that the lower intestine is capable of nett transfer to counteract excretory losses, but that these processes respond homeostatically to ecologically relevant changes in salt and water balance (mediated by co-related changes in endocrine status) which emphasises the osmoregulatory function of these segments.

Figure 2 shows parallel clines of increasing importance for water absorption by the constituent segments (coprodeum < rectum < caeca) of the lower intestine in all three species. The fowl lower intestine has been studied in greater detail and shows similar trends for several other transport functions (Figure 3). These inter-segmental differences are partly due to different serosal areas but more importantly to increasing transport capacities per unit serosal area (Thomas & Skadhauge 1988).

Gallus domesticus

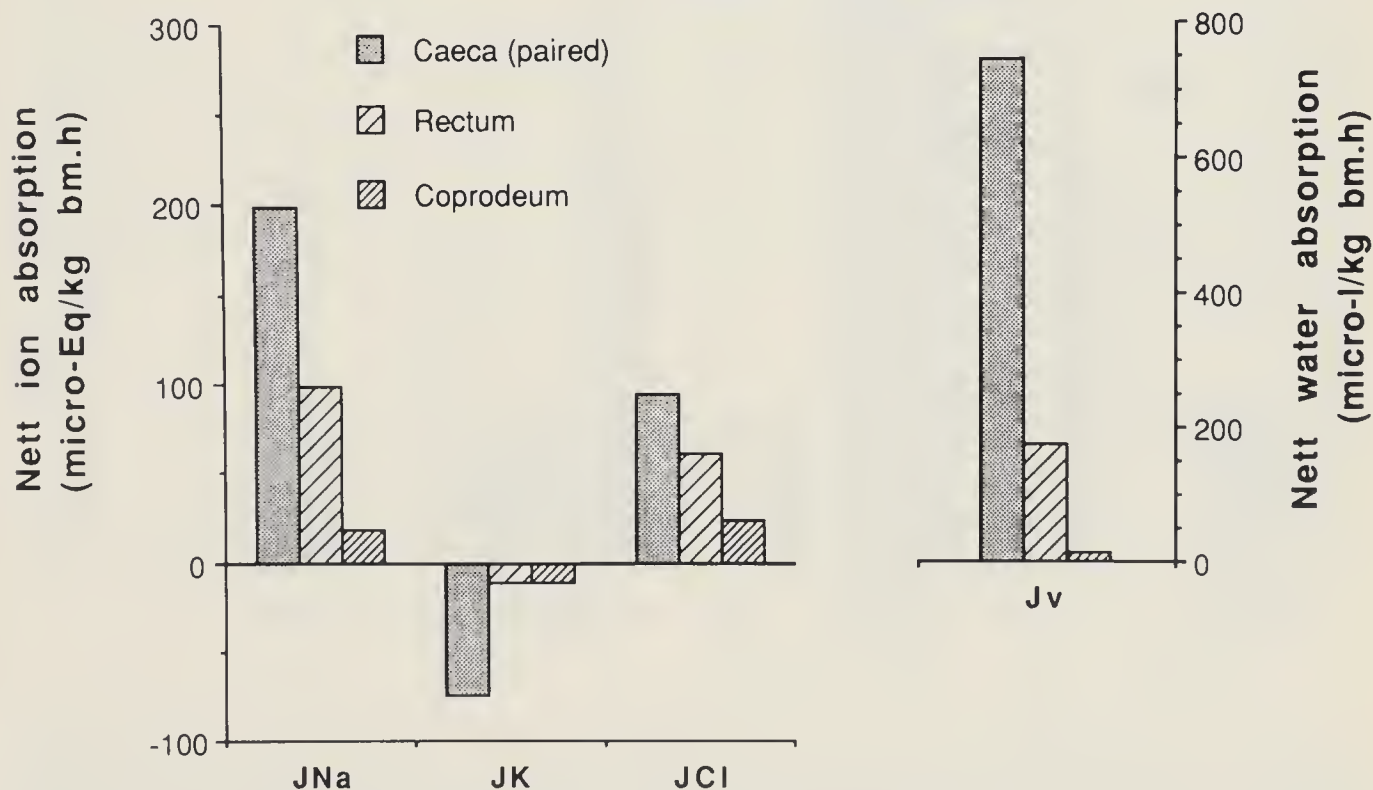


FIGURE 3 – Comparison of nett rates of ion and water absorption or secretion (negative values) by lower intestinal segments during in vivo perfusion of anaesthetised domestic fowls. Birds had been maintained on a low-Na diet (0.3-0.5 m-Eq/100 g food) which augments epithelial transporting capacities. Compiled from data of Rice & Skadhauge (1982b: coprodeum and rectum) and Thomas & Skadhauge (1989a,b: caeca).

There are pronounced parallels as well as interesting qualitative differences in function between the fowl's different lower intestinal segments (Thomas 1982, Thomas & Skadhauge 1988, 1989a), and it is clearly unsafe to extrapolate results from segment to segment in any species. In all LI segments of the fowl, active Na transport is the primary process driving active water absorption and ion fluxes. The pace of Na transport is regulated homeostatically, responding to Na- and water-balance under influence of aldosterone and arginine vasotocin (loc. cit.). Both coprodeum and rectum are aldosterone-mediated transporters of ions and water under low-Na conditions, but

whereas the coprodeum becomes virtually a non-transporter when the bird is Na-replete, the rectum switches on hexose- and amino-acid cotransport systems (lacking in both coprodeum and caeca: Thomas & Skadhauge 1989a) and still sustains a considerable solute-linked water flux (Lind et al. 1980, Rice & Skadhauge 1982a). Furthermore, the large caecal fluxes of ions and water (also aldosterone- and Na-sensitive) are facilitated by acetate (Rice & Skadhauge 1982a, Thomas & Skadhauge 1989b). This primary role of lower intestinal Na-transport and the importance of solute-linked water absorption (without or against prevailing osmotic gradients) has also been shown in Galahs *Cacatua roseicapilla* (Skadhauge 1981), Glaucous-winged Gulls *Larus glaucescens* (Goldstein et al. 1986) and House Sparrows *Passer domesticus* (Goldstein & Braun 1986).

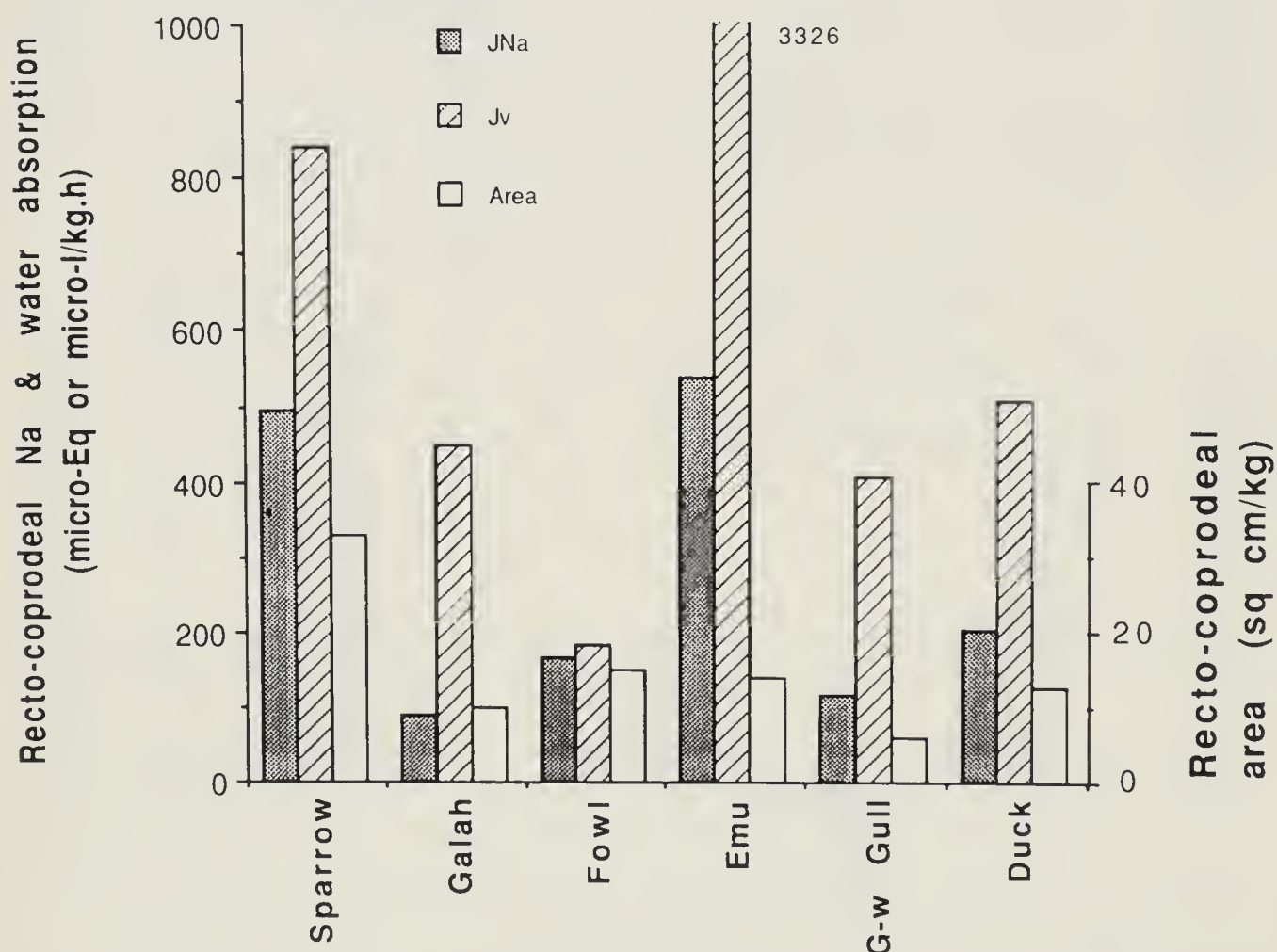


FIGURE 4 – Interspecific comparisons of lower intestinal area (coprodeum and rectum only) and transport functions, for hydrated birds maintained on a low-Na regime, and perfused in vivo with isosmotic media. Compiled from Goldstein (1989: Tables 3 and 4). Sparrow = House Sparrow; G-w Gull = Glaucous-winged Gull.

It is clearly possible that GI contents may be moved between segments to exploit their functional differences, but almost nothing is known as to whether this occurs or (if it does) how it is controlled. There is some evidence for this in two desert phasianids (Chukar *Alectoris chukar* and Sand Partridge *Ammoperdix heyi*) where urinary reflux into the lower intestine is prevented when a high NaCl intake would make NaCl-linked water reabsorption counterproductive (Thomas et al. 1984).

David Goldstein (1989) drew attention to the diversity of lower intestinal transport rates amongst species (Figure 4), and emphasised the dangers of assuming that any well-studied species is "typical". Two features of recto-coprodeal function stand out

in Figure 4: first, segmental size is only a poor guide to its physiological importance since transporting capacity per unit area varies considerably. Secondly, coupling ratio of solute-linked water absorption (J_v/J_{Na}) also shows large but somewhat systematic variation, since it was highest in the semi-arid zone species (Emu *Dromaius novaehollandiae* 6.2; Galah 5.0 $\mu l/\mu Eq$) compared with species of euryhaline (Glaucous-winged Gull 3.5; Duck 2.5 $\mu l/\mu Eq$) and mesic terrestrial habitats (House Sparrow 1.7; Fowl 1.1 $\mu l/\mu Eq$). Note that J_v/J_{Na} is also independent of segmental size or transporting capacity.

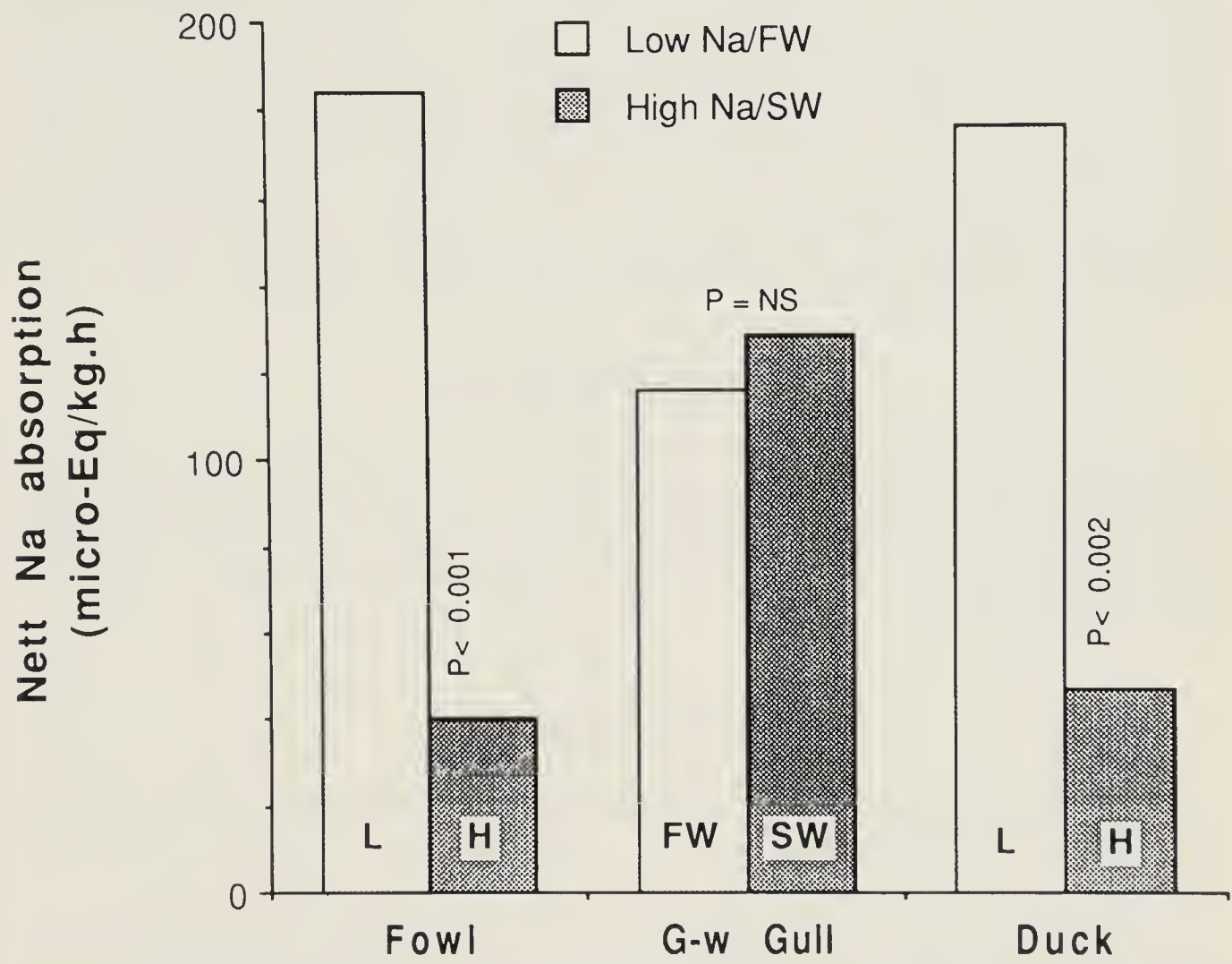


FIGURE 5 – Comparison of recto-coprodeal Na^+ absorption from isosmotic perfusates during adaptation between maintenance regimens which stimulate (high- Na^+ or seawater conditions) or depress (low- Na^+ or fresh-water) salt gland activity (where present, in Glaucous-winged Gulls and domestic ducks, but not fowls). Data from Thomas & Skadhauge (1979: fowls), Skadhauge et al. (1984: ducks), Goldstein et al. (1986: gulls).

The role of the lower intestine during salt gland function is a vexed one and still lacks comprehensive study. Schmidt-Nielsen et al's (1963) suggestion (that $NaCl$ -linked water reabsorption in the "cloaca" could be desalinated via the salt glands) has intrinsic appeal, but is not supported by the evidence (Figure 5). In Glaucous-winged Gulls, adaptation to sea-water affected neither ion nor water absorption rates nor J_v/J_{Na} (3.87-4.01 $\mu l/\mu Eq Na^+$; Goldstein et al.1986). The duck's lower intestine responded like that of fowls with diminished Na -transport in response to high- Na maintenance (Figure 5), which far outweighed a small increase in J_v/J_{Na} from 1.4 to 2.5 $\mu l/\mu Eq Na^+$ (Skadhauge et al. 1984). It seems likely, therefore, that the response to saline conditions is concentrated on the salt glands and the small rather the lower intestine.

Erik Skadhauge pointed out that, although many other groups of chordates allow urine to reflux into the lower intestine, birds are the only ones in which the urine may be hyperosmotic, although bird urine is rarely more than three-fold more concentrated than plasma (Skadhauge 1981). The problem posed by hyperosmotic urine in the GI tract is that it will drive osmotic flow towards the lumen, countervailing the kidneys' osmotic work and enhancing potential water losses. Two solutions to this problem (modification of epithelial osmotic permeability and regulated solute-linked water absorption) are both invoked in fowls, the only species in which comprehensive measurements exist (Bindslev & Skadhauge 1971a,b). There is significant rectification, with the osmotic permeability coefficient from serosa to mucosa ($P_{os(sm)} = 3.2 - 3.6 \mu l / kg.h.mOsm$) unchanged by dehydration and always less than $P_{os(ms)}$. $P_{os(ms)}$ increased during dehydration from 5.8 to 10.0 $\mu l / kg.h.mOsm$. Such differences would inhibit osmotic losses ($P_{os(sm)} < P_{os(ms)}$) when luminal fluid is hyperosmotic during dehydration, while the increase in $P_{os(ms)}$ should increase the coupling ratio of solute-linked water reabsorption, as was actually found ($J_v/J_{Na} = 1.07$ compared with 1.48 $\mu l / \mu Eq Na^+$ in hydrated and dehydrated birds respectively) (Bindslev & Skadhauge 1979b).

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THE ROLE OF THE AVIAN KIDNEY IN FLUID AND ELECTROLYTE BALANCE

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ABSTRACT. As in other vertebrate classes, the kidneys of birds play a prominent role in the control of fluid and electrolyte balance. The nephron population of the avian kidney is unique in that it is morphologically and functionally very heterogeneous. Small nephrons have low filtration rates (SNGFRs of 0.5-6.5 nl/min). These nephrons do not have loops of Henle. Deep to the small nephrons are larger nephrons with correspondingly higher SNGFRs (~16 nl/min) and loops of Henle that course parallel to the CDs and vasa recta. The avian kidney can concentrate the urine, but only to twice the osmolality of plasma. The principal end-product of nitrogen metabolism of birds is uric acid. This sparingly soluble compound is excreted in a manner that prevents the formation of large aggregates of crystals. Furthermore, uric acid is refluxed into the lower gastrointestinal (GI) tract where a significant amount (40%) of the uric acid is degraded, with the resultant formation of short-chain volatile fatty acids that can stimulate sodium absorption. Thus, in birds the kidneys and lower GI tract must function in concert in maintaining fluid and electrolyte balance.

Keywords: Kidney, structure, uric acid, urine, nephrons, ceca, intestine.

The contribution by the avian kidney to the control of body fluid and electrolyte balance is rather complex. This complexity derives in part from the fact that the kidneys of birds do not solely control this balance, but must work in concert with one or two other organ systems that also function in this capacity. These systems are the nasal salt glands and the lower gastrointestinal tract. These two systems are dealt with in detail by other contributions to this symposium. In this chapter, I will consider only renal function in birds that do not have functional salt glands. However, I will discuss some aspects of how the roles of the kidneys and lower gastrointestinal tract are interwoven in the regulation of fluid and ion balance.

I will first briefly review the anatomy of the avian kidney, then cover renal blood flow, glomerular filtration, nephron function, urinary concentration, nitrogen excretion, and some aspects of fluid and electrolyte handling by the cloaca, rectum and digestive ceca (for those birds that have rather large sacculated ceca).

In most birds the kidney is an elongated, flattened (in the dorsal-ventral aspect) organ that is fitted rather tightly into the bony concavity formed by the synsacrum. Furthermore, the kidneys are secured in place by large nerve trunks and large blood vessels that course either through the kidney parenchyma or across the surface of the kidney. In most birds, the kidneys are superficially divided into three divisions; an anterior, a small middle, and a large posterior division (Figure 1 and Johnson 1968). Internally the tissue (nephrons) is arranged in a rather organized, repeating, pattern about large efferent veins (the central veins-Figure 1). The tissue of the avian kidney cannot be readily divided into cortical and medullary regions as can be done for kidneys of most mammals. This point will become clear with a description of the nephrons of the avian kidney. The most striking feature of the nephron population when it is considered as a whole is the extreme morphological heterogeneity that is present.

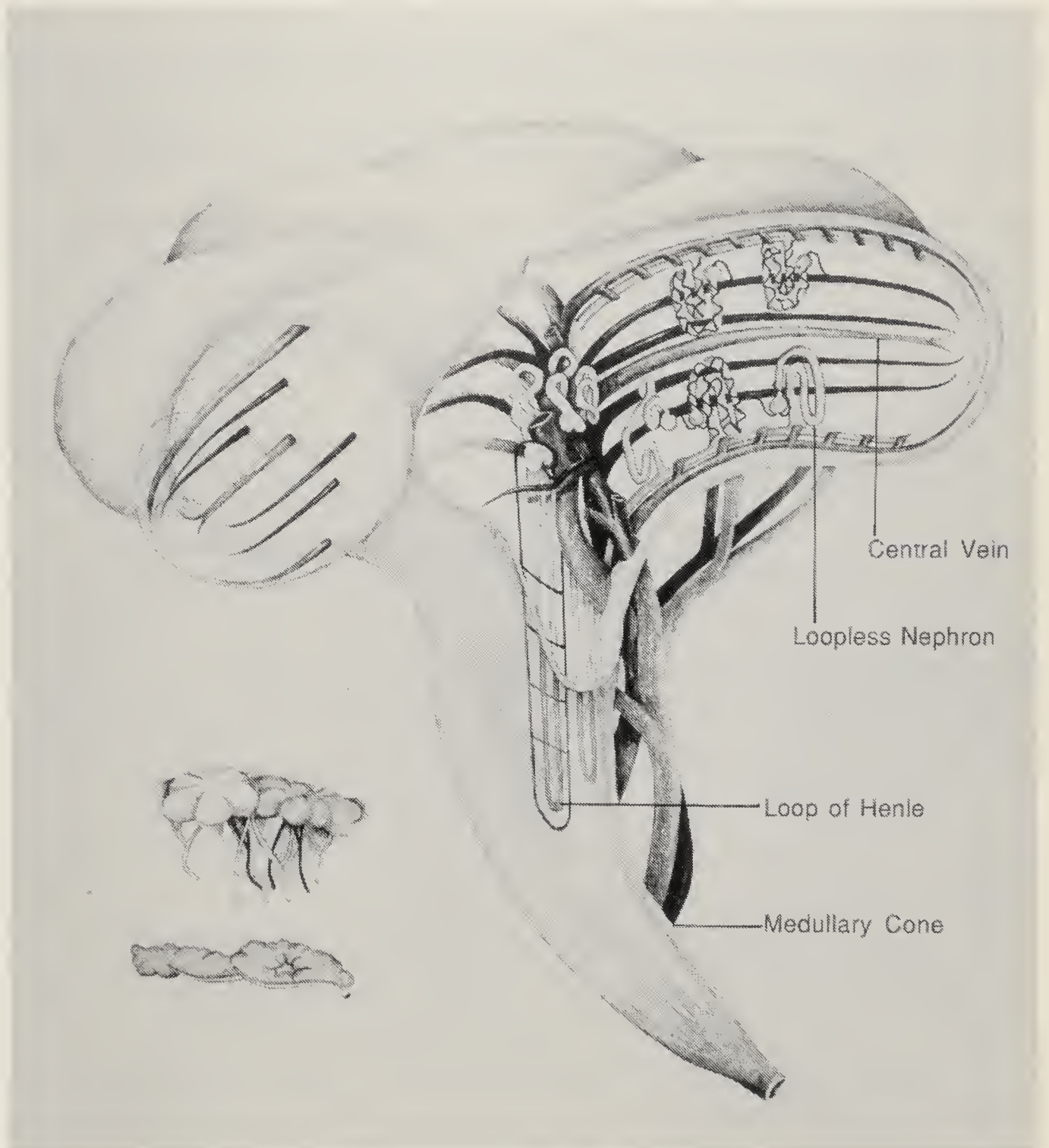


FIGURE 1 – An illustration of the avian kidney depicting the internal organization of nephrons and the associated vasculature. The whole kidney is shown at the lower left with an intermediate enlargement and the final enlargement of a small portion of the kidney. The illustration is modified from Braun & Dantzler (1972).

Arranged in a radiating pattern around the central veins are small nephrons that do not have loops of Henle, and the distal tubules of which enter collecting ducts at right angles (Figure 1). The average length of the proximal tubules of these nephrons is 1.6 mm in the Desert Quail (Braun & Dantzler 1972) and 2.6 mm in the Rhode Island Red domestic fowl (Wideman et al. 1981). At the ventral aspect of the cylinders formed by the central veins and radiating loopless nephrons (LLN) are large nephrons that have loops of Henle and much longer and highly convoluted proximal tubules. The loops of Henle of these nephrons, along with the vasa recta and collecting ducts (that drain both the LLN and the looped nephrons, LN) are organized into tapering structures called medullary cones that are bound by a light connective tissue sheath. In

most kidneys, the cylindrical units formed by the central veins and the LLN will fill the spaces between the medullary cones. This arrangement precludes dividing the tissue into distinct cortical and medullary regions. The average size of the nephrons in the avian kidney may be smaller than the nephrons of mammalian kidneys as the avian kidney contains more nephrons per gram kidney mass (Yokota et al. 1985).

The numbers of LLN and LN vary a great deal from species to species and at this point the database is inadequate to demonstrate phyletic, habitat or diet influences on the numbers of LLN or LN (Goldstein & Braun 1989). The available data are summarized in Table 1. One feature demonstrated clearly is that the majority of the nephrons in avian kidneys do not have loops of Henle. The maximum percent of LN appears to be about 30%, with a low of about 5%.

TABLE 1 – Percent loopless and looped nephrons in the kidneys of several bird species. Data from Goldstein & Braun 1989.

Species	Percent loopless	Percent looped	Total
Zebra Finch	70.2	29.8	8,783
House Sparrow	82.2	17.8	35,687
White-crowned Sparrow	89.5	10.5	53,022
Glaucous-winged Gull	70.4	29.6	564,250
Ring-necked Pheasant	93.2	6.8	394,500
Macaroni Penguin	84.7	15.3	1,222,733

TABLE 2 – Filtration rates* of individual nephrons for the Desert Quail and European Starling.

	Loopless Nephrons	Looped Nephrons	Reference
Desert Quail	6.4 ± 0.20 (41)**	15.8 ± 0.81 (20)	Braun & Dantzler 1972
Starling***	7.0 ± 0.35 (185)	15.6 ± 0.75 (208)	Braun 1978

* nl/min; ** Mean + SEM and n (number of nephrons); *** Value determined by in vivo micropuncture is 0.36 nl/min (Lavery & Dantzler 1982)

Whole-kidney glomerular filtration rates (GFRs) have been measured for a wide range of birds representing a number of phyletic groups of different habitats and diets. Roberts et al. (1985) presented GFR values for 13 species and gave an allometric relationship of: $GFR (ml/min) = 2.37 M^{0.76}$ for the data. The data suggest that GFR scales positively with body mass. This is not unexpected considering the primary function of the kidneys.

The rates at which the individual nephrons filter have been measured for only two species, the Desert Quail and the Starling. The data are summarized in Table 2. The SNGFRs of the LNs of the Desert Quail have been measured using isotopic methods (Braun & Dantzler 1972) while those of the LLN have been measured with the isotopic method (Braun 1978) and in vivo micropuncture (Lavery & Dantzler 1982). The LN of the two birds filter at rates of 15 to 16 nl/min. The SNGFRs of the LLN show a greater range of values. The lowest values (0.4 nl/min) are those measured by the

micropuncture technique of possibly the smallest nephrons in the Starling kidney; the very short LLN at the very surface of the kidney (Laverty & Dantzler 1982). The SNGFR value (7.0 nl/min) obtained using the isotopic technique is an average value for all sizes of the LLN (Braun 1978). The pattern that emerges shows that the LN, being much larger, have much higher SNGFRs – this is not unexpected.

The blood flow to the avian kidney is large, and from two sources. The first is the high pressure flow received from the arterial system. The second is low pressure, high volume flow from the renal portal system (RPS). The arterial supply is through three renal arteries. The paired anterior renal arteries branch directly from the aorta and supply the anterior divisions of the kidneys. The middle and posterior renal arteries branch from the ischiatic arteries on either side. These arteries supply the middle and posterior divisions, respectively, of the kidneys. Once inside kidneys the renal arteries form a dendritic branching system that finally terminates as the afferent arterioles leading to the glomerular capillaries. Efferent arterioles emerge from Bowman's capsules and enter the peritubular sinus network (around the LLN) and the peritubular capillaries (around the LN) and form the vasa recta that enter the medullary cones (Figure 1). Venous blood returning from the legs and terminal regions of the lower gastrointestinal tract enters the renal portal system.

The blood from the legs enters the system through the iliac vein and blood from the intestine enters by way of the posterior mesenteric vein. The portal blood supply perfuses the peritubular (outside) surfaces of the renal tubules through large capillary sinuses. The efferent arterioles of the LLN nephrons also contribute blood to these sinuses. Blood flow from the renal portal system does not appear to enter the medullary cones (Wideman et al. 1981).

As is the case for mammalian kidneys, the proximal tubules reabsorb the majority of the fluid filtered through the glomerular capillaries. The fraction of the filtrate reabsorbed has been determined directly only for the very small nephrons on the surface of the kidney. The data show that to the point of micropuncture, 40% of the filtrate is reabsorbed by the small surface nephrons (Laverty & Dantzler 1982). However, the total kidney normally reabsorbs more than 99% of the glomerular filtrate (Laverty & Wideman 1989). Thus, the remaining nephron segments and the nephrons deeper in the kidney reabsorb large amounts of fluid. The detailed aspects of how the nephron segments handle the various ions are beyond the scope of this brief review. The reader is referred to the primary literature and an excellent recent review (Wideman 1988). The one aspect I will review is nitrogen excretion by the kidney.

TABLE 3 – Forms of nitrogen excreted by birds under different conditions

	Turkey Vulture*		Pigeon**		Chicken***
	Control	HP§	LP	HP	Control
Urate	76.1	86.8	54.7	72.1	70
Ammonia	16.4	8.9	17.3	10.8	13
Urea	7.5	4.3	7.7	9.8	6.5
Other	—	—	20.3	7.3	10.5

* McNabb et al. 1980; **McNabb & McNabb 1975; ***Shoemaker 1972; § HP=High protein, LP= Low protein

The forms in which birds excrete nitrogen are shown in Table 3. Not surprisingly, the largest fraction of the nitrogen in the urine is in the form of uric acid. The fraction of nitrogen excreted as uric acid appears to vary somewhat with diet. The quantity of nitrogen excreted as uric acid appeared to increase in birds that were protein loaded and to be lower in birds on a low protein diet (McNabb & McNabb1975, McNabb et al. 1980, Shoemaker 1972). Because of its low aqueous solubility and the concentration normally found in the urine, uric acid tends to exist as a stable hydrophobic colloid in avian urine.

The colloidal suspension containing uric acid is a complex chemical association of uric acid, glycoproteins, and inorganic ions (Braun et al. 1987). The materials found or suspended in this colloidal form do not contribute to the osmotic potential of the urine. Thus, not only does the nitrogen (in the form of uric acid) not exert osmotic effects but the inorganic ions found in the colloids are also passive with respect to osmotic effects. Indeed, there appear to be significant quantities of ions bound within the colloids (Braun 1978, Lavery & Wideman,1989, McNabb & McNabb 1977). Varying amounts of calcium, sodium, and potassium as well as other ions in lesser quantities are contained within the colloids. The removal of these osmotically active particles from solution markedly reduces the osmotic potential of the tubular fluid. This is the major contributing factor for lowering the urine-to-plasma osmolar ratios (U/P_{osm}) in birds. In general, the U/P_{osm} ratios for birds are at a maximum 2.0 to 2.5, suggesting that in a conventional sense birds do not produce very concentrated urines (Table 4). However, with metabolic rates similar to mammals and inhabiting a wide variety of habitats similar to mammals, birds certainly have similar osmotic loads with which the kidney must cope. In addition to a low osmotic activity of the urine, the osmotic concentration of the plasma of birds tends to increase with increasing water deprivation. This factor will also contribute to the lower U/P_{osms} observed for birds. With the exception of the values for one species, the U/P_{osms} of birds are slightly in excess of one, suggesting that birds normally produce a urine that is only slightly hypertonic to plasma. When water deprived the values reach 2 to 2.5. The exception noted above is the salt marsh Savannah Sparrow (Poulson & Bartholomew 1962). In laboratory experiments, these birds were shown to have the capability to produce U/P_{osms} of 4 to 6. Recently, some aspects of the osmoregulatory abilities of these birds were examined in the field (Goldstein et al. 1990).

TABLE 4 – Urine concentrating ability of birds

Species	U_{osm}	P_{osm}	U/P_{osm}
Stubble Quail ^a	897	343	2.6
King Quail ^a	625	353	1.8
Savannah Sparrow ^b	601	351	1.7
House Finch ^c	850	354	2.4
Budgerigar ^c	884	384	2.3
Zebra Finch	1005	361	2.8
Senegal Dove ^c	661	379	1.7
Singing Honeyeater ^c	925	384	2.4

^a Roberts and Baudinette (1984); ^b Goldstein et al. (1990); ^c Skadhauge (1981).

In these latter experiments, ureteral urine and plasma samples were collected for analysis. These data show that the mean U/P_{osm} was 1.7. There are several major differences between the two studies. First, the Poulson-Bartholomew study was conducted on laboratory birds acclimated to drinking saline solutions and cloacally excreted fluid was analyzed for osmotic potential. The latter study (Goldstein et al. 1990) was done on birds collected in the field and held only for the purpose of collecting small ureteral urine and blood samples and immediately released. These samples should have been representative of the birds' normal osmoregulation pattern.

Birds, like mammals, have the ability to conserve body water by producing urines that are more concentrated than the plasma. The mechanism for producing the hyperosmotic urines resides within the medullary cones of the kidney. Here are found the loops of Henle, vasa recta, and the all-important collecting ducts. The countercurrent mechanism (the system that elaborates the hyperosmotic urine) of the avian kidney is somewhat simpler than that found in the kidneys of mammals. First, the morphology of the loop of Henle is different in that there are no thin ascending loops of Henle (TAL) (Braun & Reimer 1988). In all avian species examined, the epithelium of the DLLH thickens and becomes more complex before the hair-pin turn is formed (Braun & Reimer 1988). However, it should be pointed out that in some mammalian kidneys the situation is similar – i.e. the Mountain Beaver *Aplodontia rufa* (Pfeiffer et al. 1960). Second, the osmotic gradient within the medullary cones is composed of a single solute – sodium chloride (Emory et al. 1972). Furthermore, with respect to function, the fluid moving down the descending limb of Henle's loop appears to become concentrated only by solute addition (Nishimura et al. 1989). As in mammals, the thick ascending limb of Henle junctions as a diluting segment (Miwa & Nishimura 1986). The tubular fluid becomes concentrated as it passes down the collecting ducts; however, this has not been demonstrated directly (Stallone & Braun 1985). Furthermore, there is only indirect evidence that antidiuretic hormone (arginine vasotocin) exerts an effect on the collecting ducts. (Stallone & Braun 1985, Gray & Erasmus 1989).

It is not clear what effect the fluid coming from the small loopless nephrons has on the concentrating mechanism. It is certain that this fluid passes through the medullary cones. But it is not clear at what point in the collecting duct system this fluid mixes with that from the looped nephrons.

From the information presented, it is clear that the avian kidney can concentrate the urine, but to only a modest degree. Considering the fate of the ureteral urine, it may be only reasonable that the kidneys do not produce a highly concentrated urine. This urine enters the terminal portion of the gastrointestinal (GI) tract, the cloaca. The urine is not stored in the cloaca until excreted, but is moved by retrograde peristalsis into the rectum (formerly called the colon) (Akester 1967). (It is not certain that this action occurs in all orders of birds.) This retrograde movement of urine has several important consequences. First, the urine is exposed to the epithelium of the rectum, digestive ceca (in those birds that possess sacculated ceca), and the ileum (in those birds that do not have sacculated ceca). It is well documented that the composition of the urine is modified by the epithelia of the lower GI tract (Thomas & Skadhauge 1985). The degree to which the urine is modified depends on the hydromineral balance of the birds. Sodium, water, and chloride are absorbed and potassium and hydrogen ions can be secreted.

As an important component of the urine, the uric acid in colloidal suspension is also moved forward into the GI tract by the retrograde peristaltic activity. In this region of the GI tract, the uric acid is exposed to a large population of bacteria, some of which selectively use uric acid as a metabolic substrate (Barnes 1972). At least some of the uric acid is converted to short chain volatile fatty acids (VFAs) (Campbell & Braun 1986). Studies have shown that the VFAs can stimulate sodium absorption (Rice & Skadhauge 1982). It is not certain whether the VFAs are being used by the transporting epithelial cells as metabolic fuels or whether they enter the central circulation. Thus, the bacteria disassociate the colloids, freeing some of the inorganic ions, and produce a number of metabolic substrates that can be utilized by the epithelial cells or that can be absorbed and enter the central circulation. Studies have shown that about 40% of the uric acid that enters the lower GI tract is broken down (Anderson & Braun 1985).

In summary, the renal regulation of fluid and ion balance of birds involves not only the kidney but also the lower GI tract. How these two organ systems are controlled and integrated to carry out this function is not entirely clear. The regulation of fluid and ion balance is a degree more complex in birds that have functional salt glands. With some notable exceptions (Goldstein et al. 1986) few studies have been carried out on birds where the three organ systems are involved in osmoregulation.

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INTEGRATION OF AVIAN OSMOREGULATORY SYSTEMS: AN OVERVIEW

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ABSTRACT. All birds maintain extracellular fluid volume (ECFV) and Na^+ concentration $[\text{Na}^+]$ by balancing water and Na^+ uptake in the anterior and posterior gut with loss in evaporation, fecal and renal excretion, and salt gland secretion. Birds with salt glands have larger kidneys and higher water flux than birds without salt glands. Low dietary Na^+ stimulates aldosterone release facilitating Na^+ uptake in the anterior gut, renal tubules, and posterior gut. In chickens high dietary Na^+ increases plasma osmolality (Osm_{pl}) and antidiuretic hormone (AVT_{pl}) concentration and decreases plasma aldosterone and Na^+ uptake; gull Osm_{pl} and Na^+ uptake are little affected, but AVT_{pl} is increased. Decreased ECFV increases plasma Angiotensin II stimulating drinking in both species. Salt glands provide water for renal filtration. Osmoregulation is compared in a bird with (gull) and without (chicken) salt glands. Both chickens drinking freshwater and gulls drinking seawater have high gut Na^+ uptake, renal filtration, and water flux.

Keywords: Kidneys, gut, salt glands, antidiuretic hormone, arginine vasotocin, angiotensin II, aldosterone, extracellular fluid volume, plasma osmolality, sodium, chloride, water.

INTRODUCTION

Bird habitats differ as greatly in temperature, humidity, drinking water salinity, and food, water and osmotic content as those of mammals, and birds have probably evolved as many osmoregulatory solutions to environmental challenges as mammals. Birds seem to tolerate wider fluctuations in plasma osmolality (Osm_{pl}) and Na^+ than mammals (Skadhauge 1989), but avian osmoregulatory strategies are not well understood and only a few species, mainly those of economic importance, have been studied. However, as we focus more on our environment, interest in the comparative aspects of avian osmoregulation has increased. During the past decade Skadhauge's book (1981) (compiling a large volume of data and giving a general overview of avian osmoregulation); several general symposia ("Salt and water excretion in birds", Comparative Biochemistry and Physiology A 71:481-566 and "Progress in Avian Osmoregulation", Hughes & Chadwick 1989) and a symposium on cecal function (Duke & Braun 1989) have appeared. In addition, specific areas: renal function (Braun 1982) and salt gland function (Holmes & Phillips 1985) were reviewed. In this overview I will contrast osmoregulation of a terrestrial bird, the chicken *Gallus domesticus*, with supplemental data on the more xeric quail *Coturnix coturnix*, a bird which has abundant water and low NaCl intake, with that of a marine bird, the gull (*Larus glaucescens* and *L. dominicanus*), which has high salt and water intake (with supplemental data on Pekin Duck *Anas platyrhynchos*). Terrestrial birds have only the kidneys for water and NaCl excretion and have large ceca; marine birds have two excretory organs, the kidneys and the salt glands and have small ceca (Figure 1), although the Pekin Duck has large ceca.

Birds must balance the water and NaCl lost in respiration, urine, feces, and secretions with water and NaCl obtained from food, drinking water, and metabolism. They have some control over salt and water intake through food and drinking water selection and, by appropriate behavioural changes, can minimize evaporative water loss, which is dictated by environmental temperature, humidity and air movement. If water is not limiting and the thermoneutral limits are not exceeded, evaporation accounts for about 50% of a bird's total water loss (Skadhauge 1981, p. 49). Water and NaCl intake may vary greatly from season to season or during migrations. Whatever their environmental constraints, all birds must regulate the osmolality of the fluid bathing their cells, extracellular fluid (ECF) and its volume (ECFV) with some precision. To do this they must regulate water and osmolyte movement across the membranes separating the ECF from the external environment. By neuronal and hormonal modulation they balance transepithelial uptake of NaCl and water in the anterior and posterior guts with renal and salt gland excretion. Three hormones (acting either peripherally or centrally) play pivotal roles in maintaining this balance. These are antidiuretic hormone (arginine vasotocin, AVT), aldosterone, and angiotensin II (AII), which are released in response to high Osm_{pl} , low plasma sodium concentration $[\text{Na}^+]_{\text{pl}}$ and low ECFV, respectively.

OVERVIEW

Anterior gut

The anterior gut epithelium is the first boundary encountered by ingested NaCl and water. Water moves easily across the gut lining and aldosterone facilitates anterior gut Na^+ uptake when $[\text{Na}^+]_{\text{pl}}$ is low. If the water drunk contains more NaCl than the ECF, body water enters the gut until gut fluid and plasma are isosmotic and then Na^+ is absorbed. This causes a transient reduction in ECFV, the consequences of which have not been evaluated in birds. The absorbed NaCl increases both ECF NaCl content and ECFV. The elevated $[\text{Na}^+]_{\text{pl}}$ suppresses aldosterone secretion in terrestrial birds, but not, apparently, in birds with salt glands, since gut Na^+ uptake is the same (Roberts & Hughes 1984) or greater (Crocker & Holmes 1971) in saline acclimated ducks as freshwater ducks.

Extracellular fluid

Absorbed NaCl and water equilibrate within the ECF. Plasma membrane cation pumps actively segregate most K^+ within cells and most Na^+ outside cells, where, together with the Cl^- ion, it makes up about three-fourths of the total osmolality (Table 1). Marine birds have lower Osm_{pl} (to which NaCl contributes more significantly) than terrestrial birds (Table 1). The ECFV is dependent upon its NaCl content and, as either or both move away from their optimal ranges, regulatory responses are evoked. Elevated Osm_{pl} dehydrates osmoreceptor cells activating AVT release from the neurohypophysis. The $[\text{AVT}]_{\text{pl}}$ is positively correlated with increased Osm_{pl} in NaCl infused chickens (Stallone & Braun 1986), but, in ducks slowly activated to NaCl, $[\text{AVT}]_{\text{pl}}$ increased without change in Osm_{pl} (Hughes et al. unpublished data). The AVT stimulates water conserving mechanisms. ECFV decreases as its Na^+ content decreases. Low $[\text{Na}^+]_{\text{pl}}$ stimulates release of aldosterone from the adrenal cortex and (with low ECFV, the more potent stimulant) induces increased $[\text{AII}]_{\text{pl}}$. Special kidney cells release renin, initiating a cascade of reactions that finalizes with the production of AII. The AII increases blood pressure to ensure optimal distribution of the limited ECF supply and restores ECFV by stimulating drinking (Takei et al. 1989) and aldosterone and AVT release.

TABLE 1 - Comparison of plasma osmolality and sodium and chloride concentrations and contribution to osmolality (expressed as percentage of plasma osmolality) in terrestrial and marine birds. Ionic contribution to osmolality - (sum of ion concentrations x 0.9274 divided by plasma osmolality) x 100. *P < 0.05, analysis of variance, comparison birds with and without salt glands.

Number of Species		Plasma concentration mM		Osmolality	Na+Cl / OP,%
		Sodium	Chloride		
Terrestrial	9	152.2 ± 3.2	119.2 ± 3.1	332.2 ± 6.7	75.5 ± 1.2
Marine	7	150.5 ± 5.1	108.5* ± 2.7	303.7* ± 11.9	79.3* ± 1.5

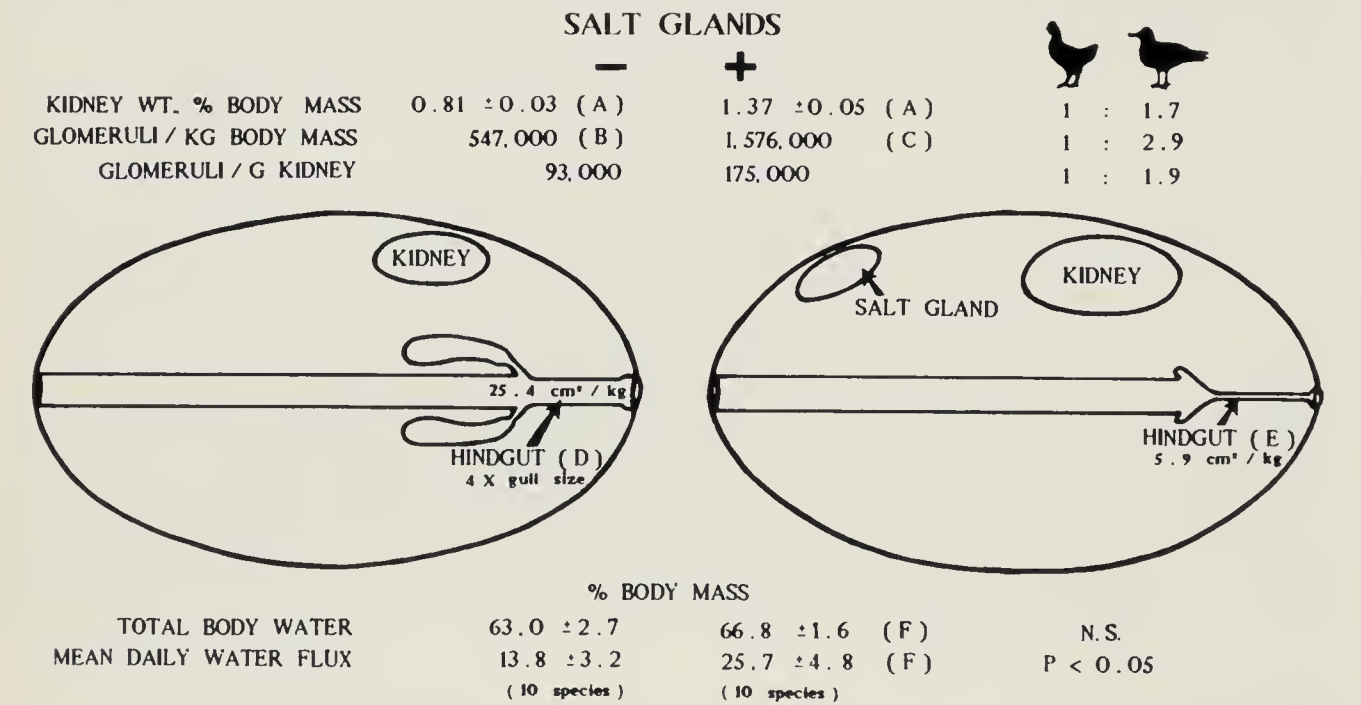


FIGURE 1 - Comparison of renal mass and total glomeruli in chicken (no salt glands) and gull (salt glands) and total body water and water flux in 10 species with and without salt glands. (A) Hughes 1970; (B) Wideman et al. 1987; (C) Braun 1984; (D) Bindsløv & Skadhauge 1971; (E) Goldstein et al. 1986; (F) Hughes et al. 1987.

Kidneys

Terrestrial birds excrete excess Na⁺ renally. The avian kidney is a mixture of reptilian-type (RT) nephrons (which lack the concentrating component, the loop of Henle) and mammalian-type (MT) nephrons (which have the loop of Henle) (Braun 1982). The number of nephrons (per gram body mass) varies widely among bird species, from about 300 in chicken (Dantzler & Braun 1980) to 800 in domestic ducks (Hughes & Fong, unpublished data) and starlings (Braun 1978), to 1600 in gulls (Braun 1984) (Table 2; Figure 1). We are only beginning to decipher avian nephron function and to correlate nephron density and renal function.

All birds filter plasma fluid through the renal glomeruli. Excess water simply leaves the body as urine, but water deficiency presents a more difficult osmoregulatory problem

because bird urine may be concentrated to only two or three times plasma concentration (Skadhauge 1981). If $[Na^+]_{pl}$ is low, retrieval of filtered Na^+ is efficient, but, if $[Na^+]_{pl}$ is high, dehydration may occur. Bird kidneys concentrate Na^+ poorly. If Na^+ ingestion exceeds the renal Na^+ concentrating capacity, body water may be used to form urine. Dehydration induces release of AVT and aldosterone which alter kidney function to restore ECFV. The AVT constricts arterioles supplying blood RT nephrons, reducing plasma filtration and the possible loss of filtered water (Braun & Dantzler 1974). Continued functioning of RT nephrons is not necessarily compromised, since their tubules are supplied by blood from the renal portal vein and secretion and reabsorption may still occur along the tubule (Wideman et al. 1987). Uric acid is secreted into the proximal tubule of RT nephrons (Lavery & Dantzler 1983). The AVT also stimulates water retrieval along tubules of those nephrons which continue to filter (Stallone & Braun 1985). Aldosterone increases Na^+ uptake. Birds seem to tolerate increased Osm_{pl} better than decreased ECFV.

TABLE 2 - Glomerular number and effect of saline on filtration rate in birds from habitats differing in free water availability. Species (*Anas platyrhynchos*, *Larus glaucescens*; *L. dominicanus*, *Gallus domesticus*, *Sturnus vulgaris* and *Callipepla gambelii*) are arranged in descending order from most aquatic to most xeric.

Species	Body mass, g	Glomeruli/ g body mass	Glomerular filtration rate ml(min kg) ⁻¹	
			Hydrated	Salt loaded (method)
duck	3230	690 ^a	4.1	3.3 ^b acclimation
gull	825	1575 ^c	1.9	4.0 ^d acclimation
fowl	2330	490 ^e	2.1	1.7 ^f infusion
			2.5	1.0 ^g infusion
			1.9	0.4 ^h acclimation
			5.8	6.1 ⁱ infusion
starling	79	936 ⁱ	1.8	0.4 ^k infusion
quail	150	313 ^j		

^a Hughes & Fong unpublished data; ^b Hughes et al. 1989; ^c Braun 1984; ^d Hughes 1980; ^e Gregg & Wideman 1990; ^f Skadhauge & Schmidt-Nielsen 1967; ^g Dantzler 1966; ^h Wideman et al. 1987; ⁱ Braun 1978; ^j Dantzler & Braun 1980; ^k Braun & Dantzler 1972.

Bird urine is a complex mixture of fluid and solids in which unneeded materials are eliminated from the plasma. Unless birds are growing, all ingested nitrogen must be excreted, creating a major osmoregulatory problem for birds. Nitrogen is excreted as uric acid (60-82%), ammonia (6-23%) or urea (2-10%) with the proportions dependent upon nitrogen intake and hydration state. The small uric acid - urate spheres are the most water efficient method of excreting nitrogen, since they are not osmotically active (Schmidt-Nielsen 1975) and contain inorganic ions in excess of their equimolar ratios with uric acid (Braun 1989). Xeric quail excrete at least five times as much urate/gram whole urine (Anderson & Braun 1985) as water replete chickens (Long & Skadhauge 1983). Thus, NaCl may be found in both the liquid and solid components of avian urine (Hughes 1972).

Hindgut

Urine mixes with residual gut contents in a common chamber, the cloaca. This material may be voided or, by reverse peristalsis, moved into the hindgut where urates may be degraded (releasing trapped ions) (Anderson & Braun 1985) and NaCl and

water may be retrieved (Bindslev & Skadhauge 1971). All hindgut segments absorb NaCl and water, but coprodeal reabsorption is limited and it functions as a storage chamber (Rice & Skadhauge 1982a) from which material passes into the colon, which has good Na⁺ transport capacity (Thomas & Skadhauge 1979, Rice & Skadhauge 1982a), or all the way into the ceca, which have even better Na⁺ transport capacity (Rice & Skadhauge 1982b; Thomas & Skadhauge 1988). About 25% of the water in ureteral urine may be reabsorbed in the colon (Skadhauge et al. 1985a) and a further 50% may be reabsorbed in the ceca (Rice & Skadhauge 1982b) along with NaCl. Therefore almost all ureteral fluid can be reabsorbed.

Adrenocortical hormones influence lower intestinal Na⁺ uptake (Skadhauge et al. 1985b). Hindgut cells have both mineralcorticoid and glucocorticoid receptors (Sandor et al. 1989) and both aldosterone (mineralcorticoid) and dexamethasone (synthetic glucocorticoid) influence Na⁺ movement (Clauss et al. 1987). Aldosterone may be the major (perhaps sole) regulator of hindgut Na⁺ reabsorption (Skadhauge 1989), but other hormones may be involved. Reabsorption of Na⁺ involves at least two transport systems, only one of which is facilitated by aldosterone (Skadhauge et al. 1985) and continues in marine birds when Na⁺ intake is high (Goldstein et al. 1986). Saline acclimation increases both fowl plasma AVT and prolactin concentrations (Arnason et al. 1986) without affecting plasma corticosterone (Thomas et al. 1980), but the effects of these hormones on the hindgut is unclear. Hindgut Na⁺ retrieval is reduced by high dietary Na⁺ in chickens (Thomas & Skadhauge 1979), but, in birds with salt glands, is only slightly reduced (Pekin Ducks, Skadhauge et al. 1984) or undiminished (gull, Goldstein et al. 1986).

Salt glands

Marine birds, some Falconiformes, and some desert birds have salt glands (Skadhauge 1981). In marine birds they are located in or above the eye orbit and eliminate excess NaCl as an almost pure hypertonic NaCl secretion. Male birds have larger salt glands than females (Siegel-Causey 1990; Hughes et al. unpublished data). The Cl⁻ ion is actively extruded into the salt gland ducts and Na⁺ follows passively, but whether the secretion is initially hypertonic (Lowy et al. 1989) or is made so by extraction of water from an isosmotic secretion (Ellis et al. 1977) has not been resolved. Since its [Cl⁻] may be twice that of sea water or more (six times plasma [Cl⁻] or more), salt gland secretion provides free water for other body functions. Salt gland size and secretion [Cl⁻] are related to environmental osmotic stress and the [Cl⁻] is correlated with the length of the secretory tubules (Staaland 1967). At low secretory rates the secretion may also have a high [K⁺] (Hughes 1970a).

Increased ECF concentration or volume or some algebraic sum of these (Hughes 1989a) activates receptors in the brain (Schmidt-Nielsen 1960) and/or heart (Hanwell et al. 1972) initiating parasympathetic stimulation (Fänge et al. 1958) of salt gland secretion. Secretion is not stimulated by increased plasma concentration without simultaneous ECFV expansion (Ruch & Hughes 1975, Hughes 1989b) and the osmolality threshold for triggering secretion is inversely related to ECFV, more specifically, the interstitial volume (Hammel et al. 1980). The regulatory role of the ECFV may be indirect, since expanded ECFV would decrease [AlI]_{pl}, a known inhibitor of salt gland secretion (Simon & Gray 1989) and increase plasma atrial natriuretic factor (ANF), a known enhancer of secretion rate and concentration (Schutz & Gerstberger 1990). Ion transport may be under beta-adrenergic control (Lowy & Ernst 1987) and vasoactive intestinal peptide (VIP) may mediate ion transport (Lowy et al. 1987) and

secretory flow rate (Gerstberger et al. 1987). Although the effect of exogenously applied hormones is clear, their normal roles are still uncertain. Secretion is elicited by dehydration (Stewart 1972), although dehydration also elevates $[All]_{pi}$, which should inhibit secretion, and by hypotonic saline (Hughes unpublished data), which should not expand ECFV or induce ANF release.

The salt glands use less water than the kidneys to excrete the same amount of Na^+ . Waste elimination and pH regulation require continuous plasma filtration, but filtered Na^+ and water may be retrieved postrenally and the Na^+ secreted via the salt glands to yield free water for further urine formation (Schmidt-Nielsen et al. 1963). Unlike chickens or quail, gulls maintain a high glomerular filtration rate even when NaCl intake is high (Hughes 1980) and gull urine is low in Na^+ even when seawater is drunk (Hughes 1970b). As long as their capacity to make free water is not exceeded, marine birds can maintain a high intake of saline water without becoming dehydrated. Marine birds actually have larger kidneys (Hughes 1970c) containing more mammalian-type nephrons (gull, Braun 1984) than terrestrial birds.

SUMMARY

Terrestrial (chicken) and marine (gull) birds use the same hormones to regulate water and NaCl balance. When water is not limiting, but dietary Na^+ is low, aldosterone facilitates Na^+ uptake from the anterior gut and its retrieval in the kidney tubule and hindgut in both species. When water is not limiting, but dietary Na^+ is high, chickens decrease plasma aldosterone and Na^+ uptake; gulls maintain high uptake of Na^+ in the anterior gut, high glomerular filtration rate, and high Na^+ retrieval in the kidney and posterior gut. Thus, the osmoregulatory responses of a gull drinking seawater and a chicken drinking freshwater are similar. When water is limiting both species release All, which induces drinking, increases $[AVT]_{pi}$ (which decreases GFR and enhances renal tubular water retrieval), and increases plasma aldosterone (which enhances Na^+ uptake).

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SYMPOSIUM 39

AVIAN NUTRITIONAL ECOLOGY

Conveners J. R. KING and F. BAIRLEIN

SYMPOSIUM 39

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NUTRITIONAL ADAPTATIONS TO FAT DEPOSITION IN THE LONG-DISTANCE MIGRATORY GARDEN WARBLER *SYLVIA BORIN*

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ABSTRACT. Garden Warblers, which breed in Europe and winter in tropical Africa, show a pronounced migratory fat deposition. To meet the nutritional demands for that body-mass increase they rely on several nutritional adaptations to maximize the uptake of specifically required nutrients. Besides seasonal hyperphagia and increased assimilation efficiency, they show a striking seasonal shift in dietary composition. They switch from a diet consisting almost entirely of insects to one that comprises mostly fruits. Specific nutrient deficiencies of fruits are compensated for by an appropriate selection of certain fruit species, regulation of daily food intake, and physiological adjustments. Facultative migratory frugivory is likely to facilitate migratory fattening in Garden Warblers.

Keywords: Garden Warbler, *Sylvia borin*, migration, fat deposition, diet selection, frugivory, food assimilation, nutrients, secondary plant chemicals.

INTRODUCTION

Twice a year, corresponding to their long-distance migration between European breeding grounds and Afrotropical wintering grounds, Garden Warblers *Sylvia borin* exhibit a pronounced deposition of body fat. Both in the field and in the laboratory, these birds gain mass of up to 100 % above nonmigratory levels. The seasonal pattern of migratory body-mass gain in captives corresponds with migratory events in free-living conspecifics. In free-living birds, migratory fattening peaks in stopover sites near the trans-Saharan segment of the journey, where daily net mass gains of up to 1.5 g, or about 10 % of lean body mass, have been reported (Bairlein 1988, 1991). In order to deal with the needs for such a tissue increase, Garden Warblers rely on a series of nutritional mechanisms to maximize mass gain. The objectives of the present paper are to summarize the state of knowledge about a long-distance migrant's nutritional ecology and to derive some ideas for future research on this subject.

SEASONAL FOOD INTAKE AND ASSIMILATION

In contrast to studies on granivorous passerines (e.g. King 1961a,b), which do not show any significant variation in food assimilation during migratory fat deposition, the few studies on insectivorous songbirds conducted thus far clearly show such variation during seasonal fattening (Bairlein 1985, Bhatt & Chandola 1985, Fry et al. 1972, Merkel 1958). Captive Garden Warblers provided ad libitum with food of invariant nutrient composition under controlled laboratory conditions increased their food intake as well as assimilation efficiency (proportion of food eaten that is digested) during periods of migratory fattening in both autumn and spring. Changes in the assimilation of fat accounted for most of the seasonal variation of assimilation efficiency, most likely indicating the birds' specific physiological demands during hyperlipogenesis (Bairlein 1985).

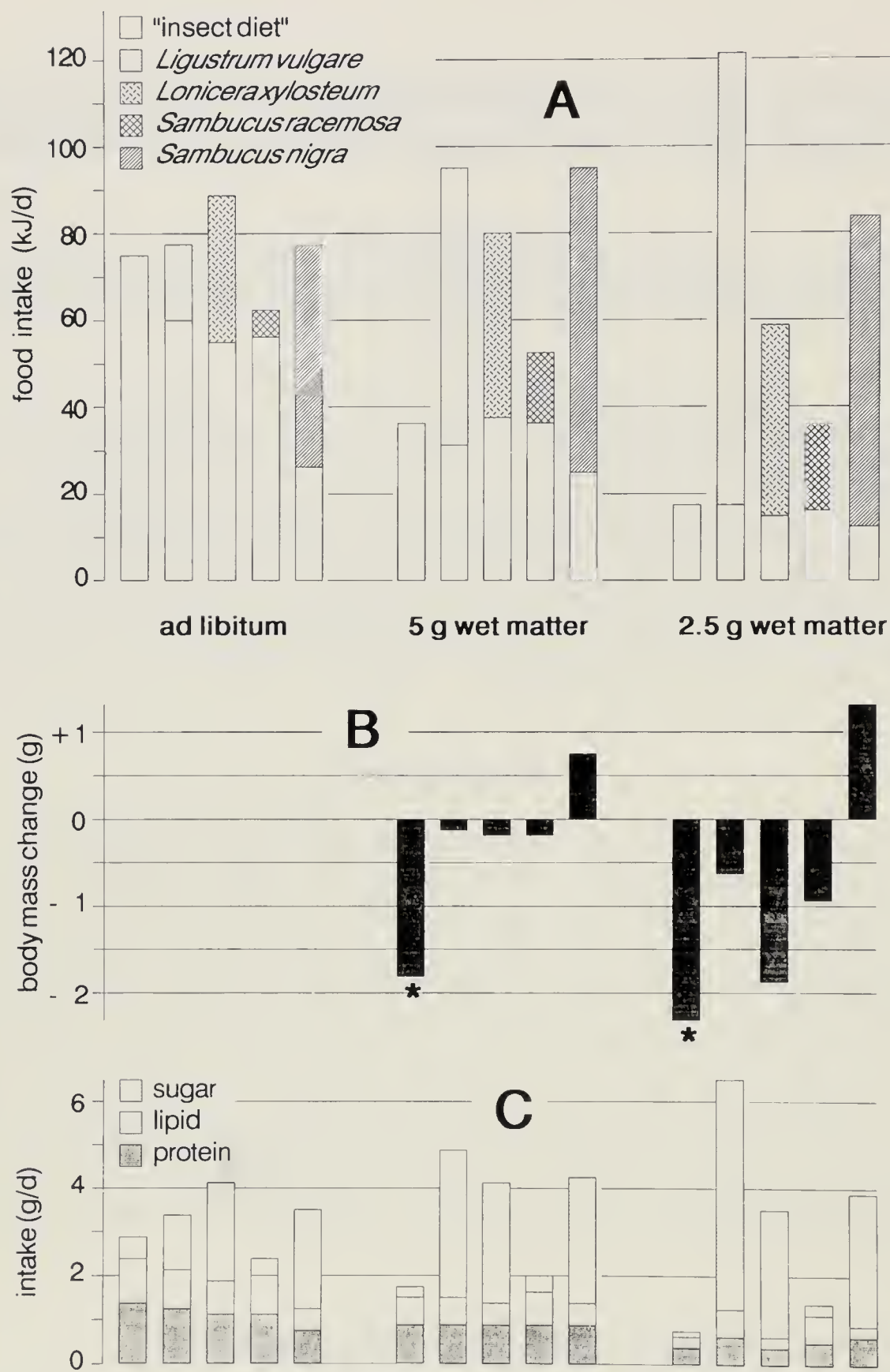


FIGURE 1 – Food intake (A), nutrient intake (C), and body mass changes (B) in captive Garden Warblers while feeding on either ad libitum “insect diet” and ad libitum fruit diets (left) or on reduced amounts of “insect diet” (5 g or 2.5 g wet mass) and ad libitum fruit diets (centre and right). Number of records per pair of alternate diets = 5-50. The asterisk beneath the body mass bar indicates that feeding 5 g of “insect diet” in the control experiment lasted only two days because of the risk of death. In the 2.5 g restriction tests no such control experiment was conducted, as all the birds were already relatively light (16-18 g). Error bars have been omitted to minimize clutter.

FRUGIVORY DURING MIGRATION

During migratory stopover, Garden Warblers feed largely on berries and fleshy fruits, unlike their insect diet in the breeding grounds. In many stomach or fecal samples fruit parts accounted for all of the identified food items (e.g. Brensing 1977, Jordano 1985), even though invertebrate prey was still available. Proportional seasonal consumption of insects and berries also occurred in controlled laboratory conditions in which both kinds of food were continuously available *ad libitum* (Berthold 1976a, Bairlein, unpubl.), thus reflecting spontaneous changes in preference rather than responses to varying availability.

Fruit consumption

Although seasonal frugivory in omnivorous songbirds is quite obvious at stopover sites, its role in the daily food requirements of fattening migrants was thought to be minor (Berthold 1976a, Izhaki & Safriel 1989). However, recent data from captive Garden Warblers clearly contradict this opinion (Simons & Bairlein 1990). Inexperienced Garden Warblers provided *ad libitum* with a standard semisynthetic "insect" diet (Bairlein 1986) simultaneously with fruit diet preferentially fed on the fruits and reduced their intake of the standard diet, compared with the amounts eaten while feeding exclusively on the latter (Figure 1a). Reducing the daily amounts of standard diet available to the birds significantly enhanced the intake of fruits by amounts that differed substantially among the species (Figure 1a). With some fruits, Garden Warblers consumed all the available standard diet (e.g. *Lonicera xylosteum*, *Sambucus racemosa*), whereas less than all was consumed when paired with others (e.g. *Sambucus nigra*), even when the daily ration of standard diet was reduced to 2.5 g (wet mass), or only one quarter of the normal amount. The Garden Warblers' body mass when they were eating only the standard diet was essentially invariant over replicated four-day trials. When they consumed mixed diets with reduced standard diet and *ad libitum* fruit intake, however, the loss or gain of body mass depended on the amount of standard diet available and the species of fruit consumed (Figure 1b). In Garden Warblers subsisting on a mixed regime of reduced amounts (5 g or 2.5 g) of standard diet and *ad libitum* amounts of fruit, body mass diminished much less than in control birds fed only the reduced amounts of standard diet through replicated 4-day trials, and even increased substantially above the control level in birds eating black elderberry *Sambucus nigra*. In the 5 g restriction groups, the losses of body mass during the four-day trials with three of the four fruit species were slight, although statistically significant. Even long term exposure (11-15 days) to that level of restriction did not affect the birds' body mass drastically if some fruits (*S. nigra* or *Ligustrum vulgare*) were available *ad libitum*. The birds almost compensated for that reduced "insect" diet by an appropriate increase of fruit consumption. In the 2.5 g restriction groups, however, the birds lost considerable body mass, except when eating *S. nigra*, and in all cases lost significantly less than when eating the standard "insect" diet alone (Figure 1b). In the restriction groups protein and fat intake was significantly lower, whereas carbohydrate intake increased due to the increased intake of berries (with the exception of *S. racemosa*). Thus, the observed body-mass loss in the restriction groups most likely resulted from protein and/or lipid deficiencies rather than carbohydrate or energy shortage. In contrast with all other fruits tested, the consumption of the berries of *S. nigra* enabled the birds to gain body mass even though the total nutrient and energy intake was less than or equal to the intake of birds that lost mass while consuming *L. vulgare* berries (Figure 1). Even when fed only *S. nigra* berries the birds did not undergo any significant long-term loss of body mass, but instead

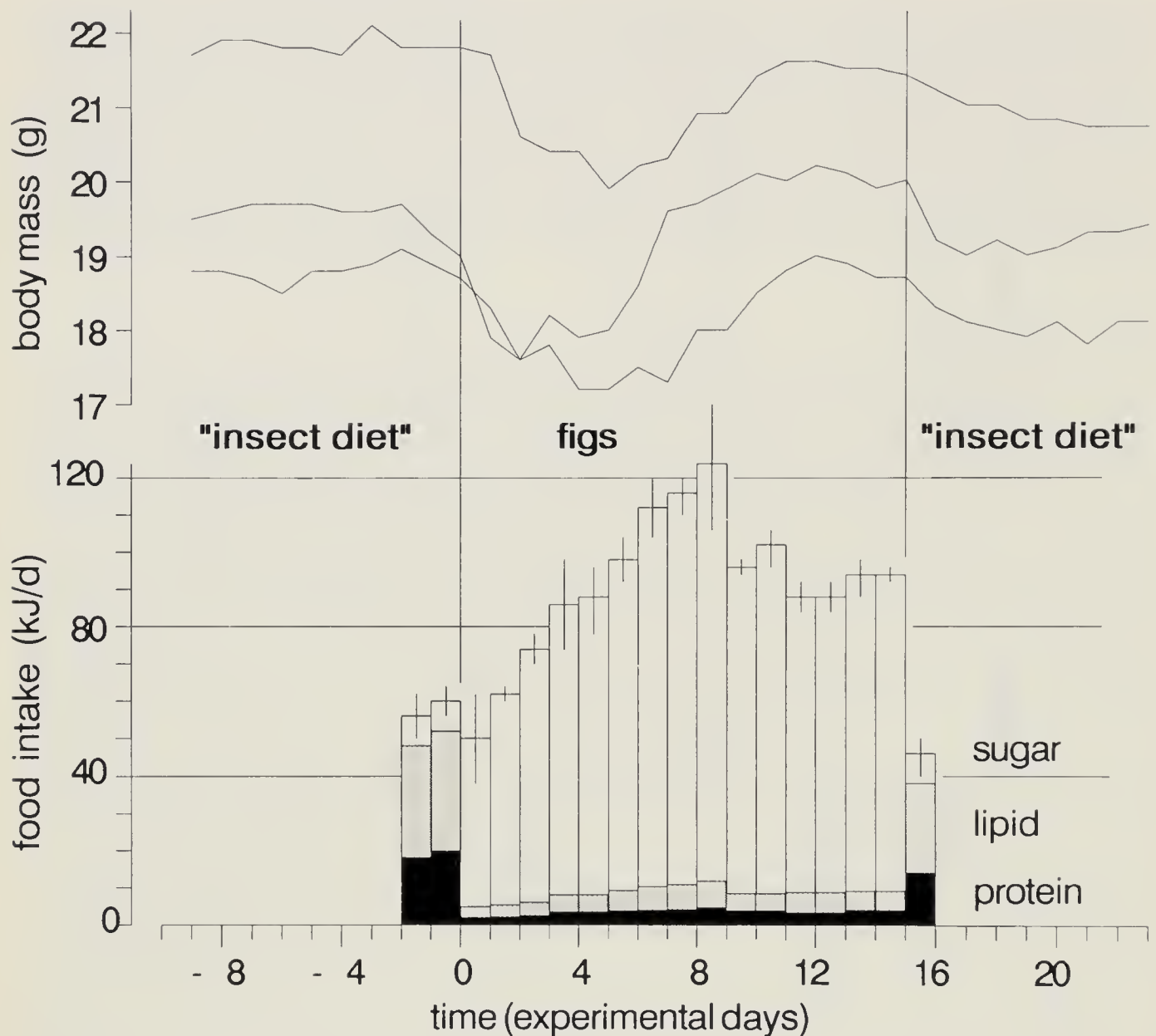


FIGURE 2 – Body mass (above) and food intake (below) of three representative Garden Warblers feeding exclusively on figs (*Ficus* sp.).

registered a slight increase. Similar results are obtained with figs (Figure 2). Both *S. nigra* and figs are important foods for Garden Warblers at stopover sites (Baccetti et al. 1985, Bairlein 1988, Kroll 1972, Schmidt 1964, Thomas 1979). Figure 2 also shows the temporal course of compensatory food intake while the birds fed exclusively on fruit. After switching from the standard "insect" diet to figs the birds lost body mass for a few days then regained normal mass although still subsisting on figs. Food intake varied substantially during this period. Initially, the intake of figs (as well as *S. nigra* berries in other experiments) was slightly lower than the intake of the standard diet. The birds then increased their fruit intake continuously for several days, followed by a significant reduction of intake as body mass regained its normal level. In that stage, while the birds maintained normal body mass and ate only fruit, they consumed about 1.5 times as much energy as when subsisting on the standard "insect" diet, but only about 17 % as much protein and lipid, respectively. The gross intake of protein

and fat while the birds fed on figs and maintained body mass averaged about 200 mg/bird-day and 130 mg/bird-day, respectively. After the birds were returned to the standard “insect” diet on day 16 (Figure 2), daily food intake was even lower than before fruit consumption (days -1 and -2). Evidently, the birds compensated for the low protein and lipid content of fruit by increasing their food intake. Moreover, maintaining body mass even though daily protein and lipid intake were greatly reduced suggests that the birds adjusted to the exclusive fruit diet by as-yet unknown physiological mechanisms. Consequently, switching back to the “insect” diet resulted in a shortfall in food intake and moderate loss of body mass, because it may take some time to adjust to the new foodstuff. These results are quite consistent with previous work with Garden Warblers using diets specifically altered in protein, lipid or carbohydrate content (Bairlein 1987).

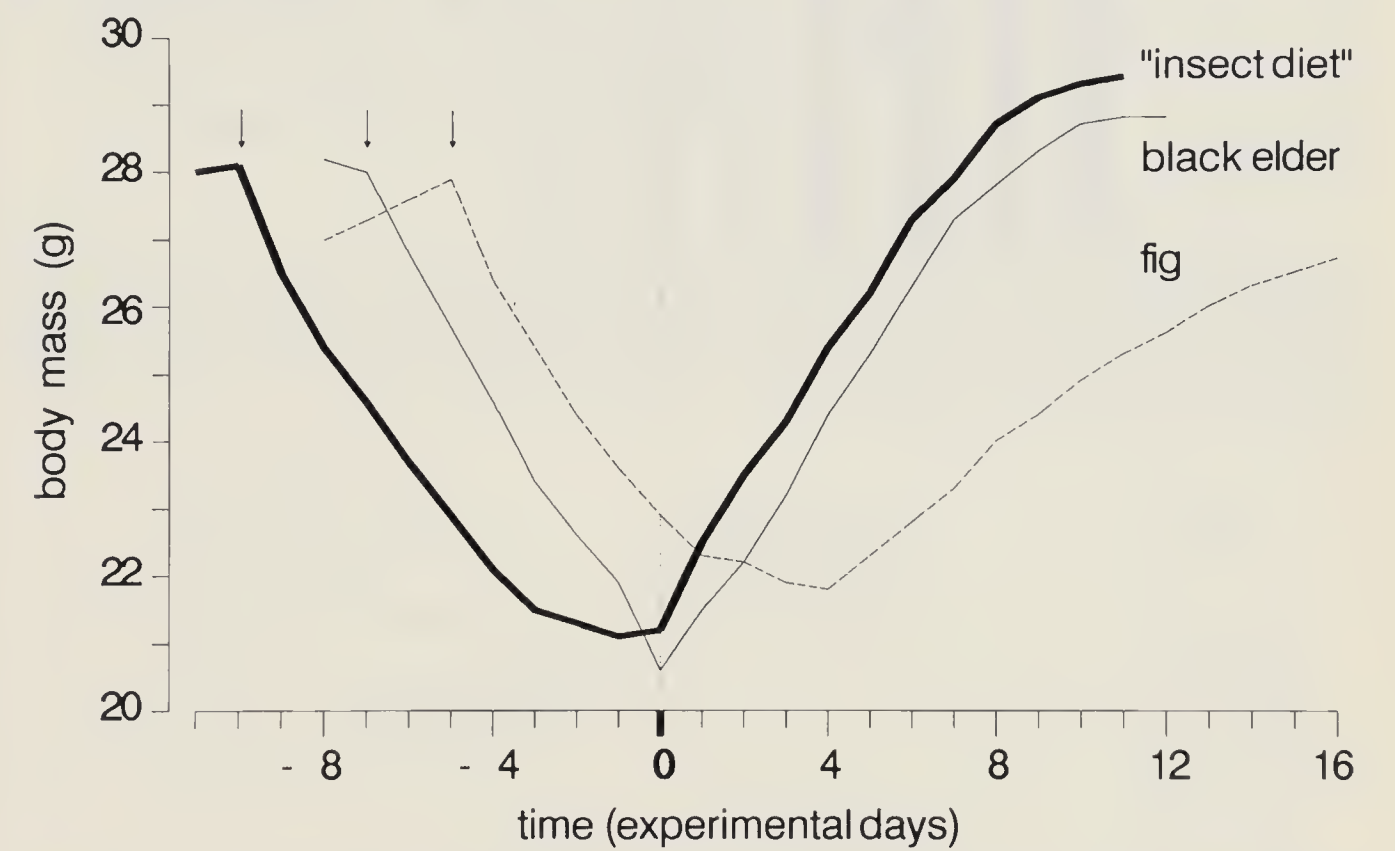


FIGURE 3 – Re-fattening of Garden Warblers refed with various foods. The broken vertical line indicates the start of refeeding. The arrows denote the onset of fasting. See text for further explanation. In this pilot experiment only few birds were tested: $n = 4$, 2 and 3 for “insect diet”, black elderberry, and figs, respectively. Error bars have been omitted to minimize clutter.

Fruit consumption and migratory fattening

Along their migratory routes migrants often refeed at stopover sites to replenish their fat reserves. Captive Garden Warblers deprived of food for several days during migratory fat deposition lose body mass but regain the normal seasonal level quickly when allowed to refeed ad libitum (Berthold 1976b). To investigate whether fruits can meet the requirements of such refueling, we fed fat birds with only small amounts of standard diet for several days in order to reduce body mass considerably (Figure 3, days -10 to -1). We then allowed subgroups of these birds ad libitum access to either standard “insect” diet, figs or *S. nigra* berries. In all cases the birds regained their initial body mass even though refeeding on fruits (Figure 3). The rate of body-mass gain was about the same in birds subsisting, respectively, on the standard “insect” diet and on *S. nigra* berries, but was slower in the birds refeeding on figs (Figure 3). In

order to obtain the same rate of mass gain when eating figs the birds needed a daily supplement of, on average, 1.68 ± 0.59 g (dry mass) of the standard “insect” diet. The continued loss of body mass by birds refeeding exclusively on figs during days 1-4 resulted from their previous inexperience with this fruit.

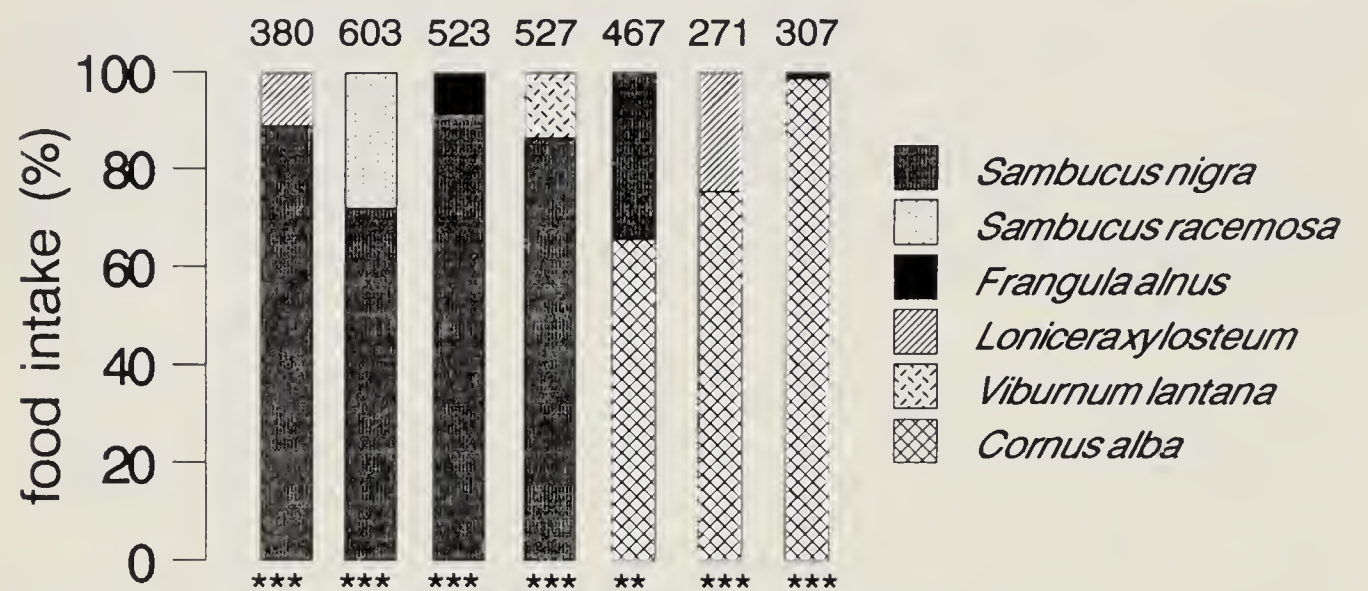


FIGURE 4 – Relative food intake of Garden Warblers (n=7) presented simultaneously with a choice of two species of berries. The numerals at the top of the bars denote the number of records. Asterisks below the bars indicate significant selection (deviation from random intake, ** P < 0.01; *** P < 0.001).

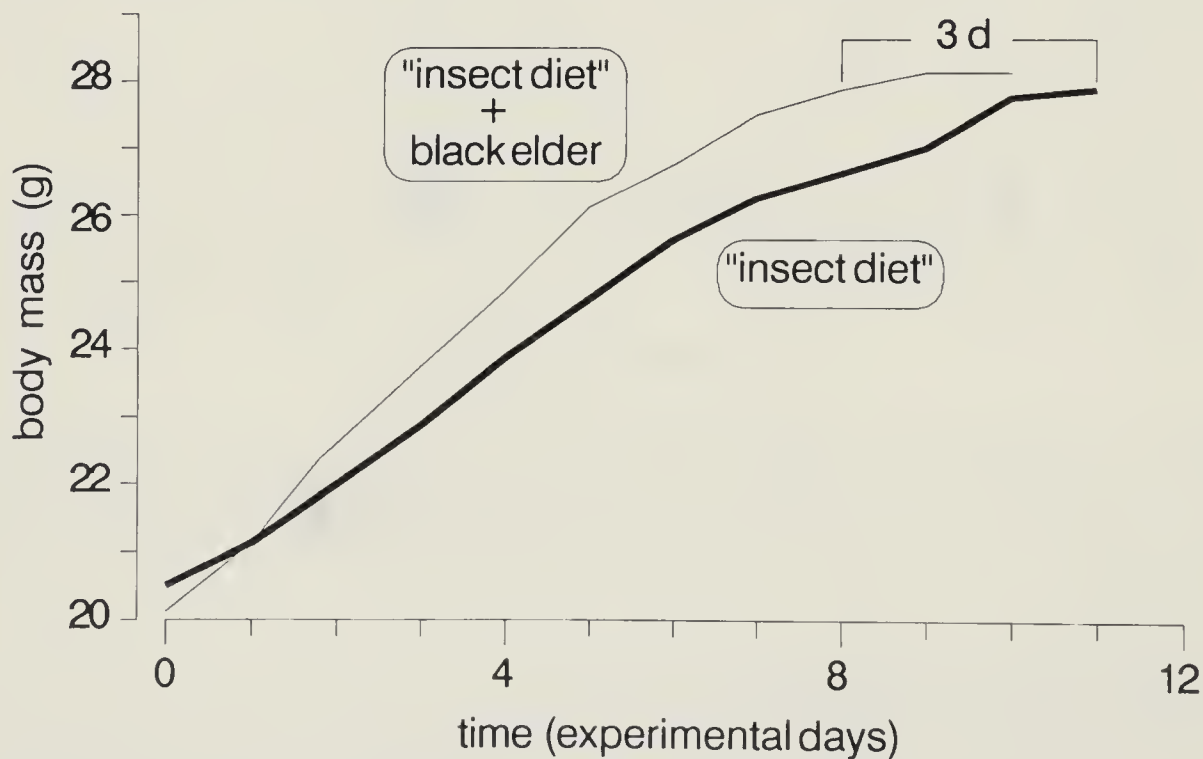


FIGURE 5 – Re-fattening of Garden Warblers refed with either a pure “insect diet” (n = 4) or a mixed diet (n = 6). For clarity, error bars have been omitted.

Fruit preference

Garden Warblers provided with various berries in replicated dual-choice clearly preferred *S. nigra* berries to all others (5 species, Figure 4) except white dogwood *Cornus alba*. There were no obvious correlations between fruits preferred and fruit characteristics (color, size, macro-nutrients, fiber content) or even handling time. Previous experiments using the semisynthetic diet, however, clearly revealed significant relationships between nutritional composition and food choice, with particular preference



FIGURE 6 – Diet selection by Garden Warblers (n = 4-6) feeding simultaneously on semisynthetic diets differing in the fatty acid composition of their lipids. The asterisks below the bars indicate that consumption differed significantly (at least $P < 0.05$) from random.

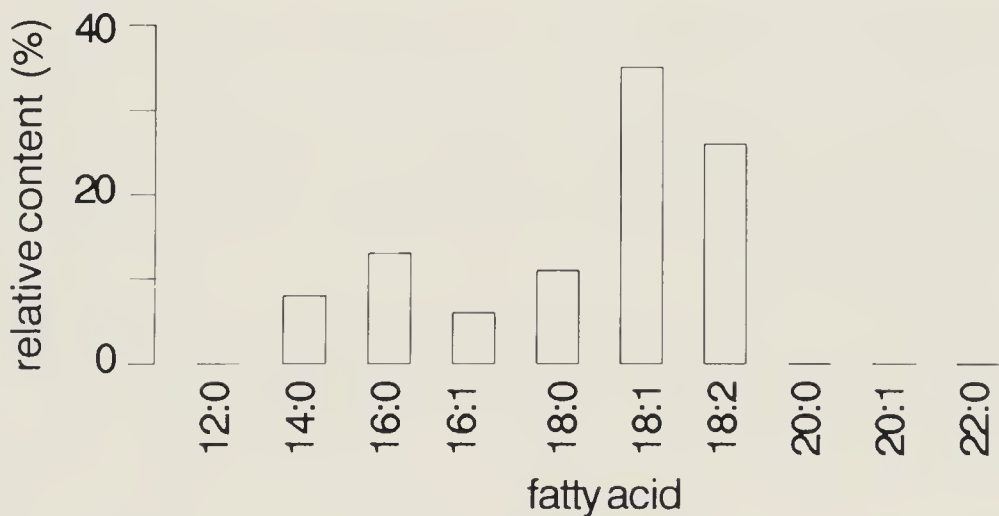


FIGURE 7 – Fatty acid composition of the depot lipids of Garden Warblers (n = 7).

for the most fat-rewarding diets (Bairlein 1990a). The failure to find such relationships while feeding whole fruits may reflect complex interrelationships between the basic fruit characteristics or the presence of other plant components not yet considered in the analysis. The observations that the consumption of berries yielding similar nutrient intakes resulted in quite different effects on the body mass of the birds (Figure 1) may indicate that plant components other than energy or macro-nutrients have to be considered. Secondary plant chemicals are often suggested as agents in the control of feeding by acting as deterrents (e.g. Izhaki & Safriel 1989, Mack 1990, Sedingner 1990). Some secondary agents, however, may stimulate food intake and metabolism (Bairlein 1990b). Garden Warblers fed ad libitum with both the standard “insect” diet and *S. nigra* berries during migratory disposition gained body mass significantly faster (0.98 g/day) than Garden Warblers fed only on the “insect” diet (0.68 g/day), thus reaching their peak body mass about three days earlier (Figure 5).

In addition to secondary plant chemicals, the specific quality of nutrients may also affect diet selection, food intake, and metabolism. Fruits are, in general, rich in unsaturated fatty acids (e.g. Altman & Dittmer 1968). Garden Warblers provided simultaneously with two diets identical in the gross lipid content but differing in the fatty acid composition of the lipids exhibited obvious preferences (Figure 6). Although these pilot data need to be replicated, they clearly indicate that Garden Warblers are able to sense the specific quality of nutrients. It may be pertinent that the birds tended to prefer foods rich in C-18 unsaturated fatty acids, which are the predominant fatty acids in the birds' depot lipids (Figure 7). Songbirds are also able to discriminate between diets that differ in essential amino acid concentration (Murphy & King 1987, 1989).

CONCLUSIONS

Garden Warblers evidently rely on many mechanisms to maximize their energy and, in particular, specific nutrient intake in relation to their specific demands during migratory fat deposition. Although the aforementioned results were obtained from captive birds, their adaptive significance in free-living birds seems most evident. In the latter, increased assimilation of ingested nutrients may reduce the costs of foraging and maximize the uptake of specifically required nutrients. The maximization of nutrient uptake is further facilitated by seasonal frugivory.

By supplementary feeding on berries and other pulpy fruits, Garden Warblers may not only compensate for a shortage of insect food but also accelerate their rate of fattening by selecting certain species of fruit. Even if fruits do not completely fulfil the birds' nutritional requirements, consumption of fruit can greatly reduce the amount of animal food needed during migratory fat deposition. Thus, feeding on fruits is indeed likely to facilitate migratory fat deposition, particularly in autumn, when fruits are locally very abundant. Although the mechanisms by which Garden Warblers sense the nutritive value of various foods are unknown, the birds' selectivity in food choice seems to be based on innate preferences for the most nutritionally rewarding fruits. In any case, the ability to recognize foods that offer the greatest specific nutritional rewards may be a prerequisite for avoiding malnutrition as nutritional demands change rapidly while the birds are engaged in seasonal fattening (King & Murphy 1985). The transitory losses of body mass that occurred in Garden Warblers when diets were switched, even to those of richer nutritional quality, indicate either behavioral responses to the novel trophic situation (Greenberg 1983) or physiological adjustment altered nutritiousness. The latter is more likely in view of the experiments in which Garden Warblers underwent a brief loss of body mass in response to changing diets even though the various foods did not differ in their outer texture (Bairlein 1987). The mechanisms involved in such physiological adjustments are, however, poorly known (e.g. Martines del Rio & Stevens 1989, Spitzer 1972, Walsberg 1975). Many banding studies report on some loss of body mass by within-day retraps and even next-day retraps. This is sometimes attributed to the effects of handling and banding the birds; but the results of studies of caged birds suggest that mass loss may instead reflect responses to the novelty of changed habitat and feeding conditions that evoke intrinsic mechanisms to seek the best habitat (Bairlein 1981) and most rewarding food.

Finally, the specific nutritional demands of migration and the accompanying physiological adjustments may significantly influence foraging decisions during migratory

stopover (Moore & Simm 1986). As recently shown (Biebach 1985, Gwinner et al. 1985, 1988, Bairlein & Moore, unpublished), the endogenous program that determines the temporal pattern of migration in many songbirds is affected by the amounts of body fat and by the rate of re-fattening. Consequently, the availability of nutrients that specifically enhance migratory fattening may have a stronger effect on the temporal course of migration than merely the gross food supply at particular stopover sites. However, the nutritional ecology of most wild birds is almost unknown (Robbins 1983), and much remains to be learned, not only about migration but also about other physiological stages in the annual cycle (e.g. molt, gonadogenesis, ovogenesis).

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ECOLOGICAL PHYSIOLOGY OF FOOD EXPLOITATION: INSIGHTS FROM MEASUREMENTS AND MODELS OF DIGESTIVE FUNCTION

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ABSTRACT. Models of digestion are useful tools for understanding the interplay between digestion and avian ecology. A model from classical nutrition is used to show how food composition (including plant secondary chemicals) influences food metabolizability in herbivorous grouse. An optimization model adapted from chemical engineering identifies relationships between foraging energetics and digestive function in nectarivores and frugivores, and predicts short term changes in gut throughput and digestive efficiency in response to variations in food composition. Longer-term changes in gut characteristics of insectivorous House Wrens *Troglodytes aedon* feeding at their probable maximal rate of energy intake are interpreted using a chemical reactor model. These examples illustrate how models serve in organizing research and explicating the integrated action of numerous facets of digestion in relation to the whole animal in an ecological context.

Keywords: Herbivores, nectarivores, frugivores, insectivores, grouse, Tetraonidae, House Wren, *Troglodytes aedon*, feeding ecology.

INTRODUCTION

The traditional role of digestion studies in nutritional ecology has been in generating data on the metabolizability of foods (reviewed in Castro et al. 1989, Karasov 1990). The metabolizable energy coefficient (Kendeigh et al. 1977, Miller & Reinecke 1984, Karasov 1990), along with a food's gross energy content, can be used to calculate feeding rate from a knowledge of energy expended in metabolism and production. More recently, it has been suggested that digestion is ecologically important also because the design and adaptability of the gut may determine diet diversity and hence niche width, and because digestion might set the limit on metabolizable energy intake and thus determine rates of growth and reproduction (Karasov & Diamond 1988, Karasov 1990). This paper reviews these developments, with special emphasis on how research in this field can be organized and advanced by application of mathematical modeling (Sibly 1981, Penry & Jumars 1987).

THE ECOLOGICAL SIGNIFICANCE OF DIGESTION

Even subtle digestive characteristics can clearly influence the feeding choices of birds. Some passerines, for example, lack sucrase, the intestinal enzyme responsible for the hydrolysis of sucrose, and therefore cannot use sucrose as an energy source (Martinez del Rio & Stevens 1989, Martinez del Rio 1990). Consequently, they avoid sucrose-rich foods (probably because of sucrose-induced diarrhea). More generally, birds' sugar preferences are often correlated with their ability to digest sugars (Martinez del Rio & Stevens 1989, Martinez del Rio et al. 1989, Martinez del Rio in review). In some cases these preferences apparently have coevolutionary significance: there is a correlation between bird sugar preferences and the sugar

composition of nectar and fruit pulp (Baker & Baker 1983, 1986, Martinez del Rio 1990, in review). Thus, the digestive characteristics of birds can have an impact on the evolution of plant populations.

Digestive processes are also important insofar as they could limit food intake (Kenward & Sibly 1977, Karasov et al. 1986, Levey 1987). Digestive limitation of intake might result from physical or biochemical limitation. In the former case the volume of the gut (or one of its compartments) and its turnover time set an upper limit on the volume (or mass) of digesta that can be processed (e.g. Belovsky 1984). In the latter case small intestinal rates of hydrolysis and absorption are limiting.

Intake limitation can have several kinds of ecological consequences. In the Kestrel *Falco tinnunculus* maximal energy intake appears to limit the performance of males when feeding young under harsh conditions due to the high energetic cost of aerial foraging (Masman et al. 1989). Besides being a proximate factor limiting a species' reproduction, digestive limitation of intake could limit a bird's geographic distribution (by limiting sustainable long-term heat production and hence survival in cold climates) (Peterson et al. 1990). Digestive limitation of intake also proves to be an important constraint in optimal foraging models (Belovsky 1984).

Frameworks for studying the physiological ecology of digestion

The preceding examples illustrate how digestive traits, interacting with the chemical characteristics of food (Moss 1983), can influence avian foraging behavior, diet breadth, digestive efficiency, and rates of energy assimilation and production. Models have been and continue to be essential tools for understanding this interplay. They are essential because a satisfactory understanding of this interplay probably cannot be achieved with simple one-factor-at-a-time analyses. The digestive system is a system – an interlocking complex of processes characterized by several reciprocal cause-effect pathways whose overall function we can best appreciate by viewing it as a whole.

I have focused on application of models because they can be critical components of the feedback loop which includes data collection, analysis, and subsequent data collection, and their use can speed the advance of knowledge. In the sections that follow I provide examples of the useful application of models from classical nutrition and chemical engineering to the problem of integrating digestive processes from the biochemical to the whole-animal level in an ecological context.

PHYSIOLOGICAL ECOLOGY OF DIGESTION: MODEL FROM CLASSICAL NUTRITION

The classical framework

Hundreds of balance trials have been performed with different avian species fed different foods in which the apparent metabolizable energy coefficient (MEC^* [food energy excreta energy]/food energy; apparent because not corrected for endogenous losses) has been determined. Recent summaries of these studies (Castro et al. 1989, Karasov 1990) concluded that the largest source of variation in MEC^* is due to chemical characteristics of food, in particular what proportion of the food energy is refractory to chemical digestion (e.g. cell walls, arthropod cuticle; Karasov 1990). Nonetheless, other factors are important such as energy and nitrogen balance status during

feeding trials and the magnitude of fecal and urinary endogenous losses of energy (Sibbald 1976, 1981).

A simple model (Karasov 1990) of MEC* incorporating these factors that is based upon principles of digestion and metabolism from animal nutrition research is

$$\text{MEC}^*_p = 1 - [\text{GE}_R] R_i / \text{GE}_i - 34.5 N_i / \text{GE}_i - (\text{E}_e - 34.5 [\text{E}_N]) / [\text{GE}_i] [\text{O}_i] \quad (1)$$

where MEC^*_p is the predicted MEC*, GE_R is the gross energy content of the material in the food that is refractory to chemical digestion, R_i is the proportion of the food dry mass that is refractory to chemical digestion, and GE_i is the gross energy content of the food (kJ/[g dry mass]). In the second term of the equation, which is part of the correction for excess N ingested and then excreted, 34.5 is the energy value (kJ/g) assigned to urinary nitrogen, and N_i is the proportion of the food that is N. In the last term, which is a correction for endogenous losses, E_e is the endogenous loss of energy (as sloughed off gut tissue, secretions, bacteria) in kJ/d, E_N is the endogenous N loss (g/d), and O_i is the rate of food intake (g/d).

Assumptions in the model include the following: (1) The bird is in energy steady state, and N intake equals or exceeds its minimum requirement. In practice, the model should hold fairly well for a bird losing mass and catabolizing protein because correction for N balance usually alters MEC* by ≤ 0.01 (e.g. Levey & Karasov 1989). (2) All of the nonrefractory portion of food (which is often measured as neutral detergent solubles) is digested and absorbed. Mammals generally digest and absorb 98% of this food fraction (Van Soest 1982) and some birds appear nearly as efficient (Karasov 1990). (3) None of the refractory portion is digested and absorbed. There are many exceptions to this (reviewed in Remington 1989, Karasov 1990). However, if one makes this assumption, perhaps the model can be used to identify those instances when birds appear to digest a substantial fraction of cell wall or cuticle, based on comparatively high utilization efficiencies. (4) There are no plant secondary chemicals (PSCs) in the food which are unmetabolizable or which render other food components less metabolizable. This also is probably not true, as discussed in the following example.

Digestive studies with herbivores

Tens of balance trials have been performed with grouse species fed wild foods (Andreev 1988, Karasov 1990). On average, they metabolize 35% of the energy in their wintertime food of buds, twigs and catkins, the lowest for all avian species and diets. Equation 1 offers a mechanistic framework for systematically evaluating whether this low efficiency is due to inherently indigestible food (high R_i), especially high endogenous losses (high E_e), or inefficient digestion of even the nonrefractory portion of food (the value 1 in eq. 1 is too high).

As indicated in the first term of eq. 1 and illustrated for Ruffed Grouse *Bonasa umbellus* (Figure 1a), the metabolizability of plant material is influenced greatly by the cell wall content (measured as neutral detergent fiber, NDF). Even assuming that none of the cell wall is digested, MECs are consistently lower than predicted by the simple model (which assumes that endogenous losses are the same as poultry). If Ruffed Grouse had particularly high endogenous losses, the third term of eq. 1 would

be large and that might explain the difference. But endogenous losses of Ruffed Grouse are not particularly high compared with poultry (Figure 1b). Even for the formulated diet (Figure 1b) the observed MEC* (0.55) was less than the predicted MEC* (0.64, based on R_i 0.31 measured as NDF). This suggests that (a) the grouse digested none of the refractory cell wall and were less efficient than assumed in digesting nonrefractory material (i.e. 0.91 rather than 1.0), or (b) that if they did digest (cell wall (highly likely and currently under study) they were less than 91% efficient at digesting nonrefractory material.

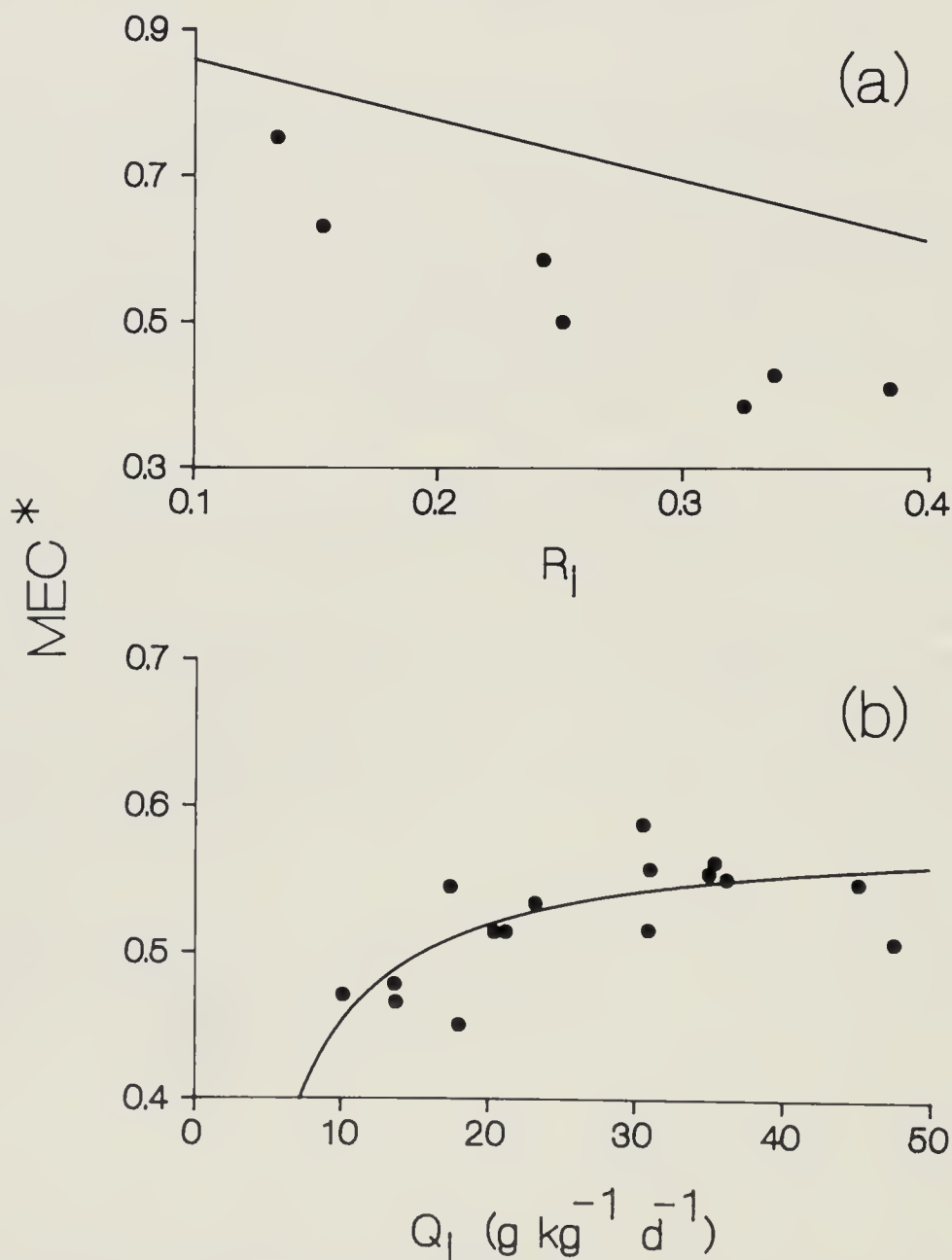


FIGURE 1 - a. MEC* as a function of R_i (measured as neutral detergent fiber) in Ruffed Grouse. Data points are from Servello et al. (1987). The solid line is the predicted relationship for a 600 g Ruffed Grouse based on eq. 1, using parameter values for grouse eating herbage (from Karasov 1990) and assuming $E_e = 24$ kJ kg⁻¹ d⁻¹ (the value for chickens; see text).

b. MEC* as a function of food intake in Ruffed Grouse. Data points are MEC* corrected to N balance from Guglielmo & Karasov (unpublished data for 8 birds [mean body mass = 601 g] fed at two levels of intake). The solid line is the predicted relationship for a 600 g Ruffed Grouse based on the third term of eq. 1, assuming that $E_e = 24$ kJ kg⁻¹ d⁻¹ (the value for chickens). The close agreement between predicted and observed indicates that endogenous losses in Ruffed Grouse are not greatly different from poultry.

Grouse species eat wintertime foods with cell wall contents (R_s) of 0.22-0.6 (Karasov 1990) and are known to digest as much as 35% of the cell wall (Remington 1989). It is difficult to rationalize this, along with 91% efficiency digesting nonrefractory material in food, with their very low MEC*s (0.35). Thus, the model prompts us to look at the last assumption. Could PSCs be partly responsible for low MEC*s? Servello & Kirkpatrick (1987) found that total phenols made up 0.06-0.11 of dry mass of buds, twigs, and catkins eaten by Ruffed Grouse. Furthermore, the accuracy of their predictions of MEC* based on forage analysis was increased when they incorporated a parameter for phenol content into their predictive equation (Servello et al. 1987). By making no assumptions about digestion inhibition but simply adding an additional 0.1 to R_s to account for phenols' presence and nonmetabolizability, one can reduce most of the difference between observed MEC* and that predicted from eq. 1.

Using a simple model (eq. 1) as a guide in data collection and analysis we conclude that (1) the presence of PSCs lowers the metabolizability of grouse foods, and (2) even so, grouse are somewhat inefficient digestors of their food. This latter observation could be further evaluated using a digestive optimization model.

PHYSIOLOGICAL ECOLOGY OF DIGESTION: MODELS FROM CHEMICAL ENGINEERING

Sibly (1981) suggested that avian digestion might be studied from the perspective of alternate strategies that maximize some function given constraints imposed by design of the gut and characteristics of the food. Penry & Jumars (1986) formalized this approach by adapting models from chemical engineering (Carberry 1976) to digestion. There are at least two important virtues of these approaches. First, they yield useful mechanistic models that explicitly identify those attributes of the digestive system that determine digestive rate and efficiency and show how they are related to each other. Second, the optimality approach offers the researcher a formalized approach to increase understanding of digestive design in relation to an animal's environment and its fitness (Calow & Townsend 1981).

An optimization model for nectarivores and frugivores

Martinez del Rio & Karasov (1990) used this approach to analyze digestion of simple sugars by avian nectarivores and frugivores. Their "hummingbird" model has a digestive gain function that is nearly linear (Figure 2a) because glucose absorption by hummingbirds appears to be almost entirely carrier-mediated and the sugar carriers are probably saturated and thus operating constantly near their maximal rate (Karasov et al. 1986). In contrast, the "frugivore" model has a digestive gain function that rises in decelerating fashion to an asymptote (Figure 2b) because glucose uptake in passerine frugivores (4 species; Karasov & Levey 1990) has a substantial passive component. For both kinds of birds, the cost of digestion is calculated as the sum of the cost of obtaining the amount of food to fill the intestine plus the cost of staying alive during the throughput time (t) required to process this amount of food. The curves for net rate of energy gain (gain - cost; illustrated for frugivores in Figure 2c,d) have the same general shape as their respective digestive gain functions, but at short t little digestion has occurred and so net rate of gain is negative and at long t net rate of gain slopes downward because digestion is complete but expenditure continues. As in many optimization models, the optimal throughput time t^* is that at which a straight line passing through the origin is tangent to the gain-cost curve. This t^* maximizes the rate of net energy gain.

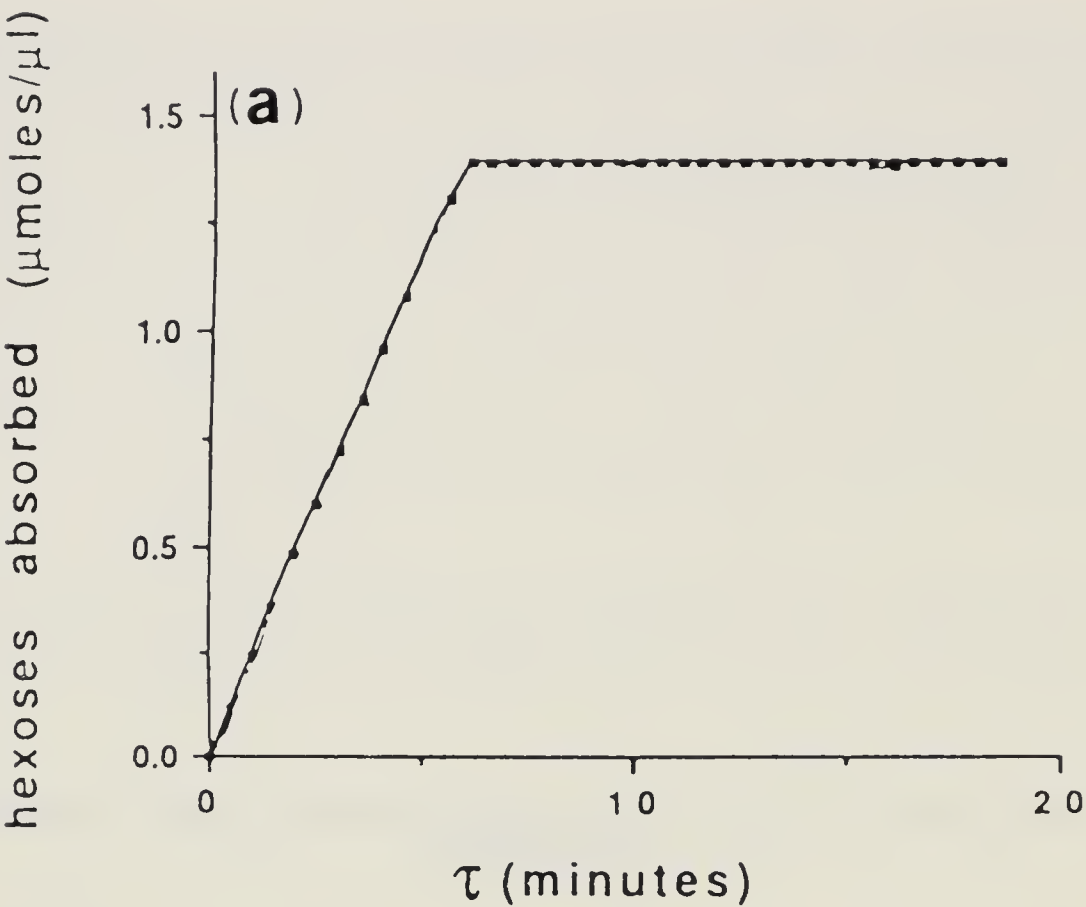


FIGURE 2 - Absorption kinetics for the hummingbird and frugivore model, and the graphical determination of optimal throughput times and digestive efficiencies under different conditions (from Martinez del Rio & Karasov 1990, with permission).
a. Predicted total absorption of hexose as a function of throughput time using a reactor model (Martinez del Rio & Karasov 1990) and intestinal absorptive parameters measured for hummingbirds (Karasov et al. 1986).

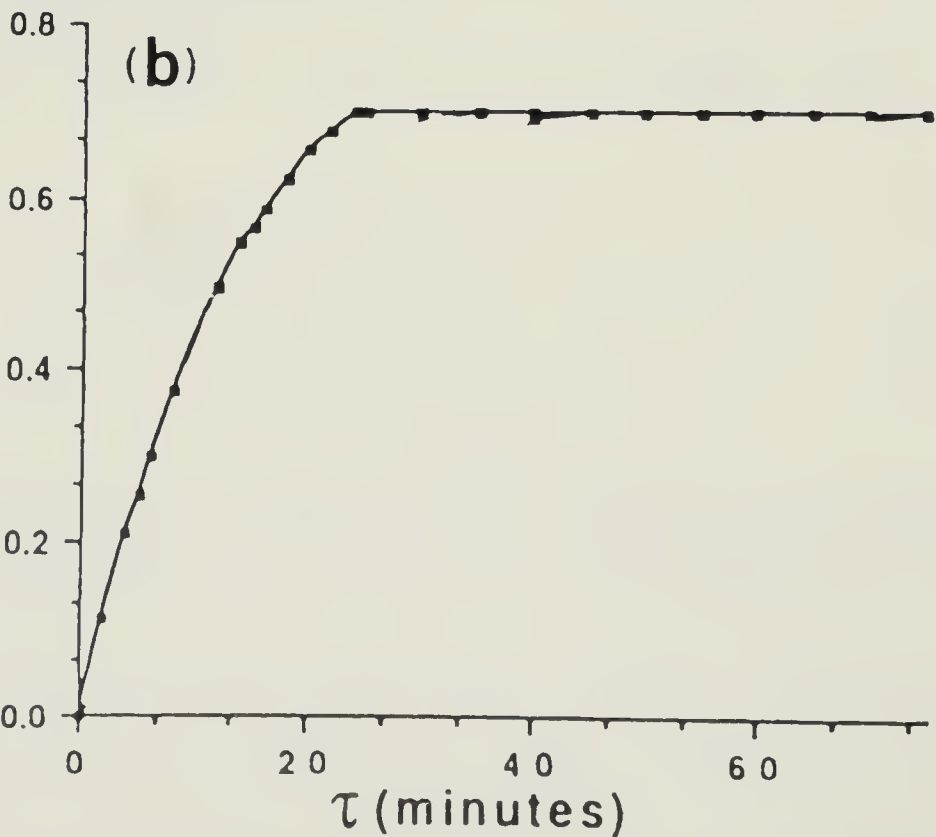


FIGURE 2b – The same as in 2a, except for frugivores, using intestinal absorptive parameters from Karasov & Levey (1990).

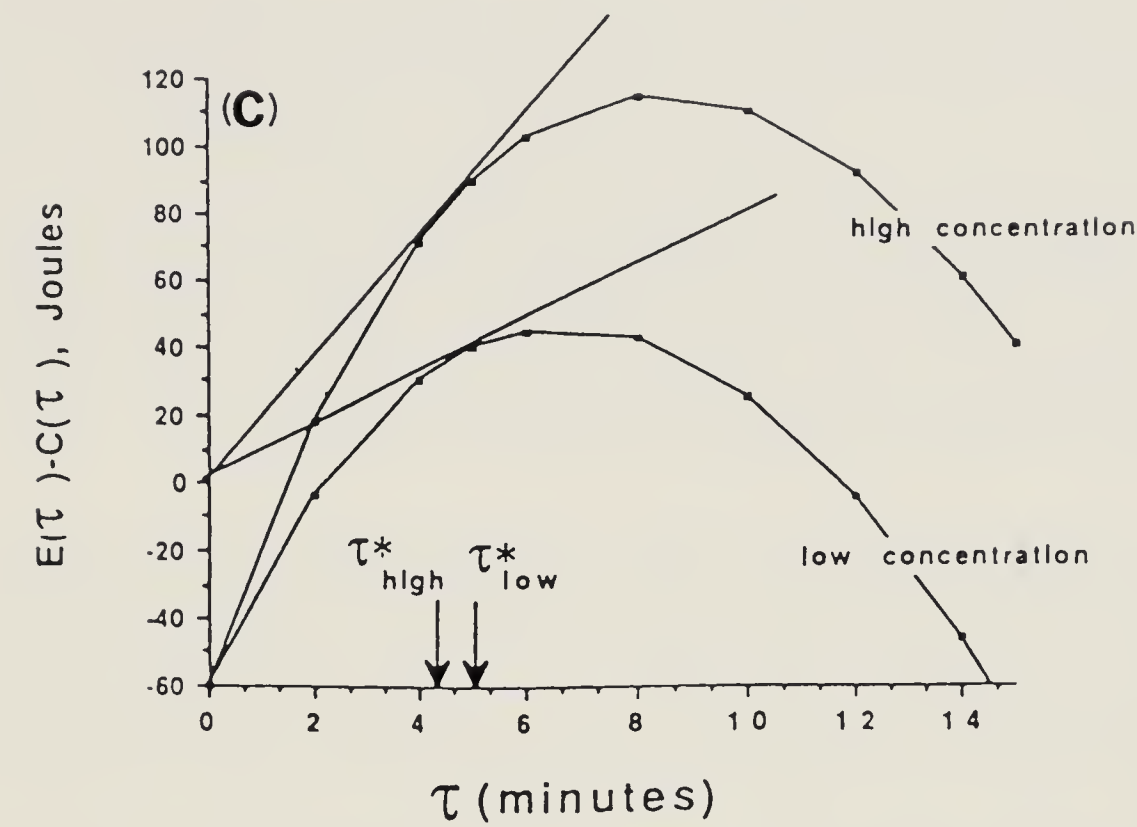


FIGURE 2c – Net energy gain (gain - cost = $E[t] - C[t]$) as a function of throughput time for the frugivore model, for two sugar concentrations (0.6 and 0.7 M). The solution for the optimal throughput time (t^*) is shown in each case (see text).

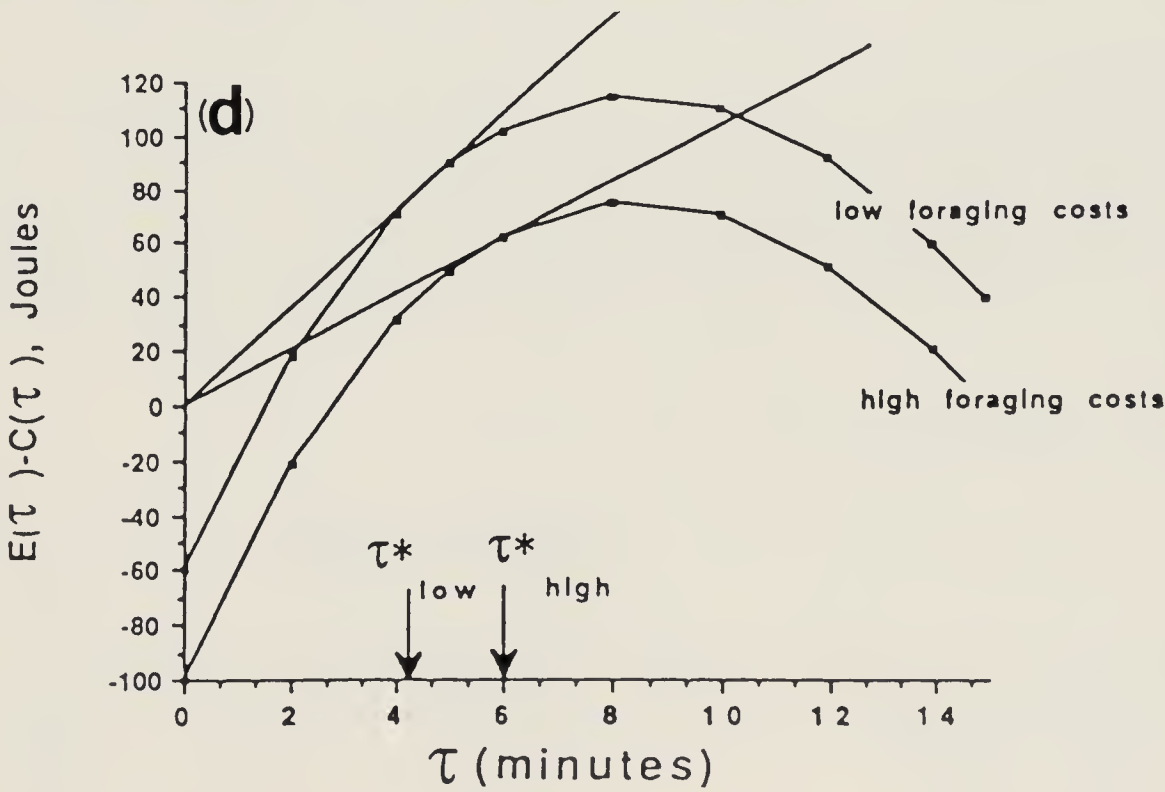


FIGURE 2d – Net energy gain (gain - cost = $E[t] - C[t]$) as a function of throughput time for the frugivore model, for two costs of filling the intestine. The solution for t is shown in each case (see text).

The biochemical differences reflected in the shapes of the two types of curve result in different predictions, explaining some past observations and suggesting some new lines of inquiry:

- (1) The frugivore model predicts digestive efficiencies < 1.0 for simple sugars and that t^* and digestive efficiency should decrease with increasing sugar concentration (Figure 2c). In other words, the optimization model predicts that, to maximize the rate of digestion, frugivores should digest fruit rapidly and be somewhat inefficient digesting even simple sugars. Frugivores do appear to have the shortest retention times of avian feeding types, and two frugivores that have been tested did show digestive efficiencies for glucose that were ≤ 0.92 (Martinez del Rio et al. 1989, Karasov & Levey 1990). Also, an analysis according to eq. 1 of balance trials with many frugivores indicated that they are inefficient digestors of soluble nutrients in food (Karasov 1990). Future studies should measure t and digestive efficiency as a function of sugar concentration.
- (2) In contrast, the hummingbird model predicts that energy-maximizing birds should exhibit digestive efficiencies close to 1.0 regardless of sugar concentration, and achieve this by increasing t^* as sugar concentration increases. (Graphically, the nearly linear incline of the net intake line is simply extended outward and the tangent moves outward.) The former prediction holds for two species of hummingbirds (Hainsworth 1974) and a honeyeater (Collins et al. 1980) and the latter prediction holds for two species of hummingbirds (Martinez del Rio in press).
- (3) In the frugivore model, but not the hummingbird model, increasing the cost of feeding (by increasing the time specific cost or total time) increases t^* and the digestibility of sugar (Figure 2d). This prediction has not yet been tested.

The frugivore-type model, wherein uptake has a substantial passive component, probably applies more generally to other kinds of feeders. In light of this, the expectation that birds will digest and absorb 100% of the nonrefractory fraction of food (assumption 2 of eq. 1 above) is probably an exaggeration. In fact, when digestion is viewed according to the optimization approach, the model described by eq. 1 is seen as too static. Birds should exhibit short term changes in gut throughput times and digestive efficiency of particular food fractions in response to variations in food characteristics and foraging costs. This is an important general prediction waiting to be tested.

TABLE 1 - Digestive parameters of House Wrens eating crickets

	Temperature to which birds were acclimated		P-value ⁴
	24 °C (n = 6)	-9 °C (n = 5)	
Body mass, g	10.4 ± 0.2	11.1 ± 0.1	0.021
Food intake ¹ , g dry mass/d	2.6 ± 0.1	5.3 ± 0.2	< 0.001
Metabolizability ¹ (MEC*)	0.72 ± 0.03	0.77 ± 0.03	0.004
Small intestine length, cm	9.4 ± 0.2	11.4 ± 0.2	< 0.001
Stomach dry mass, mg	65 ± 5	71 ± 5	0.07
Mean retention time ² , min	71 ± 13	65 ± 6	0.7
Intestinal uptake for L-proline ⁴ , umol/min,cm	266 ± 13	272 ± 23	0.83

values are means ± S.E.M.; ¹ measured in 3-d balance trials, MEC* = 1 - (energy ingested)/(energy egested); ² measured using polyethylene glycol as an inert marker, by method of Levey & Karasov (1990); ³ measured at 50 mM in vitro, by method of Karasov & Diamond (1983); ⁴ P-value for difference by *t*-test between the two groups of wrens.

The longer-term changes in gut characteristics of birds feeding on different diets (e.g. Miller 1975, Sibly 1981) or at different rates (e.g. during cold weather or reproduction; Drobney 1984) are also interpretable in light of the reactor models (Sibly 1981), as this final example illustrates.

Digestive adaptation by insectivorous House Wrens

Changes in gut structure and function that may permit large increases in food intake and digestion were studied in House Wrens (Dykstra & Karasov 1990). Birds acclimated to -9°C (the lowest temperature at which they could maintain body mass constant) had food intake rates much higher than birds at 24°C and had slightly higher assimilation efficiencies (Table 1). What changes in the gut permitted a doubling of intake and hence digestion rate with an apparent increase in digestive efficiency?

House Wrens probably have guts that approximate a stirred tank reactor (the stomach) coupled with a plug flow reactor (the small intestine) (Penry & Jumars 1986). Digesta retention time in each region is the quotient of capacity and flow rate. Total retention time in the gut (t_{tot}) is the sum of retention time in the stomach ($t_1 = V_1/v_o$) and retention time in the small intestine ($t_2 = V_2/v_o$), where V_1 is the capacity (in g) of each region, and v_o is the mass flow rate (g/d) through both regions. Within the small intestine the digestive variables are further related to each other as follows:

$$t_2 = V_2 / V_o = C_{ao} (X_a / -r_a) \quad (2)$$

where C_{ao} is the energy content of the cricket diet (kJ/g), X_a is digestibility of the energy, and $-r_a$ is the rate of reaction (joules that disappear per g digesta per unit time).

Birds acclimated to -9 °C had food intake rates (v_o') 105% greater than birds at 24 °C (i.e., $v_o' > v_o$) and small intestine lengths and hence volumes (V_2') 22% greater (i.e., $V_2' > V_2$) (Table 1). Total throughput times (t_{tot} , measured with inert markers) were not significantly different (i.e., $t_{\text{tot}} = t_{\text{tot}}$) and stomach volumes (measured as mass) were not significantly different ($V_1' = V_1$) (Table 1). Since

$$[t_{\text{tot}} = V_1 / V_o + V_2 / V_o] = [t_{\text{tot}} = V_1' / V_o' + V_2' / V_o'] \quad (3)$$

it follows that $V_2 / v_o < V_2' / v_o'$, i.e., that throughput time in the small intestine was longer in birds acclimated to -9 °C. If throughput time in the absorptive region determines extent of digestion/absorption, i.e. $X_a = t r_a / C_{ao}$, then X_a should be greater in birds acclimated to -9 °C, assuming that reaction rate ($-r_a$) was not altered. This assumption may be correct because the absorption rate per unit length intestine for the amino acid L-proline was not significantly altered (Table 1). Thus, the model offers an explanation for how intake rate could be increased in concert with an increase in digestive efficiency.

Using the simple model (equations 2 and 3) to guide data collection and analysis, we conclude that (1) a primary gut adjustment to permit increased food intake is an increase in small intestine volume and absorptive surface area (via increase in length), with no significant change in stomach volume, (2) the increased food intake is achieved with no change in total gut retention time by decreasing the retention time of digesta in the stomach and increasing it in the small intestine, (3) the increased retention time in the absorptive region permits greater digestive efficiency, with the

result that the rate of metabolizable energy intake (the product of intake and digestive efficiency) is increased >150%.

As these examples illustrate, the modeling approaches offer powerful conceptual frameworks for integrating digestive processes at the chemical, cellular, and organ level to those of the whole animal in an ecological context. They offer new opportunities for research in avian nutritional ecology.

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THE USE OF NUTRIENT RESERVES BY BREEDING WATERFOWL

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ABSTRACT. We reviewed use of nutrient reserves (lipid, protein, mineral) during egg production by female geese (3 species) and female ducks (13 species). All species, except White-winged Scoter, used lipid reserves. Use of protein reserves occurred only in geese, eiders, and herbivorous duck species; two carnivorous duck species stored protein during egg production. Use of mineral reserves occurs primarily in Arctic-nesting geese, perhaps because most temperate-nesting waterfowl have ready access to calcium via molluscs. Our review suggests that use of lipid stores is an evolved mechanism whereby lipids can be supplied to ovarian follicles at a high rate. A high rate of protein deposition is facilitated in most duck species via use of temperate wetlands that support high densities of invertebrates; species that predictably have difficulty obtaining sufficient exogenous animal protein, e.g. herbivores, use endogenous reserves. To further understand the importance of nutrient reserves to breeding waterfowl, data are needed from species inhabiting less productive habitats, e.g. boreal forests, and from species laying <1 egg per day. Intraspecific studies done in different habitats may elucidate the role of food abundance as a mediating influence on nutrient reserve use.

Keywords: Breeding waterfowl, lipid reserves, protein reserves, mineral reserves, food habits, egg production.

INTRODUCTION

Lack (1967) hypothesized that average clutch sizes of waterfowl species had evolved in relation to the average amounts of food available to laying females. This hypothesis has come to be called the "Egg Production Hypothesis" (e.g. Rohwer 1986) and has stimulated much research in the intervening 23 years. Interestingly, however, little of that work has actually involved studying *food* availability to laying females (but see Bengtson 1971). Rather, most work has focused on the use of body reserves (lipid, protein, and mineral; termed nutrient reserves by Ankney 1974) by laying females. Logistical problems in studying food availability are partly responsible for the emphasis on nutrient reserves. Perhaps a more important influence, however, was Ryder's (1970) modification of Lack's hypothesis to explain the evolution of clutch size in Arctic-nesting geese.

Ryder (1970) assumed that Arctic-nesting geese are independent of the food supply at the time and place of egg laying. Thus, he postulated that clutch size in these species had evolved in relation to the amount of energy reserves that females accumulate before arriving on the breeding grounds. Subsequent studies of use of reserves by breeding geese (Ankney 1974, Ankney & MacInnes 1978, Raveling 1979, Ankney 1984) supported Ryder's hypothesis.

Perhaps stimulated by the Arctic goose research, others investigated the use of nutrient reserves by temperate-nesting ducks. Korschgen (1977) found that use of nutrient reserves by Common Eiders (see Table 1 for scientific names) in Maine was remarkably similar to that reported for Arctic geese. Drobney (1980) and Krapu (1981)

reported that female Wood Ducks and Mallards, respectively, used large amounts of lipid reserves during laying. However, unlike investigators working on geese and eiders, who interpreted such use as a direct commitment to ova, Drobney and Krapu independently hypothesized that use of lipid reserves by ducks was an adaptation enabling them to forage for protein-rich but relatively scarce invertebrates. It was further hypothesized that a females's ability to acquire protein limits her clutch size (since termed the "Protein Limitation Hypothesis" by Ankney & Afton 1988).

Ankney & Afton (1988) noted that waterfowl eggs contain approximately equal amounts of lipid and protein. They argued, therefore, that (1) the protein limitation hypothesis overemphasized the importance of protein, (2) if female ducks normally encountered protein shortages, they would store and use protein reserves, as do Arctic geese, and (3) protein is easier to obtain than lipid in the productive wetlands used by temperate-nesting ducks and thus the size of a female's lipid reserves is more likely to limit clutch size than is rate of protein ingestion (since termed the Lipid Limitation Hypothesis by Afton & Ankney 1991).

In this paper we review use of nutrient reserves during egg laying by female geese and ducks. We discuss our findings as they relate to species specific food habits, use the data to evaluate the three aforementioned hypotheses, and suggest areas for future research.

DATA AND METHODS

The data are solely from North American studies because we are unaware of data gathered elsewhere that are appropriate to our goals. We omitted studies that only analysed use of lipid reserves, but included several studies that did not consider mineral reserves. Where two or more studies were available for a particular species we omitted those with the smallest sample size or those that had not employed regression techniques to analyse use of reserves during egg production.

As argued by Alisauskas & Ankney (1985, 1991) the following regression model is a powerful technique for analysing use of reserves during egg laying:

$$\text{Nutrient Reserve} = a + b \text{ R-Nutrient}$$

where Nutrient Reserve is somatic lipid, protein, or mineral of each female and R-Nutrient is the amount of lipid, protein, or mineral that each female has committed to reproductive tissue i.e. oviduct, developing follicles, and eggs (see Alisauskas & Ankney 1985 for a description of how R-Nutrients are calculated). So, we present data on use of nutrient reserves in two ways. First, we summarized the results from all studies using "+", "0", "-" to indicate a significant increase, no change, or a significant decrease, respectively, in size of each reserve during egg production. Second, for those studies that had employed regression analysis, or those where appropriate data were available from the author(s), we show slopes of the regressions.

We categorized general diets of waterfowl during the nonbreeding season (summarized from Bellrose 1976) as: *Herbivore* – diet primarily non-seed parts of plants; *Granivore* – diet primarily seeds; *Carnivore* – diet primarily animal matter. Food habits for birds during egg production, unless noted otherwise, came from the same

studies that reported use of nutrient reserves; herein we report percent animal matter in diets of these birds.

We followed Bellrose (1976) in use of common and scientific names.

RESULTS

We were able to find data for three goose species (including two subspecies of Canada Geese) and 13 duck species (Table 1). There is a general relationship, with some clear exceptions, between nonbreeding diets of waterfowl and their proclivity to consume animal matter during egg laying: most herbivores eat relatively little animal matter during egg-laying whereas carnivores rely heavily on such foods. For example, within the genus *Anas*, diets of two herbivorous species average 50% animal matter during laying, but the diet of the one carnivorous species is >90% animal matter. Averaging all species within groups, we found that animal matter, as a percent of diet during egg laying, equals 39% for herbivores, 78% for granivores, and 95% for carnivores.

With the exception of White-winged Scoters, females of all species used lipid reserves during egg laying (Table 1). Use of protein reserves, however, was less ubiquitous but occurred in all of the geese and three herbivorous, one granivorous, and 1 carnivorous duck species; two carnivorous duck species stored protein during egg laying. Data about use of mineral reserves were available for only 13 species and suggest that such use occurred primarily in geese, but was also noted for one herbivorous and one carnivorous duck species.

Because we were interested in an index of nutrient reserve use among species, we made the simplifying assumption that conversion of nutrient reserves to egg nutrients is 100% efficient. Given this assumption, the slope of the regression of nutrient reserves on nutrients committed to reproduction is an estimate of the proportion of egg nutrients that are derived from nutrient reserves (see Alisauskas & Ankney 1985, 1991). Thus, of the nine duck species for which data are available, lipid reserves supply from about 50% to about 100% of lipids deposited in eggs for eight species (Table 2). The change in lipid reserves during egg production by American Wigeon is non-linear; lipid reserves decline during the first half of egg production, but increase during the second half (see Alisauskas & Ankney 1991). The rate of use of lipid reserves during egg laying appears more related to body mass than to diet; the greatest use of lipid reserves occurs in females of the heaviest species (Mallard, Canvasback, Table 2). Overall, the correlation between body mass and slope of lipid use is -0.82 ($df=6$, $P<0.05$).

Females of the two *least* carnivorous species during egg laying use protein reserves (Table 2). Female Ring-necked Ducks show a non-linear relation between protein reserves and protein committed to eggs as reserves decline during peak protein allocation to eggs and increase thereafter (Alisauskas et al. 1990). Protein reserves of two highly carnivorous species increase with increased allocation of protein to eggs. But, anomalously, use of protein reserves could account for 13% of protein committed to egg production in Ruddy Ducks, the most carnivorous species during egg laying.

TABLE 1 - Use of nutrient reserves (“+” = increase, 0 = no change, “-” = decrease, “-/+” = decrease and then increase, and ? = no data) by egg-laying waterfowl in relation to diet. Note: Species are grouped by diet during the non-breeding season and not by taxonomy.

Non-breeding Species ^a Diet	Percent Animal Matter in diet during egg laying	Change in Reserves		
		Lipid	Protein	Mineral
HERBIVORE				
1. Giant Canada Goose	0%	-	-	?
2. Cackling Canada Goose	0%	-	-	-
3. Atlantic Brant	0%	-	-	-
4. Lesser Snow Goose	0%	-	-	-
5. American Wigeon	41%	-/+	-	?
6. Gadwall	57%	-	-	0
7. Canvasback	78%	-	0	0
8. Redhead	77%	-	0	?
9. Ruddy Duck	100%	-	-	-
GRANIVORE				
10. Mallard	72%	-	0	0
11. Blue-winged Teal	99%	-	0	0
12. Ring-necked Duck	63%	-	-/+	0
13. Wood Duck	76%	-	0	0
CARNIVORE				
14. Northern Shoveler	93%	-	+	0
15. Lesser Scaup	85%	-	+	
16. Common Eider	100%	-	-	?
17. White-winged Scoter	100%	0	0	0

^a Scientific names and references are given in the same numerical order as used in the table; if two references are given, the first refers to data about reserves and the second to data about diet during egg laying, whereas one reference indicates that all data were from the same study. 1. *Branta canadensis maxima*; Mainguy & Thomas 1985; 2. *Branta canadensis minima*; Raveling 1979; 3. *Branta bernicla hrota*; Ankney 1984; 4. *Anser c. caerulescens*; Ankney & MacInnes 1978; 5. *Anas americana*; Wishart 1983; 6. *Anas strepera*; Ankney & Alisauskas, unpubl. data; 7. *Aythya valisineria*; Barzen & Serie, 1990; Noyes & Jarvis 1985; 8. *Aythya americana*; Noyes & Jarvis 1985; 9. *Oxyura jamaicensis*; Alisauskas & Ankney, unpubl. data; Tome 1981; 10. *Anas platyrhynchos*; Krapu 1981; Swanson et al. 1985; 11. *Anas discors*; Rohwer 1986; Swanson & Meyer 1977; 12. *Aythya collaris*; Alisauskas et al. 1990; Hohman 1985; 13. *Aix sponsa*; Drobney 1980; Drobney & Frederickson 1979; 14. *Anas clypeata*; Ankney & Afton 1988; 15. *Aythya affinis*; Afton & Ankney, unpubl. data; Afton & Hier, unpubl. data; 16. *Somateria mollissima*; Korschgen 1977; Hicklin, unpubl. data; 17. *Melanitta fusca deglandi*; Dobush 1986; Brown & Frederickson 1986.

DISCUSSION

As noted by the original investigators, the heavy reliance on nutrient reserves by egg-laying geese and Common Eiders is predictable as these birds feed little, or not at all, then. Arctic-nesting geese generally have little food available during egg laying, whereas Common Eiders (and perhaps Giant Canada Geese) feed little so as to protect against nest predation. Clearly, this is a strategy that these birds can adopt because of their body size. That is they are sufficiently large to be able to store enough reserves to lay eggs without exogenous nutrients.

TABLE 2 - Slopes and coefficients of determination from linear regressions relating fat and protein reserves to fat and protein committed to reproduction by female ducks. Species are listed in order from lowest to highest percent animal matter in diet during egg laying (see Table 1).

Species	Body Mass ^a	Slope			
		Lipid	r ²	Protein	r ²
American Wigeon	710	b	b	-0.44	0.23
Gadwall	650	-0.85	0.39	-0.16	0.23
Ring-necked Duck	660	-0.48	0.36	b	b
Mallard	1000	-1.04	0.47	0	
Canvasback	1360	-1.06	0.60	0	
Lesser Scaup	650	-0.50	0.23	+0.25	0.27
Northern Shoveler	550	-0.72	0.27	+0.10	0.11
Blue-winged Teal	355	-0.45	0.24	0	
Ruddy Duck	510	-0.61	0.22	-0.13	0.14

^a From Alisauskas & Ankney (1991: Table 2)
b = only non-linear regression significant; see text.

Overall, our review shows that use of lipid reserves is a common feature of waterfowl reproduction. This is likely an evolved mechanism whereby lipids can be supplied to ovarian follicles at a high rate. Use of protein reserves, however, although common in geese (see above), is found in less than half of the duck species. We interpret this as evidence that most species do not normally encounter protein deficiencies during egg laying. Thus, we conclude that the data in Tables 1 and 2 are more consistent with the lipid limitation hypothesis than with the protein limitation hypothesis. Duck species that predictably should have the most difficulty obtaining invertebrates during egg laying, i.e. those that are herbivores when not breeding, apparently do so, with the exception of Ruddy Ducks. Those species, however, do not utilize lipids at a greater rate than do species that consume larger proportions of animal matter during egg laying. Rather, as predicted by Ankney & Afton (1988), species such as American Wigeon, Gadwalls, Ruddy Ducks, and Ring-necked Ducks utilize protein reserves. Furthermore, two of the most carnivorous species, Northern Shovelers and Lesser Scaup, actually store protein during egg laying and yet their use of lipid reserves is not notably low.

Ruddy Ducks and White-winged Scoters are two obvious exceptions to the general pattern described above. The scoters, which are highly carnivorous at all times, neither use nor deposit reserves during egg production (Table 1). These birds, however, have a laying rate of only 0.7 eggs per day (Brown 1981). This, coupled with their relatively large body size and therefore proportionately small eggs, apparently enables them to obtain sufficient exogenous nutrients for egg production. Ruddy Ducks lay an egg per day (Alisauskas & Ankney, unpubl. data) and their eggs are proportionately the largest of all North American waterfowl. Thus, although their diet during egg laying is very high in animal matter (Table 1), they are unable to meet their high nutrient demands, especially for protein, exogenously.

Use of mineral reserves apparently is uncommon among temperate-nesting ducks, probably because these birds have ready access to calcium via molluscs. Use of min-

eral reserves by Ruddy Ducks is likely due to their producing exceptionally large eggs; use by Lesser Scaup may relate to their inexplicably low consumption of molluscs (Afton & Hier, unpubl. ms.).

Clearly, several variables and their interactions are important in understanding the use of nutrient reserves by breeding waterfowl: body size, egg size, food habits during the non-breeding season, egg-laying rate, and food availability during laying. Of the 13 duck species for which data about use of nutrient reserves are available (Table 1), all, except White-winged Scoter and Common Eider, lay an egg per day. Further, all, except for Common Eiders, were studied in relatively productive habitats, i.e. prairie wetlands or deciduous and mixed forest wetlands (Wood Duck and Ring-necked Duck). Thus, to more fully understand the importance of nutrient reserves, data are needed from species nesting in less productive habitats, such as the boreal forest, and from species with laying rates of <1 egg per day, e.g. *Bucephala* spp. and *Melanitta* spp. Also, intraspecific studies that compare nutrient reserve use in different habitats may help elucidate the role of food abundance as a mediating influence on use of nutrient reserves.

Finally, before we can fully test Lack's (1967) egg production hypothesis, we need data about all of the "food" available to laying females, i.e. exogenous as well as endogenous sources. However, as pointed out by Ankney & Afton (1988) it is presently technologically impossible to simultaneously monitor nutrient reserves, food resources, and ingestion rates of individual females.

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LONG-TERM FASTING IN PENGUINS AS A NUTRITIONAL ADAPTATION TO BREED OR MOLT

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ABSTRACT. The life of penguins is characterized by cycles of feeding sojourns at sea and long periods of fasting on land to breed and to molt. Most quantitative information on the utilization of energy reserves throughout fasting has been obtained from Emperor Penguins. It allows comprehension of the energy strategy of these birds, a strategy where long-term fasting is the best way for minimizing energy expenditure. However, it also enables a better understanding of how birds in general may be efficient in accumulating energy reserves and in minimizing their rate of utilization, to extend fasting. It moreover gives indications on why birds may safely deplete their body fuel reserves, i.e. how refeeding is triggered before a critical depletion in body fuels has been reached. This is a first step in understanding the relationship between the level of depletion of body fuels in a bird and the possible failure in important activities such as breeding.

Keywords: Anorexia, starvation, energy reserves, lipids and proteins, induction of refeeding.

INTRODUCTION

Sea-birds alternate between feeding at sea to accumulate body fuel reserves and relying on these reserves while staying ashore to breed. This cycling between feeding and fasting is at its most extreme stage in penguins, particularly the males of the two largest species, the King and the Emperor. The male King Penguin assumes the first shift of the incubation, which lasts for 35-40 days (for review, see Cherel et al. 1988c). The male Emperor Penguin, after the time for the formation of the couple, takes over the whole task of the incubation (about 65 days). This makes a fast lasting for 90-120 days during the severe Antarctic winter. This long fast is not the only one, as both mates of Emperor Penguins thereafter alternate in feeding at sea and fasting. Each of them fasts when walking on sea-ice to the sea and when coming back with food in its stomach for the chick. At the end of the breeding cycle, both of them also fast in order to molt. Overall, male Emperor Penguins fast for half the year (see Groscolas 1990). Fasting for long periods is not exclusive to the adults. After hatching, King Penguin chicks grow rapidly during the summer, then endure a long period of fasting during the following winter. For the 4-6 winter months, they may receive on average one meal per month or even none at all (Cherel et al. 1987).

Considering the durations of their fasts, King and Emperor Penguins are certainly professional fasters. Particularly the Emperor, they live in extreme environments. It could therefore be questioned whether the way they manage to cope with energy constraints can be extrapolated to other birds. Allometric considerations should then be kept in mind. Emperor and King Penguins are very large birds. The relationship between availability of body fuel reserves and metabolic rate per unit body mass must be considered. Accordingly, an Emperor Penguin at the beginning of its four-month-long winter fast is not in a more extreme situation than a very small passerine bird facing

a single cold winter night (see Reinertsen 1989; for review, Le Maho 1991). Simply, the time scale for these two birds is completely different.

There are some obvious logistical difficulties in studying penguins in the field. However, because of the extended time scale changes in their energy reserves, their large size and the fact that they are easy to approach and find again, it is easier to get quantitative data for their metabolic response to fasting than in very small birds. Among penguins, most detailed information on the energy metabolism and utilization of body fuels during prolonged fasting pertains to Emperor Penguins.

TABLE 1 – Total energy cost of the long winter fast of the male Emperor Penguin, i.e. including the cost of the return trip on sea-ice between the open sea and the breeding colony. Comparison with the total energy cost of theoretical shorter successive fasts, including cost of return trips and of sojourns at sea.

Long fast: Calculation of cost of locomotion based on Dewasmes et al. 1980, speed of walking being assumed to be 1.4 km.h⁻¹; body fuel utilization based on Groscolas, 1988.

Shorter fasts: Mean body mass assumed to be 32 kg; cost of locomotion and resting metabolic rate based on Dewasmes et al. 1980; metabolic rate at sea estimated to be 2.8 fold resting metabolic rate, based on Kooyman et al. 1982.

	One single long fast	Several shorter successive fasts
Duration of fasting in the colony	1 x 105 days	4 x 15 days
Number of return trips	1	4
Total distance of walking on sea-ice (a single trip = 100 km)	2 x 100 km	8 x 100 km
Total duration of trips (a single trip = 3 days)	2 x 3 days	8 x 3 days
Total duration of intermediate sojourns at sea	0 day	3 x 9 days
Total energy cost	544 000 kJ	922 000 kJ

REQUIREMENTS FOR SUCCESS IN BREEDING OR MOLTING

Both Emperor and King Penguins can feed at long distances from their colonies. The King Penguin is a pelagic feeder (for review, see Wilson et al. 1989). The Emperor Penguin usually has to walk long distances on sea-ice to reach the open sea, 120 km or maybe more (review in Dewasmes et al. 1980). Moreover, due to waddling, the cost of walking per unit distance is very high (Pinshow et al. 1977). The Emperor Penguin is the only species where cost of transport has been studied in relation to change in

body mass. At 39 kg, which is the mean body mass of the males at the beginning of their winter fast, the metabolic rate for walking at the limited speed of $1.4 \text{ km} \cdot \text{h}^{-1}$ is 340 W. This is as much as 4.5 times the resting metabolic rate (RMR). The walking metabolic rate is 220 W at 23 kg, that is, 3.5 times the RMR (Dewasmes et al. 1980). The energy expenditure for a return 200 km walk may still amount for as much as 15% of the energy reserves (Pinshow et al. 1976). The strategy of Emperor Penguins, where the male fasts for months while incubating the egg and departs from the colony at the much lower body mass of about 23 kg (Groscolas 1982), could a priori appear surprising. In fact, this strategy saves the maximum amount of energy in an environment where no food is readily available. It is more efficient for one of the two mates to undergo an extended fast than for the couple to go back and forth to feed between shorter fasts at a time when the distance to the sea is further. The total energy cost for each mate, were it to alternate 15-day-long fasts in the colony and similar duration periods for treks on sea-ice added to feeding sojourns at sea, would be about twice larger than that of the male (see Table 1). We therefore end with an observation similar to that for the duration of torpor bouts in hibernators, where the energy saving is greater with fewer arousals, due to the high cost of rewarming up.

On the other way, during the rearing of Emperor Penguin chicks, when the distance of sea-ice is smaller, the fasts of the adults may be shorter and the trips more frequent. Due to the decreased requirement in energy reserves for the shorter fast and the smaller trip, prefasting energy storage may be smaller. The body mass is then lower, which accordingly reduces the cost of locomotion associated with the more frequent trips due to the increasing food demand of the growing chicks. Indeed, the body mass of both mates is around 25 kg at the time they make shorter and shorter sojourns in the colony to feed their chick, while the open sea is getting closer and closer (Prévost 1961). This means lipid reserves reduced to 3 kg (Robin et al. 1988).

Another requirement to take into account, for the success of breeding, is the always possible delay in the relief of the fasting bird by its mate. This relief is essential at the time there is an egg or a chick that still requires thermal protection. An important consequence, therefore, is that there should be a larger safety margin in energy reserves at the end of the longest fast, i.e. for the male towards the end of the incubation, in order to anticipate an always possible delay in the relief. In contrast, later on, the fasts of both mates in the breeding colony may be only adjusted to the small time that is requested for delivering the stomach content to the chick. The fasts of both mates of Emperor Penguins then become independent.

The requirements for the fast that is associated with the molt are particular, because reserves must be in excess to the energy storage necessary for a breeding fast of same duration. This is due to the additional energy requirements associated with both reduced thermal insulation subsequent to the loss of old feathers and fuel supply for building of the new plumage.

FUEL STORAGE AS A PREREQUISITE TO A PROLONGED FAST

The duration of fasting that can be sustained depends not only on the initial amount of body fuels that has been accumulated, but also on the kinds of fuels that are available. For penguins, as for other animals (Blem 1990), most of the energy is stored as

fat. In a male Emperor Penguin, at the beginning of the long winter fast, almost 80 % of the energy is stored as fat. Proteins account for 20 % of the total body energy content and glycogen for 0.3-0.5 % (Groscolas 1982).

Storing most of energy as fat has two key advantages. First, fat is the form of tissue that has the highest caloric content. This is not only because lipids yield twice as much energy as protein per unit body mass. Lipids may also be stored with very little water. In birds, triglycerides account for up to 93 % of adipose tissue mass. In contrast, energy storage of 1 g protein or glycogen requires the accumulation of 3 to 4 g of intracellular water. As a result, the caloric capacity of fat reaches 38 kJ.g^{-1} in birds (Johnston 1970), whereas the caloric capacity of skeletal muscle – the main protein reservoir – is only about 4 kJ.g^{-1} .

Second, almost all fat reserves may be used up in a fast. This contrasts with body proteins; when only about half of them have been depleted death occurs (for rev. see Le Maho et al. 1988). Thus, following this rule, only 10 % of the total prefasting energy reserves of an Emperor Penguin may be safely depleted as proteins.

The prefasting fatness, i.e. mass of lipids expressed as percentage of body mass, of an Emperor Penguin is 30% (Groscolas 1982). This value is larger than for other birds that face nocturnal or breeding fasts. It is slightly smaller than the 30-40 % value found in some small birds before a premigratory fast (Cherel et al. 1988b). In fact, based on adipose tissue cellularity at the onset of fasting, Emperor Penguins could theoretically increase their prefasting fat reserves by more than tenfold (Groscolas 1990). Why then do not Emperor Penguins reach even a higher adiposity before their long winter fast? Storing more fat would give them more leeway in the fast in relation to success in breeding.

One first answer may be again the serious limitation due to the energy cost of locomotion in Emperor Penguins. A second point to consider is an interaction between the availability of lipid and protein loss during a prolonged fast. Due to this interaction, we will see that at some stage there is no further physiological advantage of adding more lipid stores to sustain a more prolonged fast.

LIPID RESERVES INTERACT WITH UTILIZATION OF BODY PROTEINS DURING FASTING

Investigations on laboratory rats of various degrees of fatness, which were subjected to experimental fasts, are in agreement with the idea that prefasting lipid reserves determine protein loss during a prolonged fast (for review, see Belkhou et al. 1990). The changes in energy reserves of Emperor Penguins during their seasonal spontaneous fasts fit with such an interaction between lipids and proteins (Robin et al. 1988), indicating that it corresponds to basic biochemical rules.

The proportion of the energy which is derived from proteins is set at a steady state value, which appears to be dependent upon initial lipid stores. More initial fat is associated with a higher effectiveness in protein sparing, i.e. in the reduction of this proportion. For example, body proteins account for 14-17% of total energy expenditure in non-obese man and lean rat, while this proportion is reduced to about 4-5% in

obese man and rat (see Belkhou et al. 1990, 1991). A consequence is then an extension of the duration of fasting that can be sustained, as the time when cumulative protein loss will finally reach a lethal level is delayed. Accordingly, the 4-month winter fast of male Emperor Penguins, when compared with the shorter 2- to 3-week fasts that occur in spring at the time both mates alternate in feeding their chick, might be not only explained by the about three times larger availability in initial lipid reserves (11 v 3 kg) but also by a subsequent higher effectiveness in protein sparing (Robin et al. 1988).

There is, however, a limitation in the possible increase in the effectiveness in protein sparing during fasting, as a consequence of larger initial lipid reserves. The lower, i.e. obligatory, proportion of the energy that derives from proteins is of 3-5 %, as found in very obese humans or rats, and in other fatty animals like domestic geese and seals (for ref., see Belkhou et al. 1990). Since the proportion of the energy that is derived from proteins during the 4-month winter fast of male Emperor Penguins is 4 %, it means that their prefasting lipid reserves are already sufficient to reach the maximum possible effectiveness in protein sparing (Robin et al. 1988). In fact, this maximum effectiveness is already reached and maintained for a little more than a month in the female Emperor Penguin during its winter fast, although its prefasting body mass is about 30 kg (adiposity of 20%), i.e. a body mass 9 kg lower than that of the male (Groscolas, unpublished data). The duration of the fast of the female Emperor Penguin, which includes the period for formation of the couple and laying, is of 40 days (Prévost 1961).

HOW A CRITICAL DEPLETION IN BODY FUELS CAN BE ANTICIPATED

The prolonging of the metabolic situation where a steady low proportion of the energy is derived from proteins appears to be limited by lipid availability, therefore constituting another interaction between lipids and proteins. When lipid reserves reach a "critical" level, the proportion of the energy derived from proteins increases, whereas energy originating from lipids decreases. As first shown in Emperor Penguins (Robin et al. 1988), this late increase in protein utilization may occur in an animal spontaneously fasting under natural conditions; moreover, the effect is reversible and is triggered even though significant lipid reserves are still available. The coincidence of this rise and of a "signal" triggering refeeding (Groscolas 1986, Robin et al. 1987, Le Maho et al. 1988), therefore anticipates a critical depletion in body fuels.

What could be the physiological consequences of a disrupted prefasting balance in lipids and proteins due to excessive fat stores? Let us assume initial fatness is already large enough for reaching maximum effectiveness in protein sparing. The consequence of an even larger initial fatness is a further delay in the critical level in lipid fuels. The rise in protein utilization accordingly occurs later, which therefore extends the duration of protein sparing. However, there is a limitation to this possible extension due to larger initial fatness. Indeed, this fatness may be as large as it extends so much the delay in the rise in protein utilization that this rise cannot not be triggered before a lethal cumulative protein loss has been reached. This may then explain why superobese humans (adiposity up to 60 %) can die during prolonged therapeutic fasting without showing a rise in protein utilization (Le Maho et al. 1988). We have seen that refeeding of Emperor Penguins is triggered in association with the increase in

protein utilization. A lack of this rise therefore presumably means that critical depletion in body fuels cannot be anticipated. To sum up, in a wild bird, prefasting fat accumulation before a long fast has to be large in order to give some leeway, but not as far as cost of transport is excessive or the initial balance between lipids and proteins could be disrupted.

THE REQUIREMENTS OF FASTING DURING A MOLT

Molting for penguins is a much more severe process than for other birds. All feathers are replaced simultaneously and quickly, within a few weeks (Le Maho et al. 1976, Groscolas 1978, Brown 1986). Accordingly, as shown by a temporarily larger rate of body mass loss, the utilization of body fuels is more rapid than during a breeding fast. Once the new feathers are grown, the rate of body mass approaches that of a non-fasting bird (Bougaeff 1975, Le Maho et al. 1976, Groscolas 1978, Cherel et al. 1988a). The more rapid utilization of body fuels may be attributed to a higher metabolic rate, associated with a larger heat loss when old feathers fall off, and to building the new plumage. Hyperthermia occurs during the molt (Groscolas 1978). Larger heat loss is shown by a higher lower critical ambient temperature: the molting Emperor Penguin already shivers at 0 °C while the breeding bird shivers at ambient temperatures between -8 and -13 °C (Le Maho et al. 1976).

The interesting question of the changes in fuel utilization and water loss during the molt of Emperor Penguins was first discussed by Groscolas (1978). Based on data on the rate of body mass loss and on the energetic equivalent of unit mass loss, the metabolic rate of a fasting Emperor Penguin when molting is twice that during breeding (Groscolas 1978, 1988). This doubling of metabolic rate is similar to that determined from oxygen consumption in Macaroni and Rockhopper Penguins (Brown 1985).

HOW DATA FOR PENGUINS COULD BE EXTRAPOLATED TO OTHER BIRDS

It has long been thought, since most of the energy of a fasting bird is derived from fat, that protein utilization may be neglected. For Emperor Penguins, this is clearly wrong. Due to the low caloric capacity of lean tissue, although as little as 4% of the energy is derived from proteins, it contributes to as much as 38% of body mass loss (Groscolas 1988). As mentioned above, protein depletion is also a limiting factor in survival during a long fast. Therefore, its cumulative loss has to be considered. However, can data from fasting Emperors be extrapolated to other birds?

We have already seen that the contribution of body protein to energy expenditure during long-term fasting is similar in Emperor Penguins and domestic geese. Both species reach maximum effectiveness in protein sparing and show similar pattern of changes in lipid and protein utilization throughout the course of fasting (Le Maho et al. 1981, Robin et al. 1988). This might appear surprising, when considering how different birds may be a – goose from a strain selected for fat liver and an Emperor Penguin. It has, moreover, to be pointed out that the fast of the Emperors is spontaneous compared with the experimental fast of the geese. However, there is a similar prefasting adiposity of up to 30% in an Emperor Penguin (Robin et al. 1988) and in

a goose (Le Maho et al. 1981), which again emphasizes the importance of common basic metabolic determinants in the response of fat birds to long-term fasting.

The metabolic response induced by an experimental fast in domestic geese may also reflect a naturally occurring phenomenon associated with breeding. Both males and females of domestic geese have an important reduction in body mass during breeding (Robin et al. 1987), indicating spontaneous reduction in food intake. Females of wild ducks and geese eat very little or nothing while they totally assume the task of the incubation. They may lose up to 40 % of the prefasting body mass (Ankney & MacInnes 1978, Akesson & Raveling 1981). Whereas most of the energy is derived from fat, muscles are also significantly used. Available data moreover suggest that the females prematurely leaving their nest before the chicks hatch have entered the metabolic situation of further rise in protein utilization (Aldrich & Raveling 1983, review in Cherel et al. 1987).

Moreover, the energy constraints due to availability of lipid and protein reserves and their interaction should not only be considered in long-term fasts associated with breeding. Migration is another comparable situation. The extremely high level of energy expenditure contrasts with the situation of hypometabolism that is associated with a long fast. However, from the point of view of the utilization of body fuels, even if the duration of the fast that coincides with the flight is short, the importance of the total energy expenditure makes it equivalent to a prolonged fast. A recent work provides detailed information on the utilization of body fuels in the Bar-tailed Godwit *Limosa lapponica* during spring migration. This information was obtained by comparing changes in nutrient reserves at two staging sites. Lipid and protein reserves contribute respectively to 89 and 11 % of energy expenditure, therefore corresponding to a rapid fast (Piersma & Jukema 1990). Thus, at least in this godwit, body proteins are also significantly used during migration. The effectiveness in protein sparing is lower than for breeding Emperor Penguins but it is similar to that of the fasting incubating Great-winged Petrel *Pterodroma macroptera* (Groscolas et al. 1991), a sea bird which is about the size of the godwit.

In all long fasts at a low level of energy expenditure, e.g. breeding, or shorter fasts with higher energy expenditure, e.g. migration or molt, and presumably starvation due to a cold wave, not only lipid but also protein availability and utilization should therefore be considered when assessing the energetic limitations for success or survival.

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NUTRITIONAL ASPECTS OF AVIAN MOLT

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ABSTRACT. Avian molt results in a net deposition of epidermal protein that can equal one-fourth or more of a bird's protein mass. The amino acid composition of epidermal proteins differs from the typical amino acid profile of most food proteins and other body proteins. Molting birds may minimize the mismatch between the required profile of amino acids and the available profiles and enhance the efficiency of body protein and amino acid metabolism by selective feeding, by cysteine storage in glutathione, and (or) by altering the dynamics of amino acid utilization. Alterations of whole-body protein metabolism during molt, either directly or indirectly linked to cysteine need, may explain why the caloric costs of molt far exceed the apparent costs of keratin synthesis. Periodicity of access to food, and hence daylength, influences amino acid metabolism, and in turn may cause per diem molt costs (amino acids and energy) to decrease with increasing latitude. (Supported by a grant [BSR 8905783] from the US National Science Foundation.)

Keywords: Molt, nutrition, protein metabolism, energetics, glutathione, White-crowned Sparrow, feeding behavior.

INTRODUCTION

The functions of avian plumage include flight, insulation, protection, and communication (for review, see Stettenheim 1976). The loss or untimely impairment of any of these functions may reduce the probability of survival or reproduction, i.e. reduce fitness. In general, two factors serve to avert such a consequence and to maintain the structural and functional integrity of the plumage. One of these is simply the durability and inert nature of the individual feathers. Feathers are composed mainly of keratins, a specialized family of proteins characterized by their insolubility in most common solvents and by their resistance to the actions of proteolytic enzymes (Fraser et al. 1972). In spite of their durability, however, feathers are inevitably abraded, faded, or lost because of daily wear-and-tear. Moreover, for plumage to function effectively in communication and protective coloration there must be some means of altering its appearance. The second factor that helps to maintain the structural and functional integrity of the plumage is the periodic replacement of some or all of it — the molt.

Molt is undeniably important in the life of birds, as illustrated by its ubiquitous occurrence in the Class Aves. Interspecific variants in the timing and patterns of molt (Stresemann & Stresemann 1966, King 1974, Chilgren 1975) presumably reflect the balance among multiple selective pressures. The allocation of time, energy, and nutrients to reproduction, molt, and migration and the adaptive coordination of these processes among themselves as well as with environmental seasonality undoubtedly requires some compromises. Natural selection can be expected to yield the most favorable compromise possible. Nevertheless, any resolution of competing demands may include periods of stringency, as illustrated by the occurrence of natural anorexias (Mrosovsky & Sherry 1981). The evolution of a periodic rather than

continuous molt in nearly all species of birds temporally concentrates the energy and nutrient requirements of feather synthesis and attendant processes and potentially exaggerates any impairment of the insulative and aerodynamic qualities of the plumage, since a greater number of feathers will be regenerated simultaneously. On the other hand, the periodic molt allows for fairly abrupt change in plumage pattern, minimizes interference between feather regeneration and reproduction or migration, and, when timed to occur before the coldest season, provides for maximum insulation when it is most needed.

The question arises as to whether or not the evolution of a periodic molt has entrained a period of stringency wherein the energy and nutrient demands of feather synthesis and attendant processes are so concentrated in time as to challenge the bird's ability to meet these demands potentially requiring diversion of time, incoming nutrients, and/or body reserves from other vital functions. The very limited information on both the energy requirements and nutrients requirements of molting birds as well as their physiological, behavioral, and ecological adjustments precludes an unequivocal response to this question. In the following discussion we have chosen to skirt any predictions about the likelihood that molt proceeds at the expense of other vital functions, and will instead focus on means by which molting birds may minimize any mismatch between nutrient requirements (including energy) and availability.

THE NUTRITIONAL COSTS OF MOLT

Composition of the product

The apparent, or minimum, energy and nutrient requirements of a productive process can be derived from a knowledge of the composition and rate of growth of the product. The actual requirements will also include energy and nutrients lost owing to inefficiency of absorbing, processing, and utilizing nutrients, as well as the metabolic cost (above the maintenance level) involved in establishing a permissive background for production. Avian molt mainly involves protein accretion in the form of feathers and other epidermal structures (Murphy & King 1986a, King & Murphy 1990). The feathers, and the sheaths that enclose them during their development, appear to be the principal products of molt (King & Murphy 1990) and amount to about 9 to 10% of body mass (Turcek 1966). Feathers and sheath contain more than 90% protein by dry mass with the remaining fraction including lipids, ash, pigments, and various chemical remnants of the keratinocyte (water comprises about 6 to 10% of total plumage mass; for review see Murphy & King 1982, 1986, King & Murphy 1987, Murphy et al. 1990).

The family of proteins (keratins) that compose the feathers and feather sheaths are similar, in composition, among species, but differ significantly from the typical amino acid profile of mixed proteins of foods or of most other body tissues (Murphy et al. 1990 and references cited therein). In general, feathers contain lower concentrations of the essential amino acids and a much higher concentration of cystine. Together, the sulfur amino acids (SAA, or methionine, cysteine, and cystine) are the first limiting amino acids in the production of keratins from body tissues (e.g. during an overnight fast) followed by two of the branched-chain amino acids, leucine and valine. The discrepancy between the contents of the branched-chain amino acids in feathers and mixed proteins of other tissues (ca. 1.5-fold), however, is much less than is typical of

the SAA (about 3.25-fold, and 7- to 8-fold if only cyst(e)ine is considered; Murphy et al. 1990). Similar relationships are apparent between the compositions of feathers and mixed proteins of foods, but consuming adequate amounts of food to meet energy needs generally supplies an excess of most of the essential amino acids, making direct comparisons of compositions more an exercise in estimating efficiency than in estimating nutritional limitations.

The foregoing analysis of the products of molt indicates that, although many nutrient requirements may increase slightly during molt to help create a permissive background (e. g. specific mineral cofactors), the major adjustments in nutrient requirements for feather synthesis involve an increased need for total protein, the SAA, and for energy to support feather synthesis. The actual increase in the per diem requirements for these nutrients will depend on the rate of molt and, perhaps, on the photoperiod (i. e. latitude) when molt ensues (see beyond).

Protein costs of molt

The dynamics of the requirement for protein during avian molt are poorly understood. From the little that is known, it appears that the additional protein required during molt is greater than that needed for keratin synthesis alone. In the White-crowned Sparrow *Zonotrichia leucophrys gambelii* (henceforth "Gambel's Sparrow"), a species that undergoes a relatively rapid molt, an average 42 mg of protein is deposited as feathers and sheath (ca. $0.92 \times [2.1 + 0.4]$, respectively) per day of their average 54-day molt. In midmolt, when feather replacement is most intense, these sparrows may deposit as much as 55 to 65 mg of keratin per day (estimated from Morton et al. 1969, Murphy & King 1984a, 1984b, 1986a). During midmolt, in thermoneutral conditions, Gambel's Sparrows consume as much as 2 g/day of food above maintenance requirement to obtain the added energy needed for molt. During the maintenance phase, also in thermoneutral conditions, the required protein concentration of the food is 7 to 8% of good quality protein such as whole egg, corn/soy, or supplemented casein in domestic chickens and sparrows (ca. 14.75 kJ/g ME: Leveille & Fisher 1960, Martin 1968, Murphy unpublished). Eating an additional 2 g/day of food containing 7-8% protein during midmolt should supply an additional 140 to 160 mg of protein per day — more than twice the estimated need for keratin synthesis. However, molting Gambel's Sparrows fed diets containing less than 10% of high-quality protein reduce the rate of molt and have lower body masses than sparrows fed higher concentrations of dietary protein (Murphy & King 1991, Murphy unpublished). The increase in the dietary protein requirement in Gambel's Sparrow, during molt, from about 7.5% to about 10% in nearly identical foods (semisynthetic diets), suggests that additional protein is needed during molt to meet demands above maintenance and beyond keratin synthesis. The added protein requirement in molting Gambel's Sparrows could not be explained by SAA need since 8% protein in the winter maintenance diet would supply sufficient SAA to support molt (ca. 4% of the diet, cf. Murphy & King 1984b, 1984c). The picture emerging of the changes in the protein requirement during molt resembles that of energy requirements.

Energy costs of molt

In a review of the caloric costs of avian molt, King (1981) estimated that the mean (\pm SE) cost of molt in a small passerine was about 469 ± 34 kJ/g of plumage synthesized. Subsequently, we measured the energetic cost (as metabolized energy) of plumage production in Gambel's Sparrows as about 310 kJ/g dry mass of plumage

synthesized. Recently, Masman (1986) reported an estimated 109 kJ/g dry mass of plumage synthesized by European Kestrels *Falco tinnunculus*. Despite the wide range in the estimates of the cost of plumage synthesis it is apparent the energetic efficiency of molt is perplexingly low. Dividing the heat of combustion of feathers (22 kJ/g dry mass: Murphy & King 1982) by the aforementioned estimates yields energetic efficiencies for feather synthesis of only about 5 to 7% for small passerines and about 20% for the European Kestrel. Such low efficiencies contrast sharply with the estimated 40 to 60% efficiency in the utilization of metabolizable energy for energy deposited as tissue protein by growing homeotherms, and with the 30 to 80% efficiency for energy deposited as egg protein (Van Es 1980). This discrepancy suggests that energy demanding processes in addition to keratin synthesis are entrained in molt. We think that these hidden costs inflate the estimated cost of molt and account for its unusually low estimated energetic efficiency and the higher than expected increase in protein required for molt as outlined above.

Origins of the energy and protein demands of molt

We previously hypothesized (Murphy & King 1984a), and others (Hanson 1962, Newton 1968, Gavrilov & Dolnik 1974) have implied, that much of the unexplained energy cost of avian molt results from supporting "a profound disturbance of endogenous [nitrogen] metabolism" (Thompson & Powers 1924) that accompanies the renovation of the integument. Four independent lines of evidence from our studies of Gambel's Sparrows are consistent with this hypothesis: First, tissue (especially liver) glutathione (GSH) appears to be an important regulated reservoir of cysteine for overnight keratin synthesis (Murphy & King 1985, 1990). We know that cysteine donation is the main purpose of the added reserve of GSH during molt because forcefeeding or administration of cysteine through the night mutes the utilization of GSH from tissue pools. We also know that the storage of extra cysteine during daytime (feeding phase) is directly proportional to the duration of the nocturnal fast to which the birds are accustomed, and is not directly related to the daily dietary consumption of SAA. Cysteine derived from GSH is thought to improve the matching of essential amino acid (EAA) profiles between EAA derived from relatively low-cysteine tissue protein pools catabolized at night and the high-cysteine keratin synthesized at night, thus reducing the wastage of EAA (Meister & Anderson 1983, Murphy & King 1985, 1990). These special roles for GSH indicate that adjustments of protein and amino acid metabolism, in addition to keratin synthesis, accompany molt.

Second, feathers elongate at the same rate by night as by day in Gambel's Sparrows and several similar species of birds (Murphy & King 1986b). Although GSH supplies at least one-third of the cysteine required by keratin synthesis at maximum molt intensity, additional cysteine and other EAA must be obtained from the catabolism of tissue proteins if overnight keratin synthesis continues unimpeded (which it does). This entrains an overnight loss of about 400-450 mg of protein during midmolt in Gambel's Sparrows kept in thermoneutral conditions and a 12 h light phase (Murphy & King 1990). Similar amounts of nocturnal protein loss have been reported in two other passerine species under similar conditions (Newton 1968, Gavrilov & Dolnik 1974). The net nocturnal catabolism and the daily restoration (net synthesis) of the protein mass lost overnight as well as a potentially accelerated rate of daily total protein turnover may account for much of the "hidden" caloric cost of molt (see also Millward & Rivers 1988).

Third, we found in winter-phase and molt-phase Gambel's Sparrows kept in a thermoneutral environment that the valine requirement increases more during molt (from about 0.30% of diet in winter to about 0.42% of the same diet during molt) than does the SAA requirement (in both phases about 0.28% with at least 0.12% as methionine). Valine is relatively abundant in feathers but is only 65% as concentrated as cystine/2 (Murphy & King 1982). The most plausible hypotheses to explain this unexpected result are (a) that the changes in amino acid requirements during molt reflect more closely the profile of amino acids in the proteins being rebuilt by day than the profile of the keratins; (b) that cysteine-sparing physiological adjustments in addition to GSH storage occur; and (c) that the increased food consumed to meet the caloric cost of molt more nearly supplies the required cysteine than the required valine, so that food containing higher valine concentrations are necessary during molt.

Fourth, the hidden costs of molt are not explained by an alternative "aminostatic" hypothesis that molting birds consume excess calories (and hence increase their metabolic rate) in order to meet the SAA requirement of plumage synthesis (cf. Gavrilov & Dolnik 1974, Murphy & King 1984a). On the contrary, molting White-crowned Sparrows fed an SAA-deficient diet *reduce* food intake and *reduce* per diem costs of molt by slowing its rate (Murphy & King 1985, Murphy et al. 1988). [The SAA-deficient diet contained 1.5 mmoles of cystine and 8.5 mmoles of methionine, or about 0.14% SAA. This is corrected from Murphy & King (1985) and Murphy et al. (1988), wherein 5% dietary casein was the sole source of SAA, as indicated in the text (p. 281). Data in Table 2 (p. 282) were mistakenly based on 10% casein.] Likewise, added thermoregulatory costs attending plumage replacement do not appear to account for much, if any, of the "hidden" costs of molt, although the data are more ambiguous in this case (King 1980).

MINIMIZING THE MISMATCH BETWEEN NEED AND AVAILABILITY

Despite the apparent inefficiency in the deposition of protein and energy in the products of molt and the consequently high nutrient costs of molt relative to product, the actual nutrient requirements for molt could be met by a fairly broad range of natural foods (Murphy & King 1984b). Moreover, animals have many options for the frugal use of nutrients (King & Murphy 1985). These options include features of their behavior, metabolism, and life history.

Selective feeding

To ensure adequate intake of specific nutrients through the course of the molt, birds can adjust the proportions or types of available foods that they eat. Gambel's Sparrows are able to choose foods based solely on the adequacy of any one of the essential amino acids (Murphy & King 1987, 1989, and unpublished data) or based on the dietary concentration of a high-quality protein (Murphy unpublished). In a study of molting Gambel's Sparrows offered a choice of semisynthetic diets differing only in SAA content, the birds preferentially consumed the higher SAA food of a diet pair during the molt roughly in proportion to molt intensity (Murphy & King 1987). Likewise, molting Gambel's Sparrows are able to select dietary protein concentrations that are more than adequate to meet the demands of molt from a wide range of combinations

of foods that are either deficient, marginally deficient, adequate, or superadequate in protein (Murphy, MS in prep). Changes in food choice by birds during their molt have often been interpreted as signifying selective feeding to meet nutrient demands; but alternative explanations could not be ruled out and the specific nutrient being selected could not be unequivocally identified. Indeed, the extent of the abilities of wild birds to detect nutrient deficiencies in their diets and to respond with appropriate adjustments in food choice were unknown. The foregoing studies demonstrated that molting birds are physiologically and behaviorally adept at choosing foods to meet their needs for protein and specific amino acids when random feeding is ineffective.

Storage compounds

During the feeding phase (usually daylight) birds can choose foods that contain the best available balance of nutrients relative to their needs. During the fasting phase (usually overnight), however, when delivery of exogenous nutrients temporarily ceases, a molting bird must rely on endogenous reserves to sustain keratin synthesis. The mismatch between the compositions of feather proteins and the mixed proteins of other tissues and the consequent inefficient reutilization of EAA can be partially offset in molting birds by storing cysteine, the first limiting amino acid for keratin synthesis from body tissues, in the tripeptide glutathione (Murphy & King 1985, 1990, Murphy et al. 1990). As described earlier, molting Gambel's Sparrows store cysteine by day, mainly in liver glutathione, in proportion to the duration of the overnight fast. This cysteine is liberated overnight to complement the profile of amino acids liberated by catabolism of tissue proteins to support keratin synthesis. Metabolic mechanisms that enhance reutilization of EAA during molt will help to minimize the added amino acid requirements of molt and will dampen the detrimental effects of limits in EAA availability.

Life history

An important corollary of the diurnal cycle of protein turnover, described above, as a potential explanation of the high nutrient costs of molt, is that the nutritional costs of molt may be inversely proportional to daylength (directly proportional to overnight loss of tissue protein) and therefore may be related to the latitude at which a bird normally molts. Thus, species that molt in late summer at high latitudes (long days) with strict temporal constraints on the events of their annual cycles could have accelerated their molt, relative to their more southern counterparts (e. g. Mewaldt & King 1977), with little or no additional per diem costs, and thereby with a reduced cost for the whole molt. Such a relationship between latitude and costs of molt would permit a brief molt and allow a maximum amount of available time to be devoted to breeding during the brief arctic summers, making migration to these areas profitable.

A parallel consideration might explain the differences in the caloric costs of molt that we estimated for passerines and those estimated for the European Kestrel (Masman 1986). Masman (1986) also reported that the duration of the heat increment of feeding (H) in kestrels extends (but gradually declines) for nearly 20 h. If H indicates delivery and utilization of exogenous nutrients we can assume that the effective duration of the overnight "fast" in kestrels is relatively brief. If the hypothesis (above) explaining much of the hidden cost of molt were correct we would expect a lower energy cost of molt in the kestrel, as was reported.

MOLT AND MALNUTRITION

Nature is unpredictable, and occasional periods of nutritional stringency are unavoidable. When these periods encompass the molt, birds, theoretically, may adjust by (a) delaying or suspending molt; (b) reducing the rate or magnitude of production, thereby reducing per diem nutrient demands; (c) sustaining production at the expense of body tissues; or (d) exploiting some combination of these adjustments. Molting Gambel's Sparrows respond to a variety of nutritional limitations (amino acid deficiency, food shortages [Murphy et al. 1988], or protein deficiency [Murphy & King 1991]) in a similar fashion. Malnourished Gambel's Sparrows are unable either to delay or suspend molt in order to offset nutritional limitations. As a consequence of nutrient deficiency these sparrows reduce body mass and slow the rate of molt roughly in proportion to the magnitude of the deficiency. The slowing of molt involves both a decrease in the rate of growth of individual feathers and an increase in the shedding intervals between feathers. When nutritional limitations are severe molt continues, but the feathers generated can be reduced in length and mass and may be deformed (Murphy et al. 1988, Murphy et al. 1989). The feather deformities induced by amino acid deficiency are typically more pronounced than those induced by food shortages. Both types differ from fault bars, which appear to be more or less independent of nutritional status (King & Murphy 1984, Murphy et al. 1989).

The reaction of Gambel's Sparrows to nutrient deficiencies during molt, and in particular the persistence of feather growth in the face of severe malnutrition, may be specific to birds that molt at high latitudes and contend with severe temporal constraints during their annual cycles. This remains to be examined. Very few extensive studies of the specific effects of malnutrition on molt have been conducted. The alternative view is that the reactions of Gambel's Sparrows are fairly representative of not only the Class Aves but also of homeotherms in general. Mitchell (1959) suggested that keratin synthesis is a very high priority process. The persistence of keratin synthesis in malnourished homeotherms probably derives from the vital role of the integument in (a) protection against the environment, (b) thermoregulation, (c) communication, and, especially in birds, (d) locomotion.

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SYMPOSIUM 40

**HABITAT LOSS: EFFECTS ON
SHOREBIRD POPULATIONS**

Conveners P. R. EVANS and P.-O. WON

SYMPOSIUM 40

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INTRODUCTORY REMARKS: HABITAT LOSS – EFFECTS ON SHOREBIRD POPULATIONS

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INTRODUCTION

Shorebirds, in American usage, or waders in European usage, comprise chiefly the Charadriidae (plovers), Scolopacidae (sandpipers) and Haematopodidae (oystercatchers). Many species are heavily dependent on wetland habitats during at least part of their annual cycle of breeding, migration, moulting and 'overwintering' (the latter a shorthand term often applied to the non-breeding season, even though many migrants that have bred in the northern hemisphere travel to the south of the equator at that season, and thus into the southern summer).

The coastal and inland wetlands upon which they depend have been under great pressure from drainage, land-claim and degradation for many centuries and for a variety of human uses. For example, 54% of all wetlands in the United States in pre-settlement days have now been lost, and in states such as California and Iowa the losses are much higher, over 90% (Tiner 1984). Continuing losses of US coastal wetlands, largely by human action, have been occurring at the high annual rate of 0.5% since the 1950s.

In Britain, estuarine habitats have been in decline through land-claim since Roman times. Although most estuaries still remain, many have lost over 25% and some such as Teesmouth up to 90% of their intertidal land (Evans et al. 1979), most of the losses being during the last three centuries. On some British estuaries such as the Tyne and the Thaw all suitable feeding grounds for migrant waders have now been destroyed. Continuing land-claim is widespread, affecting over one-third of all British estuaries, and current proposals, especially from barrage construction, threaten up to 10% of the remaining resource (Davidson et al. in press). Many of these diminished estuaries act as migration staging areas. Similar patterns of habitat loss are widespread elsewhere in the world.

Much of the estuarine habitat loss has been from upper tidal flats and saltmarshes. Loss of such areas is not restricted to temperate latitudes. Even in arctic Norway, parts of upper tidal flats have been removed recently through road construction. Upper tidal feeding grounds can be critical for waders needing to increase their food intake before migration or during severe weather in winter. In the future, rising sea-levels will probably reduce intertidal areas in many parts of the world, since land above present high water levels is often defended by embankments.

Four papers in the symposium are devoted chiefly to habitat loss in estuarine and coastal situations. Sutherland & Goss-Custard consider general ecological and

behavioural processes which need to be quantified in order to predict effects of habitat loss on bird populations. Lambeck and Meire describe different aspects of a well-documented study of the consequences for Oystercatchers *Haematopus ostralegus* of a major loss of intertidal habitat in the Oosterschelde, Netherlands. Lambeck focuses on changes in distribution and mortality of the birds, Meire on changes in foraging behaviour. Together, they illustrate the close links between amount and density of available food and the numbers of birds surviving on a site. The fourth paper (Evans, Davidson, Piersma & Pienkowski) reviews the functions of migration staging posts for waders and deduces what might happen if particular sites are lost.

Many inland wetlands have also been drained completely; others vary in their suitability for waders from year to year according to their water levels, which are affected both by rainfall and by the rate of abstraction of water for human purposes (domestic, industrial and agricultural). Recent changes in agricultural practice have led to a general lowering of groundwater levels in many parts of the world. In the Netherlands, the sequence of "improvements" to lowland wet grasslands has been (i) lowering of the water table to allow earlier access to the fields for cattle or machinery (ii) faster growth of vegetation as a result of the drier soil conditions aided by applications of fertilizers and (iii) earlier mowing and intensive grazing. Although the wader species breeding in these grasslands have advanced their breeding season, subsequent losses of nests and eggs to trampling by cattle and mowing have affected the productivity of different species to different extents. Those species that rarely renest if they lose their first clutch have fared badly (Beintema & Muskens 1987). The problem here, and in other areas of lowland wet grasslands in western Europe, is not so much one of the habitat modification as such, but of the attendant agricultural operations. The final paper in the symposium (Baines, Grant, Jackson & Evans) summarizes the results of three separate studies comparing breeding wader densities on "improved" and unimproved agricultural habitats in northern Britain, and attempts to account for the differences found in terms of population processes.

The variety of approaches to understanding and predicting the effects of habitat loss on wader populations, presented in this symposium, may find useful application in studies of other bird taxa. This is certainly the aim of the presentations included here.

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PREDICTING THE CONSEQUENCE OF HABITAT LOSS ON SHOREBIRD POPULATIONS

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ABSTRACT. We provide a framework for analysing the consequences of habitat loss in the non-breeding areas on shorebird populations. This loss will result in higher bird densities in the remaining areas which will, in turn, intensify competition between birds as a consequence of higher rates of prey depletion and increased rates of interference. This may result in a redistribution of birds between sites, both within and between estuaries. The increased competition and associated tendency for young and subdominant birds to be forced to poorer sites is expected to result in higher rates of mortality of these birds. The conditions under which this will result in a lower equilibrium population size are summarised briefly.

Keywords: Equilibrium population size, density dependence, ideal free distribution, oystercatchers, habitat loss.

INTRODUCTION

The introduction to this symposium outlines the many changes facing estuaries. Outside the breeding season, many shorebirds depend almost entirely upon intertidal habitat for food so there is considerable concern that these changes in habitat may affect the populations of these birds.

A common consequence of many of these changes, such as reclamation, sea level rise or disturbance, is that the area of intertidal feeding areas may be reduced (Goss-Custard in press). The question therefore is whether a loss of habitat that affects shorebirds at just one time of year will affect the overall size of the population. The fundamental points are: (1) if part of an estuary is developed so that the birds have to move elsewhere, will the inevitable increase in global bird density that this entails increase the mortality rate (Goss-Custard 1977) and (2) will any change in mortality affect the total population?

One way of thinking about the effects of habitat loss locally is to formulate the question in terms of the ability of estuaries to support birds, i.e. in terms of their carrying capacity (Evans & Dugan 1984, Goss-Custard & Durell 1984). Dhont (1988) points out that the term carrying capacity has been used in so many ways that the expression may best be avoided. Thus, Leopold (1933) defined it as an "internal force which sets an upper limit on populations", Errington (1934) viewed it as a "threshold above which individuals were very vulnerable to predation", while Odum (1953) equated carrying capacity with the equilibrium value (K) of the logistic equation. Odum's definition is probably the one most used in recent textbooks though those of Leopold and Errington are still widely used by game managers. Dhont (1988) suggests that the term has become so confusing that it should now be abandoned.

On the other hand, the notion underlying the concept of carrying capacity has much intuitive appeal and conveys a useful general idea. This is that animals cannot be squeezed in ever increasing densities into an area: resources are always limited so that some upper threshold to density must exist. Though the term has undoubtedly led to conceptual confusion, the basic idea it encapsulates must be true and applies to all systems. However, it should be defined for a particular case. We apply the term to particular areas within a species range during the non-breeding season. Our particular definition rests on the assumption that various forms of feedback from bird density to the rate at which individuals can feed will cause an increasing proportion to fail to achieve adequate intake rates as the local bird density increases. Eventually, density will reach a level at which the addition of one further bird would result in another either starving or leaving that locality to seek a better feeding area. When this point is reached, no net increase in bird density can take place, and the carrying capacity would have been reached (Goss-Custard 1985).

The difficulty in using this concept is only the practical one of deciding when this point has been reached. A change in the feeding conditions or, in some cases, the social system could allow even higher bird numbers to be in a locality. Distinguishing between the maximum density yet seen in a locality and the maximum density that is possible is a fundamentally important issue, and will require extensive studies of behavioural ecology to resolve (Goss-Custard *in press*). We show in this paper how recent theoretical and empirical advances in behavioural ecology do open up the possibility of defining such limits to local density, and thus of predicting the carrying capacity of a locality.

On the occasions when predictions as to the effect of a habitat change on only local bird numbers are required, it is therefore useful to think in terms of carrying capacity. However, most attention usually focuses on the consequences for the population size as a whole, and not just local numbers. We believe that the concept of equilibrium population size is the most appropriate way for thinking about the consequences of habitat loss at the larger level of scale of entire migratory populations. To understand the concept of equilibrium population size, it is necessary to consider the interaction between the density dependent and density independent rates of births and deaths. By definition, equilibrium occurs when the birth and death rates are equal. Figure 1 shows how a change in a density independent mortality rate affects the equilibrium level in a population in which only the birth rate is density dependent. In reality, it is likely that both births and deaths could be density dependent, although the precise form of the relationships is only poorly understood (Goss-Custard & Durell 1990).

There has been considerable speculation in the past as to whether populations of migratory birds are "limited" on the wintering or breeding grounds. If some threshold population size is higher on the breeding grounds than on the wintering grounds then, it is argued, the population must be limited on the wintering grounds. Conversely, if the winter threshold occurs at a higher level than the summer threshold, then the population would be regarded as being limited in the breeding grounds. But with the concept of equilibrium population size developed in Figure 1, it is clear that the idea of a distinction between winter and summer limitation is not useful. For example, as shown in Figure 1, a change in the winter mortality rate results in a change in

population size. If ecologists observed a change in population size in response to a change in the number of predators in winter, for example, it would be argued that the population must be limited by predators in winter. But, as Figure 1 shows, all the factors that affect the balance between the total death rate and birth rate affect the equilibrium population size: why select only the one that has most recently changed and call it “the limiting factor”? Except in rather special circumstances, all the factors that affect the birth or death rates will affect the equilibrium population size, and may thus be said to be limiting (Goss-Custard 1981, Sinclair 1989).

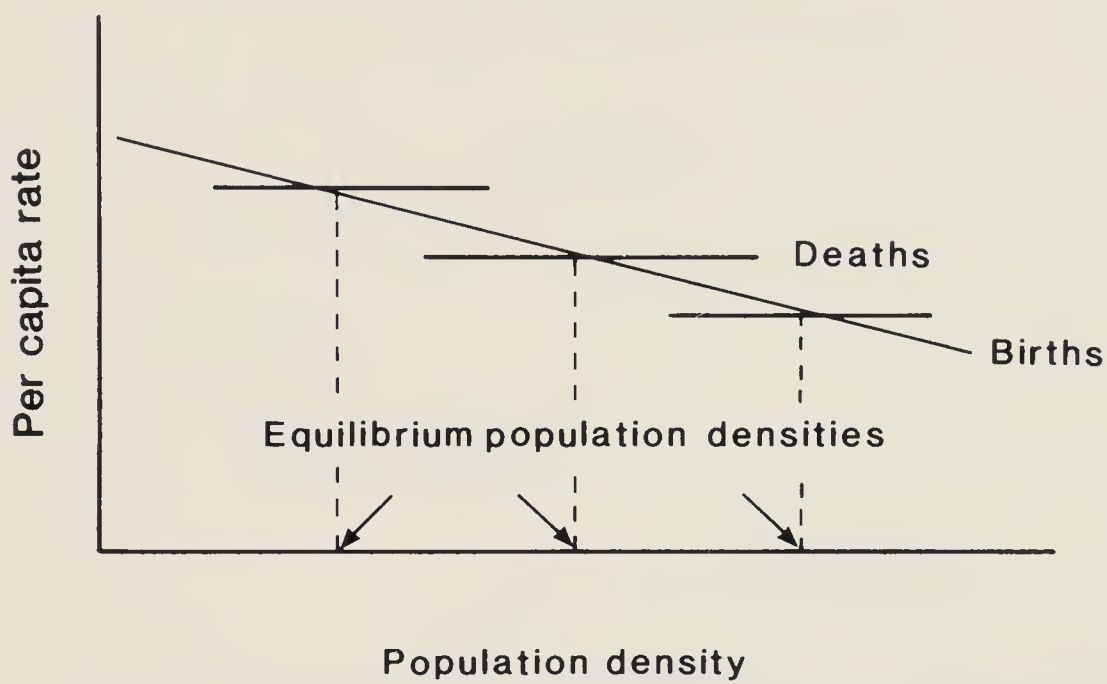
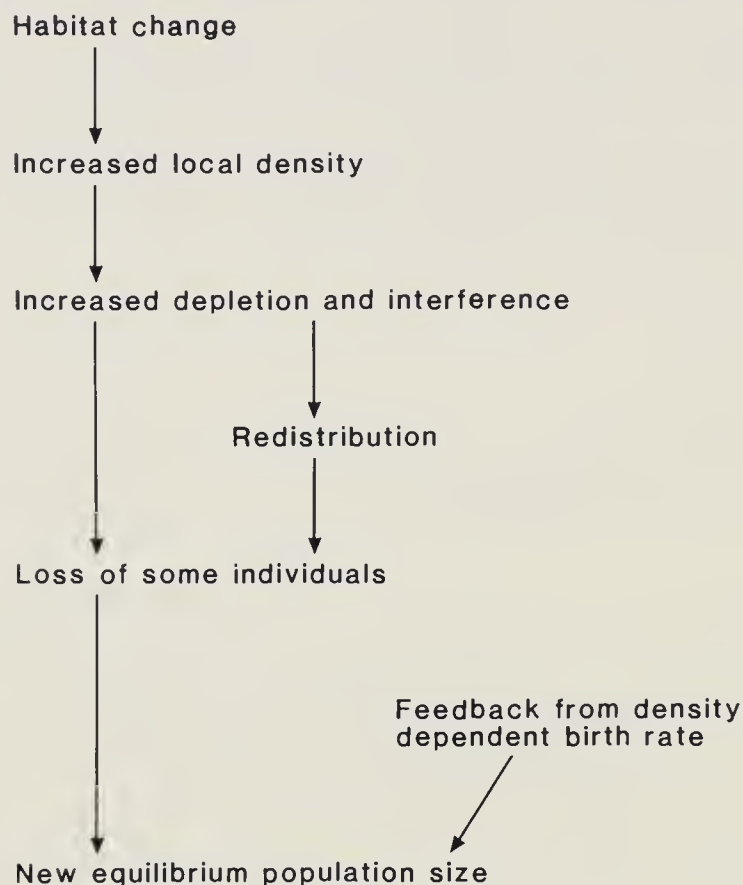


FIGURE 1 – The relationship between birth rate, death rate and population size. In this case the birth rate is density dependent and three values of density independent death rates are shown. The equilibrium population for each combination is shown by the dotted lines.

There is also frequently a confusion between limiting and regulating factors. Populations may only be ‘regulated’ by processes which are density dependent. In the example shown in Figure 1, it is the summer mortality alone that is density dependent, while winter mortality is density independent. Despite a change in population size due to a change in the conditions on the wintering grounds, the population size could not be said to be regulated in the winter, any more than it could be said to be limited by them. The key point about the effects of habitat loss, therefore, is whether it will increase the mortality rate or decrease the reproductive rate, and thus bring down the equilibrium population size (Goss-Custard 1980). Since habitat loss reduces the area of the feeding grounds, the density of birds on the winter feeding grounds as a whole would have to increase, unless some extension of the winter range was possible. In other words, we must find out whether the winter survival rates are affected by bird density (Goss-Custard 1977). If so, density-dependent mortality would increase and the population size would almost invariably decrease.

A FRAMEWORK FOR STUDYING HABITAT LOSS

Figure 2 shows a framework for considering the links between the loss of habitat and the equilibrium population size. In this paper, we will outline the justifications and evidence for each of the processes shown in this framework.

FIGURE 2 – A framework for considering the effect of habitat loss on bird populations.**Habitat loss > increased local density**

The displaced birds may either feed elsewhere within the same estuary or in other estuaries. In either case, bird density will have increased at least in part of the winter range remaining.

Increased local density > increased depletion and interference

An increase in density is likely to result in greater rates of prey depletion or interference between foraging birds (Goss-Custard 1980). Depletion is the removal of part of the food supply and, in shorebirds, can result in considerable declines over the winter in the density of the food (Goss-Custard 1980). The decline in absolute prey densities may underestimate the proportional decline in the amount of food that is actually available. For example, only mussels of a certain size and shell thickness are taken by many oystercatchers (Durrell & Goss-Custard 1984, Meire & Ervynck 1986, Sutherland & Ens 1987, Cayford & Goss-Custard 1990) so, although mussels may still be abundant in the spring, only a small fraction may be available to the birds. Interference is an immediate and reversible decline in intake rate as a result of the presence of other individuals, due to increased rates of various interactions between birds or to decreased prey detectability (Goss-Custard 1980).

Depletion and interference are likely to affect all wader species on their wintering grounds, although the relative importance of the two processes will vary. For those species which regularly fight over food, such as oystercatchers (Goss-Custard, Ens & Durrell 1982) and Turnstone (Metcalf & Furness 1987), or for those species which have easily disturbed prey, e.g. Redshank eating *Corophium* (Selman & Goss-Custard 1988), interference is likely to be important. For other species, especially those that feed in large flocks, it is likely that interference is less important than depletion.

For most species, it is likely that both processes play some role. Either way, an increase in local density causes food to be harder to collect.

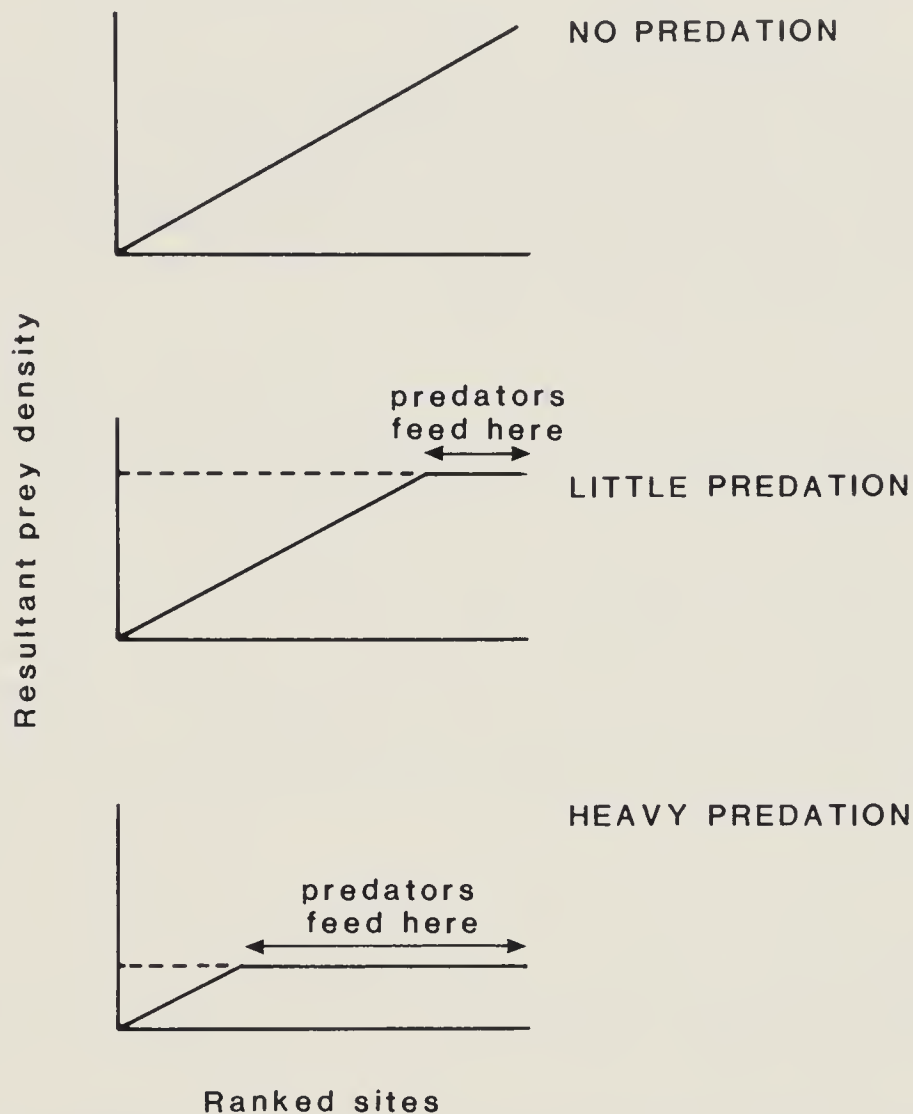


FIGURE 3 – Food availability at various sites before and after depletion. The first birds (a) to arrive feed at sites with the highest food available. As depletion occurs (b) birds use an increasing range of sites. With an increased population the rate of exploitation will increase and a wider range of habitats will be used.

Increased depletion and interference > redistribution

When birds return to their winter feeding grounds in late summer and autumn, they arrive on a food supply that varies in abundance from place to place at several levels of scale (Goss-Custard 1983). Their food supply can be viewed as a series of interlocking gradients. How birds exploit a gradient, and how they react as the total numbers of birds using it increases, depends on whether depletion or interference plays the major role in determining their distribution (Goss-Custard & Charman 1976). If prey depletion is the major process affecting bird distribution, the prey population will be exploited down to a constant density as the winter progresses, with individual birds starting at the beginning of the winter by feeding at the sites with the highest initial prey densities. As bird numbers increase, a wider area will be depleted of prey earlier in the winter, so that individuals will have to move down the food gradient earlier in the winter to find new feeding sites (Figure 3).

If interference is the major process affecting bird distribution, the birds will spread out over the food gradient right from the start of the winter as interference in the preferred

places begins immediately to drive down intake rates so birds seek new areas. As total numbers increase, a greater proportion of birds will start the winter by feeding in the poorer areas.

As the total number of birds increases, an increasing proportion is therefore expected to occur in the poorer quality sites because of either increased depletion or interference. The pattern has now been observed on food gradients within one estuary in a number of species: Teal (Zwarts 1970), Redshank (Goss-Custard 1977b), Knot (Goss-Custard 1977) and Oystercatchers (Goss-Custard 1977, Zwarts & Drent 1981, Goss-Custard et al. 1982, Meire & Kuyken 1984).

The same redistribution towards poorer sites as total numbers increase may also occur between different estuaries and on a national scale. The British population of wintering Grey Plover has increased several fold over the last 20 years, but numbers increased at a slower rate, if at all, in those estuaries where the initial density was already high, suggesting they were at or near to capacity (Moser 1988). There is a methodological problem with this analysis; if numbers at a site were underestimated in the initial counts, the estimated rate of increase in subsequent years would be too high so the proportional increase would be spuriously related to initial density. However, Moser (1988) showed that the apparently preferred estuaries with higher initial densities occurred in regions with higher winter temperatures, which probably means the feeding conditions were better. Despite the statistical problems, we feel that the approach of examining national data is invaluable in showing the redistribution that takes place as population size changes, at these large geographic levels of scale. Bird numbers on estuaries probably change between years mainly by immigration and emigration because the winter death rates are so low (Goss-Custard 1981, Evans & Pienkowski 1984). Sutherland (1982) shows how, in response to a massive increase in the cockle *Cerastoderma edule* food supply on the Ribble Estuary, the number of Oystercatchers increased four fold, primarily due to the immigration of juvenile birds and not to the increased survival of birds already there. As the cockle population declined, analogous to habitat loss, numbers declined but the birds remaining were primarily adults, the juveniles having settled elsewhere. This work suggests that young birds are particularly likely to move between sites in response to changes in habitat quality, while adults are likely to be more conservative. Accordingly, a loss of feeding habitat is likely to be followed particularly by the loss of juvenile birds, either because they fail to settle and establish themselves on the estuary in their first autumn (Myers et al. 1990), or because they subsequently emigrate.

Redistribution > death of poor competitors

Sutherland & Parker (1985) and Parker & Sutherland (1986) have shown how individuals differing in competitive ability should be distributed along a gradient of food abundance. Birds of the highest competitive ability occur on the richest parts of the gradient. The detailed field studies of Oystercatchers by Goss-Custard et al. (1982, 1984) and Swennen (1984) provide findings that are broadly in line with these predictions.

The intake rates of the poorer competitors would be reduced in two ways by habitat loss; first from a reduction in the available food due to increased depletion and interference and second by their having to move to poorer quality habitats. Both of these processes may result in an increased risk of mortality in winter, especially in severe

weather; either directly through starvation (Goss-Custard & Durell 1987) or indirectly if hungry birds are more at risk of being eaten by predators (Whitfield 1988).

Loss of poor competitors > new equilibrium population size

The strongest evidence for regulatory processes in shorebird populations is that birds compete for the best breeding places (Harris 1970, Hill 1988). This could produce a powerful density-dependence in the birth rate (Goss-Custard 1981, Galbraith 1988), quite sufficient to regulate their populations in most circumstances (Goss-Custard & Durell 1990). Though field evidence is difficult to obtain, further mechanisms may exist on the breeding grounds. For example, there may be density-dependent predation on chicks, which could add to the regulatory effect of competition for breeding territories. But, notwithstanding any regulation that occurs on the breeding grounds, simulations with an equilibrium population dynamics model show that an additional density-dependent mortality of the young birds in winter can significantly reduce the equilibrium population size. The magnitude of the reduction is, of course, larger as the strength of density dependence in the winter increases relative to that occurring on the breeding grounds. Nevertheless, over a wide range of conditions, an increase in the rate of winter mortality of young birds through an intensification of competition resulting from habitat loss can considerably affect population size. The case of the decline in the numbers of Dunlin in different estuaries, which seemed to be correlated with the amount of habitat lost by the spread of *Spartina anglica*, may be an example of this, though simultaneous changes on the breeding grounds cannot decisively be ruled out (Goss-Custard & Moser 1988).

With this approach, it is necessary to estimate the strength of any density dependence feedback operating in both seasons. These are difficult to estimate in migratory shorebird populations, but it may be done indirectly through behavioural studies, in both the breeding season (Galbraith 1988) and in winter (Goss-Custard & Durell 1990, Goss-Custard in press). Behavioural models that allow the responses of birds to the loss of parts of their gradient, such as that of Sutherland & Parker (1985) and Parker & Sutherland (1988), are likely to be particularly useful. As areas are removed in this model, birds redistribute themselves over the changed food gradient according to their competitive ability. The increased proportion of poor competitors, often young birds, that, as a consequence of habitat loss, fail to achieve the intake rates required to survive can then be predicted. The effect of this on the equilibrium population size can then be examined by simulations with population models (Goss-Custard & Durell 1990, Goss-Custard in press).

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CHANGES IN ABUNDANCE, DISTRIBUTION AND MORTALITY OF WINTERING OYSTERCATCHERS AFTER HABITAT LOSS IN THE DELTA AREA, SW NETHERLANDS

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ABSTRACT. Consequences for Oystercatchers *Haematopus ostralegus* of a reduced tidal amplitude during building and loss of 65 km² (36%) of tidal flats after completion of the storm-surge barrier and two compartment dams in the Oosterschelde estuary (Delta area, SW Netherlands) were studied. Mortality during cold spells of chiefly adult Oystercatchers increased greatly in 1986 and 1987, probably because the reduced tidal amplitude in 1985-87 caused permanent or prolonged immersion of the most preferred feeding areas. Severe weather conditions induced little emigration. Weight data and ringed corpses revealed differences in body condition and mortality risk of birds between Oosterschelde sectors. About half of the birds from former intertidal areas disappeared. A shift in the time of peak seasonal abundance from midwinter to autumn suggests that upper limits of numbers have been reached. Problems are increased by the cockle fishery. No extra mortality was found in 1988-90, when winters were very mild. Increased losses are expected in future cold spells.

Keywords: Oystercatcher, *Haematopus ostralegus*, habitat loss, coastal engineering, Dutch Delta area, winter mortality, weights, tidal amplitude, age composition.

INTRODUCTION

A central environmental question is whether a partial loss of estuarine feeding areas will reduce the size of the local wader (Charadrii) populations or will adversely affect the condition of birds and, hence, their survival during cold spells. Requirements of birds change throughout the year, dependent on weather and endogeneous cycles (Pienkowski et al. 1984). Prey abundance also shows seasonal and interannual variation. Factors such as temperature, wind speed and even density of birds affect prey behaviour and thus their availability to waders (Pienkowski 1981, Evans & Dugan 1984). Social behaviour influences the feeding success (Ens & Goss-Custard 1984, Goss-Custard & Durell 1987) and spatial distribution of birds (Goss-Custard et al. 1982).

Given this array of interrelated factors, prediction of quantitative effects of habitat loss is still difficult. Few field studies are available so far. Loss of 60% of a 4.5 km² feeding area, plus a 30% reduction in feeding time, in the Tees estuary (UK) initially reduced the numbers of some species, and the importance of supplementary non-tidal and inland feeding increased (Evans & Pienkowski 1983). Recently, numbers of most species have increased again, associated with sediment changes (Evans, pers. comm.). Reclamation of 4.5 km² of mudflats in the Danish/German Wadden Sea mainly resulted in a redistribution of waders, since population sizes in the entire sector hardly changed (cf. Laursen et al. 1984).

Large-scale habitat loss has occurred in the Delta area, the former estuarine complex of the rivers Rhine, Meuse and Scheldt in the SW Netherlands (Figure 1). After a disastrous storm flood in 1953, three of the estuaries were dammed off from the North

Sea and are now freshwater or brackish lakes. The most drastic change was the loss of 55 km² of tidal flats in the Grevelingen estuary in 1971, used by 50 000 waders in midwinter. Population numbers in the entire Delta area were not reduced, however (Leewis et al. 1984). Grevelingen birds settled in adjacent tidal areas (Latesteijn & Lambeck 1986, Lambeck et al. 1989). In 1987, the increased wader populations in the Oosterschelde, the largest of the two remaining estuaries, were faced with a loss of 65 km² (36%) of the tidal flats. This followed construction of the 8 km storm-surge barrier at its mouth and of two compartment dams, on the eastern boundary and in the northern branch, respectively (Figure 1). This paper evaluates some of the effects of (1) changes in tidal amplitude during the final stage of the building activities and (2) the loss of feeding areas since 1987 on the abundance, condition, mortality and distribution of, chiefly, the Oystercatcher *Haematopus ostralegus*. With a seasonal maximum of \approx 90 000 birds (45-50% of all waders), this is the dominant species in the Oosterschelde (Meininger et al. 1985). Effects on the feeding ecology of the species after dam construction are discussed by Meire (this volume).

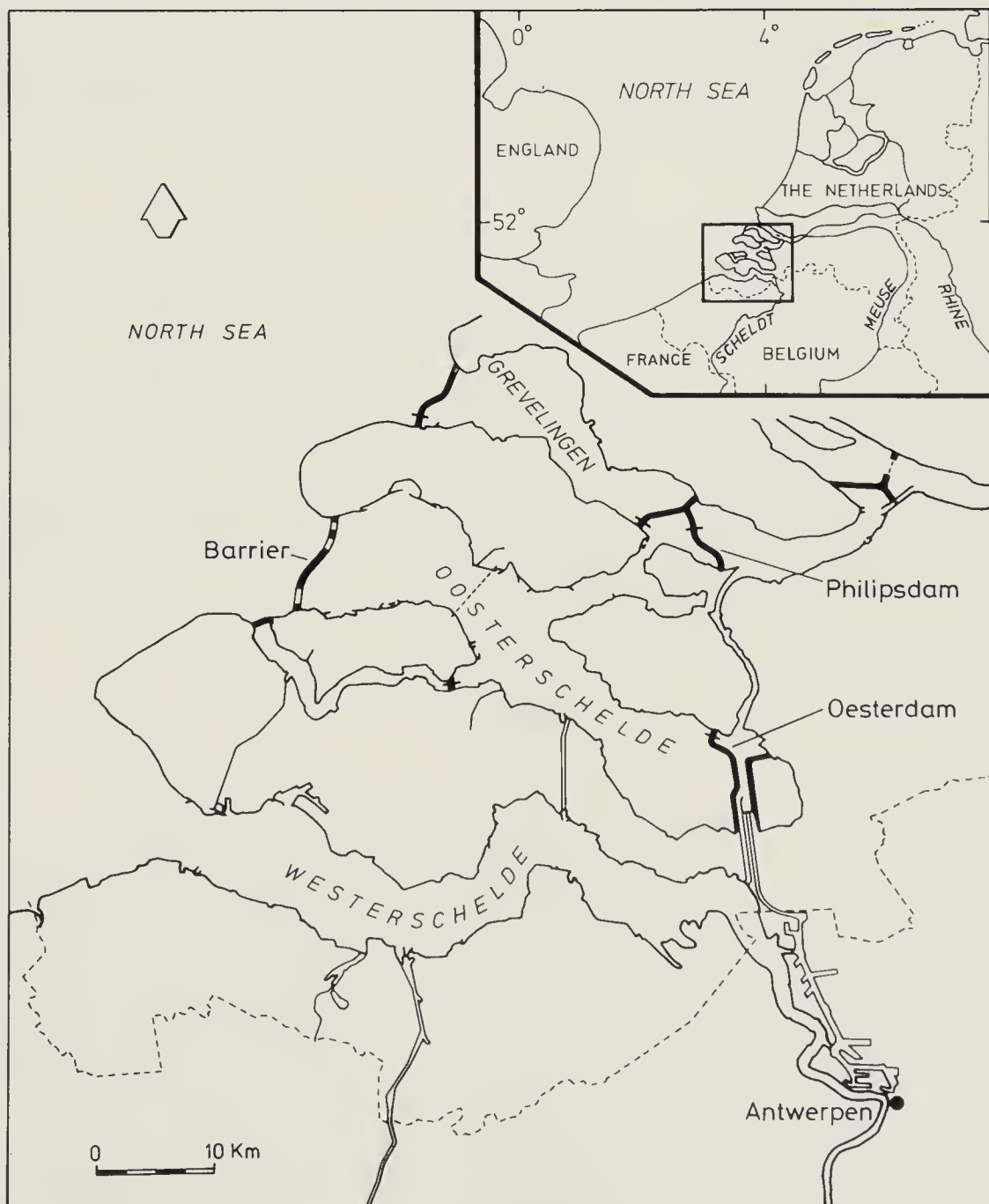


FIGURE 1 - The Dutch Delta area. Location of the storm-surge barrier and two compartment dams in the Oosterschelde estuary are indicated.

MATERIAL AND METHODS

Changes in tidal amplitude

The average difference between ebb and flood level in the former Oosterschelde was 3.7 m, as measured in the eastern sector. Due to the progressive construction of the barrier and the consequent reduction in flow profile in the entrance of the estuary, tidal amplitude gradually declined between spring 1985 and autumn 1986 to 2.4 m. With the closure of the second compartment dam in April 1987, it was brought back abruptly to 3.2 m.

Bird data

Apart from 1983-85, waders were counted each month at high tide since 1978 (e.g. Meininger et al. 1985). The accuracy of such counts is discussed by Rappoldt et al. (1985) and Lambeck et al. (1989). Parameters used in this evaluation of habitat loss are (1) the maximum number of Oystercatchers per season (July to June), (2) the seasonal totals of bird-days (the integration of abundance over time), the best index of usage of an area, and (3) the seasonal pattern of abundance, by which possible periods of reduced capacity may be identified. To facilitate a comparison between years with different population levels, all monthly counts are expressed in percents of the seasonal maximum (see Lambeck et al. 1989).

To assess possible changes in migration, survival etc., 23 000 Oystercatchers were trapped by cannon-nets in 1984-89 at high tide roosts and ringed. Individuals were classified, using differences in plumage and colour of bill, legs and eyes (Swennen 1984), into juveniles (first-winter birds), subadults (second and third winter) and adults (fourth winter and older). All birds, or a sample (≈ 100 ind.), were weighed to the nearest gram. The average time of weighing was two hours after high tide, when birds are supposed to have empty guts (Kersten, pers. comm.). Weight corrections were therefore not applied. About 4400 Oystercatchers were provided with colour rings. Distribution of these birds was monitored quantitatively at high tide roosts. Since the shooting pressure in France is high, changes in the number of recoveries from that country are used as an index of emigration from the Delta area.

RESULTS

The period 1984-87

In the three seasons of intensive bird-catching before the completion of the coastal engineering projects, winters were severe and many waders died from starvation. Roosts and beaches were surveyed during each cold spell to collect corpses. The number, species and age composition of the victims differed greatly between these three winters (Table 1). In 1986, the number of starved Oystercatchers more than tripled, compared with 1985, whilst the numbers of other species declined by two-thirds. Mortality in the third winter was less, but again with a preponderance of Oystercatchers. The proportion of Oystercatcher differed significantly between the first and the other two winters (G-test, $P < 0.001$). Census data from these frost periods showed little variation in population sizes. Rough agreement between the proportion of Oystercatcher amongst the victims and in the live wader population was found only in 1985, before tidal amplitude was reduced.

TABLE 1 - Number (D) of dead Oystercatchers and combined total of other wader species (Rest) collected in the Dutch Delta area during three successive severe winters. Also given are the percentage contribution of the two categories to the entire wader mortality (%D) and the size of the live populations during the cold spells (N; count in 1985 was incomplete). Census data from Meininger & van Haperen (1988).

	Jan-Feb 1985			Feb 1986			Jan 1987		
	D	%D	N	D	%D	N	D	%D	N
Oyster-catcher	1516	46.6	87500	5103	89.1	72200	3192	82.5	94400
Rest	1740	53.4	71200	623	10.9	102000	678	17.5	81300
Total	3256		158700	5726		174200	3870		175700

TABLE 2 - The percentage of three age classes of Oystercatchers in samples of frost victims (%D) and in cannon-net catches carried out between 1 October and the cold spell (%L), in three successive severe winters.

	Jan-Feb 1985		Feb 1986		Jan 1987	
	%D	%L	%D	%L	%D	%L
Juvenile	58.9	5.1	19.3	6.1	21.3	0.8
Subadult	16.2	17.0	20.9	14.6	11.9	11.0
Adult	24.9	77.9	59.8	79.3	66.8	88.2
Sample	1066	1901	2270	3773	3042	1530

Striking differences also existed between winters in the age composition of starved Oystercatchers (Table 2). Juveniles comprised 59% in 1985 but only ≈ 20% in the two successive winters; the absolute numbers dying were similar between years. However, more subadults starved in 1986 than in the two other winters, whilst the proportion of adults increased greatly from 1985 to 1986 and 1987. Although a cannon-net catch may give biased information about population composition (cf. Swennen 1984), the low percentage of juveniles amongst trapped birds (Table 2) indicates that juveniles were markedly over-represented in the die-offs; the reverse was true for adults (G test, $P < 0.001$). The age composition of the starved and live populations was much closer in 1986 and 1987 than in 1985.

The degree of difficulties met by birds can differ locally, as will be illustrated with ringing and weight data from 1986. The large mortality in that year was virtually confined to Oosterschelde birds. All 16 ringed Oystercatchers found in the adjacent Westerschelde estuary (Figure 1) originated from the Oosterschelde. Given an equal distribution of mortality, 13 locally ringed birds were to be expected (Table 3). Data from 422 ringed victims showed that Oystercatchers originally trapped in the central sector and in the northern branch of the Oosterschelde had a three times higher chance of dying than birds from the western and eastern sectors (G test, $P < 0.001$; Table 3). Besides limited movements to the Westerschelde, some redistribution of Oystercatchers within the Oosterschelde also occurred: 54% of the victims collected in the western sector were not originally ringed there, as opposed to 84 and 90% for

birds found in the centre and the north, respectively. In the east, where the mortality risk for local birds was as low as in the western sector, an intermediate 72% was found. The average weight of an adult Oystercatcher normally increases from 500-520 g in late summer/early autumn to 570-580 g in midwinter (Figure 2). The higher mortality risk in the central sector is reflected in the winter weight of live birds: adults at two central roosts were on average 40-50 g lighter than normal (Figure 2).

TABLE 3 - The relative risk of starvation of Oystercatchers in the four sectors of the Oosterschelde and in the Westerschelde estuary, expressed by the ratio between the number of locally ringed birds found dead and the number expected from the size of the locally ringed population.

Area	Found	Expected	Ratio F:E
Westerschelde	0	13	0.0
Oosterschelde			
West	79	141	0.56
Centre	231	144	1.60
East	31	68	0.46
North	81	57	1.42

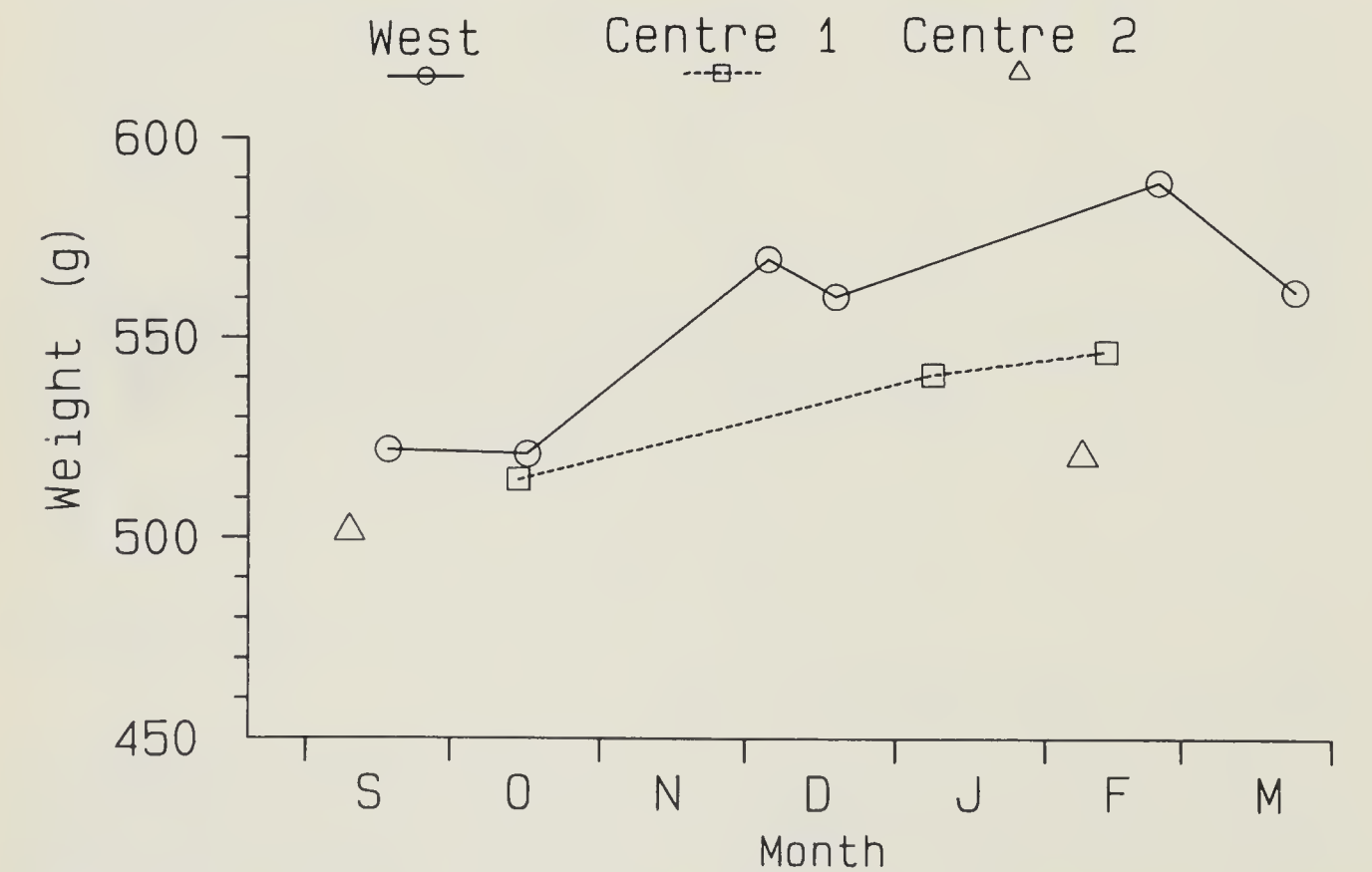


FIGURE 2 - Seasonal pattern of average adult body weight for Oystercatchers trapped at three roosts in the western and central sectors of the Oosterschelde during 1985/86.

In the winter of 1984/85, only four ringed birds were reported from France, all immatures. By February 1986, five times as many (= 14 000) Oystercatchers had been ringed. During the severe frost, 5 recoveries occurred in France, 3 of them adults. In January 1987, in spite of a smaller mortality in the Oosterschelde, 22 birds were recovered in France, including 17 adults.

Developments since the engineering projects were completed

There were no marked changes in the seasonal peak numbers in the first three years of the 'new' Oosterschelde (Figure 3), but these maxima are now found in October instead of midwinter (Figure 4). The number of Oystercatcher-days spent in the Oosterschelde tends to be lower in recent years (Figure 3). Sufficient data on body weights are available only for season 1987/88. These indicate relatively low winter weights at most roosts except those in the eastern sector (Figure 5). In this winter, a marked peak of recoveries in France occurred in December; both immature (4) and adult (5) birds contributed. These birds were shot after three frosty days, the only ones in an otherwise very mild winter. The two following winters (1988/89 and 1989/90) also broke warmth records; in both the number of French recoveries was negligible.

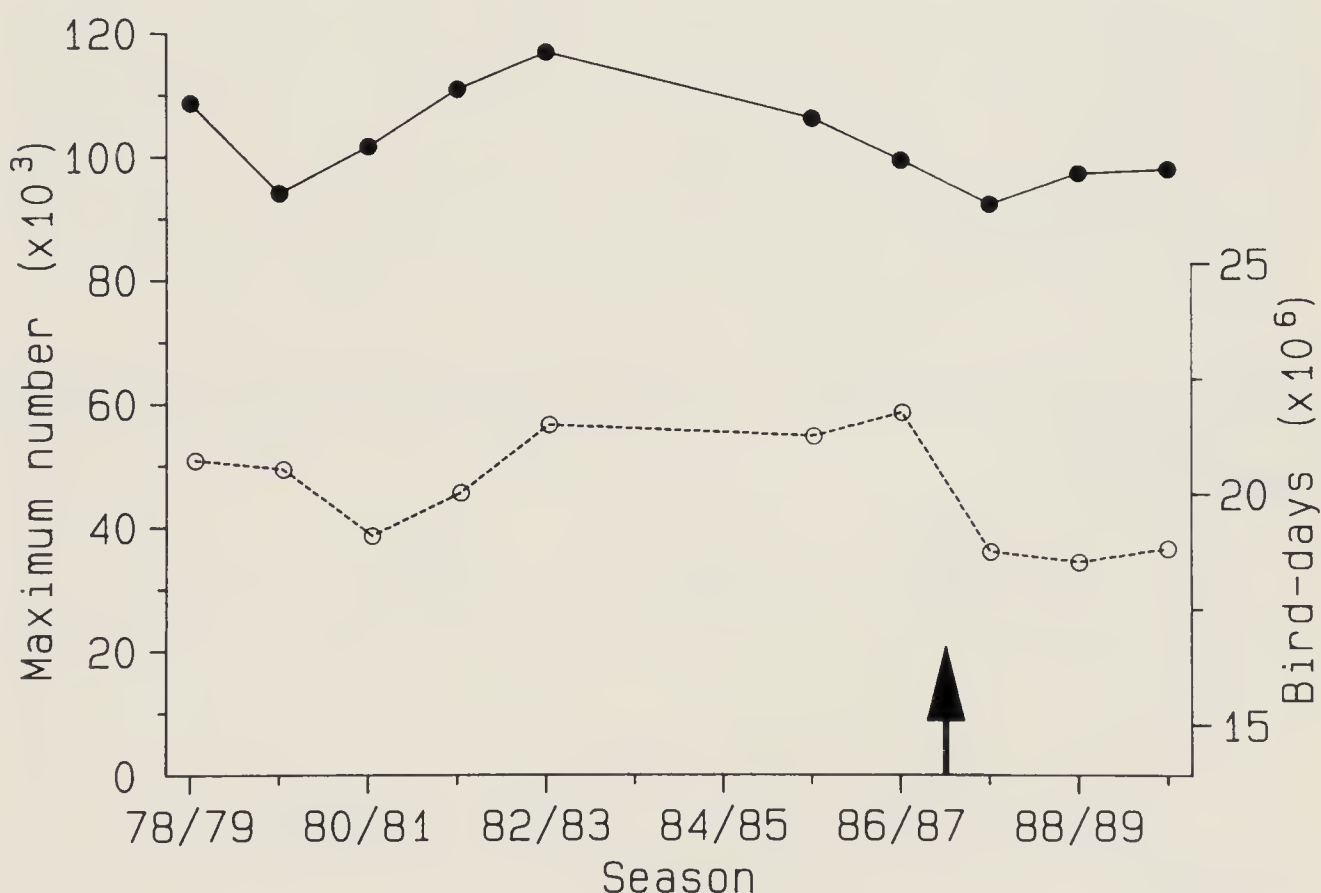


FIGURE 3 - Changes in seasonal peak counts (●) and seasonal number of bird-days (○) for the Oystercatcher population of the Oosterschelde from 1979/80 to 1989/90. The monthly census was interrupted in 1983/84-1984/85. Arrow marks the completion of the coastal engineering projects.

Some redistribution of birds took place after 10 000 Oystercatchers lost their feeding grounds behind the northern Philipsdam (Figure 1). Some of the colour-ringed individuals settled directly south of that dam and elsewhere in the Oosterschelde. However, of the birds originally colour-marked in the northern sector in 1984-87, only 40% were present in Oosterschelde and Westerschelde in 1989/90. For birds marked in the other sectors of the Oosterschelde this figure was 67% (G test, $P < 0.001$). There is no difference in the proportion of northern and other sector birds found dead since 1987.

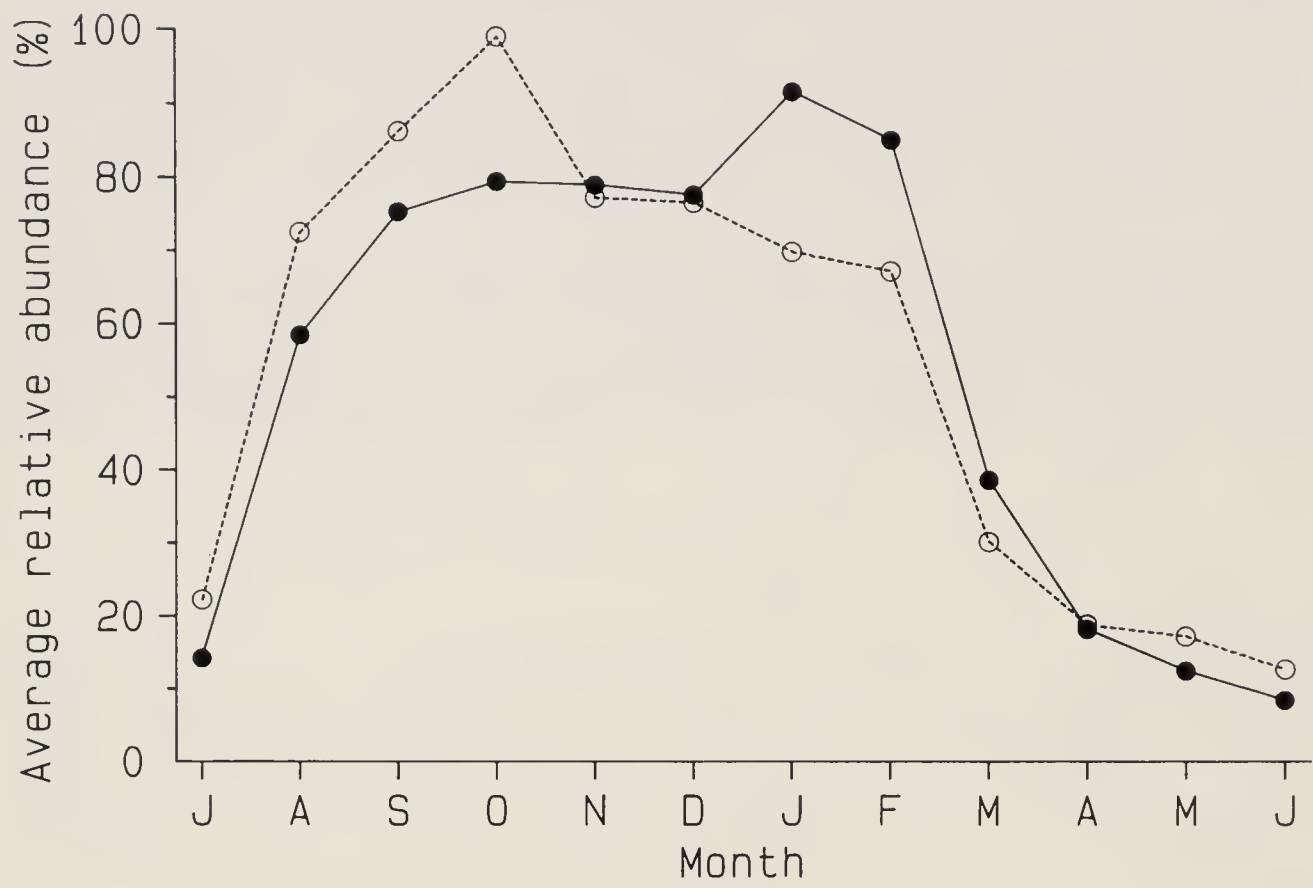


FIGURE 4 - Average relative seasonal abundance (expressed as % of peak count) for the Oystercatcher population of the Oosterschelde in the periods 1979/80-1982/83 (●) and 1987/88-1989/90 (o).

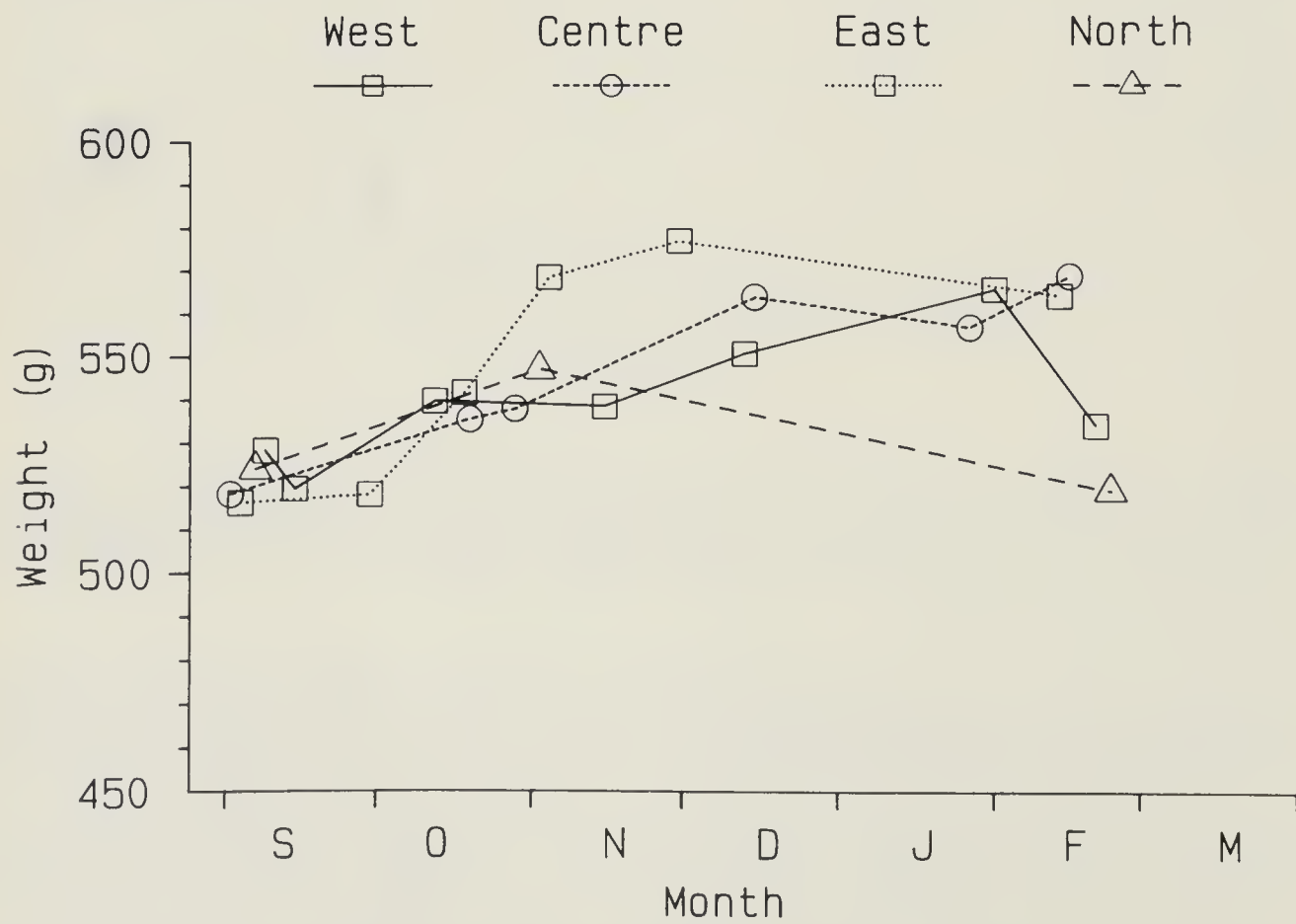


FIGURE 5 - Seasonal pattern of average adult body weight for Oystercatchers trapped in the four sectors of the Oosterschelde during 1987/88.

DISCUSSION

Mass mortalities of Oystercatchers in severe winters are well known. Juveniles are always much more vulnerable than older birds (e.g. Heppleston 1971, Swennen & Duiven 1983). Smaller fat reserves, an initially poorer feeding efficiency and subdominance in the competition for the better feeding areas will contribute to this difference (Davidson & Evans 1982, Goss-Custard et al. 1982, Goss-Custard & Durell 1987). This may also explain why juveniles and subadults migrate on average further south than adults: 70% of the wintering Oystercatchers in France are immatures (Triplet et al. 1987). Mortality in the winter of 1984/85 followed thus a classic pattern.

The frost of February 1986 had in general little effect on the Oystercatchers that winter in the Wadden Sea (Hulscher 1989). Only in the westernmost part a few hundred corpses were found, again mostly immatures (Stock et al. 1987). Because Westerschelde birds were not affected by that cold spell too, the size and age-composition of the Oosterschelde die-off must be regarded as abnormal. The key factor was probably the progressive reduction in tidal amplitude, by February 1986 already 0.5 m less than normal. Dense stocks of the two main prey in the Oosterschelde, mussel (*Mytilus edulis*) and cockle (*Cerastoderma edule*), are found chiefly in the lower intertidal (e.g. Lambeck et al. 1988). A permanent or prolonged immersion of the most profitable areas must have worsened feeding conditions. Prey of other waders is more equally distributed over the tidal range (Coosen & van den Dool 1983) and many species tend to feed along the moving tide-edge, which may explain their low 1986 mortality compared with Oystercatchers.

Goss-Custard et al. (1982) have shown that with an increasing population size more birds shift to worse feeding areas, first mainly immatures but later also adults. A linear dominance rank of individuals (Ens & Goss-Custard 1984) and a negative relationship between density of Oystercatchers and food intake of subdominant birds (Goss-Custard & Durell 1987) will be driving factors in such a redistribution (see also Sutherland & Goss-Custard, this volume). The changed pattern in mortality in 1986 agrees with these behavioural data. When the usual contingent of weaker immatures and adults with deformations (cf. Swennen & Duiven 1983) had died, healthy adults were the next victims. As shown by ringed birds, a switch to another feeding area did not necessarily save an individual from starvation. On the other hand, conditions were apparently not perceived so harsh that a cold rush was started (see below).

Whether differences in local mortality risk are related to differences in ice conditions or food supply is unknown. Data from the western sector showed cockle abundance in early 1986 to be reduced by a factor 2-3 in comparison with preceding years (Lambeck et al. 1988), while the combined biomass of other zoobenthic species hardly changed (Craeymeersch, pers. comm.). The limited mortality and high weights of birds in this sector demonstrate that Oystercatchers can cope with rather wide variations in feeding conditions.

Mortality in the Oosterschelde in January 1987 was again considerable but also occurred elsewhere. In contrast to the Delta area, hardly any cockles were left in the Wadden Sea after two severe winters (de Vlas, pers. comm.) and stocks of other prey will also have been reduced (cf. Beukema 1979). After one week of frost, the majority of Wadden Sea Oystercatchers emigrated; many of them went to France (Hulscher

1989). Delta birds also showed the most pronounced emigration (number of French recoveries) of all three severe winters. However, comparing our ringing data with those from Hulscher (1989), Wadden birds were 15 times more likely to depart. From the breeding population of the Dutch Wadden Sea Island of Schiermonnikoog 25% did not return (Hulscher 1989). In the Oosterschelde about 4% of the population was found dead. The artificial handicap of a 1.3 m reduction in tidal range was apparently less detrimental than the natural problems in the Wadden Sea.

The first season of the 'new' Oosterschelde was apparently difficult for the Oystercatchers. Considering the two following seasons, it is doubtful whether this resulted from habitat loss. Despite the lack of cockles in the Wadden Sea, the Dutch cockle fishery realised record high national landings, chiefly from the Oosterschelde. Compared with spring 1987, only 10% of the adult cockles was left at a major tidal flat in the western sector by late November, mainly at unprofitably low densities (Lambeck et al. 1988). Sufficient amounts occurred only in the eastern sector, explaining the high weights of birds there (Figure 5). In a very mild winter, such as 1987/88, impoverished feeding conditions apparently had no adverse effect on survival. Inland feeding at high tide seemed to be more common than in previous years, but quantitative data are lacking. The importance of supplementary feeding has been stressed by Heppleston (1971) and Davidson & Evans (1986). The immediate migratory response to only a little frost in that winter is an indication of the precarious situation for many birds.

The decrease in the number of bird-days found in the three seasons since the engineering works is relatively small and can be explained from just the disappearance of part of the former population of the northern branch. Moreover, the loss of $\approx 10\,000$ birds in the preceding severe winters may also have contributed to this decrease. A more important indication of possible capacity problems is the shift in seasonal maximum from winter towards autumn. Such a pattern was found also in the population of a preferred tidal flat in the Oosterschelde after the closure of the adjacent Grevelingen estuary (Lambeck et al. 1989). Results therefore suggest that after the 35% decrease in area of tidal flats the Oosterschelde is now at capacity for Oystercatchers. Birds that leave are not going to France, but their present winter destination is not yet known.

Data from three winters, particularly atypically mild ones, are too few for definitive conclusions. Adaptations to the changed environmental conditions, for example, in species composition and spatial distribution, also take time for zoobenthos. Present data suggest, however, that the final consequence of habitat loss in the Dutch Delta will be an increased susceptibility to severe winters for the local Oystercatchers.

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EFFECTS OF A SUBSTANTIAL REDUCTION IN INTERTIDAL AREA ON NUMBERS AND DENSITIES OF WADERS

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ABSTRACT. A storm-surge barrier and secondary dams were built in the Oosterschelde estuary (The Netherlands) resulting in a 30% decrease of intertidal area. Total numbers of Oystercatchers in the unaffected parts of the Oosterschelde did not increase after the loss of feeding grounds in the Krammer-Volkerak. Up to 10 000 Oystercatchers failed to establish themselves in the remaining intertidal area. On the Slikken van Vianen, a small mudflat within the Oosterschelde, total numbers and densities at low water did increase due to an increase in available biomass. On the mudflats densities of Oystercatchers feeding on cockles were within the range predicted by prey biomass - bird density relationships as measured before the environmental changes. On musselbeds densities of Oystercatchers have been much higher since 1987/88. This is caused by a different availability of mussels and cockles. It is concluded that the number of Oystercatchers in the Oosterschelde is linked very closely to their food supply.

Keywords: Waders, Oystercatcher, *Haematopus ostralegus*, habitat loss, carrying capacity, numerical response.

INTRODUCTION

Understanding the effects of habitat loss has become an essential theme in applied ecology. Ultimately one should be able to forecast the effects of the removal of part of the habitat on the total population size of the species that use it.

Birds, and especially waders, offer very good subjects for study of this problem. Several species are restricted to intertidal areas during the non-breeding season and, unlike many other organisms, it is possible to get estimates, through internationally organized counts, of their total population size. Intertidal areas are very threatened with destruction all over the world. Hence much attention is being paid, mainly in the Netherlands and the UK, to studying the influence of loss of intertidal area on waders (e.g. Goss-Custard & Durell 1990).

When assessing the impact of loss of intertidal areas on wader populations, three main issues must be resolved. First, can birds, displaced from one area, establish themselves somewhere else? Second, does an increase in density of birds affect their rates of survival and reproduction because of changes in the intensity of predation, disease or competition for food? Finally, what effect do these changed rates have on population size, from the local to the species level (Goss-Custard & Durell 1990)? The first two questions have received by far the most attention. The evidence at present indicates that bird densities reach plateau values in preferred feeding areas (e.g. Hicklin & Smith 1984, Goss-Custard 1977a,b, Meire & Kuijken 1984, Zwarts 1974, Zwarts & Drent 1981) and that interference cause the birds to disperse over the available feeding sites (e.g. Ens & Goss-Custard 1984, Goss-Custard & Durell 1987). Few studies are available however, where both the occurrence of waders and their food

supply were studied before, during and after the removal of intertidal area (e.g. Evans et al. 1979).

The Delta area in the southwestern part of the Netherlands consists of the estuaries of the rivers Rijn, Maas and Schelde. The execution of the "Delta Plan" resulted in the closure of most estuaries. In the Oosterschelde a storm-surge barrier was built as a compromise between safety and environmental considerations. Its construction resulted, however, in a substantial reduction in intertidal area. First results of the effects of this large-scale engineering project on waders, especially the Oystercatcher *Haematopus ostralegus* are presented in this paper, which also discusses some aspects of carrying capacity.

MATERIAL AND METHODS

Study area

The Oosterschelde is a major estuary in the southwestern part of the Netherlands. A storm-surge barrier was built in the mouth of the estuary and two secondary dams inland. These works resulted in a strongly reduced tidal amplitude in 1986 and 1987. On completion of the secondary dams in April 1987 the total intertidal area was reduced by some 30% from 16 239 to 11 365 ha and the tidal amplitude increased again to 3.25 m compared with 3.7 m before works started. The reduction in tidal area is caused mainly by the closure of the Krammer-Volkerak, the northern branch of the estuary (for details see Smaal et al. in press). Detailed observations on the occurrence of waders in relation to their food supply were carried out at the Slikken van Vianen, a small intertidal flat in the middle of the estuary. A description of this site is given by Meire & Kuijken (1987).

Bird counts

At high water, wader counts, organised by Rijkswaterstaat Tidal Waters Division, were carried out monthly over the whole Oosterschelde estuary. Data from 1975 to 1987 have been published (Meininger et al. 1984, 1985 and 1988). Data from 1987 until 1990 were kindly supplied by P.L. Meininger. Only data for that part of the estuary that remained tidal are used. At the Slikken van Vianen counts were carried out both at low and high water. At low water, numbers in permanent plots (0.5 - 1 ha) were counted during an entire tidal cycle on 220 days between 1979 and 1990. On each day the average density of foraging birds per plot was calculated. Six plots were followed through the entire study period and for this paper additional data from 11 plots counted in 1984 are also used. Days with very short exposure time are omitted from the analysis, as also are data from 1986/87 when the storm-surge barrier was used to manipulate the tide. For relating bird densities with prey biomass only data from December counts were used. At this time bird numbers are at their maximum.

Benthic invertebrates

At the Slikken van Vianen the benthic invertebrates in all study plots were sampled annually in September or October (see Meire & Dereu 1989 for details). In this paper the total biomass (expressed in g ash free dry weight, AFDW) of cockles and mussels is used. This includes all size-classes.

To measure the visibility of mussels, 40 cores (15 cm diameter) were taken on two musselbeds. The cores were brought to the laboratory where all mussels visible at the

surface were painted. After sieving they could easily be separated from the ones not visible. All mussels were measured (maximum length).

RESULTS

Total numbers of Oystercatchers

Before and after the completion of the storm-surge barrier and the closure of the secondary dams in 1987, total numbers of Oystercatchers using the remaining intertidal area were very similar (Figure 1). This means that the Oystercatcher population which had wintered previously in the Krammer Volkerak (up to 10 000 birds) is not accounted for. In smaller areas the situation was very different. The number of Oystercatchers at high tide on the Slikken van Vianen increased during the study period, especially after 1987, indicating local changes in the distribution of Oystercatchers.

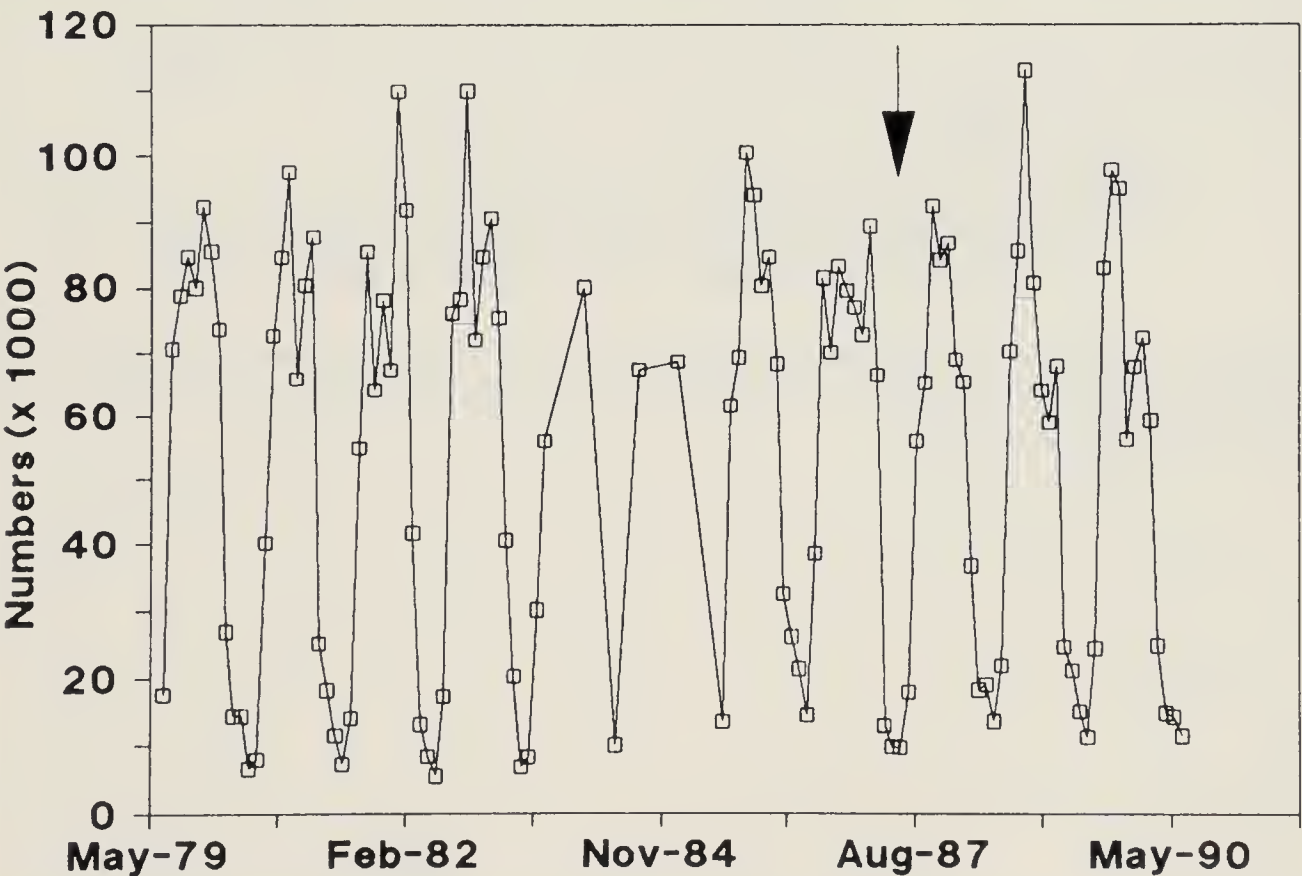


FIGURE 1 - Total number of Oystercatchers in the parts of the Oosterschelde unaffected by loss of intertidal area. Monthly totals for the seasons 1979/80 - 1989/90 are given. The arrow indicates the closure of the Philips dam, causing the loss of intertidal area.

Densities at low water: pre-barrier

As the tide falls birds spread out over the mudflats so that with low water they are distributed very unevenly. Their distribution is closely related to the available prey densities both in space and time. For Oystercatchers a clear relation between average bird density and combined biomass of cockles *Cerastoderma edule* and mussels *Mytilus edulis* was found ($r^2 = 0.81$, $N = 17$, $P < 0.001$) (Figure 2). Prey density not only influences the density of birds, it also determines the sequence in which different areas are used in the course of the season. Plots with high prey biomass are used first; as bird numbers increase, more and more feed in plots with less prey biomass (Meire & Kuijken 1984).

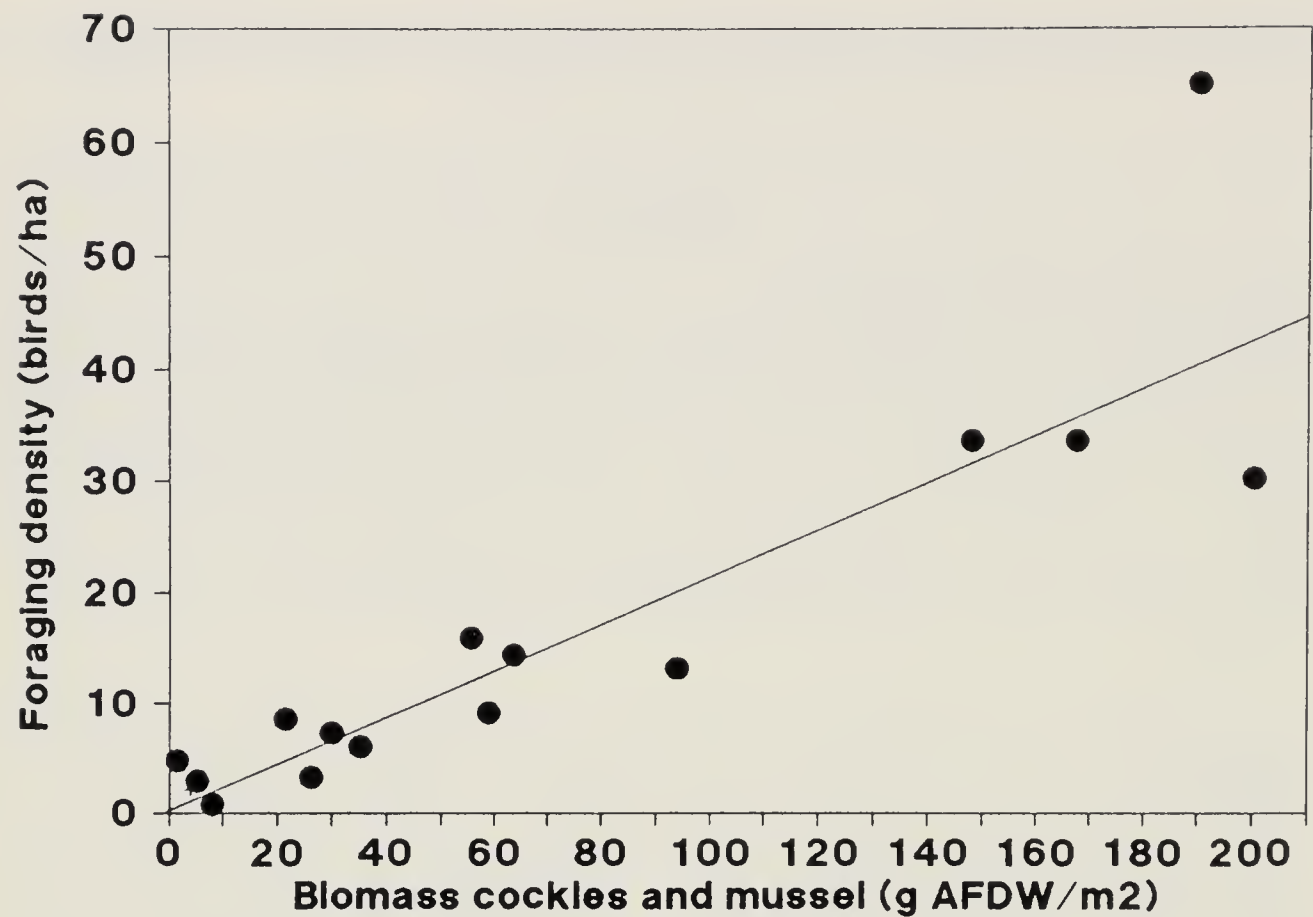


FIGURE 2 - Relation between the average density of foraging Oystercatchers and the biomass of cockles and mussel in 17 study plots of the Slikken van Vianen. The data from December 1984 are plotted.

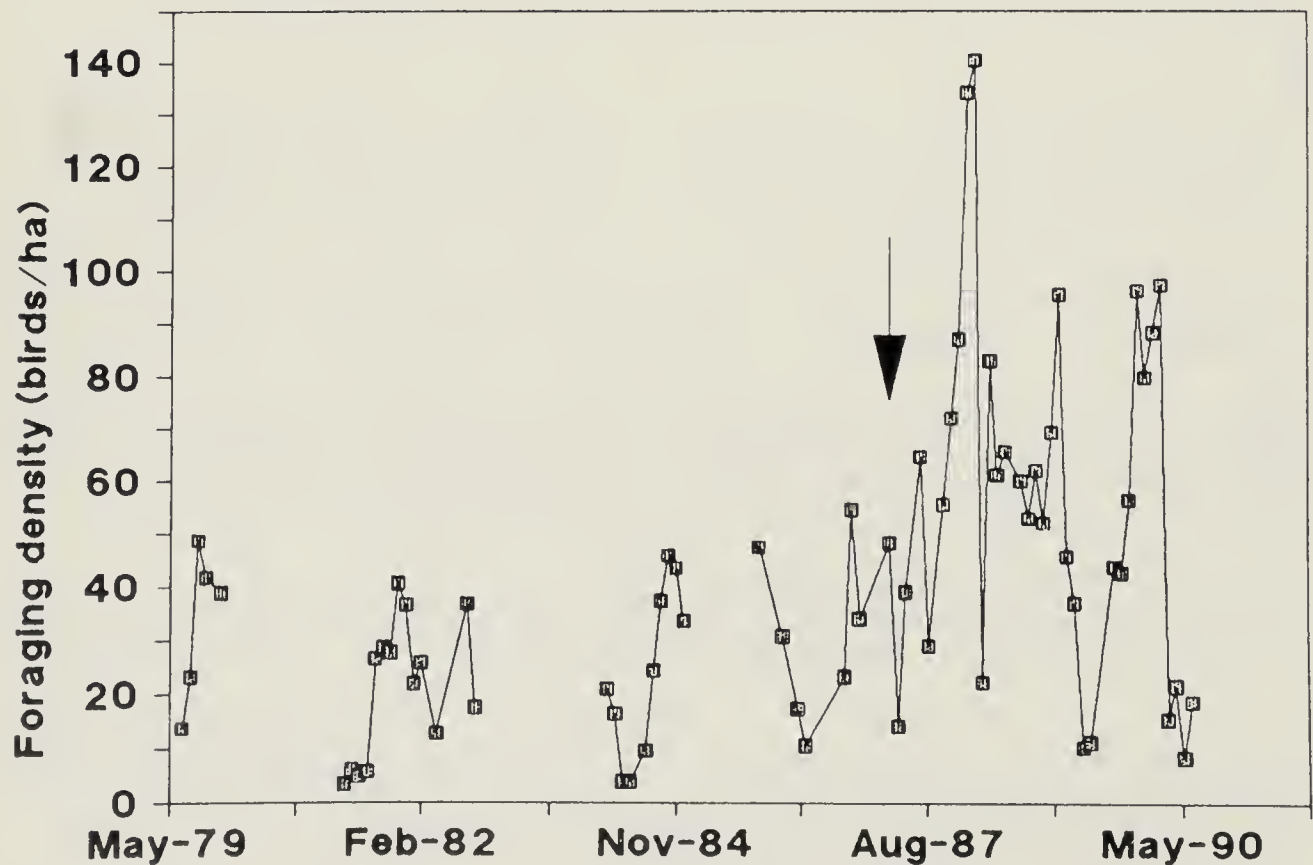


FIGURE 3 - Density of foraging Oystercatchers in one study plot (PQ 6) between July 1979 and June 1990. The arrow indicates the closure of the Philips dam, causing the loss of intertidal area.

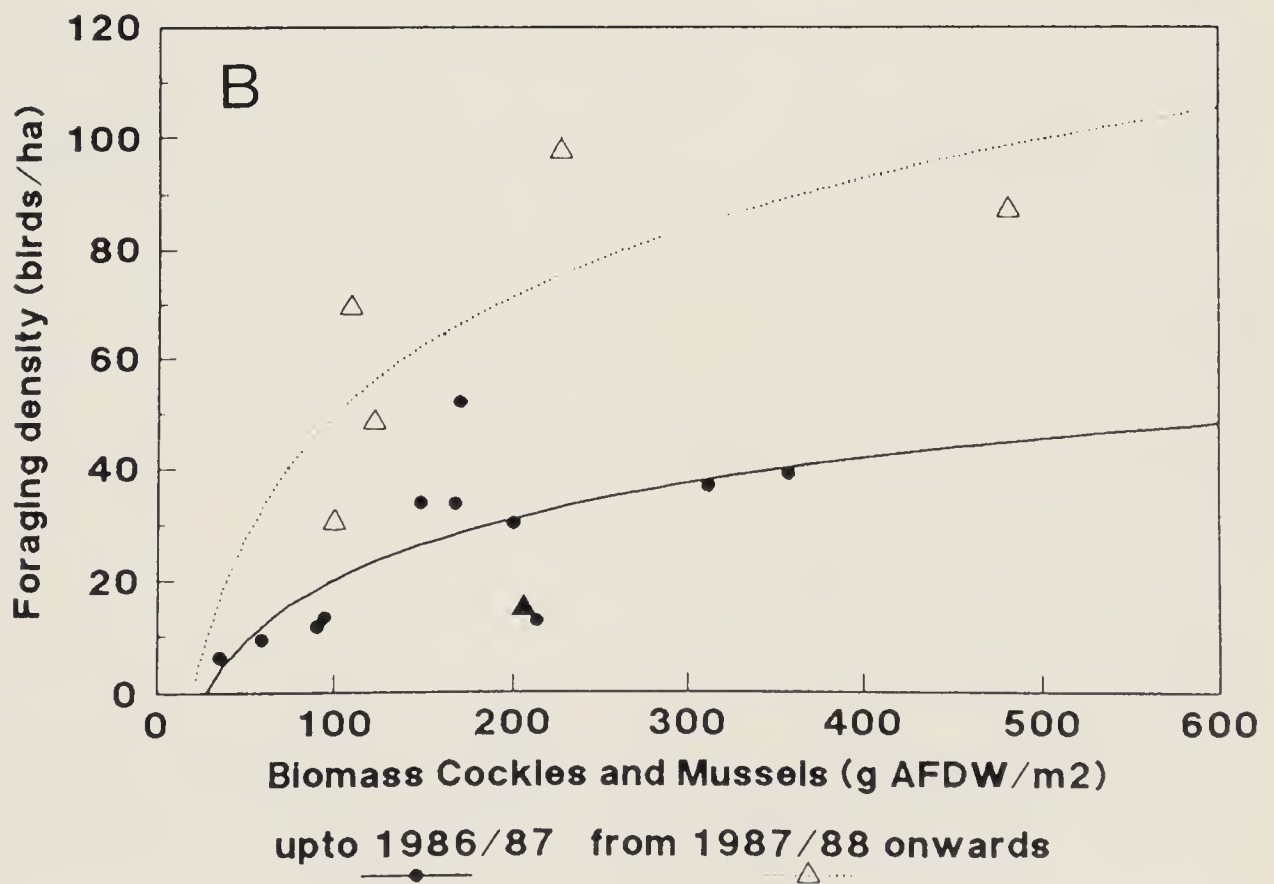
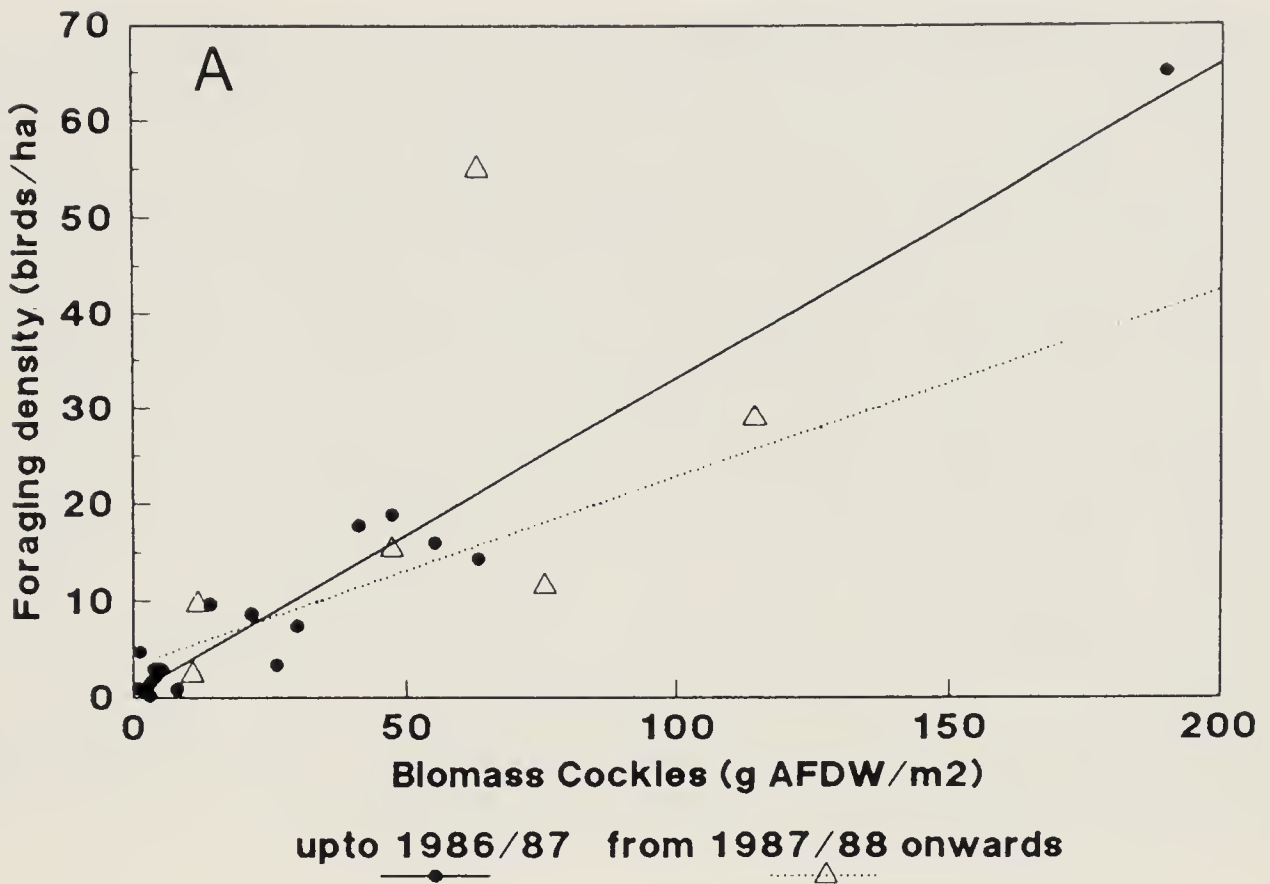


FIGURE 4 - Relation between prey biomass and density of foraging Oystercatchers in (A) non-mussel and (B) mussel plots. Data from all plots in December 1984 (17) and all December values from plots 6, 10, 13, 22, 32 and 39 were used. Values are the averages of all December counts. (Filled circle: data from 1979/80 to 1986/87; open triangle: data from 1987/88 to 1988/89; filled triangle: plot 22)

Densities at low water: post-barrier

The average density of foraging Oystercatchers per month in one study plot (PQ 6) is given in Figure 3. Between 1979 and 1986 maximum densities varied around 50 Oystercatchers per hectare and seemed quite stable. Densities increased, however, rather suddenly in the season 1987/88, and stabilized around 80 birds per hectare after a short period of extremely high densities. A similar increase in density was seen in other study plots as well. The increased densities coincided with the closure of the Krammer-Volkerak, but the question arises whether this loss of intertidal areas or another change, e.g. the available prey biomass, was the cause. In Figure 4 the relation between foraging density and prey biomass density is given for plots on musselbeds and other plots separately, based on all available data from the six plots followed during the whole study period and from all the plots studied in 1984. Before the closure of the Krammer-Volkerak a very clear relation between cockle biomass densities and Oystercatcher densities was found ($r^2=0.95$, $N=18$, $P<0.001$) (Figure 4a). After the closure, with one exception, the densities of Oystercatchers are comparable to those before closure at similar prey biomass. On musselbeds, however, with the exception of the data from plot PQ 22 (December 1988) bird densities corresponding to a given cockle plus mussel biomass density were much higher after barrier closure than before. Two different numerical responses one before the winter of 1987/88 and one thereafter are suggested by Figure 4b.

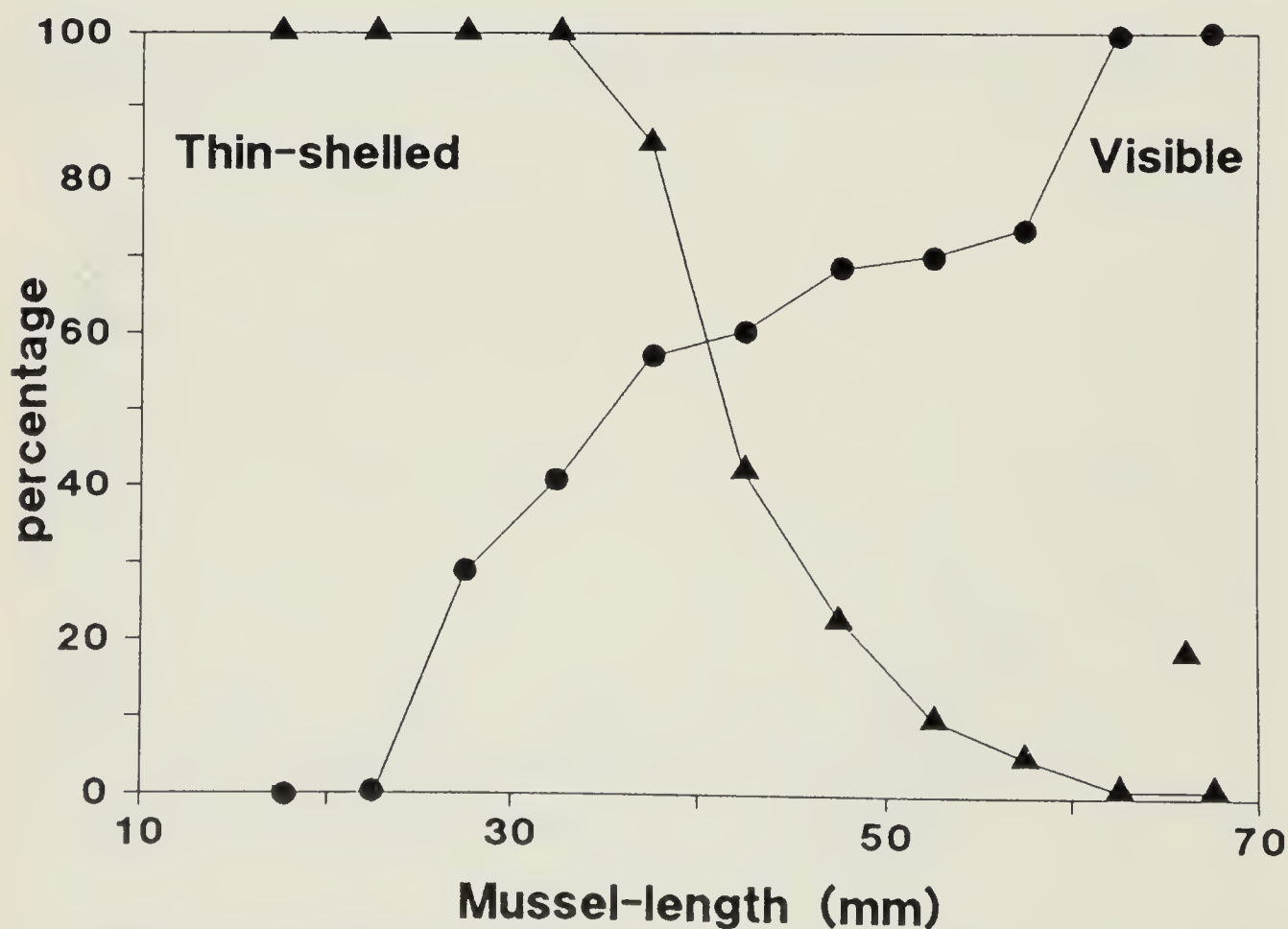


FIGURE 5 - Availability of mussels to Oystercatchers. For each length-class the percentage of mussels visible at the surface and percentage of mussels with a shell thickness within the range taken by Oystercatchers are shown.

Prey availability

The differences in the relationships between Oystercatcher densities and prey densities on the musselbeds between the two study periods might be due to differences in prey availability. On musselbeds Oystercatchers feed on cockles and mussels. Cockles contributed only 19 and 15% of the total biomass in two study plots on musselbeds between 1979/80 and 1986/87, but 68 and 77% respectively between 1987/88 and 1988/89. This change was due to an enormous spatfall in spring 1985, after the severe winter of 1984/85. How did this change prey availability? In Figure 5 the proportion of mussels visible at the surface and with a shell thickness within the range normally taken by Oystercatchers (see Meire & Ervynck 1986), is plotted by length-class. Larger mussels visible at the surface are mostly too thick for Oystercatchers. The total amount of biomass, as measured in the normal sampling procedure, is therefore not a good indicator of mussel availability for Oystercatchers, whereas it probably is for cockles. They all occur in the top few centimetres of the sediment, never one on top of the other, and thus are all available. Birds do not seem to select them by shell thickness. The very low bird densities in Plot 22 (see filled triangle and adjacent dot in Figure 4b) compared to a rather high biomass density can also be explained by low prey availability. All mussels in this plot were larger than 40 mm hence only a small fraction could have been taken by Oystercatcher.

DISCUSSION

Significantly more birds colour-ringed in the Krammer-Volkerak disappeared after dam closure than birds ringed in the remaining part of the estuary (Lambeek, this volume), strengthening the view that birds from the Krammer-Volkerak did not fit into the remaining Oosterschelde. Although total numbers using the remaining intertidal areas stayed quite constant, changes in distribution within the estuary occurred. At the Slikken van Vianen numbers did increase from the season 1987/88 onwards, coincident with, and possibly related to, the loss of intertidal area in the nearby Krammer-Volkerak. The data show, however, that on non-musselbed plots the relationship between bird and prey density was similar before and after the closure of the Krammer-Volkerak. The opposite was true for the musselbeds. From the present and earlier data (Meire & Kuijken 1984) we believed that densities had reached a plateau value on the musselbeds. The data from 1987/88 onwards, however, show that bird densities can reach much higher values. As the measured and available biomass differ in mussels, the plateau value could well be an artefact of the measure of prey biomass used. Above a certain density only a fixed amount of mussels will be visible at the surface; hence available biomass does not increase further with total mussel biomass and could explain the plateau found in the data. As the biomass became dominated by cockles in 1987/88 the total available biomass increased substantially, as did the bird densities. The data suggest a new plateau but at much higher bird densities; another artefact? At present we do not know what regulates the density of birds. Contrary to expectations (e.g. Goss-Custard 1980) their aggressiveness did not increase with bird density (unpublished data).

From this information we can conclude that the increase in bird numbers and densities on the Slikken van Vianen after the closure of the Krammer-Volkerak was entirely caused by an increased food supply. Why then did total numbers in the whole estuary not increase, as the important spatfall in spring 1985 was not restricted to the Slikken van Vianen? This was probably due to the cockle fisheries. Normally around

1 000 000 kg fish-meat of cockles are taken annually from the Oosterschelde. Because of small stocks in the Wadden Sea and the high biomass in the Oosterschelde all cockle fishermen came in September 1987 to the Oosterschelde and removed nearly 7 000 000 kg fish-meat of cockles from the estuary. On the Slikken van Vianen no cockles were fished. This probably explains why Oystercatcher numbers increased here, contrary to the rest of the Oosterschelde. Had cockles not been fished, it is most probable that birds displaced from the Krammer-Volkerak after the dam closure could have established themselves in the Oosterschelde, indicating that Oystercatcher numbers are now tightly linked to the available prey biomass or the estuary is at carrying capacity.

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IMPLICATIONS OF HABITAT LOSS AT MIGRATION STAGING POSTS FOR SHOREBIRD POPULATIONS

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ABSTRACT. Shorebirds display a wide range of migration strategies, particularly in relation to distances flown between refuelling sites. Species most at risk from habitat loss at such sites are those travelling the longest stages to reach them. These tend to be high-arctic breeding species, which have very precise time-schedules for migration, particularly in spring. Such species use their final spring staging posts to store fat and increase muscle size not only for long-distance flights but also as an insurance against food shortage on arrival at the breeding grounds. Densities of migrants on staging areas are already high, often higher than in winter. Habitat loss on staging areas could lead, through increased densities, to failure to achieve sufficiently high food intake rates to maintain correct migration timings.

Keywords: Migration, shorebirds, waders, fat reserves, protein reserves, estuaries, flight, staging post.

INTRODUCTION

Shorebirds undertake some of the longest known migrations of terrestrial species, the furthest being from circumpolar nesting areas in the high arctic to the southern extremities of South America, South Africa and Australia. Different species display a wide range of migration strategies, particularly in relation to the distances flown between refuelling sites (staging posts) on their migration routes. Even in species following the same route, some move between breeding and non-breeding areas by a series of short stages, each of a few hundred kilometres, whilst others use a few long stages, each of several thousand kilometres. These different strategies may have evolved simply because some sites are of insufficient quality for certain species for refuelling (Piersma 1987) or as a means of avoiding competition between species; but this could also be achieved by differences in timing of use of such sites (Evans & Davidson 1990). A third explanation has been suggested by Alerstam & Lindstrom (1990), who have modelled optimal migratory behaviour according to the relative importance of (1) minimizing the overall time of migration between breeding and non-breeding areas, (2) the energy used and (3) the risk from predators, as possible selection pressures. They point out that, for species in which time minimization is of overriding importance, migrants should use only those staging posts at which they can refuel (gain mass) quickly and can begin this process soon after they arrive.

The habitats used as staging posts by shorebirds on migration tend to be relatively scarce. They comprise intertidal flats and shallow (edges to) inland wetlands. At a relatively restricted number of sites, birds spend periods of a few weeks in either or both spring and autumn, often in numbers and at densities/ha greater than are found on similar habitats in the non-breeding season, and at much higher densities than on the breeding grounds (Davidson et al., in press).

The functions of staging posts

During pauses in migratory flights, birds restore fat reserves and muscle and organ masses to levels appropriate for the next stage of their migration. At least in spring, additional reserves are stored to enhance the birds' chances of survival at their final destinations if these are in mid to high northern latitudes. For example, Knot *Calidris canutus* that winter around North Sea coasts return to their breeding areas in Greenland and eastern arctic Canada by way of either Iceland or north Norway (Davidson & Wilson 1991). Those staging in north Norway leave with masses of fat and pectoral muscle larger than necessary for the flight to their breeding grounds (Evans 1991); about 68% of the increase in body mass is fat. Recent studies of spring migration at the Banc d'Arguin, Mauritania, and the Wadden Sea, however, have shown that only about 50-60% of the mass gained is fat (Piersma & Jukema 1990, Piersma & Van Brederode 1990). Since water content is about 69% of lean mass, 12.5-15.5% of the mass gained must be tissue formed largely of protein. The availability of both high protein and high energy foods at these staging areas may therefore be an important feature of site choice.

In Bar-tailed Godwits *Limosa lapponica* about half the lean dry mass increase was concentrated in the pectoral muscles of birds departing in early spring from the Banc d'Arguin, but pectoral muscle hypertrophy accounted for only 15% of the (larger) increase in late spring on the Wadden Sea (Piersma & Jukema 1990).

Pectoral muscle mass of Knots increases substantially in Balsfjord, Norway, to the size needed to power efficient flight with the much increased total mass (Davidson & Evans 1988). However, as for godwits in the Wadden Sea, the contribution of pectoral muscles to the gain in lean dry mass of Knots is surprisingly small (14.8% in males, 11.0% in females), indicating substantial protein storage elsewhere in muscles and body organs. Based on average masses of arriving and departing birds in Balsfjord (Evans 1991), this amounts to a gain of 3.5-4.0 g of protein at this staging post. The pattern of protein gain, with more 'non-flight' protein being stored at more northerly staging areas, suggests that much of the protein reserve carried to the breeding grounds is stored only on the last spring staging area. This emphasises the critical importance of such sites in the annual cycle of waders.

Studies on Ellesmere Island, Canada, confirmed that Knot arrive there with considerable reserves of fat and protein (in at least the pectoral muscles) (Morrison & Davidson 1990). Since the reserves in the pectoral muscles alone, if not needed for immediate survival, could contribute up to 40% of the requirements for production of a clutch of eggs (Davidson & Evans 1988), additional reserves elsewhere in the body mean that most of the clutch protein could come from reserves.

Departure from a staging post with more than enough fat for the subsequent flight stage has been noted not only at the final spring staging post but also at earlier staging posts along the migratory route (Davidson & Evans 1988). Various complementary interpretations are possible: (a) to guard against food shortage or bad weather at the next staging post, which might depress the rate of refuelling (Evans 1990); (b) to enable migrants flying at maximum range speeds which increases with total body mass, to set out with higher optimal airspeeds for flight stages during which they are likely to encounter headwinds; and (c), in migrants attempting to minimize the overall time for their journey, to capitalize on the higher rate of fat deposition possible at

that staging post than at the next staging post on the route; this depends in part on the distance to the next staging post (Gudmundsson et al., in press).

No matter how good are the feeding opportunities at a particular stopover site, there will be a maximum body mass attainable by each species, above which it is unable to take off. This will limit the distance which the migrant can travel before needing to use another refuelling site, unless it relies on wind-assisted flight – e.g. Bar-tailed Godwits migrating from northwest Africa to the Wadden Sea in spring (Piersma & Jukema 1990). In some springs, Knots that winter on the Banc d'Arguin break their flight towards the refuelling grounds in the German Wadden Sea by landing on the Vendee coast, France. Their body masses on arrival there are very low, averaging 120 g; they stay long enough to store sufficient fat to fly on to the Wadden Sea but not to their ultimate destination in Siberia (Dick et al. 1987). Recent analyses suggest that they land in France not because they left Mauritania with lower than normal fat reserves but because they were assisted by fewer tailwinds in flight (Piersma et al. in prep.; see also Piersma & Jukema 1990).

Partial loss of habitats at staging posts

Shorebirds preparing for migratory flights obtain the extra food they need for fat deposition and muscle hypertrophy either by lengthening their hours of feeding in the tidal cycle, e.g. Sanderling *Calidris alba* and most other species on the Banc d'Arguin, Mauritania (Zwarts et al. 1990), or by increasing their food intake rate e.g. Knots on the Wadden Sea (Piersma et al. in prep), perhaps by decreasing the proportion of time they spend in vigilance, e.g. Turnstones *Arenaria interpres* (Metcalf & Furness 1984).

Partial loss of habitats at a migration staging post could have different effects on these two types of species, depending on the precise parts of the habitat made unusable. Many land-claim schemes, on coasts and in estuaries, preferentially remove or cover the upper tidal levels of the shore and so limit the maximum duration of feeding by shorebirds in each tidal cycle. This would depress the rate of fat deposition by Sanderling-type migrant species more severely than by Turnstone-types. Removal of parts of the habitat which regularly hold the highest densities of available foods (particularly invertebrate prey) could affect both types of migrant species. Food intake rates, crucial in determining the rate at which fat and protein can be synthesized, could be reduced if available prey densities, remaining after habitat loss, fall below some threshold value, irrespective of how few birds are present. A higher rate of intake of ragworms by Dunlin *Calidris alpina* on a Moroccan estuary was measured in 1982 than 1981, associated with an increase in polychaete biomass density from 5.4 to 14.9 g/m² (Piersma 1987). (The effects on shorebirds of discharges of certain pollutants on to a migratory staging area would be similar if such chemicals reduced densities of available prey.)

Alternatively, if the densities of available food remaining after loss of the best parts of the habitat still exceed the threshold (above which intake by an individual is unaffected by prey density), crowding of migrants into a smaller area of habitat on the staging post could lead to increased interference between birds and so to lower intake rates (see Sutherland & Goss-Custard, this volume). Reduced rates of fat synthesis and muscle hypertrophy could have one of two effects:

- (1) if a species' migration is strictly time-programmed, birds would leave the staging area with lower reserves of fat and smaller muscles than usual. This would reduce their flight speed, reduce the time for which they could survive without food on the next staging post (or at their destination) and in spring might prevent early breeding; at worst, if their migration was over inhospitable land or sea, they might not reach their destination.
- (2) If a species' departure is controlled by the need to exceed some physiological threshold of fat and muscle levels, birds would leave later than 'normal'. The Dunlin in Morocco, mentioned above, stayed at their staging site for an average of 11 days when their food intake rates were high but for 16 days when they were low (Piersma 1987).

The consequences of delayed departure from a staging post near the start of the migration could be cumulative (the "domino effect" - Piersma 1987). If a migrant is able to accumulate fat and muscle protein only slowly on one site and therefore leaves later than its conspecifics, it will need to refuel faster than average on the next staging post in order to catch up with the overall time-schedule for its migration. Yet by arriving later on the next staging area than its conspecifics, it is unlikely to be able to gain access to the best feeding areas and so is unlikely to be able to refuel faster than average; if anything, the reverse. Shorebirds may remove large proportions of the standing crop of invertebrates at a staging post (Schneider & Harrington 1980), so there may be penalties attached to late arrival, particularly if food resources have been reduced below "profitability threshold" (see above).

Total loss of staging areas

The significance of total loss of a staging area depends upon the overriding selection pressures determining the migration strategy of each species. Time-minimizing species are predicted not only to depart from staging posts with an "overload" of fat but also to bypass certain possible staging sites, in an attempt to reach others further along the route where higher rates of gain of mass are possible (Gudmundsson et al. in press). Loss of one of the preferred staging sites might not, on this model, be expected to disrupt the species migration pattern completely, because they might use one of the formerly bypassed sites instead. But it would certainly delay the time of arrival at the destination. Whether the species could readjust its time-schedule by departing earlier in spring from its non-breeding areas, is open to question. Whimbrels *Numenius phaeopus* leaving the Banc d'Arguin probably cannot do so earlier because they depend on an increase in food availability brought about by the reproductive cycle of fiddler crabs (Zwarts 1990).

Another important question related to enforced change of refuelling site is the likelihood of bringing species, or even populations of the same species, into competition which they had previously avoided. This of itself could reduce the rates of replenishment of fat and muscle protein and so slow down the overall time-programme of migration, again causing delay in the date of arrival at the destination.

Clearly the most crucial staging posts of all are the final departure points for the breeding grounds in spring. Alerstam et al. (1986) have drawn attention to the difficulties facing birds which make use of breeding areas within the high arctic. There are few suitable refuelling sites from which they can prepare for the long final flight stage over inhospitable terrain which they must then accomplish. At present, the fat loads

carried by species from Iceland and north Norway are greater than needed for the flight to Ellesmere Island, for example, but may be close to the physiological or anatomical limits to flight at take-off. Thus although birds might be able to reach their breeding areas from staging sites further away, e.g. the North Sea coasts, they would arrive without any reserves which could be utilized in the arctic for survival or accelerated breeding. For example, Knots departing from the Wadden Sea in spring and flying direct to breeding grounds on northern Ellesmere Island must fly approximately 4 000 km. Assuming they depart with 35% of their body mass as fat (a typical spring departure condition - see e.g. Davidson & Evans 1988; Gudmundsson et al. in press) and fly at 65 km.h⁻¹ this distance is close to their maximum still-air flight range of 3 800-4 400 km estimated from Davidson (1984). Such birds bypassing late spring staging areas could shorten the overall distance flown since the route via Iceland or Norway they currently use is not the most direct to their breeding grounds. Such more direct routes may not, however, always be advantageous. Waders taking the shortest route from the southern North Sea to Ellesmere Island would need to cross the Greenland inland ice, where strong head-winds are much more frequent than those faced by birds on the routes via Iceland and Norway (Alerstam et al. 1986). Indeed Alerstam et al. speculate that it is for this reason that waders fly a 'dog-leg' route to the Nearctic via Iceland and Norway. Loss of a final staging area could have serious population consequences, since breeding failures and mortality of adults from starvation during very severe weather early in the breeding season has already been reported in Knots (Morrison 1975) and is implicated in a major population decline of that species (Davidson & Wilson 1991).

The importance of localized and temporary food resources at staging posts

A few sites provide superabundant invertebrate foods for shorebirds at appropriate places and times of year so that migrants can use them as staging posts. The best-known example is Delaware Bay where horseshoe crabs spawn in May at precisely the correct time for Red Knot, Ruddy Turnstone, Sanderling and other shorebird species heading for Alaska and the central Canadian arctic to utilize them. Clearly any habitat interference or degradation that would reduce the food resources available at such sites would affect very large proportions of the populations of some species. Because reproduction of particular invertebrates is often brief and highly synchronized, a site may provide shorebird foods for only part of a year and so be used only on spring or on autumn migration.

Risks of predation at staging posts

Whitfield et al. (1988) raised the possibility that raptor predation on waders on migration might be a selective pressure leading to the minimization of migration distances; but predation at staging posts could also be important. Davidson & Evans (1986) summarized data from the north Norwegian staging site of Knots which indicated that birds tended to avoid the areas where the risk of predation was highest, even though the density of available food was highest there. When birds did feed there, they were more vigilant and their food intake rates were lower than elsewhere. Thus habitat loss, even of areas of poorer densities of available prey, may reduce the potential refuelling rate of migrants, if they avoid other areas because of predation risk.

Staging posts used by juveniles on their first migration

It is a commonplace observation that juvenile waders occur in a much wider variety of sites and habitats while on migration in late summer and early autumn than they

use in winter and than are used by adults. These additional sites often resemble the habitats in which they fed either as chicks or just after fledging. Such behaviour may be beneficial for juveniles as they may not need to develop new searching and foraging techniques to take the novel prey they encounter; hence they can begin to regain fat and muscle reserves very soon after arrival on a staging post. Segregation between adults and juveniles may occur on large estuarine and tidal-flat staging posts. Such behaviour occurs in Dunlin in late summer on the Dutch Wadden Sea (Van der Have et al. 1984). They suggest that juveniles, which arrive after adults, move to less favoured areas inshore, where bird density is lower. They consider that the additional habitats used by juveniles (sand beaches, saltmarsh and margins of freshwater ponds) are marginal quality, low-density sites for Dunlin, rather than actively selected habitats. Even with use of such sites, the survival rate of juveniles (calculated from ringing recoveries) was lower for juveniles than for adults – but it is not clear whether both groups of birds wintered in the same area.

Removal of those parts of staging posts used by both adults and juveniles in autumn could lead to reduced survival of juveniles if Van der Have's hypothesis is correct. Behavioural dominance of adults over juveniles is known to occur in Grey Plovers (Townshend 1985), though it does not seem to occur in Sanderlings once they have reached a potential wintering area; indeed survival of adults and juveniles is then equal (Pienkowski & Evans 1985). However, lower dominance leading to poorer survival could still be the rule during migration.

The extent of mortality during migration is still inadequately known for juvenile shorebirds. Although, in total, it is sometimes higher than that of adults (Pienkowski & Evans 1985), it is not known whether most losses occur during flight (as a result of adverse weather or avian predators) or on the ground (through choice of inappropriate refuelling sites, with high mammalian predation, or poor food resources). Thus the importance of retaining sites used by juveniles but not by adults in autumn is not clear at present.

In the middle of the East Atlantic Flyway, possible refuelling areas are fewer and more widely spaced, e.g. along the northwest African coast (Smith & Piersma 1989). Loss of any one of these could markedly lower juvenile survival, as many birds (but an unknown percentage) reach such sites in extremely poor body condition (Dick & Pienkowski 1979). A similar situation occurs in northwest Europe for juveniles crossing the north Atlantic from Iceland or Greenland to northwest Scotland and western Norway.

Accumulation of sufficient reserves before departing from breeding grounds in autumn is known to be critical to the survival of juveniles of other arctic breeding birds. High juvenile mortality of Svalbard-breeding Barnacle Geese *Branta leucopsis* occurred in a year when autumn weather deteriorated exceptionally early on the breeding grounds and also prevented part of the population using a staging area on Bear Island. Juveniles that did manage to complete the migration despite the additional weather stresses were significantly heavier when caught on the breeding grounds in late summer than birds which failed to reach their wintering grounds (Owen & Black 1989), and these authors suggest that such losses on autumn migration, due to inadequate nutritional reserves, may be the single most important factor controlling non-hunted goose populations.

CONCLUSION

We are now beginning to understand the mechanisms by which waders make their long migrations to and from their breeding grounds, and the nature of the constraints they face in doing so. With a few exceptions, however, the extent to which individuals and populations are restricted in their choice of staging areas, and the extent to which the rate of fat and protein hypertrophy is limited in birds on their staging site, are very poorly understood. Further work is needed to establish whether species other than Whimbrels in the Banc d'Arguin are ingesting food at a maximal rate on staging sites.

There has been even less attention paid to the feeding conditions and migrational implications offered by other, potentially alternative, staging sites on a flyway. Such studies, particularly on sites that are only occasionally used as 'emergency' staging areas, are vital. They need to determine the extent to which there really are alternative, perhaps poorer quality, staging areas available to migrating waders. The prospect that some primary staging sites will be degraded by the continuing wetland habitat destruction is a real one; the full implications have yet to be assessed.

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EFFECTS OF HABITAT LOSS THROUGH CHANGES IN AGRICULTURAL PRACTICE ON WADERS BREEDING IN WESTERN EUROPE

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ABSTRACT. Agricultural intensification has led to increases in field size, replacement of hay crops by silage production, reseeded of natural grasslands or heathlands, drainage of wet pastures or marshes and elimination of crop rotation. Many shorebird species breeding in the temperate zones use agricultural land at some stage during their breeding cycles, but it is often part of a mosaic of habitats needed for successful reproduction. Increases in size of habitat units may be detrimental, particularly for species that rear broods close to their nest-sites. Disappearance of vegetation tussocks after "improvement" of pastures makes nests and young chicks more vulnerable to predators. Seasonal timing of maximum food abundance may also change. Species showing marked habitat preferences and/or fidelity to their hatching site (or previous breeding place) are at greatest risk of local extinction from habitat alteration.

SYMPOSIUM 41

**SEABIRDS AS MONITORS OF CHANGING
MARINE ENVIRONMENTS**

Conveners R. W. FURNESS and D. N. NETTLESHIP

SYMPOSIUM 41

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INTRODUCTORY REMARKS: SEABIRDS AS MONITORS OF CHANGING MARINE ENVIRONMENTS

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Fisheries exploit most of the world's major fish stocks and many of these have declined and fisheries closed as a consequence of environmental change and/or overfishing (Rothschild 1983). Many fish stocks are extremely difficult to monitor directly, which makes it difficult to reach management decisions quickly and accurately (Cushing 1988). Furthermore, many important populations of natural predators, including seabirds, depend on particular fish stocks and may be influenced by changes in stock biomass (Furness 1982, Nettleship et al. 1984). Modelling of fish consumption by seabirds has increased awareness of the quantitatively important role of some seabird populations as consumers of marine prey stocks (Croxall 1987, Furness 1990) and studies of seabird ecology have indicated that many populations are likely to be limited by food resources, particularly when tied to a local area by the need to breed (Gaston et al. 1983, Furness & Birkhead 1984, Hunt et al. 1986, Birt et al. 1987).

Generalist-feeding seabirds may respond to reductions in prey stocks by exhibiting changes in diet (Montevecchi et al. 1987), while seabirds specialising on a particular prey may increase foraging effort, suffer reduced chick growth or reduced breeding success, may opt not to breed, may emigrate, or may suffer increased mortality (Cairns 1987, Hamer et al. 1991). Thus it may be possible to use the breeding ecology of seabirds as a monitoring tool to follow changes in prey stocks (Batty 1989). Empirical observations of long-term changes in seabird population ecology, prey stocks and environmental factors can show correlated changes, although causal mechanisms may be difficult to establish (Anderson et al. 1980, Aebischer et al. 1990). However, it seems likely that we can predict which seabird species would be most suitable as prey monitors. Points we wish specifically to address are:

1. In which areas of fish stock monitoring might the data obtainable from seabirds be of value?
2. Do studies of seabirds feeding at sea support the ideas that the biology of seabirds at colonies may provide a reliable picture of prey populations at sea?
3. Which case studies of seabird breeding ecology show significant and useful correlations between seabirds and the abundance of prey stocks?
4. Which case studies show a lack of a clear response of seabirds to changes in prey stocks, and why?
5. What are the merits and disadvantages of monitoring the diet of generalist feeders compared with monitoring the breeding of prey specialists?
6. Can general rules be formulated for the use of seabirds as monitors of prey stocks or must each seabird-prey relationship be examined empirically?

We believe that consideration of these questions can lead to an enormously fruitful area of research in the immediate future and that this may have considerable applied value.

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ECOLOGICAL RESPONSES OF SEABIRDS TO REDUCTIONS IN FISH STOCKS IN NORTH NORWAY AND SHETLAND

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ABSTRACT. Between 1971 and 1990 data on seabird breeding ecology have been collected each year on Foula, Shetland, and in some years at Hornøy, northeast Norway. At both sites stocks of the major prey fish were thought to have declined considerably during the study period. Our seabird data suggest that a previously unidentified local stock of capelin *Mallotus villosus* exists in northeast Norway independently of the Barents Sea stock so that seabird breeding does not reflect changes in the Barents Sea stock. In Shetland, seabirds, especially dietary specialists that cannot reach the seabed, showed extensive changes in breeding ecology as sandeel *Ammodytes* stock declined, although the seabird data correlate much better with a fishery-independent estimate of abundance than with fishery-derived VPA estimates.

Keywords: Monitoring, seabirds, fish stocks, breeding ecology.

INTRODUCTION

With regard to the possible effects on seabirds of overfishing of their food species, Furness & Ainley (1984) identified six characteristics that are likely to predispose certain seabird species to being severely affected by decreases in their food supply during the breeding season: surface feeding habits, specialised and inflexible feeding and diet, short foraging range from the breeding colony, limited ability to increase time spent foraging, energetically expensive food-searching, low tolerance of chicks to short-term fluctuations in food supply. They identified terns and penguins as possessing most of these features and suggested that they may be particularly sensitive to changes in fish stocks. In this paper we review fieldwork in north Norway and Shetland where pronounced decreases in food supplies were believed to have occurred. We test the ideas presented above and consider some complications that affect the simple responses predicted. Our studies suggest that the use of seabirds as monitors of fish stocks will only be possible at a very crude level and will require detailed research into the relationships between particular fish stocks and seabird populations.

METHODS

The methods used are described by Furness & Barrett (1985, in press) Barrett & Furness (1990). Data on Barents Sea capelin *Mallotus villosus* stock biomass were obtained from annual reports of the Norwegian Fisheries Laboratories (mostly summarised by Hamre 1988). Data on Shetland sandeel *Ammodytes marinus* stocks were obtained from Bailey et al. (in press). Sandeel abundance was assessed by Virtual Population Analysis (based on fishery-derived data) and also by analysis of catches by a mid-water research trawl. Because numbers of sandeels caught per research trawl were highly variable between trawls and sample sizes were small in most years,

we calculated 3-year running averages of the geometric mean number caught per haul in each year and used this running mean as an index of changes in sandeel abundance around Shetland over the study period.

RESULTS

Barents Sea capelin and seabird breeding ecology in north Norway

In the Barents Sea the capelin stock (estimated acoustically) fell from 3-7 million tonnes in 1972-80 to 2.5 million tonnes in 1981-84, to 0.02 million tonnes in 1987, 0.4 million tonnes in 1988 and 0.2 million tonnes in 1989. Capelin and sandeels were the main prey of seabirds breeding on Hornøya in north Norway in 1983 (Furness & Barrett 1985). Despite the enormous decrease in capelin stock, seabirds at the same study colonies bred successfully in 1989 and their diets contained more capelin than in 1983 (Barrett & Furness 1990). The seabirds showed no evidence of food shortage while breeding, and so could not be used as an index of changes in the Barents Sea capelin stock (Furness & Barrett in press). However, we found that gravid female capelin predominated in the diet of chick-rearing guillemots *Uria* spp. in June-July. Since Barents Sea capelin spawn in March/April we suggest that the seabirds on Hornøya were exploiting a local fjordic stock of capelin with different spawning, and probably different population trends from the Barents Sea stock. The detection of this apparently distinct capelin stock, if validated by fisheries biologists, can be attributed to the study of seabird breeding ecology.

A massive decline in breeding numbers of Common Guillemots *Uria aalge* occurred when Barents Sea capelin stock collapsed in 1987, and this has been attributed to winter starvation (Vader et al. in press). This winter mortality of Common Guillemots seems to be the avian response most visibly linked to the changes in Barents Sea capelin stock biomass, and is probably linked to capelin biomass only when stock size is small.

Sandeels in Shetland

In Shetland, the sandeel is a major prey of most seabirds, at least during the breeding season. The local Shetland sandeel stock has been harvested by an industrial fishery since 1974 and this has provided data for a Virtual Population Analysis (VPA) giving estimates of stock biomass, recruitment and age structure. Research surveys by Department of Agriculture and Fisheries for Scotland (DAFS) have provided independent limited data on sandeel densities in the water column in June/July from 1970-88. The VPA and midwater trawl data show quite different patterns. Both data sets show a massive decrease in sandeels at Shetland; recruitment appears to have failed since 1984 but numbers in the water column fell from 1977 to very low levels since 1980, although VPA data suggest that the total stock increased to a peak in 1983 (Bailey et al. in press).

Seabird sensitivity

Numbers of breeding pairs of predicted 'indicator' seabirds at Foula (Arctic Terns *Sterna paradisaea*, Arctic Skuas *Stercorarius parasiticus*, Kittiwakes *Rissa tridactyla*, Great Skuas *Catharacta skua* - mostly surface feeding, inshore, with little opportunity to increase time spent feeding when rearing chicks) - generally show increasing numbers until the late-1970s with declining breeding numbers into the 1980s (Furness &

Barrett in press). Breeding failure since 1983 has been most frequent among Arctic Terns, Puffin *Fratercula arctica*, Arctic Skua and Kittiwake, species that fulfil at least some of the sensitivity criteria proposed by Furness & Ainley (1984). However, the two factors that seem to separate less affected species from those suffering severe breeding failures are ability to switch diet or ability to dive to the seabed to feed (Table 1). Common Guillemots and Shags *Phalacrocorax aristotelis* have shown no reduction in breeding success despite feeding chicks almost exclusively on sandeels, but breeding numbers of both species have fallen. As in northeast Norway, population declines in these species could reflect increased winter mortality of these relatively sedentary species.

TABLE 1 – Breeding failures of seabirds that fed predominantly on sandeels at Foula, Shetland, since 1983 in relation to the sensitivity criteria listed by Furness & Ainley (1984). For each year breeding failure is defined as achieving breeding production less than half that in the years 1971-83.

Species	Number of years of breeding failure 1983-90	Sensitivity criteria met				
		Surface feeder	Narrow diet and method	Short range	Limited time available to feed	Little fat on chick
a) species that switched to an alternative diet						
Great Skua	3	+		+		
Fulmar	1	+				
Gannet	0	+				
b) species that can dive to feed at the seabed						
Red-throated Diver	3			+		
Shag	0		+	+		
Guillemot	0		+			+
c) species that depend on sandeels and cannot reach seabed						
Arctic Tern	7	+	+	+	+	+
Puffin	5		+			
Arctic Skua	5	+	+	+	+	+
Kittiwake	4	+			+	+
Razorbill	3		+			+

Quantitative relationships between seabirds and sandeels

At Foula, Arctic Tern breeding success has been zero each year since 1984, which correlates with a reduced recruitment of sandeels at Shetland since 1984 after high levels in 1980-83. However, tern breeding success was high in 1974 and 1975 when sandeel recruitment was low according to the VPA data. In general, numbers and breeding success of predicted sensitive species correlated better with the midwater trawl estimates of sandeel abundance in the water column than with the VPA data (Table 2). Relationships can generally be described adequately by linear regressions against sandeel abundance rather than requiring sigmoid ones as predicted by Cairns (1987). The diet of nonbreeders of the generalist Great Skua shows a correlation with sandeel availability according to trawl data but not with VPA data, while presumed

sensitive sandeel specialists show changes in population size and breeding success related more closely to trawl than VPA data (Table 2). Although the midwater trawls were performed over a much wider area around Shetland than used by the industrial fishery for sandeels, were not designed to monitor sandeel stocks, and their utility in this regard is uncertain, midwater trawl data may provide a better picture of sandeel availability to seabirds than given by the VPA analysis. Indeed, it is difficult to see why seabird breeding failures should have occurred in the mid-1980s if sandeel stock biomass was really as large as the VPA suggests. If the seabird responses do reflect changes in the sandeel stock, either the VPA data do not provide an accurate picture of sandeel abundance or the availability of sandeels must have altered dramatically. The highlighting of this discrepancy by seabird data may help to clarify the uncertain picture regarding the changes in sandeel stock at Shetland over recent years, but shows another of the difficulties in establishing the value of seabirds as monitors of prey stocks; in order to establish a clear relationship between seabirds and prey the prey stock dynamics must be accurately known.

TABLE 2 – Correlations between seabird breeding numbers, breeding success or diet at Foula and measurements of sandeel stock abundance or availability around Shetland (3-year running averages of the geometric mean number of sandeels caught per haul in midwater trawls in June-July 1971-88; VPA estimated biomass of sandeels on 1 July each year and of numbers of sandeel recruits (0-group fish) on 1 July each year, 1974-88; data from Bailey et al. in press). Correlations statistically significant at $P<0.05$ are shown with an asterisk.

Seabird	Parameter	Units	Correlation with:		
			Sandeels per haul	VPA estimated number of recruits	stock biomass
Arctic Tern	numbers	pairs	0.78*	0.16	0.12
Kittiwake	numbers	nests	0.54*	0.37	0.06
Arctic Skua	numbers	territories	0.64*	0.54*	0.41
Great Skua	numbers	territories	0.60*	0.80*	0.81*
Arctic Tern	success	chicks/pair	0.34	0.47*	0.16
Arctic Tern	success	chicks fledged	0.63*	0.14	-0.13
Kittiwake	success	chicks/nest	0.64*	0.61*	0.54*
Great Skua	nonbr.diet	% sandeel	0.68*	0.09	0.10

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AVIAN INDICATION OF PELAGIC FISHERY CONDITIONS IN THE SOUTHEAST AND NORTHWEST ATLANTIC

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ABSTRACT. Avian data can be used to assess fishery conditions and trophic changes in marine ecosystems. Ornithological assays provide inexpensive, catch-independent information about the availability, spatial and temporal distributions and cohort strengths of surface-shoaling pelagic prey. Such independent data are needed to assess and complement traditional fisheries techniques, based on commercial and research catches and hydroacoustics, and to develop abundance estimates and forecasting of collapse-prone pelagic fishery conditions. Avian dietary data are useful for surveying prey that are not systematically studied, i.e. usually not commercially exploited, and for delineating changes in trophic pathways resulting from natural and anthropogenic effects. Mesoscale comparisons of prey harvests by gannets and fishermen in the southeast and northwest Atlantic show that avian data provide real-time and predictive estimates of (1) relative abundance, cohort strengths and distributions of pilchards, (2) success or failure of local squid fisheries, (3) migratory patterns of post-smolt Atlantic salmon (from tagged fish too small for entrapment by conventional gear), and (4) availability and distribution of unsurveyed, commercially exploitable pelagic fish. Advances in understanding marine ecosystems are to be expected as marine ornithology is integrated into multi-disciplinary, oceanographic research programs.

Keywords: Anchovy, Benguela region, bio-indication, gannets, northwest Atlantic, pelagic fisheries, pilchard, South Africa, salmon, saury, squid.

INTRODUCTION

Changes in avian populations are usually far too removed, temporally and often spatially, from environmental fluctuations that affect them to provide useful indication of these fluctuations (Morrison 1986, Furness 1989, Temple & Weins 1989). Such findings have led to a tendency to uniformly reject information derived from birds as being of any value in assessments of environmental condition (Morrison 1986, Temple & Weins 1989). While populations of long-lived species can be expected to be resistant to environmental change, physiological, behavioural and reproductive parameters that buffer populations from environmental flux will be very responsive to changing external contingencies. These aspects of avian biology and ecology provide potential sources of bio-indication.

Avian reactions to environmental change range from molecular through behavioural and reproductive responses and can be measured to study fluctuations in fisheries and oceanographic conditions (e.g. Crawford & Shelton 1978, Hislop & Harris 1978, Monaghan & Zonfrillo 1986, Cairns 1987). Different parameters of avian biology integrate prey availability over characteristic temporal and spatial scales. For example reproductive success may represent seasonal or annual variation in food supply, whereas foraging activity reflects prey availability on shorter time and distance scales (Cairns 1987, Croxall et al. 1988). Avian dietary studies represent direct linkages

between birds and prey and provide immediate, real-time determinations of prey species composition, availability, age (size), condition and spatial distribution. These data can be integrated over longer periods to assess decadal changes in prey conditions and trophic relationships.

Pelagic fisheries are a significant component of the world's food economy. Pelagic fish and squid are highly mobile, patchily distributed in surface waters and consequently very difficult to survey by conventional methods (i.e. catch and acoustic surveys, e.g. Clarke 1977). Pelagic species are also characterized by large interannual fluctuations in recruitment and biomass availability (e.g. MacCall 1979, Shelton et al. 1985). Purse-seine fisheries directed at pelagic prey have been prone to collapse, and management implementations have had poor success (McEvoy 1986). Avian dietary data provide catch-independent assays that are directly linked without time lag to fluctuations in prey availability and distribution (Croxall et al. 1985) and can supplement other fisheries assessment data and aid in management decisions. Avian data are also particularly useful in monitoring prey that are not systematically studied, i.e. usually not commercially exploited.

We review long-term pelagic fisheries monitoring schemes that have been developed in the eastern-boundary Benguela Current of the southeast Atlantic with Cape Gannets *Sula capensis* and in the arctic Labrador Current of northwest Atlantic with Northern Gannets *S. bassana*. For the most part, these studies involve mesoscale comparisons of annual fluctuations in the prey harvests of birds and humans.

Problems associated with surveying pelagic fish

Assessments of fish populations and biomass often pose difficult problems (Gulland 1983, Harris 1990). Owing to the behavioural, life history, and ecological characteristics of pelagic fish, their populations and spatial and temporal distributions are very variable and poorly understood. Substantial proportions of pelagic fish stocks, often including younger age classes, occur in shallow water regions that are not surveyed by fisheries vessels (e.g. Hewitt & Brewer 1983) and in the upper hydroacoustically invisible upper 10 m of the water column (Donmasnes & Røttingen 1985). For example, 76 to 93% of many thousands of pilchard shoals recorded off Namibia were within 10 m of the surface (Cram & Hampton 1976, Hampton et al. 1979). Such distributions apply to many pelagic prey, such as mackerel, herring, squid, which also exhibit ship avoidance (Cram & Hampton 1976, Diner & Masse 1987). Birds dependent on pelagic prey probably cover more area including that inaccessible to fisheries surveys and so can provide complementary information that is useful in understanding pelagic organisms. Species that are not commercially exploited usually receive little scientific attention (Croxall et al. 1985). Commercial harvesters like natural ones can benefit by sampling prey spectra to facilitate possible response to environmental change.

Problems and advantages of monitoring gannet diets

A major difficulty associated with avian assays of fish stocks is generation of biomass, population or density estimates from measurements of relative abundance. Dietary changes of polyphagous seabirds (e.g. gannets) broadly denote prey availability, but do not necessarily indicate relative, let alone absolute, abundance. Gannets eat many different pelagic prey, so fluctuations in the availability of preferred species could produce large shifts in the relative harvests of others. To ascertain the relative abundance of prey, predator preferences have to be determined, usually from comparisons of diet composition with other measures of prey abundance, such as hydroacoustic

surveys and fisheries catches. Robust data of this nature are, however, very difficult to obtain from fisheries directed at single species and constrained by market demands, quotas, fishing regions, seasons, politics, technologies, etc. Moreover, many species that are not commercially exploited are unstudied. Prey preferences can be guessed at from frequency in predator diet, energy density, size and organic composition. Even if predator preferences are determined, it is still not possible to monitor abundances of subsidiary prey whose occurrence in diet depends on availability of preferred prey. There is some evidence of prey preference among gannets. Cape Gannets' harvests of dominant prey are not influenced by increased availabilities of alternative prey (Berruti 1987, Berruti & Colclough 1987). Also drastic dietary changes involving subsidiary prey are often indicative of major fluctuations in prey abundance (Montevecchi et al. 1987). More research relating avian harvests to prey abundance, availability and distribution is needed.

One way to potentially circumvent dilemmas posed by dietary studies of polyphagous predators is to focus on predators with little dietary diversity (Monaghan & Zonfrillo 1986, Cairns 1987, Croxall et al. 1988). Predators with narrow diet breadths are vulnerable to fluctuations in prey availability (Schaefer 1970, Furness 1988), so it is expected that many aspects of their feeding behaviour, physiology and ecology will be more responsive to changes in prey availability than will those of generalists. Foraging effort and body condition have been used as indicators of the availability of the prey exploited by specialists (e.g. Costa et al. 1989). If environmental and organismic factors can be accounted for, measurements of specialist predators have the important potential of providing estimates of absolute prey availability. Dietary measurements from polyphagous species will probably at best only provide estimates of relative prey availability. Dietary data have the advantage of being easily collected and directly comparable to fisheries catches.

The interactive effects of fluctuations in the abundances of different prey on the diets of polyphagous predators can be constrained by study procedure. For example, investigations can be conducted during periods when particular prey are available within the birds' foraging range. Pelagic fish and squid that are eaten by gannets move into inshore waters during different months (e.g. Crawford 1980), and the diets of the opportunistic gannets, like the catches of pelagic fisheries, reflect seasonal availabilities (Berruti 1987, Montevecchi et al. 1987, see also Adams & Klages 1989).

Compared with vessel surveys, monitoring seabird diets is inexpensive, usually broader in spatial and temporal coverage and may better reflect prey conditions in shallow water. Avian assays are particularly useful when fish stocks are low and research surveys are less reliable (Mais 1974, Cram & Hampton 1976, Armstrong et al. 1987). The foraging ranges of gannets can be extensive (100 km or more; Kirkham et al. 1985) and hence integrate prey availability over a large area. Species with small foraging ranges are much more likely to be influenced by variation at smaller spatial scales, e.g. localized oceanographic events, spawning or recruitment, and so require that more colonies be surveyed (e.g. Barrett et al. 1990). Cape Gannets are present at colonies during nonbreeding periods and permit year-round assays of prey diversity and availability (Berruti 1987). Colony-based data characterize mesoscale variation in prey availability in adjacent waters (Montevecchi et al. 1987). Inter-colony comparisons often usefully determine oceanographic and seasonal movements of prey and can be particularly informative when birds from different colonies forage in discrete, nonoverlapping areas (Berruti 1987).

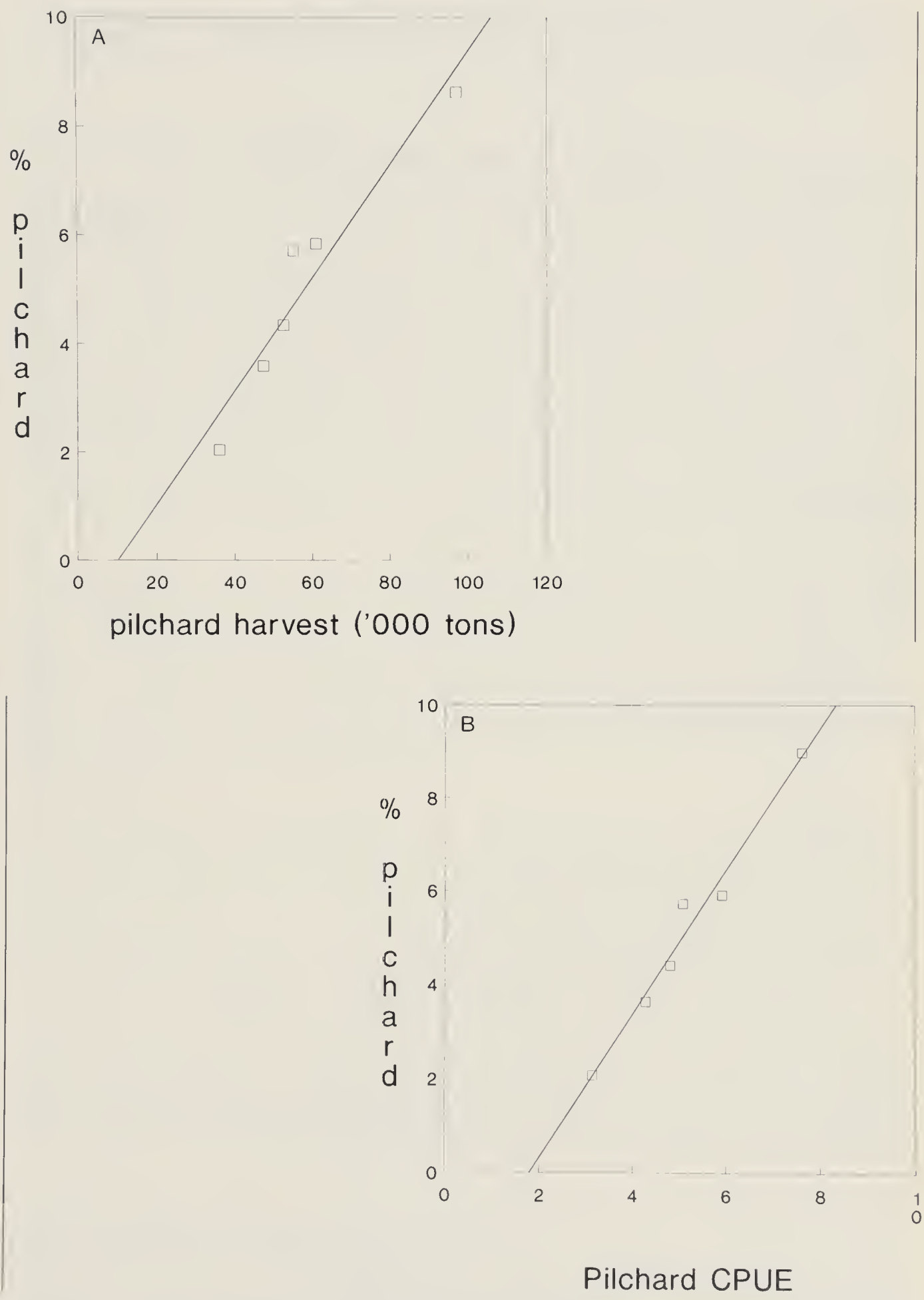


FIGURE 1 - Linear regression of annual percentages (total mass) of South African pilchard in the diets of Cape Gannets at Lambert's Bay and Malgas Island on (A) total annual South African landings of pilchards, 1978 to 1983 and (B) commercial catch per unit effort, 1978 to 1983.

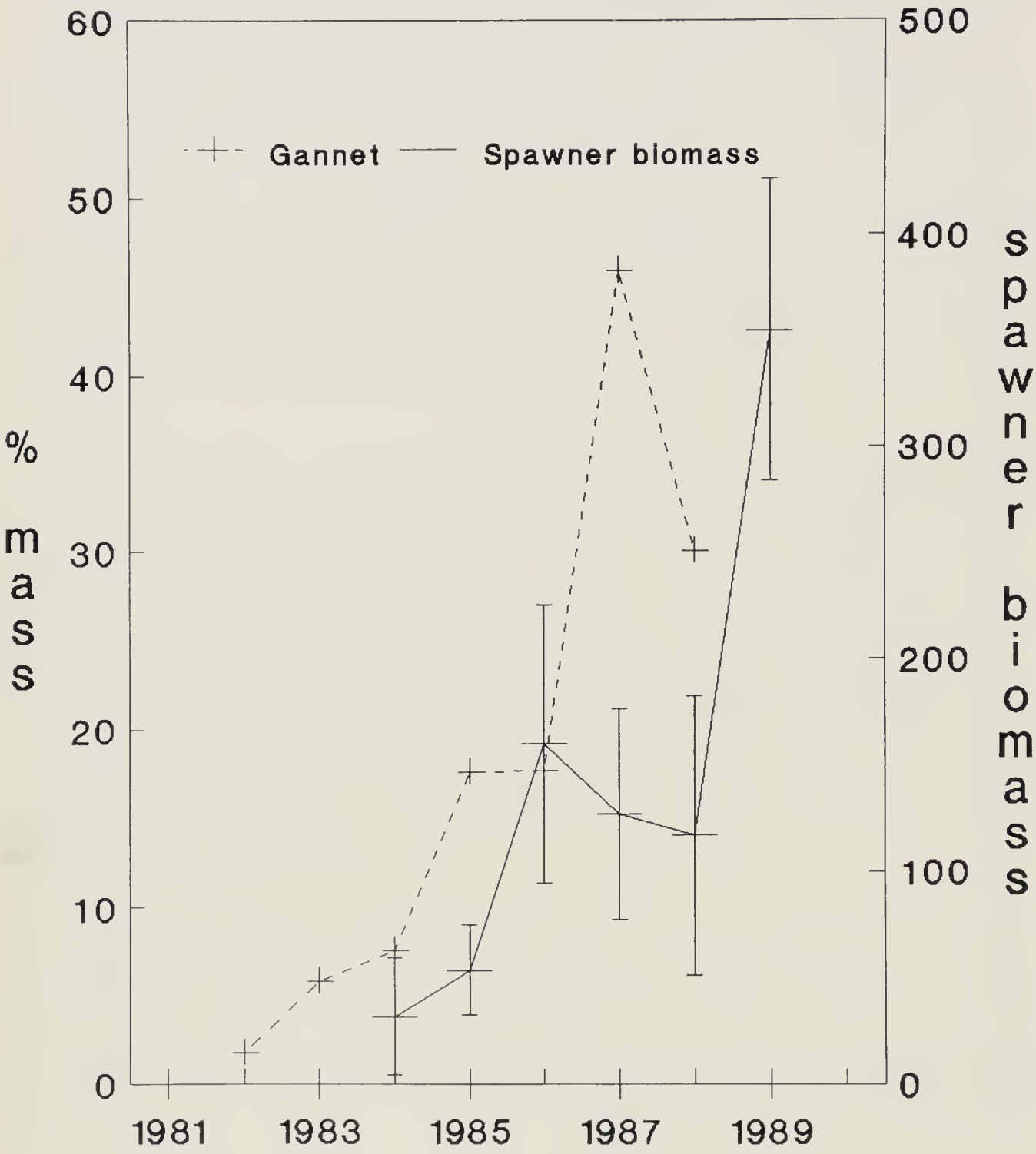


FIGURE 2 - The annual percentage (total mass) of pilchard in the diet of Cape Gannets at Lambert's Bay and Malgas Island and the estimates of pilchard spawner biomass (1000s of tonnes \pm 1 SD) from acoustic surveys (after Armstrong et al. ms).

Owing to large body size, gannets harvest the same sizes (ages) of prey as do human fisheries. This correspondence enhances the immediacy of fisheries forecasts but limits longer term predictive value. Smaller avian species often exploit younger (smaller) age classes of prey than commercial fisheries, thereby opening possibilities for evaluating year-class strength before recruitment to the commercial fishery (e.g. Hislop & Harris 1978, Monaghan & Zonfrillo 1986).

Like all independent assays, avian and fisheries assessments and harvest data need to be compared. Most such comparisons of avian (or mammalian) parameters have,

however, been made with fisheries data which do not coincide with the predators' foraging ranges and harvesting periods. Caution has to be taken in comparisons of this nature.

Cape Gannets and pilchards

Dietary studies over six years indicate that annual fluctuation in the relative harvest of pilchards *Sardinops ocellatus* by Cape Gannets is a reliable monitor of pilchard fisheries harvests and catch per unit effort when pilchard stocks are low and hence difficult to survey by conventional methods (Figure 1; Berruti 1987, Berruti & Colclough 1987). Increased availability of alternative foods (hake *Merluccius* spp. in the form of offal and anchovy *Engraulis japonicus*) has little effect on this relationship. A partial recovery in pilchard stocks off South Africa was first demonstrated by an increase in the mass of pilchard in gannet harvests. This indication preceded increases in estimates based on hydroacoustic surveys (Figure 2). Juvenile South African pilchards (<130 mm caudal length [Lc]) were much more frequent in gannet diets in winter, and larger adult fish (160-220 mm Lc) were more common food items in spring and summer (Berruti 1987, see also Batchelor 1982). Length-frequency data of pilchards collected from gannet regurgitations, commercial and research vessel landings have provided complementary evidence of year-class strength (Armstrong et al. 1987).

Trophic changes are also evident. Before the collapse of South African pilchard stocks in the 1960s, these fish were the most frequent prey taken by gannets, Cape Cormorants *Phalacrocorax capensis* and Jackass Penguins *Spheniscus demersus* in the Benguela region (Burger & Cooper 1984). Since the pilchard stock collapsed, Cape anchovy has become the gannets' major prey off the Western Cape, and pelagic gobies *Sufflogobius bibarbatus* are the primary prey of cormorants and penguins off southern Namibia (Crawford et al. 1985).

Cape Gannets and Cape anchovy

Annual cycles in the lengths of Cape anchovies harvested by gannets reveal that recruiting fish (<70 mm Lc) occur early in the year at Lambert's Bay, the more northerly gannetry in the southern Benguela region, and throughout the year at Malgas Island (Berruti 1987). Cape anchovies peaked in abundance in gannet diets in April and May, when juveniles (<90 mm Lc) dominated the catch (Berruti 1987), and when the main southward migration occurred (Crawford 1981). A subsequent peak in October and November was comprised of larger fishes (100-130 mm Lc). These spatial and temporal differences are also manifested in the exploitation of younger (smaller) anchovies by gannets at Lambert's Bay than at Malgas Island (Crawford & Shelton 1978). The Lambert's Bay region is characterized by more uniform oceanographic conditions (Shannon 1985) and is a nursery ground for juvenile fishes of several species. Juvenile anchovies are abundant in the region, though adults are rare (Crawford et al. 1987).

Northern Gannets and short-finned squid

Northern Gannets in the northwest Atlantic feed on mackerel *Scomber scombrus*, short-finned squid *Illex illecebrosus*, Atlantic saury *Scorpaenopsis saurus*, herring *Clupea harengus*, and capelin *Mallotus villosus*. These pelagic prey are harvested by birds and fishermen when they move inshore. An analysis of a 12-year data set revealed a significant association between failures of the human and avian fisheries for squid and mackerel (Montevecchi et al. 1987, in press). The gannets' landings were

significantly higher when subsequent local commercial squid fisheries were successful than when they failed ($r_{12}=0.78$, $P < 0.001$; Figure 3; Montevecchi in press).

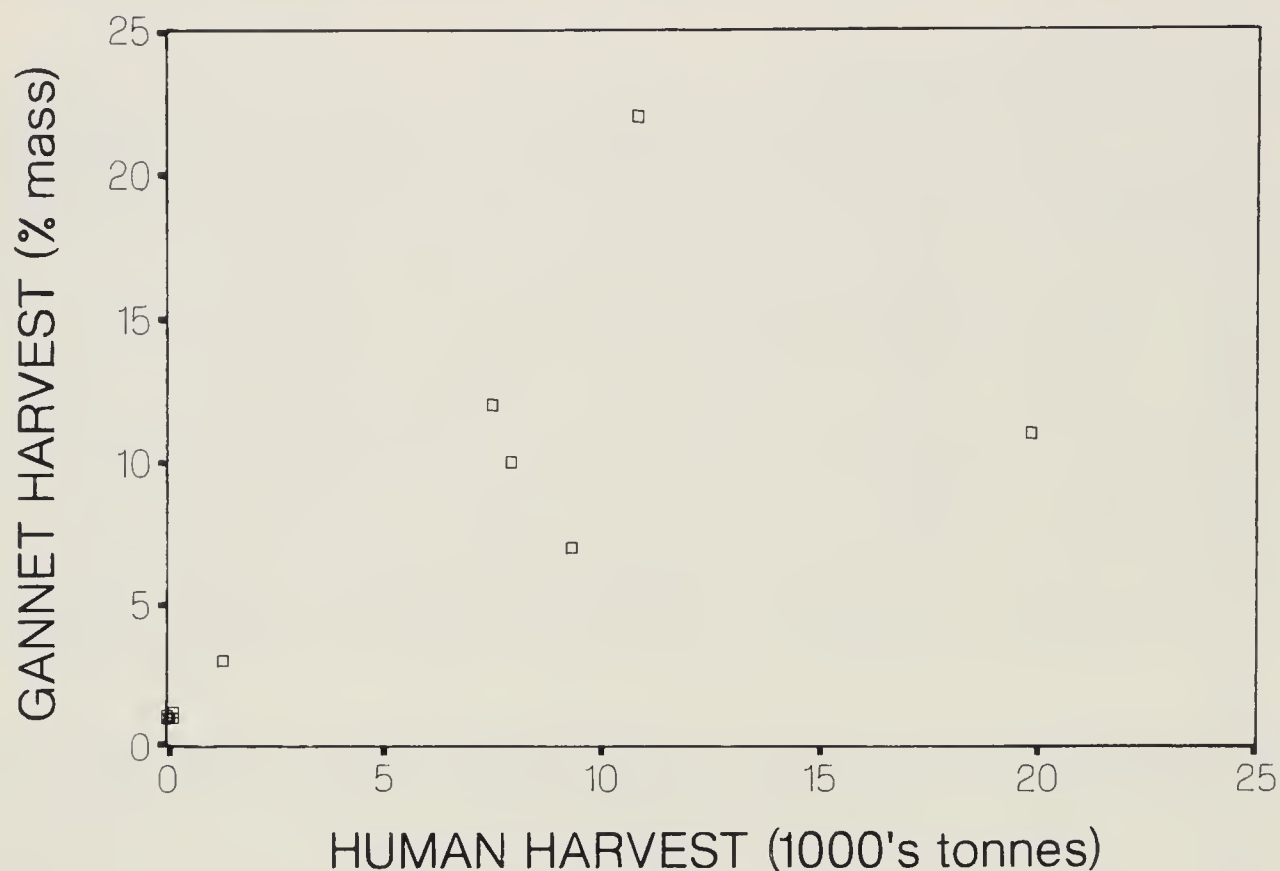


FIGURE 3 - Relationship between the harvests of short-finned squid by Northern Gannets (% total mass) and fishermen (1000s of tonnes) off northeastern Newfoundland, 1977-90 (from Montevecchi in press).

Northern Gannets and Atlantic salmon

The migratory patterns of Atlantic salmon *Salmon salar* from spawning rivers in the northwest Atlantic to growth sites in western Greenland are not well understood (e.g. Kerswill & Keenleyside 1961). The usual means of inferring fish movements is the capture of tagged fish. Because there is no directed fishery for young (small) fish, little is known about the movements of post-smolt salmon (e.g. Blair 1957).

Tag recoveries from the gannetry on Funk Island indicate that smolts from rivers in Maine, the Bay of Fundy and on the Atlantic coast of Nova Scotia migrate off Newfoundland's east coast in August, 10 weeks after release (Montevecchi et al. 1988). The recoveries also suggest that post-smolts from different rivers may travel in proximity to each other, because salmon from different origins have been landed by gannets at Funk Island within hours. Salmon have also occurred in the mixed regurgitations with mackerel, herring and Atlantic saury suggesting that pelagic schools of different species move relatively close to one another in Newfoundland waters. Warm water conditions or frontal incursions may facilitate the co-occurrence of certain pelagic species (see also Berruti 1988).

Gannets and Atlantic saury

Noncommercial species typically receive little research attention from fisheries scientists. The highly seasonal and aperiodic visits of Atlantic saury to nearshore regions in the southeast and northwest Atlantic are consistent with indications that this warm-

water species is very sensitive to fluctuations in water temperature (Dudley et al. 1985, Scott & Scott 1988). Dietary analyses of Cape Gannets have provided useful data on the seasonal occurrence and regional size distributions of Atlantic saury in the southeast Atlantic (Berruti 1988). High harvest levels of Atlantic saury by gannets in the northwest Atlantic indicate availability in recent years. Increased harvests of saury may represent compensatory responses by gannets to decreased availability of preferred more lipid-rich pelagic fish (Montevecchi in prep., Batchelor & Ross 1984). Avian information about availability of saury warrants systematic surveys by fisheries agencies. Saury are usually fished with purse seines, and if markets were available, would offer alternative prey for fisheries directed at herring, mackerel, Cape anchovy, etc. Atlantic saury have been previously exploited in the northwest Atlantic for fish meal and in the southeast Atlantic as bait for tuna. They have the potential to be harvested as a delicacy for some Asian markets, as are Pacific saury *Coloabris saira*. Major economic pulses in pelagic fisheries ventures in eastern Canada have occurred, when pelagic prey previously unvalued or exploited for bait or fertilizer found their way in "new" Asian markets (e.g. squid, capelin). As avian assays of availability indicate, Atlantic saury are worthy of further study.

DISCUSSION

Many facets of avian biology and ecology yield valuable information about prey availability. While assessments of prey abundance may not be possible, monitoring avian feeding ecology and diet produces real-time early warning of fisheries problems, such as recruitment failures, stock unavailability, distributional shifts, etc. To date, associations between avian and fisheries data have generated nominal (presence/absence) and ordinal (low, medium, high) relationships. Qualitative data, such as these, can be highly informative and useful in fisheries assessments and in more general studies of population and community ecology (Gomes MS).

Dietary and foraging studies of seabirds require thorough understanding of feeding ecology and of the ways in which seabirds respond to changes in prey availability. Particularly important aspects of study to be pursued include: (1) prey preferences, (2) species composition of diets, including length/age data, (3) foraging range and area (e.g. telemetric studies), (4) feeding/foraging behaviour (e.g. activity recorder studies). The influences of weather, physical oceanographic events, age and breeding status on prey harvest and on other predator measurements also need to be investigated.

In investigations of multi-species food webs, biophysical interactions between oceanographic factors and prey behaviour have to be understood if natural perturbations are to be distinguished from anthropogenic ones (Springer 1991). Both physical and behavioural factors influence prey availability (i.e. accessibility to avian and human predators), which is some unknown function of prey abundance. Availability and abundance are expected to covary, though the association is unlikely to be linear. Therefore, predator indices may continue to be most useful when prey fluctuations are extreme (Croxall 1989), which they tend to be for pelagic fish, squid and crustaceans. Such fluctuations in prey stocks are common, widespread, and often detected too late to allow for corrective actions. Avian research should be of value here.

In sum, ample evidence indicates the value of studying avian trophic relationships in bettering understanding of marine ecosystems. Conceptual progress will be promoted through the integration of marine ornithology, fisheries biology, hydroacoustics and physics in interdisciplinary oceanographic research programs that focus on trophic interactions in a dynamic marine environment.

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THE INFLUENCES OF CHANGES IN PREY AVAILABILITY ON THE BREEDING ECOLOGY OF TERNS

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ABSTRACT. Changes in the breeding biology and behaviour of Arctic Terns in response to changes in prey availability are examined. A reduction in prey availability influenced courtship feeding, but had no effect on laying date or egg size, but a small effect on clutch size, in birds which attempted breeding. An unknown proportion of birds are likely not to have bred at all. Hatching success, adult body condition and timing of nest failure, chick growth and chick survival were all influenced by changes in food supply. These data are discussed in the light of the usefulness of Arctic Terns as indicators of changes in fish stocks.

Keywords: seabirds, terns, prey, fish stocks.

INTRODUCTION

Understanding the relationship between predator and prey populations is a key area of ecology. It is also of considerable importance in the management of populations that are harvested by man, since it is essential to predictions of yield and to predicting the ecological effects of exploiting particular species. Furthermore, monitoring of changes in predator populations can provide valuable information on changes in the distribution and abundance of prey when the latter are not amenable to direct study. It is becoming increasingly evident that seabirds, long disregarded by fisheries biologists, can be important predators in marine ecosystems; actual assessments of their impact on fish stocks remain somewhat conjectural, being hampered by a lack of accurate information on certain key parameters, notably diets and foraging ranges outside of the breeding season (see Furness 1990). Information on changes in marine fish stocks is heavily reliant on commercial catch data. However, the efficiency of modern catching methods means that changes in the abundance of shoaling fish may not be manifested in reduced catches until the stock is seriously depleted (Murphy 1980); in addition, since fisheries data are aggregated over comparatively large regions, it may be difficult to obtain information pertaining to a localised area. For species which are not commercially exploited, virtually no data are available.

Seabirds, which forage mainly on pelagic shoaling fish, can be viewed as an effective fish sampling tool; aspects of their behaviour and population ecology can potentially be used to provide information on the distribution and abundance of their prey which could usefully complement the commercial catch data. However, care must be taken in interpreting the seabird data since a change in food supply is only one of a number of proximate factors that can give rise to changes in their biology. A good understanding of foraging ranges, dietary preferences, and foraging and reproductive strategies is essential if seabirds are to be used as effective indicators of environmental change. In this paper, we examine changes in the breeding biology and behaviour of the Arctic Tern *Sterna paradisaea* in the Shetland area which have occurred in response to changes in the availability of their main prey, the lesser sandeel

Ammodytes marinus, and discuss the usefulness of these birds as monitors of changes in the marine ecosystem.

CHANGES IN FOOD AVAILABILITY

In UK waters, sprats *Sprattus sprattus*, sandeels (mainly *Ammodytes* spp.) and young herring *Clupea harengus* are the main energy-rich prey available to seabirds (Harris & Hislop 1978). In the Shetland area, the lesser sandeel is the predominant prey; neither sprats nor young herring occur in any numbers (Kunzlik 1989). Shetland holds a high proportion of the breeding populations of several British seabirds (see Furness 1990). In recent years, there has been a dramatic decline in the breeding success of a number of species, and the most marked and persistent reduction has been in the Arctic Tern, which has produced virtually no young in the Shetland area for seven successive years, 1984-1990 (Heubeck 1989, Monaghan et al. 1989a, Uttley et al. 1989). Shetland held 33 000 breeding pairs of this bird in 1980 (40% of the UK total), but by 1989 breeding numbers had more than halved (Avery & Green 1989). Their extremely poor breeding success has resulted from a reduction in the availability of sandeels (Monaghan et al. 1989a, 1989b, 1990, Uttley et al. 1989, Uttley 1991). A sandeel fishery has existed around Shetland since 1974, and fisheries data show that the production of young sandeels (0-group, i.e. fish spawned in January of the same year) has declined considerably since 1983, and more recently the spawning stock has also declined to some extent (Bailey et al. in press). The sandeel fishery is close inshore, in the vicinity of the main seabird colonies, and there is considerable controversy over the role of the fishery in the collapse of the sandeel stock (Avery & Green 1989).

CHANGES IN THE BEHAVIOUR AND BREEDING BIOLOGY OF ARCTIC TERNS

Below, we summarise the main changes which have occurred in the Arctic Terns breeding in Shetland, in comparison with a previous study in Shetland in 1983, when Arctic Terns were breeding successfully (Ewins 1985) and with data from our own studies on Arctic Terns breeding successfully elsewhere in Britain. Full details of methodology can be found in Monaghan et al. (1989a) and Uttley (1991).

Courtship feeding

Male terns provision their mates with prey during the courtship period, and this courtship feeding is thought to play a significant role in helping the female obtain sufficient nutrients to produce eggs (Nisbet 1973). During this phase, males generally select the largest prey available for use as courtship food (Taylor 1979). In the Arctic Tern in Shetland, courtship feeding occurs in the latter half of May; 1-group sandeels (i.e. fish spawned January of the previous year) appear to be the preferred size class, comprising almost 90% of the observed prey in 1983 (extracted from data in Ewins 1985). In our study, data on courtship prey were collected in Shetland in 1987 and 1988; while over 75% of the courtship prey observed in both years were sandeels, the proportion of 1-group sandeels declined from over 90% in 1987 to 40% 1988. The utilisation of 1-group fish was lowest following a year when the production of 0-group sandeels was the lowest on record. However, the small size of courtship prey was compensated for to some extent by an increase in the provisioning rate (Monaghan et al. 1989b, 1991).

Production of eggs

We have found no changes in median laying dates, or in egg dimensions in the Arctic Terns in Shetland during the period of low food availability (Monaghan et al. 1989a, Monaghan et al. 1991). There was some decline in clutch size over the first three years of our study, but the effect was small (mean clutch size Shetland: 1987, 1.90 ± 0.03 , $n=279$; 1988 1.76 ± 0.04 , $n=115$; 1989 1.69 ± 0.07 , $n=53$; difference between years significant, one-way ANOVA $F_{2, 443} = 4.84$, $P < 0.01$, with 1987 being significantly different from 1988 at $P < 0.05$, Scheffe Multiple Range Test). In 1990, however, most pairs at our study colonies on mainland Shetland did not progress beyond the courtship phase and in virtually all cases no eggs were laid. No decrease in clutch size was observed over the same period at the successful colonies.

Production of young

Hatching success of Arctic Terns in Shetland in 1987 remained good, being similar to that recorded at the successful sites (in the region of 70%). However, in 1988, a high proportion (over 50%) of the birds deserted during incubation and hatching success was reduced to 32%. In 1989, all birds deserted during incubation at the main study colony, and the study site had to be changed repeatedly to find even a small number of birds which had successfully hatched young. The adults in Shetland subsequently brooded their young less, which is likely to increase both the thermoregulatory costs of chicks and the predation risk, thereby decreasing the probability of survival (Uttley 1991). In general, two-thirds of the observed chick food in Shetland was sandeels, with saithe *Pollachius virens* forming the bulk of the non-sandeel prey. Arctic Terns feed their young on 0-group sandeels.

The size of sandeels fed to the chicks when food supply was reduced tended to be smaller than that recorded when young were reared successfully; although the adults increased their provisioning rate, chick growth was generally poor, and the virtually all young died within the first week of life (Monaghan et al. 1989, 1991, Uttley et al. 1989). The duration of foraging trips was recorded in 1988, and the median trip length of 16 minutes did not differ from that recorded at a site where sandeels were not in short supply (Monaghan et al. 1990).

Adult condition

The body weight of adults was monitored using computer operated, remotely read weighing devices (see Monaghan et al. 1989a for details). The adults in Shetland were lighter than those at the successful sites from early in the breeding season, indicating that their condition was poor, and the lower an adult's body weight at hatching, the sooner the young died (Monaghan et al. 1989a, 1991).

ARCTIC TERNS AS MONITORS OF THE MARINE ENVIRONMENT

The change in the size of the sandeel stock around Shetland clearly resulted in marked changes in the breeding biology and behaviour of Arctic Terns. Below we summarise a number of important points which must be borne in mind when using seabirds as indicators of environmental change. While we consider these with respect to the Arctic Tern and the Shetland situation, several of the points have more general applicability.

What parameters should we measure?

DIETARY PREFERENCES. Where more than one prey is available to breeding seabirds, a reduction in the proportion of one prey species in the diet may arise, not from changes in its abundance, but from the birds switching to a preferred prey which was previously more difficult to find. The preferred prey may change seasonally according to energy demands and great care has therefore to be taken in interpreting such data. In Shetland, the only energy-rich prey available to seabirds is the sandeel, and thus dietary changes will reflect changes in sandeel abundance (see also Hamer et al. in press). Even where only one main prey species occurs, however, the preferred size class may alter seasonally, as observed in Arctic Terns which utilise 1-group sandeels in courtship and 0-group sandeels when feeding young. Detailed information on the prey utilisation at different stages in breeding can, in addition to providing an index of prey abundance, give important information on change in the demographic structure of the prey population. While sandeels remained the predominant courtship prey, changes in the proportion of 1-group sandeels utilised in courtship by Arctic Terns in Shetland clearly reflected a change in the abundance of this size class.

FORAGING BEHAVIOUR. Different species of seabirds obtain their prey at different depths in the water column. Arctic Terns, for example, are surface feeding seabirds, and therefore sample prey only in the top metre of the water column. Changes in seabird foraging success may reflect changes in prey behaviour rather than abundance. It is likely that considerable information on changes in the distribution of prey in the water column could be obtained by comparing surface and diving seabirds, but at present there is insufficient information on how the density of prey may affect foraging success. Diving species may be able to pursue prey effectively underwater, thereby continuing to foraging successfully at low prey densities, while surface feeders may be unable to locate low density shoals.

In order to utilise seabirds as sampling tools, it is also necessary to have detailed information on the range over which they prefer to forage. This makes them less useful outside of the breeding season when they are not tied to a particular land location. When breeding, especially when feeding young, they will be required to forage within an energetically economic range of the colony, and thus changes in local prey distribution may considerably alter foraging success. Arctic Terns in Shetland appear not to have altered their foraging ranges, but increased the number of foraging trips. Arctic Terns in Shetland brooded their young less than birds in areas of good food availability. Complex trade-offs are likely to occur between the energetic and time costs of foraging, the increased energy requirements and predation risk of unbrooded chicks, and reduced feeding time for adults. Since the costs of leaving small young unattended at the nest are likely to be high, changes in the attendance patterns of adults are likely to provide a good indicator of changes in foraging conditions.

LIFE HISTORY CONSIDERATIONS. Seabirds are generally long-lived, have delayed maturity and have low annual reproductive outputs. Their small clutch sizes make it unlikely that reduction in the number of eggs produced will be a response to lowered food supply. It may simply not be worth attempting to breed at all if a threshold egg production cannot be reached. There may also be little scope for delaying the onset of breeding, particularly in migratory species where the breeding season is constrained by the timing of migration. In Arctic Terns there was no change in laying dates in response to food shortage and the effect on the clutch size *of those birds which laid*. Further-

more, if prey availability during egg formation is not a good predictor of prey for feeding young, the optimum decision for the adults may be to increase effort to produce the clutch, since foraging conditions may be better later in the season. In Arctic Terns in Shetland, the abundance of the 1-group sandeels (which are pre-spawners) is not a good indication of the number of 0-group fish likely to be available that year.

Being adapted to maximise adult survival means that individual birds will either not breed or will abandon a breeding attempt when food is in short supply if the perceived risks to adult survival are too great. Monitoring the condition of adults may give a good indication of changes in foraging costs, and, as observed in the Arctic Terns, increased desertion rates during breeding are likely if the condition of the adults is poor.

BREEDING NUMBERS. Responses to a reduction in prey availability may vary between individuals and between species according to their abilities to withstand the food shortage. Changes in breeding numbers in an area may result from extensive non-breeding in response to poor food availability. However they may also result from changes in recruitment due to low young production several years previously or high adult mortality outwith the breeding season. It is extremely difficult to obtain information on the proportion of birds not breeding in a particular year, since very detailed studies of marked birds over a number of years are required to distinguish between non-breeding and mortality. However, most seabirds are very faithful to their breeding sites and seabird populations are slow to recover from periods of high adult mortality; thus in most species, large fluctuations in numbers between years are likely to be due to non-breeding. However, this does not apply to terns; entire tern colonies may shift location between years, possibly in response to predation pressure. Therefore particular colonies cannot be selected for monitoring as in other seabirds, and censuses must take place over wider areas. Where this is done, counts of breeding numbers have been shown to correlate with fish stocks (Monaghan & Zonfrillo 1986), and marked changes in numbers breeding in the Shetland area have followed the change in food availability.

CONCLUSIONS

In some seabird species, a reduction in food availability may result in an increased breeding effort, with little detectable effect on breeding success or breeding numbers. This is particularly likely to be the case with large species. Terns, on the other hand, are small seabirds with little lee-way in their energy budgets while breeding even in conditions of good food supply (Pearson 1968). They are thus likely to be particularly sensitive to changes in food availability, which will be detected in changes in attendance of young and reduced breeding success. It must be borne in mind, however, that monitoring breeding success alone may not give a true reflection of changes in food supply since only the high quality birds most able to cope with the reduced prey situation may attempt to breed. From our studies in Shetland, it is clear that terns are potentially very useful indicators of changes in their preferred prey populations within the vicinity of their breeding colonies. In practical terms, it is unlikely that such detailed studies as we have carried out would be undertaken every year. Monitoring the population production over a fairly large area is likely to give the most useful data, since this is a combination of numbers breeding and breeding success. For terns, this can most easily be done if there is a constant effort each year to ring young near

fledging, as is the case with many local bird ringing groups. In Shetland, there is a very good correlation between the production of 0-group sandeels and the number of young terns ringed each year (Monaghan et al. 1989b), clearly illustrating the usefulness of such approach.

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THE DIET OF ATLANTIC PUFFIN CHICKS IN NEWFOUNDLAND BEFORE AND AFTER THE INITIATION OF AN INTERNATIONAL CAPELIN FISHERY, 1967-1984

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ABSTRACT. The food of young Atlantic Puffins *Fratercula arctica* was examined at Great Island, Newfoundland, in 7 years between 1967 and 1984. Capelin *Mallotus villosus* was the principal prey fed to chicks in 6 of 7 years. Productivity was highest in years when capelin formed most of the diet and lowest when capelin were scarce. Mean meal size (mass), prey composition, and mass of capelin in a meal were similar during pre- and post-fishery periods, except for 1981 when puffins experienced reproductive failure and meals were significantly smaller in size, comprising mainly small gadids. The only notable differences detected in diet during the other 6 years involved the reproductive status and length of capelin. Most capelin in meals were female (all years), but more ovid females occurred during the pre-fishery period than later. And although post-fishery capelin were no smaller (mass) than those caught earlier, they were shorter in length than pre-fishery capelin. Overall, the food of young puffins is a sensitive measure of capelin availability close to the colony, and may assist in the detection of subtle changes in condition of the Newfoundland capelin stocks.

Keywords: Atlantic Puffin, *Fratercula arctica*, food and feeding, chick diet, commercial fisheries, capelin, *Mallotus villosus*, bio-indicators, Newfoundland.

INTRODUCTION

The capelin *Mallotus villosus*, a small smelt, is considered to occupy a key position in the marine food web in low arctic waters of the North Atlantic because of its importance as a food species for other marine fish, birds and mammals (Jangaard 1974, Nettleship 1977, Winters & Carscadden 1978, Akenhead et al. 1982, Carscadden et al. 1982). Its high abundances and large biomass in this region also make it important to international commercial fisheries owing to its high commercial value (Carscadden 1984, Scott & Scott 1989). In the northwest Atlantic, capelin are particularly abundant off Iceland, southern Greenland, and Newfoundland, locations where intensive offshore commercial capelin fisheries have recently been initiated. In Newfoundland waters the capelin fishery offshore began in 1972, peaked in 1976, and has declined since then with small increases inshore (ICNAF/NAFO 1967-90).

Close to 62% of the North American breeding population of Atlantic Puffin *Fratercula arctica* breeds on three islands in Witless Bay, southeast Newfoundland, the largest of which is Great Island (47°11'N, 52°49'W) where there are 110 000 to 148 000 breeding pairs (Nettleship & Evans 1985, D.N. Nettleship, unpubl.). From 1979 to 1981 unusually large numbers of puffin nestlings were found dead in their burrows, apparently due to starvation, a situation that peaked in 1981 when almost total reproductive failure occurred. Reasons for these failures seemed related to food shortages during the chick-rearing period, possibly caused by changes in the food supply (Brown & Nettleship 1984). Since capelin form an essential part of the diet of young puffins

in Witless Bay, and there is no suitable alternative prey available to the birds during chick-rearing (Nettleship 1972, Brown & Nettleship 1984), it seemed that environmental changes including capelin distribution and abundance may be reflected in characteristics of the prey fed to puffin chicks. In other words, to what extent can the chick diet of puffins in Newfoundland function as a bio-indicator of changes in the abundance and/or distribution of capelin?

This paper summarizes what is known about the food brought in to puffin chicks at Great Island, Witless Bay, Newfoundland, for seven years between 1967 and 1984. Emphasis is placed on the identification and comparison of differences in prey characteristics for the years before (1967-69) and after (1981-84) the commercial capelin fishery began, with the aim to uncover gross and subtle changes in the prey base that seem linked to changes in the abundance, biomass, or demography of capelin populations in the region.

METHODS

A total of 922 complete food samples delivered by parents to chicks were collected systematically through the chick-rearing period (late June to early September) in each year except for 1967 and 1981 when examination only began in late July and early August, respectively (Table 1). All meals came from birds nesting on the same study plots and habitats (maritime slopes) on the island. Immediately after delivery of a meal the chick was removed from its burrow, and food items collected from the burrow floor or extracted from the nestling if partially ingested. Food items comprising the meal were identified, weighed on a triplebeam balance (to the nearest 0.1 g), measured (total length to 0.1 mm), classified by sex and reproductive status (for capelin where possible), and then returned to the burrow and chick. Items not identified, mainly small larval fish and invertebrates, were labelled and retained for identification later. Incomplete meals were not used in the analysis. Feeding rates were measured on the same part of the colony each year by watching 17-20 chicks simultaneously from 1h before sunrise through to 1h after sunset for three consecutive days.

TABLE 1 - Sample sizes and time range of complete meals delivered to puffin chicks that were examined at Great Island, Newfoundland, 1967-84.

Year	June	July	August	Sept.	Totals
Pre-fishery:					
1967	-	2	6	-	8
1968	-	127	73	5	205
1969	7	117	95	1	220
Post-fishery:					
1981	-	-	94	4	98
1982	-	51	51	-	102
1983	7	99	73	-	179
1984	-	54	56	-	110
Totals	14	450	448	10	922

Comparisons are made between data for the years 1967-69, before the international capelin fishery, and those gathered later: 1981, nine years after the fishery began following two consecutive years of apparent capelin spawning failures in SE Newfoundland waters, and 1982-84 when the fish stock was recovering. For purposes of comparison, the years 1967-69 are referred to as the "pre-fishery" period and those afterwards as the "post-fishery" period; 1981, the year of puffin reproductive failure, is often excluded from certain comparisons of the two periods or treated separately owing to its obvious difference from other years. Standard statistical tests used to analyse the data are from Sokal & Rohlf (1981), and run using the Systat statistical programs by Wilkinson (1988). All tests are two-tailed and all errors reported are ± 1 SD.

Nominal catches (metric tons) of capelin in NAFO divisions 3L, 3N, 3O, 3 and 0-6, 1965-87

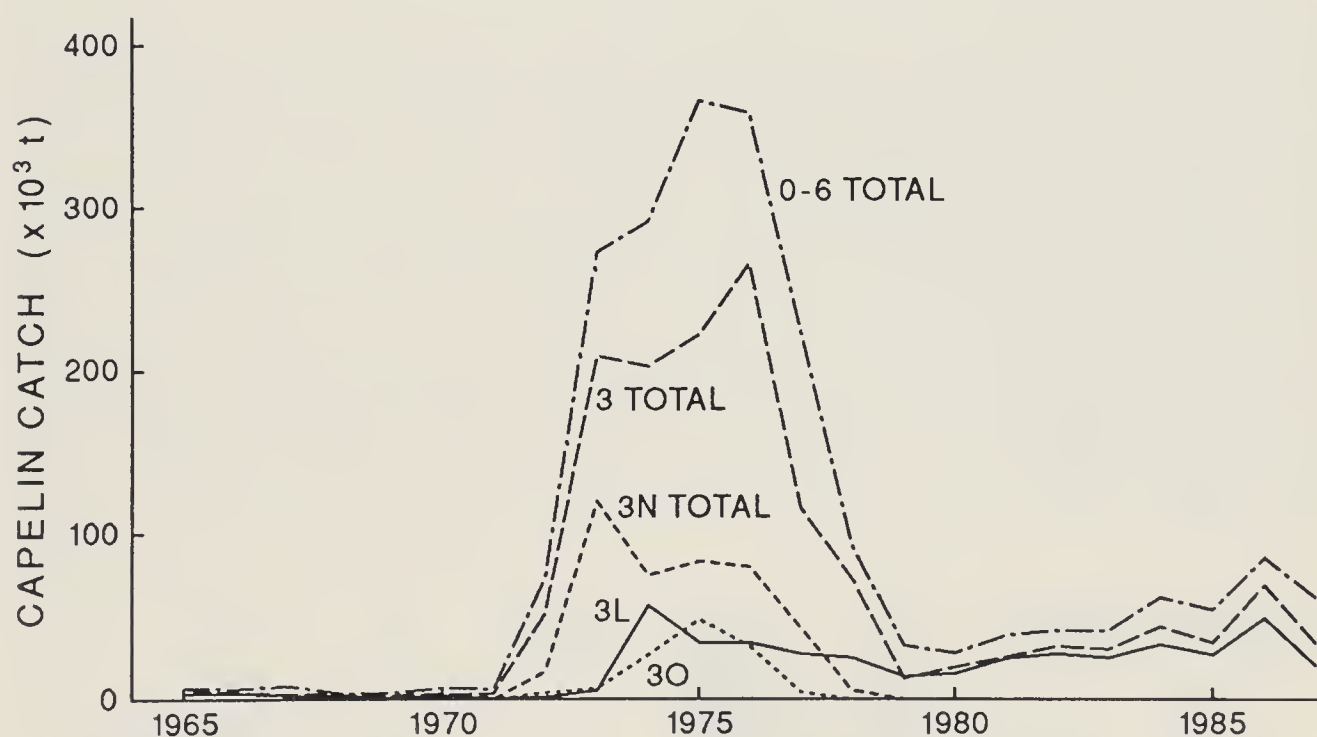


FIGURE 1 - Nominal catches of capelin in eastern Newfoundland in North Atlantic Fisheries Organization management division 3, 1965-87.

BACKGROUND AND RESULTS

The capelin fishery

Capelin have traditionally been harvested inshore in Newfoundland for food, bait, fish meal, and fertilizer (Templeman 1948, Leim & Scott 1966, Jangaard 1974, Scott & Scott 1988), with most fish taken on spawning beaches at levels ranging from about 23 000 metric tons (t) per annum in the early 1900s declining to annual levels around 5 000 t by the late 1970s and early 1980s (ICNAF/NAFO 1967-90). In the eastern North Atlantic, a major offshore capelin fishery began in the Barents Sea in the early 1960s, expanding soon afterwards to Icelandic waters and then to the Newfoundland Grand Bank region in the early 1970s (Jangaard 1974, Carscadden 1984). The international offshore fishery off Newfoundland increased dramatically from its initiation in 1972 (Figure 1), with the catch reaching a peak of about 370 000 t per year in the mid

1970s, after which capelin stocks fell with landings remaining relatively low through the 1980s (Carscadden 1984, ICNAF/NAFO 1967-90). The capelin stock spawning on the southeast shoal (Figure 1: NAFO 3N) declined during the late 1970s and was closed to fishing from 1979 to 1986 (Carscadden 1986), and reopened in 1987.

To offset the collapse offshore, the inshore fishery was expanded in 1979 in SE Newfoundland (NAFO subarea 3L), especially in Trinity and Conception bays, to satisfy the Japanese market with the roes of mature female capelin. This fishery was, and still is, wasteful and potentially damaging as all males and immature and unripe females are usually discarded dead, most unreported, resulting in marked under-estimates of the actual kill toll (Anon. 1982, Rowe and Collins 1982). The inshore capelin fishery in NAFO 3L remains active with record landings from 1986 through 1989 (Nakashima & Harnum 1987, 1989, 1990).

Food of puffin chicks

MEAL SIZE. Details of the mean wet weight of complete meals delivered to puffin chicks for the seven years examined are given in Table 2. Clearly, meal mass in 1981, the year capelin abundance was low, was different from all other years by being less than half the size of those for the pre-fishery (1967-69) and post-1981 years where meal sizes were relatively similar (Table 2). The difference between 1968 and 1969 was insignificant ($P>0.05$), and the larger size in 1967 is an artifact of the small sample size. Differences between 1982-84 were small (3-15%), though average meal size in 1982 was significantly lower ($P<0.01$) than the other two years, which were similar. Overall, the difference between years is highly significant ($P<0.0001$, $F_{6,922}=27.1$); a comparison between years for August samples only (since the 1981 sample was later, see Table 1) also indicates 1981 to be the most different of all years ($P<0.0001$, $F_{6,448}=18.2$).

TABLE 2 - Size (g) of complete meals delivered to puffin chicks at Great Island, Newfoundland, 1967-84.

Year	All meals examined			August meals only		
	N	x	SD	N	x	SD
Pre-fishery:						
1967	8	15.9	7.9	6	15.2	9.1
1968	205	11.9	6.0	73	12.2	6.7
1969	220	12.6	5.8	95	12.3	6.0
1967-69	433	12.3*	5.9	174	12.3**	6.4
Post-fishery:						
1981	98	5.9	4.9	94	5.7	4.9
1982	102	12.5	5.7	51	12.5	6.1
1983	179	14.2	5.7	73	13.1	5.9
1984	110	14.8	6.6	56	14.8	7.7
1982-84	391	13.9*	6.0	180	13.5**	6.6

*Comparison 1967-69 and 1982-84: $P<0.0001$, $t=3.91$, $df=822$

**Comparison August meals only: ns, $P=0.105$, $t=1.63$, $df=352$

However, when the unusual 1981 year is excluded, the inter-year difference remains significant ($P<0.0001$, $F_{5,824}=5.6$). If meal sizes for the years 1967-69 (the pre-fishery period) and 1982-84 (post-capelin collapse) are pooled, the differences in meal size between the two periods are also significant ($P<0.0001$, $t=3.91$, $df=822$). That means that meals in the post-fishery period were, on average, larger than those before the capelin fishery began, though the difference is insignificant when only August meals are compared ($P=0.105$, $t=1.63$, $df=352$).

FEEDING RATE. Chicks in 1981 received significantly fewer meals on average (2.3 ± 2.65 SD, $n=20$), and therefore less food, each day than those reared on the same habitats in years either before the fishery (3.6 ± 1.08 SD, $n=17$) or later (3.8 ± 1.12 SD, $n=60$); differences between the pre-fishery (1967-69) and post-fishery (1982-84) periods were insignificant ($P>0.05$).

PREY COMPOSITION. Fish were the principal component of the diet of puffin chicks in all years. Most meals consisted of a single prey species ($>94\%$), and those that had more than one usually had a single species accounting for more than 95% of the meal (by mass). Overall, the number of items in a meal was higher in 1981 than in any other year, where numbers were similar both before and after 1981. Between 78% and 100% of meals for six of the seven years comprised capelin, though the 100% value recorded in 1967 was probably due to the small sample examined that year (Figure 2). In 1981, when average meal mass was low, immature *Gadus* and sandlance *Ammodytes* spp. predominated, making up about 68% and 16% of the meals, respectively, with capelin about 10%. The proportions are similar when only August meals are compared. An examination of pre-fishery years against those after 1981 indicates a higher proportion of meals for 1982-84 contained capelin (348 of 391 meals, or 90%) than those for the 1967-69 period (359 of 433, or 83%), a difference that is significant ($P<0.01$, $\chi^2=6.26$, $df=1$).

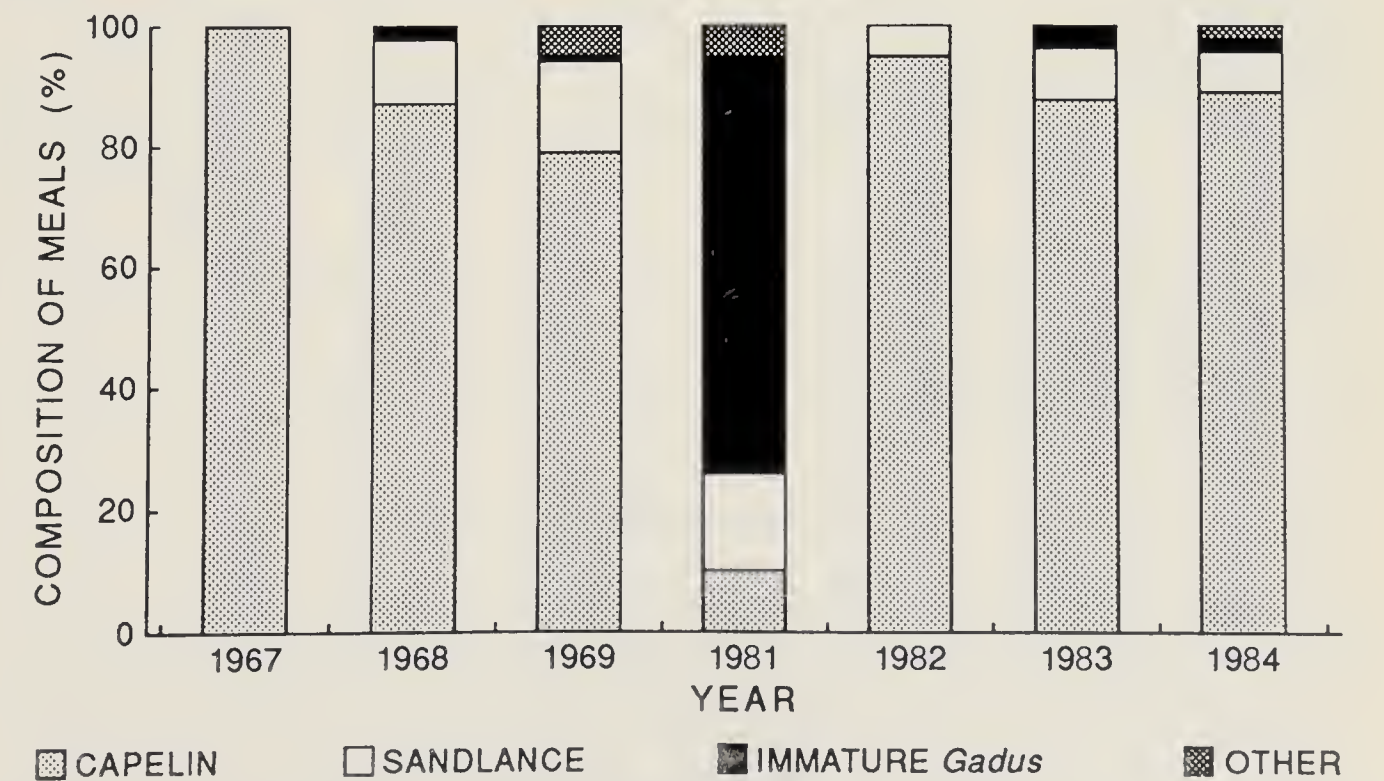


FIGURE 2 - Percent composition of prey in complete meals delivered to puffin chicks at Great Island, Newfoundland, 1967-84.

Characteristics of the principal prey

CAPELIN BODYWEIGHT. Capelin delivered to chicks in the post-fishery period (1982-84) were similar in mass to those before the fishery began (1967-69), 10.0 g and 9.9 g respectively (Table 3). In 1981, the small number of capelin that were fed to chicks were slightly smaller than either the pre- or post-fishery periods, averaging 8.7 ± 3.83 g (n=13).

CAPELIN BODYLENGTH. The mean lengths of capelin fed to chicks after 1981 were significantly shorter than pre-fishery capelin chick food, a decrease from 140.0 ± 23 mm to 134.6 ± 31 mm ($P<0.001$, $t=3.18$, $df=1132$; see Table 3). Capelin caught and delivered to young in 1981 averaged 121.4 ± 27 mm in total length, much smaller than values recorded either before or after 1981.

SEX AND REPRODUCTIVE STATUS. The proportions of male and female capelin contained in chick meals between years varied little, with females accounting for almost 92% (611 of 665) of all capelin examined for six of the seven years (Table 3). The difference between the pre- and post-fishery periods was not statistically significant ($P>0.05$). In contrast to this, significantly more female capelin fed to chicks during the prefishery period were ovid than in those delivered in 1982-84 (Table 3).

TABLE 3 - Characteristics of capelin contained in complete meals delivered to puffin chicks at Great Island, Newfoundland, in pre-(1967-69) and post-(1982-84) fishery periods.

Morphometrics:	Pre-fishery				Post-fishery		
	N	x	SD		N	x	SD
Bodyweight (g)	458	9.9	4.4	*	667	10.0	5.6
Total length (mm)	470	140.0	23.0	**	664	134.6	31.2
Sex and Status:	N	♀	♂		N	♀	♂
Sex (%)	146	129(88)	17(12)	***	519	482(93)	37(7)
No. ♀ ovid (%)	128	42(33)		****	327	53(14)	

Comparisons between periods:
* ns, $t=0.40$, $df=1123$
** $P<0.001$, $t=3.18$, $df=1132$
*** % ♀ in meals: ns, $\chi^2=2.53$
**** % ♀ ovid: $P=0.0001$, $\chi^2=20.13$

DISCUSSION

Many interesting observations arise from the preliminary comparisons of the diet of puffin chicks at Great Island, Newfoundland, before and after the initiation of a major commercial fishery. The most striking result is the importance of capelin in the diet during the chick-rearing period, demonstrated by reduced breeding performance when the supply of capelin was low and highest when capelin were abundant (Brown & Nettleship 1984). In the pre-fishery period puffins bred successfully, rearing their young mainly on capelin (78-100%), as they did between 1982-84 (87-94%), four to six years after the capelin fishery had collapsed offshore and was closed by regula-

tion. But in 1981, two years after the onset of the decline, capelin were scarce and immature gadids dominated the chicks' diet (68%) supplemented by sandlance (16%) and certain invertebrates (amphipods, squid *Illex illecebrosus*) seen only in 1981. In addition to the decrease of capelin in the diet, meal sizes and feeding rates were reduced. That reduction in daily amount (c.70% less) and food quality (caloric value of capelin exceeds all other prey; see Birkhead & Nettleship 1987) resulted in an unusually high mortality of chicks from starvation before fledging and a low likelihood of survival of those young that did fledge (Nettleship 1972, Brown & Nettleship 1984). Clearly, the absence of capelin is reflected in a reduced breeding success and performance of puffins, and in all associated determinants of successful chick rearing including diet (composition, quantity and quality), growth and feather development, vulnerability to *Larus* gull predators, and others (Nettleship 1972, 1975).

At a more subtle level are the changes recorded in certain characteristics of the prey. Although the post-fishery years of 1982-84 showed a reappearance of capelin in the chick diet, at amounts often exceeding those recorded in the pre-fishery period, notable changes occurred. While meal size and capelin fed to chicks in the post-fishery period were similar in mass to those fed earlier, the average length, sex, and reproductive condition of the fish were not. The reduced mean fish length in the postfishery period indicates an altered age structure of the capelin population. An increased proportion of female capelin in the meals after 1981 may not be significant, but the marked reduction in the percentage of females caught that were ovid (decrease from 33% to 14%) could be important both to puffin production and management of the capelin stock. Future inter-disciplinary studies between marine bird and fisheries biologists might reveal considerable insights into possible mechanisms of positive information feedback, particularly those questions related to local versus wide-ranging demographic changes in fish populations in NAFO division 3 in SE Newfoundland and elsewhere.

Why should we care about puffin chick diet and characteristics of the principal prey? Why not merely conclude that when capelin are abundant puffins do well reproductively, and when capelin are scarce puffin breeding success is reduced or fails completely?

The answer is simple. If we are ever to be able to forecast when decreases in capelin biomass are likely to occur, at least in upper water layers in the vicinity of major seabird colonies, we must identify those demographic parameters in both prey and predator that may serve as sensitive indicators of environmental change. That will permit actions to be taken for the mutual benefit of the conservation and protection of populations of capelin and puffins. Although none of the many interesting traits shown here provides any clear insight into the question of whether or not certain characteristics of the foods delivered to puffin chicks can be used to monitor changes in capelin stocks, some may form a useful step towards an analytical formulation that could link demographic changes in prey to major changes within and between local populations of capelin. The challenge is formidable and the pathway to establishing cause and effect relationships uncertain. But overall, it seems clear that the diet of chicks of specialist feeders offers broadened opportunities and promising systems for use as bio-indicators of marine environmental changes.

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HOW DO FORAGING SEABIRDS SAMPLE THEIR ENVIRONMENT?

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ABSTRACT. If seabird populations are limited by the availability of food, changes in the population size or reproductive ecology of seabirds may in some circumstances reflect changes in the availability of prey. The structure and dynamics of prey populations and the way seabirds locate prey will influence how changes in prey stocks are indicated by seabirds. The structure of prey stocks is important because birds from a given colony rarely sample entire prey populations. The extent to which the portion of the prey population sampled reflects events in the prey population as a whole is thus relevant. The method by which birds find prey and their aggregative responses to prey patches violate rules of sampling and probably act to buffer fluctuations in seabird populations and reproductive ecology. Programs that monitor seabirds as an indication of prey stocks require information on the structure of local prey populations and how the seabirds in question sample prey.

Keywords: Monitoring, predator-prey, seabirds, fisheries, foraging, aggregation.

INTRODUCTION

In many areas of the world, small "forage fish" species that are important links in pelagic food webs are increasingly subject to harvest by man (e.g. anchovies *Engraulis* spp., sandlance *Ammodytes* spp., capelin *Mallotus villosus* and Antarctic krill *Euphausia superba*). Most of these prey species are patchy in distribution, highly mobile, and difficult to sample using traditional fishing gear. These characteristics pose a challenge to organizations responsible for stock assessment and fisheries regulation.

As highly mobile and conspicuous predators on small forage species, seabirds, through various aspects of their breeding and feeding ecology, often reflect changes in the ecology of prey populations, e.g. changes following catastrophic stock failures (Cairns 1987). Thus, the monitoring of seabird populations has the potential of not only detecting changes in the status of these predators, but also of providing indirect evidence about the status of prey populations (Furness 1987, Croxall et al. 1988).

However, of the many parameters of seabird biology that are commonly assumed to relate directly to prey abundance (e.g. diet composition, chick growth, chick feeding rates, breeding success, adult mortality, foraging effort), few have been measured with concurrent studies of local prey abundance. Indirect evidence suggests that these parameters are related to prey abundance in a non-linear way (Cairns 1987), but the form and strength of these relationships are virtually unknown for seabirds as a group or for any individual species (Piatt 1990). Furthermore, assumptions that seabirds adequately sample prey stocks have not been rigorously examined.

Cairns (1987) has already summarized much of the literature pertaining to the use of seabirds as monitors of changes in the status of prey populations. In this paper, we examine some of the assumptions underlying the use of seabirds as indicators of prey stocks, and consider what at-sea studies of seabird foraging reveal about seabird-prey relationships.

PREY ABUNDANCE AND THE LIMITATION OF SEABIRD POPULATIONS

The most fundamental assumption behind the use of seabirds to monitor their prey is that seabird populations or aspects of their reproductive performance are limited by prey abundance. Implicit in this assumption is a density-dependent response of the predator to changes in the prey. If seabird populations or reproductive performance were not limited by prey abundance there would be no reason to expect them to reflect variations in prey abundance.

There is good evidence that seabirds are regulated by their prey (Birkhead & Furness 1985). Most marine birds are at or near the top of their food webs, and mortality of adults from predation (other than by man) is low. Several modeling studies suggest that marine birds crop 20% or more of secondary productivity in the vicinity of large colonies (Furness 1978, Furness & Cooper 1982, Wiens & Scott 1976). One study demonstrated prey depletion by breeding seabirds in the vicinity of their colony (Birt et al. 1987). Dramatic evidence for the impact of changes in prey populations on breeding seabirds has been provided where prey populations collapsed and seabird populations subsequently declined (Jordan 1967, Duffy 1980, Lid 1981, Barrett & Vader 1984, Vader et al. 1990). More subtle evidence for food limitation of seabirds includes apparent adjustments of colony size in relation to the size of neighboring colonies (Furness & Birkhead 1984, but see Cairns 1989) and inverse correlations between colony (population) size and measures of reproductive performance (Gaston et al. 1983, Birkhead & Furness 1985, Hunt et al. 1986).

Although studies of catastrophic prey failures have provided indirect evidence (see above), direct evidence that aspects of seabird breeding biology can be used as an index of prey abundance comes from studies where prey abundance was measured independently of avian observations. In several studies correlations between measures of prey abundance and aspects of seabird reproductive biology have been found (Hunt & Butler 1980, Anderson et al. 1982, Anderson & Gress 1984, Piatt 1987, Safina et al. 1988, Burger & Piatt 1990). These results, for dietary specialists (pelicans, Anderson & Gress 1984, terns, Safina et al. 1988, murre, Piatt 1987, Burger & Piatt 1990) and for more generalized foragers (gulls, Hunt & Hunt 1976, puffins, Piatt 1987) provide encouragement for the use of colonial marine birds as indicators of prey stock abundance. However, these studies also indicated that different seabird species responded differently to fluctuations in prey abundance and that, at least at some colonies, some bird species are able to compensate for natural variability in prey abundance.

ASPECTS OF SAMPLING DESIGN AND SEABIRD FORAGING

The most powerful sampling designs require randomly selected, independent samples of a population, the number of samples depending on the sample variance, the

degree of difference that must be detected, and the certainty required. In addition, sampling should extend beyond the edge of a population's range to detect expansions and contractions in distribution. When random sampling is not possible, alternative sampling designs, including transects and grids, must be employed. Sampling may also be stratified to adjust sampling effort in various habitats. Estimates of population size derived from non-random samples are limited in their use for detecting change because one has to assume that the points sampled are representative of the population, and one is only able to compare results from replications of a given sampling scheme (e.g. Harris et al. 1983). For the remainder of this paper, we examine what we know about seabird foraging behavior and ecology with respect to the requirements of a program designed to sample prey populations.

Independence of samples of the prey

Sampling design calls for independence of samples. However, it seems likely that information about the location of food is exchanged in colonies (see Wittenberger & Hunt 1985 for a review, Brown 1986). Thus, the smallest independent sample of prey abundance might be the colony. In addition, birds interact at sea, forming single- and multi-species foraging flocks that can attract birds over considerable distances (Simmons 1972, Hoffman et al. 1981, Bayer 1983, Duffy 1983). Therefore, colonies that overlap in the use of foraging areas may not be independent from one another in their sampling of prey. A result of these interactions is a reduction in the effective number of independent samples of the prey population, with a concomitant loss in confidence in the response of the birds.

Adequacy of sampling of prey stocks

It is unlikely, particularly during the breeding season, that seabirds will be able to sample a prey stock throughout its entirety. During the breeding season, birds must return to their colonies to feed their young. This requirement limits the time that they can be absent from the colony and forces all but a very few species (e.g. albatrosses, Jouventin & Weimerskirch 1990) to forage near the colony. It is therefore unlikely that foraging trips will be long enough to permit sampling of the entire area occupied by a prey stock. In addition, colony location may not be random with respect to resource availability. Colonies are often located on headlands and near island passes (e.g. penguins in the area of the Antarctic Peninsula, Croxall et al. 1984), where currents and gyres are likely to concentrate prey (e.g. Zelikman & Golovkin 1972, Pingree et al. 1978, Hamner & Hauri 1981, Priddle et al. 1988). Thus, for most species, random sampling of prey is precluded in all but the foraging area around the colony.

Given that the restricted foraging ranges of most species of breeding seabirds results in the sampling of a local subset of a prey population, it is of interest to know if these local populations have been representative of the prey population as a whole. In the cases of Western Gulls *Larus occidentalis* and Brown Pelicans *Pelecanus occidentalis* studied in the Southern California Bight (Hunt & Butler 1980, Anderson et al. 1982, Anderson & Gress 1984), the core spawning population of the anchovies on which these birds preyed maintained a high biomass in the inshore region sampled by both bird species, whereas peripheral portions of the prey stock fluctuated widely (MacCall 1990). In contrast, a population of pelicans at Point Lobos, which was dependent on peripheral populations of Pacific sardines *Sardinops sagax*, experienced much greater fluctuations than did the overall population of its prey (MacCall 1984). In a study of Common Murres *Uria aalge* and capelin *Mallotus villosus* in Newfoundland, inshore

capelin stocks in Witless Bay used by birds from the study colonies decreased markedly from 1983 to 1984 as indicated by hydroacoustic surveys (Piatt 1990), catch-per-effort fishery statistics (Burger & Piatt 1990), and a reduction in the number of large baleen whales foraging inshore (Piatt et al. 1989). In contrast, capelin stocks offshore on the Grand Banks, from which the Witless Bay population derives, increased slightly between 1983 and 1984 (Piatt 1987). This discrepancy may be explained in part by a differential use of offshore and inshore habitats by different age-classes of capelin, and by unusually cold water temperatures in 1984 that may have inhibited capelin migration inshore (Piatt 1987, Methuen & Piatt in press).

Random sampling of prey in the area sampled

If seabirds are random samplers of their prey, one would expect to find no statistically significant correlations between foragers and their prey. In this case, seabirds would have no foreknowledge of prey distributions, would sample parcels of water at random, and would not respond to the success or failure of nearby foragers. However, seabirds do not forage independently of one another (see above), and evidence (below) suggests that they go to areas where prey is likely to be plentiful and concentrated (e.g. Hunt & Harrison 1990, Hunt et al. 1990, Piatt 1990). If seabirds forage in this way, one would expect either all the foragers to concentrate in one or a few places, or possibly a threshold effect, with predators attending only large or dense aggregations (Piatt 1990).

The distribution and abundance of foraging seabirds frequently, but not always, show statistically significant correlations with the distribution and abundance of prey. These correlations have two components: (1) a spatial concordance, the tendency of predators and prey to co-occur, and, (2) within samples where both predator and prey are present, a numerical concordance (Heinemann et al. 1989, Erikstad et al. 1990). In Bransfield Strait and southern Drake Passage, Antarctica, Heinemann et al. (1989) found that two bird species, Cape Petrels *Daption capensis* and Antarctic Fulmars *Fulmarus glacialis*, were spatially concordant with Antarctic krill, and two species, Cape Petrels and Adelie Penguins *Pygoscelis adeliae*, were numerically concordant with krill. Most foraging individuals of these three bird species were associated with two very large krill swarms (Hunt et al. 1985). For most bird species, numerical concordances with krill were stronger when only cases with "high densities" of krill were used, suggesting a threshold effect. For three of four bird species with positive numerical concordances with krill at the scale of a nautical mile, the strength of those correlations increased as the scale of the sampling unit increased. These data suggest: (1) a high degree of stochasticity at the smallest measurement scales and a selection by the birds of oceanographically favorable areas in which to forage at larger spatial scales, (2) at intermediate scales, birds should reflect the availability of krill over periods of days or weeks, and (3) that at the largest scales, the distribution of birds is controlled by colony location, both of which would reflect the long-term expected availability of prey.

The importance of very large swarms of krill may be disproportionately great to birds (Hunt et al. 1985). Once a swarm is found, it is possible that contact with the swarm can be maintained for long periods if birds returning to the foraging grounds after visiting the colony can relocate the swarm by memory or by observing birds foraging at it. To the extent that a major portion of the foraging birds seen by Hunt et al. (1985) were associated with two large krill swarms, the bird species observed in that study were not likely to be sensitive indicators of the overall availability of krill. For those

birds not associated with the large swarms in that study, the bird-krill relationship conformed moderately well to a model based on the non-random selection of "good" areas in which to forage and "random" sampling within these areas.

In the northern Bering Sea, Hunt et al. (1990) studied associations between Least Auklets *Aetheia pusilla* and their prey (primarily *Neocalanus plumchrus*) near colonies on St. Lawrence Island. Correlations between auklets and prey biomass measured with an echosounder were strongest when auklet numbers were regressed against zooplankton biomass found at and above the thermocline. Correlations were strongest at spatial scales of 5-12 nautical miles. However, bird and plankton distributions along transects revealed many instances in which peaks in abundance of auklets and prey failed to coincide. These authors concluded that auklets were selecting for areas in which prey were relatively accessible, but auklets were not well correlated with peaks in prey abundance on a fine scale in these areas. One explanation offered for the small scale distribution of the birds was that the first bird to find an adequate prey patch would stay with that patch and subsequently be joined by other birds. The authors also suggested, as did Woodby (1989), that prey were sufficiently abundant that birds could obtain adequate food without seeking peaks in prey abundance. This argument, for an upper threshold in prey abundance above which seabirds would cease to discriminate, would reduce the range of prey densities over which seabirds could be useful indicators of prey abundance.

In the Barents Sea in winter, Erikstad et al. (1990) found both spatial and numerical concordance between murres *Uria* spp. and acoustic estimates of their potential prey. The strength of these correlations was scale-dependent. Correlations were significant at the smallest measurement scale (5 nautical miles) and reached a maximum at a measurement scale of 90 nautical miles. Numerical concordance was higher for high density ($r=0.71$) than for low density ($r=0.35$) prey patches. The high density prey patches accounted for only 5.6% of the area surveyed, but contained 58.2% of all birds seen.

These results suggest the existence of a lower threshold below which birds are not very sensitive to variations in prey density. In addition, since the birds concentrated their foraging in the most profitable areas (high prey density), they would not be likely to provide sensitive measures of the prey populations as a whole. Capelin and the other prey taken (e.g. arctic cod, *Boreogadus saida* and euphausiids *Thysanoessa raschii* form dense schools, and local densities can remain high even when region-wide stocks are depleted.

The best evidence that seabirds exhibit threshold foraging behavior is provided in the study by Piatt (1987, 1990) of Common Murres and Atlantic Puffins *Fratercula arctica* foraging on capelin in Witless Bay, Newfoundland. Both murres and puffins were temporally correlated with capelin abundance, and both species were spatially correlated with capelin schools on most surveys ($n = 72$) before the effects of scale were examined. Aggregations intensity and spatial correlations generally peaked at spatial scales of 2-6 km. Capelin density frequently explained over 75% of the spatial variability in bird density; it explained over 95% of the variation on nine surveys. Piatt (1990) concluded that these unusually strong correlations were observed because the abundance of breeding birds, close proximity of the survey route to colonies, and the use of Witless Bay for spawning by large numbers of capelin increased the likelihood that

most capelin schools in the study area would be exploited by foraging murres and puffins (i.e. prey schools were saturated by predators).

At the scale of aggregations, murres and puffins exhibited sigmoidal aggregative responses to capelin density. Inflection points (thresholds) in sigmoidal response curves occurred at higher densities of capelin for murres than for puffins, and foraging thresholds for both species varied daily (and annually) with overall capelin abundance in Witless Bay. Piatt (1987, 1990) concluded that threshold foraging behavior had important implications for interpreting the feeding ecology and population biology of seabirds. For example, the diet composition of murres and puffins will not necessarily reflect fluctuations in local prey abundance unless prey densities fall below some "critical" threshold level - which is lower for puffins than for murres. Both species have considerable flexibility in dealing with prey fluctuations above "critical" threshold levels - as evidenced by variable thresholds and foraging ranges. Also, murres rear their chicks during a period of maximal prey densities near the colony (c. 4 weeks) whereas puffins extend chick-rearing for a much longer period (c. 8 weeks). Thus, murres are less likely to reflect variations in abundance of prey except in extreme cases. As long as prey densities remain above "critical" levels, murres appear to deal with "normal" fluctuations by spending more (or less) time foraging, thereby maintaining constant meal delivery rates to chicks (the Time-Buffer Hypothesis - Burger & Piatt 1990).

CONCLUSIONS

The results of the above studies suggest that there may not be a simple, linear relationship between the ability of birds to obtain prey and the size of prey stocks. In some cases, the lack of spatial and numerical concordance between seabirds and their prey indicates that seabirds may be operating as random samplers of prey, at least at small spatial scales. At larger scales, stronger correlations between predators and their prey, often involving a majority of individual predators concentrating their foraging on one or a very few unusually large concentrations of prey, suggest that seabird foraging success will not reflect the status of overall prey stocks. To the extent that prey stocks are patchy and that patches are non-uniformly distributed, the likelihood that seabird foraging success will reflect prey stocks is further diminished. Both upper and lower threshold effects also complicate the interpretation of the results of seabird foraging success. There is little doubt that under certain circumstances changes in the population biology or reproductive performance of birds will reflect changes in their success in obtaining prey. However, before we can interpret these signals from the birds, we will have to learn a great deal more about the at-sea relationships between birds and their prey. In particular, we must learn how changes in prey distribution and numbers are reflected by the foraging activities of the birds and subsequently how these interactions are reflected by avian population parameters and reproductive performance. To this end, coordinated, long-term studies of the bird and prey populations of interest are necessary to validate the use of birds as monitors of prey stocks.

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SYMPOSIUM 42

**BIRD CONSERVATION AT A LANDSCAPE
SCALE**

Conveners M. L. HUNTER and Y. HAILA

SYMPOSIUM 42

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INTRODUCTORY REMARKS: BIRD CONSERVATION AT A LANDSCAPE SCALE: SEEING THE WORLD FROM A BIRD'S-EYE VIEW

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The geographic scales of conservation are often very limited—measurable in tens or hundreds of hectares—because conservation biologists typically focus on a single population or community and because resource managers usually develop their plans one ecosystem at a time. In recent years conservationists have realized that large scale phenomena, notably habitat fragmentation, are of profound importance and they have begun to broaden their perspectives to consider landscapes measured in tens and hundreds of square kilometers. This shift is of particular importance to bird conservationists because birds have large home ranges compared to most organisms and because they are exceptionally mobile. Thus birds' use of landscapes is usually profoundly different from that of the insects, other invertebrates, and plants that comprise the bulk of the world's biota, and is only crudely similar to that of other endotherms, i.e. mammals.

The uniqueness of birds means that as we begin to develop conservation plans at the landscape scale we must avoid blindly applying paradigms developed for other taxa to birds. Conversely, we cannot necessarily apply bird-based paradigms to other biota—a prospect that is far more likely given the popularity of birds. For example, I have heard and read much discussion about the design of a reserve system that would protect the Central American habitat of neotropical migrant birds (Hagan & Johnston in press), but almost no one asks how this effort would integrate with the habitat needs of the local biota. A reserve system designed for birds is likely to have units of sufficient size for most other organisms with the exception of large carnivorous mammals, but the connectivity between reserves may be inadequate for less mobile taxa.

Inaccurate generalizations can also confound the management of different bird species. Consider the differences in the scale and pattern of spatial use among colonial, migratory seabirds (e.g. Arctic Terns *Sterna paradisaea*), year-round resident raptors, (e.g. Harpy Eagles *Harpia harpyja*), year-round resident nectarivores (e.g. Golden-winged Sunbirds *Nectarinia reichenowi*), and irruptive species (e.g. Red Crossbills *Loxia curvirostra*). Again, there are examples of short-sighted applications of inappropriate paradigms. Management for game species such as quail *Colinus virginianus* and woodcock *Scolopax minor* has traditionally emphasized the creation of edges between different successional stages and assumed that this was good management for the entire avifauna (Hunter 1990). Now we know that many species of passerines experience elevated nest predation and brood parasitism near edges (Angelstam 1986, Brittingham & Temple 1983). The importance of using species-specific, spatially explicit models is explored in this symposium in papers by Haila and Van Horne.

Much of our understanding of habitat fragmentation comes from studies of forest birds in temperate regions where the forest remains as isolated patches following historical conversion to an agricultural landscape. We know little of the impacts of forest fragmentation where forests continue to dominate the landscape but are currently being divided into patches by clearcuts and roads. Most research suggests that fragmentation may be important in forested landscapes (Helle 1985, 1986, Angelstam 1986, Small & Hunter 1988), although Rosenberg & Raphael (1986) and Haila (1986) illustrate limitations to this generalization. We also have learned little about the prospects for fragmentation in environments where it may be less obvious: grasslands, wetlands, and marine habitats. In this symposium we move beyond agricultural landscapes in papers by Angelstam on forest fragmentation in Fennoscandia and by Gaston and Brown on the use of marine environments by seabirds.

Our knowledge of the ways birds use the landscape is focused largely on their selection of habitat for establishing home ranges. We also have moderately good information about how birds migrate between winter and summer ranges or move daily between foraging and nesting/roosting areas. However, our understanding of the dispersal of juveniles to new habitat is strikingly poor. This is unfortunate because models of population viability have taught us that dispersal often has a significant influence on the probability of a population persisting. Temple considers this topic and its implications for several species in his paper.

Conservationists' use of a landscape perspective has been particularly evident in the use of island biogeography theory and related ideas to design nature reserves. In many regions however, reserves are too few and too small to stand alone, and conservationists should not think solely in terms of buffering nature reserves from surrounding ecosystems where human activities are dominant. They must also consider how to integrate reserves into managed landscapes, and how to modify natural resource management practices to foster biological diversity in the managed ecosystems themselves.

To summarize, I have tried to make five points: (1) a bird is not a beetle – birds' use of space is very different from other organisms; (2) a bird is not a bird – species should be considered individually; (3) a farm is not a forest – fragmentation studies must extend beyond forest patches in agricultural landscapes; (4) a day can be a lifetime – a brief event, dispersal, is of great importance to population viability; and (5) a park is not an island – reserves must be integrated into landscapes managed for natural resource exploitation.

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IMPLICATIONS OF LANDSCAPE HETEROGENEITY FOR BIRD CONSERVATION

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ABSTRACT. When evaluating the challenges of bird conservation in heterogeneous landscapes, it is fruitful to define landscape characteristics from an organism-centred perspective. The critical features of a particular landscape diverge depending on the focal species. This gives rise to three types of questions: first, is it possible to classify species according to the threats they face?; second, is it possible to recognise landscapes presenting similar challenges for bird conservation?; third, can these generalisations be applied to bird conservation in human-modified environments? As answers to these questions I suggest empirical generalisations that can be used to direct further, specific studies. An important general principle remains, however, that the more specific the conservation problem addressed, the more necessary it is to resort to thorough autecological knowledge of the species concerned.

Keywords: Landscape heterogeneity, landscape dynamics, fragmentation, disturbance.

ORGANISM-CENTRED PERSPECTIVE ON LANDSCAPE HETEROGENEITY

In the conservation of endangered species there is no substitute for thorough autecological knowledge of the species. Similarly, when the challenges of bird conservation in heterogeneous landscapes are evaluated, it is appropriate to adopt an organism-centred approach toward identifying critical characteristics of the environment. By organism-centred approach I mean simply that we should let the organism considered define what features of the environment matter.

This statement calls forth several conceptual clarifications.

First, the critical elements of a landscape need to be defined. Landscape is a general, descriptive term referring to how various environmental structures are distributed in space, but in ecology and conservation we are primarily interested in how those structures, and their configuration, influence ecological processes. Following Margaleff (1979) I distinguish, in an organism-centred framework, among three aspects of a landscape, namely, structure, pattern and process. By "structure" I refer to the physical environment not modified by the organisms considered. Landscape structures have their own generative mechanisms which may be either physical or biological or both, but they operate on time-scales much longer than the ecological units of concern. Recurring disturbances are an important type of generative process of landscape structures. By "pattern" I refer to the spatial distribution of the organisms considered. Landscape structures act as a constraint on organismal patterns. By "process" I refer to the causal, ecological mechanism(s) creating the pattern considered.

There is genuine interpenetration between the organism and the landscape (Levins & Lewontin 1985). That is, the difference between structure and pattern is relative and depends on the time-horizons of the respective generative processes, and the role of

the organisms in modifying those processes. The distribution pattern of an organism on the landscape scale results from how the organisms choose and modify the landscape structures they use. Vegetation heavily and continuously modified by a particular species may be regarded as a part of the "pattern" of that species.

When identifying important landscape structures we may use criteria defined either on the individual or on the population level. The former case relates to factors influencing individual survival, and the latter to factors important for population maintenance (Haila et al. 1989, Van Horne, this volume). For instance, forest fragmentation in boreal environments causes an alteration in the spatial distribution of breeding pairs by changing the suitability of particular sites for reproduction, but it is not a priori clear whether this has a detrimental effect on population maintenance (Helliwell 1976, Haila 1986). Individual level and population level phenomena are more closely related in southern areas with a more sedentary bird fauna, for instance western Australia (Saunders 1989).

The distinction between individual level and population level is fuzzy. An individual-centred approach to population dynamics may allow more realistic models than those traditionally used, but in evaluating the survival of small populations, population structure needs to be considered in its own right: what an individual does depends on the surrounding population. Sociality, of course, is a manifestation of this effect. Another potentially important factor is the Allee effect, that is, a decrease in reproductive performance with declining group size.

Evaluating the significance of landscape heterogeneity for bird conservation gives rise to three types of questions: First, is it possible to identify types of species facing similar threats?; second, is it possible to recognise types of environments presenting similar challenges for bird conservation?; third, is it possible to classify human-modified environments according to criteria that prove fruitful in answering the two first questions? In the following I discuss these questions on a phenomenological level. That is, I try to formulate empirical generalisations that could direct further, specific studies.

FRUITFUL GENERALIZATIONS ACROSS SPECIES?

The situations faced by endangered birds tend to be idiosyncratic. This is for several reasons. Endangered species comprise, almost by definition, small populations. Endangered birds are often greatly specialized in their requirements. Birds are long-lived organisms with an important component of habituation and learning in their behaviour, which increases the situation-specificity of protection problems.

Further, contingent details of population structure relative to the structure of the environment may be important. For instance, who are the dispersers and who occupy and monopolize the remaining favourable sites? Such factors may be mediated through landscape configuration as in the Capercaillie *Tetrao urogallus* in southern Norway (Angelstam, this volume).

However, I suggest the following generalizations for classifying species according to threats they face:

1. Colonial and territorial birds differ as regards their habitat requirements. Preservation of a particular, unique site is probably more important for the former. Also, it is likely that colonial birds need a combination of different habitats for different activities, whereas territorial birds more probably spend the whole breeding season on more restricted areas. On the population level the relationship may be reversed, however. Territorial birds are spaced out in the landscape whereas colonial species can make it on more restricted areas. This implies that the total area of suitable habitat is critical for territorial species.
2. The allometric relation between the size of birds and their area requirements predicts that larger species require larger home ranges (Calder 1984). However, the response of birds to landscape heterogeneity as a function of body size is ambiguous. Small species have probably more specialized, and hence smaller-scale, requirements than large species but they are, on the other hand, more vulnerable to unfavourable conditions. Large species can select the habitats they need from a large area but may, on the other hand, be very sensitive to the availability of particular combinations of habitats.
3. Birds often have particular requirements of within-habitat structural elements such as snags in which they find food or excavate nest cavities. Wetland and shore birds may be specialised concerning foraging areas. Within-habitat structures may be critical for the conservation of such species independently of large-scale landscape structures.
4. Life-history characteristics of birds vary systematically across biogeographic regions. Birds disperse over longer distances at high latitudes than close to the equator, presumably also in highly seasonal dry environments compared with more stable regions at similar latitudes. This implies that barriers with identical dimensions as measured by metres and hectares have a vastly different significance for population isolation depending on what is the biogeographic zone and climatic domain. Habitat "islands" need to be scaled according to the ecological processes of concern (Haila 1991). Sedentary species are particularly vulnerable to changes in habitat configurations, as has been demonstrated in northern Europe (Helle & Järvinen 1986, Virkkala 1987).

However, when the population trends of all endangered species in a regional bird fauna have been considered together, the conclusions have diverged. The degree of habitat specialisation seems important as an overall characteristic of vulnerable species (Järvinen & Koskimies 1990, Ranjit Daniels et al. 1990). This conclusion underlines the need of specified approaches.

FRUITFUL GENERALIZATIONS ACROSS LANDSCAPES?

Landscapes can be classified according to their characteristic generative processes. For instance, many landscape types are maintained by characteristic disturbance regimes. The generative processes of landscape structures thus form a background for the habitat templates that have moulded the life-history strategies of extant species. This suggests that in characterizing types of landscape heterogeneity in conservation contexts it is fruitful to focus on physical structures of landscapes and their

generative processes rather than the ephemeral extant communities found in them today (Hunter et al. 1988). Unfortunately, very few useful comparative data are available on the relationships between landscape structures and life-history traits of birds living in those environments. Nevertheless, I suggest the following generalizations:

1. Environments differ as regards the spatial scale of their characteristic disturbance regimes. The tree-fall gap dynamics in tropical forests is smaller-scaled than the wild-fire dynamics in boreal forests. Temperate deciduous forests lie somewhere in between: fires have been less important than in the north but heavy winds may have destroyed quite large areas at a time. Bird communities in tropical forests differ in many important respects from those in temperate and boreal forests which are more similar to each other (Terborgh et al. 1990).
2. Patterns of variation in environmental conditions vary across climatic regimes. Of particular significance is the relation of between-habitat and within-habitat variations to each other. If between-habitat patterns are highly synchronized, the degree of habitat specialisation in breeding birds will probably be low: breeders in all habitats are exposed to basically similar environmental hazards. This seems to be the case in northern Finland (Virkkala 1989).
3. Migratory birds require a combination of habitats distributed over vast geographic regions. In some environments, for instance, temperate mountains, migratory movements are conducted over relatively short distances (Dorst 1962) and the migrating birds require particular combinations of habitat types on a fairly small regional scale. Irregular bird movements triggered by varying food availability as in "invasion" birds (Svårdson 1957) or by large-scale environmental fluctuations (Dorst 1962) cover regions of variable extent. The habitat requirements of different types of migratory birds relative to landscape dynamics diverge: for long-distance migrants conditions on breeding grounds and wintering grounds are completely uncoupled, but more localized bird movements take place within landscapes moulded by specific disturbance regimes.
4. Readily identifiable habitats which remain relatively constant through time such as particular types of wetlands are important for specialized species. The relation of the patches of that particular habitat to the surrounding matrix is important (e.g. Kushlan 1979).

THE CHALLENGE: PRESERVING ECOLOGICAL DIVERSITY IN HUMAN-MODIFIED ENVIRONMENTS

Because preserves will always cover a relatively small proportion of the earth's surface, a major conservation challenge for the future is to preserve species diversity in human-modified environments. In intensively modified environments original habitats are completely destroyed and the landscape becomes ecologically uniform and barren. However, in less-intensively modified conditions natural landscape elements are supplemented with human-created structures and the heterogeneity of the landscape is increased. The new structures may represent pure disturbance — for instance, highways — but human activities have historically also produced genuinely new habitats. The challenge is to understand how different types of bird species respond to the human-induced dynamics of modified landscapes.

The first step is to distinguish between major types of human-modified environments, for instance, urban-industrial, suburban, recreational, agricultural, and silvicultural. In evaluating the prospects of preserving ecological diversity in these landscape types we should both specify the environmental dynamics of modified landscapes and use focal species. I suggest the following four points for attention:

1. The dynamics of structural change of human-modified landscapes can be compared with the dynamics of change of corresponding natural environments. Two aspects of structure can be distinguished, namely, within-patch structure and between-patch structure. In boreal forests, for instance, snags, undergrowth and tree-species composition represent the former, and regional distribution of forest stands of different age and type represent the latter. Both factors have been demonstrated to be important for forest birds in Finnish boreal forests (Haila et al. 1987, Helle & Järvinen 1986). One can surmise that the more closely human-induced habitat dynamics follow the dynamics of corresponding natural landscapes, the better the prospects of preserving diversity there (Hunter 1989).
2. The large-scale configuration of remaining habitats is likely to be important, but in different ways in different biogeographic zones.
3. Human influence may create new types of disturbances and/or change the efficiency of propagation of disturbances through the landscape (Turner 1989) — e.g. predators, parasites, disease, and physical disturbance by fire or wind.
4. Specific habitat types, important for potentially vulnerable species, may be particularly threatened by specific activities, for instance, shore habitats by recreational development.

It is particularly important to evaluate the effects of such human activities that cover large areas, and develop guidelines for modifying them so that the effects on bird populations be minimized. Human-induced environmental changes need to be scaled. Drastic but localized effects are unimportant provided they do not destroy unique sites — on the other hand, habitat changes that occur over large areas in a uniform manner are critical although barely distinguishable at local sites.

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CHANGES IN FOREST LANDSCAPES AND BIRD CONSERVATION IN NORTHERN EUROPE

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ABSTRACT. Usually the effects of alteration, fragmentation and finally loss of natural habitats is measured as the local, regional and finally irreversible loss of species. At a community level, however, the ecological situation may be altered, and fitness and density of important key species may be reduced, long before any individual species actually disappears. To solve such problems one must consider not only the dynamics of the target species but also the changes in the biotic and abiotic surroundings. This requires studies also of species whose situation is not yet critical, as well as covering larger geographical areas than is usual in population studies, i.e. at a landscape scale. In boreal forest, populations track changes in forest age ratios well but declines (mainly residents) are steeper than is to be expected from the successional change, due to lowered habitat quality, increased fragmentation and associated edge-related processes. In the forest/farmland edge, several habitat qualities found in pristine forest are retained due to less intensive management of forests. Here several species demanding a very high degree of naturalness of forest habitats are being temporarily rescued after having gone extinct in the taiga landscape. However, in this environment predation from generalist predators affects the dynamics of populations. To conclude, conservation of species and natural communities can be undertaken by restoring many of the natural qualities of the forest landscape. We must, however, also initiate landscape planning for long-term conservation.

Keywords: Habitat fragmentation, boreal forest, edge-effects, restoration ecology, predation.

INTRODUCTION

Forests in Fennoscandia have been subjected to alteration, fragmentation and reduction in extent for centuries (Nilsson 1990). This process has created two principal edges or fragmentation fronts: one between natural and managed taiga forests and one between managed forests and farmland. This has led to changing proportions of young forest, old forest and farmland as well as to reduced habitat quality because of reductions of the amount of old deciduous trees, dead wood, vertical complexity, wetlands, etc.

Bird populations react to these changes by altered range boundaries and dynamics. From the highly altered and fragmented boreal forests in Scandinavia (Gamlin 1988) the populations of several bird species depending on old successional stages, dominated by resident species, have declined while species preferring open ground or young forests, mainly migratory species, have shown a corresponding increase (Järvinen et al. 1977, Järvinen & Väisänen 1977, Väisänen et al. 1986). These changes have to a great extent been explained by a changed age structure due to loss of old boreal forest stands (Haila et al. 1980, Helle & Järvinen 1986). Because migrants greatly outnumber residents, patterns among the former are likely to mask patterns among the latter, thus illustrating the dangers of generalizing about long-term faunal changes.

Furthermore, differences in forest quality in similar successional stages cause differences in bird species richness and composition. The density of dead trees (Haapanen 1965, Järvinen et al. 1977, Haila et al. 1987, Niemi & Hanowski 1984), the density of old deciduous trees (aspen *Populus tremula*, and birch *Betula* spp.) (Angelstam 1990, Angelstam & Rosenberg unpubl.) and existence of large continuous tracts of forest (Boström 1988, Rolstad & Wegge 1989, Virkkala 1990) have been found to influence bird species composition and richness in the taiga forest. Resident species seem to be especially sensitive to reductions in these qualities.

EFFECTS OF HABITAT FRAGMENTATION AND LANDSCAPE GRAIN SIZE

One of the birds depending on old forest, the Capercaillie *Tetrao urogallus*, has been studied in great detail with respect to the effects of habitat fragmentation (Rolstad & Wegge 1989). The main factor explaining variations in Capercaillie density is the proportion of the landscape covered by old forest. As the size of old forest stands and the proportion of old forest in the landscape declines territories of individual cocks are lost. This leads to a reduction in the number of cocks per lek and, finally, to the disappearance of leks. There are three different kinds of critical area requirements for the amount of old forest that the Capercaillie needs in order to maintain a stable population level: (1) 20-50 ha of old forest - the territory size of one individual Capercaillie cock at the lek. (2) 200 - 500 ha dominated by old forest - the size of all the cock territories, i.e. a local lek population. (3) Approx. 10 000 ha of forest landscape with a balanced age distribution - the size of an area required in order to have a core area satisfying the needs of a local population throughout the breeding cycle.

Rolstad & Wegge (1989) also studied how the Capercaillie population size and fitness vary in relation to the grain of the landscape mosaic. At an intermediate grain size, i.e. the home-range size of Capercaillie, the negative effects on survival are the worst. In a coarse-grained landscape the local occurrence of populations will move around with the occurrence of suitable patches, while if the size of clear-cuts is sufficiently small, the Capercaillie may perceive the forest landscape as one single old forest area and be permanent.

Using bird census data, Helle (unpubl.) modelled the effects of variations in landscape grain size on north taiga forest bird communities from the start of exploitation by clear-cutting of continuous forest. Three grain sizes were used: 5, 20 and 50 hectares and the rate of exploitation was 75% being logged in 100 years. He then simulated the effects on total bird density, bird biomass, species richness and number of sedentary species. The simulation predicted that bird density will be highest when the smallest clear-cut area is used; the adult biomass will be highest with the largest grain size. Bird species diversity shows the greatest values when medium-sized clear-cuts were used. However, the species group suffering from forest management in north Finland is the sedentary species (Väisänen et al. 1986, Virkkala 1990). Thus, if the desired option is to reduce the decline of this group a coarse-grained landscape is to be preferred provided that the age distribution is even. For migratory birds, the smallest cuts were the optimal option. In conclusion, since there is no consensus of what is optimal patch size, provisional advice is to create a diversity of landscape grains (see also Hunter 1990).

EFFECTS OF SURROUNDING HABITATS ON FITNESS AND DYNAMICS

Apart from the direct effects of habitat loss and fragmentation, life in a patch can be affected by the surrounding landscape (Angelstam 1991). One such edge effect is predation which leads to higher nest predation rates in small than in large forest fragments (Andrén et al. 1985, Andrén & Angelstam 1988). In North America, predation and nest parasitism appear to cause declines in forest-interior bird densities. There are, however, alternative untested explanations that could work in the same direction, such as the rapid disappearance of forest in the tropical winter-quarters of these forest-interior species. In Europe there are no recent comparable patterns of population declines of predation-prone species.

In northern Europe the effect of predation may vary regionally. Population cycles of birds and mammals in the holarctic zone disappear towards the southern part of the taiga. In northern Fennoscandia grouse populations undergo regular population fluctuations every 3-4 years (Angelstam et al. 1984, 1985). By contrast, grouse populations farther south on the European continent are non-cyclic. Evaluation of several potential explanations for the cyclic fluctuations in grouse (Angelstam et al. 1985) show that temporal and spatial variation in predation pressure may explain both the occurrence and distribution of Fennoscandian grouse cycles. Predation from a generalist predator community upon grouse (an alternative prey with low abundance) varies in relation to the abundance of small rodents (the main prey of generalist predators) (Angelstam et al. 1984).

Regarding the disappearance of population cycles towards the south, overall predation increases from north to south (Angelstam et al. 1985, Angelstam 1988) due to a more complex set of food items being available to predators (Angelstam et al. 1985), which increases the number of generalist predator species as well as their population density (Andren 1985). Hence, the consequences of predation as an edge effect can be seen also at a landscape level near the edge of the continuous boreal forest.

There also appear to be differences in predation pressure among forested landscapes with different degrees of fragmentation at the northern edge of the managed boreal forest (Hansson 1979, Angelstam 1991), suggesting that fragmentation of surrounding forests may negatively affect the breeding success of ground-nesting birds in forest fragments.

INDIRECT EFFECTS OF HABITAT FRAGMENTATION

One of the first effects of habitat fragmentation is the loss of large predators. Several studies show that as herbivore populations are released by lack of predation the vegetation structure changes due to increased browsing pressure on preferred food plants, thereby altering future tree species composition (Alverson et al. 1988, Pastor et al. 1988). Because large herbivorous animals are often habitat generalists, the effects of this edge effect may extend into the whole landscape.

The dominating browser in taiga forests is the moose *Alces alces*. In Sweden the moose has increased dramatically during the last 50 years due to lack of natural mortality and increased amounts of young forest providing a good food supply (Strandgaard 1982).

In boreal forest there are two coniferous tree species (Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*) and five main deciduous tree species (aspen, rowan *Sorbus aucuparia*, birches *Betula pubescens* and *B. verrucosa* and willow *Salix caprea*). Of these, the deciduous trees and shrubs are preferred as winter food throughout the range of moose. According to Ahlén (1975) moose prefer the species mentioned above in the following order: rowan > aspen > willows > birches > pine > spruce. Today moose densities are so high that pine, and occasionally spruce, is severely damaged indicating that the supply of preferred foods is depleted (Lavsund 1987).

Hence, intensive browsing is preventing the deciduous tree species preferred by moose from growing into an adult shape and reproducing. This is a serious long-term conservation problem for hole-nesters since aspen is the tree species in which the majority of nest holes are found in boreal forest (Angelstam & Mikusinski unpubl.). This indirect effect of browsing adds to the active reduction by forest management of the previously common old deciduous trees in taiga forests. The occurrence of adult deciduous trees is now largely confined to the edge between taiga forest and abandoned farmland (Lövgren, Ihse & Angelstam unpubl.). Given that today's high browsing pressure is not reduced, species requiring adult rowan and aspen may become threatened regionally.

MANAGEMENT IMPLICATIONS

The literature on biological conservation has focused mainly on the formation of nature reserves or national parks. This is not enough. The long-term conservation of boreal forest communities must also depend on maintaining viable populations of the various species within the framework of a managed and sustainably used forest landscape in which consideration of fauna and flora is a necessary part. Parks and reserves may be important core areas for some species with small area requirements in this system.

To preserve natural processes (such as low levels of predation and herbivory), however, is probably not possible unless reserves are unrealistically large. We must also accept that it is dangerous to be too orthodox when setting aside reserves. It is better to accept an assemblage of species that may not be complete but that nevertheless allows the main interactions to operate. In addition there is great potential for restoring habitats which have been lost. Research in natural areas in north-eastern Europe may give advice on how this restoration can be done.

As well as concentrating on populations with negative trends in density, we must cope with the faunal changes following intensive exploitation of the environment by man allowing certain species to attain super-normal densities. Abnormally positive trends of, for example, generalist predators such as gulls and corvid birds, must sometimes be broken. Likewise, we must deal with the direct effects of super-normal densities of large herbivores affecting the future composition of plant communities and forests as well as the indirect effects on generalist predators (see also Westmore 1990). In addition our goals should be:

- to preserve the remaining natural forests.
- to create buffer zones around reserves.

- to develop strategic land-use planning.
- to enhance the natural variation in forests.
- to increase the numbers of (old) broad-leaved trees.
- to plant native trees.

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THE ROLE OF DISPERSAL IN THE MAINTENANCE OF BIRD POPULATIONS IN A FRAGMENTED LANDSCAPE

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ABSTRACT. The conversion of a naturally extensive and contiguous ecosystem into small and isolated fragments has negative consequences for three types of birds: (1) area-sensitive species that require extensive tracts of habitat to accommodate large individual home range requirements, (2) edge-sensitive species that suffer reductions in their survival and natality in fragmented habitats dominated by ecological edges, and (3) isolation-sensitive species that have poor dispersal movements between widely separated fragments of habitat and consequently become isolated subpopulations. Dispersing individuals that move between habitat fragments can reduce the probability of extirpation of each type of species from isolated fragments in three ways: (1) they can recolonize fragments from which a previously extant population disappeared, (2) they can augment a local population whose intrinsic rate of growth is negative and, hence, maintain a population that would otherwise decline to extinction, (3) they can insure gene flow adequate to overcome loss of genetic variability and inbreeding depression that may occur in small, closed populations.

Keywords: Dispersal, habitat fragmentation, metapopulations, population dynamics.

INTRODUCTION

When once large contiguous areas of habitat become fragmented, usually by human development, the areas of the remaining patches of habitat become steadily smaller, and the distances between remaining patches become progressively greater (Temple & Wilcox 1986). These landscape-scale changes in bird habitats are proceeding apace in most of the earth's ecosystems, and they are resulting in regional changes in the structure and composition of avian communities because of differential responses of species populations to the challenges of living in a fragmented habitat.

At the community level, bird species richness in each remaining fragment of habitat is known to be strongly dependant on the area of the fragment (Ambuel & Temple 1983). A typical species-area relationship (MacArthur & Wilson 1967) results, in which certain types of birds are predictably missing from the community in fragments below a certain size (Temple 1988). Understanding the population-level processes that generate this community-level pattern involves describing the functioning of a metapopulation, in which a regional species population exists as a number of more or less discrete subpopulations distributed among habitat fragments.

A regional metapopulation composed of subpopulations living in many scattered fragments of habitat has its own set of population parameters, including size and rates of growth, birth, death and dispersal. These metapopulation characteristics are, however, the sum of the characteristics of the constituent subpopulations, each of which will have its own set of values for various population parameters.

There are predictable differences between the characteristics of subpopulations living on fragments of habitat with different attributes of size, shape, and isolation from

other fragments. Reproductive rates of birds living in habitat fragments have been particularly well studied (Brittingham & Temple 1982, Wilcove 1985, Temple & Cary 1988), but rates of survival and dispersal have been more difficult to study and are, as a result, less well understood. It is my intention to review the role of dispersal movements in the dynamics of avian metapopulations that are composed of subpopulations living in habitat fragments. I shall focus on the role of dispersal in maintaining the size, persistence and distribution of a regional metapopulation as well as the size, persistence and distribution of constituent subpopulations.

BIRDS HARMED BY HABITAT FRAGMENTATION

The dynamics of populations of several types of birds are predictably disrupted when the habitat becomes fragmented: area-sensitive species, edge-sensitive species, and isolation-sensitive species. Area-sensitive birds have large spatial requirements that cannot be met in fragments of their habitat below a critical minimum size, often determined by home-range size requirements. Their problem is simply that small fragments become non-habitat; individuals that attempt to live on fragments of inadequate size are unable to reproduce and do not live long. When their habitat within a region is composed entirely of fragments of inadequate size, these species disappear from the regional avifauna.

Edge-sensitive species generally evolved in ecosystems that were extensive and contiguous and featured few ecological edges where different ecosystems were abruptly juxtaposed. They are poorly equipped to cope with the unusual physical and biotic environments that characterize edges; as a result, their fitness is reduced near edges but enhanced in interior situations far from edges. As their habitat becomes increasingly fragmented, edge-sensitive birds are faced with a habitat that is composed of steadily greater proportions of edge. In severely fragmented landscapes, virtually all of the remaining habitat may be edge habitat. As the proportion of edge in a region increases, the dynamics of a regional metapopulation of edge-sensitive species can be impaired when widespread edge-induced changes in survival and fecundity occur (Temple & Cary 1988).

Isolation-sensitive birds have difficulties dispersing between isolated fragments of their habitat. Usually the interstitial habitat type is hostile to these species and forms a barrier to dispersal or the distances between fragments are great enough to exceed the effective dispersal distances for the species, especially for poor fliers. The result is that the subpopulations on each fragment become isolated from one another so that gene flow and exchanges of individuals are interrupted. Each subpopulation, so isolated, must maintain itself intrinsically.

As isolated subpopulations become smaller in size, owing to the limited carrying capacity of smaller fragments, they become susceptible to extirpation as a result of stochastic changes in their environment, demography and genetics (Shaffer 1987, Temple 1989). The regional metapopulation is, therefore, affected by the loss of constituent subpopulations that have failed to maintain minimum viable population size.

DISPERSAL MOVEMENTS IN FRAGMENTED LANDSCAPES

Dispersal movements in bird populations generally occur as a result of two independent phenomena: either natal (also called intrinsic or passive) dispersal from the site of birth to the site of breeding or density-dependent (also called environmental or active) dispersal away from areas of high density and intense intraspecific competition for important resources (Lidicker & Caldwell 1982). Natal dispersal is often the result of an innate drive among offspring to move away from their parents' home range, the timing, distance and direction of the movement often being unrelated to changes in resource availability per se. In many migratory species that leave parental home ranges when they undertake their initial migration, the return to the breeding range may be characterized by inaccurate homing and loose philopatry that result in individuals being scattered about the region surrounding their birthplace.

Density-dependent dispersal, in contrast, is a movement away from areas where densities are high and competition for scarce resources is intense to areas where competition for scarce resources is less severe. The timing, distance and course of the dispersal movement are tightly correlated temporally and spatially to patterns of resource availability and densities of competing individuals.

For birds living in a fragmented landscape, dispersal movements can play an important role in the dynamics of a regional metapopulation whose constituent subpopulations are interconnected through immigration and emigration movements. Subpopulations inhabiting different habitat fragments have independent schedules of births and deaths that result in some subpopulations having positive intrinsic rates of growth (r), whereas other subpopulations have negative intrinsic rates of growth. Subpopulations that maintain $r > 0$ are intrinsically viable "sources" whereas subpopulations with $r < 0$ are intrinsically unstable "sinks" (Pulliam 1988, Temple 1990). Within a metapopulation, source subpopulations can often bolster a failing sink subpopulation through a "rescue effect" (Brown & Kodric-Brown 1977) provided by immigrants that compensate for the excess of deaths over births. A dynamic equilibrium can be reached in a metapopulation when both source and sink subpopulations are maintained at the carrying capacities of their respective habitat fragments because births and immigrants counterbalance deaths and emigrants among the subpopulations. This situation is, however, unusual, and typically source subpopulations persist while sink subpopulations are subject to within-fragment extirpation.

The respective roles of natal and density-dependent dispersal in the dynamics of a metapopulation occupying a fragmented landscape can be complex. The role of natal dispersal within a metapopulation depends on a number of factors: the species' normal tendency to undergo natal dispersal, the extent to which interstitial areas of nonhabitat form barriers to dispersal between habitat fragments, the probability of dispersing juveniles surviving to reach another habitat fragment, and the probability that a dispersing juvenile will successfully colonize a habitat fragment it has reached. The role of density-dependent dispersal depends on the size of potential source subpopulations relative to the carrying capacity of the habitat fragments on which they live, barriers to dispersal, the probability of survival while dispersing, and the probability of successful colonization.

An important difference exists between natal and density-dependent dispersal movements within a metapopulation. Natal dispersal will result in emigration and immigration movements regardless of a subpopulation's size relative to the carrying capacity of the habitat fragment it inhabits. In contrast, density-dependent dispersal will cause emigration movements only from those fragments of habitat that hold subpopulations near or in excess of the fragment's carrying capacity. Natal dispersal, therefore, allows all subpopulations, both sources and sinks, to produce emigrating individuals. Density-dependent dispersal allows only source subpopulations to generate emigrants.

WHEN IS DISPERSAL BENEFICIAL TO A METAPOPOPULATION?

Dispersal movements within a metapopulation can be viewed as beneficial if they enlarge the metapopulation's size, increase the number of subpopulations, cause rescue effects that prevent extirpations of subpopulations, increase genetic variation within and between subpopulations, or allow a declining metapopulation to persist longer.

Density-dependent dispersal can result in an overall increase in the size of a metapopulation if dispersing individuals find habitat and survive better than they would have by remaining stationary and coping with density-dependent mortality factors. Natal dispersal may afford the same advantages, but it is less certain in most cases that the risks of dispersing are lower than the risks of staying close to home. Natal dispersal may lead to a risk-filled emigration away from a population that is actually below carrying capacity.

A metapopulation composed of many subpopulations has a higher probability of persistence than one composed of a few. Subpopulations are subject to stochastic extirpations, and large numbers of subpopulations provide one important hedge against simultaneous collapse of all subpopulations and, hence, the extinction of the entire metapopulation.

When a metapopulation is composed of source and sink subpopulations, dispersal that results in rescue effects can cause sink subpopulations to persist which otherwise would collapse. These additional subpopulations enhance the viability of the metapopulation. Although natal dispersal can be involved, density-dependent competition is the common cause of emigration from the source subpopulation. Natal dispersal does, however, become particularly important when all subpopulations are below the carrying capacity of their respective habitat fragments but still differ with respect to their intrinsic rates of growth. Natal dispersal allows subpopulations that are below carrying capacity to become sources.

Dispersal movements within a metapopulation can reduce the drastic losses of genetic variability and inbreeding depression that occur within subpopulations isolated on small habitat fragments (Lande & Barrowclough 1987). To the extent that this reduces the probability of a subpopulation being extirpated, the gene flow that is promoted by dispersal can be beneficial to the metapopulation. Although this benefit accrues primarily with very small subpopulations, there is another side to the relationship between dispersal and genetics of a metapopulation. Differences between isolated

subpopulations can contribute to the overall genetic variability within a metapopulation. A subdivided population may, in fact, support more genetic variation than an equal-sized panmictic population, if all the subpopulations remain viable (Denniston 1978).

Natal dispersal within a declining metapopulation can extend the time to extinction. If dispersing juveniles are able to colonize habitat fragments, even ones that are only capable of supporting sink populations, they survive and avoid the inevitable mortality that would result from not locating an area of suitable habitat. In this way the overall size of the metapopulation is enhanced by the retention of individuals that would otherwise have been lost, and the rate of metapopulation decline is reduced. Within a declining metapopulation, density-dependent dispersal becomes rare as subpopulations drop below the carrying capacity of their respective habitat fragments. Natal dispersal, therefore, takes on increased significance.

WHEN IS DISPERSAL DETRIMENTAL TO A METAPOPOPULATION?

Dispersal movements within a metapopulation can be viewed as detrimental if they result in reductions in metapopulation size because subpopulations are consistently held below carrying capacity, because dispersing individuals suffer much higher mortality rates than if they remained stationary, because dispersal leads to a reduction in genetic variability in a small panmictic metapopulation, or because dispersal movements hasten the demise of a declining metapopulation.

Most of the detrimental consequences of dispersal in a metapopulation distributed over a fragmented landscape are related to the fates of individuals undergoing natal dispersal. If the rate of natal dispersal is high, and dispersing individuals suffer heavy mortality before reaching another fragment of habitat, subpopulations may be chronically below the carrying capacities of their habitats. In such cases, natal dispersal essentially becomes mortality that is additive to normal mortality. This could happen in a fragmented landscape in which fragments of habitats are far apart and hazards of crossing interstitial habitats are great. Natal dispersal becomes a drain on the population that keeps it from achieving a higher size or hastens the rate at which a declining metapopulation approaches extinction.

Dispersal movements in a small metapopulation can result in rates of gene flow between subpopulations that render them uniform in genetic makeup. A greater amount of genetic variability may be retained in a small subdivided metapopulation than in a small, panmictic metapopulation.

SOME SELECTED CASE HISTORIES

I have selected as examples of these processes four birds that are suffering because their habitat has become severely fragmented: the Northern Spotted Owl *Strix occidentalis caurina*, the Sharp-tailed Grouse *Pediocetes phasianellus*, several songbirds of North American deciduous forests, and several songbirds of North American tallgrass prairies.

Northern Spotted Owl

This owl's habitat is primarily mature, old-growth coniferous forests of the northwest coast of the United States. Because those forests have become extensively fragmented by logging activities, the owl population has become a metapopulation divided into subpopulations living on widely isolated fragments of forest left uncut (Dawson et al. 1986). One consequence of this fragmentation is that natal dispersal, and to a lesser extent density-dependent dispersal, takes emigrating owls through areas of nonhabitat in which they suffer excessively heavy mortality through predation from other raptors and starvation (Gutiérrez & Carey 1985). As the probability of finding or reaching a fragment of habitat is reduced by progressive forest fragmentation, dispersal becomes a drain on the population, reducing the size of the metapopulation, eliminating rescue effects of source subpopulations on the sink subpopulation, and allowing local extirpations of isolated subpopulations.

Sharp-tailed Grouse

These grouse inhabit prairies and brush-prairies in central North America. Their habitat has been extensively altered by agriculture, fire suppression, and forestry practices (Hamerstrom & Hamerstrom 1952). Agriculture destroyed native grasslands throughout portions of the species' range and left behind small, widely scattered remnants of grouse habitat. Fire suppression in many of these remaining fragments allowed trees to invade areas that were previously kept open by periodic fires, rendering the areas unsuitable for these grouse, which avoid forested areas. In other areas, particularly in the northern and eastern portions of the range, open lands have been planted with forestry plantations, again converting remnant habitats into forested nonhabitat. Because these grouse rarely disperse far across forested lands, regional metapopulations composed of almost completely isolated subpopulations have resulted. The size of those subpopulations is set by the area of their habitat fragment, and many subpopulations have dropped below viable population size. Without rescue effects and recolonizations, these nonviable subpopulations have suffered extensive local extirpations owing to stochastic events, especially when the remaining fragments are below about 4000 ha in size and spring breeding populations fall below about 200 birds (Gregg 1987, Temple 1989).

Deciduous forest songbirds

Several species of deep-forest songbirds — mostly members of the families Tyrannidae, Turdidae, Vireonidae, Parulidae, and Thraupidae — are having problems in the deciduous forests of eastern North America. These species seem to be especially edge-sensitive, and the most conspicuous component of their edge-sensitivity seems to be impaired reproduction near edges. In edge situations their nesting success is reduced because of brood parasitism by Brown-headed Cowbirds *Molothrus ater*, nest predation by a number of avian and mammalian predators, and competition from edge-inhabiting birds (Ambuel & Temple 1983, Brittingham & Temple 1983, Temple 1986, Temple & Cary 1988). As a result of reproductive failures, subpopulations living on forest fragments with a high edge-to-interior ratio become sink subpopulations. Only large, compact forest fragments support source subpopulations, in which births exceed deaths. Regional metapopulations have declined (Ambuel & Temple 1982), and many forest-interior songbirds now exist at densities below the apparent carrying capacity of the forest habitat.

Natal dispersal plays an important role in the dynamics of these metapopulations. Upon returning to the breeding range, migrating juveniles show loose philopatry and

settle onto breeding territories with little apparent avoidance of forest fragments dominated by edges. This habitat selection pattern results in birds being scattered among forest fragments that are sink and source habitats, with sink subpopulations being subsidized by source subpopulations. The problem is that good source habitat is not fully utilized when returning juvenile birds opt for sink habitats. Depending on the proportions of a regional metapopulation occupying source and sink habitats, the size of the metapopulation can decline because overall reproduction fails to compensate for mortality (Temple & Cary 1988).

Prairie songbirds

The tallgrass prairies of central North America have largely disappeared as agriculture took over the fertile soils of this ecosystem. Many grassland songbirds have essentially lost their natural habitat, which today exists only as minute scattered remnants of a once vast prairie ecosystem (Johnson & Temple 1986). Many of these songbirds have adopted modified agricultural lands, such as hayfields and pastures, as an ecological substitute, and regional populations of most species rely heavily on this secondary habitat. Changes in the way these lands are managed have resulted in many areas becoming sink habitats. Early and frequent hay mowing, pesticide residues, and intense edge-related predation combine to reduce reproduction. Like forest-interior songbirds, prairie songbirds undergo natal dispersal that distributes returning migrants over both source and sink habitats. When the proportion of sink-to-source subpopulations is high, metapopulations decline, and even high-quality habitats become underutilized.

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DYNAMICS OF SEABIRD DISTRIBUTIONS IN RELATION TO VARIATIONS IN THE AVAILABILITY OF FOOD ON A LANDSCAPE SCALE

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ABSTRACT. Seabirds are generally more mobile than their terrestrial counterparts. In coastal and continental shelf waters, distance from shore, bottom depth and type, and processes causing local upwelling, and hence increasing the availability of food near the surface, are the most important in determining species distributions and abundance. Distributions may change over very short spans of time. Processes affecting seabirds at this scale are relatively poorly understood, and this may affect their conservation because the coastal zone is subject to increasing disturbance from industrial and recreational developments.

INTRODUCTION

Marine birds have traditionally been divided into those which remain most of the time within sight of land (inshore, or coastal species) and those which occur largely out of sight of land (offshore, or pelagic species). Species of the inshore zone include many loons, grebes, cormorants, ducks, gulls and terns. Offshore species belong mainly to the specialized orders Sphenisciformes, Procellariiformes, and Pelecaniformes, with the addition of various Charadriiformes – gulls, terns and auks, and outside the breeding season, jaegers and phalaropes.

For most marine birds, feeding their nestlings depends on travelling long distances between their breeding sites and feeding areas (Ashmole 1971). Consequently, many marine birds habitually forage over much greater areas than terrestrial birds of equivalent size. In addition, reversible changes in marine environments occur on a variety of time scales, in addition to the circadian and circannual ones affecting most ecological communities. The speed with which changes take place in marine environments, and the birds' ability to respond to them, make marine bird communities more dynamic than terrestrial bird communities.

The distributions of marine birds, like those of their terrestrial counterparts, are governed by variations in the physical environment. Whereas climate, determining vegetation, is the main driving force behind the distributions of terrestrial birds, physical oceanography, affecting productivity and the development of food webs, is the main determinant for marine birds (Bourne 1963, Pocklington 1979).

On the largest scale, major oceanographic provinces support distinct marine bird communities (Hunt & Schneider 1987). Aggregations of marine birds in the open ocean occur on a variety of scales, but the minimum size of patches is generally too large to be considered here (Schneider & Duffy 1985). Moreover, at scales below 40

km, marine birds feeding on krill showed a poor concordance with the distribution of their prey, suggesting that small-scale distribution patterns may relate to random dispersal, as much as to the distribution of food (Heinemann et al. 1989). Consequently we concern ourselves mainly with processes occurring in coastal or continental shelf waters, where aggregations on a landscape scale (1-100 km) are more predictable.

FACTORS AFFECTING DISTRIBUTIONS ON A LANDSCAPE SCALE

Haury et al. (1978) have described the spatial and temporal scales of different oceanographic events. These are summarized, and adapted to a marine bird perspective, in Figure 1. The natural phenomena most important on a landscape scale ("coarse scale", of Haury et al. 1978) are water depth, coastline configuration, including river inflow, tidal currents, upwellings and fronts which are dependent on bathymetry, local wind-driven upwellings, and the distribution of sea ice, especially land-fast ice-edges and glacier fronts (Hunt & Schneider 1987). In addition there are various human-induced effects: fishing, sewage disposal, breakwater construction, the provision of artificial structures at sea, oil spills and other forms of contamination.

The effect of water depth and proximity to land

Because offshore waters are frequently deeper than the diving capability of even the deepest-diving birds (Kooyman & Davis 1987), most offshore species are either surface or mid-water feeders (Ashmole 1971). Conversely, many inshore species feed on, or close to, the sea bed. Those which specialize on benthic prey are restricted to water which is shallow enough to allow them to reach the bottom with sufficient time left to feed (Dewar 1924). Cormorants *Phalacrocorax* spp., and other birds that habitually roost on land, must remain within flying range of shore. These, and other effects, mean that water depth and proximity to land are major determinants of marine bird distributions (Briggs et al. 1987).

Species found offshore are not merely a subset of those found inshore, but instead form a distinct community (Diamond 1978). Pelagic species rarely occur in coastal waters, except when driven by exceptional weather or feeding conditions, or when sick or contaminated with oil. However, predominantly inshore species may occur far offshore over shallow banks.

Observations in Hecate Strait, to the east of the Queen Charlotte Islands, British Columbia, in April-June of 1984-1990 allowed us to analyze the occurrence of marine birds in three zones; coastal (found only within 1 km of shore), inshore (>1 km from shore and <6 km from islands larger than 500 ha), and offshore (found only >1 km from land and >6 km from islands larger than 500 ha). Coastal and offshore communities were found to be very distinct, with 55% (N=20) and 54% (N=25) respectively of species recorded being exclusive to that zone. Only one species was exclusive to the inshore zone (N=16), which can therefore be regarded as a transitional zone.

We examined the effect of water depth and proximity to land on marine bird distributions in inshore waters adjacent to the Queen Charlotte Islands in May 1990. Regular transects were conducted at fixed times of day at different distances from shore, and all birds seen feeding were counted. Species diversity was calculated from the Shannon-Weaver formula ($H' = - \sum p_i \ln p_i$, Hurtubia 1973). Species diversity was

highest on transects within 1 km of the shoreline ($H'=1.38$, Figure 2), lower between 1-3 km offshore ($H'=1.35$), and lowest 3-6 km offshore ($H'=0.74$). To examine the effect of water depth, we used only those transects within 3 km of shore, for which aggregate diversity indices were similar. For this sample, water depth explained 51% of variation in the total number of species recorded per transect.

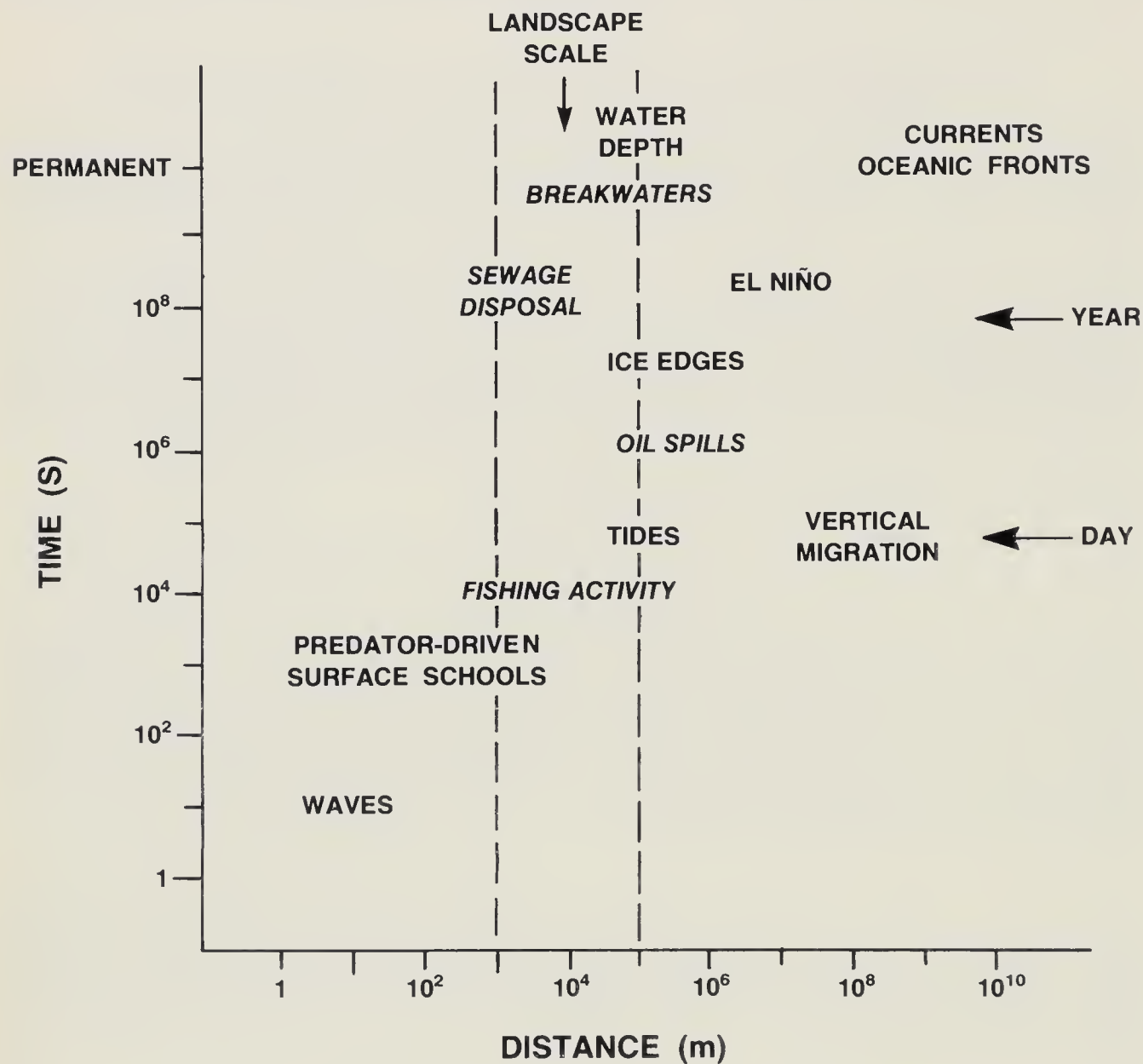


FIGURE 1 – Time and distance scales of oceanic events affecting marine bird populations.

Bathymetry may be important in determining the distributions of surface and mid-water feeding seabirds. Areas of local upwelling, where tidal currents encounter steep changes in bottom topography, may cause slow-swimming prey organisms, such as zooplankton, to aggregate or be forced towards the surface (Brown 1980; Wolanski & Hamner 1988). The timing of bird aggregations in relation to the tidal cycle may differ, depending on the configuration of the bottom relative to the set of the current.

The effect of tidal currents in inshore waters on marine bird distributions has been extensively investigated around Deer Island, New Brunswick. In this area, large tides pass between a network of islands and reefs between the Bay of Fundy and Passamaquoddy Bay. The distribution of migrant Red-necked Phalaropes *Phalaropus lobatus* was closely correlated with the distribution of their copepod prey, which was

determined by tidally induced upwellings (Mercier & Gaskin 1985). Similarly, Bonaparte's Gulls *Larus philadelphia* and terns *Sterna hirundo* and *S. paradisaea*, which fed on euphausiid crustacea and small schooling fishes, shifted feeding areas to take advantage of prey concentrations created by upwellings and downstream eddies (Braune & Gaskin 1982). Areas of concentration differed between the ebb and flood. Black Guillemots *Cephus grylle*, which fed largely on benthic fishes, showed a different response to tidal currents. At slack water they were well dispersed, but during the ebb and flood they fed mainly where reefs and underwater ledges provided protection from strong currents, which apparently disrupted feeding activity (Nol & Gaskin 1987).

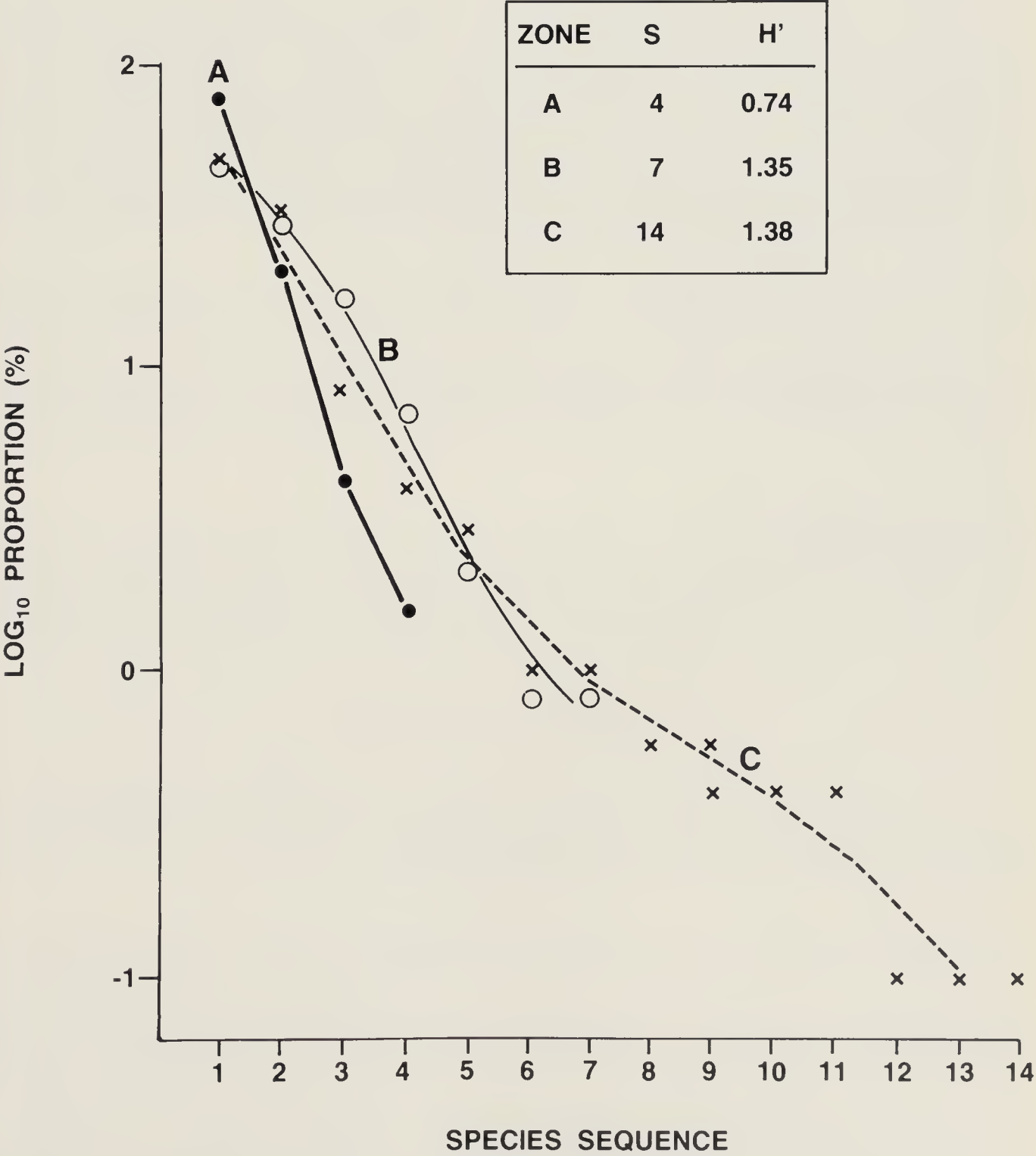


FIGURE 2 – Species diversity of marine birds in three inshore zones of western Hecate Strait in May 1990; A 3-6 km from shore, B 1-3 km from shore, C <1 km from shore. Species are ranked in order of abundance.

Other local habitat effects

For benthic feeders, bottom types (sandy, weedy, rocky, etc.) may be important determinants of local distributions. Along the New Hampshire coastline, Stott & Olsen (1973) found that scoters *Melanitta* spp. and *Oidema nigra* fed mainly on sandy bottoms, Red-breasted Mergansers *Mergus serrator* and Common Goldeneyes *Bucephala clangula* fed on rocky bottoms, and Buffleheads *Bucephala albeola* on soft ooze bottoms. Bottom type may affect both the distribution of prey and its visibility. Shallow water over sandy or muddy bottoms is frequently made opaque when wave-motion stirs up bottom sediments. Sediment discharge from stream and river mouths can have a similar effect.

The effects of land-fast ice edges and glacier fronts in concentrating marine birds have been well documented (Bradstreet 1982). The discharge of fresh water from the ice front causes a countercurrent in the seawater, generating upwelling. This brings zooplankton within reach of surface feeders such as Black-legged Kittiwakes *Rissa tridactyla* and Northern Fulmars *Fulmarus glacialis*. Underwater pursuit divers, such as Thick-billed Murres *Uria lomvia* and Black Guillemots *Cepphus grylle* aggregate at fast ice edges, where they feed on fish and zooplankton concentrated at the undersurface of the ice, but not at glacier faces.

Salinity can also be an important factor in marine bird distributions on a landscape scale, presumably taking effect through alterations in the marine food web. In southern Chile, Brown et al. (1975) found differences in marine bird densities and community structure between fjords of lower and higher salinity. Marine bird densities and diversity indices were generally greater in higher salinity waters, irrespective of temperature.

Human influences

Practically all marine ecosystems have been considerably altered by human activities. Harvesting of marine mammals, especially the large baleen whales, may have greatly reduced competition with seabirds for certain prey stocks (Laws 1983). At the same time, fisheries compete directly with seabirds for other prey, especially small schooling fishes (Brown & Nettleship 1984). Contaminants discharged into the marine environment, especially oil, have been responsible for the deaths of millions of marine birds in this century (Clark 1984). Modelling of oil spill impact suggests that the effects on seabird populations may last from a few years to one or two decades, depending on the demography of the species concerned (Samuels & Ladino 1983). Repeated exposure to oil may have already caused some local extirpations, such as the virtual disappearance of auks from the English Channel.

Not all human activities are harmful. For marine birds of inshore waters, coastal developments, in the form of jetties, breakwaters, buoys, navigation beacons, and other structures at sea, provide potential roosting and nesting sites. In some situations they allow species to extend their distributions to previously unoccupied areas. Oil rigs have been shown to concentrate seabirds in the Bering Sea, although the causal mechanism is unknown (Baird 1990). At the same time, increased feeding on garbage, and at sewage outflows, has led to increases in the populations of large gulls *Larus* spp. (Kadlec & Drury 1968), which threaten potential prey species, especially terns, and other shore-nesters (Hatch 1970).

CONCLUSIONS

Because of the relative inaccessibility of the habitat, our understanding of causal mechanisms determining the distributions of seabirds lags behind that for terrestrial birds. There is a particular gap in our understanding of seabird ecology at the landscape scale. On a smaller scale, the detailed ecology of coves and inlets can be studied by shore-based observers. On a larger scale, much information has been accumulated by ornithologists based on oceanographic research vessels. Distributions and processes on the scale with which we have been dealing are best studied from small, inshore vessels equipped to collect physical, as well as biological, data. In practice there are few such vessels available, and consequently, studies of the inshore zone lag behind those of the open ocean.

From a conservation perspective, the inshore zone is much more likely than the open ocean to be affected by human activities, so that gaps in our understanding of this area are potentially damaging. For example, all of Canada's threatened or endangered marine birds are inshore feeders (Harlequin Duck *Histrionicus histrionicus*, Roseate Tern *Sterna dougallii*, Marbled Murrelet *Brachyramphus marmoratus*). Inshore waters are being used increasingly for fish-farming, tidal power, oil extraction, recreational boating, and for the discharge of an increasing variety of chemical and organic wastes.

The dynamic nature of the marine environment, and the mobility of the marine avifauna, makes it unlikely that habitat fragmentation of the type seen in terrestrial situations will be a major factor in marine bird conservation.

However, the marine environment is far less uniform to a hungry seabird than it may appear to us. Great variations in the availability of food for marine birds occur at the landscape scale. Without a detailed knowledge of the processes causing such variation we cannot predict the effects of human interventions on seabird populations, and hence cannot institute effective conservation measures.

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SPATIAL CONFIGURATION OF AVIAN HABITATS

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ABSTRACT. Models that can be used to predict the effects of habitat change on avian populations often use some measure of habitat quality as their basis. Generality of such models is achieved in part through simplicity. Simplicity resulting from the averaging of variable measurements across a habitat that the bird perceives and uses in a patchy fashion, however, can produce misleading results. I advocate that explicit spatial heterogeneity be recognized at two levels. Individual-scale patches (within a seasonal home range) can be defined based on the behavior of the animal. Cost/benefit approaches can be used to describe the effects of spatial configuration at this level. Population-scale patches contain seasonal populations with relatively homogeneous probabilities of survival and reproduction. Population models can be used to describe the effects of observed patch structure on population change. In both cases, attention should be paid to “negative value” patches.

Keywords: Habitat models, geographic information systems, spatially explicit models, habitat patchiness, scale.

EFFECTIVE HABITAT MODELS

Models describing avian habitat relationships are frequently used to predict the effects of habitat change on populations. Often such models are either too general to provide useful predictions in specific instances, or too detailed to be applicable at different times or in different geographic locations. Indeed, the twin dangers of oversimplification and excessive detail might be considered to be the Scylla and Charybdis of biological models in general. I propose that the way to navigate these dangerous waters and achieve models that are both general and predictive is to develop models that are (1) simple — the number of functions and variables is minimal; (2) based on biological processes (mechanistic); and (3) spatially explicit — incorporating information about patch size and arrangement.

For a model to be simple, the number of functions and variables included in the model (and thus the number of sources of error) must be minimal. No mathematical description of a biological system is biologically correct. The art of making a model simple, therefore, is the art of making as many biologically incorrect assumptions as possible while having a tolerably small effect on the results of the model. What is tolerably small can be explored by relaxing model assumptions (adding complexity) and noting the result.

I consider a model based on biological processes to be one that relies on factors that directly affect fitness, that is, survival and reproduction. For birds such factors might include food, nest sites, cover, water, presence of competitors and predators, or thermal gradients. It may be sufficient, in light of the desirability of simplification, to quantify the factors that affect fitness with simple linear relationships between habitat variables that can be easily measured and the presumed suitability of the habitat with regard to the fitness factors thought to be measured by the habitat variables. For instance, the number of dead trees of a specified age and diameter could be translated into a measure of nest site suitability for a cavity-nester. The limits of such broad

correlations should be carefully defined, however, as it may be necessary to change these relationships with geographic location, season, or annual climatic variance. Seasons should be clearly defined. For example, a definition based on some phenological cue (e.g. bud break) might serve to standardize the onset of “spring.” Annual climatic variance may be incorporated, for instance, by changing the relationship between distance to water and suitable nesting habitat with categories based on ranges of annual precipitation.

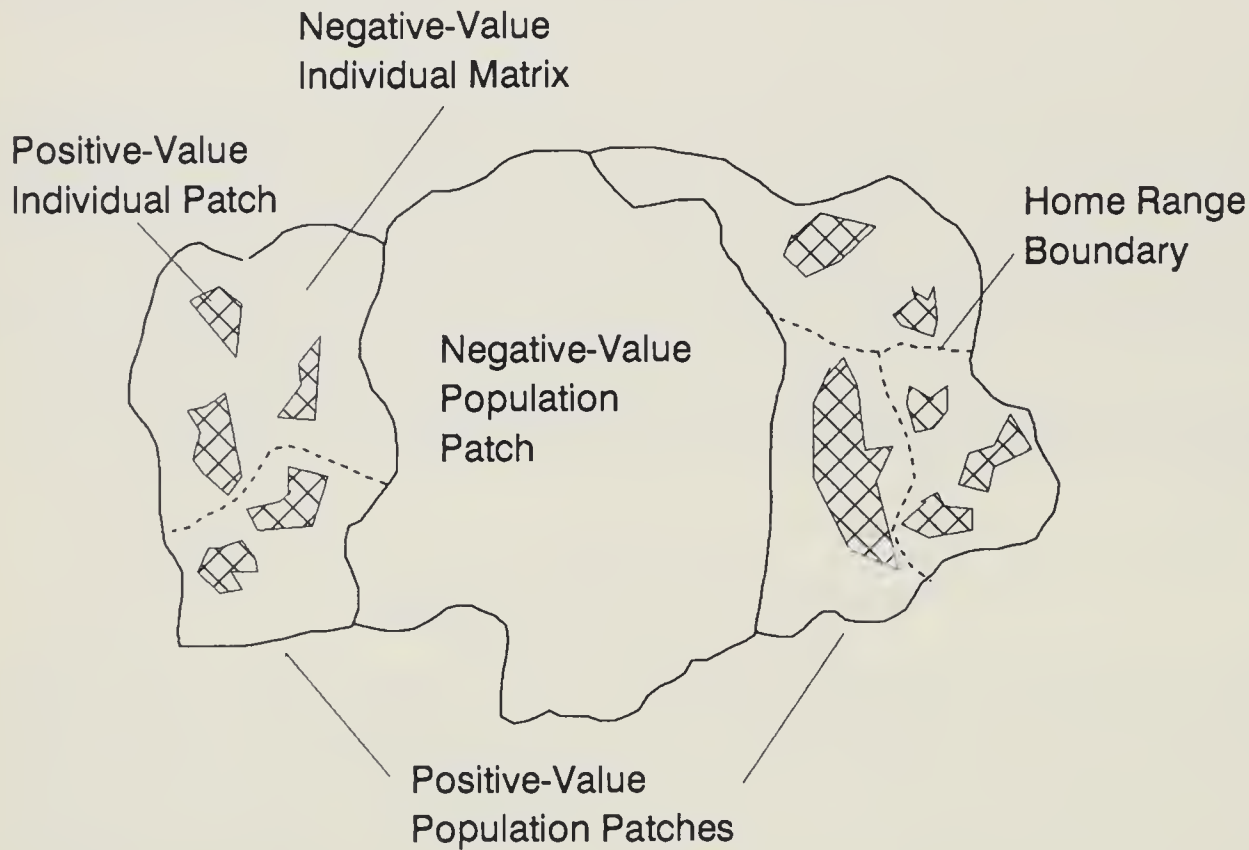


FIGURE 1 - Population- and individual-patches relative to home range size.

SPATIALLY EXPLICIT MODELS

The requirement that models be spatially explicit means that habitat factors that directly affect fitness will contribute to habitat quality for the species depending on two elements of spatial pattern. First, the size of a habitat patch is important. Second, the spatial relationship between a habitat patch and other habitat patches may influence the value of the patch. One way to illustrate the importance of size and spatial context is to consider the minimum size of useful patches. For example, the Habitat Suitability Index models developed by the U.S. Fish and Wildlife Service to evaluate wildlife habitat for individual species (Fish and Wildlife Service 1981) define the minimum habitat area for a useful patch as the minimum amount of contiguous habitat that is required before an area will be occupied by a species. This definition is vague. (Does an occasional visit count as occupation? What is “contiguous habitat? Won’t the amount of required habitat vary with its quality and internal spatial structure?) It does not explicitly describe the minimum habitat area required to support a self-sustaining population, or even a reproducing individual. Thus, a habitat might be assigned a high suitability value without being able to sustain a population. Its actual value depends on whether the larger landscape has sustainable populations that use the habitat in a way that enhances the ability of individuals to survive and reproduce (see Haila et

al. 1989). If not, it seems improper to give it a positive suitability value. Clearly, minimum size must be defined relative to the species and not some arbitrary scaling factor, such as the minimum pixel size available through remote sensing. For a given species, the area required by an individual is likely to vary in relation to its seasonal activity (e.g. breeding), its energy demands (e.g. thermoregulatory costs during winter), and the cover types it occupies.

Many biologists at this point would throw up their hands and say that the spatially explicit requirement adds a hopeless layer of complexity to models. There is no doubt that complexity is added, but by making models spatially explicit, even in a rather simplistic fashion, we remove one of the largest sources of error in existing modeling procedures, and we allow ourselves to simplify what would otherwise be a hopelessly complex (and varying) relationship among the factors influencing fitness. I will argue that this approach is the key to successfully integrating the benefits of simplicity and complexity, as well as the prerequisite to scaling models properly and to integrating models across species.

PATCH DEFINITION

In the subsequent discussion I make two critical assumptions. The first is that the boundaries of habitat patches can be identified and mapped. Where there is ambiguity about the boundary location, for instance, in the case of a shrubland changing gradually to a grassland with distance, it would be ideal to use the behavior of the focal animal to define the important boundary.

The second assumption is that identification and mapping can take place at either of two scales (Figure 1). At the small or individual scale, patches that influence individual movements can be defined. This influence may be mediated through the need for cover from predators, for food, or for reproductive requirements. At the large or population scale, patches that are relevant to within-season population processes can be mapped. For species that move seasonally, individuals will use several of these patches within an annual cycle. The boundaries must be drawn such that there is sufficient within patch homogeneity among fitness characters of individuals of the same age and sex to justify averaging seasonal survival and reproductive parameters within a patch. The boundaries may depend on the objectives of the study as well; for instance, in one study of a riparian bird species such population parameters might be averaged over patches consisting of small valleys while in another study of the same species with different objectives, values might be averaged over a larger watershed that included many such valleys.

The identification and scaling of patch types depends on the scale at which population and individual processes operate in the focal species, and consideration may be given to patches within patches (e.g. Kotliar & Wiens in press). For instance, we might envision a series of mountain meadows in which both a hummingbird and a sparrow forage. The hummingbird moves among meadows, so that these might be the relevant patches, surrounded by negative-value forest patches. Within a meadow, one could also describe patches of nectar producing flowers. In contrast, several sparrows may maintain breeding territories within a given meadow and forage in shrub patches within these territories, such that groups of shrubs are the largest small-patch type that can be identified. The meadows are population-scale patches for the sparrow but

individual-scale patches for the hummingbird that includes several meadows in its daily foraging bouts. The grain size, or minimum size of the measurement unit (Wiens 1989) should be larger for population-scale than for individual-scale patches.

USE OF SPATIAL AVERAGES FOR HABITAT VARIABLES

It is particularly important at the individual-patch scale that the use of habitat averages be avoided. For example, the Winter Wren *Troglodytes troglodytes* in coastal Oregon coniferous forests spends most of its time within 3 m of the ground. The birds use patches of thick shrubs or logging slash for nesting and foraging but these seemingly must be surrounded by a mosaic of open areas within the home range (pers. obs.). Adults avoid setting up territories in areas that are either solidly open or solidly closed in this stratum. The nature of the higher canopy seems relatively unimportant; the birds nest in both forested habitat with a dense high canopy and clearcut-logged habitat with a completely open canopy, as long as there is a horizontal patchiness structure consisting of thick and open patches in the lowest 3 m. Averaging values for vegetation cover over a home range might be useful for predicting habitat-use patterns within a geographic area that tended to have a certain horizontal patch structure, but would be misleading in an area in which an "ideal" coverage value could be achieved with a relatively uniform rather than patchy horizontal distribution of cover.

Another example in which the use of area-wide averages rather than explicit patch structure might be misleading can be found in the hole-nesting woodpeckers. A series of Habitat Suitability Index models for woodpeckers (Schroeder 1982a,b, Sousa 1982, 1983) use the density of snags as an indication of optimality for nesting habitat. Equivalent snag densities in two areas, however, might have very different population effects if the trees were clumped in one area but not in another. In the first area all suitable snags might occur in a few territories, whereas in the second area they might be dispersed among all territories.

LINKING INDIVIDUAL AND POPULATION SCALES

At the small or individual scale, patch-use patterns can best be understood through intensive and detailed behavioral observations of individuals. Energetics modeling and, in some species, local microclimatic considerations can be used to develop predictive models of patch use. One may think of individual-scale patches as having associated costs and benefits associated with their use. Costs might include predation risk or energy cost of traversing the habitat, while benefits might include energy gained in the patch, or increased survival associated with cover from predators. Costs and benefits must be expressed in a common currency, such as energy loss/gain, that is of sufficient importance to be directly linked to survival and reproductive parameters. Experimental approaches using artificial patch configurations can provide insights into costs and benefits. Envision positive-value patches separated by negative-value patches or a matrix that must be traversed in foraging (Figure 1). To investigate this situation, one could evaluate the effects of clumping of nectar-bearing shrubs on a hummingbird territory by measuring the energetic costs of traversing the negative-value areas between shrubs or shrub clumps. The cost of these negative-value areas depends on the spatial distribution and arrangement of the shrubs, not simply on their overall percent coverage in the territory.

The effects of individual-scale patchiness must be expressed in terms of fitness or individual reproduction and survival effects. These can, in turn, be expressed as population averages within the larger population patches, as modified by immigration and emigration rates that depend on patch size and arrangement, to determine habitat quality for the larger area that includes several population patches (Figure 2; see Van Horne 1983 for definition of habitat quality).

Habitat patches at the population scale can then be evaluated in part based on the individual-scale patches they contain. Survival and reproductive values obtained at the smaller scale must be combined with among-patch dispersal information to develop population-level models that incorporate explicit patch structure (Figure 2).

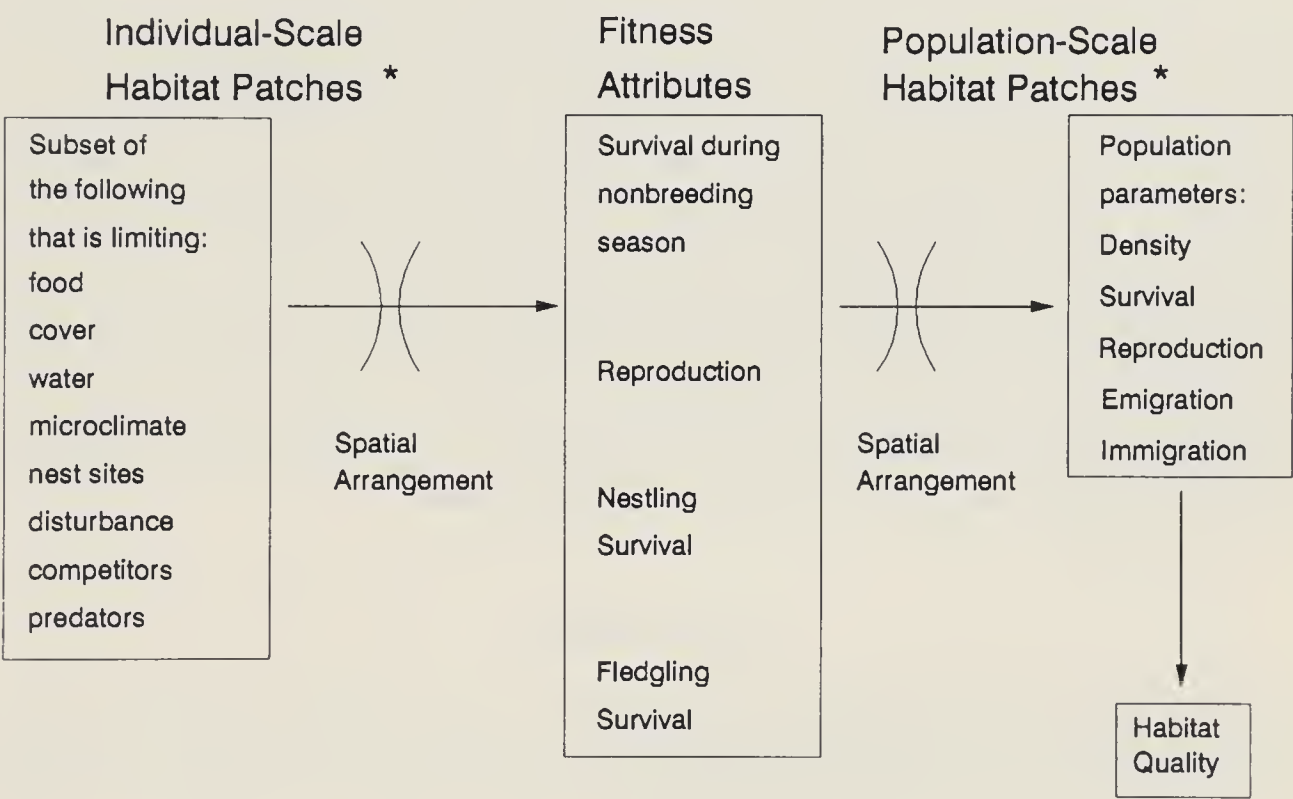


FIGURE 2 - The structuring of habitat models that are spatially explicit and incorporate both individual and population scales. * Includes both positive- and negative-value habitats.

Once again, the models depend not only on the correct identification of patches that are used by the species, but also on an evaluation of patches (or a matrix) that are of negative value. Survival and reproduction are much lower in these negative value patches than in the surrounding patches. These may serve as population sinks in which there is little successful reproduction, or they may be areas that are traversed by dispersers. Because the strength of the negative effect will differ among habitat types (e.g. a traversable grassland v an equal area of non-traversable urban development for a riparian-dependent rail), the effects of these negative patches or matrices on dispersal between population-scale patches should be carefully evaluated and included in the habitat model. For instance, we might have two patches containing subpopulations, separated by a patch that may be traversed but not occupied (Figure 1). The positive-value patches may have different parameters for survival and reproduction in each age class, as well as dispersal probabilities. Animals dispersing between the two patches would have an increased risk of mortality while they were

traversing the negative-value patch, such that the absolute risk depended upon the distance of negative-value patch that must be traversed. This distance depends on the geometry of patch configuration, or the explicit spatial structuring of the patches.

GEOGRAPHIC INFORMATION SYSTEMS (GIS)

The emergence of GIS applications to habitat evaluation has real potential to provide us with usable, spatially explicit information for large and mobile animals. In this approach, satellite images that show reflectance values for different vegetation and other coverage types are used to classify habitat polygons, or areas with uniform reflectance values. Thus it provides a map of patches whose size is the lower limit of resolution, or pixel, of the image. This map can be used as a basis for habitat classification and management. The danger of this approach is that the biological processes that determine the fitness effects of different patch sizes and arrangements will be lost to an averaging approach that ignores the important, spatially explicit information that the GIS provides. Models based on this approach alone may be extremely difficult to verify, and it may be difficult to determine the limits to their applicability. Grain sizes and patch boundary determinations should be based on the biology of the species rather than the distinctions inherent in the technology that is used (e.g. minimum pixel size and vegetation with distinguishable reflectance values). GIS-based correlations cannot substitute for intensive investigation of the effects of patch size on population processes, and the effects of negative-value habitats on movement patterns, but these approaches used together have the potential to greatly enhance the predictive accuracy of habitat models for large and mobile species.

CONCLUSIONS

Correct interpretation of spatial models depends on an understanding of individual movement patterns at individual and population scales and the effects of negative-value habitats, as well as the effects of patch size on patch use and value. Scaling in this approach is based on the movement patterns of the focal species, with differentiation between individual-scale movements within a home range and population-scale immigration, emigration and migration movements. Model integration across species must require that the species-specific scaling of habitat patches be retained. Only in this way can one avoid inappropriate averaging of survival, reproduction, and density across habitat patches whose explicit spatial relationship is important in determining habitat quality for a species.

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SYMPOSIUM 43

**DISEASE ECOLOGY AND THE CONSERVATION
OF AVIAN SPECIES**

Convener M. FRIEND

SYMPOSIUM 43

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INTRODUCTORY REMARKS: DISEASE ECOLOGY AND THE CONSERVATION OF AVIAN SPECIES

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Welcome to the symposium, "Disease ecology and the conservation of avian species". Response within the conservation community to disease in birds varies widely as do perspectives regarding the importance of disease in the conservation of our avifauna. An objective of this symposium is to stimulate proactive disease management for the benefit of free-living avian species.

There are four basic levels of response to disease problems that occur within the conservation community (Friend 1981).

- (1) The first level is simply awareness that disease exists. This is a critical first step because problem recognition is a prerequisite for problem resolution. Too often, however, awareness is accompanied by a fatalistic perspective that disease in free-living birds is a "natural" event that must be endured.
- (2) At level two, concern generated by awareness motivates a desire to do something. However, seldom are actions taken because means for problem mitigation are not envisioned. As a result, frustration characterizes this response level.
- (3) At level three, frustration is replaced by active response to disease outbreaks, primarily reactions to major epizootics and other crisis situations. Fire-fighting is the characteristic for this level of response.
- (4) Level four is characterized by problem solving and disease prevention. Disease impacts are truly being mitigated against at this level.

Those who question the need for increased efforts to combat disease in avian species should consider the effects DDT had on avian populations (Hickey & Anderson 1968) and the devastating losses occurring from diseases of microbial origin, such as the single event loss of more than 40% of 100,000 Mallard Ducks *Anas platyrhynchos* wintering at the Lake Andes National Wildlife Refuge, South Dakota (Friend & Pearson 1974). Consider also that the habitat base many species depend upon is being continually eroded relative to quantity and quality. Habitat fragmentation is another factor in reducing the resiliency of species to overcome losses from disease.

It is also important to recognize that there are inherent disease risks associated with changing ecological conditions that alter established relationships between species and their environment. The major geographic expansion of avian cholera and avian botulism that has occurred within the United States during the past 15 years appears to be closely associated with environmental changes. Predicted global climate

changes may also enhance infectious disease activities. "In coming years, viruses are expected to expand their ranges and diversify into new epidemic strains in response to global warming, as well as to increased geographic movement and concentration of people and livestock" (Miller 1989). It is folly to think that wildlife will be spared from this expansion of infectious disease activity.

Disease concerns have increased over time within the conservation community. That concern is reflected here; disease is the focus of three separate sessions in the scientific program of this Congress. "Disease and environmental contamination" is the theme of a contributed paper session and "Avian disease - implications for species conservation" is the subject for a round-table discussion. However, these concerns must be transformed into proactive disease management if disease impacts are to be successfully mitigated against.

The first two presentations within this symposium provide concepts and specific recommendations that serve as a basis for significantly reducing disease impacts in free-living avian populations. The third presentation addresses the consequences of "real world" concurrent exposures to multiple biological insults, chemical contaminants and microbes in this instance. Data provided in that presentation raise serious questions regarding the adequacy of risk assessments associated with chemical registrations. The fourth paper addresses the international problem of lead poisoning in birds. Considerable progress has recently been achieved in eliminating this disease as a significant cause of wild bird mortality in the United States. However, much remains to be done worldwide if needless bird losses from this disease are to be avoided. The final symposium paper addresses the role of birds in the distribution and transmission of Lyme disease. Lyme disease has been known for many years in Europe but is second only to AIDS (acquired immune deficiency syndrome) as an emerging disease problem of concern within the United States.

"Emerging Diseases are usually not "new", just freed from obscurity by acts of man" (Morse 1990). This is true for humans, domestic animals, and wildlife. If the acts of man can unleash these problems, the acts of man can also bring them under control. However, a question that must be addressed is whether the conservation community is willing to take the necessary actions to do so. This is one of the challenges before us as we prepare to enter the twenty-first century.

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CONTROL AND MANAGEMENT OF DISEASE IN WILD BIRDS

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ABSTRACT. Disease in wild birds may be managed with many of the same methods used to control disease in humans and domestic animals. These include reduction or elimination of the causative factor, population manipulation, habitat modification, alteration of the birds' resistance, alteration of human activities, or combinations of these methods. There have been notable successes in the control of disease caused by toxic agents, but attempts to control infectious diseases have been less successful. The most promising methods involve habitat modification. These require a detailed understanding of disease ecology. There is a need to assess the cost of disease and to measure the effectiveness of disease management techniques.

Keywords: Disease, management, control, eradication, prevention, population, mercury, pesticide, infection.

Management of wild animals is a new science, although humans have been practising the art of management for centuries e.g., the rearing of captive Mallard Ducks *Anas platyrhynchos* in the mid-17th century. Management directed specifically at disease is an even more recent phenomenon, and it is only in the past few decades that this has been considered possible. Most forms of wildlife management are aimed at producing the maximum number of animals possible on the habitat available, and this is particularly true for those mammals and birds that are to be hunted. The emphasis is usually on maximal, rather than optimal, numbers, although these are often different. Aldo Leopold stated in *Game Management* (1933) that, "in its more advanced stages, game management is in effect the art of maintaining a population which is vigorous and healthy in spite of its density". The problem for the wildlife manager is still the same today. The aim of this talk is to advance the idea that disease should be considered as one of the factors in the management equation.

If we are to consider managing disease in wild birds, the first step is to define the term "disease". We tend to think of disease in wild animals simply in terms of dead bodies. This is certainly a definable end-point or criterion to measure disease. However, when we consider humans or domestic animals, disease has a much less restrictive definition - one doesn't have to die to be excused from a day of work because of illness! We often consider a few nematodes or cestodes in the gut, or the occasional *Leucocytozoon* gametocytes in the blood to be "normal" in wild birds and dismiss them as being of no importance. However, it is vital to remember that these are disease agents living at the expense of the host. Every parasite has some cost to the animal. We may not know how to measure the cost; but the cost is still real. The definition of disease I prefer includes any impairment that interferes with or modifies the performance of normal functions. This definition is sufficiently broad to include sublethal and lethal effects, and it makes no mention of causation.

Early management of game birds and many other wild species simply consisted of dividing the resources among those who wished to partake. However, in many or most

circumstances, we find now that the supply or resource available for division has dwindled, and there is no longer an adequate supply to meet the demand. The wildlife manager confronted with this situation has two options - either to increase the supply by increasing natality or to reduce the wastage to other factors, such as natural mortality in the form of disease. Disease, by the definition just described is important in both these options, since the "cost" of the disease might reduce the productive capacity of the population, as well as resulting in direct losses.

The greatest problem for those trying to establish the value of disease management is the difficulty in measuring the cost of disease. In domestic animals, we know the major cost of disease is diminished productivity, rather than in direct mortality, but we are not in a position to measure productivity well in wild birds. For example, we know that the number of eggs laid by Snow Geese *Chen hyperborea*, is determined by the body condition of the female when she arrives on the breeding ground (Ankney & MacInnes 1978). However, we do not know how many extra eggs would be laid if the "average" goose did not have to feed lice, nematodes, cestodes, trematodes and a variety of protozoa, or if she had no chemical residues in her body.

Some people argue that disease is a natural phenomenon and we should not play God by interfering. I agree that disease, in a natural environment, is a natural phenomenon, and it is likely an important evolutionary force. However, most wild birds no longer live in a natural environment, and I cannot agree that many of our current disease problems, such as selenium poisoning from irrigation run-off water, lead poisoning, enhanced transmission of avian cholera among birds crowded on refuges, or massive botulism outbreaks among birds on artificially-created marshes, are natural phenomena. These are man-created problems, and most disease management is, in reality, an attempt to mitigate the effect of some other human action. In such cases, I believe disease management is justifiable.

The other question that should be addressed is whether it is possible and feasible to manage disease in free-flying birds.

There are really only three basic methods of trying to manage any disease. These are to:

- prevent its occurrence,
- control or reduce its frequency or severity, or
- eradicate it.

These are probably listed in the order of preference, and in the order of feasibility, as well. The ideal method, and often the easiest method, is to prevent the occurrence of disease, because in this way the bird does not have to pay any cost. The most obvious situation for using this method is when a disease is not present in an area, and management efforts can be directed at preventing its introduction. Regulations on the importation of animals and animal products, while not designed specifically to protect wild birds, have undoubtedly prevented the movement of many foreign infectious diseases that would infect indigenous birds. Unfortunately, we have failed to prevent the translocation of some diseases, such as the introduction of avian malaria to Hawaii. We can also prevent many diseases by not creating situations that we know will result in disease, e.g., by stopping release of certain toxins into the environment.

If a disease is already present in an area, we have only three possible choices:

- (1) Do nothing - which implies that we accept the costs as tolerable, or that the disease is unmanageable.
- (2) Attempt to control the disease - in which case we accept that the disease will continue to occur but we will try to reduce its frequency of occurrence or its severity. This type of management must be continued indefinitely.
- (3) Eradicate the disease. Total elimination has been accomplished for some non-infectious diseases, i.e., certain types of intoxication of wild birds, but no infectious disease has been eradicated from wild birds. (The only successful eradication of any disease on a global scale has been the elimination of human small pox). Eradication usually implies a massive effort, but once accomplished, no further input is required.

We can direct these three basic methods, prevention, control and eradication, at four different targets. These include the three standard components of the disease triangle, always recited by epidemiologists: the agent, the host, and the environment; to which I've added a fourth - humans. Humans are obviously a part of the environment, but modification of human activity is so important in managing disease in wild birds it deserves special attention.

The most obvious way to "attack" any disease is to act directly against the causative agent or factor. The agent may be dealt with either outside the bird, or within the bird. To date, I'm not aware of any large scale disease management program based upon attacking disease agents while they are within wild birds (i.e., by mass treatment), except for limited attempts to use antitoxin for birds paralysed by botulism. The disadvantage of such a treatment program is that the disease has already had some *cost* to the bird before management is applied. Normally we want to manipulate the causative factor before it affects the birds. Some of the best examples available of this type of disease management concern toxins. Two particularly successful programs involved the elimination of mercury poisoning in terrestrial birds in Sweden (Borg & Hugoson 1980), and the elimination of hepatochlor intoxication of geese in the northwestern USA (Blus et al. 1984). In both these situations, cessation of release of toxin into the environment was followed rapidly by disappearance of the problem. Programs to eliminate certain insecticides have been less or only partially successful, with problems continuing to occur because of the continued use of the compounds in some parts of the world, unlicensed use in areas where the compounds are banned, and persistence of residues in the environment.

There have been relatively few attempts to manage infectious diseases of birds by attacking the infectious agents; except for occasional attempts to "disinfect" wetlands during outbreaks of disease, such as duck plague. Research in Scotland on *Trichostrongylus tenuis*, a cecal parasite of the Red Grouse *Lagopus lagopus*, however, has demonstrated that reduction of parasites by treating birds with anthelmintics can have significant population effects (Hudson 1986). This technique, and others based on treatment, are limited by the ability to deliver the drugs and therapeutic agents to individual birds.

It has been much more common to attempt to manage disease by manipulating the host population than by attacking the causative factor. The general principle behind

this type of management has been to change the distribution or density of the birds to reduce exposure to causative factors or to reduce transmission of infectious agents. There has been relatively little attention given to changing the level of resistance of the host population. Programs that act by manipulation of the host population are usually designed to prevent or control disease, rather than attempting elimination.

The most commonly employed method of host manipulation is hazing or harassment of birds to move them away from recognized dangers. This only works for localized problems, but it has been employed in outbreaks of botulism, avian cholera, duck plague and some toxicity problems. The effort required to move birds must not be underestimated, and harassment must often be accompanied by provision of suitable alternate habitat if it is to work. This same technique can be used in a preventive sense if problems can be anticipated in a particular area. Thus one of the strategies used to reduce the risk of selenium poisoning in some areas of California was to make the contaminated wetlands unattractive to birds.

An important factor in the population biology of infectious diseases is population density, because of its effect on disease transmission. Reduction of bird density would appear to be an obvious strategy to use in combatting many infectious diseases, such as avian cholera in waterfowl in North America. This could be done by creating new habitat and spreading birds out, or by reducing the number of birds on existing habitat. Unfortunately, neither of these options is available to the waterfowl manager on a large scale, because (a) the habitat base is declining in size, not expanding; and (b) the population of many species is already very low. The present system of waterfowl management encourages dense assemblages of birds for long periods of time on small areas; leading to very heavy contamination with infectious agents and facilitating disease transmission. While we cannot miraculously increase the total amount of habitat overnight, efforts must be directed at methods to spread birds out locally in problem areas, and perhaps to try some innovative form of rest-rotational use of wetlands within refuge complexes, to reduce the level of environmental contamination.

The use of vaccines to increase the resistance of individuals to infections and to block transmission of infectious diseases is standard practice now in humans and domestic animals. The use of vaccination to control at least one disease in free-living wildlife, rabies in wild foxes, is now a reality; (Steck et al. 1982) however, vaccines have not been employed to date in wild birds. There is no reason to think that vaccines would be less effective in wild birds than in other species; but no methods are currently available for the mass immunization that would be necessary to have population effects.

Management of disease in wild birds through manipulation of the environment appears to offer the greatest chance for success. Most such programs involve changing human activities in some way, and the effect on disease is often by a rather indirect route. Use of this form of disease management requires a much more detailed knowledge of the ecology of the disease than is required to harass birds away from an area, or to dump disinfectant into a marsh to kill a bacterium. In many cases, our level of knowledge is still insufficient to allow effective use of habitat manipulation for disease management.

However, this type of program has been used in various areas to prevent and control diseases. An example of a simple form of habitat manipulation relates to electrical transmission lines and avian botulism. Botulism is a disease that occurs when the bacterium *Clostridium botulinum* type C grows and produces toxin within decaying organic material. The best possible organic substrate for toxin production appears to be a vertebrate carcass. Maggots formed in the carcass carry the toxin and cause poisoning when they are ingested by healthy birds. Anything which produces carcasses in a marsh may provide the initial toxin source to start an outbreak. One such factor is an overhead electrical transmission line passing over a marsh. A simple form of preventive habitat manipulation is to route power lines away from botulism-prone marshes.

Similarly, we know that ducklings can not survive on wetlands with a certain degree of salinity (Mitcham & Wobeser 1988); a good preventive measure in this case is to discourage biologists from building nesting islands on such wetlands and exert their efforts elsewhere, and to encourage the building of small impoundments at the freshwater inlets to such wetlands to provide drinking spots for ducklings. Another simple example has been a program to encourage farmers to plow waste peanuts under the ground to eliminate mycotoxin poisoning of cranes in certain areas of the USA (Windingstad et al. 1989).

We can sometimes manipulate habitat to reduce the level of exposure of birds to infectious agents. For example, a few years ago, I was asked to look at a Common Eider *Somateria mollissima* nesting colony in eastern Canada that had suffered repeated outbreaks of avian cholera. The island was densely vegetated, shaded, damp and without good air circulation, and with numerous shallow ponds of freshwater in which we were able to isolate *P. multocida*. Conditions on the island were nearly ideal for persistence of the bacterium, and the shallow pools were an ideal site for transmission of the disease. The recommended action was to open the vegetation canopy and to drain the standing water, so that the island became dryer, and more sunlit and windswept. This habitat change has been followed by a marked reduction in the occurrence of disease, but I hasten to add that this has been a totally uncontrolled experiment.

The final environmental manipulation I want to mention is the current program to eliminate the use of lead shot for waterfowling in the USA. This is an attempt to change deeply ingrained human activities to prevent introduction of a toxin into the environment, and as such is an attempt to **eradicate** (not control) an important and preventable disease.

There is an unlimited number of ways in which habitat can be manipulated to reduce exposure to toxins, to reduce vectors or carriers of disease agents, and to influence the distribution and timing of bird movements. The use of such techniques is limited only by a lack of detailed knowledge of the ecology of many diseases, by the ingenuity of the manager, and by the ability to convince others to undertake or allow the change.

One other form of alteration of human activity I want to mention is the need to alter the perception of disease in the mind of the public, the politicians and of some biologists. We need to instill the idea that disease is a significant factor that should

neither be under or overestimated in importance but that should be considered in all management programs. Disease can be managed for the good of the birds, but effective management will require a thorough understanding of its ecology so that we can manage by manipulating the environment, for as stated by Leopold (1933), "the real determinants of disease mortality are the environment and the population, both of which are being "doctored" daily, for better and for worse, by gun and axe, and by fire and plow".

Disease management measures employed to date in wild birds are all of unknown efficacy. For example, we found last summer that carcass cleanups during a botulism outbreak only resulted in the collection of about 30% of the carcasses present in the marsh. We must develop sensitive methods for determining (a) the actual "cost" of disease to populations, and (b) the effectiveness of disease management procedures, so that we can clearly show that a dollar spent in preventing or controlling disease is a better investment than a dollar spent in some other type of management. At present, waterfowl biologists know roughly how many extra ducklings can be produced by building nesting islands or by reducing predation on a marsh, but no one has attempted to determine how much a Mallard hen saved from botulism is worth, or which type of management has a greater effect on the population.

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DISEASE PREVENTION AND CONTROL IN ENDANGERED AVIAN SPECIES: SPECIAL CONSIDERATIONS AND NEEDS

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ABSTRACT. Mortality and other disease impacts are seldom addressed in the routine management of endangered species. The National Wildlife Health Research Center, Madison, Wisconsin, has conducted more than 6,000 disease evaluations on carcasses and tissues from endangered and threatened species. These evaluations have documented avian tuberculosis, neoplasia, lead poisoning, and inclusion body disease of cranes to be significant causes of mortality in endangered avian species. To combat these and other diseases special attention needs to be given to: (1) determination of causes of debilitation and death; (2) detection of new and emerging disease problems; (3) protection of captive populations from disease epizootics; (4) protection of relocated and released stock from indigenous disease; and (5) minimizing disease losses in free-living populations.

Keywords: Disease, avian tuberculosis, neoplasia, tumors, lead poisoning, eastern equine encephalitis, inclusion body disease of cranes, pigeon herpes, endangered species, endangered birds.

INTRODUCTION

"Pathogens and parasites are one of the most important though frequently unconsidered aspects of conservation biology" (Dobson & May 1986). The importance of these disease agents is their potential negative impact on recruitment, survival, population size, and population distribution. Disease should be given great attention when endangered species are involved because population recovery is a basic program objective. "Recovery is the process by which the decline of an endangered or threatened species is arrested or reversed, and threats to its survival are neutralized, so that its long-term survival in nature can be ensured" (USDI 1990).

Unfortunately, disease impacts are seldom addressed in the routine management of endangered species. Disease eruptions of crisis proportion result in a transient "emergency" response that terminates when the immediate threat to the population/species has ended. Our interactions with field biologists and wildlife managers suggest that the reasons disease does not receive greater attention are a belief that the occurrence of disease is independent of wildlife management activities, and that little can be done to effectively alter this "natural" process. There is also reluctance to accept the magnitude of losses from disease as being sufficiently substantial to warrant action except for major crises. We do not share those beliefs and address the importance of disease in endangered avian species. We also provide recommendations for reducing disease impacts.

DISEASES AND THEIR IMPORTANCE

General

Disease occurrence and its effects on threatened and endangered species is only infrequently documented in the scientific literature (Thorne & Williams 1988).

Documentation that does occur consists mostly of epizootics and unusual host records for a disease or parasite; the diversity of causes, frequency of occurrence, and magnitude of loss are not adequately recorded. During the past decade our program (the National Wildlife Health Research Center, Madison, Wisconsin) has conducted disease evaluations on approximately 800 carcasses, and on tissues from more than 2,500 other endangered and threatened species exclusive of Bald Eagles *Haliaeetus leucocephalus*. Our Bald Eagle data base contains postmortem findings from approximately 2,800 eagles dying since 1963.

Both data sets contain a potpourri of causes of mortality that in total include infections caused by viruses, bacteria, fungi, and internal and external parasites; plant toxins; chemical contaminants including heavy metals, pesticides, economic poisons, and barbituates; physical processes such as gunshot, electrocution, trapping, and impact trauma; and a variety of other conditions such as capture myopathy, visceral gout, and neoplasia. Our data clearly illustrate that disease is common in free-living and in captive-for-life (zoological collections) endangered species.

Disease impacts

FREE-LIVING POPULATIONS. Since 1982, avian tuberculosis *Mycobacterium avium* has been diagnosed in 7 of 21 free-living Whooping Cranes *Grus americana* necropsied at our Center; all but two of these were from the Rocky Mountain experimental cross-fostered flock. Whooping Crane numbers within this flock have declined from a high of 33 in 1984-86 to 13 in 1989-90 (peak winter counts). Our findings strongly suggest that avian tuberculosis is an important factor in this decline.

Neoplasia is infrequently found in free-living birds. A previous analysis of avian necropsies at our Center disclosed 9 of 18,000 birds with tumors. In contrast, 5 of 17 free-living Mississippi Sandhill Cranes *Grus canadensis pulla*, necropsied during the period of 1974 to 1989 had fatal tumors. This problem appears to be site-specific because Mississippi Sandhill Cranes are non-migratory and no tumors have been found in the captive propagation flock located elsewhere. As with avian tuberculosis in the cross-fostered flock, neoplasia has been a major impediment for Mississippi Sandhill Crane restoration.

Lead poisoning accounts for approximately 50% of all poisoning diagnosed in Bald Eagles in our Center data base. We are likely to exceed 250 cases of lead poisoning in Bald Eagles by the end of 1990, the vast majority of these occurring during the past decade. Lead poisoning has also been an important cause of mortality for the California Condor *Symnogyphs californianus*. This disease was a major factor in removing the last California Condors from the wild and placing them in captivity to prevent species extinction. Of five wild Condors necropsied between 1980 and 1985, three died from ingestion of particulate lead from the carcasses upon which they fed.

Introduced diseases, particularly avian pox and malaria, are reported to be a major factor in limiting the current distribution and abundance of native Hawaiian land birds (van Riper et al. 1986). Hawaiian water birds also face a significant disease threat. A recent avian botulism outbreak on the Island of Oahu resulted in losses of Hawaiian Duck *Anas wyvilliana*, Hawaiian Stilt *Himantopus mexicanus knudseni* and Hawaiian Coot *Fulica americana alai*. Current conservation efforts are focused on protecting Hawaii's remaining wetlands and intensively managing manmade and highly

altered natural impoundments to produce the greatest number of endangered water birds possible (Scott et al. 1988). Avian botulism is often a disease of disturbed and altered wetlands. Therefore, management of Hawaiian wetlands and impoundments must address this disease to prevent the creation of "death traps" that kill more birds than are produced.

CAPTIVE POPULATIONS. Captive-breeding programs for endangered birds are also impacted by disease. These impacts include reduction in the breeding colony due to adult mortality; suppression of recruitment due to diseases causing infertility, embryo or chick mortality, and the unsuitability of birds for release or breeding when they become disease carriers. A classic example of the importance of disease carriers involves spontaneous mortality of 5 to 10-day-old Mauritius Pink Pigeon *Columba mayeri* chicks due to pigeon herpesvirus (Snyder et al. 1985). These chicks became infected from latently infected Domestic Pigeons *Columba livia* used as foster-parents.

The only documented United States outbreak of inclusion body disease of cranes was also triggered by a latent herpesvirus infection in captive birds. This virus killed a substantial number of endangered and non-endangered cranes at the International Crane Foundation, Baraboo, Wisconsin, and jeopardized the existence of this important program (Docherty & Henning 1980). The Hawaiian Goose *Nesochen sandvicensis* captive-breeding program also suffered losses from a previously unexperienced disease problem caused by a gapeworm *Cyathostoma* sp. Prompt diagnosis followed by control actions prevented decimation of the captive flock. Indigenous diseases can also pose a serious threat to captive-breeding programs. Mosquito-transmitted eastern equine encephalitis virus killed 7 of 39 Whooping Cranes at the Patuxent Wildlife Research Center, Laurel, Maryland, (Dein et al. 1986). This event contributed to a decision to relocate half the flock elsewhere to protect the total captive population from catastrophic loss.

ACTIONS NEEDED

The examples cited are neither isolated nor unique events. They reflect a broad spectrum of disease. Infectious microbes, parasites, bacterial, and man-made toxins, and tumors are the causative agents involved. In each instance there was a reactive response by resource managers, but proactive disease initiatives could have prevented or significantly reduced the impact for at least some of these events. Disease considerations need to be fully incorporated into species recovery plans. Also, the following management actions are critical to minimize disease impacts on endangered populations.

Determination of causes of debilitation and death

Determining specific causes of debilitation and death is a critical first step in preventing additional losses. For example, our Bald Eagle necropsy findings have been used to: support law enforcement efforts to reduce the shooting of eagles; obtain design modifications in power poles to reduce electrocution; plan power line placement and bird aversion marking devices to reduce wire strikes; change trap baiting regulations to reduce losses from steel traps, and hasten the banning of lead shot for waterfowl hunting. Also, timely postmortem findings of cyanide poisoning, capture myopathy, and aspiration pneumonia associated with endangered species manage-

ment activities were used to modify predator control, and bird trapping and relocation protocols to prevent additional losses.

Detection of new and emerging problems

Disease problems are most manageable before they become well established within a population. Methodical surveillance of health status and causes of mortality provides a basis for identifying new problems within a population or species. The emergence of carbamate and organophosphate poisoning in Bald Eagles due to pesticide use and misuse was detected in this manner. Documentation of these findings has led to prosecution of intentional offenders within the United States and reviews of several compounds for environmental hazards. Detection of five cases of avian pox in Alaskan eagles followed by the finding of an additional case in the state of Washington caused us to recommend that Alaskan eagles not be relocated to other areas without further investigation. These recommendations were not heeded. The subsequent first appearance of this virus within eagles in several locations in the eastern United States may have been coincidental or related to the transfer and release of Alaskan eagles.

Protection of captive populations from disease epizootics

The opportunity for clinical disease to occur and be transmitted is often increased by confinement, and the severity of disease intensified. Infectious disease transmission is facilitated when animals are in close proximity, have limited space, are confined in areas with minimal air exchange, and utilize the same environment for protracted time periods. Frequent (as appropriate for the species) surveillance to detect early onset of disease, timely examination of sick and dead animals by competent laboratories, and aggressive disease prevention and control measures are required to protect captive-breeding programs. Vaccines and other veterinary biologics can prevent catastrophic loss by protecting animals from disease problems indigenous to the geographic location of the breeding program. However, the species-specific safety of these products must be carefully determined before they are used. Black-footed Ferrets *Mustela nigripes* died of vaccine-induced distemper from a modified-live virus vaccine routinely used in other species (Carpenter et al. 1976).

Protection of relocated and released captive-propagated stock from indigenous disease

Captive propagation or animal relocation are often needed for population enhancement and recovery. The success depends upon released stock surviving long enough to produce progeny that enhance population levels. If this objective is not obtained the great costs associated with these programs become highly questionable. Therefore, disease status in the environment where animals are to be released should be seriously considered in selection of release sites. Preventive measures (such as vaccination) may be needed to protect this critical investment when disease risks can't be circumvented by release site selection. For example, Center scientists developed a highly efficacious avian cholera bacterin to immunize Aleutian Canada Geese *Branta canadensis leucopareia*. Geese being released on their Alaskan breeding grounds were to be vaccinated to protect them from avian cholera on their California wintering grounds and thereby to enhance their chances to return to breed. Although the captive-breeding program was terminated before use, the bacterin has had considerable success in protecting captive Giant Canada Geese *Branta c. maxima*.

Minimizing disease losses in free-living populations

Preventing losses from disease is more desirable than minimizing losses during disease outbreaks. This should always be the highest priority for endangered species since animals that die have been lost from an already limited population. Anticipation of problems and contingency planning are important aspects of minimizing disease losses. Whooping Cranes serve as an example. Since these birds often stage in Nebraska during spring migration, a major avian cholera outbreak in waterfowl during the spring of 1975 caused concern that Whoopers would become exposed to this disease. Plans were developed and necessary clearances obtained to haze cranes away from wetlands where the disease was occurring should they arrive during the die-off. These plans were implemented when nine Whoopers (15% of the total free-living population) landed on a wetland undergoing major waterfowl losses from avian cholera. In 1979 similar procedures were used to move three Whoopers from another wetland during the most severe avian cholera outbreak to ever occur in Nebraska. No Whooping Cranes died during either epizootic.

Treatment and rehabilitation of individual animals may be possible and should be encouraged for endangered species. Antitoxin can be administered to treat botulism, oiled birds can be cleaned, and raptor rehabilitation programs have returned many injured birds to the wild, or salvaged birds for captive-breeding programs. In extreme instances, it may be necessary to capture, relocate and apply preventive biologics to protect endangered species from catastrophic loss.

DISCUSSION

Endangered species command a great deal of attention within the conservation community because of the close proximity these species have with the irreversible status of extinction. Despite large expenditures of resources, worldwide species extinctions are projected to rise from 1,000 per year to 5,000 per year (Meyers 1979). We believe increased attention to disease prevention and control can inhibit the rate of loss for wildlife species. For this to happen, disease must be elevated as a concern within the conservation community and these concerns incorporated into recovery plans and species management. Recently issued Recovery Plan Guidelines (USDI 1990) state, "It is important to consider all strategies that may alleviate known threats, such as research on disease, habitat protection, protection from taking, captive propagation, reintroduction, control of competing species, etc." It is encouraging to see disease included for consideration since disease has seldom been addressed beyond a very cursory level in previous recovery plan development.

As noted above, diagnostic findings are a critical first step in problem identification. Methodical diagnostic evaluations should always be sought when confronted with sick, injured, or dead endangered species. Unless diagnostic evaluations are reasonably rigorous, terminal findings (cause of death) may not reflect the problem needing to be addressed. For example, the fungus, *Aspergillus fumigatus*, can be directly responsible for mortality (e.g., waterfowl feeding on moldy grain) or be an opportunistic pathogen secondary to the immunocompromise from a primary event such as lead poisoning. Problem orientation would be misdirected in the opportunistic situation if the diagnostic evaluation was not sufficiently thorough to detect tissue lead levels and properly interpret them.

Because of small population sizes, there is limited opportunity to gather information on decimating factors. Therefore, there is a major need for long-term methodical collection, compilation, and evaluation of data on the causes of illness and death in endangered species. We need to establish species-specific repositories for morbidity and mortality information. However, these data are of limited value unless they are used to formulate and carry out aggressive disease prevention and control activities. For example, now that we have determined that avian tuberculosis is a serious detriment to one Whooping Crane reintroduction effort, it is critically important to determine how and why that occurred. This information may be essential to guide future management of this population and to prevent a similar problem in other Whooping Crane reintroductions currently under planning. Resolution of the other problems cited is just as important.

Greater efforts are warranted to minimize mortality in endangered species than for species with more secure population status. The loss of even one individual from a small population may be of considerable significance. Either chronic or catastrophic losses in species with low reproductive potential may push the species closer to extinction. Diseases that reduce reproductive success and/or survival of young are especially detrimental. Failure to adequately address mortality (including disease) in small populations can lead to population levels so low that severe genetic bottlenecks occur. In turn, genetic homogeneity may lead to increased susceptibility to disease and accelerated losses. O'Brien et al. (1985) describe such a problem involving feline infectious peritonitis in captive cheetah *Acinonyx jubatus*.

The fate of specific endangered species may hinge upon our success, or lack of it, in preventing disease introductions or establishment and our ability to minimize losses when disease erupts. The task before us is a formidable one. Difficulties in combatting disease in mobile and secretive species, and limited technology currently available for this task provides an extreme challenge to our abilities and ingenuity. It is critical that this challenge not overwhelm or frustrate us to the point where it retards our efforts to combat disease. Disease in endangered populations can and must be effectively addressed.

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INTERACTIONS OF ENVIRONMENTAL CONTAMINANTS AND INFECTIOUS DISEASE IN AVIAN SPECIES

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ABSTRACT. The effects of chemical toxicants (insecticides, heavy metals, oil) or disease caused by infectious agents (botulism, avian cholera, herpesviruses, internal parasites) on avian species have been recognized for some time. Interactions between environmental contaminants and infections were reported and may be important in the conservation and management of wild populations of birds. Resistance of Mallard Ducks *Anas platyrhynchos* to bacterial (avian cholera, *Pasteurella multocida*) and viral (duck hepatitis virus 1, a picornavirus) disease is decreased after exposure to oil, and to polychlorinated biphenyl, DDT, dieldrin, or high concentrations of selenium, respectively. Immune function assays are being developed to monitor changes in disease resistance from environmental contaminants. Changes in skin (delayed-type hypersensitivity) and blood tests (phagocytosis or white cell concentrations) after exposure to high concentrations of selenium will be discussed.

Keywords: Environmental contaminants, toxicants, disease resistance, immune function, infectious disease.

INTRODUCTION

Agricultural use of fertilizers, herbicides and pesticides, hazardous substance spills, and a growing problem of waste disposal from industrial and urban areas are sources of chemical contamination of the environment. Exposure of wild birds to these chemicals often results in mortality. Examples range from limited die-offs following consumption of pesticide treated seed or invertebrates recently sprayed with a pesticide, to the Exxon-Valdez oil spill where 33,000 bird carcasses were collected. Egg-shell thinning due to chlorinated hydrocarbons (Hickey & Anderson 1968) is an example of the chronic effects chemicals can cause. Chronic intoxication, such as that from lead, can also cause death, decreased fitness, and increased vulnerability to predators (Sanderson & Bellrose 1986, Friend 1987).

Concern with the effects of environmental contaminants on wild bird populations greatly exceeds that for infectious and other disease processes. This is partly because in many countries there has been little monitoring of avian diseases. Dead and sick birds are often not found because death occurs in remote areas, the birds hide before death, or they are removed by predation and scavengers. Death or sickness from disease is more likely to be detected if a large proportion of a population is affected at one time. For example, a single epizootic of duck plague (duck virus enteritis) killed approximately 40,000 of 100,000 Mallard Ducks *Anas platyrhynchos* at a National Wildlife Refuge in South Dakota, USA (Friend & Pearson 1974). Large die-offs from other avian diseases are common in North America (Friend et al. 1987). Apparent increases in the occurrence and distribution of major die-offs from disease has raised questions regarding the effects of exposure to environmental contaminants on the

susceptibility of birds to microbes and parasites. We present evidence that exposure to some chemicals results in decreased resistance to disease.

EFFECTS ON IMMUNE FUNCTION

The immune system is a basic life-sustaining mechanism that facilitates survival. Natural and altered environments abound with a wide variety of microbes and parasites, and impairment of the immune system can result in increased occurrence and severity of host infections and death. The immune system of birds consists of white blood cells, the lymphocytes and monocytes or macrophages, which are found in the blood, lymph nodes, spleen, thymus, and bursa of Fabricius. Immune mechanisms are essentially the same in mammals and birds, and are responsible for the formation of antibodies and cellular defenses against infections. These mechanisms are primed by previous exposure to a specific antigen. Non-specific host defenses involve mechanisms that protect against any infection, and are not affected by earlier exposure.

There are three categories of immune mechanisms, and some tests have been developed to measure their function (Table 1). The concentration of white blood cells or leukocytes, and phagocytosis of bacteria by these cells is often used to measure non-specific host defenses. Antibody-mediated immunity is commonly measured by assessing concentrations of antibodies in serum or of antibody-forming cells in the bird's spleen. Delayed-type hypersensitivity skin tests or the ability of blood lymphocytes to replicate in response to an antigen are measurements often used for cell-mediated immunity.

TABLE 1 – Immune function tests.

NON-SPECIFIC HOST DEFENSES

- Total and differential leukocyte (white blood cell) concentrations
- Phagocytosis and killing of bacteria or particle by blood cells
- Clearance of carbon from blood by reticuloendothelial cells
- Natural killer (NK) cells
- Interferon (IFN) production
- Complement

ANTIBODY-MEDIATED IMMUNITY

- Weight and histopathology of bursa, spleen, lymph follicles
- Blood-serum antibody concentration
- Number of antibody-forming cells in spleen
- B lymphocyte blastogenesis

CELL-MEDIATED IMMUNITY

- Weight and histopathology of thymus, spleen, lymph follicles
- Delayed-type hypersensitivity (DTH) skin test
- Skin graft rejection
- Proliferative response of lymphocytes to antigen or mitogen (lymphocyte blastogenesis)
- Cytotoxic T lymphocytes (CTL)
- Mixed lymphocyte reaction (MLR)

EXPERIMENTAL STUDIES

Research using Mallard Ducks as a model has demonstrated that disease resistance and immunocompetence are reduced after exposure to some environmental contaminants. Early studies used mortality as a primary endpoint. Enhanced technology and increased understanding of avian immunology have allowed more sensitive assays to be applied during recent years (Rocke et al. 1984, Goldberg & Yuill 1990, Fairbrother & Fowles 1990, Whiteley 1989).

To determine the impact of selenium on disease resistance and immune function, we maintained Mallard Ducks for 95-99 days on streams treated with 0, 10, or 30 ppb sodium selenite. Selenium was biomagnified through the food chain in these streams, resulting in higher exposure levels than stream treatment levels. Fifteen-day-old ducklings produced by Mallards raised on these streams were challenged with duck hepatitis virus 1, a picornavirus. Mortality was increased significantly with selenium exposure. Liver selenium concentrations increased at the highest exposure level. Immune function in adult Mallards measured by phagocytosis and monocyte concentration, was increased at the 30 ppb treatment level.

Our studies add selenium to a list of compounds (polychlorinated biphenyl, DDT, and dieldrin) that have reduced resistance of Mallard Ducks to duck hepatitis virus 1 (Friend & Trainer 1970, 1974a, 1974b). Mallard Ducks exposed to oil (Bunker C fuel and Louisiana crude) have also had decreased resistance to the bacterium *Pasteurella multocida* (Rocke et al. 1984).

DISCUSSION

Captive Mallard Ducks exposed to polychlorinated biphenyl, DDT, dieldrin, petroleum oil (crude and distillates), or selenium had significantly reduced disease resistance to a virus or bacteria (Table 2). Immunomodulation occurred following exposure to elevated selenium concentrations indicating that immune function was altered. Cell-mediated immunity (delayed-type hypersensitivity) was decreased and non-specific host defenses (phagocytosis and blood monocyte concentration) were increased. Disease resistance in ducklings decreased. Antibody-mediated immunity was not affected by exposure to oil or to selenium in these studies.

The increased susceptibility to infectious disease reported here occurred following exposure to sublethal concentrations of contaminants. In experiments with laboratory animals many chemicals that occur in the environment have also reduced disease resistance to viral, bacterial, or parasite infection and/or immunity. The list of toxicants includes organophosphates, carbamates, chlorinated hydrocarbons, halogenated aromatic hydrocarbons, and heavy metals such as arsenic, cadmium, lead, mercury, and zinc.

A difficulty in investigating the interaction between contaminants and infectious disease is the need for special isolation facilities for the disease challenge, and for the death of the bird. Further development of immune function tests may enable non-lethal studies to be done in the field and laboratory. However, these assays require time to develop and need to be related to disease resistance. Several of the assays listed

in Table 1 use radioactive reagents or require sophisticated laboratory equipment not suitable for field studies, but are useful for laboratory investigations.

TABLE 2 – Effects of toxicants on disease resistance or immune function of Mallard Ducks.

TOXICANT	DISEASE RESISTANCE	IMMUNE FUNCTION	REFERENCE
Polychlorinated biphenyl	D ¹ Duck hepatitis virus 1		Friend & Trainer (1970)
DDT (130 ug/g wet wt. brain)	D Duck hepatitis virus 1		Friend & Trainer (1974a)
Dieldrin (11.5 ug/g wet wt. brain)	D Duck hepatitis virus 1		Friend & Trainer (1974b)
Oil	D <i>Pasteurella multocida</i>		Goldberg & Yuill (1990)
Selenium (16 ug/g dry wt. liver)		D Delayed-type hypersensitivity	Fairbrother & Fowles (1990)
Selenium (7.6 ug/g dry wt. liver)	D Duck hepatitis virus 1	N ² spleen plaque-forming cell assay N serum antibody titer I ³ phagocytosis of killed <i>P. multocida</i> I blood monocyte concentration	Whiteley (1989)

D¹ decrease, N² no effect, I³ increase

The toxicity of chemicals is a function of route of exposure among other factors. Exposure of wild birds to immunosuppressive chemicals may occur by direct contact, such as spraying or during an oil spill, or via ingestion of contaminated water or food. Chemicals in water may move from the source of contamination and be concentrated as water is reused several times for agricultural purposes before becoming available for wetlands used by wild birds. In the experimental studies reported here polychlorinated biphenyl DDT, dieldrin, and sewage sludge were mixed with the feed, selenomethionine was added to the water, the oil was intubated into the gizzard, and sodium selenite was added to water and biomagnified through a natural food chain. The effects of exposure to sublethal levels of environmental contaminants on the magnitude of wild bird losses from disease remains unknown due to limited investigation. Results from the experimental studies cited and empirical field observations suggest contaminant-disease interactions are an important aspect of environmental contamination. Wild birds exposed to chemical contaminants may be more susceptible to die-offs and chronic attrition from infectious disease. Avian mortality from this

source is likely to increase due to diminishing wildlife habitat resulting in increased concentrations of contaminants and environmental conditions that facilitate the transmission of infectious disease. It is imperative that these relationships be better understood so that appropriate actions can be initiated to minimize the potential for catastrophic losses from disease.

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LEAD POISONING IN BIRDS: AN INTERNATIONAL PERSPECTIVE

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ABSTRACT. Lead is a very toxic metal, with many industrial uses, which is ubiquitous due to anthropogenic activities. An important source of lead poisoning in birds is spent lead gunshot, the ingestion of which is estimated to kill several million waterfowl annually in the USA. There is a paucity of published information on lead poisoning in non-waterfowl avian species, from ingested shot and other sources. This paper summarizes the problem of lead poisoning in waterfowl and reviews the information available concerning lead poisoning in captive and wild non-waterfowl avian species.

Keywords: Lead, poisoning, gunshot, paint.

INTRODUCTION

The physical properties of lead make it ideal for a wide range of industrial uses. As a consequence, lead is ubiquitous in urban and natural environments. Unfortunately, lead is also a non-specific poison affecting all body systems, particularly the haematological, neurological and muscular systems.

Once absorbed into the blood stream lead is deposited in a range of tissues including the liver. Liver lead concentrations are used to indicate exposure. Waterfowl and raptors with concentrations >6–10 ppm w.w. (wet weight) are considered to be acutely exposed to lead (Longcore et al. 1974, Pattee et al. 1981, USFWS 1986) and birds with 2–6 ppm may be sublethally poisoned. Lead toxicity is influenced by many factors, particularly diet. Birds with diets high in protein, calcium and/or phosphorous are more resistant to the effects of lead poisoning than birds with diets poor in these constituents.

Lead poisoning is responsible for the deaths of millions of wild birds (Sanderson & Bellrose 1986, Pain 1990b) and is also a cause of mortality among captive birds. Most published information on lead poisoning in birds involves waterfowl poisoned through the ingestion of spent gunshot. However, even for these species little information is available outside Europe and the USA. Observations of lead shot in the intestinal tracts and lesions of lead poisoning have often been noted during necropsy or while conducting unrelated research in many nonwaterfowl species. Unfortunately, these observations are rarely published and contribute to inadequate recognition of the extent of lead poisoning as a cause of mortality in avian species throughout the world. This paper provides an overview of lead poisoning in birds.

LEAD POISONING IN WILD BIRDS

Poisoning from lead ammunition

There are two main groups of birds likely to ingest spent gunshot. The first group includes those birds feeding in substrates in shot-over areas. Such areas include many

wetlands, clay pigeon shoots and upland game areas. Densities of up to 2 million shot/ha. have been recorded in wetlands (Pain 1990c) and even higher densities (up to 200 million shot/ha.) around clay pigeon shoots (Peterson & Meltofte 1979). Birds particularly at risk are those which ingest grit and small stones; included are waterfowl, many waders, rails, coots, pigeons and doves. There is some evidence that species normally ingesting grit of a similar diameter to shot are more likely to ingest shot (Pain 1990a). Bill length may also influence shot ingestion by shorebirds as longer billed birds have more shot available to them.

Appendix 1 illustrates the wide range of birds reported to have either ingested shot and/or suffered lead poisoning following shot ingestion. In addition, White et al. (1980) have recorded elevated lead concentrations (>6 and up to 28.5 ppm) in the livers of 3 of 15 Western Sandpipers *Calidris mauri*, the source of which may have been previously ingested shot.

The other group of birds at risk from poisoning are those species which ingest shot whilst feeding on dead or live animals carrying shot in their flesh, or themselves lead poisoned. In the USA, an estimated 19% of ducks and 15% of geese shot by hunters go unretrieved (USFWS 1976). These waterfowl and other unretrieved animals provide a lead contaminated food source that is utilized by many avian scavengers and predators, including eagles, harriers, buzzards and vultures. As raptor populations are often small, and reproductive rates low, their populations are particularly vulnerable to increases in adult mortality (Grier 1980).

The National Wildlife Health Research Centre (USA) has documented more than 170 Bald Eagle *Haliaeetus leucocephalus* deaths due to lead poisoning (pers. comm.). The primary cause of these deaths is ingestion of shot embedded in tissues of prey, rather than lead concentrations in tissues being consumed (Pattee & Hennes 1983). The high rate of lead exposure in some populations is illustrated by up to 71% of egested pellets containing shot (Platt 1976). Even when pellets are regurgitated poisoning may occur. Pattee et al. (1981) found experimentally that repeated ingestion/regurgitation of lead pellets caused mortality in the Bald Eagle. Lead poisoning is considered to have accounted for between 5.2 and 7.6% of total Bald Eagle mortality between the mid 1960s and early 1980s (Pattee & Hennes 1983, Reichel et al. 1984).

The Californian Condor *Gymnogyps californianus* has also suffered the effects of lead poisoning. Between 1982 and 1986, blood samples from 5 of 14 Condors (representative of the remaining population) had elevated lead concentrations (>70 µg/dl - Wiemeyer et al. 1988). Also, 3 of 5 Condors necropsied between 1980 and 1986 died of lead poisoning. Bullet fragments probably present in carrion fed on was found in the ventriculus of one of the Condors. The last wild Californian Condors were taken into captivity in 1986 to enhance the captive breeding population.

Other raptors have also been diagnosed as dying of lead poisoning (Appendix 1). In addition, elevated bone lead concentrations were found in 10 of 16 Turkey Vultures *Cathartes aura* examined (Wiemeyer et al. 1986), and Snyder et al. (1973) found a lead concentration of 19.6 µg/ml in the egg of one Coopers Hawk *Accipiter cooperii* compared with a mean of 0.2 µg/ml in 23 other eggs.

In the USA, concern over lead-related waterfowl and Bald Eagle mortality has resulted in replacement of lead by non-toxic steel shot for waterfowl and coot hunting

nationwide by 1992. Lead poisoning also affects large numbers of waterfowl in Europe, especially in the heavily hunted wetlands of the Mediterranean basin (Pain 1990a, Pain & Handrinos 1990). Denmark and Holland are considering the use of non-toxic shot (which has been used on RAMSAR sites in Denmark since 1986), but most other European countries have done nothing. Outside Europe and the USA, little information is available concerning lead poisoning in waterfowl or other species.

Poisoning from non-ammunition sources

Wild birds may be exposed to non-ammunition sources of lead contamination including lead in petrol, industrial effluents and waste dumps. Although few records of avian mortality are associated with such sources, elevated tissue lead concentrations, and associated physiological effects, have been reported in association with local environmental contamination, or lead contamination of specific feeding sites (Black-headed Gull *Larus ridibundus* and Herring Gull *Larus argentatus* (Leonzio et al. 1986); Pigeon *Columba livia* (Hutton & Goodman 1980, Ohi et al. 1974); Knots *Calidris canutus* (Goede & de Voogt 1985)).

Several species have been suggested as indicators of lead and other metal contamination in human environments. The pigeon appears to be one of the most suitable as it frequently feeds at ground level where food and small gizzard stones ingested are likely to be contaminated with lead rich dust. In urban areas, petrol additives may be the origin of much of this lead. Significantly higher tissue lead concentrations have been found in urban than rural pigeons (France - Jenkins 1975, Japan - Ohi et al. 1974, England — Hutton & Goodman 1980, USA - Tansy & Roth 1970), and a range of passerines (Getz et al. 1977). Tissue lead concentrations in pigeons in Tokyo decreased, with a two year time lag, following a reduction in the amount of leaded petrol used (Ohi et al. 1981). The time lag presumably occurred as much of the lead to which pigeons were exposed may have been lead rich dust. Removal of urban pigeons to uncontaminated rural areas resulted in significant reductions in tissue lead within months rather than years.

London pigeons accumulated very high tissue lead concentrations without several of the signs associated with acute lead toxicity, although other signs (altered activity of hematopoietic enzymes, increased kidney weight and altered mitochondrial structure and function) were present. Exposure regime (acute or chronic) may alter the subcellular distribution of lead and consequently its toxic effects (Hutton 1980).

Most lead contamination of the type described above results in sub-lethal poisoning that is difficult to quantify regarding effects on the biological fitness of a bird. One notable exception occurred in the Mersey estuary in the UK in 1979 and the early 1980s. Several thousand birds, mainly shorebirds and gulls were found dead or dying of alkyl lead poisoning after eating prey contaminated with industrial effluents from a petrochemical works. Liver concentrations of alkyl lead were generally >10 ppm w.w. (Bull et al. 1983). Trialkyl lead is regularly released in industrial effluent and it was considered possible that the general decrease in pollution in the estuary had resulted in an increase in prey, which attracted birds to feed in areas of alkyl lead contamination.

Another example of avian mortality from non-ammunition lead exposure is that involving the Mute Swan *Cygnus olor* in Britain due to the ingestion of lead fishing weights.

Concern over declining Mute Swan populations on the Thames and other rivers resulted in the banning of lead fishing weights in Britain in 1986 (Birkhead 1983, Sears 1988).

LEAD POISONING IN CAPTIVE BIRDS

The sources of lead poisoning in captive birds are diverse, ranging from lead shot to the disposable self-developing camera film believed to have poisoned a Kori Bustard *Choriotis kori* (Zook et al. 1972). However, most cases of poisoning in captive birds occur in one of two ways (Appendix 2), being fed game (waterfowl, pigeons, rabbits, deer etc.) containing lead shot or bullet fragments embedded in the flesh, or from the ingestion of lead-containing paint used to coat cages, enclosures, or objects such as perches or feeders (Zook et al. 1972, Kennedy et al. 1977).

METHODS OF REDUCING LEAD POISONING IN BIRDS

A reduction in the incidence of lead poisoning in captive birds simply requires the control of the two main sources of lead contamination; game killed with lead ammunition and lead paint on enclosures, to which they are exposed.

A general reduction in exposure of many birds and other animals to lead, particularly in urban areas, could be brought about by a reduction in petrol lead or the use of lead-free petrol. Lead-free petrol was first introduced in the USA in 1974 and in 1987 75-80% of petrol sold was unleaded. Europe was slow in following this example but in 1985 a European Economic Community Directive was adopted requiring all member states to make available unleaded petrol by 1989.

It is evident that the most important source of lead poisoning for both waterfowl and non-waterfowl avian species is lead shot which causes the unnecessary deaths of millions of birds each year, and may put some avian populations at risk. This is particularly true for species with small populations and low reproductive potentials. The significance of lead shot related avian mortality has resulted in its replacement by non-toxic steel for waterfowl and coot hunting throughout the USA. Similar regulations in other countries would help prevent the deaths of large numbers of waterfowl each year, and would protect the many other species at risk.

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APPENDIX 1

Lead poisoning in wild birds

1) Poisoning from or ingestion of lead shot

a) Direct shot ingestion

SPECIES	SITE	REFERENCE
Waterfowl (Many species)	USA & Europe	Reviewed in: Pain 1990b; Sanderson & Bellrose 1986
Sora Rail <i>Porzana carolina</i> , King Rail <i>Rallus elegans</i> , Clapper Rail <i>Rallus longirostris</i> , Virginia Rail <i>Rallus limicola</i> , Moorhen <i>Gallinula chloropus</i> , American Coot <i>Fulica americana</i> .	USA	Jones 1939 *
Coot <i>Fulica atra</i> , Water Rail <i>Rallus aquaticus</i> , Black-tailed Godwit <i>Limosa limosa</i> , Snipe <i>Gallinago gallinago</i> , Ruff <i>Philomachus pugnax</i> .	France	Pain 1990a *
Long-billed Dowitcher <i>Limnodromus scolopaceus</i> , Black-necked Stilt <i>Himantopus mexicanus</i> , White-faced Ibis <i>Plegadis chihi</i> , Marbled Godwit <i>Limosa fedoa</i> .	USA	Hall & Fisher 1985 *
Jack Snipe <i>Lymnocyptes minimus</i>	France	Veiga 1985
Dunlin <i>Calidris alpina</i>	Canada	Kaiser & Fry 1980
Western Sandpiper <i>Calidris mauri</i> , Sandhill Crane <i>Grus canadensis</i> , Herring Gull <i>Larus argentatus</i> , Glaucous-winged Gull <i>Larus glaucescens</i> .	USA	NWHL 1985 *
California Gull <i>Larus californicus</i>	USA	Quortrup & Shillinger 1941
Bobwhite Quail <i>Colinus virginianus</i>	USA	Stoddard 1931 *
Turkey <i>Meleagris gallopavo</i>	USA	Stone & Butkas 1978 cited in USFWS 1986
Scaled Quail <i>Callipepla squamata</i>	USA	Campbell 1950
Pheasant <i>Phasianus colchicus</i>	UK USA Denmark	Calvert 1876 NWHL 1985 * Clausen & Wolstrup 1979
Partridge <i>Perdix perdix</i>	Denmark UK	Clausen & Wolstrup 1979; Keymer & Stebbings 1987

Appendix 1 – continued

Wood Pigeon <i>Columba palumbus</i>	Denmark UK	Clausen & Wolstrup 1979; Harradine pers. comm.
Mourning Dove <i>Zenaida macroura</i>	USA	Locke & Bagley 1967 *
Rock Dove <i>Columba livia</i>	USA	Dement et al. 1987

b) Ingestion of lead fragments in flesh of prey/carrion

Bald Eagle <i>Haliaeetus leucocephalus</i>	USA	Pattee & Hennes 1983 *
Golden Eagle <i>Aquila chrysaetos</i> , Red-tailed Hawk <i>Buteo jamaicensis</i> , Rough-legged Hawk <i>Buteo lagopus</i> .	USA	NWHS 1985 *
Californian Condor <i>Gymnogyps californianus</i> (bullet fragments rather than shot ingestion)	USA	Wiemeyer et al. 1988

2) Poisoning from non-shot sources

SPECIES	SOURCE	SITE	REFERENCE
Sandhill Cranes <i>Grus canadensis</i>	Fishing weights	USA	Windingstad et al. 1984
Common Loons <i>Gavia immer</i>	Fishing weights	USA	Locke et al. 1982
Laysan Albatross <i>Diomedea immutabilis</i>	Paint chips	USA	Sileo & Fefer 1987
Shorebirds and gulls	Industrial effluent from petrochemical works	UK	Bull et al. 1983

Most records cited involve cases of lead poisoning. However, some are cases of shot ingestion, which may not always result in poisoning.

APPENDIX 2
Lead poisoning in captive birds

* indicates that other references are available (contact author for full list)

1) Poisoning from or ingestion of lead shot

SPECIES	SITE	REFERENCE
Buzzard <i>Buteo buteo</i>	UK Germany	Macdonald & Randall 1983; Stehle 1980
Sparrowhawk <i>Accipiter nisus</i> , Peregrine <i>Falco peregrinus</i> , North American Peregrine <i>Falco peregrinus anatum</i> , Lager Falcon <i>Falco jugger</i> , Snowy Owl <i>Nyctea scandiaca</i> .	UK	Macdonald & Randall 1983
Andean Condor <i>Vultur gruphus</i>	USA	Locke et al. 1969
King Vulture <i>Sarcorhamphus papa</i>	USA	Decker et al. 1979
Turkey Vulture <i>Cathartes aura</i> , Bald Eagle <i>Haliaeetus leucocephalus</i> .	USA	Janssen et al. 1979
Prairie Falcon <i>Falco mexicanus</i>	USA Germany	Benson et al. 1974*; Stehle 1980
Goshawk <i>Accipiter gentilis</i>	Germany	Stehle 1980
Honey Buzzard <i>Pernis apivorus</i>	USA	Lumeij et al. 1985
Bobwhite Quail <i>Colinis virginianus</i>	USA	Stoddard 1931
Sandhill Crane <i>Grus canadensis</i>	USA	Windingstad et al. 1984 (ingestion of entire rifle cartridge)
Domestic poultry	USA	USFWS 1986*

2) Lead poisoning from non-shot sources

SPECIES	SOURCE	SITE	REFERENCE
Sandhill Crane <i>Grus canadensis</i>	Paint	USA	Kennedy et al. 1977

APPENDIX 2 – Continued

SPECIES	SOURCE	SITE	REFERENCE
Rhea <i>Rhea americana</i>	Paint	USA	Zook et al. 1972
Parrots various	Paint	USA UK Germany	Zook et al. 1972 Theissen 1976
Cockatoo	Paint	USA	Panigraphy et al. 1979
Cockatiel	Lead on stained glass window	USA	Rosskopf & Woerpel 1982
Amazon Parrot <i>Amazona ochrocephala</i>	Lead perch Lead caulking	USA USA	Giddings 1980; Fudge 1982
Kori Bustard <i>Choriotis kori</i>	Self-developing camera film	USA	Zook et al. 1972

THE ROLE OF WILD BIRDS IN THE TRANSMISSION OF *BORRELIA BURGDORFERI*

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ABSTRACT. Lyme borreliosis is the most frequently reported tick-borne disease in the United States. It is a spirochetal zoonosis with a global distribution. Transmission is primarily by the bite of an Ixodid tick. Birds can act as hosts for the ticks and for the spirochete with 49 species of birds reported as carriers of the tick. The migratory habits of birds give them the potential to transmit ticks over a wide geographic range. The disease in humans can cause a skin rash, arthritis, cardiac, and neurologic problems. People who trap and handle birds should be aware of the potential exposure to Lyme borreliosis and take protective measures.

Keywords: Lyme borreliosis, *Borrelia burgdorferi*, Lyme disease, birds, Ixodid ticks.

INTRODUCTION

Lyme borreliosis, caused by a spirochete *Borrelia burgdorferi*, is the most frequently reported human tick-borne infection in the United States (Steere 1989) with 7402 cases reported in 1989. The majority of cases have been from the East coast, Midwest and far western states but cases have been reported from 43 of the 50 states. The disease was first recognized in Sweden in 1909, where it was called erythema chronicum migrans. In Europe cases have been primarily reported from Germany, Austria, Switzerland, France, Sweden, and Italy, but cases have occurred in most other European countries. The disease is also reported in the Soviet Union, China, Japan, and Australia. The first identification of this disease in the United States was in 1975 in Lyme, Connecticut where a tick-borne arthritis was given the name Lyme disease (Steere et al. 1986). A spirochete was discovered as the cause of the illness in 1982 when the organism was recognized in *Ixodes dammini* and in the blood of two patients (Burgdorfer 1982, Benach et al. 1983). The spirochete was given the name *Borrelia burgdorferi* after the researcher, Willy Burgdorfer, who first discovered it in ticks.

DISEASE IN MAN

Infection can cause illness in both humans and animals. The disease in humans can cause multiple syndromes. The earliest manifestation is an expanding circular skin rash (erythema chronicum migrans) that occurs in 60-80% of people infected with the organism. The rash can appear from two to twelve weeks after the tick bite and may be accompanied by flu like symptoms such as fever, vomiting, joint pain, and occasionally photophobia and conjunctivitis.

The intermediate stage of the disease occurs from four to nine weeks after the bite and may include neurologic symptoms, cardiac and musculoskeletal signs. The

neurologic signs may include Bell's palsy, pain of the extremities, headache or stiff neck. These symptoms may occur in 15% of infected humans. Cardiac signs are characterized by heart block or tachycardia. Musculoskeletal signs consist of painful swollen muscles and chronic Lyme disease may involve the joints and peripheral nervous system. Arthritis may affect the large joints such as the knees. Dementia may develop years after the initial infection in a small percentage of infected people.

Diagnosis of Lyme borreliosis is made by a combination of clinical signs, serologic test results, and response to treatment. Best results of treatment are obtained when the disease is treated promptly in the early stages. Several antibiotics can be used for treatment depending upon the stage of the disease and the response of the individual. Examples of some antibiotics used for treatment include tetracycline, doxycycline, penicillin, amoxicillin, and ceftriaxone.

ANIMAL STUDIES

Transmission is primarily by the bite of certain Ixodid ticks including *I. dammini* and *I. pacificus* in the United States, *I. ricinus* in Europe, and *I. persulcatus* in Asia. Thirty-one species of mammals and 49 species of birds have been shown to act as carriers for *Ixodes dammini*. While the White-tailed Deer is the main host for the adult form of *Ixodes dammini* and the White-footed Mouse for the larval and nymphal stages, birds can also serve as hosts for the larval and nymphal stages.

Immature stages of *I. dammini* have been found on one species of Meleagrididae, one species of Phasianidae, one species of Scolopacidae, one species of Tyrannidae, one species of Corvidae, two species of Paridae, one species of Sittidae, one species of Certhiidae, one species of Troglodytidae, two species of Mimidae, five species of Turdidae, two species of Vireonidae, 14 species of Parulidae, one species of Surnidae, three species of Ploceidae, and 10 species of Fringillidae.

Of 62 birds captured in Connecticut, 71% were infested with immature stages of *I. dammini* and approximately 500 larvae were removed from 200 birds along coastal Massachusetts, suggesting birds may be transmitting the tick between islands. In a study of 9200 migratory birds in the St. Croix River Valley in Wisconsin and Minnesota 58 birds carried 250 *Ixodes dammini* ticks and 56 of the 250 ticks were infected with *B. burgdorferi*. Birds carrying infected *I. dammini* included Veery *Catharus fuscescens*, Nashville Warbler *Vermivora ruficapilla*, Myrtle Warbler *Dendroica coronata*, Ovenbird *Seiurus aurocapillus*, Waterthrush *Seiurus noveboracensis*, Mourning Warbler *Oporonis philadelphia*, Common Yellow Throat *Geothlypis trichas*, Wilson's Warbler *Wilsonia pusilla*, Song Sparrow *Melospiza melodia*, and Swamp Sparrow *Melospiza georgiana* (Weisbrod & Johnson 1989).

Birds can also be infected with the spirochete and may be able to infect ticks feeding on them. *B. burgdorferi* was isolated from the blood or tissue of 7 species of birds naturally infected with *B. burgdorferi* including: Veery, Common Yellow Throat, American Robin *Turdus migratorius*, Catbird *Dumetella carolinensis*, Prairie Warbler *Dendroica discolor*, Orchard Oriole *Icterus spurius*, and House Wren *Troglodytes aedon*. Mallard Ducks *Anas platyrhynchos platyrhynchos* have been experimentally infected with *B. burgdorferi* by the oral route and shed spirochetes in their droppings

for up to 30 days. Ten of 22 wild turkeys from Oklahoma had antibodies to *B. burgdorferi* and a *Borrelia* spp. was isolated from the droppings of one. *B. burgdorferi* was detected by polymerase chain reaction test in a kidney from a House Sparrow. These findings suggest that birds may be able to transmit the spirochete to each other by the fecal-oral route (Burgess 1989).

DISCUSSION

No signs of disease have been recognized in any infected birds so the main importance of infected birds is in their role in the spread of ticks and spirochetes. The role of birds in the distribution of Lyme borreliosis and transmission of this disease to man appears to be greater than previously recognized. This role involves distribution of the disease vector (ticks) and transport of the disease agent via infected ticks and as an infected host.

Migratory birds may travel up to 7,000 miles from breeding habitats to overwintering grounds. *Ixodes* spp. ticks feed for several days before dropping off their hosts thus allowing for the possibility of transport and dispersal of ticks over several hundred miles of the migration route. Immature stages of ticks feeding on birds may become infected with *B. burgdorferi* and unattached nymphs may crawl onto humans.

People who work in outdoor environments are at a higher risk of exposure to ticks and therefore infection with *B. burgdorferi*. A study of individuals engaged in outdoor employment and anonymous blood donors demonstrated a 5.9 times greater positive rate of infection in employees working outdoors (Smith et al. 1988). People who trap and handle birds should check themselves carefully for ticks and also be aware of the potential of spirochete transmission via the blood or droppings of infected birds. Protective measures that should be taken include: wearing protective clothing (long sleeves and pants tucked into socks), insecticides (Permethrin or Deet on clothing), careful inspection for ticks and prompt removal by grasping the mouth parts with tweezers and pulling the tick out.

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CONCLUDING REMARKS: DISEASE ECOLOGY AND THE CONSERVATION OF AVIAN SPECIES

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We have heard about a variety of disease-related subjects in this session and more will be discussed in another session this afternoon and in a roundtable tomorrow. This reflects the growing awareness of disease as a factor that must be considered in the management of wild birds.

Disease in free-living wildlife has received increasing attention by natural resource managers during the past two decades. Some agencies have developed internal disease capabilities and others have provided fiscal support for regional and other programs to serve their needs. These actions are encouraging but efforts and perspectives need to be expanded considerably if the impact of disease is to be significantly mitigated. The basis for this statement lies in the fact that current actions are focused on the proverbial tip of the iceberg (i.e. major die-offs) while the greater scope of disease impacts is hidden from view. This was clearly eluded to by several speakers in this session.

Survival in nature is a highly competitive daily struggle for many wild species. Factors that even slightly compromise normal body function and responses may result in the individual animal being unsuccessful. Mortality is one end-point, but until the true cost of disease is known we will continue to underestimate its effects. Wobeser, and Friend and Thomas noted in their presentations that the greatest impacts of disease often involve sublethal effects such as suppression of reproductive success and survival of young. Those presentations also stressed that disease prevention is more cost-effective and efficient than disease control.

Eradication of infectious disease in free-living wildlife populations is not a realistic goal. This reality strengthens the need for aggressive disease prevention because of the potential for new infections to spread over broad geographic areas. The presentation by Burgess on the role of birds in the transmission of Lyme disease serves as an example.

Wobeser stressed the importance of man in the development and maintenance, and conversely, the prevention and control of disease in free-living wild populations. The role of man in these processes should not be underestimated. Lead poisoning and other direct toxicity problems associated with environmental contaminants are clear examples of wildlife health problems directly caused by man. The cause of waterfowl losses from lead poisoning has been known for more than a century. But these losses

persist as a significant cause of mortality due to lack of acceptance of the magnitude of the problem or of the need to take corrective actions. The focus on lead poisoning in waterfowl has been expanded to other species by Pain in her review of this subject. The potential for corrective actions to deal with far more complex situations than lead poisoning, such as the chemical-microbial interactions discussed by Whiteley and Yuill, is inherently much more difficult. The ramifications of the data they presented are such that natural resource managers need to integrate their programs of contaminant assessment and "classical" disease investigations.

Translocation of free-living wildlife and release of captive-propagated stock are appropriate wildlife conservation strategies. However, these activities have inherent disease risks which are seldom addressed; it is illogical not to take the appropriate measures for minimizing the potential for disease introduction. Failure to do so jeopardizes the populations these programs are intended to help. The needs of endangered species are interwoven within this issue because of the emphasis on captive-propagation programs for some species.

Endangered species should receive the most attention regarding disease but, as a group, receive less attention in North America than most other species. The presentation by Friend and Thomas clearly illustrated that endangered species are suffering considerable losses from disease. In several instances, disease is having an undeniable negative impact on species recovery efforts. The lack of attention to disease is in part a result of the failure of habitat oriented managers to appreciate the linkage between environment (habitat) and disease. One of the purposes of this symposium was to enhance recognition of this relationship.

Lyme disease, unlike the other presentations in this symposium, does not involve a disease with direct impact on bird populations. However, this subject was included because it illustrates the complexity of disease ecology and because of the current importance of Lyme disease for man and domestic animals. The ability of birds to move disease agents and vectors many miles from the site of original exposure is analogous to enhanced distribution of human disease, resulting from the transport of people from one area to another by jet aircraft. Infections in mobile populations must be diagnosed and dealt with before movement takes place, to prevent spread to new populations and new locations. Disease prevention and control must be proactive rather than reactive to be effective.

Disease will always be a part of the biological world. However, the choice is ours whether we attempt to manage disease or continue to accept uncontrolled losses and the establishment of preventable new problems.

SYMPOSIUM 44

**SUPERABUNDANCE IN GULLS: CAUSES,
PROBLEMS AND SOLUTIONS**

Conveners H. BLOKPOEL and A. L. SPAANS

SYMPOSIUM 44

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INTRODUCTORY REMARKS: SUPERABUNDANCE IN GULLS: CAUSES, PROBLEMS AND SOLUTIONS

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INTRODUCTION

The large family of the Laridae contains some 45 species of gulls which can be found in most geographical areas and all climatic zones of the world. They do not nest on the Antarctic pack-ice or in the Central Pacific (Löfgren 1984). There are more gull species in the Northern than in the Southern Hemisphere, probably because of their evolutionary origin in the northern half of the globe. Many gull species favour temperate climates and prefer to live in coastal areas, although they can also be found inland near lakes and rivers (Löfgren 1984). Gulls are born generalists: they are able to walk, swim and fly, and some species even plunge-dive well. Many *Larus* species are omnivorous, adaptable, opportunistic and gregarious. Because of their morphological and behavioural characteristics many gulls are highly adapted to live in human-altered habitats.

In the temperate portions of the northern hemisphere people have populated coastal areas and built large cities. Many people and many gulls have similar habitat preferences. On both coasts of the Atlantic Ocean and on the west coast of the Pacific Ocean, rich nations still enjoy material wealth fostered by an economic system based on intense consumption coupled with a throw-away mentality. Put simply, gulls flourish in the effluence of affluence. This is, of course, an oversimplification, but increasing numbers of gulls thrive in the human landscape where, in the absence of many natural predators, they capitalize on new food sources (garbage dumps, offal from fish processing plants, hand-outs in parks, etc.). Gulls also benefit from their association with people because humans make natural food sources more readily available (gulls feeding behind the plow, following fishing boats, foraging on manure, etc.).

Gulls are webfooted and like to rest on sites that offer a flat substrate, protection from ground predators and good visibility in many directions. Roofs, runways, school yards and sport fields are attractive human-made loafing sites for gulls. In addition, increasing numbers of several gull species are also nesting in or near urban and suburban areas.

GULL POPULATION INCREASES

During most or all of the last several decades, several gull species have expanded their range and increased their populations in Europe (Vauk & Prüter 1987) and in northeastern US (Drury 1973). It is generally accepted that these increases result

mainly from protection (against human disturbance) and increased food supplies (made available directly or indirectly by human activities), but cause-and-effect relationships are not always clear and other factors (climatic change and long-term ecological interactions) may also play a role (Drury & Nisbet 1969, Harris 1970, Murton 1972, Drury 1973, Vauk & Prüter 1987).

In some cases continued population growth has led to superabundance, i.e. the gulls are "abounding in great or too great quantity". Superabundance is a value judgement and, as such, open to discussion.

WHAT IS A GULL PROBLEM?

Gull population increases can result in conflicts between gulls and the interests of people and those of other bird species. When gulls are in conflict with human interests, a variety of "gull problems" of different degrees of seriousness arise. The main problems usually include general nuisance, damage to property, potential health hazards, and threats to flight safety. Vauk & Prüter (1987) provide a detailed review of gull problems in western Europe. Gulls are often involved in collisions with aircraft, especially in North America and Europe (Blokpoel 1976).

Different people often have different opinions about the seriousness of any particular gull problem. Many problems are insignificant on a nation-wide scale, but of serious and legitimate concern for the few people directly affected. As gulls are legally protected in many countries, gull problems are often referred to the appropriate government agencies. Public servants must then decide whether a problem is indeed a problem, i.e. is serious enough to warrant government sanctions for gull control measures. There is, not surprisingly, some awkwardness when agencies that are mandated to protect gulls are forced to become involved in projects to control them. In remote areas, affected landowners probably decide for themselves that they have problems with gulls and deal with them directly, and often illegally, without involving government officials.

When gulls are in conflict with terns and other bird species (reviews by Thomas 1972, Vauk & Prüter 1987), concerns are usually first expressed by knowledgeable naturalists, park wardens, etc. Controlling overabundant gulls for the benefit of other bird species such as terns has been questioned. Until people greatly modified the natural environment, gulls and terns were presumably in some dynamic, but natural equilibrium. If gulls, by benefitting greatly from human-made changes in the environment, are thus able to cause local extirpations of terns, wildlife management agencies are justified in controlling gulls for the benefit of terns. This is not "interfering with the natural order of things" but a simple desire to maintain some species diversity in an already highly non-natural world. Obviously, such gull control operations should be undertaken only if the gulls are the problem and if the control operations will solve that problem.

GULL PROBLEMS IN HISTORIC PERSPECTIVE

Gull problems are not recent phenomena. In 1950 at the Tenth IOC in Uppsala, Gross (1951) reported on a large-scale, long-term program to reduce Herring Gull *Larus*

argentatus numbers along the coast of Maine, USA, to a level where they would no longer be "a serious menace to man's interests". He sprayed eggs with a mixture of high-grade carrier oil and formaldehyde to prevent hatching. The Maine gull population levelled off and perhaps even declined during 1944-1951, but the program was abandoned in 1952 because the results were not considered spectacular enough to justify the high cost (Graham & Ayres 1975). In the late 1960s there were some 135,000 nesting pairs of Herring Gulls in the eastern USA and they created flight safety hazards at several airports along the Atlantic seaboard. Drury & Nisbet (1969) described a strategy for reducing this number but their proposed large-scale control program was never put in place.

In Europe, Herring Gulls were controlled on a large scale as early as 1939 in Holland (Mörzer Bruyns 1958). Currently, gulls are controlled only to deal with local problems. There are no large-scale multi-national programs to reduce gull populations in Europe and in Germany large-scale culling is prohibited by law (Thomas 1972, Vauk & Prüter 1987). Thomas (1972) concluded "There is no record of an effective method for reducing gull populations over large areas". Basically, that conclusion still holds today. A multi-year program of incomplete culling of nesting adults at a large Herring Gull colony in the UK resulted in a decrease in nest numbers and nest density, increased immigration to that colony, nesting by younger recruits, and an improvement of the condition of breeding birds (Coulson et al. 1982).

As long as the factors that caused the present superabundance in gulls continue to operate and as long as gull problems are dealt with on a site-by-site basis, gull populations are not likely to decline, nor are the numbers of complaints about gull problems. Solving a local problem usually means shifting it to another site rather than eliminating it altogether.

GOALS OF SYMPOSIUM

This symposium focuses on superabundance in five gull species in different parts of the developed world, explores the reasons for population increases, reviews problems caused by superabundant gulls, and discusses solutions to deal with these problems.

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THE HERRING GULL IN NORTH-WEST EUROPE

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ABSTRACT. In north-west Europe, Herring Gull *Larus argentatus* numbers exploded during the twentieth century, but have recently stabilised and started to decrease. The population explosion was triggered by protective measures taken around the turn of the century after a period of heavy persecution. The extent of the growth in numbers is thought to be related to the increased availability of food directly or indirectly provided by man. The increasing numbers have brought the birds more and more in conflict with human activities: gulls being a nuisance in urban areas, damage to agriculture, horticulture and shell-fish cultures, collisions with aircraft, and spread of pathogens. Gulls can also have impact on flora and fauna. Gulls are deterred from areas where they are not wanted by preventing the birds obtaining access, scaring and killing, and collecting eggs.

Keywords: Herring Gull, *Larus argentatus*, population explosion, gull problems, north-west Europe.

INTRODUCTION

Herring Gulls *Larus argentatus** are large gulls inhabiting the arctic, boreal and temperate zones of North America and Europe. Like other larids, they are highly social and very opportunistic in their habits. They rapidly take advantage of food directly or indirectly provided by man, and easily use human-made habitats for feeding, loafing and nesting. Herring Gulls became a problem for people and for other bird species after they had increased dramatically in numbers during the twentieth century. This paper focuses on the species' status and the problems the gulls cause in north-west Europe.

THE NORTH-WEST EUROPEAN HERRING GULL

In the Old World, Herring Gulls breed from north-west Russia and north Norway southward as far as south-west France (Glutz von Blotzheim & Bauer 1982). During the 1920s the species successfully colonised Iceland, and it recently spread southward along the French coast (Yésou 1989).

Herring Gulls breed primarily at rocky and sandy coasts, but in recent times increasingly also on islands in freshwater lakes and on heaths and moorland (reviewed in Vauk & Prüter 1987). The birds increasingly nest on roofs of buildings and on other human-made structures.

* *Footnote:* Common and scientific names follow Voous (1977).

Roof-nesting is most wide-spread in Great Britain and attributed to saturation of colonies at natural sites (Monaghan & Coulson 1977). In The Netherlands the increase of nesting on buildings coincided with re-colonization of the mainland dune area by Red Foxes *Vulpes vulpes* and their subsequent predation upon gulls, resulting in a large numerical decline of gulls at original breeding sites (Spaans unpub. data).

There is much geographical variation in the migratory behaviour, with northern populations undertaking long-distance movements to the south-west, and southern populations being dispersive to a varying degree and usually predominantly along coasts and in a southerly direction (e.g. Cramp & Simmons 1983). Individual birds may roam widely during the winter (e.g. Coulson et al. 1987).

Herring Gulls are omnivorous, taking a wide range of live and dead animals, vegetative material, as well as various kinds of offal and garbage provided by man. Types of food actually eaten depend on local situations, resulting in a great geographical variation in diets (reviewed in e.g. Cramp & Simmons 1983, Götmark 1984, Vauk & Prüter 1987). The species is a well-known predator of eggs, chicks, and sometimes also adults of other bird species.

Considerable variation exists in the published survival rates (briefly reviewed in Chabrzyk & Coulson 1976 and Coulson & Butterfield 1986). Taking all evidence together, survival rates of adults and older immatures are probably well over 90%, whilst the survival rate of first year birds is about 70-80% (Chabrzyk & Coulson 1976, Migot 1987). Birds do not start breeding before three years old, the average age of first breeding being about five years (Chabrzyk & Coulson 1976). Annual offspring production varies widely between colonies but amounts on average to about one fledged young per pair (reviewed in Glutz von Blotzheim & Bauer 1982).

POPULATION DEVELOPMENT

At the turn of the century numbers of Herring Gulls were small due to extensive shooting and eggging. Following the introduction of protective legislation, numbers have increased exponentially, with an interruption in growth in Germany and The Netherlands during the 1930s through 1960s when large-scale control measures were taken (Figure 1). Using local data for age of first breeding, offspring production, and mortality rates, Chabrzyk & Coulson (1976) and Migot (1987) found a close agreement between calculated and actual rates of increase for a British and a French population, respectively.

The gulls did not use refuse tips before the population explosion was well under way (Spaans 1971, Bergman 1982). Therefore, it is likely that the population explosion was triggered by a decreased adult mortality rate and an increased recruitment resulting from the introduction of protective legislation. The increasing availability of food provided by man at sea (discarded fish, offal) and on land probably affected mainly the extent to which populations were able to expand (Spaans 1971, Monaghan 1983). The boost in west Germany during the 1970s coincided with a numerical increase in other seabirds and is believed to reflect the eutrophication of the local marine environment during the last few decades (Vauk et al. 1989).

Numbers have recently stabilised and started to decrease over a wide area (Figure 1), but locally (e.g. west Scotland, north-west Ireland, Schleswig-Holstein) numbers are still increasing. The recent decline has been most dramatic on the British and Irish coasts, where numbers decreased from 750,000 pairs in the late 1970s to fewer than 500,000 in 1987 (Lloyd et al. 1991).

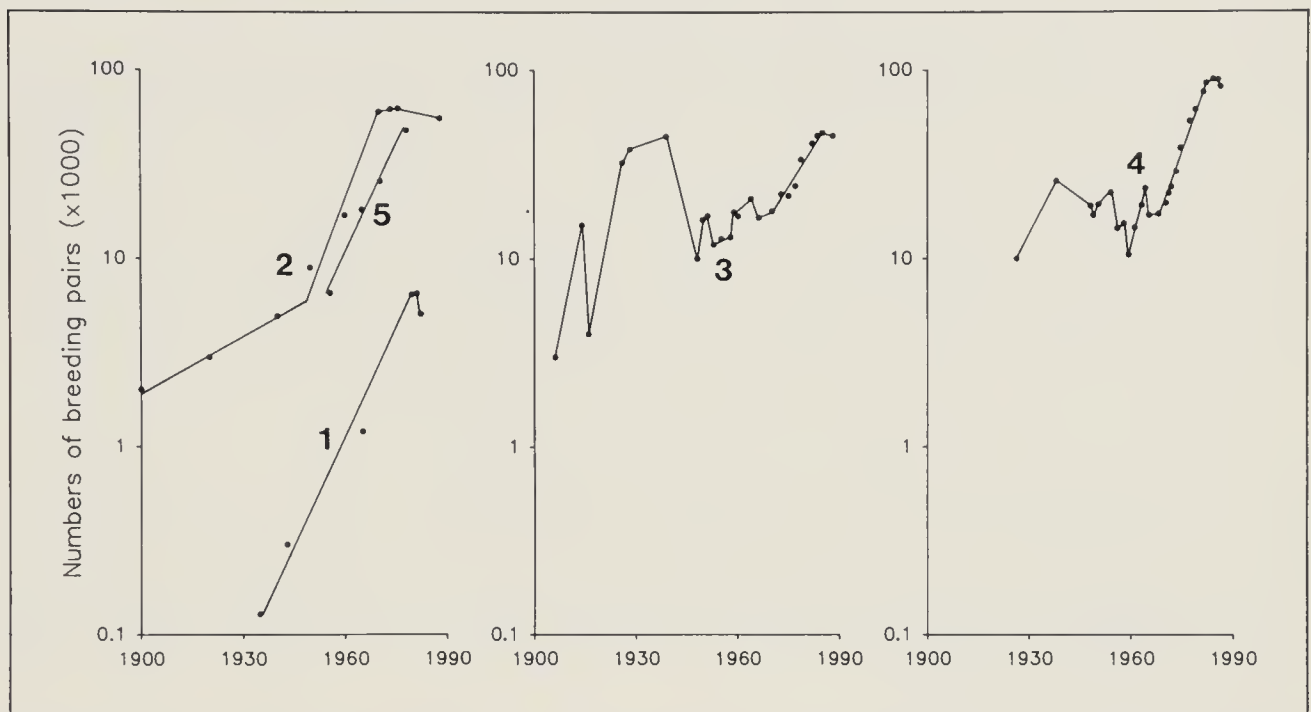


FIGURE 1 - Population development (numbers on logarithmic scale) of Herring Gulls in different areas in north-west Europe during the twentieth century, from north to south: (1) archipelago south-west of Helsinki, south-west Finland, (2) Denmark, (3) East and North Frisian Islands, Germany, (4) The Netherlands, and (5) Brittany, north-west France.

Causes of stabilisation and decline are at present unknown. For certain areas there is good evidence that offspring production has declined dramatically due to shortages of offal (W. Vader unpub. data) and garbage (J.-M. Pons unpub. data) or to a deterioration of the general feeding situation resulting from an increased intra- and interspecific competition (R. Noordhuis & Spaans unpub. data), but it is unknown whether this has occurred extensively. J.-M. Pons (unpub. data) found a 66% decline in offspring production in a colony in Brittany on the heels of a 80% reduction in waste disposal at a nearby refuse tip. Using a Leslie-matrix model, he showed that such a reduction in reproductive success is enough to stop the population increase.

GULL PROBLEMS

The population explosion has brought Herring Gulls increasingly in conflict with man. Herring Gulls are a nuisance at rubbish tips, industrial complexes and in towns, in particular at sites where the birds nest. Noise, attacks on people, fouling of human beings, buildings and equipment, and damage to fabrics of buildings are the major complaints (Monaghan 1983).

Conflicts with agriculture and horticulture include consumption of grain, treading of soil as well as trampling on and pecking at plants at loafing sites, transport of indigestible material from tips to nearby fields harming livestock or damaging equipment, and

spread of pathogenic bacteria (reviewed in Vauk & Prüter 1987). The birds can cause considerable damage to Blue Mussel *Mytilus edulis* cultures (Camberlein & Floté 1978, R. Noordhuis unpub. data).

Herring Gulls are frequently involved in aircraft strikes. For military jets in The Netherlands, L.S. Buurma (unpub. data) arrived at a proportion of 2.3% Herring Gulls in 1984-89, when 82% of the birds found in strikes were identified to species level. The proportion in collisions with civil aircraft is higher because collisions with military jets are mostly en route (Dekker & Buurma 1990), whereas those with civil aircraft are mostly during take-off and landing where the chance of hitting gulls is higher. Breeding colonies and refuse dumps close to runways constitute a particular hazard. Problems arise also when flight routes of aircraft cross flightlines of gulls to and from roosting sites. Sixty percent of accidents with military aircraft in which Herring Gulls are involved result in damage, sometimes including crashes (L.S. Buurma unpub. data).

Herring Gulls are well-known carriers of bacteria pathogenic to human beings and domestic animals. Salmonellae, causing gastro-enteritis in human beings and livestock, are predominant in this respect. In the British Isles the prevalence of salmonellae in Herring Gulls is increasing (e.g. Butterfield et al. 1983), whereas in west Germany it is decreasing (Vauk & Prüter 1987). The opposite trends in the two countries probably reflect differences in environmental contamination by the countries' sewage outflows and refuse tips, the main sites where gulls ingest salmonellae (Monaghan et al. 1985). Serious problems for people may arise when large numbers of gulls roost at potable water supplies (Benton et al. 1983). Herring Gulls can also easily spread *Mycobacterium avium*, the causative agent of avian tuberculosis, from tips to loafing sites at nearby fields, thus contaminating livestock grazing in these fields. *M. avium* is seldom injurious to cattle, but breeding-cattle carrying the bacterium show a positive reaction when tested for bovine tuberculosis, which disqualifies them for export and thus lowers their value (Spaans unpub. data).

Because of their predatory habits, Herring Gulls are often held to be harmful to other bird species. However, the impact on the population level of the species involved is questionable (Spaans 1971, Vauk & Prüter 1987). A good example is the predation on Eider *Somateria mollissima* ducklings (99% of all ducklings taken in some years) in the Dutch Wadden Sea. Swennen (1989) experimentally showed that ducklings taken are weak birds and doomed to starve, the predation therefore being synonymous to a sanitary removal of already moribund birds. Direct competition for nesting sites with terns (*Sterna* spp.) is a problem when no alternative sites for the terns are available (e.g. Thomas 1972, Vauk & Prüter 1987). At some places, Herring Gulls compete for nesting sites with alcids as well (e.g. Vauk & Prüter 1987). Breeding in areas with rare plant species presents locally a conservation problem. Also birds may pull out Marram Grass *Ammophila arenaria* cuttings planted to reclaim sandy dunes. Losses may be so heavy that Marram Grass has to be re-planted (costs about US\$ 5,000.00 ha⁻¹; Bureau Waardenburg unpub. data).

SOLUTIONS

A wide range of methods are presently used to deter Herring Gulls from sites where these birds are not wanted. The most effective measure is to prevent the birds obtaining access. Gulls can be effectively barred from refuse tips by means of a mobile

cover net (Ferns & Johnston 1982). Because nets are expensive (US\$70,000.00, 1988 price level), an overhead wire barrier may be a good alternative (McLaren et al. 1984). Wires have also been used successfully in Germany for deterring gulls from open fish stores (Vauk & Prüter 1987). Wires and monofilament lines are effective also against roof-nesting gulls, but they may cause the gulls to move to other buildings.

A policy of less intensive farming for Dutch airfields has led to tall grass and a smaller prey biomass, resulting in fewer gulls visiting these fields (L.S. Buurma unpub. data; see also Vauk & Prüter 1987).

Distress calls have been effectively used in deterring gulls from water storage reservoirs in Scotland (Benton et al. 1983) and from shell-fish cultures in north-west France (Camberlein & Flote 1978). Such calls are also useful in scaring birds from airfields, in particular when used in combination with pyrotechnics, shell crackers and occasionally shotguns, thus avoiding habituation to the devices (L.S. Buurma unpub. data).

A prolonged use of raptors and shotguns have been effective in deterring Herring Gulls from shell-fish cultures and small, open refuse dumps. The success of actions increases with increasing frequency and when actions are unpredictable (Vauk & Prüter 1987).

Birds rapidly habituate to propane exploders. However, employees of a small refuse tip in The Netherlands kept their working-area at the dump free from gulls using exploders only during working-hours (Spaans unpub. data).

Nesting of Herring Gulls in areas where they are not wanted can be discouraged by removing eggs and nests a few times each season. This is not effective in towns, because birds may move to adjacent buildings after egg removal. In large colonies this is effective only if a small portion of the colony site has to be cleared. Otherwise birds will spread over a wider area and worsen problems (e.g. Spaans et al. 1987).

In west Germany, colonization by Herring Gulls of traditional breeding sites of other species is locally discouraged by shooting gulls. Shooting is most successful when carried out from a blind (Vauk & Prüter 1987).

Large-scale culling of adults in larger breeding colonies is less effective than one would expect, and the effects are soon annulled once culling is discontinued, mainly because maximum recruitment occurs at a relatively low level of nest density (Chabrzyk & Coulson 1976). Culls that cover such colonies entirely, reduce nest density but do not change the extent of the colony (e.g. Chabrzyk & Coulson 1976). If efforts are put into clearing particular areas or sub-colonies entirely, this will probably work better. A considerable proportion of the birds has to be killed annually to cause substantial reduction in a breeding population. For an inland colony in the British Isles, for example, Wanless & Langslow (1983) came to a figure of at least 30%. Culling upsets the dynamics of recruitment over a wide area (Duncan 1978), and generally speaking the method is therefore unattractive. However, it can be an effective solution when, for example, a breeding colony presents a serious threat to nearby air traffic (e.g. Rochard 1987) or to breeding sites of terns (Migot 1987).

In some cases man has adjusted his activities to the gulls. The Royal Netherlands Air Force, for example, initiated a re-routing of a NATO link route to avoid a large roosting flight of Herring Gulls from an inland refuse tip to the coast (Buurma & Bruderer 1990). Losses of planted Marram Grass by gulls can be reduced significantly by using newly cut plants and by planting early in the season. However, a long-term reduction in the numbers of Herring Gulls and in the complaints the birds cause, can probably be achieved only by reducing the amount of food which has come available to the gulls as a result of human activities.

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THE RING-BILLED GULL IN THE GREAT LAKES OF NORTH AMERICA

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ABSTRACT. European colonists decimated the original Ring-billed Gull *Larus delawarensis* population on the Great Lakes. The population increased from 27,000 pairs during 1940-1960 to 710,000 pairs in 1990. Bird protection laws changed human attitudes towards gulls and gulls, in turn, lost most of their fear of people. By capitalizing on opportunities provided by humans, many gulls have become "urbanized", i.e. they feed, rest and nest in or near urban areas. Gull problems include conflicts with interests of people (flight safety hazards, disease transmission, crop damage, roof-nesting, interference with industrial operations, and general nuisance) and of other bird species. Problems are dealt with on a site-by-site basis using the following approaches: (1) scaring gulls, (2) excluding gulls, (3) removing or modifying attractions, and (4) preventing gull reproduction.

Keywords: Ring-billed Gull, *Larus delawarensis*, superabundance, problems, solutions, the Great Lakes, North America.

INTRODUCTION

The Ring-billed Gull* *Larus delawarensis* is a North American species with a breeding range that stretches virtually across the continent, encompassing much of southern Canada and portions of the northern USA. There are two populations: a western population which winters along the Pacific coast of California and Mexico, and an eastern population which spends the winter mainly along the southern part of the Atlantic seaboard and the northern part of the Gulf of Mexico (reviewed by Blokpoel & Tessier 1986).

Most birds of the eastern population nest in the Great Lakes and the St. Lawrence River. The eastern population has increased greatly in recent years and in the Great Lakes area the Ring-billed Gull has become a nuisance or a problem at several locations (Blokpoel & Tessier 1986, 1987). In this report we review the population growth in the Great Lakes, examine possible causes for that growth, and discuss some gull problems and their solutions.

POPULATION GROWTH

Historically, the Ring-billed Gull probably was numerous because J.J. Audubon referred to it as the Common American Gull. As North America became gradually settled by colonists, the ring-bill's breeding range decreased and its numbers dwindled. During 1906-1925 only small numbers may have nested in a remote portion of Geor-

* *Footnote:* Common and scientific names follow American Ornithologists' Union (1983).

gian Bay, Lake Huron (reviewed by Blokpoel & Tessier 1986). The Great Lakes population was fairly stable at 27,000 pairs during 1940-1960, then increased to at least 141,000 pairs in 1967 (Ludwig 1974), some 280,000 pairs in 1976 (based on counts and estimates, Blokpoel & Tessier 1986), and about 710,000 pairs in 1990 (based on inventories in 1989 and 1990, Blokpoel & Scharf unpub. data).

Lakes Superior and Huron contain many small natural islands suitable for nesting, but most of the better islands have already long-standing Herring Gull *L. argentatus* colonies. In the lower Great Lakes (i.e. Lakes Erie and Ontario) there are relatively few natural islands and several colonies are on human-made habitats, such as harbour developments and industrial yards. Average colony size varies between lakes, being larger on the lower Great Lakes. Seven of the eight largest colonies are on the lower Great Lakes (Figure 1).

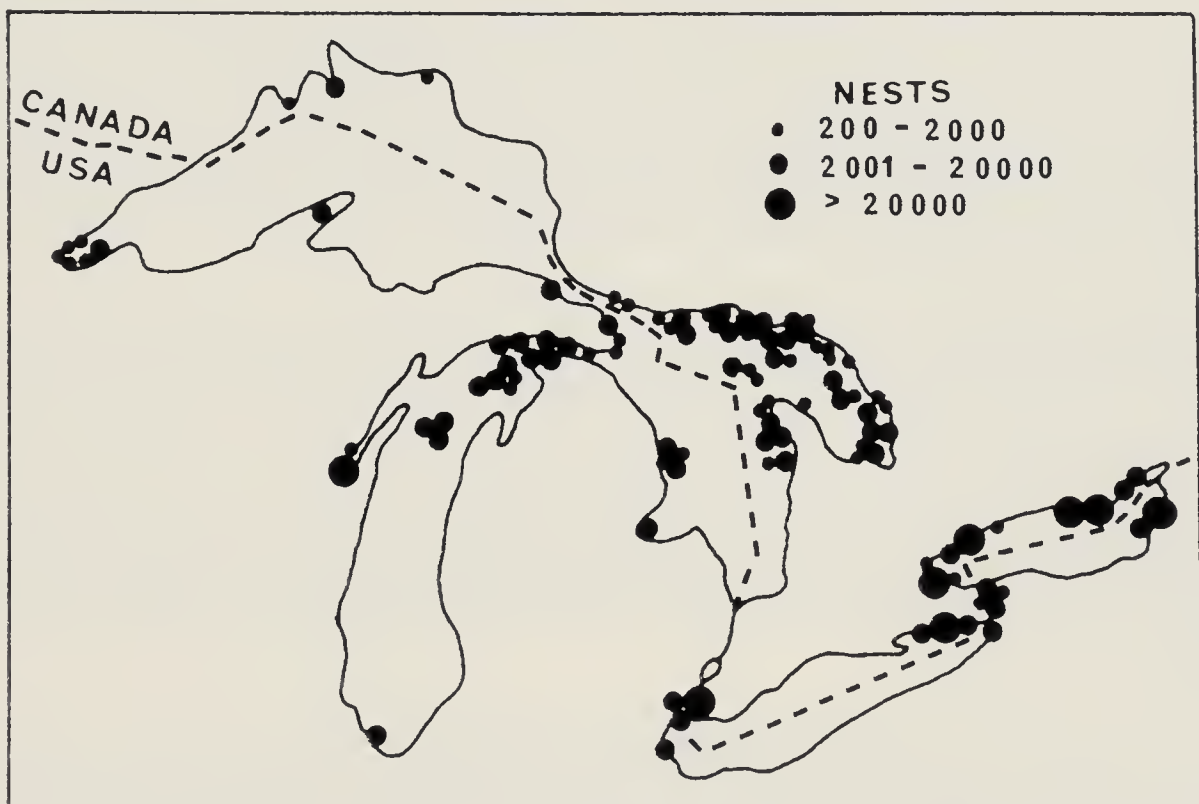


FIGURE 1 - Distribution of Ring-billed Gull colonies in the Great Lakes during 1989-90 (77 colonies with fewer than 200 nests were not plotted).

Ring-bills in the Great Lakes use a wide variety of nesting habitats including natural islands, parklands, slag yards, lawns, roofs, breakwaters, and various landfill sites. Nesting substrates vary accordingly and include bare or sparsely vegetated soil, sand, rocks, driftwood, rubble, and concrete (Blokpoel & Tessier 1986).

Ring-billed Gulls are highly gregarious and often nest in high densities. In 1988 nest densities in preferred habitats at Tommy Thompson Park, Toronto, varied from 1.8 to 2.5 nests m^{-2} . Especially in the lower Great Lakes, a colony tends to increase rapidly once a good-quality site has become colonized. At Tommy Thompson Park, for example, the population increased from some 20 pairs in 1973 to 67,300 pairs in 1980 (Blokpoel unpubl. data).

Recently, ring-bills have begun to nest on roofs in the Great Lakes area (Blokpoel & Smith 1988). Colonization of a new site usually follows extensive use by loafing birds. It is likely that gulls that were loafing on roofs eventually began to nest there.

POSSIBLE REASONS FOR POPULATION GROWTH

The Migratory Bird Convention Treaty between Canada and the USA was signed in 1916 to provide federal protection in both countries for most migratory birds, including the Ring-billed Gull. The end of human persecution presumably allowed the population to return to its previous (and unknown) size. However, in the last few decades two more changes in the gulls' environment have fuelled their population increase: availability of many new food sources and availability of new nesting habitat.

The ring-bill's varied diet contains natural items (fish, insects, earthworms, berries, voles and small birds) and human-made food (garbage, left-overs and hand-outs) (Blokpoel & Tessier 1986). An exotic fish, the Alewife *Alosa pseudoharengus* invaded the Great Lakes and became very abundant. Its availability as prey fish contributed to the growth of the ring-bill population (Ludwig 1974). Alewife populations are likely to decline, now that the lakes are being stocked with salmonids for the sport fishery. Similarly, the ready food supplies on open garbage dumps on the winter range may dwindle with the current trend towards incineration of garbage (Patton 1988). However, given the ring-bills' opportunistic foraging behaviour, they may be able to shift successfully to other food sources and their population level may not be affected.

Great Lakes water levels fluctuate from year to year, resulting in changes of nesting habitat availability. When lake levels are high, low-lying islands are inundated or washed-over during storms. Low lake levels created suitable habitat not yet occupied by the larger Herring Gulls and thus facilitated the recolonization of the Great Lakes by ring-bills (Ludwig 1974). In more recent years, ring-bills have successfully colonized many artificial sites which are usually less affected by changing lake levels than natural sites. However, several of these artificial sites are located on the mainland and are thus prone to mammalian predation and human disturbance, resulting in lowered reproductive success.

It is the behavioural adaptability of the Ring-billed Gull that is behind its current success. Once persecution stopped and people began to tolerate or even appreciate gulls, the gulls lost most of their fear of people and were thus able to capitalize on many new opportunities in the human landscape. In the lower Great Lakes many ring-bills have become urbanized in that they feed, rest, and nest in or near urban areas.

Although ring-bill die-offs are occasionally reported in the Great Lakes area, the population appears to be little affected by diseases, parasites and contaminants. We think that the Great Lakes population will continue to grow before levelling off due to lack of natural food (especially on remote colonies in the upper lakes) and lack of suitable nesting habitat (especially in the lower lakes).

Taking into account the large and growing breeding range in the Great Lakes, the long period of population growth (1960-1990), the variety of nesting habitats, and the changes in abundance of key prey fish, little is known regarding natality, mortality, emigration and immigration of Great Lakes Ring-billed Gulls (reviewed by Blokpoel & Tessier 1986). Calculation of mortality is complicated by band loss (Ludwig 1967). We know of no published population model that describes the ring-bills of the Great Lakes during 1960-1990.

PROBLEMS CAUSED BY GULLS

The increasing numbers of gulls nesting, resting and feeding in the Great Lakes area are creating conflicts with the interests of people and of other bird species.

Conflicts with the interests of people include: threats to flight safety, hazards to human health, damage to agriculture and horticulture, nesting on roofs, interference with industrial operations, and general nuisance. Ring-billed Gulls frequent many airports in the Great Lakes area and are often involved in collisions with aircraft (Blokpoel 1980, R.O'Brien and D. Parr pers. comm.).

Gulls carry several pathogens that could be transmitted to people and cattle (briefly reviewed by Blokpoel & Tessier 1986). However, in the Great Lakes only two outbreaks of histoplasmosis in people have been reported in association with a Ring-billed Gull colony (Southern 1986).

Damage to agriculture and horticulture includes eating, pecking, trampling and defecating on crops such as tomatoes, corn, beans, wheat, strawberries, cucumbers (Blokpoel & Tessier 1986) and, more recently, cherries (Blokpoel & Struger 1988).

Known roof-nesting by Ring-billed Gulls is of recent origin (Blokpoel & Smith 1988) and the associated problems include: fouling of roofs and vicinity, noise, smell, plugging of drainage system by feathers and nest materials, and distraction of people working on roofs.

Many companies have large, fenced properties along the shores of the Great Lakes. Ring-billed Gulls readily colonized several of these industrial yards, and as their colonies grew problems emerged: noise, smell, nesting on roadways, distraction of personnel, and fouling of equipment.

For many people ring-bills have become a nuisance in parks, beaches, marinas and picnic areas by aggressively begging for food and defecating. However, other people enjoy the company of the gulls and encourage them by feeding.

Conflicts with other bird species pertain primarily to the distinct Great Lakes population of Common Terns *Sterna hirundo* which is declining (Courtney & Blokpoel 1983, Shugart & Scharf 1983). Arriving at the colony sites well in advance of the terns, the gulls simply take over traditional tern nesting habitat and thus force the terns to nest in less suitable areas (e.g. close to the waterline) or to abandon the site (reviewed by Courtney & Blokpoel 1983).

SOLUTIONS TO GULL PROBLEMS

Gull control programs, or even discussions about their need or feasibility, are apt to provoke controversy (Blokpoel & Tessier 1986, 1988; Southern 1987). In the Great Lakes area gull problems are dealt with on a case-by-case basis, and there is no large-scale control program. Special permits are issued by government agencies to affected landowners to scare gulls or to disturb gull colonies on their land. Killing of gulls has not been approved except for airports and in cases of serious damage to crops.

Three approaches are used against both loafing and nesting gulls: (1) scaring (shell crackers, bangers, distress calls, falconry, blank and live shells), (2) excluding (installation of wires and monofilament lines), and (3) removing or modifying attractions (prohibition of gull feeding, gull-proof garbage cans, razing of nesting habitat). A fourth approach, prevention of reproduction (egg removal, egg oiling), is used against nesting gulls.

At some Ontario airports gulls are scared away by bird control consultants (Blokpoel 1980). A study of the effectiveness of a bird control operator in getting rid of ring-bills at a dump-site near a military airport in Trenton, close to Lake Ontario, concluded that the long-term, cumulative effect of daily harassment resulted in a large drop in gull numbers despite the fact that individual bird-scaring visits had only limited success (Risley & Blokpoel 1984). An incipient ring-bill colony at Toronto Island Airport, Lake Ontario, was disrupted by repeated egg collections and harassment of the adults (Blokpoel & Tessier 1987).

After the outbreak of histoplasmosis at Roger's City, Lake Huron (Southern 1986), the local ring-bill colony associated with the disease was eliminated by grading the nesting habitat repeatedly using bulldozers and by destroying eggs and nests using pigs (D. Parr pers. comm.). Damage to agriculture and horticulture is reduced by scaring gulls away (shell crackers, blank or live shells, bangers).

Roof-nesting by ring-bills has been discouraged at two sites by removing egg and nests repeatedly (Blokpoel & Smith 1988), while at another site eggs were oiled to prevent reproduction (Blokpoel, unpub. data). Ground nesting at several industrial sites has been reduced or eliminated by scaring, installing wires and monofilament lines, frequent grading of nesting areas, and removing eggs (Blokpoel & Tessier 1987, D. Parr pers. comm.). At two sites reproduction was eliminated by spraying eggs with oil. Nuisance at public places was reduced by installing wires at two sites (Blokpoel & Tessier 1984) and by forbidding the feeding of gulls at another site.

Nesting by Ring-billed Gulls encroaching on Common Tern habitat was discouraged successfully by persistent removal of eggs and nests early in the season at a Lake Erie colony site (R.D. Morris pers. comm.) and was prevented by installing parallel monofilament lines over traditional tern nesting habitat at a Lake Ontario site (Blokpoel unpub. data).

Because no adults are killed and relatively few eggs are prevented from hatching, it is unlikely that the local gull control projects have a significant impact on the overall population size. As long as the overall population does not decline, new gull problems at other locations are likely to arise.

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THE GLAUCOUS-WINGED GULL ON THE PACIFIC COAST OF NORTH AMERICA

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ABSTRACT. The 1988 nesting population of Glaucous-winged Gulls *Larus glaucescens* along the North Pacific coast of North America was estimated at 200,000 pairs. Populations in British Columbia, Washington and in the western Aleutians, Alaska, are increasing due to the cessation of eggging, the availability of garbage and fish offal, and the removal of predators. Nesting on roofs of city buildings in British Columbia and Washington is becoming a nuisance. Gulls are also a nuisance at garbage dumps and a safety risk at airports. The nuisance created by gulls on roofs and on garbage dumps can be addressed by installing parallel overhead wires. The risks at airports can be reduced by playing gull distress calls, closing garbage containers, covering bare ground between runways with grass, and removing gull nests from roofs of airport buildings.

Keywords: Glaucous-winged Gull, *Larus glaucescens*, status, Pacific coast, North America, problems.

INTRODUCTION

The breeding range of Glaucous-winged Gulls* *Larus glaucescens* encompasses the east coast of Kamchatka, Aleutian and Bering Strait islands, the Gulf of Alaska, and the coasts of southeastern Alaska, British Columbia, Washington and Oregon. Glaucous-winged Gulls nest either solitarily or in colonies throughout their range. They usually nest in grass on islands, but also on barges, beacons, bridge supports, cliff ledges, derricks, log booms and pilings, as well as in cliff cavities (Vermeer & Devito 1987). Glaucous-winged Gulls recently started to nest in large numbers on roofs of buildings in coastal cities in British Columbia and Washington, thus indicating much plasticity in their choice of nesting habitat. This roof-nesting habit and the high numbers at garbage dumps have recently made the species a nuisance (Vermeer et al. 1988). In addition, Glaucous-winged Gulls are a safety risk at airports (LGL Limited 1973). To understand the underlying factors responsible for the created nuisance and safety risks, we review population status and trends of the Glaucous-winged Gulls in Pacific North America and the factors behind those trends. We also discuss problems caused by the gulls and measures for alleviating them.

STATUS OF NESTING POPULATION

Censuses of nesting Glaucous-winged Gulls in the North Pacific arrived at a conservative estimate of 133,000 pairs in Alaska (A.L. Sowls pers. comm.), 29,000 pairs in British Columbia (Vermeer 1989), and 10,000 pairs along the inner coast of Wash-

* Footnote: Common and scientific names follow American Ornithologists' Union (1983).

ington (Seattle, Puget Sound and San Juan Islands; Speich & Wahl 1989). There are no separate counts for Glaucous-winged and Western *L. occidentalis* Gulls along the outer Washington coast, as the two species hybridize extensively there. Speich & Wahl (1989) estimated the combined nesting number of these two species on the outer Washington coast to be 8,250 pairs. Using the extent of hybridization reported by Hoffman et al. (1978), the total number of Glaucous-winged Gulls was estimated to be 4,000 pairs. We conservatively estimate the overall, present nesting Glaucous-winged Gull population along the North Pacific coast of North America at 200,000 pairs.

POPULATION TRENDS

The best documented long-term trend of a nesting population of Glaucous-winged Gulls is from the Strait of Georgia, British Columbia, where the population increased from about 6,200 pairs in 1960 to 9,800 pairs in 1975, and to 13,000 pairs in 1986, or an average annual growth rate of 2.9% between 1960 and 1986. Numbers of roof-nesting gulls in the Strait of Georgia are increasing at a rate of 9.1% (Vermeer et al. 1988).

Elsewhere in British Columbia the nesting population in the Queen Charlotte Islands, one of the most isolated and sparsely populated areas along the coast, increased from 2,000 pairs in 1977 to 2,600 pairs in 1986 (Rodway et al. 1988), at an average rate of 3% per year.

For Washington, population data are limited, but increases in nesting populations in Puget Sound colonies are documented (Thoresen & Galusha 1971), and quantitative observations by many observers indicate increases have been widespread (Speich & Wahl 1989). Eddy (1982) observed about 30 Glaucous-winged Gull nests scattered on roofs along the Seattle waterfront in the 1950s and 1960s; by 1981 the number of roof nesters in the same area had grown to an estimated 300 pairs. Eddy (1982) also noted that gulls had nested progressively farther inland from the water over the years.

In Alaska, the overall population trend is poorly documented. In the Gulf of Alaska, gulls were counted in 15 coastal colonies and in one offshore colony (Middleton Island) in 1958-1972 and again in 1976-1984. Most coastal colonies decreased in size (total change was 1,300 to 2,600 pairs), while that on Middleton Island increased (Nysewander et al. 1986). In 1956 no gulls nested on Middleton Island, but in 1976, 570 pairs nested there (Sowls et al. 1978) and in 1987, 3,650 pairs were counted (S. Hatch pers. comm.). The only other available information is for the western Aleutian Islands. The total number of gulls on four islands increased from 5,175 pairs in 1970 to 9,760 pairs in 1979 (U.S. Fish and Wildl. Serv. 1988), at an average rate of 7.3% per year.

FACTORS BEHIND THE POPULATION TRENDS

Cessation of egging

Before and during early European settlement of British Columbia, native Canadians utilized gull colonies as a food source on a sustainable basis, but egging by both

European fishermen and natives reached alarming proportions during the first quarter of this century. Consequently, wardens were posted at some colonies to preserve them (Drent & Guiguet 1961). Since the 1940s, eggling has stopped in southern British Columbia, but it still continues in some parts of northern British Columbia (Vermeer unpub. data).

Garbage

The increasing supply of refuse on garbage dumps near urban centres in the southern portion of the Strait of Georgia attracts tens of thousands of gulls (Vermeer unpub. data). The Glaucous-winged Gull is the most abundant species exploiting those dumps, particularly in winter. Glaucous-winged Gulls are attracted to dumps away from nearby estuaries and intertidal feeding areas, which, compared to the dumps, are only marginally used by the gulls (Vermeer unpub. data). Glaucous-winged Gulls feed extensively on the dumps in winter because marine invertebrates, which are an important natural food (Vermeer 1982), are then less accessible to them because of the pattern of the tides. Glaucous-winged Gulls chiefly feed diurnally at low tides in the intertidal zone. Along the British Columbia coast, the tides are of a 'mixed' type, meaning that either one marked low water is experienced per 24 hours or two slight ones; thus at best one opportunity cycle is offered the gulls to feed in the intertidal zone (Drent & Guiguet 1961). Limited access to invertebrates in the intertidal may have controlled gull survival in the past. Much of the recent Glaucous-winged Gull expansion in the Strait of Georgia is thought to result from an increasing supply of garbage (Drent & Guiguet 1961, Vermeer 1963).

Fish offal

The largest Glaucous-winged Gull colony in Alaska is in the Gulf of Alaska on Egg Island near Cordova. Patten & Patten (1983) observed 10,000 pairs on Egg Island and suggested that the large artificial food supply from canneries in Cordova supported this large colony. When access to fish offal is limited or halted, gull populations will presumably decline. The recent decline of coastal Glaucous-winged Gull colonies in the Gulf of Alaska is probably the result of changes in fish handling techniques. Up to the early 1970s, most fish were canned, a process that produces much waste. Freezing fish became popular in the late 1970s, reducing the amount of offal. Also, new regulations forced canneries to grind up offal, making it less accessible to the gulls (P. Isleib pers. comm.).

Predators

The absence of natural as well as the removal of introduced predators could contribute to an increase in the nesting population of gulls. The high rate of increase of the roof-nesting population in downtown Vancouver is thought to result at least in part from the absence of natural predators, such as Bald Eagles *Haliaeetus leucocephalus* and River Otters *Lutra canadensis* (Vermeer et al. 1988). These two species are predators of Glaucous-winged Gull colonies in the Strait of Georgia, where they cause extensive reproductive failure of small gull colonies (Vermeer & Devito 1989).

Arctic *Alopex lagopus* and Red *Vulpes vulpes* foxes were introduced to many Aleutian islands for the purpose of fox farming in the early 1900s. The foxes had a deleterious impact on seabirds on some islands, taking 40,000 or more seabirds (Murie 1936). Introduced foxes have been removed from the Aleutians and as a result numbers of Glaucous-winged Gulls and other ground nesting birds increased (C.R. Zeillemaker & J.J. Trapp pers. comm.).

GULL PROBLEMS AND CONTROL MEASURES

Airports

In February 1987, a Glaucous-winged Gull destroyed a jet engine on a plane taking off from Victoria International Airport, British Columbia, resulting in tens of thousands of dollars of damage (D. Eastholme pers. comm.). At Vancouver International Airport, British Columbia, Glaucous-winged Gulls are the most common birds.

They visit the airport most frequently during spring, summer and autumn (K. Summers pers. comm.). The gulls feed on earthworms and crane flies in the grass between runways. They create a hazard when visiting or flying over the airport: from 1963 to 1973 gulls were involved in 29 bird strikes, many of which occurred around sunrise (LGL Limited 1973). The number of bird strikes at the Vancouver International Airport has recently decreased: 47 (11 by gulls) strikes in 1987, 22 (5 by gulls) in 1988, and 19 (1 by a gull) in 1989. R. Grondin (pers. comm.) attributes this reduction to preventive measures initiated in 1988, i.e. playing of gull distress calls, closing of garbage containers, covering of bare ground between runways with grass, and removing Glaucous-winged Gull nests from roofs of airport buildings. Continued application of these measures is necessary.

Garbage dumps

The greater Victoria regional dump is the largest refuse landfill on Vancouver Island. In 1987, in response to complaints that Glaucous-winged Gulls were dropping large amounts of garbage into nearby Prospect Lake, the Capital Regional District (1987) installed parallel overhead wires across the active landfill site. The feeding activity of gulls there was consequently much reduced. The spacing of the wires above the landfill has been further reduced since the first year of installation, which further reduced feeding activity by gulls and eliminated the dropping of garbage at Prospect Lake. Only a handful of Glaucous-winged Gulls visit the active landfill site now, by walking to it beneath the wires. The program has one drawback: it costs \$10,000 a year to maintain the wiring system, as garbage trucks frequently snap wires (A.W. Summers pers. comm.).

Roof-nesting

Roof-nesting Glaucous-winged Gulls are a nuisance to humans, primarily due to their faeces falling on homes, automobiles and people. In addition, gulls nesting on private homes disturb the sleep of people by their loud calls in the morning. Roof-nesting gulls also cause chemical erosion of roofs by their faeces, and water damage by the blockage of drainage pipes by feathers and nest material. A new \$315,000 roof of a building was expected to last only half as long as originally planned because of chemical deterioration caused by the faeces of roof-nesting Glaucous-winged Gulls (Vermeer et al. 1988).

The problem with roof-nesting gulls will likely become larger if their numbers continue to increase. The high reproductive output of urban nesters, if maintained, will result in a large population increase of gulls along developed waterfronts (Vermeer et al. 1988).

Gulls can be discouraged from nesting on a roof by the installation of stainless steel wires or monofilament fishing lines a short distance above the roof (Blokpoel &

Tessier 1986). Although such a method would provide relief for an individual building, it would not prevent roof-nesting behaviour from becoming more widespread. The only means of completely solving the problem is to kill the adult gulls that nest on roofs.

Health risks

With the growth in Glaucous-winged Gull numbers visiting garbage dumps, sewage disposal sites, fish canneries, drinking water reservoirs, city roofs, city parks and other public places, gulls may increasingly become vectors in the dispersal of organisms harmful to human health. Patten & Patten (1983) reported that Glaucous-winged Gulls spending time at sewage outlets and fish canneries were implicated in the transmission of *Salmonella* spp. and in the dissemination of human cestode and nematode parasites. They also stated that gulls had been demonstrated to be susceptible to human influenza strains, and to display antibody titers to avian influenzas, Newcastle disease and toxoplasma. At present, the number of instances in which Glaucous-winged Gulls have been implicated as the actual carriers of any pathogen affecting a person is surprisingly small. Gulls are perhaps not a serious risk to human health or there may have been a lack of documentation of gull-borne pathogens affecting people. We recommend a study of gull-borne pathogens and their dissemination in the human environment.

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THE BLACK-HEADED GULL IN EUROPE

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ABSTRACT. Superabundance in the Black-headed Gull *Larus ridibundus* in Europe represents a textbook example of how human interactions with the environment in industrialized countries have had a paramount influence in some birds' recent demographic boom and range expansion. Increasing access to foraging grounds, utilization of new and artificial food sources, and protective measures changed its status during this century from a species at risk to the most abundant gull species in the Palearctic zone. A marked spread northward and a less pronounced spread towards the south, a redistribution within the breeding area, as well as a tremendous increase in numbers took place. In the last ten years, there have been signs that the breeding figures are beginning to level off. The species' superabundance creates only a few minor problems and its influence on other species is largely positive.

Keywords: Black-headed Gull, *Larus ridibundus*, range expansion, demography, superabundance, problems, Europe.

INTRODUCTION

The recent superabundance in the Black-headed Gull *Larus ridibundus** (hereafter BHG) has been largely the result of human activities as was the earlier decline of the species. Owing to the BHG's relatively small size, its superabundance has obviously created fewer problems (many of them, if not all, considered of minor importance) than those created by the larger-sized gulls (Vauk & Prüter 1987). It is the aim of this paper to review the current population trend and to discuss the different factors involved in this superabundance, as well as the few problems raised by the species' increase.

RANGE EXPANSION AND POPULATION INCREASE

The BHG is known to breed now in nearly all European countries (Figure 1). A survey in 1976 (Isenmann 1976, 1977) indicated that about 1,000,000 pairs bred in Europe (Baltic States included but not the rest of the Soviet Union). A more comprehensive survey in 1982 (Glutz von Blotzheim & Bauer 1982) indicated 1,570,000 breeding pairs in this area. Using the recent, more complete breeding figures for Bulgaria, Finland, Italy, Spain, The Netherlands, Turkey and Yugoslavia, the total figure for 1985-1989 is between 1,782,000 and 2,082,000 pairs. An unknown part of this overall increase may have resulted from more accurate censusing of the breeders in recent years in some countries. In Mediterranean Europe the status of the BHG has not markedly changed in recent years. Italy and Spain, both colonized since 1960, do not harbour more than about 800 and 1500 pairs respectively, and North Africa has not yet been colonized. Furthermore, it has recently established a small but geographi-

* *Footnote:* Common and scientific names follow Voous (1977).

cally widespread reproductive base in northeastern North America (Montevecchi et al. 1987).

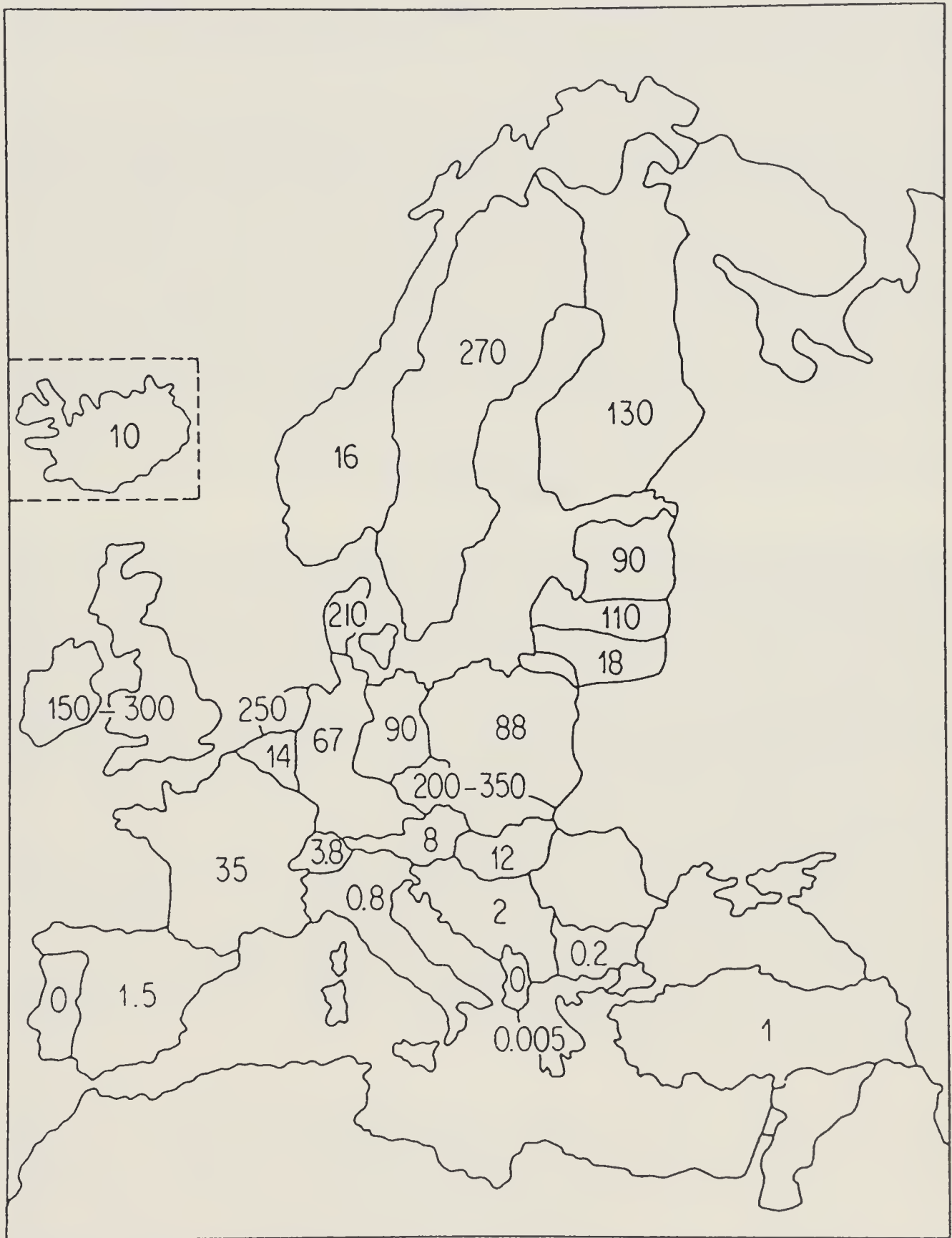


FIGURE 1 - Number of breeding pairs (x 1000) of Black-headed Gulls in Europe (1985-1989).

The spread and the increase were very impressive from 1950 to 1980, except in Denmark where a decline occurred at that time. In the last ten years, signs of a lower rate of increase or even of stability have appeared. For example the breeding figures remained stable between 1983 and 1988 in northeastern Germany (Arnold 1988 and

unpub. data). The species has also shown spectacular redistributions within its original breeding range, invading in huge numbers certain coastal areas (e.g. the coast of the North Sea and the Baltic) as well as inland areas (e.g. around reservoirs). Such colonization has compensated for the loss of natural wetlands, the species' original breeding habitat, through reclamation.

Some changes have also occurred in the wintering distribution. A slight tendency to winter at higher latitudes (owing to the availability of artificial food sources) has been suggested by Andersen-Harild (1971), who compared old (1920-1939) and recent (1959-1969) recoveries of birds ringed in Denmark. Ritter & Fuchs (1980) found the same trend for gulls breeding in Switzerland. The species has also extended its wintering range southward. The BHG is now regularly seen in Africa as far south as Gabon on the Atlantic coast, and Kenya and Tanzania on the eastern coast, and thrives along inland rivers in the Niger and Nile basins. A southward extension of the wintering range has also been observed in Asia where the species now winters abundantly in Hong Kong (Glutz von Blotzheim & Bauer 1982, Cramp & Simmons 1983).

DEMOGRAPHY

Little is known about the demographical processes which may have contributed to the increase in BHG numbers. Most published estimates of survival rates are based on analyses of recoveries of birds marked as chicks. After accounting for the most obvious bias (i.e. the fact that some birds are still alive at the end of the study period), the estimated annual survival rates come close to 0.8 for adults and to 0.4 for first-year birds (Lebreton & Isenmann 1976). Although these estimates are more compatible with population growth than earlier ones (e.g. 0.72 for adults in Britain, and 0.67 and 0.73 in two Baltic populations, reviewed by Lebreton & Isenmann 1976), simple demographic models show that they cannot explain the large-scale increase in numbers (Table 1). For instance, Lebreton & Isenmann (1976) concluded from such models that the rapid increase in the Camargue, southern France, required an adult survival rate of at least 0.84. This discrepancy is apparently due to the unreliability of survival estimates based on recoveries of birds marked as young (Anderson et al. 1985). In a study of the inland population of the Forez region in central France, Clobert et al. (1987), analysing resightings of birds marked as breeders, obtained an adult survival of 0.822 (SE 0.032), which might still be an under estimate (Pradel, Allainé & Lebreton unpub. data).

Most birds of the Baltic populations start to breed when two (females) or three years (males) old, with some variation between years (reviewed by Lebreton et al. 1990). Lebreton et al. (1990) showed that full breeding status in a large and successful colony of the Forez population is reached only at age five. Moreover, the local recruitment rate to this large colony was inversely related to the initial number of chicks in the cohort. This pattern is consistent both with the stabilization in numbers at a regional scale and with the adult survival rate mentioned above. Many birds are being forced to nest in poor quality sites because of the saturation of good quality habitats (Lebreton 1987).

The number of young fledged per pair has been determined in only a few studies. Published values show an average of 1.3 - 1.7 chicks per pair, but in some years good

colonies can produce two chicks per pair (Glutz von Blotzheim & Bauer 1982). Large-scale and long-term averages may well be lower. An adult survival rate in the range of 0.82 - 0.86 is plausible and may have led to rapid population growth with early successful reproduction (Table 1). The rate of increase is sensitive to adult survival because of the fairly long generation time (around six years) of the BHG (Lebreton & Isenmann 1976). Therefore a range of 0.82 - 0.86 for adult survival rate is needed to explain the large-scale increase. When reproduction is delayed and reproductive success lowered by density-dependent factors, an adult survival rate in the range of 0.82 - 0.84 would lead to stability in numbers (Table 1). The fragmentary demographic information available on the BHG can be summarized by the following scenarios:

- 1) Survival increased with an increase in human activities. Stabilization has recently been reached in some populations as a result of a decrease in reproductive output with no change in survival.
- 2) The same as under 1) but with a recent decrease in survival rate in some populations.
- 3) Survival has always been high. Natality was low because of human persecution and increased when persecution stopped. This has led to the observed increases in numbers.

Scenario 3 seems the least plausible, because great changes in natality, at a very large spatial scale, would have been needed to induce the observed changes in numbers. The example of the Forez population provides some limited evidence against scenario 2. So we believe that scenario 1 is the most likely.

TABLE 1 - Rate of change (in %) of a theoretical Black-headed Gull population, under various sets of demographic parameters (asymptotic rate obtained by a Leslie matrix model; see Lebreton & Isenmann 1976).

AGE-SPECIFIC PROPORTIONS OF BREEDERS		Recruitment at an early age			Recruitment at a late age				
		Age % br.	2 50	≥3 100	Age % br.	2 30	3 50	4 75	≥5 100
FECUNDITY		Low	Medium	High	Low	Medium	High		
Fledglings/pair		1.1	1.5	2.0	1.1	1.5	2.0		
SURVIVAL									
Low									
1st year	0.40	-3.4	1.2	6.4	-5.2	-1.5			2.6
>1st year	0.80								
High									
1st year	0.42	1.5	6.3	11.7	-0.5	3.5			7.8
>1st year	0.84								

The BHG shows a highly flexible generalist feeding strategy taking rapid advantage of a wide diversity of food sources. The superabundance of this species is probably the result of many factors. The major factor seems to be the various artificial food sources provided by man, especially in western Europe. This has buffered the impact

of fluctuating natural food sources and increased the overall food availability for this gull. Feeding on coastal mudflats, a previously rarely used habitat during the breeding period, has also greatly widened the species' feeding grounds.

Moreover, some of the new breeding habitats (e.g. sea coasts, salt pans, reservoirs) offer even better conditions for breeding than natural marshland habitats do. Furthermore, various protective measures have enhanced the species' breeding success and overall survival.

PROBLEMS OF SUPERABUNDANCE

On a local scale the superabundance of BHG can create problems. The most commonly cited inconveniences are the eutrophication of water around breeding colonies, the spread of diseases, nuisances to fish ponds, and various kinds of damage to agriculture (e.g. the species is thought to kill too many earthworms and damage hay) (Glutz von Blotzheim & Bauer 1982, Vauk & Prüter 1987). But these inconveniences were either largely overestimated or dealt with locally in a satisfactory way (Vauk & Prüter 1987). The BHG is frequently involved in collisions with aircraft. Routine bird-scaring operations at airfields are necessary to minimize this hazard to flight safety (L.S. Buurma unpub. data).

The influence of the gulls on other bird species, especially in the recently invaded sea coast habitats, has frequently been studied because the BHG can compete for available nesting space (reviews in Glutz von Blotzheim & Bauer 1982, Vauk & Prüter 1987). Locally, it may even become a predator of eggs and young, or klepto-parasitize feeding adults of other species. However, Becker & Erdelen (1987) found no direct influence of the BHG increase on the numbers of other species, especially terns (*Sterna* spp.), along the German North Sea coast.

The interspecific conflicts noticed here and there, are largely balanced by the BHG's role in attracting other species such as the Sandwich Tern *Sterna sandvicensis* (Veen 1977), the Black-necked Grebe *Podiceps nigricollis* (Trouvilliez 1988), and ducks that settle in the neighbourhood of gull colonies, and have enhanced breeding success as a result. If local culling is nevertheless deemed necessary, it must be done with caution and only where the superabundance of the BHG really becomes a serious problem for other species. Finally, the superabundance of the BHG has no dramatic consequence either for man or for other bird species. There is no need for further concern as the population of the species is showing the first signs of stability.

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THE SILVER GULL IN AUSTRALIA AND NEW ZEALAND

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ABSTRACT. The Silver Gull *Larus novaehollandiae* is becoming more abundant throughout most of its range, especially in the urban areas of south-eastern Australia. Increased foraging at refuse tips and sewage treatment plants has been associated with a decrease in natural mortality. Fresh water appears to limit their range within Australia and all major colonies are situated close to the reservoirs of large cities. Silver Gulls pose potentially serious threats to human health via the transmission of *Salmonella* spp. and through congregating on airfields. A coastal scavenger, the Silver Gull is a persistent predator of some nesting seabirds. Scaring techniques and culling adults with narcotic baits (alpha-chloralose) are the commonest local control measures, but changes in waste disposal techniques are required for long-term control.

Keywords: Silver Gull, *Larus novaehollandiae*, abundance problems, Australia, New Zealand.

INTRODUCTION TO THE SPECIES

Dwight (1925) listed five geographical subspecies of the Silver Gull: *Larus n. novaehollandiae* of southern Australia, *L. n. gunni* of Tasmania, *L. n. forsteri* of New Caledonia and northern Australia, *L. n. scopulinus*, the Red-billed Gull of New Zealand, and *L. n. hartlaubii*, Hartlaub's Gull of south-western Africa. Other authors recognise Hartlaub's Gull as a full species due to its geographical isolation and different colouration and the same may hold true for the Red-billed Gull in New Zealand (Johnstone 1982).

The Silver Gull is common in coastal regions throughout its range and usually breeds on coastal islands (Gurr & Kinsky 1965; Blakers et al. 1984). Recently, increased breeding numbers and decreased natural mortality have been linked with the availability of urban waste (Skira & Wapstra 1990).

FOOD HABITS AND DISPERSAL

During the breeding season there are major differences in the feeding ecology of Australian and New Zealand populations. Most gulls at colonies in New Zealand eat krill *Nyctiphanes australis* (Mills 1969) and only 6% of their diet is human refuse and fishery waste. In contrast, gulls nesting in Australia appear largely dependent on food from human sources, although, as in southern Africa (Ryan 1987), clutch initiation often coincides with peak abundance of small invertebrate prey emerging from stranded kelp (Dunlop 1986). Outside the breeding season, Australian and New Zealand gulls feed opportunistically at both artificial and natural sites, such as garbage dumps, sewage outfalls, coastal mudflats and tidal beaches.

Australian Silver Gulls do not migrate but disperse from their breeding colony to habitats providing ample food and freshwater during the long, dry summer months. Most banded birds are recovered within 30 km of the coast (Ottaway et al. 1988). Silver Gulls usually return to their natal colony to breed (Mills 1973).

POPULATION TRENDS AND EXPLANATIONS

In New Zealand, Gurr & Kinsky (1965) conservatively estimated the breeding population of Silver Gulls at 40,000 pairs (Figure 1). Individual colonies have generally increased since the 1960s. However, the Kaikoura population, which by 1969 had doubled over 15 years to 5,700 pairs, is now stable at around 6,000 breeding pairs (Mills 1973, unpub. data). At this colony there are an equal number of non-breeding adults, mostly females (Mills 1989). Conversely, gull populations in Wellington Harbour decreased 50% between the mid-1960s and the mid-1970s, when the dumping of food waste into the sea from meat and fish processing works stopped, remaining stable thereafter (Mills unpub. data).

In Australia, the largest gull breeding colonies occur near major cities (Figure 1). New colonies are becoming established upon man-made areas, and the highest densities of gulls, during both breeding and non-breeding seasons, occur in coastal areas disturbed by human activities. Cities where human-generated food is readily available, provide major feeding areas for Silver Gulls (Ottaway et al. 1988). Although Silver Gulls can fly 80 km per day to feed (van Tets 1969), few do so. Near Melbourne, hundreds of birds move daily 25-50 km from the coast to feed at inland dumps (Blakers et al. 1984).

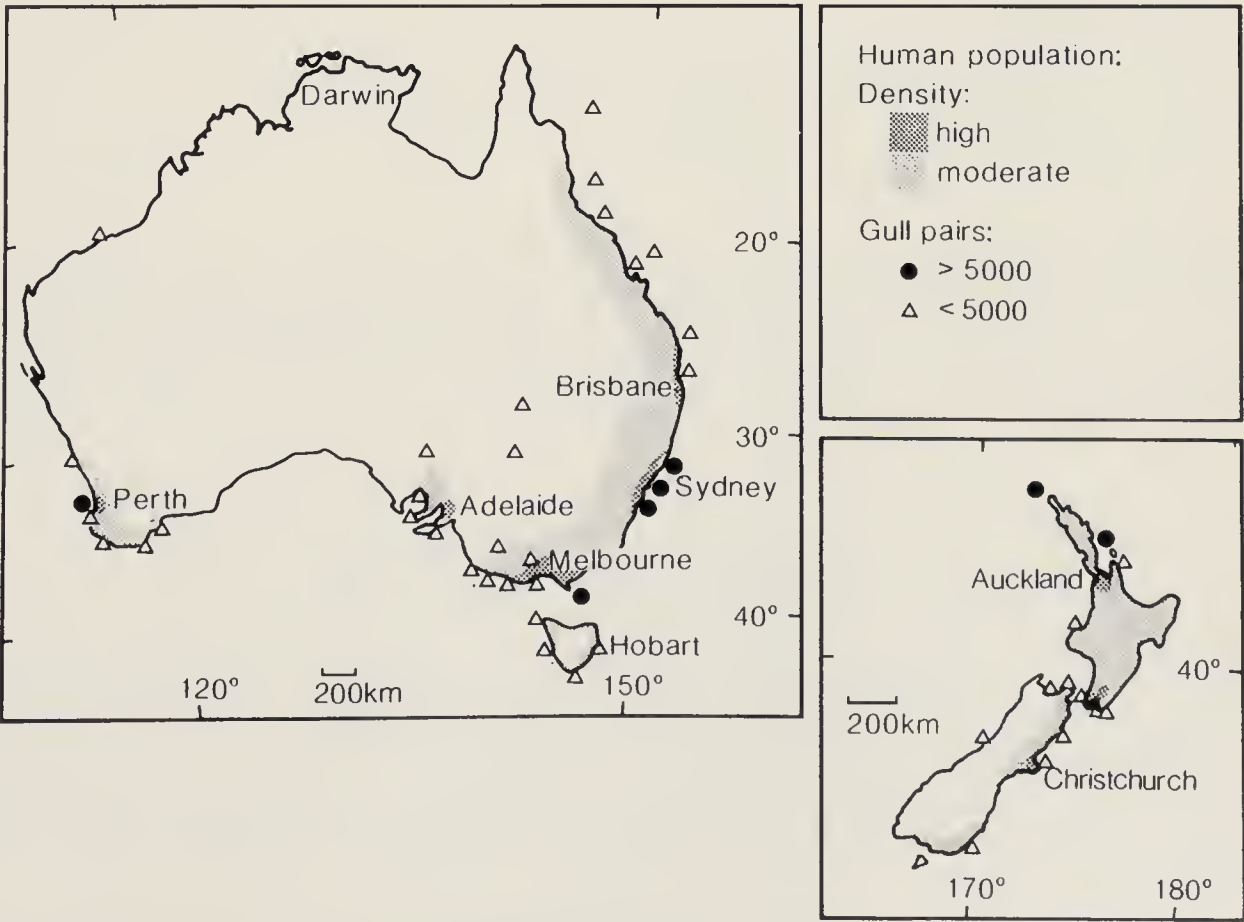


FIGURE 1 - Location of nesting colonies of Silver Gulls in relation to human population density in Australia and New Zealand.

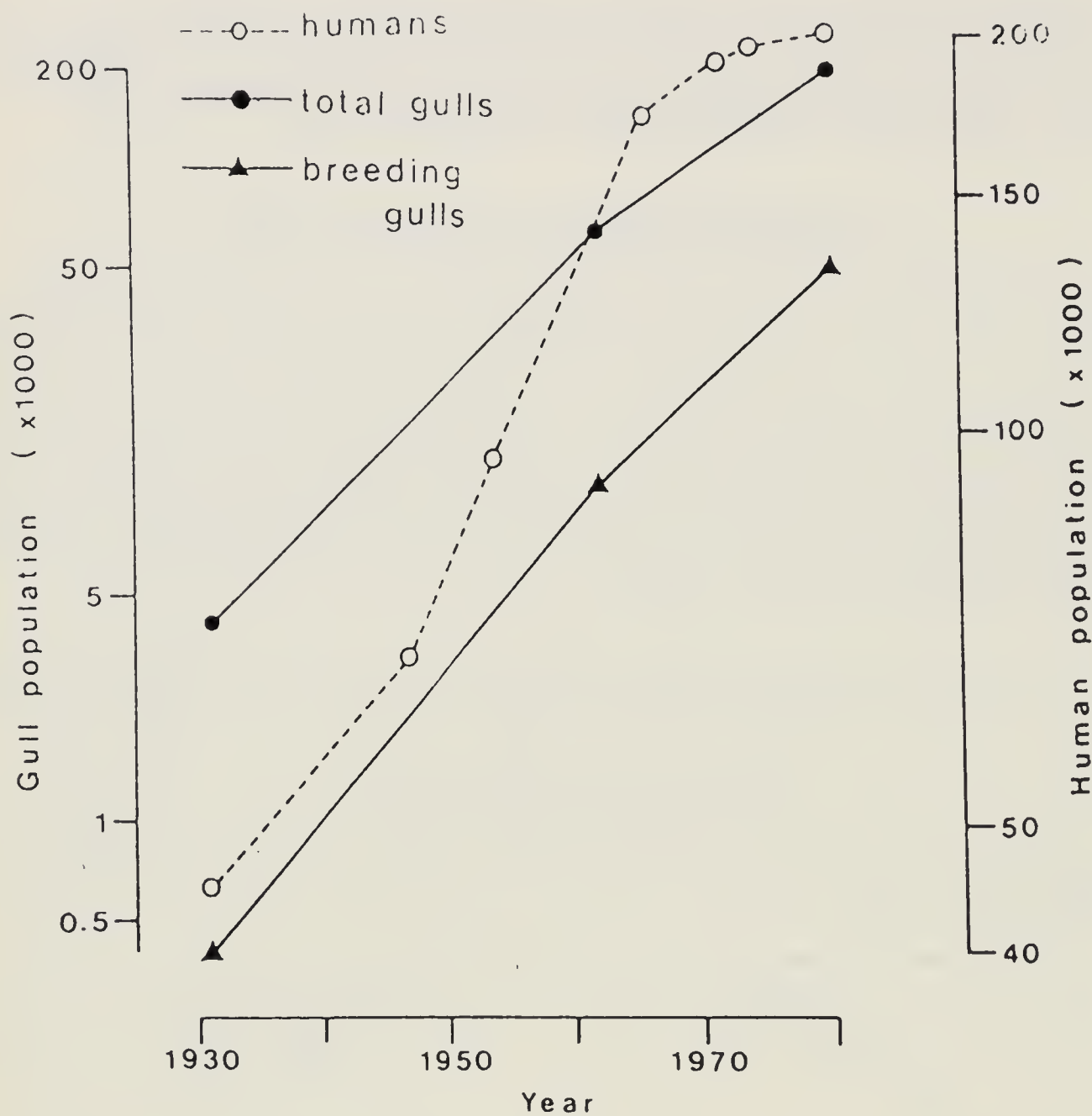


FIGURE 2 - Changes in the resident human population in the Wollongong and Port Kembla region (---○---), the total gull population (---●---), and the gull population breeding on the Five Islands group (---▲---), south of Sydney, Australia, from 1930 to 1980 (after Gibson 1979).

The few data available suggest that Australian Silver Gull populations are increasing at a rate similar to that of gulls elsewhere (e.g. 10-13% yearly). At the Five Islands group, south of Sydney, numbers increased from fewer than 1,000 pairs in 1940 to 51,500 pairs in 1978 (Figure 2; Gibson 1979). In 1990, there are estimated to be more than 80,000 breeding pairs around Sydney (G.C. Smith pers. comm.). At the Mud Islands, near Melbourne, eight pairs in 1959 (Wheeler & Watson 1963) had increased to an estimated 50,000 breeding pairs in 1984 (I. Temby pers. comm.). Such increases in Australia are almost certainly the result of increased putrescible waste, foraging in pastoral regions, and the advent of freshwater irrigation and reservoirs.

The link between increasing gull numbers and human activity is particularly evident in remote Australia. The gull population on the Capricorn-Bunker Islands group of the

Great Barrier Reef north of Brisbane is considered to be unnaturally high because, although these gulls scavenge fishing offal, 75% of their diet is food-waste generated by tourists from the nearby holiday resort of Heron Island (Walker 1988; P. Ogilvie pers. comm.). Figure 3 shows the relationship between gull and tourist numbers. Similar correlations between human and gull numbers have been reported by Burbidge & Fuller (1989) in the Abrolhos Islands, off central Western Australia, and by McKean (1981) in Darwin, Northern Territory.

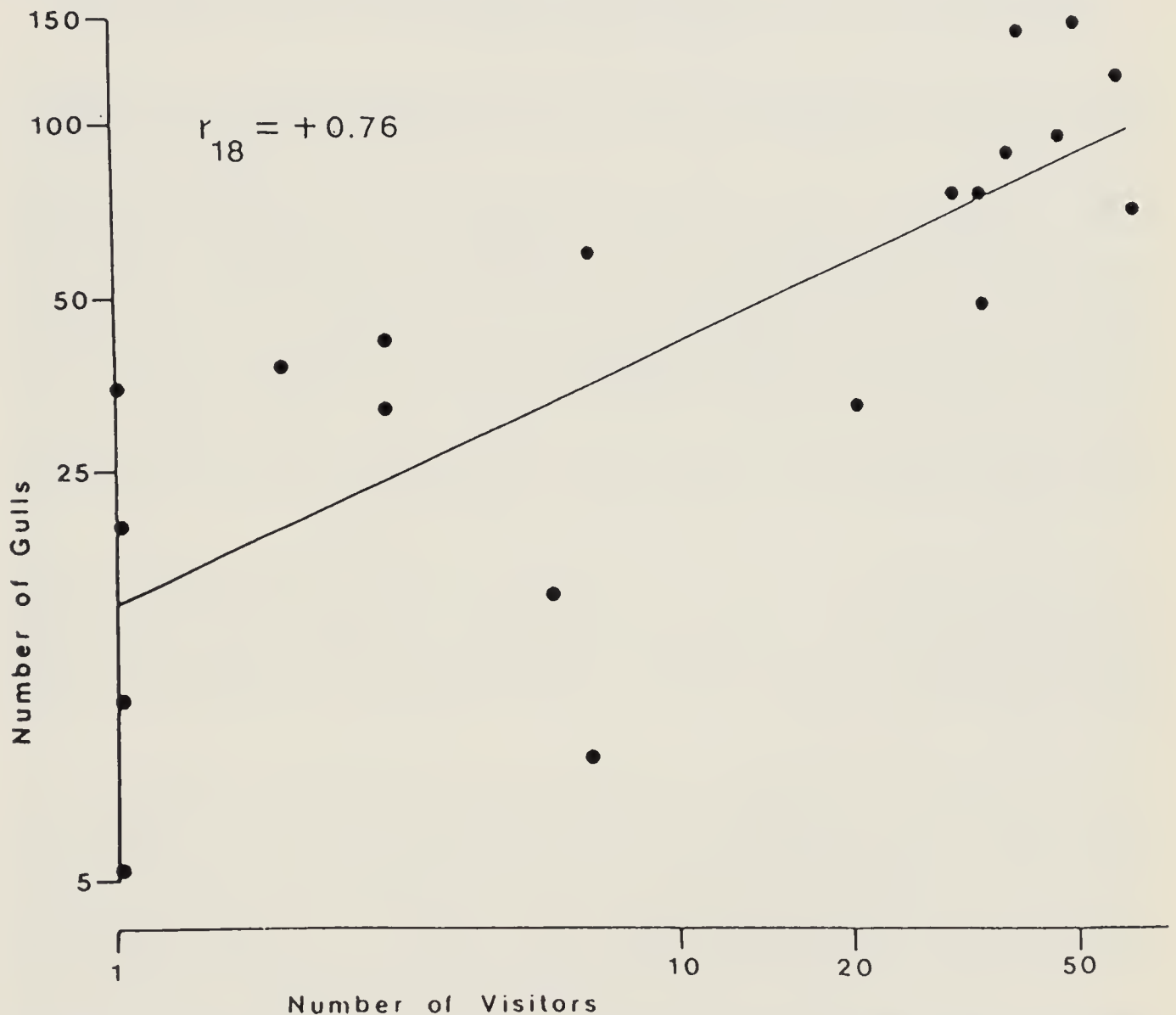


FIGURE 3 - The daily numbers of non-breeding Silver Gulls on a Great Barrier Reef island in relation to the numbers of people present (after Walker 1988).

REPRODUCTION AND MORTALITY

Underhill & Underhill (1986) calculated the average mortality of the subspecific Hartlaub's Gull between chick banding and first-nesting to be 60%. Assuming that survival rates are similar for Silver Gulls and Hartlaub's Gulls, and that most birds breed first aged three to five and produce an average clutch of 2.5 eggs (Mills 1973, Ottaway et al. 1988), with a probability of survival to first breeding of 0.4, then the mean number of young produced per pair per year is 1.0. This relatively low reproductive rate is probably offset by the long breeding lifespan of Silver Gulls, estimated at five to ten years (Wooller & Dunlop 1979).

In Australia, the natural mortality of Silver Gulls, both adult and juvenile, is greatest during the long, hot and dry summer (van Tets 1968). The lack of freshwater causes shortages of natural food. The remarkable behavioural flexibility of Silver Gulls has offset their natural mortality rates by utilising year-round supplies of human sewage, rubbish and freshwater.

PROBLEMS AND SOLUTIONS OF INCREASING SILVER GULL ABUNDANCE

We estimate the breeding population of Silver Gulls in Australia and New Zealand at roughly 250,000 breeding pairs, giving a total population of around 800,000 gulls.

Viewed as pests in Australia, gulls may ingest pathogens, such as *Salmonella* spp., at tips and outfalls so that carriage rates are higher in areas of high human population density (Iveson 1979). Roosting on inland waters, including water supply reservoirs, means that gulls are potential vectors of food poisoning in humans. In Western Australia, Iveson (1979) isolated 37 *Salmonella* serotypes from gulls, but concluded that "Silver Gulls are the unwitting victims of human environmental degradation, and no substantial evidence exists to implicate them as a major public health hazard". Solutions to disease transmission include covering sewage treatment plants and improved rubbish disposal (e.g. relocating tips away from reservoirs and baling or covering garbage), but expense often limits their implementation.

Silver Gulls have been viewed as a threat to human life due to their habit of foraging and roosting on airfields, particularly in Tasmania, where gulls nest on man-made causeways beside the Hobart airport (Skira & Wapstra 1990). In Melbourne, up to 32,000 gulls have been seen daily at five rubbish tips adjacent to the airport (I. Temby pers. comm.).

Sydney Airport was an ideal gull habitat created by humans (van Tets 1969). An average of 10,500 gulls visited the airfield during a six month period in 1964/65 (van Tets 1969) but, after habitat modification, numbers dropped to around 2,600 gulls by 1968. This decrease was achieved not by culling adults with alpha-chloralose, a technique used earlier by Caithness (1968) in New Zealand, but rather by limiting food sources. Improved drainage, frequent mowing, insecticide, closure of one tip and covering of another all helped to reduce aircraft strikes by gulls, but only after gull numbers had declined by 80% (van Tets 1969).

Direct competition for nesting space and food may occur between Silver Gulls and species with similar nesting or feeding requirements, including White-faced Storm Petrels *Pelagodroma marina* in New South Wales (Gibson 1979) and Crested Terns *Sterna bergii* in Western Australia (Wooller & Dunlop 1979). In New Zealand, Mills (1973) reported Silver Gulls preying on White-fronted Tern *Sterna striata* eggs and chicks and, occasionally, scavenging food from sympatrically breeding seabirds.

Attempts to control breeding gulls by lowering their reproductive output are likely to have only limited, short-term success because Silver Gulls are long-lived with a low annual reproductive rate. Their deferred maturity and the large pool of non-breeding, potential recruits in populations means that culling must be continuous to be effective. A culling programme in Tasmania, using alpha-chloralose only decreased the

breeding population for a relatively short period (Skira & Wapstra 1990). If the numbers of Silver Gulls are perceived as too high, the only long-term way to reduce numbers is effective control of waste disposal. As noted earlier, the prevention of waste discharge from fish and meat processing works has reduced the gull problem in New Zealand considerably. Direct control of Silver Gulls seems inappropriate for a native species (Anderson & Keith 1980), and may well be ineffective (Skira & Wapstra 1990).

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CONCLUDING REMARKS: SUPERABUNDANCE IN GULLS: CAUSES, PROBLEMS AND SOLUTIONS

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The five case studies from around the world reported in this symposium show that at present these species are superabundant and that most of these gull species pose problems to mankind and to other bird species. The studies show many similarities in population development, in problems caused by the gulls, and in solutions to solve these problems, despite the fact that these species occur in very different parts of the world.

CHANGES IN GULL POPULATIONS

The present situation of superabundance in the five species dealt with here follows a period in which the gulls have exponentially increased in numbers. For all the species it is assumed that present numbers are much higher now than they have ever been before. Overall numbers of Glaucous-winged *Larus glaucescens*, Ring-billed *L. delawarensis* and Silver Gull *L. novaehollandiae* are still continuing to grow, although locally numbers of Glaucous-winged and Silver Gull have stabilised. However, in the Black-headed Gull *L. ridibundus* overall numbers have recently levelled off and in the Herring Gull *L. argentatus* they have even started to decline.

For all species there is good evidence that the increase of food directly or indirectly provided by man is, or has been, the prime factor for the high level to which the birds could increase. However, little is known about the changes in adult mortality and survival of young to breeding age since the time that gulls began to use anthropogenic food sources to a great extent. The underlying demographic processes for the observed increases in gull numbers since then are therefore not well-known.

The causes of stabilisation of Black-headed Gull numbers and the decline of Herring Gull numbers are not known at present, but the models presented in the symposium suggest that stabilisation in numbers resulted from a severe reduction in offspring production rather than from an increase in adult mortality. One may speculate whether the observed population changes in these two species reflect recent changes in the disposal of human refuse and sewage in Europe. For example, in west Germany and in The Netherlands there has been a pronounced drop in the numbers of open garbage dumps and a great improvement in the treatment of sewage water during the last 10-20 years (Prüter & Spaans unpub. data). In the modelling study of a Herring Gull colony in Brittany, France, it was shown that a drop of 66% in reproductive success was related to a 80% decline in the availability of food at a nearby garbage dump when this dump was converted to an incinerator, and that this reduction in reproductive success was indeed sufficient to stabilise the colony size.

To account for the present decline in Herring Gull numbers in Great Britain, much larger changes in the population dynamics must have occurred. A reduction by at least two-thirds in the number of young surviving to breeding age, or a tripling of adult mortality, or some combination, would be required to give the present decline of about 3-4% per annum in the British population (Monaghan unpub. data).

PROBLEMS AND SOLUTIONS

The problems which are caused by the five gull species generally fall in the same categories. In most species they are a matter of serious concern. Generally speaking, the larger the population of both gulls and humans in a certain area, the greater is the chance that conflicts will arise. Of the various gull problems, collisions with aircraft and the spread of pathogens probably have the most serious consequences for humans. Gulls are often involved in bird strikes because they frequent airports, fly in groups, and, as slow flyers, often are unable to get out the way of approaching aircraft. All five gull species appear to be carriers of pathogens of human beings and domestic animals, suggesting that all over the world gulls, as transmitting agents for such pathogens, constitute a health risk.

Many problems which are caused by gulls are directly related to the wasteful lifestyle and unsanitary waste disposal methods in the rich countries. People in these countries will therefore be faced with gull problems as long as the abundance of human refuse will continue.

From a wildlife conservation point of view, gull predation on eggs and chicks of other bird species is relatively minor in all five species, but encroachment by Ring-billed and Herring Gulls on nesting habitats of terns *Sterna* spp. is of serious concern.

In the last five decades, wildlife agencies in different parts of the world have tried to reduce numbers of gulls by region-wide culls at breeding sites under the assumption that fewer gulls would mean fewer gull problems. Although such culls sometimes significantly reduce local numbers, overall numbers usually remain the same because potential recruits settle to a greater extent elsewhere. Moreover, to keep numbers depressed at treated sites, intensive culls have to be carried out annually. In Europe, a public outcry followed large-scale cullings of Herring Gulls, with the result that at present culls are carried out only at certain locations and only in exceptional situations.

Superabundance in gulls is primarily caused by the superabundant food supply resulting from human activities. A long-term reduction in gull numbers can therefore probably be achieved only when people are seriously willing to reduce the amount of food that becomes available through waste disposal, sewage outflows, fisheries, etcetera. However, as pointed out by Meathrel et al. in this symposium, high costs often limit the implementation of radical changes in waste disposal practices. Nevertheless, locally some progress has been made in recent years. Where waste disposal methods are changed, local problems are solved almost overnight. On the other hand, as long as the amount of human-generated food remains available to gulls, people must learn to live with a superabundance of gulls in the human landscape, and people must be prepared to continue to tackle problems on a site-by-site basis. Good planning of human activities can help prevent conflicts between humans and gulls.

Methods used on a site-by-site basis are of the same types for the five species and include those that exclude birds from areas where they are not wanted, scaring gulls from sites, and prevention of reproduction. Methods for excluding birds, such as a mobile cover net or an overhead barrier of wires or monofilament lines appear to be the most effective. However, the need to move net or wires at refuse tips can give problems, and lines easily snap. At some airfields, sizable improvements have been obtained by habitat modification. At airfields where gulls remain a problem, scaring techniques are to be applied. Because birds easily habituate to the various scaring devices, they should be used in different combinations to maximise their effectiveness. Nevertheless, occasionally a few gulls may have to be shot, in order to prevent habituation. The success of scaring actions varies and depends not only on the local situation but also on skills and motivation of the people who carry out the control program. Success will be greater when nearby alternative sites for the gulls are available. Collecting eggs is currently used to discourage gulls from breeding, and oiling eggs is used to prevent reproduction. The success of large-scale egg-collections is rather species-specific. Black-headed Gull colonies can be relocated rather easily by this method, even when colonies are large, whereas this method is less effective against Herring Gulls. At large colony sites, Herring Gulls, whose eggs are collected en masse, tend to disperse to nearby areas. Thus problems are spread rather than eliminated.

CONCLUSIONS

Due to the on-going changes in gull populations, there is a continuing need for monitoring gull numbers over large areas and for ecological studies to determine the various demographic parameters required for population modelling.

In addition, in many cases better documentation of gull problems is required. There is also a need for improving and refining gull control methods, and for monitoring their effectiveness and side-effects.

The various control methods reported in the symposium papers are at best rather temporary solutions. More permanent solutions can only be achieved by dealing with the underlying cause of all problems, i.e. the superabundance of food. This superabundance of food is related to the wasteful lifestyle of man in the rich countries dealt with in this symposium.

As long as large amounts of food continue to be available in these countries, people will have to face up to gull problems.

SYMPOSIUM 45

**CONTRIBUTIONS OF CAPTIVE BREEDING
TO THE CONSERVATION OF
ENDANGERED SPECIES**

Conveners F. J. CUTHBERT and D. M. BIRD

SYMPOSIUM 45

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INTRODUCTORY REMARKS: CONTRIBUTIONS OF CAPTIVE BREEDING TO THE CONSERVATION OF ENDANGERED SPECIES

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Loss of global biological diversity has been a major conservation issue for the later part of this century. Currently we are challenged to the task of large scale protection and management of the earth's living resources combining two imperatives: development and conservation. There presently are numerous small populations of birds in the world, both in the wild and in captivity, that are surviving on the edge of extinction. In many cases these populations could be restored to non-endangered status if reliable techniques were available to increase populations size, to reintroduce birds to historically used habitat or to establish entirely new populations at alternative locations. Captive breeding has been used extensively as a primary tool to enhance small populations of birds (e.g Conway 1977, 1989, Wemmer & Derrickson 1987, Griffith et al. 1989). During the past several decades, these research efforts have proliferated and advanced in sophistication as investigators all around the earth have struggled to prevent extinctions. The purpose of this symposium is to examine some of these studies to evaluate the contribution of captive breeding to endangered species conservation, to provide general guidelines for successful captive breeding efforts, and to identify directions for future research.

To demonstrate the breadth of this area of avian research, symposium participants summarize a diversity of programs. S. Derrickson will discuss the prospects and problems of reintroducing captive-bred birds back into the natural environment and S. Haig will summarize work on captive management for genetic demographics. Two presentations will focus on the role of captive breeding in two long-term large-scale species recovery efforts, the Whooping Crane captive breeding programme (D. Ellis, G. Gee, and D. Smith) and the California Condor project (M. Wallace). The final paper (A. Powell) will examine early experience in captive-reared shorebirds.

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PROSPECTS AND PROBLEMS OF REINTRODUCING CAPTIVE-BRED BIRDS

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ABSTRACT. Reintroduction of captive-bred birds can be an integral component of recovery programs when conventional and more cost-effective measures are unavailable. Reintroduction should be undertaken as soon as possible following program initiation, and should complement rather than compete with other recovery activities. Successful reintroduction depends upon: (1) knowledge of key biological factors in the wild and captive environments; (2) adequate numbers of genetically diverse founder stock; (3) genetic, demographic and behavioural management; (4) effective disease/parasite screening and control; (5) adequate production of birds suitable for release; (6) development and refinement of pre- and post-release training, monitoring and management procedures; (7) continuity of staffing, administration and funding; and (8) effective public education. Post-release survivorship of captive-bred birds is normally enhanced by "soft" release procedures, such as supplemental feeding and predator training, which facilitate transition from the captive environment to the wild.

PAST AND POTENTIAL CONTRIBUTIONS OF CAPTIVE BREEDING TO POPULATION RECOVERY OF THE WHOOPING CRANE

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ABSTRACT. A captive Whooping Crane colony was established at the Patuxent Wildlife Research Center in Maryland in 1966. This colony first produced eggs in 1975 and has produced 252 eggs through 1990. From 1976 to 1984, 73 eggs were sent to Grays Lake, Idaho, the site of the first Whooping Crane reintroduction attempt. Canada also provided 216 eggs (1976-1988) from the wild population. Although 84 chicks fledged, the egg transfer program has been discontinued because of inordinately high mortality and lack of breeding. In recent decades, several new methods have emerged for introducing captive-produced offspring to the wild. The largest introduction effort involves the rearing of Mississippi Sandhill Cranes, either by captive Sandhill Crane foster parents, or by costumed humans in close association with live cranes and with taxidermy mount feeding models and brooder models. These two techniques have resulted in high post-release survival rates and will likely be used in future Whooping Crane reintroduction programs. Current recovery objectives for the Whooping Crane include the establishment of three captive colonies and the building of two other wild populations. A full-scale reintroduction effort (at least 20 birds/year) is scheduled to begin at the first site (Florida) with birds reared in 1994 or 1995.

Keywords: Whooping Crane, *Grus americana*, recovery, captive breeding.

INTRODUCTION

Whooping Crane population decline

Historically, the breeding range of the Whooping Crane *Grus americana* extended from Iowa northwest through Minnesota and the Dakotas into Alberta, Saskatchewan, and southern Manitoba (Allen 1952). In 1939, a small, widely disjunct population was also found breeding in the marshes north of White Lake, Louisiana (Lynch 1984). In the 1800's, a combination of habitat destruction, human disturbance, hunting, and egg and specimen collection for museums and private collectors contributed to a rapid population decline (Allen 1952). In 1945, the population consisted of two disjunct flocks totalling about 21 birds (Figure 1, U.S. Fish and Wildlife Service 1986). Following this nadir, the Whooping Crane population began its slow recovery.

PATUXENT'S CAPTIVE COLONY

The ponderous expansion of the Whooping Crane population in the 1940's and 1950's prompted captive breeding attempts (McNulty 1966). Lynch (1956) proposed that a sizeable captive flock be established by removing progeny from pairs breeding in Wood Buffalo National Park (Wood Buffalo) in Canada. Hyde (1957) noted that Sandhill Cranes and Whooping Cranes usually laid two eggs but rarely raised two young. He suggested that a captive flock could be established without detriment to the wild population by removing one egg from each clutch. Erickson (1968) recommended that the idea first be tested by developing a surrogate flock of nonendangered Sandhill

Cranes. In the early 1960s, this surrogate flock was built in Colorado. In 1966, the surrogate flock and Canus, a flightless male Whooping Crane recovered in Canada in 1964, were moved to Patuxent Wildlife Research Center (Patuxent) in Laurel, Maryland. In 1967, the second eggs from six nests in Wood Buffalo were taken to Patuxent. Egg taking has continued sporadically ever since, with eggs going either to Patuxent or to Grays Lake National Wildlife Refuge (Grays Lake), Idaho, or, more recently, to the International Crane Foundation (ICF), Baraboo, Wisconsin.

In 1975, the first eggs were produced by captive females at Patuxent. Thereafter, problems with artificial insemination, incubation, and chick rearing were identified and solved, and annual productivity increased accordingly (Kepler 1977, Gee 1978, Archibald 1974). Between 1975 and 1990, the Patuxent flock produced 234 potentially fertile eggs (of 252 total eggs), of which 73 were transferred in an attempt to establish a second wild flock at Grays Lake. In November 1989, 22 birds, representing all families in the captive flock, were transferred to the ICF. A third captive flock is also being planned for the Calgary Zoo in western Canada (Cooch et al. 1988).

REINTRODUCTION ATTEMPTS

The first attempt, translocation of a single bird

By 1947, only one wild bird remained in the marshes near White Lake, Louisiana (McNulty 1966, Doughty 1989). On 11 March 1950, this crane was captured by helicopter and translocated by truck to join the flock wintering at Aransas National Wildlife Refuge (Aransas). The crane survived through the spring and summer but was found dead in September.

The Grays Lake experiment

The only reintroduction effort, so far attempted, consisted of placing nearly 300 Whooping Crane eggs in Greater Sandhill Crane *G. canadensis tabida* nests at Grays Lake. This experiment was designed to create a disjunct population of Whooping Cranes that, like their Sandhill Crane foster parents, would nest in Idaho and winter along the Rio Grande in west-central New Mexico (Drewien & Bizeau 1978).

According to plan, the Sandhill Crane foster parents incubated the eggs and reared the young Whooping Cranes that hatched. The chicks also accepted their foster parents and followed them on migration. However, only 209 (72%) of the 289 Whooping Crane eggs transferred to Grays Lake hatched, and only 84 (40% or 29% of the original 289) of these young fledged. High egg and chick mortality rates were associated with inclement weather and coyote *Canis latrans* predation (Drewien & Bizeau 1978, Drewien et al. 1985). Many fledged birds died from powerline strikes (Brown et al. 1987) or avian tuberculosis (Doughty 1989). Recruitment has not kept pace with mortality, and the Grays Lake Whooping Crane flock has declined from a high of 33 birds in 1984-85 to 13 birds in 1990 (Lewis 1990).

Few females reached breeding age and those that did failed to pair with males on the wintering grounds and scattered on northward migration, thereby further diminishing their chances of finding mates. Because no pairing occurred naturally, two Patuxent-reared females were introduced to males at Grays Lake in 1981 and 1989. Both females formed temporary pair bonds with wild males, but neither experiment resulted

in eggs, or in pairs that migrated south together (Drewien et al. 1989). Due to these unfavorable demographic trends, the Grays Lake experiment is being phased out.

CHOOSING FUTURE REINTRODUCTION SITES

Preferred reintroduction sites should: 1) provide extensive suitable habitat, 2) be at a considerable distance from other wild populations, 3) for the next attempt, be at a latitude and location that would not require introduced birds to migrate, and 4) be within the historic range of the species. For biological reasons, the marshes north of White Lake in southern Louisiana are a favored choice for reintroduction of a sedentary population. It seems logical to return the birds to the wild where they most recently lived. The creation of a nonmigratory population is also preferred because of experience gained from the Grays Lake experiment and the increased risks during migration, wherever it occurs.

During the last decade, White Lake appeared to be unavailable as a reintroduction site because the state wildlife management agency disfavored the idea (Lewis pers. comm.). As a consequence, three other sites were considered: the Kissimmee Prairie in central Florida, the Okefenokee Swamp in southeastern Georgia and the Seney National Wildlife Refuge on the Upper Peninsula of Michigan. Habitat is believed to be favorable at all three sites. All areas have extensive wetland, are somewhat removed from urban areas, and support sizeable Sandhill Crane populations. Whooping Crane breeding, however, has never been documented for any of the three areas. In 1988, the U.S. Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS) decided to proceed with a Whooping Crane introduction experiment in Florida. Unfortunately, the region poses considerable risk of Eastern Equine Encephalitis (EEE) and Venezuelan Equine Encephalitis. An initial release of about nine young Whooping Cranes, scheduled for 1992, will assess this danger.

REINTRODUCTION TECHNIQUES

Reintroduction techniques for fledged cranes were described by Derrickson and Carpenter (1983), Konrad (1976), Nagendran and Urbanek (in prep.), and Ellis et al. (in prep.) and are outlined below. Some or all of these techniques will likely be employed in future Whooping Crane introduction attempts.

Pairing of captive and wild cranes

In Hokkaido, Japan, flightless male Red-crowned Cranes *G. japonensis* have lured females into their enclosures. The resulting pairs produced chicks that fledged into the wild flock (Konrad 1976). Occasionally, captive cranes of other species have lured wild mates (Hyde 1957, Archibald pers. comm.), and the technique, although logistically difficult with a large number of birds, appears to hold promise for forming small numbers of pairs.

Abrupt releases

The first controlled release of captive-reared cranes occurred in 1971 when 14 Florida Sandhill Cranes *G. c. pratensis*, which had been reared at Patuxent, were transported to a site near Lake Okeechobee, Florida, and released without acclimation. None of

13 hand-reared birds integrated into the wild flock, and within a few months all had died of exposure, starvation or accident (Nesbitt 1978). The single crane in this release, that had been reared by foster parents, survived three years.

During and following the experiments with hand-reared cranes in Florida, abrupt releases of parent-reared Greater Sandhill Cranes were attempted at Grays Lake in 1976 ($n=1$) and 1980 ($n=11$). Of eight young that survived to migrate south, none reappeared at Grays Lake the following spring (Drewien et al. 1981). These results, especially when compared with results from the gentle releases described next, further demonstrate the need for pre-release conditioning at the release site.

Gentle releases of parent-reared cranes

In gentle releases, cranes (normally juveniles) are brailed (i.e. rendered temporarily flightless) then confined in large pens at the release site for about 30 days. They are then debrailed and allowed to come and go at will for a period of months. During this time, food is constantly available, and each crane weans itself from the artificial food source at its own rate.

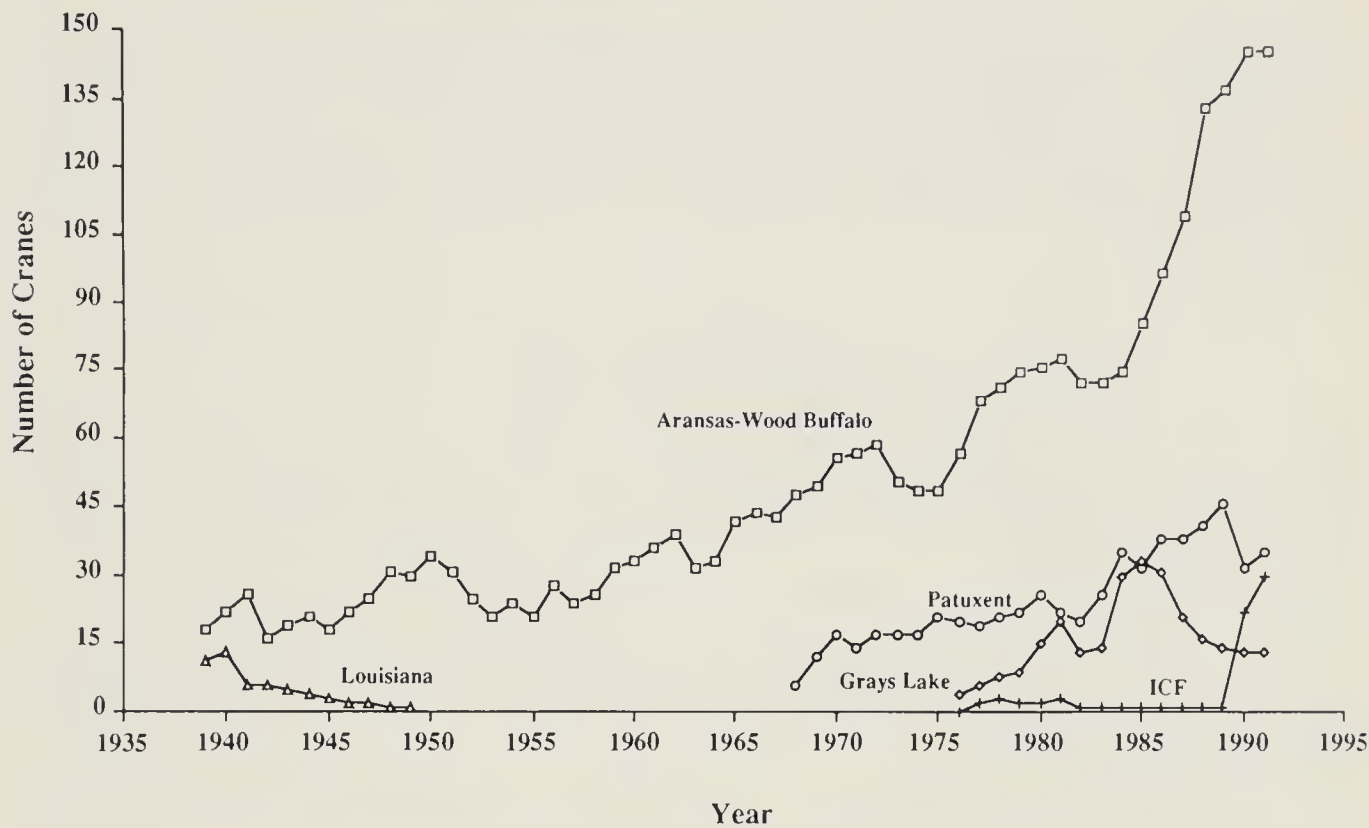
Since 1981, a number of gentle releases have been made with cranes parent-reared at Patuxent. The highest survival rates have been achieved in Patuxent's extensive program of releasing parent-reared Mississippi Sandhill Cranes *G. c. canadensis*; two-thirds (67 of 97) of the birds released from 1981 through 1989 survived for at least one year (McMillen et al. 1987, Zwank & Wilson 1987, and unpub. data), and at least 30 of 67 birds released from 1981 through 1988 have survived at least two years (Ellis et al. in prep.). All birds surviving more than a few months have successfully integrated into the wild flock. During the last five years, at least 13 captive-reared Mississippi Sandhill Cranes have paired or bred in the wild.

Gentle releases of hand-reared cranes

Various attempts have been made to rear and/or release hand-reared cranes that were held in some degree of isolation from their human caretakers (Archibald & Archibald 1991, Horwich 1986, Nagendran 1989 unpub., Urbanek 1989a unpub., 1989b unpub., and Ellis et al. in prep.). In the 1960s, silhouette heads were first used at Patuxent to train chicks to feed. Today, chicks are fed using a terry cloth puppet (ICF and Michigan) or a taxidermy mount (Patuxent). In addition, some chicks are penned in visual and auditory (but not physical) contact with adult cranes. Some chicks are also led afield by a costumed human to learn to forage for natural foods.

Fledged birds from releases in Wisconsin, Michigan, and Mississippi have had high survival rates, many have effectively socialized, and at least two birds have paired with wild cranes (Urbanek 1989a unpub., Urbanek & Bookhout 1987 unpub., Archibald, pers. comm.). Some cranes released in northern latitudes have also completed fall and spring migrations unassisted. Others required intensive assistance to move them to staging areas after they failed to move south unaided (Horwich, pers. comm., Urbanek 1989b unpub.). Hand-rearing in isolation from unclothed humans seems most useful in producing birds for release in nonmigratory situations and will probably be employed in Whooping Crane releases in Florida.

FIGURE 1 – Whooping Crane population; winter counts.



FUTURE RECOVERY GOALS AND SCHEDULE

The USFWS and CWS have separately published recovery plans for the Whooping Crane (U.S. Fish and Wildlife Service 1986, Cooch et al. 1988). Common goals in the recovery plans are increases in the size of current wild and captive flocks and establishment of two additional, disjunct wild flocks.

Although extraordinary efforts have been made to build captive Whooping Crane colonies and to create a wild flock at Grays Lake, all expansion of the Aransas-Wood Buffalo flock (Figure 1) has been due entirely to endogenous production. As in the past, all future increases in the Aransas-Wood Buffalo population are to be from natural reproduction and recruitment. Although no eggs or birds are to come from captive flocks, fertile eggs in the nests in Wood Buffalo will continue to be distributed so that as many as possible of the nesting pairs have at least one viable egg.

With the expansion of the Aransas-Wood Buffalo population to 140-plus birds, the growth of the Patuxent flock to 30-plus birds, and the establishment of the ICF flock with 30 birds, we are optimistic about Whooping Crane recovery. The USFWS recovery plan (U.S. Fish and Wildlife Service 1986) calls for expansion of the Aransas-Wood Buffalo population to 40 breeding pairs by the turn of the century (32 pairs were present in 1990) and the establishment of two additional wild populations by 2020. The CWS plan (Cooch et al. 1988) calls for a separate population of 25 pairs in the United States and another population of at least five pairs in Canada by 2010.

In the 1940s, the Whooping Crane teetered on the brink of extinction; fewer than 30 birds remained in the world. In the intervening five decades, the wild population has expanded seven fold, while sustaining a massive effusion of over 300 eggs to build the Grays Lake flock and captive flocks. The recovery of the Whooping Crane, although not yet complete, stands as a singular marvel in the annals of wildlife management.

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GENETIC CONSIDERATIONS FOR REINTRODUCTION OF GUAM RAILS TO THE WILD

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ABSTRACT. Guam Rails *Rallus owstoni*, flightless rails formerly endemic to the Pacific island of Guam, became extirpated from the wild in 1986 as a result of the 1940's introduction of the Brown Tree Snake *Boiga irregularis*. The 21 rails brought into captivity formed founder stock for birds to be released in the 1990 introduction of Guam Rails to the nearby island of Rota. To choose appropriate reintroduction stock, protein electrophoresis was performed on Guam Rails and other congeners to evaluate overall genetic diversity and to quantify inbreeding among the founders. DNA fingerprinting was then used to determine genetic relatedness among founders. Finally, a gene drop pedigree analysis was used to evaluate various options for choosing birds for the reintroduction. The study illustrates how quickly genetic diversity can be lost in small populations and the importance of examining multiple genetic factors in designing reintroductions.

Keywords: Guam Rails, *Rallus owstoni*, genetic diversity, DNA fingerprinting, gene drop, pedigree analyses, electrophoresis, reintroductions, founder genome equivalents, founder contribution.

INTRODUCTION

Captive breeding programs have long been heralded as last resorts for species that can no longer survive in the wild, usually due to the actions of man. While this role enhances public awareness of the plight of endangered species, it does not help the particular species recover unless careful population management is undertaken and reintroduction plans are explored. Zoo's and other captive breeding programs are beginning to incorporate these ideas into their animal management philosophies and are making steady progress towards accomplishing significant conservation goals. Initiation of the Species Survival Program (SSP) in 1981 by the American Association of Zoological Parks and Aquaria (AAZPA) set precedent in developing and implementing recovery plans for captive endangered species.

While zoos are making major changes in population management policies, emphasis is being placed on creating "masterplans" (SSP recovery plans) for large mammals and primates. Relatively little effort has been placed in recovering captive avian species. Of the 54 SSP programs currently underway, only 14 deal with birds (Seal 1990).

Policies are changing partially as a result of current research efforts in population genetics and conservation biology that focus on development of techniques that provide better quantification of genetic and demographic factors leading to population isolation, instability, and extinction. New molecular technology has provided us with the tools to genetically differentiate among populations and determine overall population stability for endangered birds such as Piping Plovers *Charadrius melodus* (Haig & Oring 1988) and Dusky Seaside Sparrows *Ammodramus maritimus nigrescens*

(Awise & Nelson 1989); we have evaluated population viability for endangered Red-cockaded Woodpeckers *Picoides borealis* (Reed et al. 1988) in the wild and wild/captive Puerto Rican Parrots *Amazona vittata* (Lacy et al. 1989); and we have set up pedigrees to begin population management of captive endangered birds such as the Micronesian Kingfisher *Halcyon cinnamomina* (Bahner 1990) and Bali Starling *Leucopsar rothschildi* (Siebels 1990). However, in order to truly evaluate a species status, manage that species in captivity, and then reintroduce a viable population to the wild, multiple factors and techniques must be considered. This has rarely, if ever, been accomplished for an avian species. The remainder of this paper describes an uncommon example of comprehensive genetic management efforts for an endangered bird that has gone extinct in the wild, has bred in captivity, and is now being released back into the wild.

Guam Rails *Rallus owstoni* were once common on the Pacific island of Guam. They are flightless rails, endemic to Guam, with population estimates of over 80,000 individuals on this tiny 10 x 45 km island. Introduction of the Brown Tree Snake *Boiga irregularis* to Guam during World War II caused precipitous decline or extinction for all eleven of Guam's avian native forest species including the rails (Savidge 1987). By 1983, less than 100 Guam Rails remained on Guam and they were concentrated in the northern 1/8 of the island (Engbring & Pratt 1985). The last Guam Rail was seen in the wild in 1986.

Guam Rails were taken into captivity in 1983 and subsequently brought to U.S. zoos where a captive breeding program was begun in 1984. Initially, 21 birds were brought into captivity and are considered *founders* to the captive population. As of December 1990, the captive population contained over 150 birds. Now that a captive population and pedigree are established, the next step is to reintroduce birds back into the wild. Guam continues to be overrun with snakes (over 3 million in 1988, Fritts 1988), hence the decision was made to introduce Guam Rails to the nearby island of Rota (U.S. Fish and Wildlife Service 1989). Rota has no history of competing rails, no Brown Tree Snakes, and contains suitable habitat.

Numerous genetic, demographic, logistical, and environmental factors need to be addressed for proper population management, hence this paper summarizes resolution of three primary issues needed to manage genetic diversity in both captive and reintroduced Guam Rails. First, overall genetic diversity was assessed in relation to other non-endangered rails to determine if Guam Rails were genetically depauperate. Second, genetic relatedness among founders was unknown and needed to be established in order to properly assign kinship values to future offspring and to determine the number of independent founder lines. Finally, various options were assessed in designing strategies for choosing birds that would maximize genetic diversity in reintroduced Guam Rails.

METHODS

Methods are briefly summarized here as they are outlined in greater detail elsewhere. Overall genetic diversity was assessed using protein electrophoresis (Haig et al. in prep.). Blood samples were collected from all living Guam Rails (n=102) and from heart, liver, and muscle samples from Guam Rails (who had died in captivity), King

Rails *Rallus elegans*, Clapper Rails *Rallus longirostris*, Virginia Rails *Rallus limicola*, and Sora Rails *Forzana carolina*. Non-Guam Rail samples were collected from hunters shooting rails during the 1987 fall migration on the United States Atlantic coast. All 29 enzymes screened for the interspecific rail study were included in further analyses. Twenty-eight enzymes were initially screened for the intraspecific Guam Rail study and 23 were included in further analyses.

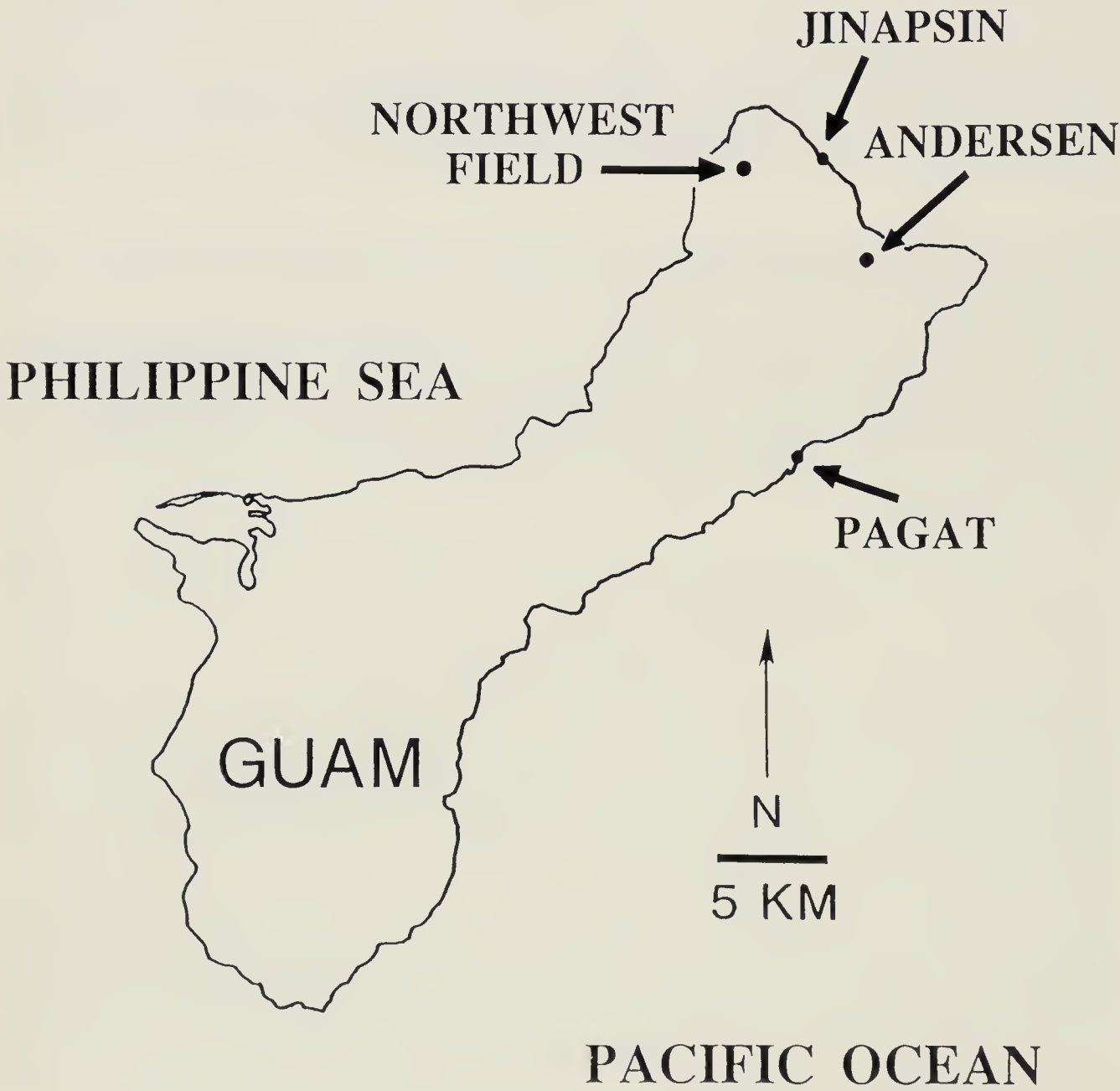


FIGURE 1 – Capture sites of founder Guam Rails on Guam.

Relatedness among founder Guam Rails was evaluated through correlation of various hypotheses explaining founder relatedness with DNA fingerprinting data. Hypotheses are as follows (see Figure 1 for founder collection locations): 1) founders are unrelated; 2) founders are unrelated with the exception of two nests where chicks from each are considered siblings; 3) founders within each *major* site descended from one set of parents; 4) founders within each major site are first cousins except that same-nest chicks are sibs; 5) founders within each *local* site are descendent from one set of parents; 6) founders within each local site are first cousins except same-nest chicks are sibs; 7) founders within each major site have the same greatgrandparents; within each local site founders are first cousins except same-nest chicks are siblings. These

pedigrees were compared using a least squares linear regression analysis that regresses DNA fingerprinting band sharing data for all 102 birds sampled with kinship coefficients calculated from the Guam Rail pedigree (molecular methodology and pedigree analyses are detailed in Haig et al. in prep.). The pedigree most closely aligned with molecular band sharing data was considered the best representation of founder relatedness.

Once an accurate pedigree was established, a gene drop pedigree analysis technique was used to evaluate various options for choosing pairs of Guam Rails to produce 90 chicks to be introduced as adults to Rota (Haig et al. 1990). The gene drop is a Monte Carlo simulation where two unique alleles are assigned to each founder and survival of founder alleles is then tracked through the pedigree to assess genetic variability in what would be the Rota population. The goal is to maximize genetic diversity in the Rota population without causing loss of genetic diversity in the captive population. Options included choosing pairs: 1) randomly; 2) based on their past reproductive success; 3) based on maximizing allozyme variability; 4) based on equalizing genetic contribution of each founder; 5) based on maximizing number of unique founder alleles surviving in the reintroduced population; and 6) based on maximizing founder genome equivalents (i.e. a combination of equalizing founder contribution and maximizing number of unique founder alleles). Results were evaluated in terms of percent heterozygosity retained, allelic diversity, and founder genome equivalents.

TABLE 1 – Allozyme variability among *Rallus* and *Porzana* species and within Guam Rails (from Haig et al. in prep.).

	n	Alleles/locus (x + SE)	% Poly. loci	Heterozygosity/locus (x + SE)	
				Direct count	Hardy-Weinberg expected
INTERSPECIFIC COMPARISON					
Guam Rail	2	1.1 ± 0.0	6.5	0.048 ± 0.036	0.038 ± 0.026
King Rail	1	1.0 ± 0.0	3.2	0.032 ± 0.032	0.032 ± 0.032
Clapper Rail	10	1.1 ± 0.1	3.2	0.006 ± 0.006	0.006 ± 0.006
Virginia Rail	8	1.1 ± 0.1	9.7	0.016 ± 0.010	0.021 ± 0.014
Sora Rail	19	1.3 ± 0.1	16.1	0.024 ± 0.012	0.022 ± 0.011
INTRASPECIFIC COMPARISON: GUAM RAILS					
Founders	13	1.1 ± 0.1	12	0.028 ± 0.016	0.025 ± 0.014
Population w/o founders	89	1.1 ± 0.1	12	0.026 ± 0.019	0.026 ± 0.018
Total population	102	1.1 ± 0.1	12	0.026 ± 0.018	0.026 ± 0.017

*Using 0.99 criterion for polymorphism.

RESULTS AND DISCUSSION

Overall genetic variability

Electrophoretic results indicated that Guam Rails have levels of genetic diversity as high or higher than non-endangered rails sampled from mixed populations and that

levels of heterozygosity for Guam Rails were not significantly different from Hardy-Weinberg predictions for population equilibrium (Table 1, Haig et al. in prep.). Interspecific comparisons of electrophoresed rail samples indicated 18/36 presumptive loci were polymorphic. The number of alleles per locus did not vary significantly among species, however, the percent of polymorphic loci varied considerably with Guam Rails having the third highest value. While none of the species examined indicated a significant deviation from Hardy-Weinberg predictions, Guam Rails had the highest level of heterozygosity among all species. Results from intraspecific Guam Rail samples indicated 4/26 presumptive loci were polymorphic. Genetic diversity among founder, non-founder, and the entire Guam Rail population was not significantly different from Hardy-Weinberg predictions for expected heterozygosity. Founder Guam Rails had slightly higher heterozygosity than non-founders but the difference was not significant.

Founder identification

Least squares linear regression analyses indicated that hypothesis 1 (founders are all unrelated) yielded the most significant correlation with kinship values from the pedigree (Table 2). Hypothesis 2 (assigning sibling status to same-nest chicks) also correlated significantly with kinship data. Analyses continue in an effort to determine the exact nature of the difference between hypotheses 1 and 2. Until the difference is resolved, hypothesis 1 will be used to define the relationship among founders.

TABLE 2 – Evaluation of hypotheses to determine Guam Rail founder relatedness using least squares linear regression analyses of DNA fingerprinting band sharing data with kinship values from Guam Rail pedigrees (N=number of different kinship values in pedigree). See text for further explanation of hypotheses (from Haig et al. in prep.).

Founder hypothesis	N	R ²	SE	p≤ 0.01
1. Not related	7	0.98	0.01	*
2. Same-nest chicks related	14	0.88	0.03	*
3. Each major site has 1 set of parents.	16	0.31	0.17	(* @ .05)
4. Founders in each major site are cousins; same-nest chicks are sibs	33	0.66	0.06	*
5. Each local site has same parents	15	0.77	0.06	*
6. Founders from local sites are cousins; same-nest chicks are sibs	27	0.80	0.04	*
7. Founders from each major site share great-grandparents; founders in each local site are first cousins; same-nest chicks are sibs.	49	0.62	0.05	*

Reintroduction options

Gene drop analyses were run using the pedigree established from hypothesis 1. Genetic management options 4,5,6 produced the most genetically diverse release populations for Rota (Table 3). All three options represent genetic management strategies for pedigrees rather than the more common approaches illustrated in options 1,2,3. Managing founder genome equivalents provided a balance between equalizing founder contribution and maximizing allelic diversity, and provided the most genetically diverse population. Therefore the Rota reintroduction was begun using option 6. The captive population is now also managed using option 6 as a guideline.

TABLE 3 – Consequences resulting from various Guam Rail reintroduction options (from Haig et al. 1990).

Option	Heterozygosity retained ¹	Allelic diversity ¹	Founder genome equivalent
Initial	1.00 ± .000	42.0 ± 0.00	21.0
Current	0.98 ± .000	31.5 ± 0.62	10.5
Random ²	0.95 ± .027	24.1 ± 1.10	9.4
Fitness	0.98 ± .054	20.5 ± 0.53	8.3
Allozyme	1.00 ± .000	18.9 ± 1.10	7.1
EFC	0.98 ± .022	27.2 ± 1.20	13.4
MAXA	1.00 ± .000	29.3 ± 0.76	13.7
FGE	1.00 ± .000	29.2 ± 0.84	14.4

¹ ± standard deviation
² means of 100 random simulations

SUMMARY

The process described here represents a multifaceted approach to determine optimal genetic management strategies for captive and newly-established wild populations of an endangered bird. One technique alone would not have been adequate to address the problem of managing captive and wild Guam Rail gene pools. By posing a series of alternative hypotheses to explain results of each technique and then systematically testing them, a clearer picture of the path to take emerges. Specific life history patterns and causes of population decline may alter the choice of these hypotheses for other species of concern, but the overall approach toward managing Guam Rails should provide guidance for future genetic management programs.

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USE OF ANDEAN CONDORS TO ENHANCE SUCCESS OF CALIFORNIA CONDOR REINTRODUCTION TO THE WILD

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ABSTRACT. The last wild California Condor *Gymnogyps californianus* was trapped from the wild in 1987 and increased the captive flock to 27. As adults became more relaxed and juveniles matured, sexual activity led to one chick being hatched in 1988, 4 chicks in 1989, and 8 chicks in 1990. While the flock builds to better genetic representation, Andean Condors *Vultur gryphus* have been released in an experimental dry run to refine release techniques and test areas for problems and mortality factors where California Condors will be released in the future. Seven Andeans were released in 1988-89, and six in 1990. They have not fed significantly at food other than proffered carcasses at specific sites yet, they have ranged over 100 miles from the release site. Two mortalities have occurred to date, one three-month-old juvenile died during transportation and one flying bird collided with a power line. Andeans may be allowed to remain in the wild for a few months to help the first California Condors adjust to the environment.

The California Condor *Gymnogyps californianus* is among the world's most endangered species of birds. Indeed, by the mid-1980's the wild condor population had reached a low of 22 individuals. Although in the early 1980s it was hoped that California Condors could be maintained in the wild, the realization that excessive, uncontrolled mortality would soon drive this species to extinction urged the U.S. Fish and Wildlife Service to seriously consider capturing the entire wild flock. Amidst intense controversy, the last free flying condor was trapped and brought into captivity on April 19, 1987. This action permanently altered the recovery program to now rely entirely on captive propagation and eventual release to the wild of genetically surplus young.

Condors fit the model for extreme K-selection; i.e. they are large, long-lived birds that take six years to reach sexual maturity and reproduce at a low rate of only one chick every two years during a successful season. Any species with this kind of natural history strategy must also have a low rate of mortality to counterbalance the low reproductive input. For condor populations to be maintained, annual mortality rates have been calculated at 5 to 7% (Verner 1978, Temple & Wallace 1988). During the mid-1980s, 23-40% annual mortality was documented in the wild condor population. (Snyder & Snyder 1989). The rate of mortality seemed to differ depending on where the birds chose to fly. The range of the condor population during that period could be separated into two distinct areas: the rugged mountains around the southern end of the San Joaquin Valley that provided nest caves, safe roosting sites, and sufficient updrafts for easy soaring. In contrast, condors foraged the less vegetated foothills over to the San Joaquin basin by either discovering carcasses themselves in the relatively open habitat or by observing the behavior of other scavengers that would indicate the presence of carrion.

Although many details about condor mortalities are poorly understood, it was obvious that losses were greater in the foraging areas than in the area within the mountains where nesting occurred. During deer hunting season, foraging condors tended to spend more time in areas of high hunter use where they fed on "gut piles" left behind after a dead deer was field-dressed by a hunter or on wounded deer that were unretrievable by hunters and later found by the scavengers.

Both food items often contain a fragment of lead, which is highly toxic if ingested by a condor. Three condors were recovered dead or dying from the toxic effects of lead fragment ingestion. One bird (AC3) that had survived gunshot wounds later died from lead ingestion. Other evidence of dangers encountered in the traditional foraging grounds include a case where a breeding female was contaminated with DDT, as her crushed egg indicated. It is not known where she ingested such a high concentration of the pesticide, but a possible source is from cattle carcasses that had been treated with chemicals to control parasites. Another bird died from ingesting cyanide when, out of curiosity, it tugged on a trap called a "coyote getter" during a federally-run predator control program.

An aggressive program of taking wild-produced eggs and chicks into captivity began in 1983. By 1987, the captive condor population consisted of 14 wild-caught adult and juvenile condors and 13 young that had been artificially hatched from eggs taken from wild nests. These 27 individuals were evenly distributed between two facilities: the Los Angeles Zoo and the San Diego Wild Animal Park, according to sex, age, and genetic line.

Compared to hawks, eagles, falcons, and owls (the true birds of prey), condors adapt to captivity with relative ease. In 1987, two adults that had been in captivity for only one year were showing signs of pair formation, such as following behavior where one bird displayed increased interest in the activities of the other and follows it to different areas of the pen, joining in the other's activity. In 1988, after what appeared to be successful copulations, this same pair laid one fertile egg that produced a healthy chick. In 1989, five pairs produced seven eggs, four of which were fertile and successfully hatched, raising the total to 32 condors. In the 1990 season, nine pairs produced fifteen eggs. Eleven of these were fertile, and eight hatched healthy individuals, bringing the population total to 40. We have noted that, similar to other species in captivity, condor eggs produced by first-time breeding females, even if fertile, do not hatch, whereas their subsequent eggs have proven viable. Captive management of condors has certain advantages over natural production in the wild. The ability of reproductive females to lay a replacement egg if the first or even the second egg is removed provides the opportunity to increase the reproductive rate up to sixfold, which is one reason why captive breeding has such promise.

Two reproductive events appear to be occurring concurrently with respect to the increasing productivity of the captive flock. The wild-caught birds are now sufficiently adjusted to captivity to form pair bonds and reproduce. Secondly, the young of the "wild" eggs hatched in captivity in the early part of the program are reaching maturity and show no reluctance to begin breeding. Some have even shown a tendency to breed as early as four and five years of age. Whereas, the earliest wild condors are known to breed is at 6-7 years. We have found that keeping potential breeding pairs within sight of each other seems to produce a synergistic effect in the sexual

excitement of the birds. When one pair begins to display and copulate, so will two or three other pairs housed in adjacent pens.

The timetable for future releases is set by criteria recommended by the California Condor Recovery Team, a panel of biologists that advises the U.S. Fish and Wildlife Service on program direction. With the current reproductive performance of the captive pairs, releases of captive produced condor chicks are imminent.

The four genetic and behavioral requirements for release candidates are:

- (1) At least 96% heterozygosity of each of the 9-11 founding lines must be retained in captivity before subsequent progeny can be considered for release, i.e. five young per genetic line.
- (2) At least 3 pairs of founders are breeding.
- (3) Candidates are physically and behaviorally releasable.
- (4) There are at least 3 birds in any one release group.

The reproductive pace of the birds themselves determines the timetable under which releases will occur. A few founding lines are close to meeting these criteria and, if reproduction in the coming season is exceptional, releases could commence in 1991, although they are more likely to begin the following year.

Releases of California Condors are scheduled to occur first in sites tested within their most recent range in southern California. However, other possible sites within, as well as outside, California are also being carefully considered. This species will be recommended for down listing from endangered to threatened status when two disjunct populations numbering at least one hundred individuals each have been established in the wild. Since these birds may range over 160 kilometers in a day, diverse areas are being studied, e.g., the Grand Canyon in Arizona and Gray Ranch in southwest New Mexico.

The Andean Condor *Vultur gryphus* has served as a surrogate for many kinds of research on the California Condor over the years. Although endangered as well, populations still number in the thousands within its range along the length of the Andes mountains. Its behavior, size, and ecology are similar to the North American species (Brown & Amadon, 1968). Thus, techniques developed on Andean Condors have, so far, been equally applicable for use in California Condor recovery.

Andean Condors have been bred in many zoos throughout the world (Kasielke & Wallace 1990). These institutions have accumulated extensive experience with eggs and young of this species. Artificial incubation and captive management techniques used on California Condors at the Los Angeles Zoo and San Diego Wild Animal Park are based on that long history (Kuehler & Witman 1988). Also, radio telemetry transmitters and tracking techniques were developed with Andean Condors, along with trapping and field handling methods, prior to their use on California condors (Wallace & Temple, 1987).

Based on release experiments conducted by Wallace & Temple (1983) in Florida using Black Vultures *Coragyps atratus* and Turkey Vultures *Cathartes aura*, eleven Andean Condors were released in northern Peru. Seven survived and successfully

integrated into the wild population over a two-year period (Wallace & Temple 1987). The results of these experiments suggested that captive-reared California Condors could also be successfully released into the wild using appropriate methods. Because the climate, topography, food dispersion, and human activity level differs drastically between the site where Andeans were released in Peru and the area in which California Condors will be released in California, it was important to test the potential release sites before native birds were freed. Since it would be several years before California Condor young were available for release to the wild, an opportunity to release Andean Condors existed to help improve release methods developed in Peru to better fit conditions in the southern California mountains. In 1988, experimental releases using captive-produced Andean Condors were begun under joint supervision by the Los Angeles Zoo and U.S. Fish and Wildlife Service personnel. The California Department of Fish and Game provided additional support.

Nine zoos cooperating in the program contributed 29 fertile eggs in the 1988 and 1989 seasons. The eggs were transported in portable incubators to the Los Angeles Zoo and the San Diego Wild Animal Park for the 56-62 day incubation period. The chicks were reared in isolation from human contact behind one-way glass with the use of hand puppets resembling adult condors. At three to five months of age the nestlings were transferred to pens in the area in which they would be released. During the transport to the field, one three-month old nestling died inexplicably. The two hour trip should have been only a minimal stress, but apparently that was the cause of death as diagnosed by the zoo pathologist. Three release pens were constructed in different areas each several miles apart. Although of different styles, they all have certain features in common including a small roost area, an outside pen covered with netting, and an adjacent blind that has a view through one-way glass into both the roost and outside pen. All three areas can be approached by researchers undetected by the birds, and food and water can be delivered through portholes in a way researchers cannot be detected. The birds were reared and released in groups of three to four; seven in 1988-89 and six in the 1989-90 season.

Conducting "dry runs" with a surrogate species in release programs such as these are the most reliable means of developing techniques that are efficient and safe. The zoo production and management during the Andean program allowed the opportunity to assess the logistics of egg transport, improve incubation parameters, and revise the chick rearing methods based on the results of the releases. We found that the release site must be carefully selected, considering the management logistics of maintaining visual isolation while caring for the chick's physical needs, that the immediate topography must afford protection from large mammalian competitors such as bears, and that the release site must provide adequate updrafts for flying conditions for the inexperienced birds. Also, important in site selection is the amount of human activity in the surrounding landscape.

Soon after their release the birds in our first group were attracted to particularly windy slopes over 1.5 km from the release area. An active petroleum field was located there and workers used the roads and the area daily. It appears that close exposure to the high level of human activity, power lines and vehicular traffic during the first months of their fledging experience habituated the birds to these features in their environment. They responded to the presence of people and man-made structures as they later ranged over a hundred mile area, with far less fear of humans than we hoped. An

inexperienced Andean Condor died as a result of a collision with a power line a few weeks after it had fledged in the same "practice" area on a prominent ridge, thereby underscoring the necessity of selecting sites with a sufficient buffer of unobstructed slopes. Subsequent discussions with oil company executives over the incident have led to a cooperative effort to bury the most hazardous of the offending lines.

Because of their tameness, the remaining six condors released in 1988-89 were trapped and returned to captivity in 1990. Another six young Andean Condors were released in 1990, this time from a more remote site without nearby human activities. Lacking the influence of the former tame birds, the 1990 birds chose a more secluded slope to practice soaring and continue to respond much less positively to human activity when they encounter it.

Lead poisoning by ingestion of bullet fragments from hunter-killed deer and possibly other similarly killed animals during the hunting season appears to be an important mortality factor of condors. A major question about the behavior of released condors is whether their feeding activity and foraging pattern could be controlled in a way that would minimize their exposure to lead. Wild condors learn how and where to forage from following their parents and the local condor population. Foraging patterns vary among habitats (Wallace & Temple 1988). By feeding the released Andeans exclusively on mountain peaks where soaring for inexperienced birds is easy, but where natural carcasses are scarce, the young condors have fed solely on the safe food we offer, even though they have traversed over more than a hundred miles of habitat. By training the birds to forage in areas less dangerous it is likely to reduce mortalities in the first few years or possibly decades of California Condor releases. However, that training is not likely to eliminate lead poisoning as a mortality factor in the long term.

Copper is now being investigated as an alternative to lead bullets. A pure copper bullet is now on the market in most all of the deer hunting size loads and is claimed by the manufacturer to be well received by hunters because of its superior ballistics and competitive price. If copper bullets prove to be nontoxic to the birds and their use can be encouraged in areas where condors and deer hunters coexist, then a major source of mortality can be reduced and natural carrion can once again be safely eaten.

If the current six Andeans are still free and behaving appropriately when California Condors are ready for release, the surrogates may be allowed to remain in the wild for the first few months after the release of the first California Condors and thereby used to teach the first native condors their activity pattern. The Andeans would show the California birds where to forage and roost and the location of the drinking and bathing pools before the surrogates are again taken into captivity. Utilizing the experience of the Andeans in this way could significantly reduce the chances of the newly fledged Californians acquiring behaviors that are maladaptive, or at least speed their adjustment to a wild environment.

Both condor species are benefiting from this program. In order to eliminate some concern over the possibility of Andeans proliferating in the wilds of North America, only females were allowed to be released. Fourteen male Andeans were hatched during the California experimental program and were also reared in isolation from human contact. They were eventually shipped to Colombia, South America, and released in areas where this species has either declined or no longer exists. When the

female Andean Condors are retrapped at the end of the California study, they will also be going south to join their brothers in the wilds of their own species range.

If captive propagation of California Condors succeeds to the degree we anticipate, adequate numbers of young should be available for annual releases to reestablish the species in the native range. With basic release methods in hand, we are likely to have significant increases in populations as we attempt to establish them in various selected sites. No doubt some mortalities will occur but, with increased understanding of each circumstance, we may be able to deal with the causes on an individual basis. It appears that we can expect a reasonable amount of success in establishing populations – at least in the short term. What cannot be determined, at this point, is the long term viability of a population recovering from such a narrow genetic bottleneck. It could possibly be many decades before we really know the success or failure of these efforts. Nevertheless, success to date gives reason for considerable optimism.

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EARLY EXPERIENCE IN CAPTIVE-REARED SHOREBIRDS: IMPLICATIONS FOR ENDANGERED SPECIES MANAGEMENT

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ABSTRACT. This study determined how the early experience of captive-reared shorebirds differed from experiences of young raised by their natural parents. Captive rearing was then evaluated as a viable tool for enhancing populations of endangered shorebirds. Killdeer *Charadrius vociferus* were used as experimental shorebirds because they are common yet taxonomically similar to the endangered Piping Plover *Charadrius melodus*. In 1988 and 1989 a combined total of 19 Killdeer chicks was raised in captivity and released to the wild. Wild Killdeer families were observed in 1987 and 1989, and behavioral differences between captive-reared and wild chicks appeared in time spent feeding and resting. Captive chicks spent a greater proportion of time resting and less time feeding than wild chicks. This can be attributed to constant heat and concentrated, high quality food sources provided to the captive-reared chicks. Growth rates and response to alarm calls and potential predators were the same between groups. Hatching success and survival to fledging were significantly higher for captive-reared young. Because of precocial characteristics of young shorebirds, captive rearing is a viable tool for enhancing populations. Political rather than biological obstacles now need to be overcome.

Keywords: Killdeer, Piping Plover, *Charadrius*, shorebirds, captive rearing, endangered species, small populations.

INTRODUCTION

Captive breeding is a technique that has been utilized with varying success for the management of rare and endangered birds. Attempts have been made to breed endangered birds in captivity for future reintroduction to the wild. These efforts have focused primarily on species in the orders Anseriformes, Falconiformes, Galliformes, Gruiformes and Psittaciformes (Wemmer & Derrickson 1987). There has been little work done on Charadriiformes (Senner & Howe 1984), although several species of shorebirds are listed as threatened, endangered, or of special concern by the United States Fish and Wildlife Service (Dept. of Interior 1986).

The Piping Plover was given federal status as endangered or threatened in 1986. The total population of Piping Plovers is less than 4700 birds (Haig & Oring 1988) and is divided into three geographically separated breeding populations. The Great Plains and Atlantic Coast populations were given threatened status. The Great Lakes population of Piping Plovers was listed as endangered. By the time the Great Lakes and Northern Great Plains Piping Plover Recovery Plan was developed only 17 breeding pairs remained in the Great Lakes population, and viable breeding areas were reduced from eight Great Lakes states to one (U. S. Fish and Wildlife Service 1988). In the past several years, the Great Lakes population has remained relatively stable at 17 breeding pairs, all within the state of Michigan. However, in 1990 the population decreased by 35% (Allen & Powell, unpublished data).

This study was initiated because captive rearing is a potential management tool for augmenting Piping Plover populations before they become critically reduced. Captive

rearing differs from captive breeding in that clutches of eggs are taken from the wild, allowing wild parent birds to lay and raise a second clutch of young. This technique not only potentially doubles the reproductive success of individual breeding birds, but it also bypasses the expense and difficulties of keeping adult birds in captivity and inducing them to breed. Captive rearing may be particularly suitable for managing small shorebirds populations. Unlike cranes or vultures (Drewien & Bizeau 1977, Wallace & Temple 1987), shorebird chicks have a rapid rate of physical and behavioral development (three to five weeks), a short period of parental dependency, and foraging is primarily innate. The possibility of imprinting to humans is diminished because most Charadriids exhibit plumage monomorphism (therefore male chicks do not have to learn female plumage), young are raised with siblings, and there is little similarity between human foster parents and their avian "adopted" young (Immelmann 1972). Killdeer were used as experimental shorebirds because they are common yet taxonomically similar to the endangered Piping Plover.

METHODS

This study was conducted in northern Michigan in Cheboygan and Charlevoix counties (45° 45' N, 85° 40' W). This area includes nesting habitat for both Killdeer and Piping Plovers. The sites in Charlevoix County included two island locations; High and Beaver. Killdeer nests were located and either assigned to use for observations of wild Killdeer or the eggs were collected for captive rearing. In 1988 captive rearing efforts were conducted on an island where there was no electricity and eggs could not be incubated; instead newly hatched chicks were taken from nests to be reared in captivity. In 1989 eggs were collected and incubated at 39° C. As chicks hatched they were removed from the incubator and placed into a box with a heat lamp and kept at 35° C. Chicks were provided water and tubifex worms. On the day after hatch captive chicks were individually color banded and placed in sibling units in large outdoor pens. A heat lamp placed at one end of the pen provided warmth as needed. Chicks were fed a mixture of tubifex worms, mealworms, earthworms, and commercial moist cat food. In addition, chicks fed on insects attracted to the heat lamps. Twelve one-minute observations were made on each individual chick for two-hour observations per sibling unit each day. Data recorded included time spent feeding, resting, preening, and other activities, distance from nearest sibling, and response to taped Killdeer alarm calls. Chicks were weighed every other day. Human exposure to the captive chicks was minimized. After the chicks were fully feathered and had been observed flying in the pens (at approximately 30 days), they were released in sibling groups on an isolated beach. Observations on the released birds continued until they left the area.

Wild Killdeer nests were observed until the chicks fledged or the nest was destroyed. Observations on family units with chicks were similar to those for the captives but included data on response to predators and spatial relationships to parent birds. Comparisons of behavioral data were analyzed with unpaired t-tests.

In subsequent years the study areas were searched for banded Killdeer that may have returned to the area to breed. Notices were placed in several ornithological journals and local parks to alert people to watch for banded Killdeer.

RESULTS

Hatching and fledging success

Five Killdeer chicks were successfully reared in captivity and released to the wild in 1988. In 1989 14 Killdeer chicks were released. Twenty-two eggs were taken from seven Killdeer nests and incubated in 1989 (Table 1). Two of these eggs did not hatch and two chicks died in the process of hatching. It is believed that poor humidity regulation in the incubator may have played a role in these deaths. Three chicks died within three days of hatching; only one chick died in subsequent weeks. Fledging success for captive rearing was one chick per clutch in 1988 and two chicks per clutch in 1989.

TABLE 1 – Percent survival of wild and captive-reared Killdeer from hatching to fledging. No eggs were incubated in 1988 for captive rearing.

	Total Number Eggs (# Nests)	Eggs Hatched	Chicks alive 1 week	Chicks alive 2 weeks	Chicks alive 3 weeks	Known Fledged
Wild Killdeer						
1987	61 (16)	52%	44%	22%	13%	13%
1989	23 (6)	48%	36%	36%	27%	27%
Captive Killdeer						
1988	? (5)	N/A	63%	63%	63%	63%
1989	22 (7)	82%	68%	64%	64%	64%

Of the 22 wild Killdeer families observed, hatching success was 52% and 48% in 1987 and 1989, respectively (Table 1). Egg failure was due primarily to predation, although one nest was abandoned in 1987. Sixty percent of the wild Killdeer chicks died within the first week of hatching (Table 1). Fledging success of wild chicks ranged from an average of 0.25 fledged per nest in 1987 to 0.5 fledged per nest in 1989. These figures for egg and chick mortality are within the ranges reported in the literature (Lenington & Mace 1975, Schardien 1981).

Growth rates

Growth rates for both wild and captive-reared Killdeer were similar in all years. The mean weight (\pm SE) at hatch was 9.58 ± 0.12 g for captives and 9.8 ± 0.13 g for wild chicks. Although the oldest wild Killdeer caught and weighed was 17 days old, the growth curve for wild Killdeer follows that of captive-reared young (Powell in prep.).

Behavior

Behavioral data for wild and captive-reared Killdeer were divided into three age groups: less than one week old (when the mortality is highest in wild chicks), between one and two weeks, and older than two weeks (when feather formation and attempts to fly begin). There were significant differences between wild and captive-reared chicks in the time spent feeding ($P = 0.01$, $P = 0.004$) and resting ($P = 0.04$, $P = 0.0003$) in the second and third age groups (Table 2). At ages less than one week, there were no significant differences in any behaviors. Wild Killdeer chicks spent a greater proportion of their time feeding at all ages. Both captive and wild chicks spent a greater proportion of time resting at less than one week of age. Captive chicks always spent more time resting than wild chicks (Table 2). Both groups spent a greater

amount of time preening after two weeks of age, corresponding to feather development. Time spent in other activities (running, antipredator behavior, etc.) was similar in both groups.

TABLE 2 – Mean percent time spent by wild and captive-reared Killdeer. (N = number of individual sibling groups; the number of individual chicks is given in parentheses). Significant differences ($P < 0.05$) are noted with an asterisk.

Age of Young	N	Feeding	Resting	Preening	Other
Less than 1 week					
Wild	6 (25)	66.8±9.2	22.7±9.1	2.0±0.7	16.5±7.6
Captive	9 (18)	60.7±3.1	24.2±4.7	0.9±0.6	14.1±2.8
Between 1 and 2 weeks					
Wild	3 (11)	84.0±6.4 *	3.0±3.0 *	3.7±2.7	9.3±3.2
Captive	9 (15)	59.2±4.1 *	23.2±4.8 *	3.2±1.2	14.5±2.2
Over 2 weeks					
Wild	4 (7)	83.2±8.4 *	2.4±2.4 *	8.7±1.2	14.6±4.5
Captive	9 (14)	53.9±4.0 *	20.7±2.4 *	8.5±5.3	10.0±9.9

Response to Killdeer alarm calls was the same for captive and wild chicks. Both groups displayed the antipredator behavior of crouching and freezing in place when exposed to alarm calls before age one week. Wild and captive chicks older than one week gave alarm calls and either ran to cover or crouched and froze. In addition to alarm calls, both groups of chicks responded with these antipredator behaviors when approached by humans. Captive chicks did not habituate to human observers.

Return rates

Of the 19 captive Killdeer fledglings that were released only one was seen as a yearling. This bird had been reared and released on High Island in 1988 and was seen among a flock of wild Killdeer on the mainland in 1989 after the breeding season. None of the wild Killdeer were sighted in subsequent years. Natal site fidelity is extremely low for Killdeer (Lenington & Mace 1975)

DISCUSSION

Captive rearing is a potential management technique for augmenting small populations of shorebirds; both hatching and fledging success were significantly increased using this method. Captive rearing resulted in an additional one to two birds fledged per nesting pair of adults. This is an increase of 75% in young produced in a single breeding season by a given number of breeding adults. Assuming that captive-reared fledglings have a similar survival rate to breeding age as wild fledglings, captive rearing can add considerably to the overall population.

Killdeer chicks raised in captivity behaved similarly to wild Killdeer chicks. Although captive-reared chicks spent a greater proportion of time resting and a smaller amount of time feeding than wild chicks, these differences are artifacts of captivity where a constant, consistently located food supply and heat source were available. Captive fledglings were observed foraging on natural food sources and were capable of locating food and cover after release to the wild. The released fledglings fed and rested

at a rate similar to wild Killdeer of the same age. Released captives were also frequently observed in the presence of wild Killdeer and showed appropriate interactive behaviors. Both in 1988 and 1989, released fledglings joined groups of wild Killdeer as they formed pre-migration flocks. Although returns of captive-reared Killdeer were limited to one individual, this was to be expected for this species. None of the wild Killdeer chicks returned to their natal area to breed.

This study indicates that early experience of captive-reared Killdeer does not have negative ramifications on successful release and survival in the wild. The next logical step would be to initiate a program of captive rearing to augment the endangered Great Lakes Piping Plover population. Currently management of Piping Plovers in the Great Lakes consists of basic monitoring, habitat protection, public education and the use of predator exclosures to protect nests. Haig and Oring (1988) have shown that there is little genetic differentiation between the two threatened populations of Piping Plovers. It is unknown whether the Great Lakes plover population suffers from decreased genetic variability. Augmentation efforts could use eggs obtained from the two threatened populations. The resulting captive-reared fledglings could then be released in areas where wild Piping Plover fledglings were located in the Great Lakes region. In addition eggs from abandoned nests or those atrisk from high water levels and storms could be taken from the endangered population for captive rearing. However, eggs from the Great Plains or Atlantic Coast would be preferable because the small population in the Great Lakes may already suffer from inbreeding and or decreased genetic variability.

Page et al. (1989) reported that released captive-reared Snowy Plovers *Charadrius alexandrinus* successfully bred and fledged young, increasing productivity within the local population. Breeding success of adult Killdeer that were raised in captivity was difficult to determine because of low natal site fidelity. The occurrence of captive-reared adults returning to successfully produce young in the wild should be more evident in Piping Plovers than in Killdeer because Piping Plovers are more likely to return to their natal area. (Haig & Oring 1988). It is difficult to measure the subsequent breeding success of adult Killdeer that were reared in captivity because Killdeer exploit a wide range of habitat types and are common throughout the United States. In contrast, the nesting habitats of Piping Plovers are quite specific and geographically limited. In addition, all three populations of Piping Plovers share a common wintering area. Piping Plovers are monitored closely by researchers in both the breeding and wintering areas, and banded birds are easily sighted. These factors would facilitate the measurement of success in a captive rearing effort for Piping Plovers.

The management of rare and endangered species is typically "crisis management" (Soule 1989). We now have an opportunity to treat the proximate causes of the declining Great Lakes population of Piping Plover before a true crisis (extirpation of a centrally located population) occurs. But before a captive rearing effort can be initiated for Piping Plovers political obstacles must first be overcome. The Piping Plover Recovery Team and the U.S. Fish and Wildlife Service must approve of the augmentation plan and issue permission to proceed. Bureaucratic decisions are usually slow, and federal funding is tenuous. An official response by the Piping Plover Recovery Team to an augmentation proposal submitted in 1990 indicated that captive breeding for release is not a favorable option. The team also suggested two more years of experimentation with plovers from the threatened Great Plains population. This option

would be ideal if funding and time permitted. However, the Great Lakes Piping Plover population has rapidly reached a crisis situation. This population currently consists of less than 25 individuals. Genetic and environmental stochasticity greatly increase the risk of extirpation of this population in the next few years. Population augmentation may no longer be a viable management tool if the number of birds continues to decline. In such a scenario, a reintroduction program may be the only remaining option if Piping Plovers are to continue to exist in the Great Lakes region. Reintroducing captive-bred or captive-reared birds to the wild is difficult both biologically and politically once extirpation has occurred (Griffith et al. 1989, Wemmer & Derrickson 1987). Reintroductions are expensive, controversial and less likely to succeed than augmentation. Hopefully, we are not destined to continue the current pattern of crisis management for rare species and the resultant poor success of halting local extinctions.

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CONCLUDING REMARKS: CONTRIBUTIONS OF CAPTIVE BREEDING TO THE CONSERVATION OF ENDANGERED SPECIES

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The “green thumb” art of captive breeding of wildlife has by necessity virtually transgressed into a science in recent decades. Whether it need be applied to each and every endangered species though is still a subject of hot debate. For example, while endangered Peregrine Falcon *Falco peregrinus anatum* populations extirpated in North America have benefited enormously from such programs, there was no apparent need to do likewise with British populations which, through the banning of injurious chemicals and careful wardening of wild eyries, have made a tremendous comeback. Nor was any captive breeding required in the amazing return of the Chatham Island Black Robin! On the other hand, some argue that captive breeding should have been undertaken well before the species reached its precarious state.

Nevertheless, no one will argue that captive breeding has its place in today’s wildlife management practices. Moreover, there is a right way and a wrong way to go about it. The following discussion will briefly outline the steps needed for a successful captive breeding program for an endangered bird species.

First, it must be decided who will undertake the work. The choices can be boiled down to governments at various levels, backyard aviculturists, zoos, and breeding centres, both private and university-based. Influencing that decision are things like funding, geographical location, proximity to the wild population, climatic factors, and the critical need to preserve wild habitat into which to release captive-bred birds.

Often, funding is the key ingredient in any decision. In short, whoever pays, plays! In most situations, captive breeding programs are expensive. If undertaken by governments, certain guidelines must be adhered to. For example, salaries must be set at a level consistent with those of other government employees. Volunteers are sometimes not allowed due to liability problems. In developing countries that have little funding for such programs, perhaps the best pathway is to distribute what little money there is to backyard aviculturists who would relish the challenge of breeding an endangered species. Above all, it must be remembered that any captive-breeding program require long-term funding.

Perhaps one of the most difficult aspects of captive breeding programs, especially for endangered species, is the procurement of permits for the capture of stock, its keeping, and its shipment across international borders. Public sentiment has much to do with obtaining permits and it is for that simple reason alone that one must do their homework before even considering such a program. After gleaning every bit of information from field research, backyard breeding projects, published and unpublished literature, and work on surrogate species, an overall aim accompanied by specific

objectives and a chronology of events must be established. One may have to consider such aspects like species and subspecies. In short, it is critical to define exactly what the target species or subspecies is.

Once the funding is in place, the objectives have been set, and the homework done, facilities can then be created. Things like size, furniture, and special needs, e.g. photoperiod, temperature, water, and 'live' v 'dead' food might have to be considered. Depending on the scope of the project, the best experienced staff money can buy should be hired. Educational degrees are not necessarily the most important criterion; sometimes backyard breeders can be invaluable in this regard.

Another critical decision is the breeding stock. Some programs keep things simple and inexpensive by only releasing surplus birds bred by aviculturists and/or zoos. However, if the object is to establish a captive breeding population, one must decide upon, if the luxury exists, a basic minimal number of birds to overcome potential problems with inbreeding and skewed sex ratios. As stated earlier, the most practical move would be to obtain stock bred in captivity. They will likely be less stressed and more prone to breed in captive conditions. If birds must be taken from the wild and there is a choice, eggs and/or nestlings are more desirable than juveniles or adults. The latter have been successfully used in captive breeding programs however, e.g. the California Condor.

Further prevention of inbreeding can be achieved through use of the various studbook programs. There are computer programs available which facilitate the pairing of birds in the most effective way. Studbooks also help to maximize the effectiveness of captive breeding programs by advertising the availability of breeding stock.

One cannot overstate the importance of disease considerations and of working closely with veterinarians and pathologists.

As for particular techniques in stimulating the birds to breed in captivity, these are too numerous to mention here. Most species will respond to some form of artificial insemination, even semen freezing, if natural copulation does not occur. Artificial incubation of eggs removed by renesting techniques is a very popular technique to increase output of progeny. Sexing techniques for breeding stock are becoming quite sophisticated now.

Once success has been achieved and there is suitable habitat free of the conditions which placed the species in jeopardy in the first place, captive birds can be released. Release techniques have been classified into two distinct categories: 'soft' and 'hard'. Each has its own merits, but more and more, biologists and managers are tending toward the former method.

Monitoring of the released birds is extremely important, as it is by this step that one can gauge the success of the program. Telemetry and direct observation offer the best possibilities here.

Last but not least, breeders must come to grips with the final problem — the dispensation of unwanted and/or aged breeding stock. While some birds can be used for research or education programs, a humane form of euthanasia with public fanfare is probably the most merciful route.

SYMPOSIUM 46

**GENETIC ASPECTS OF POPULATION
STRUCTURE**

Conveners A. J. VAN NOORDWIJK and P. STANGEL

SYMPOSIUM 46

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INTRODUCTORY REMARKS: GENETIC ASPECTS OF POPULATION STRUCTURE

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In the past decade several aspects of genetics have rapidly gained the interest of ornithologists. This was clearly reflected in the program of the previous congress in Ottawa, which included papers on the use of genetic markers such as enzymes or DNA-recombining properties for taxonomic purposes, heritability estimates for life-history traits and the results of selection experiments. Since then techniques using DNA-probes and especially the so-called genetic fingerprinting have become available to answer interesting questions that could previously not be addressed, especially those involving pedigree analysis. Most recently a technique called 'Polymerase Chain reaction' has made it practical to study avian population genetics and systematics at the level of the DNA sequence.

The genetic structure of populations is an important parameter in virtually all evolutionary processes. Further, conservation biologists recognize that preservation of a species should include the preservation of a major part of its gene pool. The maintenance of the gene-pool is, of course, related to the potential for further adaptive evolution. The continued ability to change is a necessary condition for survival in a changing environment. The word conservation conveys an image that is too static, instead we need programs that provide opportunities for change and adaptation to new conditions.

The recent findings of large amounts of genetic variation for life history traits allow considerable evolutionary response in five to ten generations. Where rapid local adaptation is possible, the distribution of selective pressures and gene flow will determine how much local adaptation really exists. One is here dealing with a double-edged sword: genetic variation may allow rapid adaptation to local environments, but environmental heterogeneity probably also plays a major role in the maintenance of genetic variation. It is the purpose of this symposium to try and give an overview of what we know about the genetic variation within and among populations, in order to see where the main gaps in our knowledge are.

The first two papers in this symposium will describe genetic variation at the DNA-level. The contribution by Quinn (not in *Proceedings*) concentrates on the between population variation. Parkin's contribution demonstrates that both electrophoresis and DNA-fingerprinting show that about one in every seven House Sparrow *Passer domesticus* offspring results from an extra-pair copulation, which is thus an important element of the genetic population structure. Moreover there are indications that the successful EPCs follow a definite pattern. The middle paper in this symposium by Stangel describes enzyme variation and the broad-scale within-species patterns of genetic variability that can be obtained by them. The last two papers in this

symposium deal with genetic variation in body size as an example for quantitative traits. In both of them the interaction between genotype and environment in building the phenotype plays a central role. James reports on the covariation of size and shape across populations. Van Noordwijk reports on experiments to investigate the interaction of genotype and environment in shaping the phenotypic variation in body size within a population.

I hope that the symposium will help in a better definition of the gaps in our knowledge of the genetic population structure, and that it will stimulate new studies in this area.

SPERM COMPETITION AND FERTILITY IN THE HOUSE SPARROW

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ABSTRACT. DNA fingerprinting, enzyme polymorphisms and observational data from a rural population of House Sparrows *Passer domesticus* were used to determine the extent of extra-pair fertilization and intra-specific parasitism. No egg dumping was found, but cuckoldry was widespread, affecting 26.8% of broods and 41.7% of males. Despite a low (2%) observed rate of extra-pair copulation, 13.6% of nestlings were sired extra pair. We have evidence from the distribution of EPF's between broods that success in sperm competition is strongly influenced by the fertility of the cuckolded male, and that females may benefit from EPC as an insurance against their mate's infertility.

Trivers (1972) predicted that males could attempt to gain extra-pair copulations (EPCs) in order to increase their reproductive output. It has been shown using a wide range of genetic markers, including DNA fingerprinting (Jeffreys et al. 1985, Jeffreys 1987, Burke 1989) that this occurs in several species of monogamous birds (Birkhead et al. 1987). The fitness advantage to males is obvious, although it is less clear whether females will gain any benefit from such behaviour. The fact that females tolerate, or even actively solicit, EPC attempts by males is circumstantial evidence for an advantage. However, there is little direct evidence. We have recently obtained results from a study population of House Sparrow *Passer domesticus* that suggests there may be good biological reasons why a female might benefit from EPC, and the consequent extra-pair fertilization (EPF) of some of her offspring.

Observational data and blood samples have been collected at a colour-ringed nestbox population at Brackenhurst, Nottinghamshire, UK since 1980 (Burke 1984, Wetton et al. 1987). The blood is used to score 6 polymorphic protein loci by starch gel electrophoresis (see Table 1). Allele frequencies at the 6 loci are in Hardy-Weinberg equilibrium, and do not vary significantly between years, sex or age classes. Examination of known true families confirms normal Mendelian inheritance of the allozyme banding patterns observed in starch gels.

Between 1985 and 1989, repeated observations of feeding visits to 183 broods resulted in the identification of both attendant adults. These families comprise a total of 151 adults and 536 nestlings, and were analysed firstly by enzyme electrophoresis which revealed 39 instances of incompatibility with the adults. In almost all cases where one or other adult could be excluded from parentage, it was the male (14m: 1f, $P < 0.001$), suggesting cuckoldry rather than egg dumping as the major cause. Estimates of the EPF rate were derived using exclusion probabilities (Chakraborty et al. 1988) calculated to compensate for undetected cases of cuckoldry (Tables 1, 2).

The same families were then analysed by DNA fingerprinting using the pSPT 19.6 minisatellite probe (Carter et al. 1989). Extra-pair offspring (EPOs) were readily identified by their possession of several bands (mean 4.88 ± 0.46) found in neither of the adult fingerprint patterns. In all cases these EPOs shared more bands with the female, the proportion being consistent with known parent-offspring comparisons

whilst the number shared with the male was typical of that found between unrelated individuals (Table 3). This confirms that all cases of non-parentage were due to EPC. The single case of female exclusion in the electrophoretic survey was probably due to a very rare and previously undetected null allele at PEPD3.

TABLE 1 – Extra-pair fertilization (EPF) rates calculated using 6 protein loci. Allele frequencies at the 6 loci used in the parentage analysis were derived from 574 presumed unrelated birds sampled between 1985 and 1988 at Brackenhurst. Electrophoretic and staining methods follow Cole & Parkin (1981) (transferrin (Tf) was scored from Gahne gels using a general protein stain). Exclusion probabilities (Chakraborty et al. 1988) (P_E) represent the proportion of extra-pair offspring (EPOs) which are expected to genetically mismatch with the attendant male. The estimated EPF rate = $P_E/(N_E N_T)$, where N_T is the number of attendant/offspring trios for which genotypes were determined for all three individuals. (NB - the combined total of observed exclusions (N_E) includes three cases of nestlings which mismatched at two loci).

LOCUS	Allele Frequencies					P_E	N_E	EPF Rate (%)	N_T
	A	B	C	D	E				
6PGD	0.041	0.959				0.0393	1	5.0	509
PEPD2	0.051	0.949				0.0484	6	24.2	513
PEPD3	0.010	0.911	0.015	0.064		0.0568	5	21.0	420
IDH	0.709	0.291				0.2063	14	13.1	517
PEPT	0.006	0.047	0.027	0.914	0.006	0.0413	2	9.3	521
Tf	0.200	0.786	0.014			0.1550	14	17.9	506
Combined						0.5532	39	14.2	

TABLE 2 – Comparisons of EPF rate estimates from protein electrophoresis and DNA fingerprinting analysis

Year	Observed Exclusions		Estimated EPF rate (%)		No of Nestlings Finger- printed
	Enzymes	Fingerprints	Enzymes	Fingerprints	
1985	5	8	11.7	10.4	77
1986	7	14	9.6	10.6	132
1987	12	24	13.5	14.9	161
1988	4	5	14.5	10.0	50
1989	11	22	17.1	19.0	116
Total	39	73	14.2	13.6	536

The proportion of nestlings identified as EPOs by DNA fingerprinting (the EPF rate) varied between 10 and 19% between years (Table 2). Evidence from additional fingerprinting and electrophoretic studies suggest similar frequencies in every year since 1981 (JHW unpublished data and T. Burke, pers. comm.). Between 1985 and 1989, 26.8% of broods and 41.7% of males were affected by cuckoldry. First year and experienced males were equally susceptible, but certain males appear to be particularly

prone to being cuckolded (Figure 1). The majority of cases occurred in broods where paternity was shared with the attendant male ($N = 35$). In those broods where the attendant male was excluded from parentage of the entire brood ($N = 14$), the male was observed to feed the nestlings on more than one occasion, and most (8 out of 12 males) raised 'legitimate' offspring in previous or subsequent broods with the same female. The similarity between fingerprints of EPOs within broods implicate a single non-mate as sire in almost all cases, and in several instances this was also true of EPOs from consecutive broods (Table 3 and Figure 1). We have started to survey neighbouring males for diagnostic bands, and in several cases have been able to assign paternity (Wetton et al. 1987, and in prep).

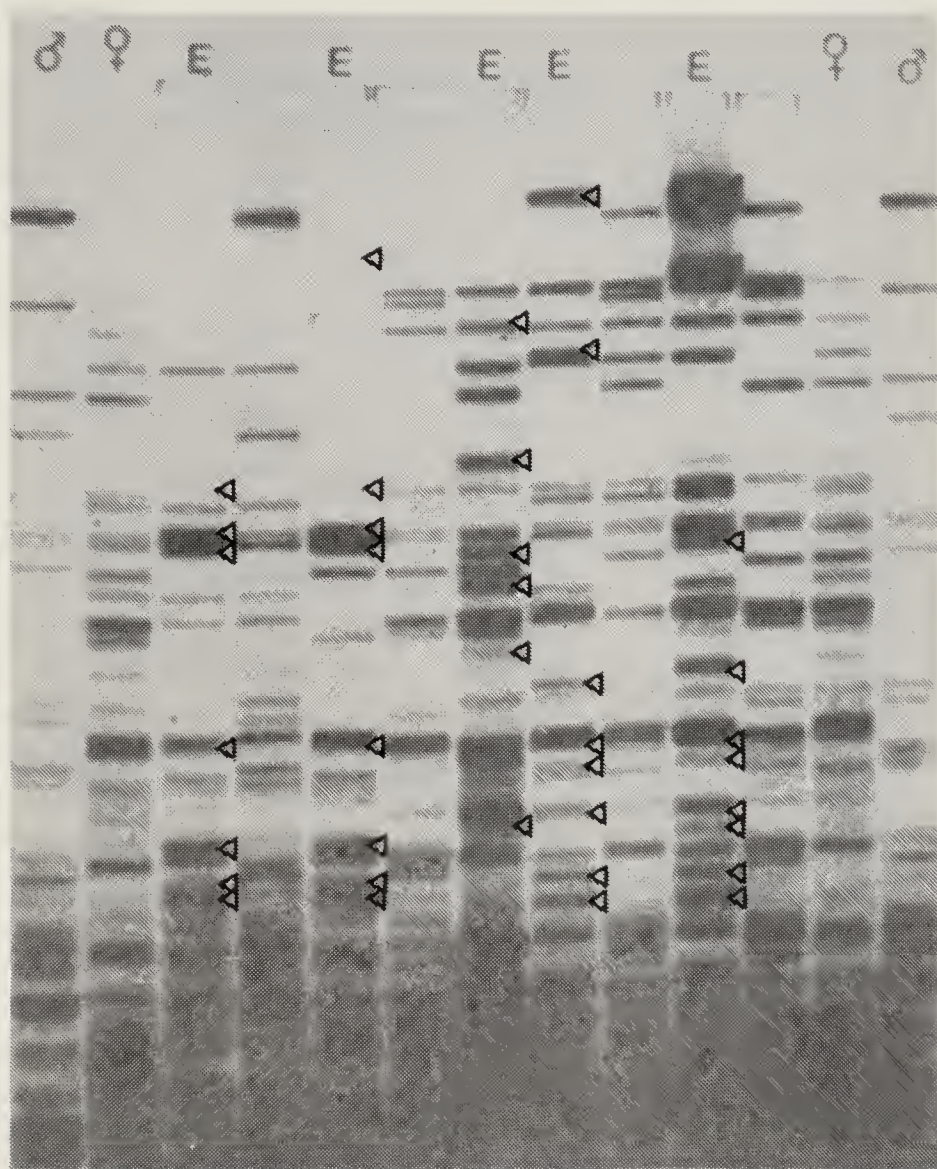


FIGURE 1 – DNA fingerprints of five broods reared by a single pair of House Sparrows over three years. The pair repeatedly suffered from poor hatching success, only the last clutch hatched totally successfully and produced the sole brood with no evidence of cuckoldry, three broods showed mixed paternity. The first contains two EPOs (E) with similar paternal components in their fingerprints, suggesting that the same male fathered both. The same applies to the EPOs in the third and fourth broods. Bands incompatible with the attendant adults are marked (Δ). The fingerprints were produced from 6 μ g of Hae III restricted DNA electrophoresed through a 22 cm 0.8% agarose gel at 2V/cm until fragments <3kb were lost. DNA was alkaline transferred to a nylon membrane. Hybridization to pSPT19.6 RNA probe was carried out at 65°C in 1 x SSC, 1% SDS, 1 x BLOTTO and washed at 65°C in 1 x SSC, 0.1% SDS. The autoradiograph is a 4-day exposure without intensifying screens. The filter was reprobbed with pSPT18.15 (Carter et al. 1989) which detected additional mismatching bands in the EPOs (data not shown).

Studies of other monogamous birds have often implicated forced extra-pair copulations (FEPCs) as the main source of EPOs (McKinney et al. 1984). In the House Sparrow, FEPC is associated with communal displays (Summers-Smith 1955, Møller 1987) which decline rapidly in frequency through the season, but fingerprinting revealed no evidence of a corresponding decrease in the proportion of EPFs. Communal displays are very conspicuous, but rarely result in successful sperm transfer due to the lack of an intromittent organ, and the vigorous resistance of the female. Solicited EPCs may be more important and will go unrecorded if carried out furtively. We recorded several copulations whilst observing birds for other purposes, and one mating was extra-pair amongst 54 where both partners could be conclusively identified (1.8%). The female co-operated in the mating, but the preceding behaviour was not observed. However, on another occasion, a female was seen to actively solicit an EPC, but both birds flew off before mating occurred. The copulations that we observed share an almost identical temporal distribution with a published report of copulation behaviour (Møller 1987), and therefore probably represent a random sample of matings.

TABLE 3 – Similarity coefficients (Wetton et al. 1987), $D = 2N_{AB}/(N_A + N_B)$, where N_A and N_B are the number of bands scored in two individuals and N_{AB} is the number shared between them were calculated using fingerprints from 36 families giving an estimate of 0.15 for band sharing between unrelated individuals from both mate pair ($N = 36$) and random male ($N = 16$) comparisons. Males possessed more bands (13.75 ± 0.568) than females (10.72 ± 0.549) ($T = 4.41$, $P < 0.0001$) through suspected sex linkage of several large Hae III fragments dispersed on the Z chromosomes (males are ZZ and females ZW in birds). Z linkage results in a higher mean D for male/legitimate offspring (LO) comparisons due to the low similarity between mothers and daughters which share no sex linked bands. The mean full sib D lies between those for parent offspring comparisons, all of which correspond to a coefficient of relatedness of $r = 0.5$. EPO/LO comparisons were intermediate between full sib and unrelated values, i.e. they are half-sibs, whilst male/EPO values clustered with the unrelateds and female/EPO comparisons with female/LO. EPOs within broods have similarity coefficients characteristic of full sibs being significantly greater than half sibs.

RELATIONSHIP	Mean D	±	SE	N
Male/RRITZØEfemale	0.1511	±	0.0186	36
Male/Male	0.1492	±	0.0216	16
Male/LO	0.5983	±	0.0085	173
Female/LO	0.5362	±	0.0118	173
LO/LO	0.5802	±	0.0086	451
LO/EPO	0.3411	±	0.0193	76
Male/EPO	0.1370	±	0.0218	24
Female/EPO	0.5775	±	0.0309	24
EPO/EPO	0.6507	±	0.0680	8

A deficiency of observed extra-pair copulations relative to extra-pair fertilizations has been found in other monogamous birds (Weatneat 1987a, b, Møller 1985, 1987) and suggests either that EPCs are less easily observed or that they are more likely to produce viable young. The latter could be due to the higher fertility of cuckolding males, or the optimal timing of EPCs to ensure that they place a high titre of sperm

in the female reproductive tract at ovulation. No data were available to test the effect of timing, but using data from 1985-88, we found that broods containing EPOs did not differ from 'legitimate' broods in either initial clutch size or post-hatch survival. However, there was some evidence of association between the proportion of EPOs within a brood and the proportion of eggs that hatch (Table 4, $G = 22.5$, $df = 15$). Testing for a trend within this table (McCullagh 1980) showed a progressive negative relationship ($G = 7.3$, $df = 1$, $P < 0.01$).

In the Brackenhurst population overall, 11.9% of eggs failed to hatch. These were not all examined, but the results were consistent with a previous study (Seel 1968) that showed 8% of House Sparrow eggs to be infertile, and 4% to contain embryos that died during incubation. Thus, two thirds of the eggs that fail to hatch may be infertile, even though a single copulation can provide sufficient sperm to fertilize an entire brood in other passerine species (Birkhead et al. 1988).

TABLE 4 – Percentage mismatch after nestling mortality

% Hatch	% Mismatch				Total
	0	25-33	50-67	75-100	
25-33	2	0	0	3	5
50	2	0	2	0	4
60-67	4	0	1	1	6
75	12	1	1	0	14
80-83	7	3	1	2	13
100	82	6	7	5	100
Total	109	10	12	11	142

We attempted to identify the cause of the correlation between cuckoldry and hatching success by examination of the seven eggs which failed to hatch in the 39 finger-printed broods sampled in 1989. Four of the eggs were found to be infertile. Using these data we constructed a contingency table categorizing broods by the presence of EPOs and infertile eggs. Four of the 14 broods containing EPOs had a single infertile egg, but none were found amongst the 25 legitimate broods. This result provides significant confirmation that cuckoldry is most likely to succeed when the pair produces infertile eggs ($P = 0.012$, Fishers Exact Test).

Although very few EPCs were seen at Brackenhurst, intensive observations of other House Sparrow populations indicate that most females solicit EPCs (D. Harper, pers. comm.). These results support the hypothesis that females do so as an insurance against low fertility of their mate (McKinney et al. 1984). In such cases, a female may reduce the risk of laying a largely infertile brood by gaining a relatively small number of EPCs, thereby increasing the likelihood of viable sperm being available to fertilize a proportion of the eggs. However, if her mate produces a normal amount of viable sperm, the greater number of within-pair copulations will swamp the contribution from other males, leading to a lower frequency of EPOs in fully fertile clutches. EPOs would only appear when the cuckolder was the last male to mate, assuming the last insemination has precedence (Birkhead et al. 1988).

The two main paternity assurance mechanisms adopted by socially monogamous birds are mate guarding and frequent copulations (Birkhead et al. 1987). The former is usually impracticable in colonial species such as the House Sparrow. In this species high copulation rates (40/day) (Birkhead et al. 1987) may deplete the sperm reserves of males with small testes or low viable sperm counts, thus increasing their susceptibility to cuckoldry. The males which benefit through cuckoldry remain to be identified but observational studies suggest that females prefer large billed males as mates (Møller 1988). These are also the birds most likely to participate in EPCs and communal displays (Møller 1987). Interestingly bib size is positively correlated with testis size and probably ejaculate quality (Møller & Erritzøe 1988). Females may thus choose to participate in EPCs with males of high genetic quality and fertility.

This survey demonstrates the successful application of DNA fingerprinting in a large population survey. A high frequency of EPF was suspected from enzyme electrophoresis but fingerprinting provides precise information without sampling error thereby allowing the detection of a subtle association between cuckoldry and infertility which may help to explain the discrepancy between the observed frequencies of EPC and EPF and the cooperation of females in some extra-pair copulations.

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DIFFERENTIAL GEOGRAPHIC PARTITIONING OF NUCLEAR VERSUS MITOCHONDRIAL DNA SEQUENCE VARIATION IN THE LESSER SNOW GOOSE

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ABSTRACT. Most gene flow between breeding colonies of the Lesser Snow Goose (LSG) occurs as a result of male intercolonial movement. Thus, maternally inherited DNA (mitochondrial and W chromosomal) is more restricted than autosomal DNA in its geographic movement. Previous studies (T.W. Quinn, F. Cooke and B.N. White) showed that nuclear genetic differentiation is very low across the subspecies range. By sequencing the control region and surrounding genes of the LSG mitochondrial genome, we have (1) detected a major rearrangement in gene order; (2) developed primers which can be used with widely divergent avian taxa to amplify and sequence the control region using the Polymerase Chain Reaction; (3) shown that, as in mammals, that region is evolving rapidly and (4) used these primers to show that, in contrast to the nuclear genome, there is distinct geographic partitioning of variation of the mitochondrial genome. The implications of this with respect to Snow Goose populations and speciation concepts will be discussed.

GENIC DIFFERENTIATION AMONG AVIAN POPULATIONS

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ABSTRACT. Variations in allele frequencies among avian populations were summarized. No significant differences among orders were found, but F_{st} values did vary significantly among geographic range and life zone categories. F_{st} values were significantly higher in island and nonmigratory than in mainland and migratory species. F_{st} values were significantly correlated with geographic distance between sample localities, number of polymorphic loci, and sample size but not with the number of loci or populations sampled.

INTRODUCTION

The advent of starch-gel electrophoresis for the detection of variation in allele frequencies in natural populations heralded a new age for the study of geographic variation within species (Hubby & Lewontin 1966, Lewontin & Hubby 1966). Molecular techniques offered several advantages not available with traditional characters (Barrowclough 1983) and promised increased understanding of the processes contributing to geographic variation. Ornithologists were quick to use electrophoresis (e.g., Bush 1967) and information on geographic variation in allele frequencies has accumulated at an increasing rate (M. W. Smith et al. 1982, M. H. Smith et al. in press).

Variation in allele frequencies can be studied by examining the actual frequencies themselves or through the use of summary statistics like genetic distance (Rogers 1972, Nei 1972) and Wright's F-statistics (Wright 1978). Wright's F_{st} , which measures the among-locality component of the genetic variance, has been widely used and provides a convenient measure of differentiation among populations. In its basic form, Wright's F_{st} is the ratio of observed variance in allele frequencies between localities (demes) to the maximum possible variance in allele frequencies that occurs when alternate alleles at a locus are fixed (Workman & Niswander 1970). The F_{st} can therefore be considered a measure of population divergence due to random genetic drift or population subdivision due to biological or environmental factors. F_{st} values can be calculated using a number of methods (Zink 1986, p12), but the most common incorporates a correction factor allowing for finite sampling of genes within demes (Wright 1978).

The objectives of this paper were to 1) summarize F_{st} values from the avian literature, 2) estimate mean levels of F_{st} values within various taxonomic and biotic categories, and 3) associate levels of F_{st} values with ecological, demographic, and life history factors to assess their relative influence on geographic variation in allele frequencies. This study was modelled after that of Nevo et al. (1984).

METHODS

The data set presented in the Appendix includes F_{st} values for 63 species representing 18 families of birds. F_{st} values were taken directly from the literature, and were in each case calculated from electrophoretic surveys of allozyme variation in wild populations. The percentage of each species total distribution sampled was approximated to orient the reader as to the geographic coverage of each study. The season during which collections were made is presented when available because samples from non-breeding populations may contain individuals from different geographic areas.

Biotic data

Original research papers and a variety of other sources were used to place species into biotic categories. Categories were chosen to represent factors that might be likely to contribute to genetic divergence among populations. Each species was classified as to breeding strategy (monogamous or polygamous) and migratory behavior (migratory or nonmigratory). Species were also grouped by life zones (temperate, tropical, temperate and tropical, and cosmopolitan), geographic range (narrow, regional, cosmopolitan, relict, introduced) and distribution (island, mainland, or both).

Statistical analysis

Spearman's rank correlation was used to examine associations between F_{st} values and the number of populations examined, the total number of loci, the number of polymorphic loci, and the mean sample size per population. Differences between species categorized for breeding strategy and migratory behavior were analyzed using t-tests. Analysis of Variance (ANOVA) was used to test for differences among taxonomic groups (order), life zones, geographic range, and distribution. The effect of geographic distance was investigated by correlating the maximum distance between samples (km) with F_{st} . Significance was accepted at the 0.05 level.

RESULTS

F_{st} values calculated from allele frequencies are available from 9 of 27 orders (37%) and 18 of the 159 families (11%) listed in Howard and Moore (1980). The mean number of populations examined was six (range 2 - 31) and the mean sample size per population was 30 (range 2 - 217). The mean number of loci and polymorphic loci examined was 27 (range 1-44) and 8 (range 1-24), respectively. The mean F_{st} for all species examined was 0.046 (range 0.000 - 0.321).

F_{st} values were not significantly correlated with the number of loci ($r_s = 0.110$, $P = 0.38$) or localities examined ($r_s = 0.226$, $P = 0.07$). F_{st} values were significantly and positively correlated with the number of polymorphic loci ($r_s = 0.246$, $P = 0.05$) and significantly and negatively correlated with mean sample size per locality ($r_s = -0.273$, $P = 0.04$). There were no significant differences in mean F_{st} values among the nine avian orders for which data were available (Figure 1; $F = 1.07$, $df = 8.61$). F_{st} values varied significantly among geographic range categories (Figure 2; $F = 51.57$, $df = 4.55$). F_{st} values were also significantly correlated with the maximum distance between sample locations ($r_s = 0.337$, $P = 0.02$).

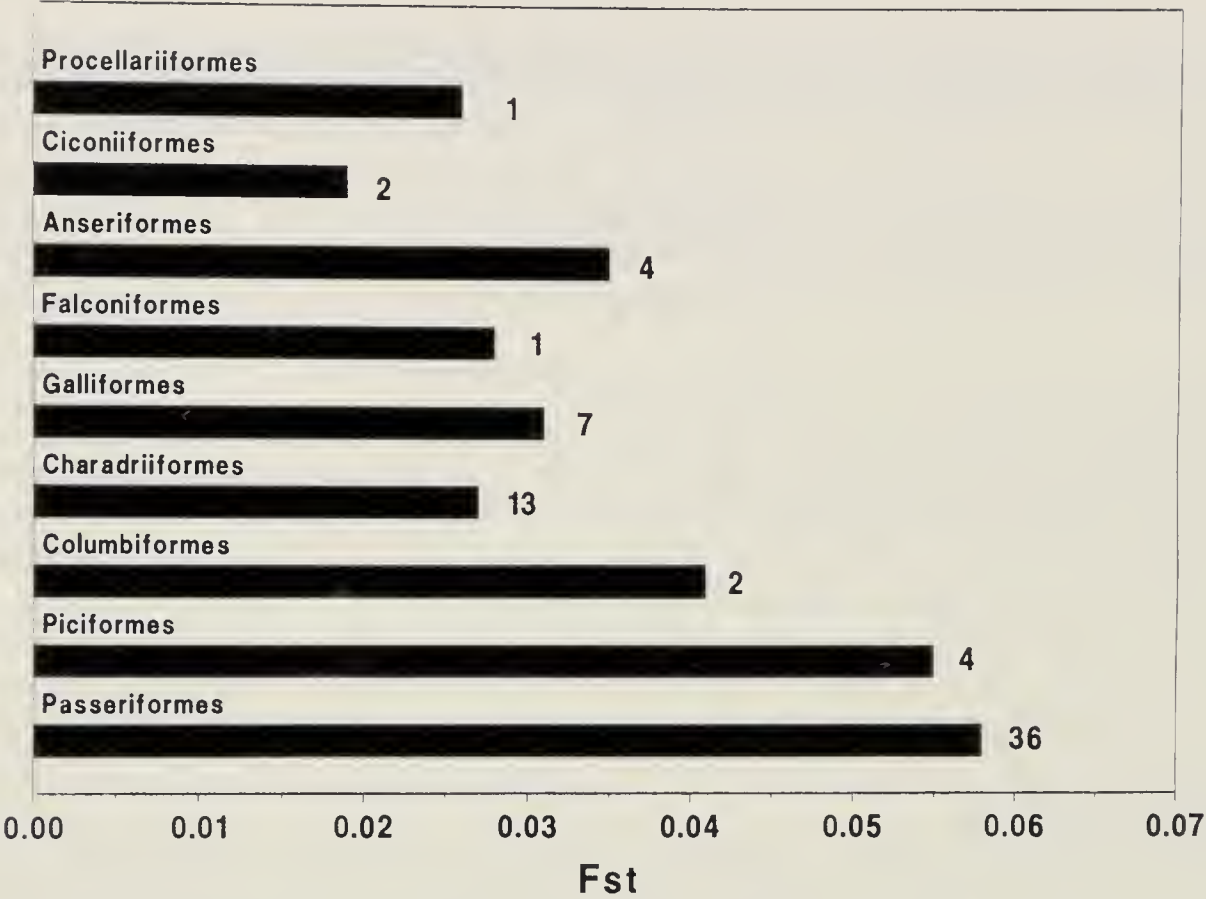


FIGURE 1 – F_{st} values for nine avian orders. The number of species sampled is at end of bar.

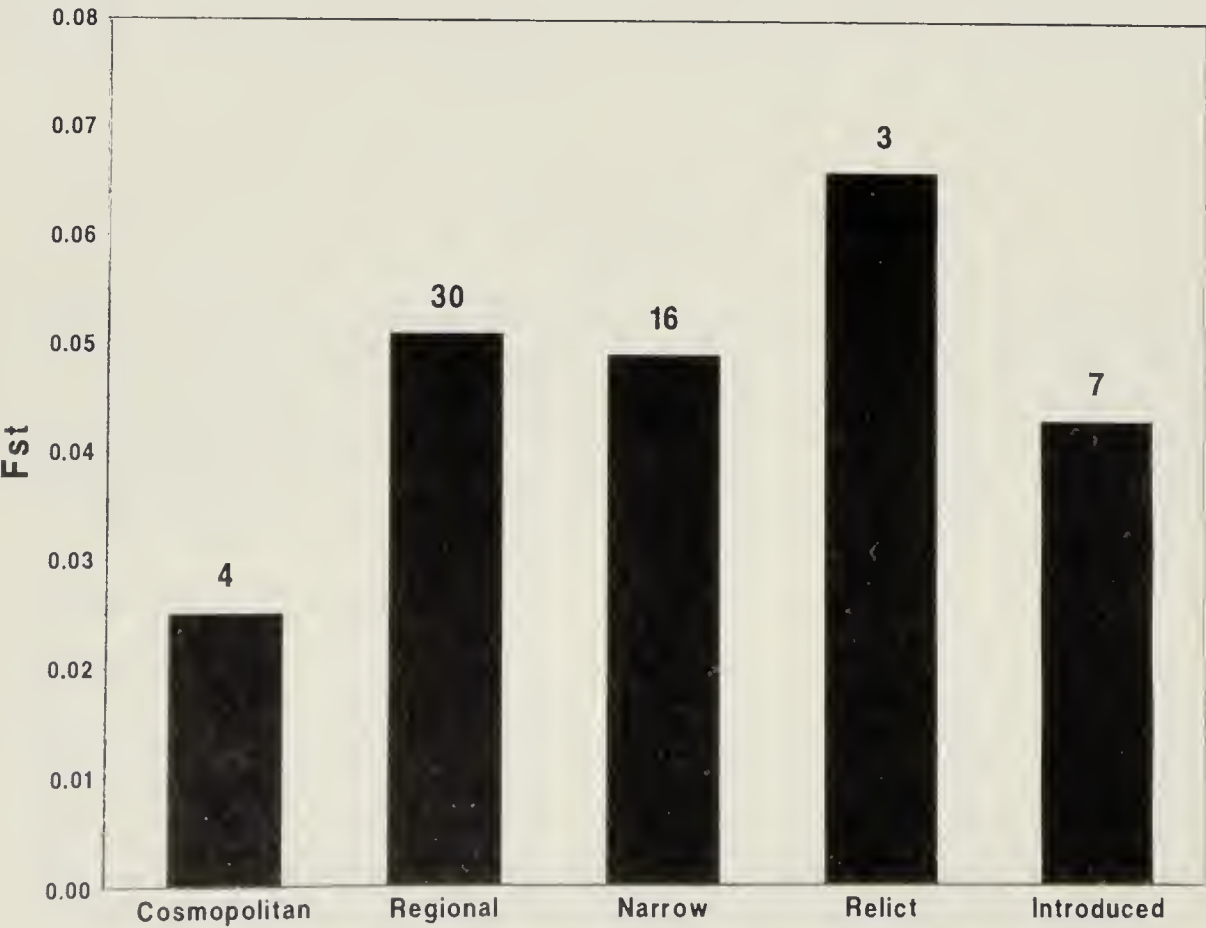


FIGURE 2 – F_{st} values among birds categorized by geographic range. The number of species sampled is at top of bar.

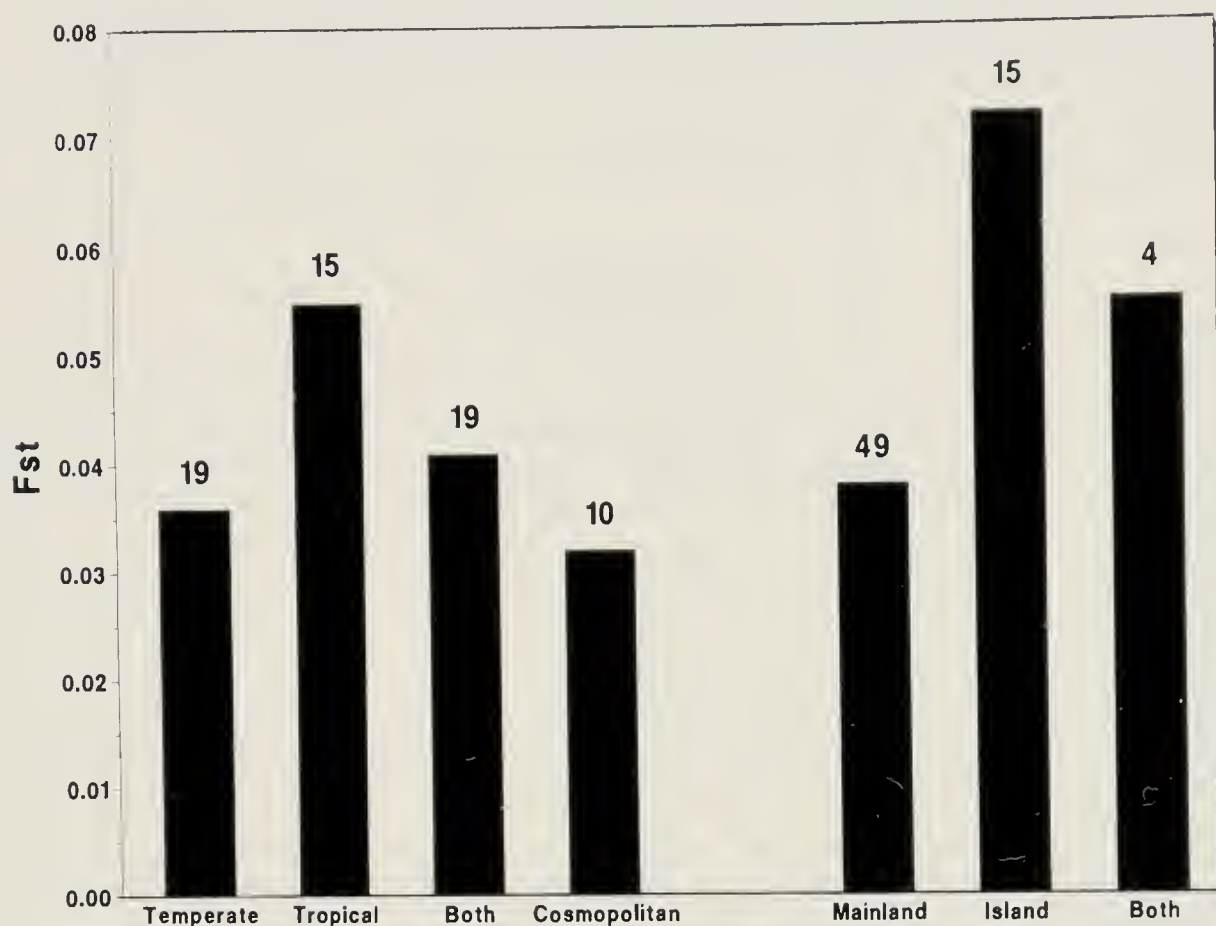


FIGURE 3 – F_{st} values among birds caterogized by life zone and mainland v island distri-
bution. The number of species sampled is at top of bar.

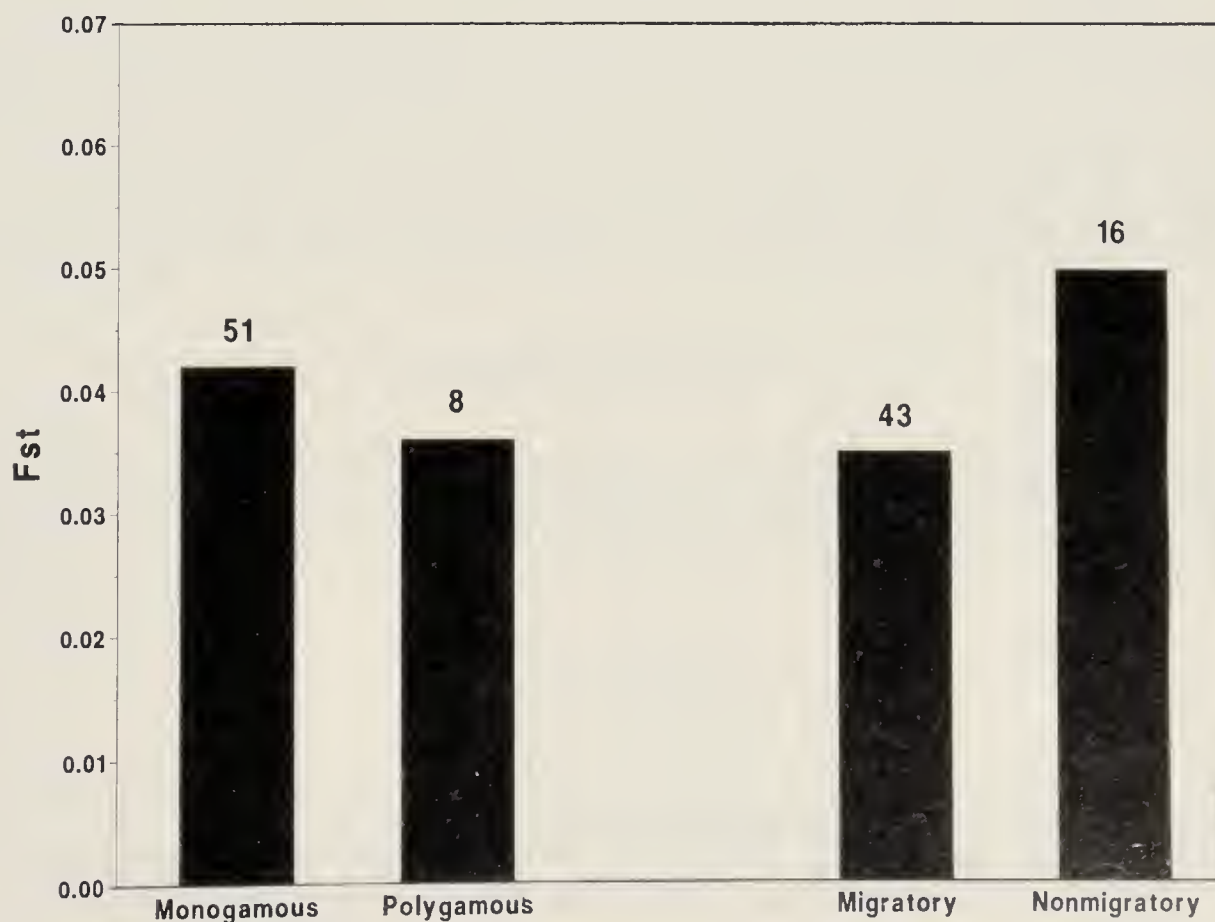


FIGURE 4 – F_{st} values among birds categorized by breeding structure and migratory
behavior. The number of species examined is at top of bar.

There were significant differences in F_{st} values among life zones (Figure 3; $F = 14.00$, $df = 3.59$), and island vs mainland species (Figure 3; $F = 159.40$, $df = 2.65$). Nonmigratory species had significantly higher F_{st} 's than those considered migratory (Figure 4; $t = 9.25$, $df = 57$), but there were not significant differences between monogamous and polygamous species (Figure 4; $t = 0.347$, $df = 55$).

DISCUSSION

Not unexpectedly, species with insular populations exhibit relatively higher F_{st} values. Relict and island populations are likely to be subject to increased random genetic drift if they are small in size. Similarly, introduced populations are likely to be genetically divergent due to founder effects (Nei et al. 1975). Introduced populations as a group had moderate F_{st} values, but F_{st} values were usually higher in introduced relative to native populations. Cosmopolitan species exhibited the lowest F_{st} values and species with narrow or regional distributions had similar F_{st} values. F_{st} values were higher for tropical than for temperate species and this may reflect larger effects of environmental factors on the distribution of tropical species (Capparella 1988). Surveys of Galapagos Islands endemic species (Yang & Patton 1981) also contributed to the high F_{st} value in the neotropical sample. That F_{st} was correlated with geographic distance between samples suggests an isolation by distance effect (Wright 1943). This also indicates that studies of geographic variation should include a broad geographic scale.

Nonmigratory species had a slightly higher F_{st} than did those that migrate. Although many migratory species are considered philopatric, the opportunity for gene flow among regions is probably higher for species with interregional or intercontinental movements. The lack of significant differences between monogamous and polygamous species is somewhat surprising given the important effects of breeding structure on F_{st} (Chesser in press). Polygamous species are poorly represented, however, and additional studies on this group are warranted. The effect of breeding structure on F_{st} values may also be more important on a microgeographic rather than larger scale.

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APPENDIX 1
Summary of F_{st} estimates for birds

Family/Species	% Total Range Sampled	Season Collections Made ¹	Breeding Strategy ²	Migratory or Non-migratory ³	Number of loci sampled (polymorphic)	Number of populations sampled	Average sample size (range)	F_{st}	Reference
Procellariidae									
<i>Calonectris diomedea</i>	<10	B	M	M	36(6)	3	48;14-100	0.026	31
Ciconiidae									
<i>Mycteria americana</i>	<5	B	M	M	20(9)	15	26;16-33	0.019	37
Threskiorinithidae									
<i>Eudocimus albus</i>	<5	B	M	M	19(8)	2	27;24-30	0.019	40
Anatidae									
<i>Cygnus buccinator</i>	100	S	M	NM	19(2)	3	75(43-128)	0.003	6
<i>Branta bernicla</i>	30	W	M	M	28(7)	3	31(13-41)	0.013	28
<i>Branta canadensis</i>	100	B, W	M	M	35(24)	11	23(10-33)	0.065	41
<i>Somateria mollissima</i>	<5	B	M	M & NM	1(1)	5	48(11-50)	0.057	27
Accipitridae									
<i>Rostrhamus sociabilis</i>	<5	B	M	M	12(3)	5	36(24-76)	0.028	40
Phasianidae									
<i>Dendragapus obscurus</i>	<5	S	P	M	1(1)	9	200(14-389)	0.000	32
<i>Callipepla californica</i>	100	–	M	NM	37(16)	7	14(5-17)	0.032	46
<i>Colinus virginianus</i>	<5	F	M	NM	19(7)	3	41(12-85)	0.016	17
<i>Perdix perdix</i>	<5	–	M	M	17(6)	2	27(25-29)	0.023	9
<i>Phasianus colchicus</i>	<5	A	P	NM	26(14)	2	42(37-48)	0.086	34
	<5	F	P	NM	1(1)	4	217(113-603)	0.006	42
<i>Meleagris gallopavo</i>	<5	B	P	NM	28(7)	2	29(20-37)	0.055	39

Family/Species	% Total Range Sampled	Season Collections Made ¹	Breeding Strategy ²	Migratory or Non- migratory ³	Number of loci sampled (polymorphic)	Number of populations sampled	Average sample size (range)	F _{st}	Reference
Scolopacidae									
<i>Charadrius melodus</i>	50	B	P	M	35(4)	5	24(6-41)	0.022	22
<i>Calidris canutus</i>	<10	F, W	M	M	39(12)	4	10(-)	0.041	2
<i>C. maritima</i>	<10	F	M	M	29(3)	2	17(-)	0.023	2
<i>C. minutilla</i>	>50	B, F		M	39(8)	3	8(-)	0.054	2
<i>C. fuscicollis</i>	<10	F, W	P	M	39(8)	2	28(-)	0.019	2
<i>C. alpina</i>	<10	B, W	M	M	29(4)	3	8(-)	0.056	2
<i>C. mauri</i>	<10	B, W	M	M	39(6)	2	15(-)	0.020	2
<i>Catoptrophorus</i>									
<i>semipalmatus</i>	<10	B, W	M	M	40(2)	2	12(-)	0.020	2
<i>Limnodromus griseus</i>	<10	B, W	M	M	40(3)	2	12(-)	0.004	2
Laridae									
<i>Larus californicus</i>	<10	-	M	M	35(8)	2	30(30)	0.004	45
	<10	B	M	M	32(7)	2	12(10-13)	0.067	26
<i>Sterna hirundo</i>	<10	B	M	M	18(12)	4	21(20-21)	0.002	12
Columbidae									
<i>Columba livia</i>	<10	A	M	NM	1	2	177(140-204)	0.030	18
<i>Columba palumbus</i>	<10	A	M	NM	1	2	43(24-63)	0.051	18
Picidae									
<i>Sphyrapicus nuchalis</i>	>50	-	M	M	39(9)	3	11(7-15)	0.019	24
<i>Sphyrapicus ruber</i>	>50	-	M	M	39(7)	2	14(13-15)	0.019	24
<i>Picoides borealis</i>	>5	B	M	NM	16(11)	26	17(2-97)	0.140	38
<i>Colaptes auratus</i>	<5	B	M	M	36(15)	2	6(5-7)	0.042	20, 21
Dendrocolaptidae									
<i>Glyphorhynchus</i>									
<i>spirurus</i>	<10	B	M	NM	25(6)	5	23(22-24)	0.073	13

Family/Species	% Total Range Sampled	Season Collections Made ¹	Breeding Strategy ²	Migratory or Non-migratory ³	Number of loci sampled (polymorphic)	Number of populations sampled	Average sample size (range)	F _{st}	Reference
Formicardiidae									
<i>Pithys albifrons</i>	<10	B	M	NM	31(7)	4	12(12)	0.032	13
Pipridae									
<i>Pipra coronata</i>	<10	B	P	NM	31(8)	5	30(30)	0.090	13
Tyrannidae									
<i>Empidonax traillii</i>	<5	S	M	M	36(13)	2	15(16-19)	0.011	35
<i>Empidonax alanoorum</i>	<5	S	M	M	36(16)	4	16(14-19)	0.043	35
<i>Empidonax difficilis</i>	50	B	M	M	41(17)	11	19(10-27)	0.153	25
Sturnidae									
<i>Aplonis cantoroides</i>	>50	S	M	NM	16(20)	4	24(11-32)	0.127	16
<i>Aplonis metallica metallica</i>	>50	S	M	M, NM	16(2)	6	22(17-38)	0.029	16
<i>Aplonis metallica nitida</i>	>50	S	M	M, NM	16(2)	4		0.040	16
<i>Sturnus vulgaris</i> (New Zealand)	<5	W	M	M	24(10)	6	24(24)	0.032	33
<i>Sturnus vulgaris</i> (United Kingdom)	<5	W	M	M	24(10)	6	24(24)	0.010	33
<i>Acridotheres tristis</i> (native)	<50	–	M	M	39(21)	7	29(20-41)	0.032	1
<i>Acridotheres tristis</i> (introduced)	<50	–	M	M	39(14)	12	47(27-86)	0.123	1
Emberizidae									
<i>Passerina cyanea</i>	<5	B	M	M	–(9)	3	21(16-25)	0.004	30
<i>Dendroica coronata</i>	<10	B	M	M	32(8)	5	24(13-27)	0.005	7
<i>Zonotrichia leucophrys</i>	<5	S	M	M	44(12)	7	18(10-21)	0.032	14
<i>Zonotrichia capensis</i>	<5	S	M	M	19(3)	9	–	0.047–	5
<i>Zonotrichia capensis</i>	<5	–	M	M	14(6)	5	40(25-50)	0.015	23
<i>Passerella iliaca</i>	10	B	M	M	38(14)	31	22(3-65)	0.014	44

Family/Species	% Total Range Sampled	Season Collections Made ¹	Breeding Strategy ²	Migratory or Non-migratory ³	Number of loci sampled (polymorphic)	Number of populations sampled	Average sample size (range)	F _{st}	Reference
Emberizidae – continued									
<i>Junco hyemalis</i>	25	B	M	M	37(9)	6	–	0.008	8
<i>Icterus galbula</i>	<5	S	M	M	19(2)	8	25(20-33)	0.015	15
<i>Agelaius phoeniceus</i>	50	B	P	M	1(1)	3	–	0.037	10,11
<i>Geospiza fortis</i>	70	B	M	NM	27(12)	8	7(-)	0.065	43
<i>Geospiza scandens</i>	30	B	M	NM	27(11)	3	9(-)	0.020	43
<i>Geospiza fuliginosa</i>	80	B	M	NM	27(12)	10	8(-)	0.054	43
<i>Geospiza difficilis</i>	30	B	M	NM	27(9)	3	2(-)	0.057	43
<i>Geospiza magnirostris</i>	30	B	M	NM	27(7)	4	4(-)	0.046	43
<i>Camarhynchus parvulus</i>	40	B	M	NM	27(8)	4	5(-)	0.057	43
<i>Camarhynchus crassirostris</i>	40	B	M	NM	27(4)	4	2(-)	0.034	43
<i>Certhidea olivacea</i>	30	B	M	NM	27(8)	4	4(-)	0.125	43
<i>Pipilio erythrophthalmus</i>		40	S	M	M	16(1)	6	-0.229	36
Fringillidae									
<i>Fringilla coelebs</i>									
(New Zealand)		B	M	NM	44(17)	8	28(20-36)	0.040	3
(Atlantic Island)		B	M	NM	42(19)	14	47(27-62)	0.321	4
(Continent)		S	M	M	42(18)	5	28(27-30)	0.092	4
Passeridae									
<i>Passer domesticus</i>	<5	W	M	NM	(4)	7	64(13-120)	0.008	19
	<5	–	M	NM	23(10)	13	74(29-150)	0.003	29

APPENDIX 1 – Continued

¹ B = Breeding; S = Summer; F = Fall; W = Winter; A = All seasons

² M = Monogamous; P = Polygamous

³ M = Migratory; NM = Nonmigratory

Key to References Cited

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GEOGRAPHIC DIFFERENTIATION IN THE RED-WINGED BLACKBIRD: A CHECK ON ONE OF LANDE'S ASSUMPTIONS

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ABSTRACT. Based on principles of quantitative genetics, Lande (1979) has proposed a theoretical model by which the forces of natural selection on character complexes can be reconstructed. This model presumes that the genetic variance-covariance matrices among the characters remain stable as the means of the characters change. Lande suggests that an indirect way to explore the validity of this assumption is to assume that phenotypic variance-covariance matrices among characters are similar to their genetic matrices and then to check to see whether the phenotypic matrices change as the means of the characters change through time or across localities. For a data set of 545 adult male Red-winged Blackbirds *Agelaius phoeniceus*, organized by 17 two-degree latitude-longitude blocks, we found high allometric covariation across blocks between size and shape ($r = 0.89$). Nevertheless, the within-block variance-covariance matrices were not equal (Box's M, $P < 0.0001$). Only 8 of 17 within-block correlations (standardized covariances) between size and shape were significantly different from zero, and with the conservative Bonferroni correction for multiple tests, only three were significant. A test of more importance here, that the within-block correlations are from the same population, could not be rejected. The reason that the covariance matrices are not the same is not that the correlations are not the same, but rather that both the variances of size and the variances of shape are statistically different. It would be interesting to know how variance-covariance matrices behave as mean values change across localities in other species. We think that, when genetic variances and covariances are unknown, applications of Lande's (1979) model to field data should be preceded by empirical description of within- and across-locality phenotypic correlations, variances and covariances.

Keywords: Microevolution, allometry, Red-winged Blackbird, *Agelaius phoeniceus*, multivariate analysis, covariance.

INTRODUCTION

An area of evolutionary biology that is poorly understood concerns how the genetic structure of populations is related to their phenotypic structure. For bird populations, this question is particularly troublesome because determination of the genetics of quantitative traits requires extensive breeding experiments and difficult studies of parent-offspring relationships. Such studies are more easily performed on animals that are easier to breed in captivity than are most wild birds. Although the phenotypic variation in bird populations can be characterized well, the genetics of their quantitative variation and the effects of the environmentally-dependent expression of genes is poorly understood.

The conventional neo-Darwinian explanation of the mechanism that maintains clinal patterns of phenotypic geographic variation in birds is based on the assumption that the dominant process is natural selection (Mayr 1954). The result is presumed to be adaptation toward an optimal phenotype for each environment, albeit probably dampened by gene flow. The predominance of natural selection as a cause of intraspecific

differentiation in birds is supported by research that seems to confirm several of its predictions. For example, the prerequisite for natural selection that local variation must have a genetic basis has been confirmed in nearly every case that has been tested (Wright 1978, Boag & van Noordwijk 1987, see Hailman 1986 and Boag & van Noordwijk 1987 for some caveats and Smith & Arcese 1988 for an exception). Another prediction, that the average phenotypic values of traits can be changed in predictable directions by selection, is nicely confirmed by long-term artificial selection experiments on the size of quail (Marks 1988). Also, although clines of character variation (gradual changes across large geographic areas) can result from genetic drift among local populations and gene flow between them, only natural selection is likely to cause parallel variation among species. Such parallelism is widespread in the color of the plumage of birds (Zink & Remsen 1986) and many other organisms.

Ornithologists disagree about the existence of parallelisms among species in size variation. Much of the literature on this subject concerns criticisms of Bergmann's expectation of larger forms in colder regions rather than empirical comparisons of patterns and analyses of their environmental correlates (Aldrich & James, in press). James (in press) drew a random sample of 21 species of passerines in North America that exhibit geographic variation and compared their pattern with that of the American Robin *Turdus migratorius*. Nineteen species showed positive rank correlations with the American Robin. The probability of obtaining as many as 19 out of 21 by chance is 0.00011. Natural selection plus some gene flow is the most likely cause of this congruence in size variation among passerines.

In spite of support of the predictions for the current view of how microevolution works, clearer understanding may come from additional tests of models and attempts at refutation. In this paper, we use data on Red-winged Blackbirds *Agelaius phoeniceus* to test an assumption of Lande's (1979) model for the estimation of the past forces of directional selection that have resulted in differentiation in character complexes between populations. This model presumes the validity of two assumptions:

1. There is no correlation between genetic and environmentally induced variation.
2. Intraspecific phenotypic variances and covariances (the elements of the variance-covariance matrix) within populations are constant. They do not change as the mean values of characters change across localities or through time. The correlations of the log characters within populations are the same in different populations.

A check of the first assumption requires reciprocal transplant experiments to discover the magnitude and directions of environmental effects. For the Red-winged Blackbird (James 1983, James & NeSmith 1988), such experiments have suggested that there are statistically significant environmental correlations between genetic and environmentally induced variation. In one such experiment in 1987 between Colorado and Florida (James, NeSmith & Rebon, manuscript), in which eggs were exchanged among localities and young were reared by foster mothers, the correlations between genetic and environmental effects on bill measurements were negative. See also the experimental work of Ricklefs & Peters (1981) and Ricklefs (1984) with Starlings *Sturnus vulgaris*, Slagsvold & Lifsjeld (1985) with the Great Tit *Parus major*, and Via (1984) with insects.

Lande (1979) suggested that a way to check the second assumption, when the genetic variance-covariance matrices within localities are unknown, is to assume that phenotypic variances, covariances and correlations among characters mirror their genotypic ones and to see whether these are stable in closely related populations. In this paper we explore this possibility for the Red-winged Blackbird.

METHODS

In an attempt to characterize the general overall phenotypic covariation between the size and shape of adult redwings, we define size variables and shape a priori. Then we examine the geographic covariation between size and shape and the extent to which this covariation is present within populations.

Our morphometric analysis of variation in adult male Red-winged Blackbirds is based on measurements of 545 individuals, made primarily on museum specimens by RL, organized by two-degree latitude-longitude blocks. These data were supplemented by additional measurements by FCJ for specimens taken at the six study sites where former transplant experiments have been conducted (James 1983, James & NeSmith 1988). The four measurements reported here are of bill length (culmen, BL), bill depth (at the nostril, BD), wing length (unflattened chord, WL), and tarsal length (TS). These are four measurements that can be made on museum study skins of birds with minimal measurement error. Adjustments were made for differences between measurements of the same specimens by RL and FCJ, and all were multiplied by 100.

Construction of a graph for the display of allometric relationships within and across populations

The analysis of shape and the interpretation of the allometric relationship between size and shape is facilitated by application of the methods of Mosimann & James (1979). We use \log_{10} WL as a size variable, and we express shape as a set of ratios transformed to differences between logs. The ratio of wing length to bill length changes dramatically across localities. The smallest individuals tend to have the longest bills. The ratio of wing length to tarsal length is also larger in larger birds, but in this case both variables increase. The ratio of bill length to bill depth has direct functional significance for feeding. Transformed to logs, these variables (log WL minus log BL, log WL minus log TS, and log BL minus log BD) are a vector of shape variables for each bird. Of course they do not capture all the shape variation between the forms, but their change with size should give a reasonable estimate of major allometric changes within and across localities. Principal component 1 of the covariance matrix of the means of the three shape variables for 17 geographic blocks gives the primary axis of shape variation for the species. Because no size information entered the principal component analysis, it represents only variation in shape (Darroch & Mosimann 1985).

An equal-frequency ellipse (Wilkinson 1988) around the distribution of the means of size and shape by latitude-longitude blocks in a graphic space can show the extent of their allometric covariation across blocks. Correlations (Table 1) and equal frequency ellipses (Figures 1 and 2) in this space allow direct comparisons of the extent to which the overall geographic covariance of size and shape is present within blocks.

RESULTS

Size variation

The order of the 17 geographic blocks in Table 1 and the x-axis in Figures 1 and 2 is the order of increasing size (wing length). The smallest birds (average wing length 108 mm, weight 57 g) occur in the southeastern United States and the lowlands of southeastern Mexico. There is little size variation among blocks 4 and 14, but in the high plateaus of Colorado and Mexico redwings are exceptionally large (average wing length 138 mm, weight 75 g).

TABLE 1 - Correlations between size and shape in adult male Red-winged Blackbirds for 17 two-degree latitude-longitude blocks and for the average values among blocks. Size is defined as log wing length and shape as principal component 1 of a covariance matrix among three log ratios (increasing WL/BL, WL/TS, decreasing BL/BD). A locality is named in each block, and the blocks are ordered by increasing size of the birds.

	Two-degree Lat.-Long. Block	n 545	Locality in block	Correlation (r) between size and shape**
1 *	26-80	66	Everglades, Florida	0.42
2 *	18-94	13	Tlacotalpan, Mexico	0.70
3 *	30-84	27	Tallahassee, Florida	0.39
4	42-82	34	Ann Arbor, Michigan	0.52
5	42-70	38	Boston, Massachusetts	0.21 ns
6	36-118	34	Fresno, California	0.25 ns
7	38-118	66	Reno, Nevada	0.36
8	34-118	38	Los Angeles, California	0.25 ns
9	32-114	50	Yuma, Arizona	0.42
10	36-114	25	Las Vegas, Nevada	0.29 ns
11	36-120	35	Monterey, California	0.43
12 *	46-94	11	Park Rapids, Minnesota	0.39 ns
13	41-116	24	Battle Mountain, Nevada	0.24 ns
14	36-122	30	San Francisco, California	0.15 ns
15 *	40-104	21	Greeley, Colorado	0.26 ns
16 *	18-98 W	20	Coatetelco, Mexico	0.57
17	18-98 E	13	El Carmen, Mexico	0.00 ns
Across blocks				0.89

* Study sites where transplant experiments have been conducted (James 1983; James & NeSmith 1988).
** All correlations are significant at $P = < 0.05$ unless marked ns.

Shape variation

The principal component analysis based on the average values for each of three shape variables for adult male redwings for the 17 blocks shows that there is a strong geographic pattern of covariation among these ratios. Principal component 1 accounts for 84% of the variance in shape. It has an eigenvalue of 17.3. The standardized coefficients for the equation describing PC1 are 0.68 log WL/BL, 0.17 log WL/TS, and -0.24 log BL/BD.

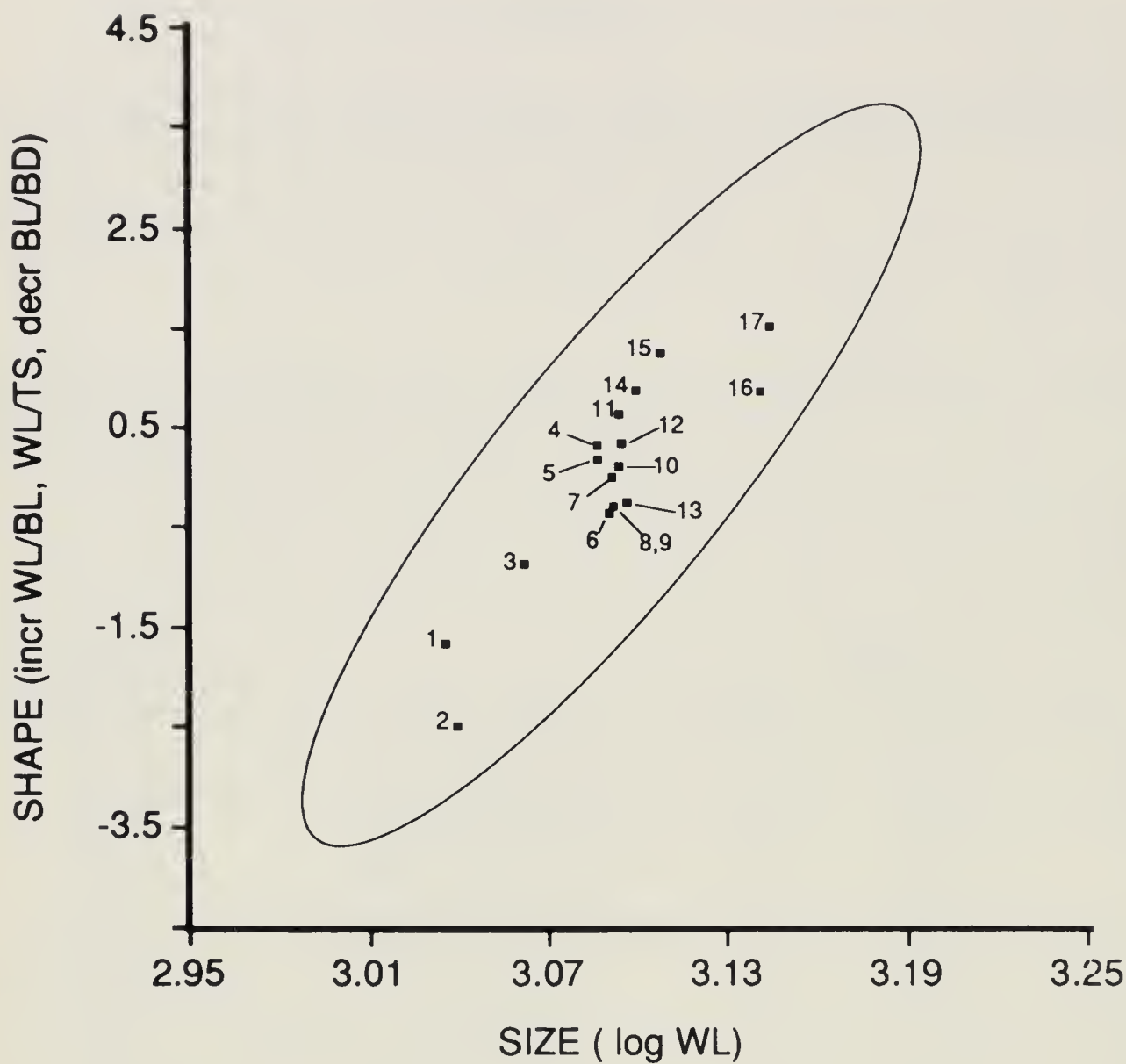


FIGURE 1 - Geographic variation in the size and shape of Red-winged Blackbirds across 17 geographic blocks. Size is expressed as log wing length (multiplied by 100) and shape as principal component 1 of a covariance matrix of three log ratios (see text). The ellipse is a 0.99 equal-frequency ellipse for means for size and shape of redwings for each block (Table 1).

The covariation of size and shape

Average PC 1 scores for each geographic block plotted against average log WL show substantial allometric covariation between size and shape across localities. A 0.99 equal frequency ellipse captures this overall pattern (Figure 1). Note, however, that the spread of points in the central area of Figure 1 is vertical. In the middle of the size range of redwings (blocks 4 through 14), there is geographic variation in shape but not size. The scores for each bird ($n = 545$) on the shape axis (principal component 1) and the size axis (log WL) were calculated, and 0.5 equal-frequency ellipses were plotted for each of the 17 geographic blocks (Figure 2). Comparisons between the large ellipse for the means of blocks and the small ellipses for variation within blocks show that the same direction of covariation in some cases, but in the middle of the size range of redwings there is almost no indication of an association of size and shape either across (Figure 1) or within (Figure 2) blocks.

Another way to examine the association of size and shape within and across localities is to examine their Pearson product moment correlations (Table 1). The overall among-block correlation between size and shape is high, 0.89. Correlations within blocks are all positive, but 9 of 17 are not statistically different from zero at $P < 0.05$. When the conservative Bonferroni correction is applied to account for experiment-wide error rate, only three are significant (1, 4, 9). The more crucial hypothesis (Snedecor & Cochran 1980, p. 187) that these sample correlations are from the same population could not be rejected (chi square 11.2, 16 df, $P = 0.79$).

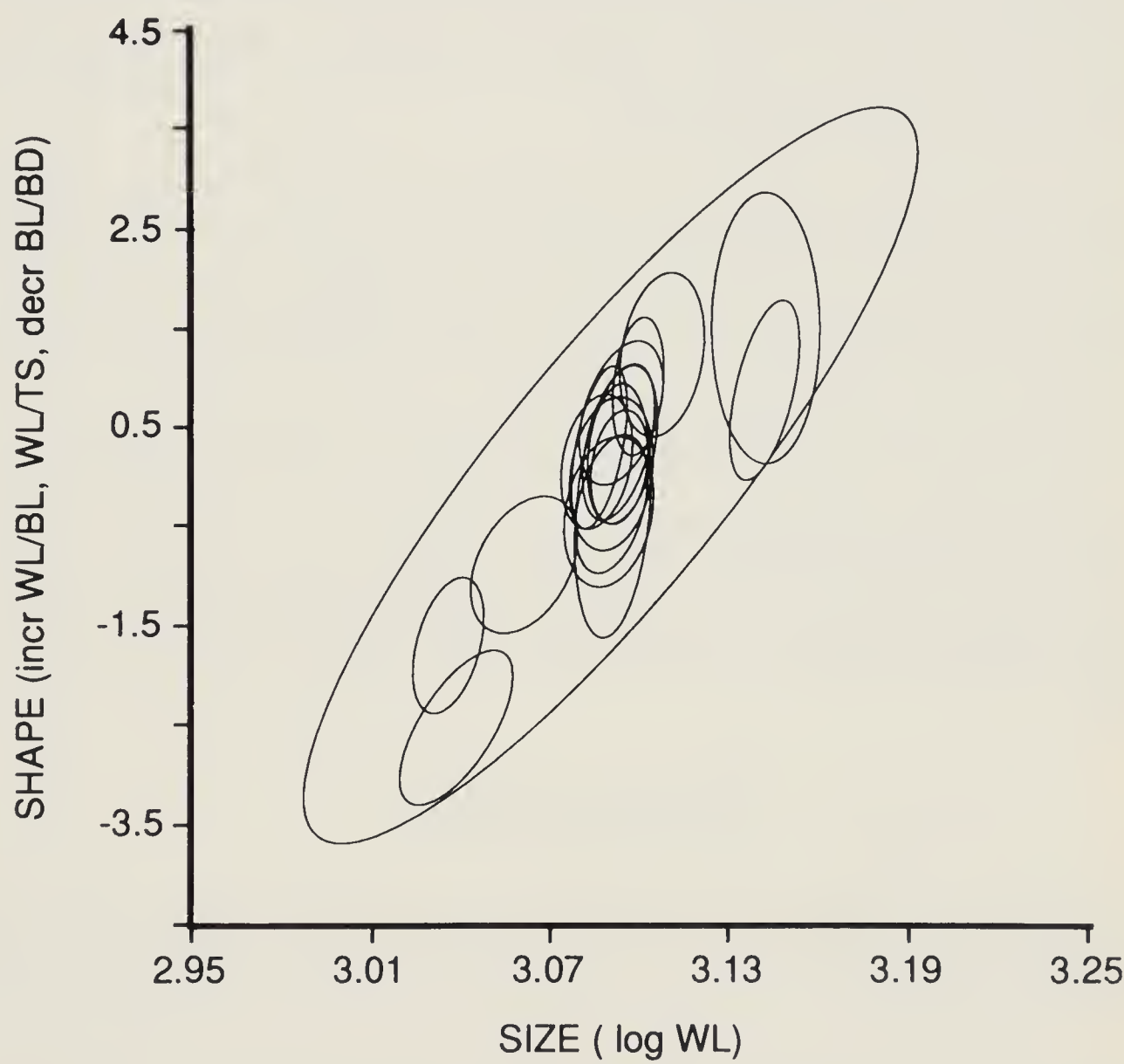


FIGURE 2 - Small (0.5) equal-frequency ellipses for each of 17 geographic blocks show the extent of within-block covariation in size and shape with the geographic (large ellipse) covariation.

Although these within block correlations of size and shape are not statistically different from each other, their covariance matrices, which are made up of their variances and covariances, are different (Box's M rejected at $P = 0.0001$). The inequality of the covariance matrices does not result from unequal correlations (standardized covariances) but rather from unequal variances for both size (chi square 36, 16 df, $P = 0.003$) and shape (chi square 46, 16 df, $P < 0.001$).

DISCUSSION

The correlation of size and shape across localities in Red-winged Blackbirds is striking. A rigorous check of the assumption of the constancy of genetic variance-covariance matrices for the allometric relationship between size and shape for the 17 populations would require extensive captive breeding experiments, such as those recently reported by Lofsvold (1988) for *Peromyscus* and by Atchley and coworkers (Atchley et al. 1981, Kohn & Atchley 1988) for captive mice and rats. Such studies are not feasible on birds. However, a check on the constancy of phenotypic character variance-covariance matrices in birds need not be assumed. It can be checked on the basis of measurements of large samples of museum study skins, preferably even larger than the samples reported here.

We found that the phenotypic covariance matrices did change as the average size and shape of the birds changed across geographic blocks. By plotting ellipses, we found that there seemed to be a geographic pattern to the change. By further testing, we found that the major cause of the change was not a change in the correlations between size and shape among populations, but rather a reduction in the variance of both size and shape in populations in the middle of the ranges of these two variables.

More empirical analyses of correlated evolution among quantitative characters would be welcome, as would more examples of the extent to which phenotypic variation represents genetic variation (Cheverud 1989, Zeng 1988, Turelli 1988a,b). Because interest is increasing in applications of Lande's model for estimation of the intensity and direction of natural selection in field situations and for reconstruction of past selection events (e.g. Lande & Arnold 1983, Price et al. 1984, Price & Grant 1985, Price & Boag 1987), we recommend prior analyses in which assumptions of the model are tested.

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GENOTYPE-ENVIRONMENT INTERACTION FOR BODY SIZE IN THE GREAT TIT *PARUS MAJOR*

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ABSTRACT. The genotype provides a developmental program which builds the phenotype in interaction with the environment. These programs may lead to a plastic phenotype that is better adapted to each environment, but this requires that a number of conditions are fulfilled. At the same time, phenotypic plasticity plays an important role in adaptation to varying local conditions and plasticity has important consequences for the maintenance of genetic variation through variable selection regimes. I will report on attempts to measure the genetic variation in nestling growth under different conditions in the Great Tit. We employ two strategies: field experiments in which sibs are raised in broods of different size, and attempts to measure the environmental conditions at the level of individual territories at the time when the ontogeny of the traits actually takes place. I will discuss these two research strategies in relation to the measurement of genetic variation within and among populations. It becomes clear that we need a better understanding of the underlying physiological processes and detailed measurements of the relevant environmental variables before we can return to the study of genotype-environment interaction.

INTRODUCTION

In a reasonably constant environment, the amount of genetic variation for a quantitative trait can be described by the heritability and the phenotypic variance in that trait. This information allows one to make estimates of how rapid the mean value of the trait in the population might change due to directional selection. Several studies have reported significant amounts of genetic variation within populations for fitness related traits (see Boag & van Noordwijk 1987).

The observed amounts of genetic variation would allow a fairly rapid response to selection. Changes in the order of a few tenths of a per cent to a few per cent of the mean value per generation are possible at moderate selection pressures, in the order of 5 - 50% mortality.

MAINTENANCE OF GENETIC VARIATION

The question how genetic variation for quantitative traits is maintained in natural populations is largely unsolved. There are three major groups of processes that can contribute to the continued presence of within population genetic variation; 1) overdominance, 2) mutation-selection balance and 3) genotype-environment interaction.

- 1) For a locus with two alleles, genetic variation will be maintained if the heterozygote has a higher fitness than either of the homozygotes. This mechanism is probably not very important, because it requires substantial selection (i.e. the death of genetic individuals) every generation.

- 2) Mildly deleterious mutations arise continuously, and it takes time before these mutants are eliminated. The genetic variation results from a balance between mutation giving rise to new alleles and selection eliminating them (see Lande 1976). There is some doubt whether this process can really maintain large amounts of variation in quantitative traits (e.g. Bürger 1986, 1988).
- 3) There is no single optimal genotype. Instead there is a mixture of genotypes whose relative performance depends on the environmental conditions. In this group of processes, not only the average environmental conditions are important, but also the variability in conditions. To an ecologist, this explanation seems very plausible, but the processes involved are difficult to study, since there are many variables involved.

GENOTYPE ENVIRONMENT INTERACTION

This is an area where little theoretical work and little empirical work has been done (but see e.g. Scharloo 1987). Intuitively, it makes sense that e.g. whether having enzyme variant a or variant b will be favoured will depend on substrate concentrations, temperature etc. The major question now becomes how big are the differences between these enzymes relative to the variation in conditions encountered (van Noordwijk 1989, 1990a).

One of the most interesting aspects of the interactions is phenotypic plasticity. It will however also complicate studies of genotype-environment interaction. Phenotypic plasticity is a general term for the phenomenon that a single genotype may give rise to different phenotypes depending on the environmental conditions during the ontogeny of the trait. A good way to deal with it is through the concept of reaction norms. The reaction norm is defined as the set of phenotypes displayed by a single genotype depending on the environmental conditions. It can be measured directly whenever it is possible to test the same genotype in different conditions. This is possible for clonal organisms and for traits that are formed repeatedly without significant learning or age effects. Where it is not possible to have exactly the same genotype in different environments, one can, at least in principle, draw inferences from groups of relatives.

In performing experiments, it is essential to manipulate those aspects of the environment that do indeed play an important role in the genotype-environment interaction. In other words, the investigation of genotype-environment interaction requires substantial knowledge of eco-physiology. Moreover, with respect to its potential role in maintaining genetic variation, one wants to study those environmental parameters that are indeed variable among individuals. In other words, one requires insight in the distribution of environmental conditions among individuals (van Noordwijk 1989). Thus, genotype-environment interaction and phenotypic plasticity are not only interesting because of their potential role in maintaining genetic variation, but also and probably especially so, because they provide links between the proximate determination of phenotypic traits and their ultimate consequences. In other words, we get close to a study of the evolution of proximate mechanisms.

A CASE IN POINT

Using the existing knowledge about heritability in the Great Tit *Parus major* (e.g. van Noordwijk 1987, van Noordwijk & van Balen 1988), we chose to work on variation in fledgling weight with food availability as the main environmental factor (see Henrich 1989, Henrich & van Noordwijk 1991). The heritability of nestling weight is strongly dependent on the environmental conditions during growth (van Noordwijk 1988b, et al. 1988). We manipulated brood size together with reciprocal cross-fostering, in the expectation that nestlings in enlarged broods would receive less food and would grow less well. The design of these experiments is illustrated in Figure 1. Although the expression of genetic variation did indeed depend on the experimental manipulation and on the environmental conditions, it proved impossible to investigate genotype-environment interactions systematically (see Henrich 1989).

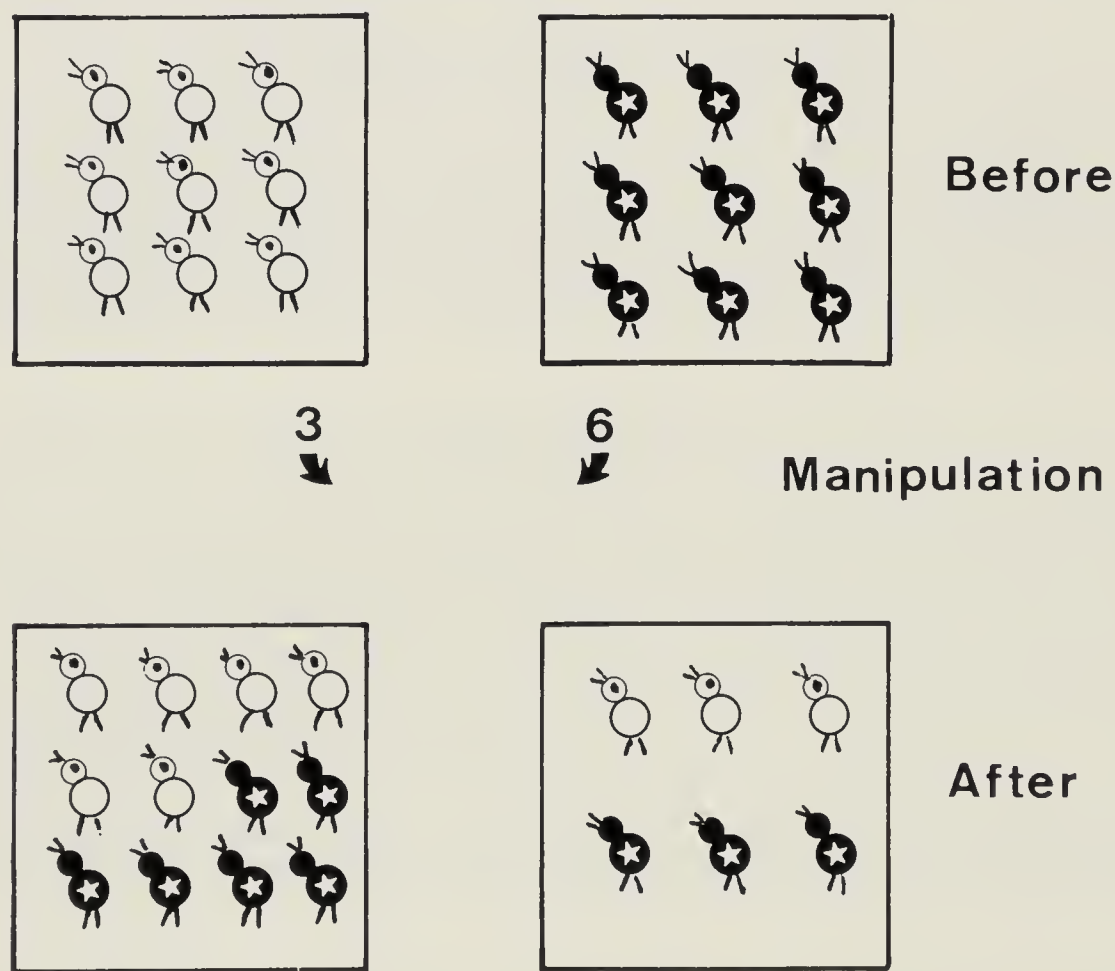


FIGURE 1 – The experimental design used for investigating genotype-environment interaction for body size. Nestlings are exchanged between two broods on the second day after hatching to create an enlarged and a reduced brood, with half the nestlings in each of these originating from each of the original broods. This allows comparisons of genetic differences between the two sib-groups within each nestbox and an environmental comparison between the two nestboxes within a sib-group (see Henrich 1989).

Two major problems precluded an analysis of genotype-environment interactions. The first was that the effect of our brood size manipulations was small compared to the natural variation in food availability. The second problem was that in the enlarged broods competition for food among nestlings became an important qualitatively different process, that did not occur in the reduced broods. Moreover, it is unavoidable that through our experiment the initial size heterogeneity is somewhat enhanced, making

competition more important. The importance of sib-competition can be demonstrated by simulation (van Noordwijk 1988a), and also by the experiment described below.

Experimental Methods

The experiment described here is an extension of the design in Figure 1 in which the hatching of two to three eggs is delayed. The first part of the experiment and standard methods are described in detail by Henrich & van Noordwijk (1991). The experiment was carried out in the Blauen study area, a woodland dominated by Beech *Fagus sylvatica* on a north-facing slope about 10 km south of Basel (see Nager 1990 for a description). In this area the breeding density of tits as well as their breeding success in terms of nestling survival and fledging weights are substantially lower than in the Hard study area where the main experiments were performed by Henrich (1989).

During egg-laying two eggs (when five were present) or three eggs (when six or seven were present) were removed from the nestcup and stored in a vial in a corner of the nestbox. These eggs were returned to the nest about two days after the suspected onset of incubation. In practice the delayed eggs hatched 0-4 days later than the unmanipulated eggs.

From one day before the expected hatching date, daily inspections were made to establish the hatching date of the brood, defined as the day on which the first eggs hatched. This day is counted as day 0. When two broods hatched on the same day, nestlings were exchanged according to the scheme in Figure 1, where the enlarged brood was given to the birds with the larger clutch size in alternate experiments. The smallest nestlings and delayed eggs that had not yet hatched remained in their nestbox. All nestlings were individually marked with felt-tip pens and later with colour rings. Nestlings were weighed every two days from day 3 till day 15.

Although we attempted to sex the nestlings based on colour differences in the thumb coverlets, these estimates are too unreliable to be useful, especially since there is a strong interaction between weight and reliability of sex estimate. Since the average difference between male and female nestlings of about 0.6 g is small relative to other sources of variation, I will ignore it in the present context.

We expected that under favourable conditions, in small broods with little sib competition, the retarded hatchlings would grow well, whereas poor growth was expected in the enlarged broods.

Experimental Results and Discussion

It is not possible to analyse these experiments in any quantitative way, because there are too few complete experiments and the differences between them are too great. However, a number of features can be illustrated qualitatively with the two experiments illustrated in Figure 2.

There is a large effect of brood size on final weight. The retarded nestlings survive and grow well in the reduced broods, but die rapidly in the enlarged broods. A short period with poor weather occurred between days 7 and 9 in experiment A and between days 9 and 11 in experiment B. Whereas this poor weather had a large effect on the growth curves in the enlarged broods, there is no visible effect in the reduced

broods. Even the two individuals in the reduced brood in experiment A that hatched four days late grew almost normally during this period. The interaction of growth and weather makes it difficult to combine the analysis of experiments that are not simultaneous.

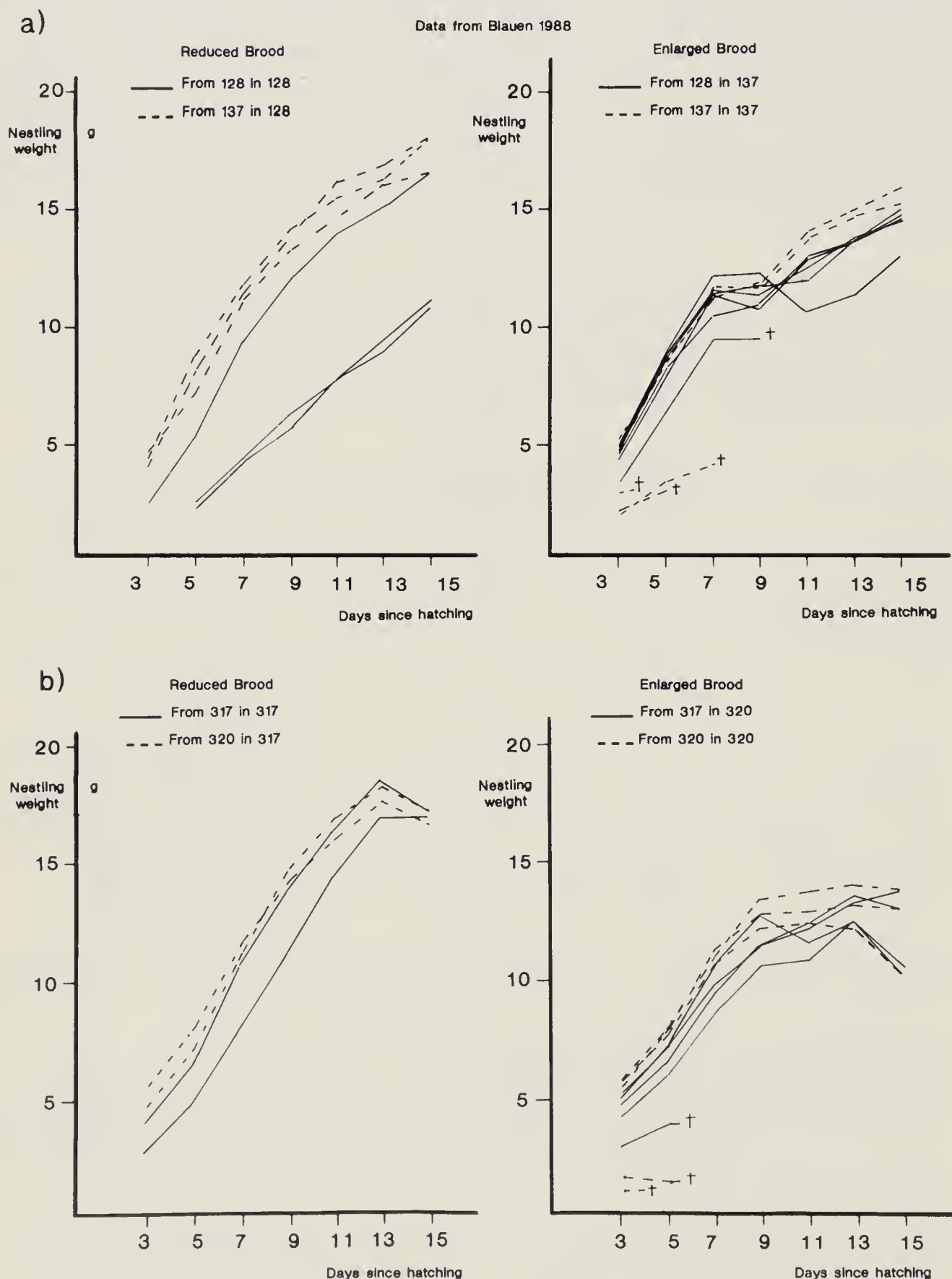


FIGURE 2 – The results of two experiments as outlined in Figure 1 with additional retarded hatching of some chicks (see methods). The nestlings were transferred on day 2 after hatching and weighed every three days from day 3 to day 15. The experiment in a) was performed two days after the experiment in b). See text.

If we ignore the retarded hatchlings, there is a tendency for a decrease in within brood variance, in weight, in the reduced broods, and for an increase in variance in the enlarged broods. This is to be expected as a consequence of the establishment of a weight hierarchy, which is in turn enhanced by sib competition (van Noordwijk 1988a, Henrich in prep.). However, the establishment of a weight hierarchy is contradicted by many changes in relative weight in the enlarged broods, especially in the period when growth is depressed. In theory such changes could be caused by genetic differences in the reaction to adverse conditions. In fact the alternative explanation, namely that chance events play a large role, seems more likely. Such chance events could consist of being fed a large caterpillar. Chance events with large effects will in turn have dramatic effects on the sample sizes required to have any hope of establishing genotype-environment interactions.

One is thus faced with a situation where each experiment demonstrates a number of singular features. At the same time, however, it seems that we understand the whole system sufficiently to be able to interpret nearly all singularities. Nestling growth, or in other terms the ontogeny of body size, is to be seen as a chain with many links. An irregularity in any of these links reduces the strength of the chain. It seems that we can recognize many of the causes for weakening of the individual links, but that there are so many natural causes for weak links that it is impossible to evaluate our experimental changes in some of the links at the level of the strength of the whole chain.

Hindsight

In hindsight, one should have noticed that in a study area where nestling mortality in first broods can be as high as 70%, the range of naturally occurring environmental conditions is so large, that experimentally induced variation is relatively small. If we use experiments as a standardized stimulus and observe very different responses, we are still left with the question that the different response results either from environmental or from innate differences.

There is thus no hope of analysing genotype-environment interaction in field-experiments. The experiments have nevertheless been very helpful in a better understanding of the eco-physiology of growth without reference to the genotype. It is clear that we need a better understanding of the underlying processes and detailed measurements of the relevant environmental variables before we can return to interactions with the genotype. Several projects along these lines have been initiated (see van Noordwijk 1990a,b).

CONCLUSIONS

One can observe that there are significant amounts of genetic variance for many quantitative traits in natural populations. It seems likely that genotype-environment interaction plays a role in maintaining this variation. However, it is too difficult to demonstrate the importance of this interaction in a heterogeneous environment at the level of the phenotypic traits we are interested in such as body size and various life-history traits. Instead, the only approaches open are indirect ones, such as comparative analysis and a more detailed study of the critical aspects of the environment in the ontogeny of the traits in which we are interested.

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CONCLUDING REMARKS: THE GENETIC STRUCTURE OF POPULATIONS

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Molecular techniques have been widely used over the last two decades to document genetic variation within and among populations. These techniques have greatly increased our knowledge of the genetic variation in natural populations. However, the relationship between variation in nuclear and mitochondrial genes that have been studied molecularly and morphological or life-history traits is not well understood. The latter types of traits are those for which natural selection has been studied. Moreover, most traits that make a species or population distinct have a quantitative genetic basis. The understanding of genetic variation in quantitative traits is labour intensive and often requires testing of individuals from each environment in each environment in which the species is found.

We are therefore faced with a discrepancy: We have already learned a great deal about the genetic population structure through the study of genetic markers, but we have no empirical information to relate this to the traits involved in the ability of the population to survive changes in conditions.

We believe that the large majority of the properties that make a population especially adapted to a particular environment, or the properties that give a species its ecological characteristics are based on polygenic variation. This type of polygenic variation is presently beyond rigorous general analysis.

Practical advice (e.g. to conservationists on maintaining genetic variation) is largely based on the assumption that the genes used as markers in molecular studies are representative of all genes and thus also for the genes that supposedly make populations and species to be what they are. Although this belief is based on the best available information, there is a disturbing discrepancy in the fact that the genes used as markers are believed to be selectively neutral and that conversely morphological and life history traits are believed to be under fairly intensive natural selection.

For finding satisfactory solutions for this discrepancy, birds may be the ideal group of organisms, since we know much about their ecology and the natural selection pressures. It is also possible to follow reasonable numbers of individual genealogies in natural populations. One might quote Maynard Smith (1987): "There was a time, not all that long ago, when the "modern synthesis" of evolutionary biology consisted, not of a synthesis of ideas . . . , but of a synthesis based on the paleontology of marine molluscs, the genetics of *Drosophila*, and the taxonomy and ecology of birds." [We are now reaching a stage where] ". . . birds may offer the best chance for a genuinely

synthetic theory of evolution." One might add that we need a better insight in evolutionary processes both for the sake of understanding the observed diversity of life, and for an assessment of how human activities affect nearly all forms of life.

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SYMPOSIUM 47

BIRDS AS INDICATORS OF GLOBAL CHANGE

Conveners I. L. BRISBIN and D. B. PEAKALL

SYMPOSIUM 47

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INTRODUCTORY REMARKS: BIRDS AS INDICATORS OF GLOBAL CONTAMINATION AND CYCLING PROCESSES

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It has often been said that imitation is one of the sincerest forms of flattery. If this is true, then when it comes to concerns for our earth's present environmental crisis, ornithologists must feel very flattered indeed. Many years before scientists in the other life sciences had begun to express concerns for the growing levels of contaminants in our forests, air and waters, the concept of the "canary in the mine" and Rachel Carson's (1962) clarion call of the *Silent Spring* had begun to look at birds as warnings of the degrees to which man-made pollutants were already beginning to threaten many of the other inhabitants of this planet. Today in fact, it has now become almost fashionable to champion the particular group of organisms with which one has become familiar, as an ideal "early warning system" to detect and evaluate various forms of threat to our environment. One of the groups which has recently gained much attention in this regard for example, has been the world's frogs, toads and other amphibians.

Although the forms of environmental threats and impacts are varied, the widespread release of environmental contaminants has long been at the forefront of concerns by both the public and scientists alike. Over the past several years a number of incidents of accidental contamination have resulted in significant environmental impacts on a regional and in some cases, a global scale. Many of these incidents have resulted in the widespread release of contaminants of a variety of kinds and have demonstrated in turn, the need to develop more effective means to assess the fate and effects of such pollutants across extended geographic scales. Birds as a group possess a number of characteristics that make them ideally suited to serve as indicators across such extended distances, as a result of their flight mobility. Birds are also visible and well-known to the general public and changes in their numbers, health or vigor are generally quickly reported and thus readily documented. Birds also sample a wide variety of food webs, and according to environmental monitoring needs, appropriate species can usually be identified representing any of the major trophic levels of a particular ecosystem.

All of these factors have combined to increasingly suggest the use of birds as bioindicators of environmental change (Temple & Wiens 1989). When it comes to the use of birds as indicators of the release and cycling of contaminants in the environment however, a strong foundation of basic principles of chemistry, ecology and ornithology must be established upon which specific research/assessment scenarios can then be built. The papers in this symposium are designed to present some representative case histories of such scenarios as well as to describe some of those basic principles forming the foundation upon which they have been built.

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HERONS AND EGRETS AS PROPOSED INDICATORS OF ESTUARINE CONTAMINATION IN THE UNITED STATES

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ABSTRACT. The National Contaminant Biomonitoring Program of the U.S. Fish and Wildlife Service includes the sampling of freshwater fish, starlings, and duck wings. In order to include an estuarine component, herons and egrets are being evaluated. Organochlorine concentrations were measured in eggs and chicks of Snowy Egrets *Egretta thula*, Great Egrets *Casmerodius albus*, and Black-crowned Night-Herons *Nycticorax nycticorax* collected in Rhode Island, Texas, and California. Chicks of all species at all locations accumulated DDE and polychlorinated biphenyls (PCBs), and accumulation rates may serve as the basis for an indicator program of estuarine contamination. Biochemical responses of embryos and chicks were also evaluated. Microsomal arylhydrocarbon hydroxylase and benzyloxyresorufin-O-dealkylase activities in livers of 10-day-old night-heron chicks were elevated at a contaminated site in San Francisco Bay, CA, when compared to a "reference" site in Virginia. Quantification of liver enzyme activities may serve as a rapid cost-effective biomarker of pollutant exposure.

Keywords: Biomonitoring, estuaries, organochlorines, Black-crowned Night-Heron, *Nycticorax nycticorax*, Snowy Egret, *Egretta thula*, Great Egret, *Casmerodius albus*, cytochrome P-450, monooxygenases, United States.

INTRODUCTION

The National Contaminant Biomonitoring Program (NCBP), formerly named the National Pesticide Monitoring Program, was initiated by the U.S. Fish and Wildlife Service in 1964 to monitor concentrations of DDT and other persistent chemicals in the environment. Research is now underway to add a new component focused on estuaries.

Herons and egrets are good candidates for an estuarine component to the NCBP. Rationale for their use includes their high trophic level position, bioaccumulation of contaminants, wide geographic distribution, nest site fidelity, and the relative synchrony of the nesting season within a region. Both contaminant burdens and biochemical markers of contaminants in herons and egrets are being evaluated for the NCBP.

CONTAMINANT MONITORING

Early attempts to describe geographic and species-specific contaminant profiles in United States colonial waterbirds used eggs (Ohlendorf et al. 1979a). However, herons and egrets may be migratory, so their eggs are of limited value for monitoring

because they may reflect contaminants the female accumulated elsewhere. Another disadvantage to eggs in a monitoring program is that although organochlorines and some trace elements (e.g., selenium and mercury) can be measured in eggs, other contaminants (e.g., cadmium, lead, chromium) do not accumulate in eggs or do not show a relation to degree of exposure (Leonzio & Massi 1989).

To overcome the limitations of eggs as indicators of contaminant exposure, heron chicks have also been collected and tissues analyzed (Ohlendorf et al. 1979b). Because the food fed to heron chicks comes from within a few km of the nesting colony (Custer & Osborn 1978), their tissues should reflect local contamination. One confounding factor related to use of chicks is that residues present in the egg may be incorporated into the chicks and thus still influence the measured values. However, there is a rapid loss of contaminants from the embryo to the chick, thereby diminishing the influence on contaminants in eggs to those measured in chicks (Becker & Sperveslage 1989, present study). Furthermore, rapid growth minimizes the influence of egg contaminants, such that most of the contaminant burden in chicks probably reflects levels in the local food supply (Charnetski 1976).

To determine the most suitable species and tissues (including eggs) to sample for contaminant analysis, eggs and chicks of Black-crowned Night-Herons *Nycticorax nycticorax*, Great Egrets *Casmerodius albus*, and Snowy Egrets *Egretta thula* were collected and analyzed for organochlorines. Samples will also be analyzed for trace elements and polycyclic aromatic hydrocarbons (PAHs).

Collection and Analytical Protocols

Night-heron and egret eggs and chicks were collected in 1987 from one colony each along the Rhode Island, Texas and California coasts (Custer & Ohlendorf 1989). Within each clutch sampled, an egg was collected late in the incubation period, the chick from the first egg to hatch was collected when about 15 days old, the second when about 10 days old, and the third when about five days old. Eggs and carcasses were analyzed for organochlorines as described by Cromartie et al. (1975) and Kaiser et al. (1980). The lower limit of quantification was 0.01 µg/g wet weight for organochlorine pesticides and 0.05 µg/g wet weight for polychlorinated biphenyls (PCBs).

PCB Accumulation

As one example of uptake kinetics, PCB concentrations are presented for eggs and skinned carcasses of night-herons collected in Rhode Island (Figure 1). The mean concentration of PCBs (µg/g) in eggs was higher than in chicks of any age. This difference was due partly to the rapid weight gain of chicks between 5 and 15 days of age. Concomitantly with this increase in body mass, total burden of PCBs (µg) in chicks also increased. PCBs (µg) accumulated in all species at all sites, but the accumulation in night-herons from Rhode Island was the most dramatic. Based on limited data, the total body burden was about twice that of the skinned carcasses.

Accumulation rates (µg/day) of a particular contaminant within a brood could serve as a sampling unit. This approach overcomes the problem of contaminants in eggs reflecting exposure distant to the colony site. One assumption of this method is that contaminants do not vary significantly within the clutch, a finding previously demonstrated in night-herons (Custer et al. 1990). Unless contaminant concentrations in

eggs affect their subsequent accumulation in chicks, this approach is not biased by contaminants transferred from eggs to chicks. A possible scenario would be to collect two chicks from n broods, one chick at about 5 days of age and another at about 15. The accumulation rate (e.g., μg gained/day from 5 to 15 days) for each nest would then be used as a dependent variable indicative of environmental contaminant levels, and means could be compared among locations and years as treatment classes.

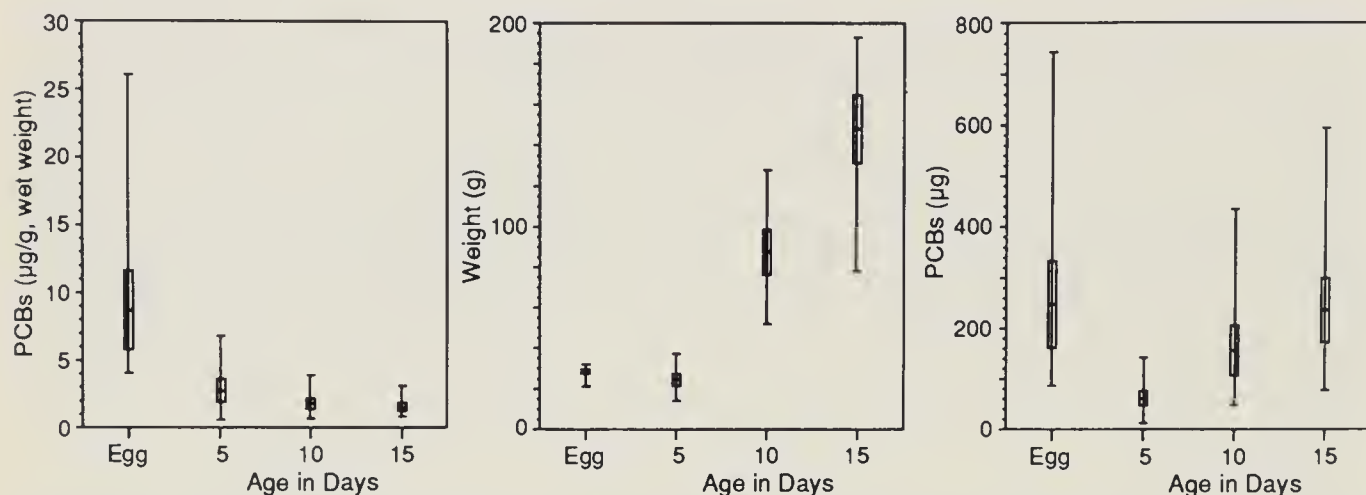


FIGURE 1 - PCB concentrations, body weights and total PCB contents of eggs and 5-, 10-, and 15-day-old skinned carcasses from seven broods of Black-crowned Night-Herons collected on Gould Island, Narragansett Bay, Rhode Island, 1987. In each graph, horizontal lines are the arithmetic mean; enclosed bars represent standard errors and vertical lines indicate ranges.

BIOCHEMICAL MONITORING

Monitoring of environmental contaminants traditionally involves quantification of potentially hazardous compounds in various matrices (e.g., soils, plants and animals). Although this approach works well for many contaminants (especially those with high bioaccumulation and lengthy persistence), these chemical analyses are often time-consuming and costly. An alternate approach for monitoring exposure involves measurement of biochemical responses that result from exposure to specific pollutants.

Induction of cytochrome(s) P-450 and related monooxygenase activities in fish and wildlife has been proposed as one biomarker that could serve as a rapid and cost-effective "early warning system" of environmental contamination (Payne et al. 1987, Rattner et al. 1989). The central role of cytochrome(s) P-450 in detoxication would seemingly make them better indicators of xenobiotic exposure than some other biochemical parameters (e.g., serum protein and enzyme activities, amino acid profiles) which are more indicative of generalized stress and cellular damage. Recent field studies of terns and herons indicate that induction of monooxygenase activity is associated with exposure to organic pollutants (Hoffman et al. 1987, Rattner et al. 1989, Bellward et al. 1990).

Methods

To evaluate the usefulness of cytochrome(s) P-450-related measurements as biomarkers of pollutant exposure, pipping embryos and 10-day-old Black-crowned Night-Heron chicks were collected during 1989 at Chincoteague National Wildlife Refuge ($37^{\circ}56'$ N, $75^{\circ}25'$ W; Ohlendorf et al. 1979a), Northampton County, Virginia,

a relatively clean “reference” site, and from sites presumed or known to be polluted, including Cat Island (44°34' N, 88°00' W) in Green Bay, Brown County, Wisconsin, and Bair Island (37°32' N, 122°12' W), San Mateo County, and West Marin Island (37°58' N, 122°28' W), Marin County, in San Francisco Bay, California. In the field, pipping embryos and chicks were weighed and sacrificed. The liver of each was removed, minced in glycerol, snap-frozen in cryotubes and stored at -70°C. The remainder of each sample was frozen for subsequent analysis of organic pollutants.

Samples were thawed and homogenized, and microsomes were prepared by differential centrifugation. Activities of arylhydrocarbon hydroxylase (AHH), ethoxyresorufin-O-deethylase (EROD), benzyloxyresorufin-O-dealkylase (BROD), pentoxyresorufin-O-dealkylase (PROD), and ethoxycoumarin-O-deethylase (ECOD) were quantified to evaluate potential induction of cytochrome(s) P-450. These types of responses have been documented in several species of wild birds (Rattner et al. 1989).

Microsomal enzyme activities of chicks were compared by analysis of variance and Tukey’s method of multiple comparison. Upon completion of organic pollutant analyses, the association between enzyme activities and pollutant burdens will also be examined. Methods are being developed to analyze P-450 isozymes by sodium dodecylsulfate polyacrylamide gel electrophoresis and western blotting. Such methods would serve as a potentially rapid, inexpensive, and sensitive tools for screening large numbers of samples.

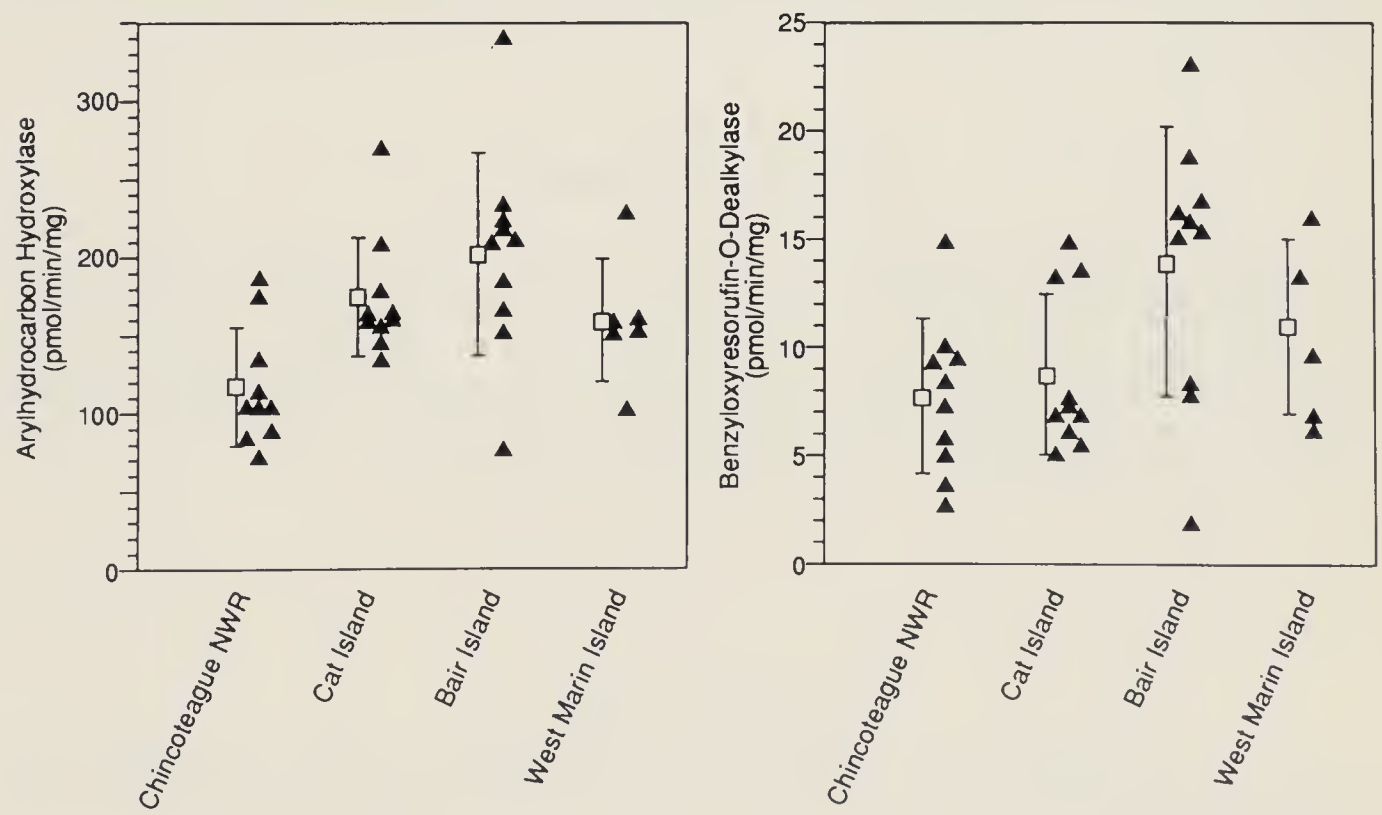


FIGURE 2 - Hepatic microsomal arylhydrocarbon hydroxylase and benzyloxyresorufin-O-dealkylase activity from Black-crowned Night-Heron chicks, 1989. Open squares and vertical lines are mean \pm SD; closed triangles are individual observations.

Enzyme Activity

Hepatic microsomal AHH and BROD activities of chicks from Bair Island in San Francisco Bay were significantly greater ($P<0.05$) than values from Chincoteague National Wildlife Refuge (the reference site, Figure 2). Inspection of enzyme activity values for individuals revealed that 6 of 10 AHH values and 7 of 10 BROD values from Bair

Island were greater than 2 standard deviations above the reference mean site. Notably, the 6 elevated AHH values were a subset of the 7 chicks with elevated BROD from Bair Island. Two of the 10 AHH values for chicks from Cat Island in Green Bay were greater than 2 standard deviations above the control site mean. Activities of EROD and PROD of chicks did not differ among the sites that were studied. Activity of ECOD in Cat Island chicks (mean \pm SD = 113 \pm 51 pmol/min/mg) was significantly less ($P < 0.05$) than those from the Chincoteague National Wildlife Refuge reference site (332 \pm 172); ECOD activity at other sites was intermediate (Bair and West Marin Islands = 258 \pm 189 and 192 \pm 31). Analyses of organic pollutants and monooxygenase activities of pipping embryos have yet to be completed.

These data suggest that some chicks are being exposed to types and quantities of organic pollutants that induce cytochrome(s) P-450 and monooxygenase activities. It is anticipated that contaminant burdens in carcasses of chicks will lend support to this hypothesis. Absence of an EROD response in night-heron chicks that exhibited AHH induction suggests either a qualitatively different pattern of induction or a different substrate specificity of cytochrome P-450 isozymes compared to the laboratory rat. The toxicological consequences of monooxygenase induction may include increased xenobiotic detoxication and elimination, enhancement of metabolic activation of some carcinogens, tumorigenesis and impairment of reproduction (Rattner et al. 1989). However, the association between monooxygenase induction and population-level effects in wildlife is equivocal. Nonetheless, quantification of monooxygenase enzymes may serve as a useful biomarker of pollutant exposure and environmental quality.

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INDICATOR SPECIES, BIRDS, TOXIC CONTAMINANTS, AND GLOBAL CHANGE

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ABSTRACT. It has been pointed out that the concept of "indicator" species must be strictly and narrowly applied to be meaningful and useful, particularly in using birds as an index of environmental quality or as a measure of environmental change. The concept is used to consider global changes in fluxes of heavy metals, trace elements and the persistent organochlorine biocides, and is expanded to consider uses of birds to: 1) measure changes in oceanic food webs, particularly the effects of overfishing; 2) document consequences of acidic deposition; and 3) record the impact of large-scale changes in habitats. Birds are generally unsuitable for detecting or measuring large-scale global changes in the fluxes of metals or trace elements. Globally, these pose no threat to avian populations; their principal effects, and those of the newer-generation biocides, are local in scope. Seabirds are particularly useful for measuring changes in organochlorine contamination of the oceans; programs that include periodic collection of seabird eggs for frozen storage should be expanded in the Northern Hemisphere and be initiated in the Southern to determine long-term changes in organochlorine contamination of the marine environments in both hemispheres.

Keywords: Indicator species, organochlorines, PCBs, marine pollution, global change.

INTRODUCTION

The first draft of this paper was restricted in its scope to a brief review of the generalizations that can now be made about the impacts of the principal environmental contaminants on bird populations, and to a discussion of the uses of selected avian species to measure hemispheric changes in the environmental levels of the persistent organochlorine biocides. It proved impossible, however, not to mention that the 'Silent Spring' predicted by Rachel Carson (1962) has become a reality over much of eastern North America, but not for the reasons that she foresaw. The significance of this process for conservation policies is vastly greater than the impacts of biocide use. Since a recent review of the effects of contaminants on bird populations (Risebrough 1986) is now only partly out-of-date, this topic was eliminated in favor of an expanded discussion of the concept of 'indicator species'. Space constraints permit only a representative bibliography.

BIRDS AS 'INDICATOR SPECIES'

This topic has been addressed in two recent reviews. Morrison (1986) concluded that the "use of birds as direct indicators of specific environmental changes is tenuous at best", pointing out that birds usually respond to secondary or tertiary effects of a primary cause. In such cases birds can not be considered as satisfactory indicators of environmental change. The case was made for a narrow and restricted use of the term "indicator". The best way to measure the anticipated global warming would therefore be by taking temperatures, rather than attempting to document any changes in populations of birds or of other species potentially affected by the warming process.

Temple and Wiens (1989) reviewed the results of a workshop devoted to the question of whether bird populations can be used as indicators of environmental change. The conclusions reached were generally those already made by Morrison (1986) that "the prospects for using birds as sensitive bioindicators are not especially good". The primary population parameters of birth rate, death rate, and dispersal are more immediately affected by environmental change than are a host of secondary parameters that affect total population size and population abundance. Consequently it is very difficult to sort out causal relationships. Temple and Wiens (1989) strongly recommended improvements in census methods and in data storage and retrieval, and long-term monitoring of both primary and secondary population parameters.

Both reviews mentioned the use of birds to assess contaminant effects and to measure changes in environmental levels of persistent contaminants. Neither, however, mentioned the current and potential uses of birds to measure the impacts of over-fishing and of acidic depositions, impacts that are significant and that are increasing in their magnitudes. Nor did either specifically address the changes that have produced the 'Silent Spring'.

HEAVY METALS AND TRACE ELEMENTS

Local contamination by any of the more toxic heavy metals and trace elements may result in avian mortalities or other adverse effects, even if, as is the case for selenium, the element is essential at lower concentrations. Examples are the mortality of aquatic birds by lead deriving from a factory producing alkyl lead compounds in Britain (Bull et al. 1983), mortalities of seed-eating birds in Sweden caused by seed dressings containing alkyl mercury (e.g. Jensen et al. 1972), and embryonic deformities of aquatic birds breeding in ponds receiving agricultural drainage waters in California that contain high levels of selenium (e.g. Ohlendorf et al. 1987).

Globally, however, the accumulated evidence indicates no threats to avian populations from metals and trace elements. Changes in the fluxes of aluminum, iron, manganese, cobalt, nickel and copper into the marine environment beyond the coastal zone have not been found; current fluxes appear to be of the same order as those over recent geological timescales. The fluxes, however, of zinc, cadmium and mercury (Yeats & Bewers 1983) and lead (e.g. Flegal et al. 1984) into the sea have increased as a result of man's activities.

There have been major changes in the global biogeochemical cycle of lead; most of the lead in the oceanic water column is anthropogenic (e.g. Flegal et al. 1984). Species such as the California Condor *Gymnogyps californianus* and the Bald Eagle *Haliaeetus leucocephalus* have suffered significant mortalities from the ingestion of bullet fragments or lead shot. This, however, is not legitimate trophic accumulation and the effects are local rather than global. However undesirable from other considerations, the accumulation of lead in the sea is not a threat to birds or other wildlife.

Like lead, cadmium is dispersed through the atmosphere but unlike lead it is incorporated into marine food webs and is rapidly re-cycled in surface waters (Knauer & Martin 1981). "High" levels of cadmium have been reported in seabirds, but these are considered to consist principally of "natural" cadmium, e.g. Bull et al. (1977).

Global fluxes of mercury are considered to have approximately doubled as a result of man's activities. Analysis of the mercury content of feathers of birds preserved in museums, particularly the White-tailed Eagle *Haliaeetus albicilla*, has shown a local increase in the Baltic Sea, (Berg et al. 1966). Elsewhere, however, no increase has been evident; e.g. analysis of museum specimens of tuna and swordfish (Miller et al. 1972). Mercury has been implicated in the population declines of White-tailed Eagles in the Baltic, but a critical review of the data and a re-assessment of the role of mercury is now needed. Are fish-eating species in coastal environments, which are exposed to higher levels of mercury than are terrestrial species, less sensitive to the effects of mercury? A defense mechanism has been demonstrated in fish-eating species of marine mammals, that sequesters mercury in a relatively non-toxic chemical complex.

Data on levels of metals and trace elements in avian tissues are difficult to interpret in the absence of comparable data from other areas of the species' range and without consideration of factors such as age. Levels of selenium and heavy metals in diving ducks in San Francisco Bay have been considered "high", e.g. Ohlendorf et al. (1986), but high in comparison with what?

Undetermined variances in uptake and retention, undetermined effects of variables such as age, and unknown contributions of anthropogenic and "natural" components of trace elements and metals in avian tissues make birds poor indicators at best of changes in environmental levels of these elements.

ORGANOCHLORINE CONTAMINATION: A HISTORICAL PERSPECTIVE

In 1967 we found DDE levels of 29 ppm in the whole body of a Short-tailed Shearwater *Puffinus tenuirostris*, 2-12 ppm in whole bodies of Sooty Shearwaters *Puffinus griseus* and 84 ppm wet weight in the breast muscle of a Brown Pelican *Pelecanus occidentalis* from Monterey Bay on the California coast. These levels greatly exceeded those being measured in terrestrial species and were in the range, then suspected, later confirmed, of being capable of causing deleterious physiological effects in at least some species. In the following year PCBs were determined in these and other samples; levels were frequently of the same order as those of the DDT compounds (Risebrough et al. 1967, 1968). The big unknown at that time was the dimension of the terrestrial inventory. Was it sufficient to cause levels in the sea to increase further by many times?

The research that followed determined that the high DDE levels were not coming from the cotton fields of California but from the world's largest manufacturer of DDT in Los Angeles. They were not therefore typical of global levels. But an unhatched egg of the New Zealand Falcon *Falco novaeseelandiae* obtained in 1973 on Adams Island in the subantarctic Auckland Islands contained 3.8 ppm DDE wet weight (Bennington et al. 1975). This level is associated with virtually complete reproductive failures of the Prairie Falcon *Falco mexicanus*, indicating a very real potential for harm even in such a remote location. Many papers have since reported levels in the marine environment that must be considered "high" not only of the DDT and PCB compounds, but also of the hexachlorocyclohexanes, the chlordane compounds, and toxaphene. Determination of long-term trends in the global marine environment of these compounds should become a priority in the environmental sciences.

TRANSPORT PROCESSES AND MONITORING PRIORITIES

There has been a subtle shift in the thinking about how the persistent organochlorine compounds move through the global environment. Formerly, we thought of long-range transport processes largely in terms of transfer from land to sea through the atmosphere. A PCB or toxaphene molecule would volatilize from a water surface, a leaf, or the soil at point A and travel through the atmosphere to point B. But from point B a molecule could travel back to point A, or to A through points C,D, etc. Transport processes are therefore not one-way but are a component of the continuing fluxes of the organochlorines into and out of the atmosphere (Risebrough, in press).

Because of limited exchange of gases in the troposphere between the northern and southern hemispheres, the two hemispheres must be considered separately in determining longer-term changes in the environmental levels of the organochlorines. In my opinion, eggs of seabirds have emerged as the best, or potentially best, indicators of the longer-term changes in the global levels of the organochlorine biocides and related industrial compounds. Systematic, periodic collection of the eggs of appropriate species, archival in frozen storage, and periodic chemical analyses constitute the protocol. The Canadian Wildlife Service began archiving frozen samples in the late 1960s, and has used this collection to document the magnitude and direction of longer-term changes (as reported at the 1989 meeting of the Society of Environmental Toxicology and Chemistry). On the Atlantic coast of Newfoundland, DDE was shown to decline in Atlantic Puffins *Fratercula arctica* and Leach's Storm-Petrel *Oceanodroma leucorhoa* over 1968-1988; PCBs declined in the petrels but not in the puffins. Both DDE and PCBs declined from 1975-77 to 1987-1988 in three species breeding in the Arctic which winter in the North Atlantic, but in the resident Ivory Gull *Pagophila eburnea* DDE, PCBs, HCB, HCH, and mirex were stable or increased, and chlordane-related compounds doubled over the period.

Because methodologies continually improve, eggs should periodically be reanalysed. Toxaphene could not be measured in the late 1960s, but the Canadian Wildlife Service was able to measure a two-fold increase in toxaphene levels in the petrel eggs from Newfoundland over 1968-1988 by using techniques not available until the late 1980s.

Might wildlife departments, environmental agencies and the national ornithological societies in the southern hemisphere consider such a program? Expansion of the efforts in the northern hemisphere should also clearly be encouraged. The persistent organochlorine compounds are still being used in many countries, and continue to be globally dispersed. Birds are in many cases appropriate "indicators" of local contamination and potential effects on human health as well as on the avian populations themselves.

ENVIRONMENTAL CONTAMINANTS: OTHER PRIORITIES

Although less persistent, many of the newer-generation biocides are nevertheless toxic to birds; mortalities due to carbofuran, famphur, diazinon, etc. have been reported in the recent literature. Although habitat remains the primary concern for conservation efforts, continued vigilance is clearly required to maintain also the integrity of the chemical environment.

CHANGING MARINE ENVIRONMENTS

"Seabirds as monitors of changing marine environments" is the theme of another symposium at this Congress. Changes of specific concern are those that result from over-fishing (e.g. Bailey 1989). I mention two examples.

Juvenile of the Walleye Pollock *Theragra chalcogramma*, for which there is a major commercial fishery in the northeastern Pacific, are an important prey of Kittiwakes *Rissa* spp. in the southeastern Bering Sea, and reproductive success is lowered when pollock abundance declines (Springer et al. 1986). Monitoring of the reproductive success of Kittiwakes in this area provides therefore an index of the local abundance of pollock, needed for the management of the fishery, - and for the protection of all species that prey upon the pollock.

In Antarctica, populations of the Chinstrap Penguin *Pygoscelis antarctica* generally increased with the decline of the large baleen whales, attributed to a "surplus" of the principal prey species, the Krill *Euphausia superba* (e.g. Laws 1985). As whale populations respond to protection, and as the commercial krill fishery expands, a decrease in krill abundance is anticipated. Since the production of young is a very sensitive indicator of food supply, monitoring of the reproductive success in several Chinstrap colonies would appear to be the best "indicator" of an anticipated decline in the numbers of krill available to these penguins.

ACIDIC DEPOSITIONS

The number of cases of documented deleterious effects of acidic deposition on selected bird populations in northeastern North America and Europe is increasing (e.g. Mitchell 1989). Overall, the consequences of the atmospheric dispersal of sulfates and nitrates, which include the acidification of freshwater systems and alterations in the uptake of nutrients and selected trace elements by plants, are potentially if not already of a much greater magnitude than those so far inflicted by biocide use. Moreover, powerful economic arguments are advanced by the automobile and utilities industries to delay a response to this problem. The greater the number of documented effects on birds, indicating adverse changes, the more powerful will be the counter conservation argument that can be put forward.

An elegant example of the use of a bird species to document damage, and to serve as a sensitive "indicator" of local acidity, is found in the paper in this symposium by Vickery and Ormerod. The ultimate causes of the acidity in the streams of Wales that affects the distribution and breeding success of the Dipper *Cinclus cinclus* are diverse. Although nothing can be concluded from the data on the depressed productivity of the Dippers about the sources of the acidity, the data provide a good "indicator" of an integrated effect. They also provide a basis and rationale for political action. Ultimately the distribution of Dippers in Wales may provide a measure of success or failure in the effort to re-orient a major portion of our technology.

THE SILENT SPRING

In his recent book, John Terborgh (1989) described his personal observations of the decline or disappearance of song birds in the area in which he grew up in northern Virginia. Many of us can describe similar experiences. The dawn chorus in early June at my parents' house in suburban Toronto used to include the songs of a Warbling Vireo *Vireo gilvus*, a Yellow Warbler *Dendroica petechia*, and a Northern Oriole *Icterus galbula*. Now, except for an occasional American Robin *Turdus migratorius*, the dawns in June in the Toronto suburbs are silent.

Terborgh (1989) has discussed the causes of the decline of songbirds in eastern North America which include deforestation in the tropics, fragmentation of breeding habitats, the population explosion of the parasitic Brown-headed Cowbird *Molothrus ater*, and an increase in local populations of mammalian predators which include domestic cats. It would be naive to propose "indicators" of the complex processes that are responsible for the declines. Nevertheless, might not the expanded monitoring programs proposed by Temple and Wiens (1989) place particular emphasis on selected species that are more sensitive to specific changes, such as the destruction of forest habitat in Central America or the Caribbean?

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LONG-TERM MONITORING OF ORGANOCHLORINE AND MERCURY RESIDUES IN SOME PREDATORY BIRDS IN BRITAIN

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ABSTRACT. Residue levels of organochlorine pesticides (HEOD, DDE), polychlorinated biphenyls (PCBs) and mercury (Hg) in the livers of five predatory bird-species were monitored in Britain over a 27-year (1963-89) period. Of two raptor species, Sparrowhawks *Accipiter nisus* contained higher levels of most chemicals than did Kestrels *Falco tinnunculus*, and among three fish-eaters, Grey Herons *Ardea cinerea* contained the highest levels, followed by Kingfishers *Alcedo atthis* and then Great-crested Grebes *Podiceps cristatus*. Species differences were related to diet and habitat. Over the 27 years, most species showed significant downward trends in HEOD, DDE and Hg levels, but only two fish-eaters showed significant declines in PCB levels. The downward trends in DDE and HEOD followed successive restrictions in the use of organochlorine pesticides, and were accompanied by recoveries in the populations and breeding success of affected species.

Keywords: Sparrowhawk, *Accipiter nisus*, Kestrel, *Falco tinnunculus*, Grey Heron, *Ardea cinerea*, Kingfisher, *Alcedo atthis*, Great-crested Grebe, *Podiceps cristatus*, aldrin, dieldrin, DDE, DDT, HEOD, PCB, mercury, monitoring, pollution.

INTRODUCTION

This paper reports the levels of certain pollutants in the bodies of some raptorial and fish-eating birds examined in Britain during the 27-year period, 1963-89. The chemicals involved include pp'-DDE (the main metabolite of the insecticide DDT in avian tissues), HEOD (the active ingredient in the insecticide dieldrin and a metabolite of the active ingredient in the insecticide aldrin in avian tissues), PCBs (industrial polychlorinated biphenyls) and Hg (mercury, from industrial and agricultural sources). The bird species involved include the Sparrowhawk *Accipiter nisus* and Kestrel *Falco tinnunculus* which eat land-based prey, and the Grey Heron *Ardea cinerea*, Kingfisher *Alcedo atthis* and Great-crested Grebe *Podiceps cristatus* which eat primarily fish. All of these species obtain pollutant residues with their food.

The main aim was to assess temporal trends in chemical residues against the background of successive government restrictions on organochlorine and mercurial pesticide-use. As the scheme was countrywide, it was also intended to assess regional variations in levels. A secondary aim was to provide longterm residue-data, against which to assess the changing population status of affected species. The chemicals involved were known to be highly persistent, and some of the pesticides were known to have caused mass mortalities and reproductive failures in birds (Cramp et al 1961, Borg et al. 1969, Ratcliffe 1970, Newton 1979). As predators, all the species chosen for study accumulated residues of these chemicals to a high level. Most also have shown some degree of eggshell thinning (Ratcliffe 1970), attributed to DDE, and some have shown obvious population declines, attributed to poor breeding (from DDE) and enhanced mortality (from HEOD). The Sparrowhawk was the most affected of the species studied.

METHODS

Specimens for analysis were obtained each year by making requests in bird journals for bodies of birds found dead. These birds may not have been representative of the living population of each species with respect to contaminant levels, but they formed a consistent sample throughout. Carcasses were stored deep frozen (at -20°C), and examined in batches, using samples of liver for chemical analysis (for methods, see Newton et al. 1990). The limit of detection was about 0.01 ppm in wet weight for the organochlorines, and about 0.01 ppm in dry weight for mercury. Analyses for HEOD and DDE were started in 1963, analyses for PCBs in 1967, and for Hg in 1966-79, depending on the species. To achieve consistency in analyses over the years, results were continually checked against standards of known concentration. Because of the non-normal distribution of residue data, annual geometric means, rather than arithmetic means, have been used to indicate temporal trends. Throughout this paper, levels of organochlorines are given as wet weight values, and of mercury as dry weight values, fitting the usual convention.

Treatment of data

To examine geographical patterns in contaminant levels, the country was divided by agricultural land use, distinguishing four zones, where the proportion of tilled land in 1960 was less than 10%, 11-30%, 31-60% and more than 60% respectively. In general, the zone with least arable land covered much of the north and west of Britain, the zone with most arable land covered much of the east, while the other zones were intermediate (see map in Newton & Haas 1984).

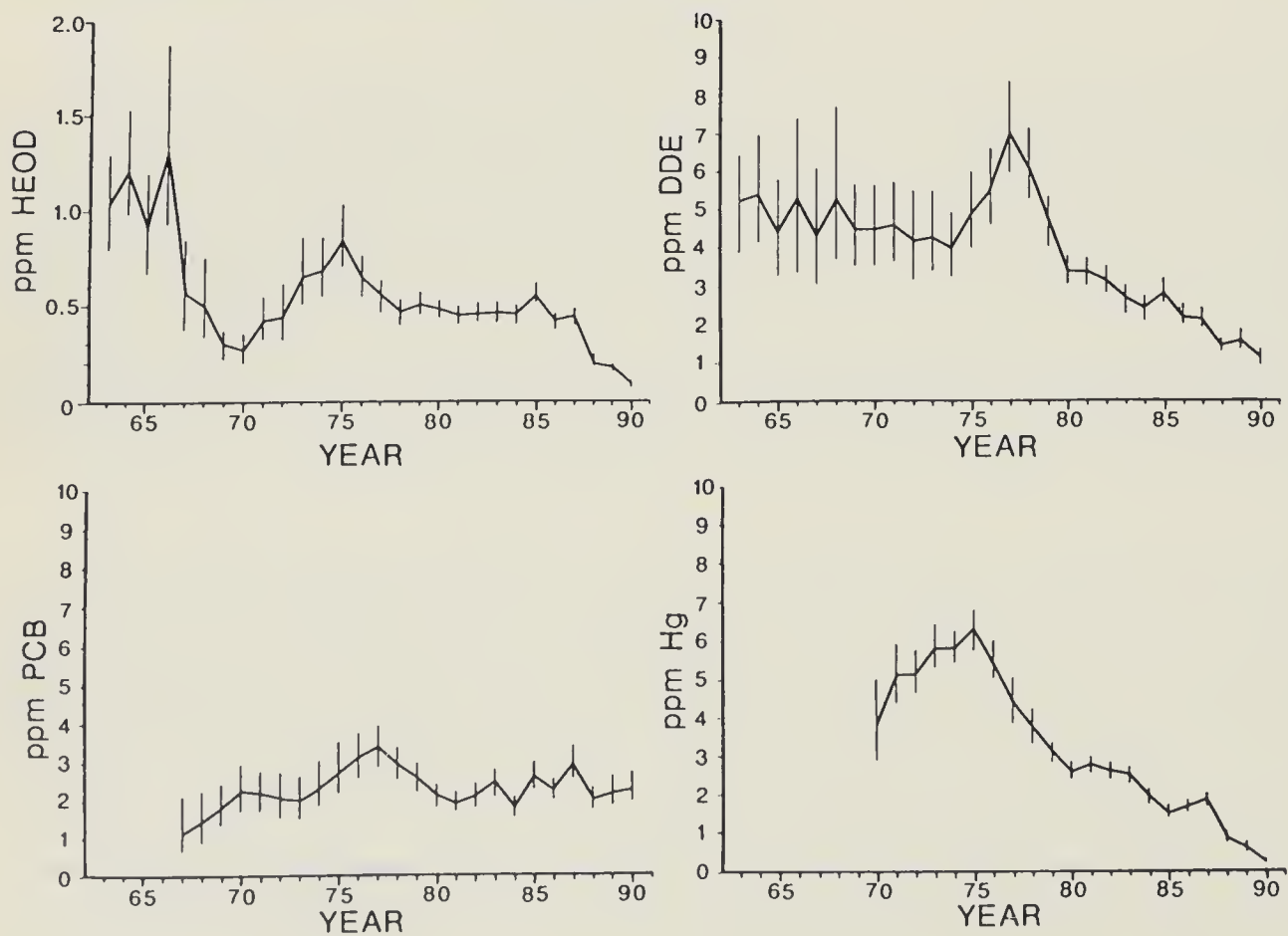


FIGURE 1 – Levels of chemical contaminants in the livers of Sparrowhawks, 1963-89. Lines show 3-year moving geometric means of residue levels, and bars show geometric standard errors.

Temporal trends in residues over the 27-year period were examined by linear regression analyses, with individual \log_{10} residue levels as the dependent variable and year as the independent variable. A linear regression model may not always have given the best fit to the data, but the aim was merely to find whether a significant net decline in residues had occurred over the period as a whole. In each analysis all relevant specimens were included, irrespective of age, sex, mode of death or condition (for examination of these aspects, see Cooke et al. 1982).

RESULTS

Among the terrestrial-feeders, the bird-eating Sparrowhawk had generally higher levels of most residues than the mammal-eating Kestrel (Figures 1 and 2). Among the fish-eaters, the Heron contained the highest levels of all residues (Figure 3), while the Great-crested Grebe contained the lowest.

In Sparrowhawk and Kestrel, HEOD and DDE levels were initially higher in the two most arable zones, but in later years these regional differences largely disappeared (Figure 4). In contrast, the Heron showed no differences between agricultural zones, and no other consistent regional variation. Too few Kingfishers and Grebes were obtained to examine regional variation in detail, but no obvious variation was apparent.

The overall data for most species revealed a significant downward trend in DDE, HEOD and Hg residues over the period concerned (Figures 1-3, Table 1).

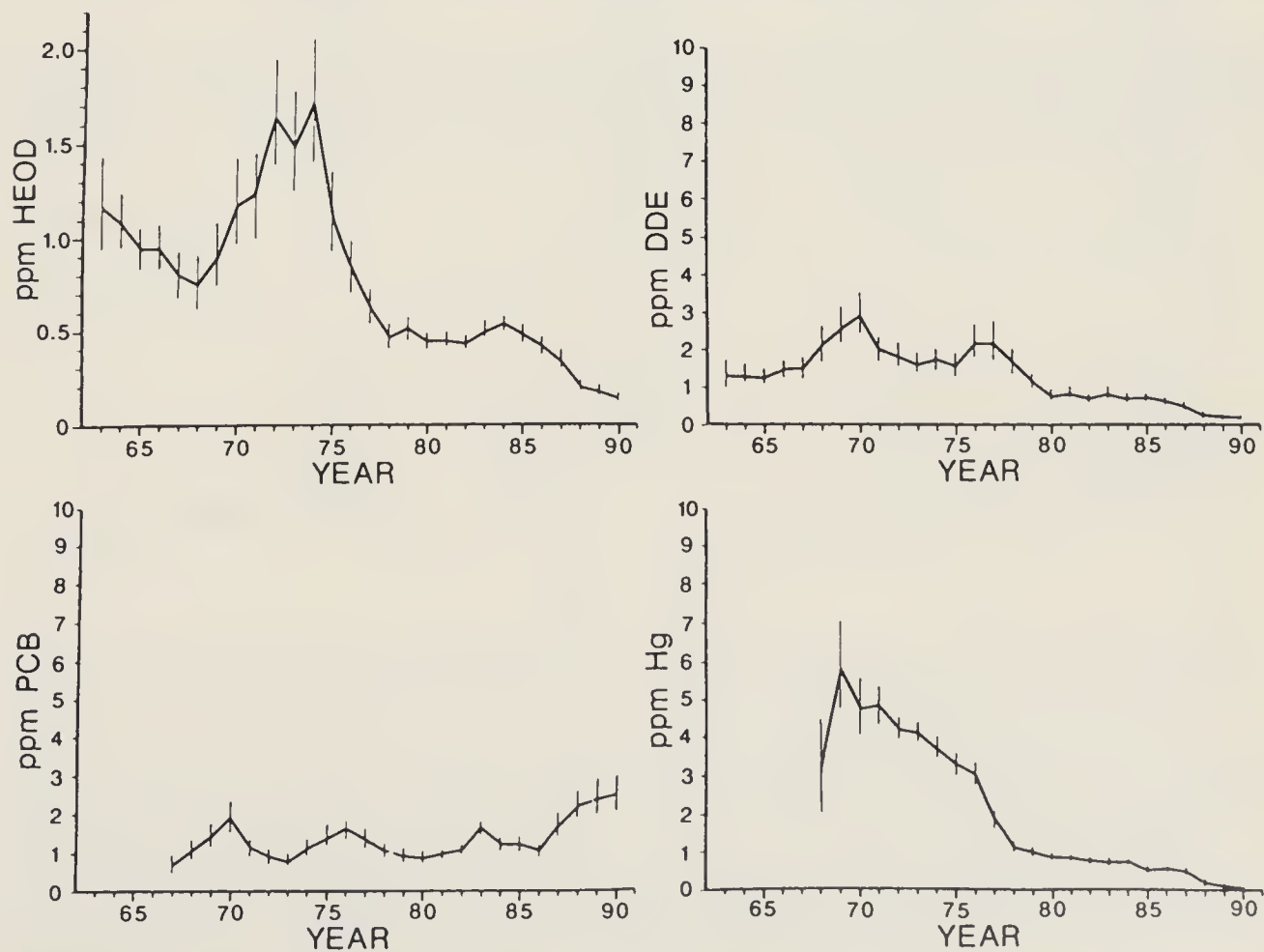


FIGURE 2 – Levels of chemical contaminants in the livers of Kestrels, 1963-89. Lines show 3-year moving geometric means of residue levels, and bars show geometric standard errors.

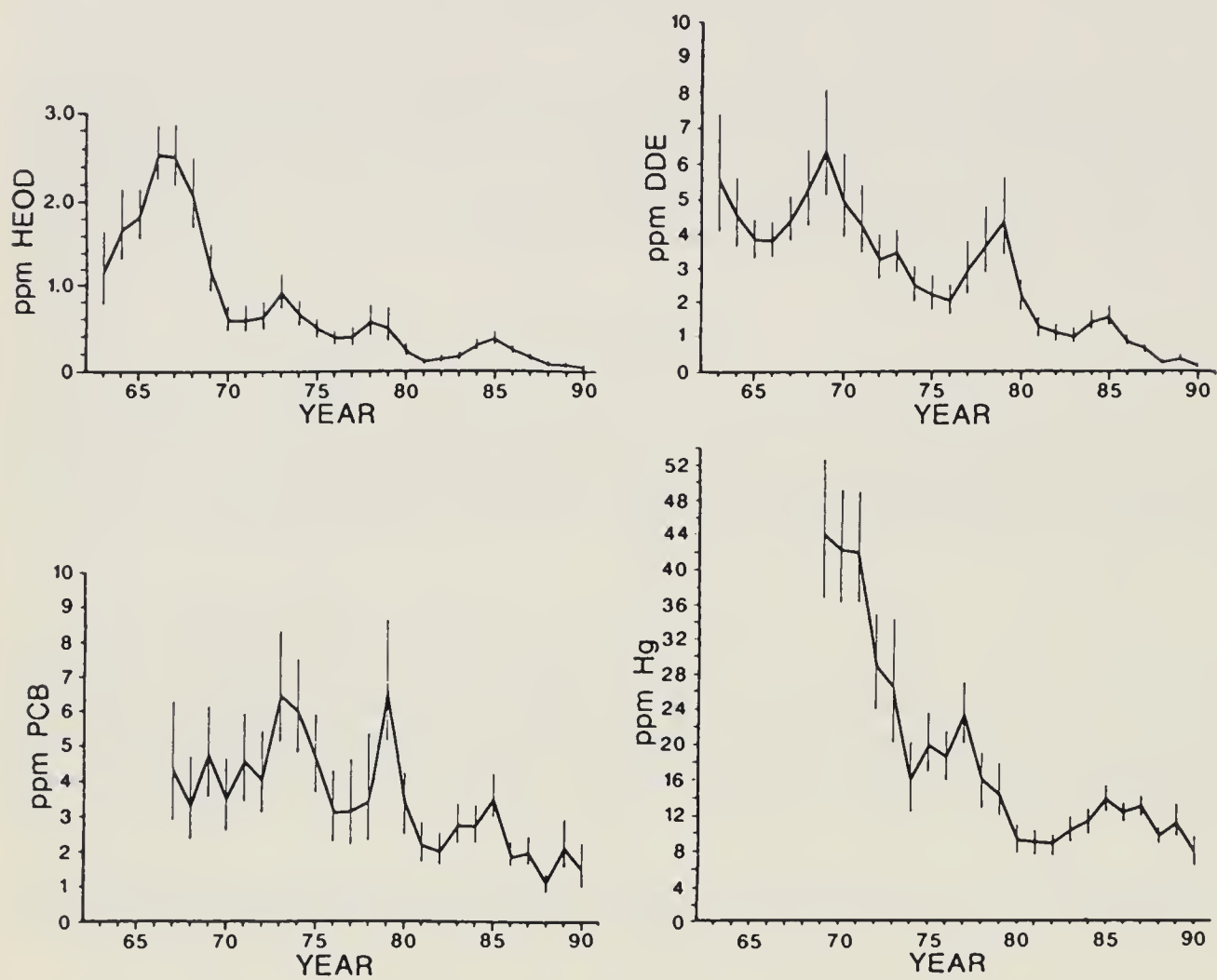


FIGURE 3 – Levels of chemical contaminants in the livers of Herons, 1963-89. Lines show 3-year moving geometric means of residue levels, and bars show geometric standard errors.

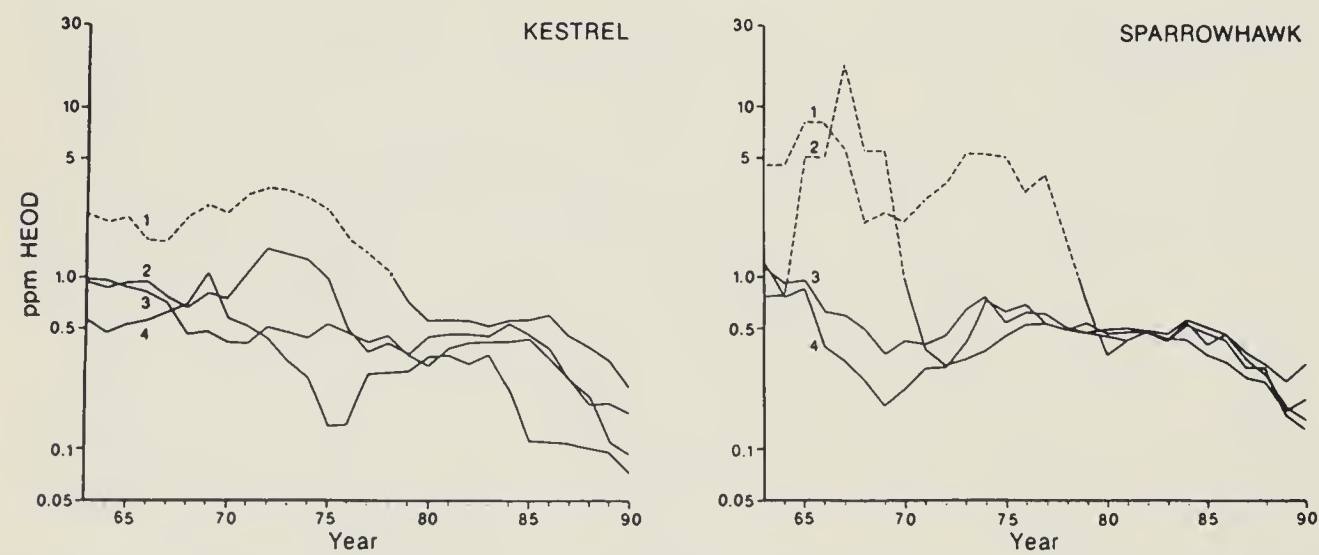


FIGURE 4 – Trends in DDE and HEOD levels in Sparrowhawk and Kestrel livers from different agricultural zones in Britain (see text). Lines show 5-year moving geometric means. Broken lines show periods when populations in each zone were depleted or declining, and solid lines show periods when populations were normal or increasing. The latter occurred when geometric mean HEOD levels in livers were less than about 1 ppm in wet weight. Zone 1 – proportion of tilled land >60%; Zone 2 – 31-60%; Zone 3 – 11-30% and Zone 4 – <10%. Redrawn and extended from Newton (1988).

In contrast only the fish-eaters showed downward trends in PCB levels (significant in Heron and Grebe), while the raptors showed increases (significant in Kestrel). Separating the data by agricultural zones, declines in DDE, HEOD and Hg residues were apparent in all zones, and in most cases were statistically significant.

TABLE 1 – Time trends in pollutant levels in the livers of various bird-species. Trends were examined by regression analyses of individual residue levels (log transformed) as the dependent variable, against years as the independent variable. The slope of the trend is indicated by the regression coefficient, and negative values indicate declines. *P<0.05, ** P<0.01, *** P<0.001.

Species	Chemical	Period	Number of livers examined	Regression coefficient
Kestrel	HEOD	1963-89	1,052	-0.029***
	DDE	1963-89	1,074	-0.030***
	PCBs	1967-89	933	0.010*
	Hg	1968-89	744	-0.083***
Sparrowhawk	HEOD	1963-89	987	-0.020***
	DDE	1963-89	1,001	-0.025***
	PCBs	1967-89	957	0.001
	Hg	1966-89	777	-0.060***
Heron	HEOD	1963-89	678	-0.051***
	DDE	1963-89	688	-0.039***
	PCBs	1967-89	554	-0.022***
	Hg	1969-89	391	-0.025***
Kingfisher	HEOD	1964-89	165	-0.023**
	DDE	1964-89	165	-0.045***
	PCBs	1967-89	158	-0.021
	Hg	1970-89	88	-0.033*
Great-crested Grebe	HEOD	1963-89	143	-0.013
	DDE	1963-89	164	-0.011
	PCBs	1968-89	151	-0.032*
	Hg	1979-89	83	0.012

DISCUSSION

There were probably three reasons why the Sparrowhawk had higher levels of most pollutants than the Kestrel. First, it eats other bird-species (herbivores and carnivores), and hence feeds higher in the food chain than does the Kestrel, which eats mainly herbivorous voles. Secondly, birds in general are less able to metabolise organochlorines and some other pollutants than are mammals (Walker 1983), so for this reason too the bird-eating Sparrowhawk would tend to accumulate higher levels than the mammal-eating Kestrel. Thirdly, Sparrowhawks are less able than Kestrels to metabolise organochlorines within their own bodies (Walker et al. 1987). It was not

surprising, therefore, that Sparrowhawks suffered a more marked and widespread population decline than Kestrels.

Among the fish-eaters, Herons had the highest residue burdens, followed by Kingfishers and then Great-crested Grebes. In inland areas, Herons and Kingfishers feed largely from rivers, as well as still-waters, while Grebes are almost restricted to still-waters. The fact that rivers more often receive industrial effluent than do still-waters may partly explain the species-differences in residue burdens.

The general decline in DDE and HEOD levels in all the species studied was associated with progressive reductions in the uses of DDT, aldrin and dieldrin. Over the same period populations of depleted species recovered, while shell-thickness and breeding success improved (Newton 1979, Ratcliffe 1980). In the Sparrowhawk, population recovery began in the west in the mid-1960s and spread eastward, occurring latest (in the mid-1980s) in the more arable eastern areas (Newton & Haas 1984). In the Kestrel, decline was obvious only in the east, and recovery occurred in the late 1970s (unpublished data). Interestingly, the recoveries of Sparrowhawk numbers in different agricultural zones, and the recovery of Kestrel numbers in the eastern zone, all began when the geometric mean HEOD residue in livers from those zones fell below about 1.0 ppm (Newton 1988). As the population decline in these species was attributed mainly to increased mortality from aldrin and dieldrin, this HEOD level indicated a critical threshold below which population recovery occurred.

In contrast to other chemicals, PCB levels declined only in the aquatic species, but not in the Kestrel and Sparrowhawk. This was despite the withdrawal in 1970 of PCBs from all uses except in 'closed systems'. However, no system is completely closed, and continual escape of PCBs to the environment would be expected from products made in earlier years. Moreover, the great chemical stability of PCBs could ensure their persistence in the environment for long periods.

Because much more mercury has been used in Britain in industrial processes than in agriculture (Anon. 1976), industrial processes are likely to have provided the main source of residues for at least the fish-eaters. The industrial uses and disposal of mercury have been more rigorously controlled in recent years, and agricultural uses have also been reduced (Anon. 1964). Thus, it was not unexpected that residues declined in all species examined.

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DIPPERS AS INDICATORS OF STREAM ACIDITY

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ABSTRACT. The acidification of upland streams and lakes in Britain has been a cause of growing concern over recent years. Fast-flowing streams, typical of such regions of the U.K., are the favoured breeding habitat of the Dipper *Cinclus cinclus*. This bird is unique amongst passerines in its close association with water, upon which it depends for nesting and feeding sites. Studies in two areas of the U.K., Wales and Scotland, have shown that the density and productivity of breeding pairs of Dippers declines with increasing stream acidity. These birds feed almost exclusively on aquatic invertebrates, the abundance and diversity of which is low at acidic compared with non-acidic sites. Stream acidity affects the distribution and breeding success of the Dipper through pH-related differences in prey availability. It is concluded that Dippers are suitable indicators of stream acidity.

Keywords: Acidification, Dipper, *Cinclus cinclus*, distribution, breeding success, prey availability, bio-indicators.

INTRODUCTION

It is now widely recognised that acid deposition, in some areas exacerbated by large-scale planting of non-native conifers, causes pronounced chemical and biological changes within aquatic ecosystems. Birds and mammals which rely on aquatic organisms for food may also be adversely affected (Ormerod & Wade 1990). Many of the biological changes which occur are robust and predictable between regions, leading to the view that biological systems can provide a cost-effective and convenient indicator of change in time and space. Indicator species which have had a long history of exposure to certain environmental conditions (Zonneveld 1983) may be particularly effective where pollution phenomena are episodic, as in the case of acidification (McNicol et al. 1987, Wade et al. 1988). The biological system is able to integrate the effects of chronic and episodic change in a way not easily reproduced using chemical sampling.

Some authors have maintained that organisms at higher trophic levels, such as predatory birds, are well placed as indicators relying on the quantity and quality of production at other trophic levels (McNicol et al. 1987). At the same time, however, others have questioned the usefulness of such species as bio-indicators (Landres et al. 1988). A clear understanding of the mechanisms by which a species responds to chemical and biological changes in the environment is thus essential in order to assess whether a given organism is an appropriate bio-indicator.

In the U.K., research concerned with the impact of acidification on waterbird populations has focussed on the Eurasian Dipper *Cinclus cinclus*. This bird is unique amongst passerines in its close association with streams upon which it depends for food and nesting sites. The diet is almost exclusively freshwater invertebrates and

small fish, many of which are scarce in streams of low pH (Ormerod & Tyler 1987). Dippers are thus potentially sensitive to changes in water quality.

In this paper we examine the distribution and breeding performance of Dippers in two areas of the U.K., in relation to the acidity of adjacent streams. The suitability of Dippers as indicators of surface water acidity is discussed.

THE STUDY SITES

The Welsh (52° 20'N, 3° 30'W) and Scottish (55°10'N, 4° 15'W) study sites are described elsewhere (Ormerod et al. 1988). Both areas are approximately 2-3000 km², and within both, stream chemistry varies widely, (annual mean pH ranging from 4.5-8.5), largely as a result of the variable nature of the soil systems and underlying bed-rock. The major land-use is rough pasture but both areas also include extensive areas of conifer plantation and small areas of improved pasture. Human populations are low (0.1-0.25 persons ha⁻¹).

METHODS

Water chemistry and environmental variables

The detailed methodology is also given elsewhere (Ormerod et al. 1988). The pH of most sites was determined at weekly and fortnightly intervals from February to July. A number of less accessible sites were sampled on a monthly basis. Altitude and gradient have been suggested to influence the density of riparian birds (Sharrock 1976, Marchant & Hyde 1980) and these were assessed, for all streams, using 1:25 000 Ordnance Survey maps.

Density and territory lengths of breeding pairs of Dippers

Dippers are conspicuous on their breeding territories; their breeding density was assessed for a total of approximately 112.5 km of waterway in south-west Scotland in 1987 and for over 220 km of waterways in Wales in 1983. All streams were surveyed at least seven times (at approximately ten-day intervals) between early March and late July. Sightings of adult Dippers were recorded on visit maps and a minimum of three sightings was used as evidence for a breeding pair. Breeding was confirmed by locating the nests of 97% of the pairs. The stream lengths of breeding territories were estimated using the 'doubling back' technique (Ormerod & Tyler 1987).

Breeding success of Dippers

The nests of breeding pairs of Dippers were located during the building stage of the breeding cycle. Data were collected over three years in Scotland (1985-1987) and over two in Wales (1985-86). Information recorded included the following: (a) first egg date, (b) clutch size, (c) brood size (number of nestlings at day ten; day of hatching = day 0).

Diet of adults and nestlings

The diets of adults and nestlings were assessed by faecal analyses, following the techniques of Ormerod (1985). Fresh faecal samples were collected at weekly intervals from stones near the nest and during visits to the nest throughout the nestling

period. Dietary composition was determined by identifying and counting all prey mouthparts present in samples collected from ten acidic and ten non-acidic sites. The diet was expressed in terms of biomass composition after calculating prey biomass using mouthpart dimensions (see Ormerod 1985, Ormerod & Tyler 1987). Detailed dietary analysis is presented elsewhere (Ormerod 1985, Vickery 1988).

Statistical analyses

One-way and multivariate analyses were performed using MINITAB. The dependent variables considered were the densities and territory lengths of Dippers, first egg date, clutch size and brood size. For ANOVAS the pH of sites (238 sites in Wales and 119 sites in Scotland) was divided into four treatment categories: 4.5-5.5, 5.5-6.5, 6.5-7.5 and 7.5-8.5. All other independent variables (altitude, gradient and lay date) were placed into four categories depending on whether they were above or below the mean and whether they were greater or less than one standard deviation from the mean. None of these variables deviated from normality.

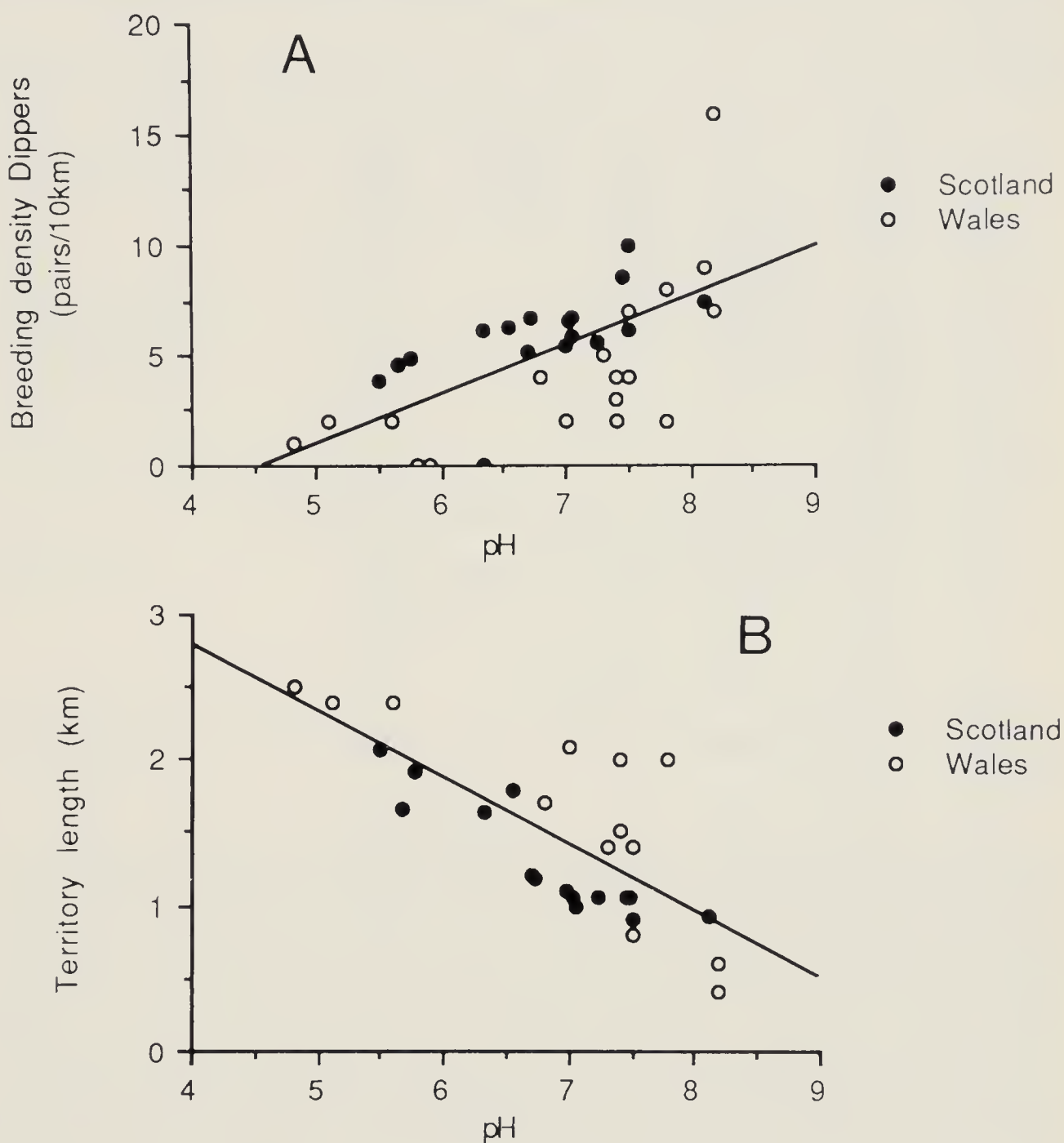
RESULTS

Breeding density

The density and mean territory length of breeding pairs of Dippers was recorded for a total of 36 streams of known pH, 18 in Wales and 18 in Scotland. The mean density of breeding pairs was 5.10 ± 3.11 prs/10 km (Wales: 4.33 ± 3.91 prs/10 km, Scotland: 5.87 ± 2.04 prs/10 km). There was a significant positive relationship between pH and density of breeding pairs ($F_{1,35}=18.52$, $P<0.0001$, Figure 1a). Breeding density decreased by approximately 2.5 pairs per 10 km with a decrease of one pH unit (increase in acidity). Using a multivariate analysis, the effect of area, gradient and pH, on breeding density, was determined. Having controlled for the effects of the former two variables there was still a highly significant effect of pH on density ($F_{3,35}=7.48$, $P<0.001$), pH accounted for 35.3% of the variation in density of Dippers (Table 1). There was no effect of gradient, but there was a significant difference in density between the two areas ($F_{1,35}=6.48$, $P<0.02$), the mean density of birds, on streams of similar gradient and pH, being lower in Wales than in Scotland. However the relationship between pH and density within the two sites did not differ (pH*area interaction term was non-significant).

The territory length of breeding pairs was measured on 31 streams of known pH, 14 in Wales and 17 in Scotland, and ranged from 0.4 km to 2.4 km. The mean territory length was 1.48 ± 0.61 km (Wales: 1.66 ± 0.67 km, Scotland: 1.34 ± 0.42 km). There was a significant negative relationship between pH and territory length ($F_{1,30}=52.64$, $P<0.0001$, Figure 1b). Territory length declined by approximately 0.5 km with an increase of one pH unit (decrease in acidity). When the effects of area and gradient were controlled for using multivariate analysis, pH still had a significant effect on territory length ($F_{3,30}=17.54$, $P<0.0001$) and accounted for 48.4% of the variation in territory length (Table 1). Gradient also had a small, but significant, effect, territory length decreasing with increasing gradient ($F_{3,30}=3.17$, $P<0.04$). There was a significant difference between the two areas, with territory lengths on streams, of similar gradient and pH, being generally longer in Wales than in Scotland ($F_{1,30}=5.73$, $P<0.03$). There was, however, no difference in the relationship between territory length and stream acidity within the two areas (pH*area interaction term was non-significant).

FIGURE 1 – The relationship between pH and (A) the density and (B) mean territory length of breeding pairs of Dippers in Wales and Scotland.



Breeding success of Dippers

FIRST EGG DATE. The first egg date was recorded for a total of 314 nests at sites of known pH, 104 in Scotland and 210 in Wales. There was a highly significant effect of pH on first egg date ($F_{1,313}=88.11$, $P<0.0001$). Clutch initiation was delayed by four to five days with a decrease of one pH unit. There was, however, also a highly significant effect of year (one way analysis: $F_{3,334}=28.10$, $P<0.0001$), with birds breeding in 1985 laying approximately ten and seven days earlier than those in 1986 and 1987 respectively. In order to control for this large year effect, first egg date was standardised across years (by subtracting the annual mean from the Julian laying date and dividing by standard deviation). Altitude is also known to influence first egg date of Dippers (Cramp et al. 1988). Having controlled for any effects of altitude, area and year, a multivariate analysis, still revealed a significant effect of pH ($F_{3,313}=30.33$, $P<0.0001$) on first egg date, but pH explained only 15.1% of the variation in first egg

date (Table 1). There was also a significant effect of altitude ($F_{3,313}=9.75, P<0.0001$), birds at lower altitudes laying earlier, but there was no difference between Wales and Scotland.

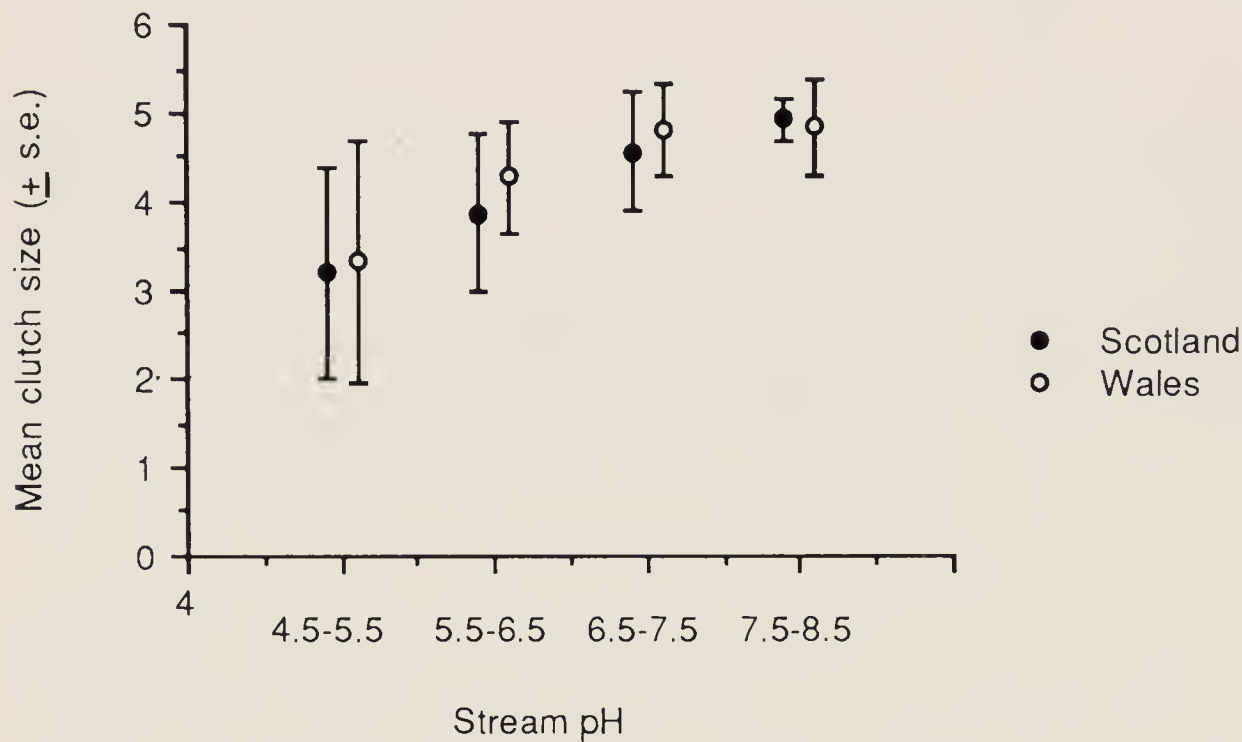


FIGURE 2 – The relationship between pH and clutch size of Dippers in Wales and Scotland.

CLUTCH SIZE. The size of first clutches was recorded at 267 sites of known pH, 110 in Scotland and 157 in Wales. There was a highly significant positive relationship between pH and clutch size ($F_{1,266}=40.47, P<0.0001$). Clutch size decreased by approximately 0.5 eggs with a decrease of one pH unit. A multivariate analysis was performed in which any effects of lay date, altitude, year and area were considered in addition to pH. There were no significant effects, on clutch size, of any of the variables considered except pH ($F_{3,249}=22.33, P<0.0001$), which accounted for 15.6% of the variation (Table 1). To determine whether the relationship between pH and clutch size was consistent between the two areas data from the two areas were considered separately. There was a significant effect of pH on clutch size in Wales (one way analysis: $F_{3,156}=16.62, P<0.0001$) and Scotland ($F_{3,109}=17.55, P<0.0001$) and the relationship was highly consistent between the two areas (Figure 2).

BROOD SIZE. The brood size at day ten was recorded at a total of 226 nests at sites of known pH, 154 in Wales and 73 in Scotland. The effect of pH on brood size was highly significant ($F_{1,225}=72.65, P<0.0001$). This would be expected, given the significant relationship between pH and clutch size. The effect of clutch size, first egg date, altitude, year, and area was considered in a multivariate analysis. The only variable that had a significant effect on brood size was that of clutch size ($F_{4,178}=9.34, P<0.0001$), explaining 11.6% of the variation. Thus there was no effect of pH on brood size over and above that of its effect via clutch size. Neither was there any significant effect of first egg date, altitude, year, or area. When clutch size was omitted from the analysis only pH has a significant effect on brood size ($F_{3,223}=4.72, P<0.003$). There was no significant difference between the two areas in any of the analyses.

TABLE 1 – Factors accounting for the variation in density, territory length, first egg date, clutch and brood size of Dippers. Results are for multivariate analyses using MINITAB; details are given in the text.

Dependent variable	Factor	df	F	P	% variation explained
i) Density breeding pairs	pH	3	7.48	0.001	35.3
	gradient	3	0.25	0.859	3.3
	area	1	6.42	0.017	7.4
	error	28			54.0
ii) Territory length	pH	3	17.54	0.001	48.4
	gradient	3	3.17	0.044	7.4
	area	1	5.73	0.025	8.6
	error	23			35.7
iii) First egg date	pH	3	30.33	0.001	15.1
	altitude	3	9.75	0.001	6.5
	area	1	1.34	0.249	0.1
	error	306			78.3
iv) Clutch size	pH	3	22.33	0.001	15.6
	first egg date	3	1.07	0.360	0.4
	altitude	3	1.61	0.187	1.8
	year	2	0.59	0.557	0.1
	area	2	0.03	0.856	0.0
	error	237			82.1
v) brood size	pH	3	0.93	0.429	2.6
	first egg date	3	1.10	0.341	0.2
	clutch size	4	9.34	0.001	11.6
	altitude	3	0.34	0.799	0.2
	year	2	0.08	0.920	0.2
	area	1	1.14	0.287	4.5
	error	162			80.7

Dietary analysis

At all sites and throughout the nestling period trichopteran larvae were extremely important components of the biomass of the diet for both adult and nestlings. Trichopteran larvae comprised 80 to 95 percent of the diet of nestlings older than five days at both acidic (Wales: 95.5%, Scotland: 88.3%) and non-acidic (Wales: 80.9%, Scotland: 90.3%) sites. This order comprised a smaller percentage of the diet of nestlings before day five (acidic sites: 73.6% and 23.3% in Wales and Scotland respectively and at non-acidic sites: 45.7% and 31.6%). The invertebrate order that comprised the major part of the diet of young nestlings and adults differed between acidic and non-acidic sites. At the latter the dominant prey items were ephemeropterans, whilst large numbers of plecopterans were taken at acidic sites.

DISCUSSION

In order to provide a useful indicator of stream acidity a waterway bird should (a) be sensitive to changes in water acidity (b) respond to such changes in a predictable fashion across its range and (c) respond in a way that is relatively easily measured

or assessed. In addition, the causative mechanisms underlying these responses should be understood. The data presented here support these requirements and suggest that Dippers are suitable indicators of stream acidity.

There were clear and significant relationships between the distribution and breeding success of Dippers and the pH of the adjacent waterways in two areas of the U.K. Birds resident along streams of high acidity were present at lower breeding densities, defended longer territories and exhibited reduced breeding productivity compared with birds on streams of lower acidities. Birds at low pH sites exhibited delayed laying and reduced clutch size compared with non-acidic sites. There was, however, no effect of pH on brood size, over and above that of its effect on clutch size. Data concerning a number of other parameters of breeding success of Dippers, in both these study sites, are presented elsewhere. These include egg weights, shell thickness (Ormerod et al. 1988), nestling weights and growth rates, the rates of food delivery to nests and nestling growth (Ormerod & Tyler 1987, Vickery 1988, Ormerod et al. in press).

These effects of pH on the distribution and productivity of Dippers, were very similar in two distinct parts of their breeding range in the U.K.; Scotland and Wales. This indicates that the response of this species, to differences in pH, are robust and predictable within and between different regions.

Demonstrating the existence of a relationship between water acidity and Dippers does not provide adequate criteria in itself alone, for the selection of this bird as a suitable bio-indicator. It is important to also understand the possible mechanism by which these effects are mediated (Landres et al. 1988). The effect of pH on distribution and productivity of Dippers is almost certainly a result of pH-mediated differences in food availability. Data concerning the diet of Dippers and the distribution of invertebrates in adjacent streams support this hypothesis. Dietary analysis reveals a strong dependence of Dippers on trichopteran larvae, particularly when feeding nestlings greater than five days old (Ormerod & Tyler 1987, Ormerod 1985, this paper). The scarcity of trichopteran larvae at acidic sites is well documented in the literature (e.g. Townsend et al. 1983, Sutcliffe & Hildrew 1989, Weatherly et al. 1989). The evidence for an effect of stream pH on other parameters of Dipper breeding success is also consistent with the hypothesis that pairs occupying acidic streams experience reduced prey availability (Ormerod et al. 1988, Vickery 1988, Ormerod et al. in press, O'Hallaran et al. in press). This may result in increased time and energy expenditure during foraging (O'Hallaran et al. in press). The influence of food availability on both density and territory size has been demonstrated elsewhere for Dippers (daPrato & Langslow 1976, Price & Bock 1983) and for several other passerines (e.g. Krebs 1971, Enoksson & Nilsson 1983). Prey abundance is known to effect breeding performance in many birds (e.g. Ewald & Rohwer 1982, Murphy & Haukioja 1986) and reduced prey quantity and/or quality may also lead to lower productivity of Dippers on acidic streams.

In summary, both the density and productivity of Dippers are affected by the pH of the adjacent stream. The response of this species to water acidity is similar in two separate regions of the U.K., suggesting that the results could be generalised throughout its breeding range. Much evidence exists to support the fact that the causal mechanism, underlying the relationships between Dippers and stream acidity, is via pH-related differences in prey quantity and quality. Dippers may therefore, provide highly

suitable indicators of stream acidity. Unlike other indicators of acidity, such as diatoms (Battarbee et al. 1988), they are easy to census and identify. Furthermore, the Cinclidae family is widespread in its distribution with species occurring in Western Europe, North and South America, the Himalayas and western pacific islands (Tyler & Ormerod 1987). The Dipper may, therefore, be a suitable indicator species over a wide geographical area.

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BIRDS AS INDICATORS OF GLOBAL CONTAMINATION PROCESSES: THE CHERNOBYL CONNECTION

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ABSTRACT. The 1986 Chernobyl nuclear accident has resulted in worldwide concern for the possibility of regional and even global distribution of the released radioactive contaminants. However, relatively little information has been available concerning the direct uptake and concentration of these contaminants by birds and other forms of wildlife even though some species such as migratory waterfowl could serve as potential vectors of contamination to the food chain of man. Studies of waterfowl and other birds at sites of smaller scale accidental releases of radionuclides have shown that some of the basic principles of contaminant cycling theory, when examined under freelifving conditions, may not be true. While biomagnification or trophic level concentration is invariably shown by chlorinated hydrocarbons and heavy metals for example, this was not true for radiocesium in wintering waterfowl inhabiting a reactor cooling reservoir in the southeastern United States. Preliminary calculations are presented estimating the possibility of radiocesium uptake and transport by migratory waterfowl visiting or residing within the extensive Pripyat Marsh wetlands directly adjoining the Chernobyl reactor site. A final determination as to whether or not these calculations indicate an appropriate "margin of safety" against the contamination of waterfowl to a level that would make them unfit for human consumption will require more information on the levels of radiocesium in the biota of these wetlands. The collection of such data should be a high priority for cooperative research by the international ornithological community.

Keywords: Contaminant cycling, biomagnification, radiocesium, Chernobyl accident, waterfowl.

INTRODUCTION

The Chernobyl nuclear reactor accident in the Soviet Union in April, 1986 has become a particularly prominent event of environmental contamination on both a regional and global scale (Medvedev 1986, Anspaugh et al. 1988). Relatively little information is available concerning the direct contamination of birds as a result of this accident. However, birds and particularly migratory waterfowl which may become contaminated and then be eaten by humans as food, have subsequently become the focus of considerable speculation with regard to the possibility of effects on the birds themselves (e.g., DeSante & Geupel 1987) as well as with regard to the role of birds as biomonitors of radionuclide contaminants released from that accident (e.g., Ruiz et al. 1987, Baeza et al. 1988). Considerations of the fate and effects of radioactive contaminants in birds are dealt with in the discipline of avian radioecology as has been described at length elsewhere (Brisbin in press).

It is the purpose of this report to summarize some of the most important principles of avian radioecology as developed in that earlier paper, and then to indicate how the successful development and application of these principles to an event such as the Chernobyl accident requires not only an understanding of radioecology but also of basic ornithology as well. At the same time however, it can be shown that important basic ornithological information can also be gained as the result of applied studies of the environmental cycling and fates of "tracer" radioactive contaminants. This is

particularly true for long-lived gamma-emitting radionuclides such as $^{137}\text{cesium}$ (hereafter referred to as “radiocesium”) which was one of the most abundant of the radioactive contaminants released by the Chernobyl accident (Anspaugh et al. 1988). Previous studies have indicated how knowledge of the accumulation and cycling of this radionuclide in bird populations can not only provide important information about the birds themselves but can also be relevant to concerns for other forms of environmental contaminants as well (Brisbin et al. 1973, Clay et al. 1980, respectively). Like other gamma-emitting radionuclides, radiocesium can be detected and total body burdens quantified in living birds without harm to the subjects. This feature has enabled this radioisotope to become the focus of several radioecological studies using birds as “sentinel animals” to evaluate some basic “textbook” principles of contaminant cycling. Although most of these principles were developed through laboratory studies, this approach now allows them to be tested under natural free-living conditions. The results of such work can then be combined with some basic ornithological information for the movement and migration of birds in eastern Europe and the western Soviet Union, to make some preliminary predictions and pose some testable hypotheses concerning the role of birds, particularly waterfowl, as possible vectors of radiocesium contamination from the site of the Chernobyl accident.

CONTAMINANT UPTAKE: THE SENTINEL ANIMAL APPROACH

The “sentinel animal” approach to contaminant monitoring involves the use of individuals which have either been tamed or otherwise rendered vulnerable to multiple recapture while living free under “natural” conditions in contaminated habitat. The periodic recapture and return of these individuals to the laboratory can produce time-series data for the uptake of contaminants from the environment as well as for the assessment of effects which the contaminant may have as it accumulates in the animal’s body (e.g. George 1990). In the case of birds, sentinel animal studies of the uptake and effects of radiocesium have been undertaken using tamed and imprinted Mallard Ducks *Anas platyrhynchos* and feral Bantam Chickens *Gallus gallus* in both aquatic and terrestrial habitats (George 1990, Brisbin in press, respectively). A modification of this approach is also possible, using untamed wild birds which can be subjected to multiple recaptures through routine banding/ringing operations (Brisbin & Swinebroad 1975) or by wing-scissoring and radio-tracking to assist in multiple recaptures (Fendley et al. 1977, Potter 1987).

The results of the studies cited above have now shown that the classic “textbook” model for radionuclide uptake (Davis & Foster 1958) does not appear to be valid under free-living conditions. Rather, radiocesium uptake from contaminated habitats under natural conditions seems to be better described by a three-parameter Richards sigmoidal model (Brisbin et al. 1989). This model is characterized by a slight but significant time-lag in the rate of initial contaminant accumulation, as compared to the “classic” model which has been largely based on laboratory studies. Although the magnitude of this initial time-lag was quite small in the studies cited above, the consequences of this deviation from the predictions of the classic uptake model could assume a greater importance in the case of contamination events of a larger scale such as the Chernobyl reactor accident (Brisbin in press).

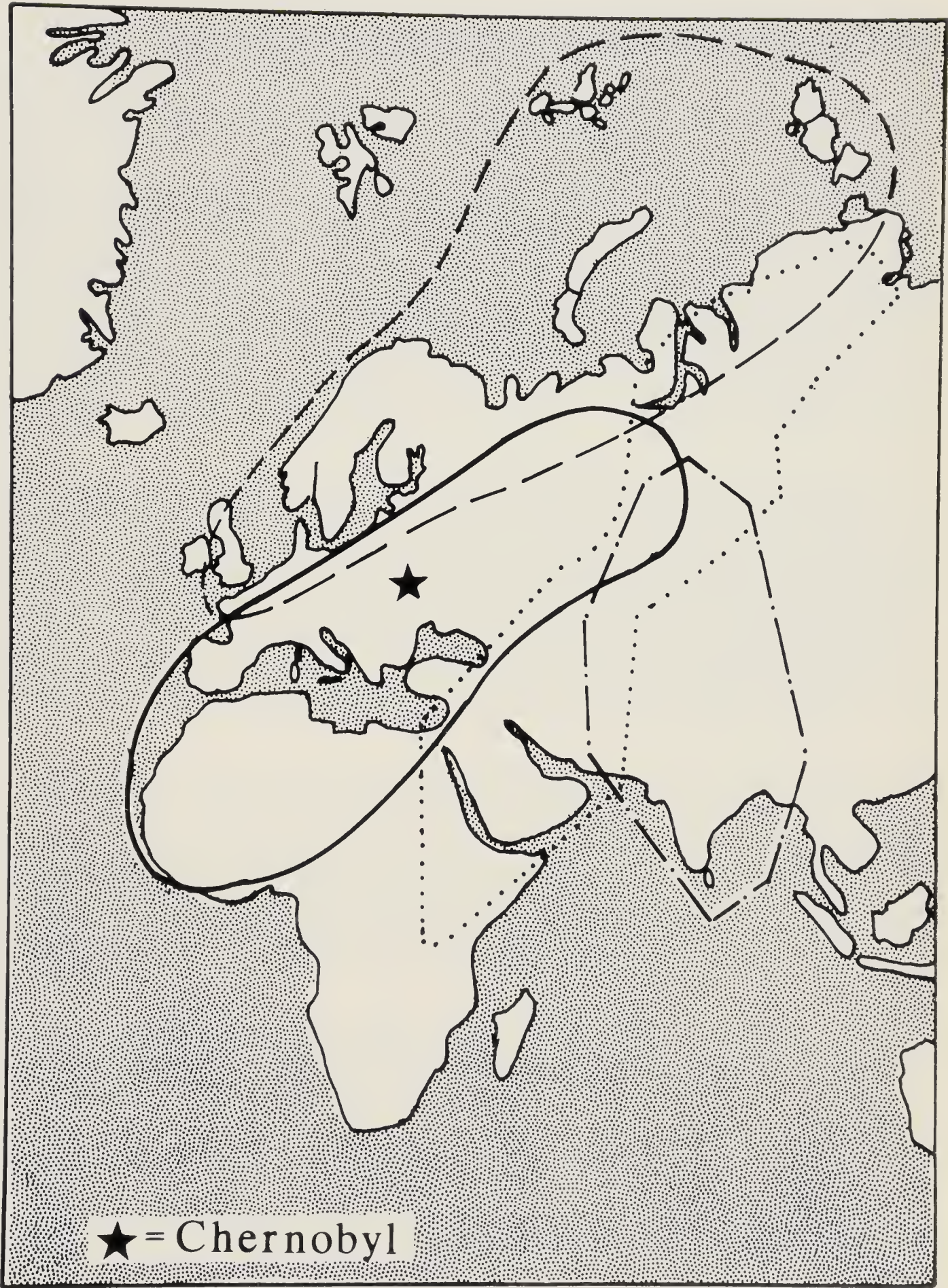


FIGURE 1 - Outlines of the major waterfowl flyways of eastern Europe and European Russia in relation to the Chernobyl reactor site. The solid line outlines the only flyway including the Chernobyl site within its boundaries. From Brisbin (in press), as redrawn from Isakov (1966).

APPLIED AVIAN RADIOECOLOGY: THE CHERNOBYL NUCLEAR ACCIDENT

Assessments of the release of radiocesium and other radionuclides as a result of the Chernobyl nuclear accident have so far dealt almost exclusively with dispersal by physical, principally meteorological, transport mechanisms and with domestic animals and other agricultural products which are likely to be consumed by humans. To date there has been little or no published information on the direct contamination of birds or other wildlife species living in the immediate vicinity of the reactor explosion, or on the possibility of biotic transport of these contaminants by migratory species, particularly waterfowl, which may also be consumed by humans as food. The wetlands adjoining the Chernobyl reactor site, the so-called "Pripyat Marshes" have been previously identified as representing important habitat for waterfowl (Isakov 1966), and may extend for over 300 km to the northwest from the reactor site, including an area possibly as large as 15,000 km², as estimated from standard geographic maps (Hall 1981).

The migratory patterns of waterfowl passing through the general region of the Chernobyl accident have been described by Isakov (1966) who described five major flyways, only one of which includes the reactor site. Such knowledge of the general migratory flyway patterns of the waterfowl of this region can both explain the lack of elevated radiocesium levels in wintering populations of waterfowl in certain parts of the western Europe (e.g. Hancock & Woolam 1987), as well as predict those regions where elevated levels of this contaminant might be more likely to be found. The latter for example would include southwestern France, Spain and northwest Africa as well as much of the Mediterranean region (Figure 1).

The likelihood that migratory waterfowl visiting these Chernobyl wetlands might serve as vectors of radiocesium contamination to the food chain of man has been preliminarily estimated by calculations presented by Brisbin (in press). These calculations have been based on estimates of parameters for the uptake, concentration and transport of radiocesium by waterfowl inhabiting similar aquatic habitats that have been contaminated by lower-level releases of this isotope from nuclear industrial activities at the U.S. Department of Energy's Savannah River Site (SRS) in the southeastern United States (Brisbin et al. 1973).

In addition to estimating radiocesium uptake parameters for the Richards sigmoidal model as described above, these studies at the SRS have also found that radiocesium does not show biomagnification into the higher trophic levels of this waterfowl community, as would be expected for other forms of environmental contaminants (Carson 1962). Rather, it was the herbivorous American Coot *Fulica americana* which consistently showed the highest body burdens of radiocesium in this wintering waterfowl community (Brisbin et al. 1973). Like many other rallids, related species of *Fulica* in the Chernobyl region are known to be frequently consumed as food in many of the countries in which they are likely to winter (Ripley 1976, Figure 1), thus suggesting a potentially overlooked pathway for released radioactive contaminants to reach the food chain of man.

The calculations of Brisbin (in press) suggest that cooked meat from migratory waterfowl harvested on their wintering grounds as much as 3000 km from the Chernobyl

site could exceed the maximum level of radiocesium generally permitted for human consumption (600 Bq/kg fresh weight; EEC 1986), if the areal deposition of this isotope in the 100 km² of marsh wetlands closest to the reactor site exceeded 17.7×10^{10} Bq/km². This is only 25 times the average radiocesium deposition rate estimated for the entire European U.S.S.R. (6.98×10^9 Bq/km², Anspaugh et al. 1988).

Whether or not the magnitude of this difference indicates that there is cause for concern, will depend on later more refined estimations of the actual radiocesium deposition rates in the Pripjat Marsh wetlands and particularly on the collection of data for actual contaminant body burdens of waterfowl and/or other birds or wetlands biota from this site. The collection and assessment of such data both from the Chernobyl region and from along the flyways, wintering and breeding grounds of birds that may pass through that region should be a priority item for cooperative research within the international ornithological community.

ACKNOWLEDGEMENTS

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CLOSING REMARKS: BIRDS AS INDICATORS OF GLOBAL CONTAMINATION AND CYCLING PROCESSES

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Taken together, the papers presented in this symposium, although only five in number, span the gamut from terrestrial to freshwater and marine environments; they also reach across a variety of contaminants and scales of impact from local to regional and particularly global concerns. If there is a single theme that seems to be common under all of these conditions it is that efforts to evaluate contaminant fate and effects in bird populations cannot be successful without a thorough understanding of the principles of basic ornithology and the natural history of the particular birds under study.

This message of the need to “know your bird” is of course, good news to those of us who are concerned for the future of ornithological employment within the mainstream of environmental science. However, there still seems to be a need to “spread the word” in this regard amongst many of today’s engineers, health physicists, administrators and political decision-makers who find themselves in positions of responsibility for designing programs of environmental monitoring and assessment.

Finally, it is also important to emphasize the corollary of the above situation. Namely, important benefits can accrue to our understanding of basic ornithology as the result of information gained from applied studies of contaminant cycling in bird populations. Indeed these two sides of the same coin not only can but must go hand-in-hand, if we are ever to be successful in using birds as indicators of global contamination and cycling processes.

SYMPOSIUM 48

**INTEGRATING NEW ZEALAND
CONSERVATION**

Conveners J. L. CRAIG and G. S. DUMBELL

SYMPOSIUM 48

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INTRODUCTORY REMARKS: INTEGRATING NEW ZEALAND CONSERVATION

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By convening this symposium, we have taken the opportunity to bring together five very different papers covering a range of conservation activities and issues. Conservation, especially avian conservation, is very topical here in New Zealand, and as has been previously pointed out in this congress, New Zealand has a small ornithological community which is highly conservation oriented. This is also reflected in the range of authors who have contributed papers to this symposium, which includes conservation managers, applied scientists from governmental agencies, and university based research scientists.

In addressing our title, we hope to examine the role that science can play in integrating conservation. In doing this, we believe that we should all remember that science is a methodology which gives us the machinery to help us achieve our declared conservation goals. As a result, science must also be integrated with the political, social and economic components of conservation. Science is not, and must not become a conservation end in itself. Having said that, we believe that science is essential for identifying conservation options. This can only be achieved through the development of theory which is being constantly re-evaluated against data from the real world. This generates a dynamic feedback between theory and data to maintain a balance and to allow an informed choice between conservation options. We hope the five papers in this symposium will demonstrate this.

The first paper addresses three case studies of manipulative management in the field aimed at improving the status of endangered species. The second paper is a wide ranging review of the impacts that introduced mammals, especially predators and competitors, are having on New Zealand birds. Following on from this, the third paper contains more specific information about the control operations which have been launched against introduced mammals in New Zealand, and the effects of those operations on bird populations. The fourth paper considers both the problems and advantages of managing small populations of birds, especially on islands, before the final contribution which is a more general paper warning us of the problems of limiting our approaches to the acceptance of one entrenched conventional research methodology.

BEHAVIOURAL MANIPULATION OF ENDANGERED NEW ZEALAND BIRDS AS AN AID TOWARD SPECIES RECOVERY

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ABSTRACT. New Zealand contains 11% of the world's endangered bird species. The introduction of mammalian predators and competitors, and the destruction of native habitats by humans have been prime causes of the decline in numbers and distribution of many species. However, human intervention has resulted in the recovery of some species. Management techniques such as cross-fostering, supplementary feeding and captive breeding have manipulated individual and population behaviour or physiology in the wild. These techniques have boosted productivity to well above that occurring naturally, while avoiding inappropriate filial imprinting. Case studies from the Black Robin, Black Stilt and Takahe recovery programmes are discussed.

INTRODUCTION

New Zealand is an island archipelago which has evolved some unique endemic bird species. Geographical isolation and an environment free of mammals has led to both flightless and nocturnal species which were ill-equipped to deal with predators such as cats *Felis catus*, ferrets *Mustela furo* and stoats *Mustela erminea*; and competitors such as deer *Cervus* spp. and possums *Trichosurus vulpecula* which were introduced by humans in the 1800's. Habitat destruction, degradation or fragmentation has also contributed to the decline of species, especially on the North and South Islands and on many offshore islands. New Zealand now contains 11% of the world's endangered bird species.

Active management to halt the decline of many species began in 1947 when the NZ Wildlife Service was established. Initially the management of endangered birds concentrated on translocating birds to predator-free islands. For example, South Island Saddlebacks *Philesturnus carunculatus carunculatus* were saved from extinction using this method (Merton 1975). However, the use of management techniques which manipulate the breeding biology, physiology and behaviour of endangered species has increased over the past 10 years and now includes egg and nest manipulations, fostering, cross-fostering, supplementary feeding, hand-rearing and captive breeding.

Of these, the technique which poses the greatest risk to the long-term behavioural characteristics of a population is cross-fostering. Imprinting onto the foster parents of another species (Cooke & McNally 1975, Owen 1975, Kruijt et al. 1982), the learning of their song (Immelmann 1972) and the migration of a sedentary species with migratory foster parents (Harris 1970) are three serious problems which have been identified in the past. Similarly, rearing birds in captivity may result in individual behaviour such as taming and filial imprinting on humans (Kear 1977) which is inappropriate for life in the wild.

This paper will describe three case studies; Chatham Island Black Robin *Petroica traversi*, Black Stilt *Himantopus novaezelandiae*, and Takahe *Notornis mantelli* all of which have used one or more of these techniques. The success of each technique and the steps taken to avoid inappropriate imprinting are discussed.

TABLE 1 – Productivity of Black Robin pairs.

1. PRIOR TO ANY MANAGEMENT

1973-1976 1 chick survived to breeding age

2. FOLLOWING TRANSFER TO MANGERE ISLAND

Season	No. pairs	No. independent young per pair	% independent young per eggs laid
1976/77	2	0.5	–
1977/78	2	1.0	–
1978/79	2	0.5	–
1979/80	2	0.5	–

3. CROSS-FOSTERING BEGAN

1980/81	1	4.0	40
1981/82	1	2.5	42
1982/83	2	1.0	18
1983/84	2	5.5	46
1984/85	5	3.8	61
1985/86	5	2.0	29
1986/87	9	2.4	47
1987/88	11	3.6	63
1988/89	22	2.2	43
AVERAGE		3.0	43

CHATHAM ISLAND BLACK ROBIN

The Black Robin is endemic to the Chatham Islands, 850 km east of the New Zealand mainland. Once widespread in the Chathams group, the Black Robin has disappeared from the larger islands following European colonisation early last century. A remnant population of about 25 birds survived in approximately five hectares of bush habitat on Little Mangere Island. Following rapid degeneration of their bush habitat in the 1970's, the sole population of Black Robins plummeted from eighteen birds in 1972 to seven (including two breeding pairs and three males) in 1976. From 1973 to 1976, only one chick survived to breeding age. In 1976, as a result of the small population size and low recruitment, all the birds were transferred to four hectares of forest on nearby Mangere Island (130 ha) where by 1979, the population had sunk further to only five birds. Following the transfer, chick survival improved with five chicks being produced in four years (Table 1). However, the recruitment of young birds into the population was lower than natural mortality of older birds. Unaided, no rapid recovery was possible and further management was needed. Black Robins can live to 13

years of age but have a low reproductive rate. Usually two eggs were laid per clutch and a successful nesting cycle lasted three months. As Black Robins are capable of renesting, productivity could be increased by manipulating nesting behaviour. Just one effective breeding pair existed in 1979, so a cross-fostering and nest manipulation programme was begun to boost productivity. Eggs were taken from robins and fostered to Chatham Island Warblers *Gerygone albofrontata* on Mangere Island. Warblers were able to hatch the eggs and care for the nestlings but could not raise them beyond 10 days of age because unlike Black Robins, they did not remove faeces from their nests. Nests became contaminated and the nestlings died. However, in 1981 it was discovered that Chatham Island Tomtits *Petroica macrocephala* could successfully hatch and rear robin chicks through to independence, so the use of warblers was discontinued. As no tits occurred on Mangere Island, eggs were carried 15 km by sea and fostered to Tomtits on South East (Rangatira) Island (210 ha). Nestlings were transferred back to Mangere Island and between 1980 and 1988, a total of 40 robin eggs, 10 nestlings and 25 independent birds were eventually transferred between the two islands without loss. The 1983 transfer of two pairs of adult Black Robins to South East Island to establish a second population was the turning point in the recovery of the species.

During each breeding season, poorly sited or insecure nests were secured with string or gradually moved to safety a few metres at a time. Natural nests of warblers, tits and robins were also relocated into nest-boxes, to increase security and to facilitate management of the nest contents and this was completely accepted by parent birds. Each spring approximately 30 pairs of tits were used to ensure a continuous supply of foster parents. All breeding robins were closely monitored and the first and second clutches were removed from each pair and fostered to tits for incubation. Third clutches were normally left with the natural parents. Where possible, the incubation of several clutches was synchronised so that broods of similar ages could later be united and returned to a robin nest prior to flying. One of the major successes of the programme was that robins, tits and warblers could all be induced to incubate for almost twice their normal incubation period and accepted fostered eggs and nestlings without problem.

At approximately 15 days of age, robin chicks hatched by tits were returned to robin nests, where they were often united with a brood of similar age. Fledging occurred at about 23 days. Robin nests were augmented with up to four extra nestlings above the normal brood size of one or two. To help robin parents cope with the additional food demands of enlarged broods, supplementary feeding was undertaken. This consisted of hand-feeding natural (e.g. wetas) and cultivated (e.g. mealworms) invertebrates to Black Robin parents who then fed them to their chicks.

In the early stages of the tit fostering, some Black Robin chicks were reared completely to independence by Tomtits. Some tit-reared Black Robins uttered contact calls identical to those of the foster species, particularly those tit-reared robins raised in a single chick brood. Male song also resembled that of Tomtits, but was not an accurate copy. Tit-reared robins remaining on South-East Island amongst their foster species never switched to robin song and generally did not attempt to breed with other Black Robins. Conversely, male tit-reared robins transferred back to Mangere Island began singing robin song in the presence of other robins which had been reared by their own species. In the absence of tits, transferred robins bred within two years with

conspecifics. This reversal of malimprinting could be induced even after three years and several attempts to mate with the foster species. No such reversal of malimprinting was apparent in robins which remained with Tomtits on South East Island. Once back on Mangere Island, the adult tit-reared robins socialised with other robins and learnt to sing robin song from conspecific males in adjacent territories. The timing of song switching closely followed the transfer to tit-free Mangere Island and was not affected by the age of the birds.

Since the 1983 transfer of adult Black Robins to South East Island to form the second population, the population density of Black Robins on South-East Island has increased to over 100 birds and the remaining tit-reared robins have made the transition to robin song behaviour and pairings in the presence of tits.

BLACK STILT

Once widespread throughout the South and lower North Islands, Black Stilts declined in number and range in the late 1800's following the introduction of mammalian predators by humans. Loss of swamp and river habitats through agricultural development and hydro-electric power development, and hybridisation with the closely-related Pied Stilt *Himantopus himantopus leucocephalus* has also contributed to their decline. In the 1950's, the population decreased from 500-1000 individuals to approximately 50. It reached a low of 32 adults in 1982, including only 13 breeding pairs found nesting only on the braided riverbeds of the Mackenzie Basin, South Canterbury, South Island. Without management, only 1% of all eggs laid survived to fledging as most were lost to predators or flooding (Pierce 1986). In a similar manner to Black Robins, this level of recruitment was lower than adult mortality and the population was unable to recover unaided. Black Stilts were capable of laying up to four clutches per breeding season if early clutches were lost, so a cross-fostering programme began in 1981 where the first and second clutches of each pair were removed for eventual placement under Pied, hybrid or mixed pairs of stilts. Black Stilt parents were left to rear clutches laid later in the season. All eggs were taken freshly laid and were artificially incubated for 23 days. If the parent Black Stilts were to receive their own hatching eggs back after artificial incubation, they were given "dummy" ceramic eggs to avoid nest desertion. Otherwise, if their eggs were to be fostered to other parents at hatching, Black Stilt pairs were induced to re-lay by leaving the nest bare. All foster parents were given dummy eggs in place of their own. This way, stilts could be induced to prolong their attendance at the nest for up to two months, until required as parents to Black Stilt chicks. Foster parents accepted eggs and newly hatched chicks fostered to them and on one occasion, a Black Stilt pair accepted chicks before they had completed laying their own eggs. To further enhance success, many nests were surrounded by a ring of traps to remove local ground predators.

Between 1981 and 1989, 332 chicks were fostered to Black, hybrid or Pied Stilt parents and 159 (48 %) of these fledged. The main reasons for chick death prior to flying were floods and predators. Between 1985 and 1989, 50% of eggs which hatched in trapped areas (n=90) survived to fledging (Murray et al. 1990) whereas in untrapped areas this proportion was reduced to 29% (n=63). Generally, only those fledged chicks fostered to two black parents are known to have survived to breeding age (Figure 1). Almost all hybrid and Pied Stilts migrated from the Mackenzie Basin during winter to

the South Island coast or North Island harbours, whereas 90% of the Black Stilt population were nonmigratory. It became evident that Black Stilts given to Pied or hybrid stilts migrated out of the basin in winter with their foster parents. They either did not return, or returned only in spring and summer and did not breed with other Black Stilts. Juveniles reared by two black parents remained in their natal areas and although post-fledging mortality was high, some were recruited into the breeding population.

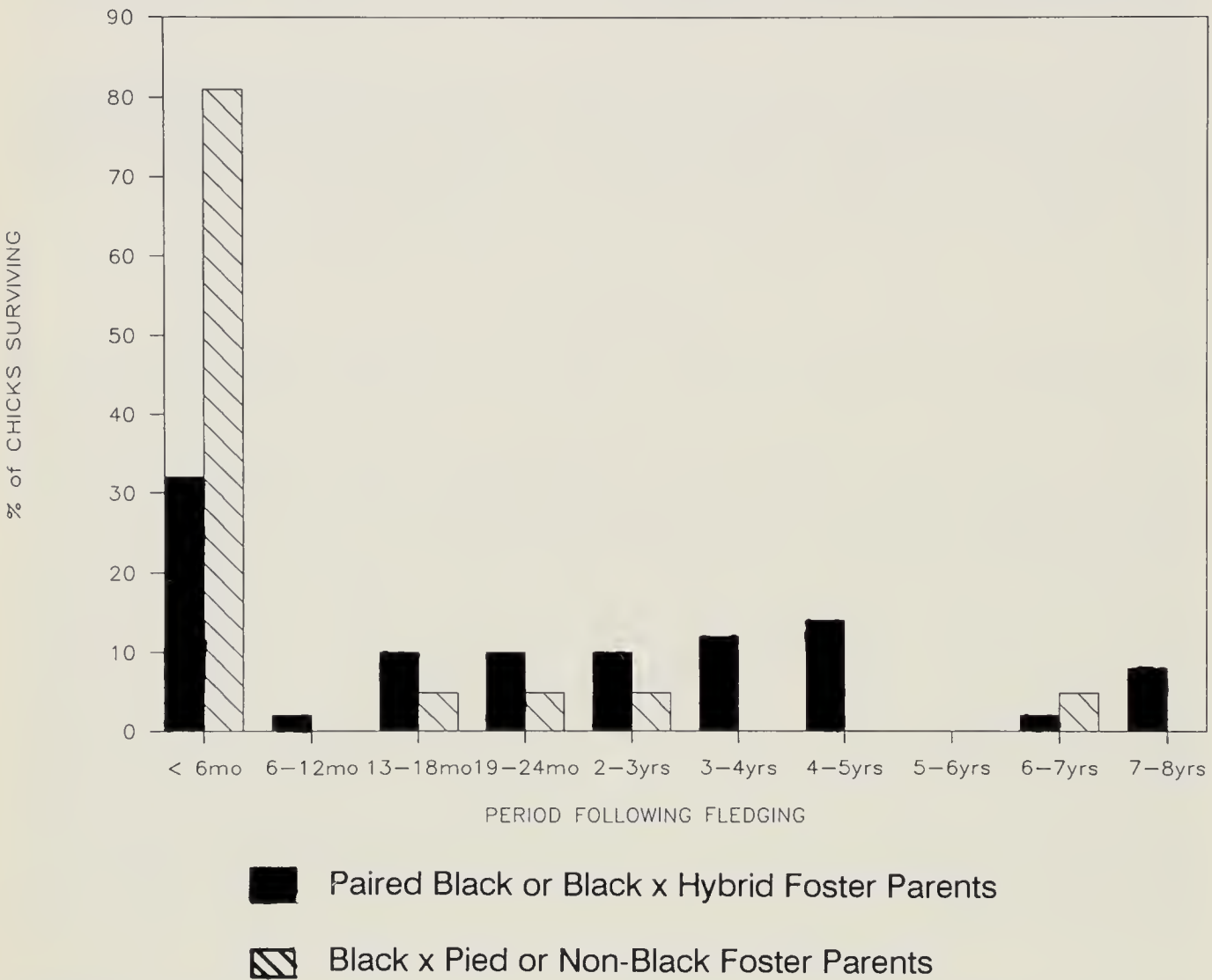


FIGURE 1 – Sightings of banded Black Stilt chicks fledged 1981-1987.

These results led to a shift of management in 1985 to allow Black Stilt parents to rear their first clutch and fostering to migratory Pied and hybrid stilts was scaled down. Fewer chicks were produced but the quality of rearing improved and the migratory behaviour of the Black Stilt population was reduced. Black Stilt nests were still manipulated by fostering eggs of other black pairs where necessary. For example, pairs with flood or predation or disturbance prone nests were given eggs from other Black Stilt pairs which were due to hatch before their own. Where Black Stilt nests and the dummy eggs contained within them were lost to predators or floods, eggs previously taken from that nest and held in the incubator were fostered to other Black Stilt pairs.

Egg manipulation, artificial incubation and predator trapping techniques have increased the percentage of eggs surviving until fledging as chicks, to between 19% (1982) and 42% (1983) (Table 2). This was a significant improvement on natural recruitment of 1% recorded by Pierce (1986) and the population now stands at around 80.

TABLE 2 – Productivity of Black Stilt pairs

1. PRIOR TO MANAGEMENT			
1977—1979 1% of eggs laid survived to fledging (Pierce 1986)			
2. CROSS-FOSTERING BEGAN			
Season	No. pairs	Average no. chicks fledged per pair	% chicks fledged per eggs laid
1981/82	7*	1.8	35
1982/83	13	1.4	19
1983/84	11	2.5	42
1984/85	11	1.4	23
1985/86	12	1.8	28
1986/87	10	1.7	37
1987/88	11	1.3	28
1988/89	12	1.1	21
AVERAGE		1.6	28

* Not all areas surveyed

To supplement production of chicks in the wild, a captive breeding and release facility was constructed near Twizel in 1987, within the range of the wild Black Stilt population. Nearby permanent spring water was diverted through the aviaries to provide natural feeding areas. Three captive Black Stilt pairs were transferred to the aviary from the National Wildlife Centre near Masterton. They were allowed to hatch and rear their first clutch of eggs. At nine months of age, the juveniles were separated and released into the wild.

Allowing Black Stilt parents to breed in semi-natural captivity has reduced the risks of malimprinting, which results from hand-rearing. Young chicks improved their foraging success, through experience with natural invertebrates within their aviary ponds (Reed 1986) and social behaviour within and between family groups was experienced during the “semi-natural” rearing. Parent birds also reinforced antipredator behaviour of chicks, through their own vocal and display behaviour.

By the time of release, young Black Stilts could capture insects very successfully (Reed 1986) and reacted strongly to predators, particularly Harriers *Circus approximans*.

Four of the seven juveniles released since November 1989 survived in the wild and one attempted breeding during the 1990 season. A further seven young birds were released in September 1990 and their progress is being monitored. At least three are still alive.

TAKAHE

Takahe were thought extinct until the rediscovery in 1948 of a single population of less than 200 birds in the alpine tussock grasslands of the Murchison Mountains near

Te Anau. Competition with red deer for their preferred tussock (*Chionochloa* spp) food plant and predation by stoats and wekas *Gallirallus australis* have all contributed to their decline. The wild population stood at approximately 120 individuals in the early 1980's.

Since 1985, a small percentage of eggs laid by wild birds have been removed for captive rearing. Before removal, all eggs were candled and the wild pairs were left with one fertile egg as they rarely rear their second egg successfully and do not re-lay a second clutch. Eggs removed from the wild were hatched and the chicks hand-reared at Burwood Bush, 40 km from Te Anau. They have been used to establish a captive breeding population and to provide young birds for release into the wild.

To prevent hand-reared chicks imprinting on humans, hand-puppets and models were used as "parents" to feed and brood chicks. Eggs were artificially incubated and at hatching, taped brooding calls were played to emerging chicks which were placed under heated Takahe models. Speakers concealed inside the model's head allowed the chicks to continue to hear the brooding calls. Takahe hand-puppets were used to feed chicks and feeding calls were played from the puppet via a speaker in each glove. Chick-rearing was done with minimal handling and chicks rarely saw a human.

Young birds were gradually introduced to natural grasses at six weeks of age and at three months, they were moved to 60 x 30 m red tussock enclosures. At five months, the young birds were pulling tussock tillers on their own and feeding naturally.

Between October 1987 and December 1989, 25 young birds were released into the Glaisnock catchment of the Stuart mountains near Te Anau where survival has been greater than 50% and one failed breeding attempt is known.

SUMMARY

By using manipulative techniques to increase recruitment into a population, how much better off is that population having been manipulated than if it were left alone? (Cade 1978). The results from these case studies give positive answers. Manipulation of nest contents, nest protection, fostering, cross-fostering and supplementary feeding have increased the number of Black Robins from 5 to over 100 birds in 9 years. Manipulation, protection and fostering of Black Stilt eggs, in addition to a captive breeding and release programme have increased this species' population number from 32 to approximately 70 birds. Egg manipulation, captive breeding, puppet-rearing and release of Takahe, has made use of wild eggs unlikely to survive in the wild and the liberation of chicks has established a second population which has contributed to an increase from 120 individuals to over 200 in total.

In all cases the interventionary management techniques had to be modified as each programme progressed, to avoid the acquisition of individual behaviour that would be inappropriate to the long-term behavioural characteristics of the wild population. Filial and sexual imprinting theory (Immelmann 1972) predicts that the rearing of one species by another will result in imprinting on the foster species. The sexual imprinting process has been reversed in laboratory studies of some species, such as the Zebra Finch *Poephila guttata* (Immelmann 1972, Sonnemann & Sjolander 1977) by remov-

ing the foster species. The fostering of Black Robins to Tomtits and their subsequent return to Black Robin parents prior to or at fledging, is one of the few examples where reversal of the imprinting process has been induced in a field situation. The reversal of sexual imprinting on Tomtits was also achieved after fledging in the wild through transfer to an environment free of the foster species.

Singing behaviour has been demonstrated to alter with experience after the normal sensitive phase of learning has occurred. Zebra Finches denied the opportunity to learn song during the normal sensitive phase may remain open to learning until a suitable song tutor is available (Eales 1987). A similar result was obtained in Black Robins where social contact rather than age was the most important factor determining the acquisition of their own species song. Confinement on an island without the foster species promoted the rapid reversal of the sexual and song imprinting processes, even in older individuals.

One behavioural characteristic of a fostered species which cannot be easily reversed is the tendency to migrate. Once Black Stilts migrated with their foster parents, those few individuals which did return to the breeding population continued with few exceptions to migrate annually. As the cross-fostering technique could not be modified to overcome this problem, the use of the technique had to be reduced.

The establishment of a self-sustaining population as a result of the reintroduction of a species from captivity into the wild, has rarely been achieved in endangered species management (Fyfe 1978). Although the instinctive behaviour necessary for survival in the wild is present in captive birds, much behaviour is learnt or perfected by practise. Learning of behaviour inappropriate in a wild situation such as taming and failure to avoid predators was minimised through the use of puppets in hand-rearing Takahe and by parent-rearing Black Stilts under as natural conditions as possible.

A slow method of release ("gentle-release") is necessary to allow gradual acclimatisation to the new environment. However, release back into areas where factors responsible for species demise are still operating (such as in introduced mammals) may seriously compromise the establishment of a self-sustaining population. Short-term techniques such as trapping around nest-sites and surrounding breeding areas with predator-proof fences can aid survival and recolonisation of these populations, at least in the short term. But in the long-term, unless the cause(s) of the decline are identified and remedied, predator-naïve species such as Takahe and Black Stilts will require continuing, intense long-term management if they are to survive within their current mainland ranges.

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THE INTERACTIONS OF NEW ZEALAND FOREST BIRDS WITH INTRODUCED FAUNA

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ABSTRACT. Historically, New Zealand forest birds suffered declines and extinctions due to animals introduced by Polynesians after ca. 750 AD and by Europeans after 1769. The evidence linking these declines with introduced fauna is largely circumstantial, but nonetheless compelling. We suggest that the details of present-day interactions between forest birds and introduced fauna on the New Zealand mainland are different from those pertaining to historical declines, since the forest community has changed; introduced animal populations are post-peak, and some forest birds may have changed their behaviour to cope better with predators and competitors. Nevertheless, introduced fauna are still regarded as the most important proximate cause of current New Zealand forest bird declines. Increasingly, manipulative experimental designs are being used to explore the causes of these declines.

Keywords: New Zealand, forest birds, introduced fauna, predation, competition, causes of decline.

INTRODUCTION

Introduced fauna

All forests on the New Zealand mainland now contain animal species of foreign origin, either deliberately or accidentally introduced by humans. In addition, most coastal and offshore islands harbour such species, either introduced or adventive. Polynesians introduced Kioore *Rattus exulans* and Kuri *Canis familiaris* about 1000 years ago, but most species arrived with Europeans after 1769 (Williams 1973). Twenty one of the 34 successfully introduced terrestrial mammal species dwell principally in forest interiors, or are widespread there (King 1990a). In contrast, only two introduced bird species, Blackbird *Turdus merula* and Chaffinch *Fringilla coelebs*, are widespread in intact native forests, although 11 others occur in disturbed forest or on forest edges (Robertson 1985). Forest waterways contain introduced fish, especially, Brown and Rainbow Trout *Salmo trutta* and *Oncorhynchus mykiss* (McDowall 1990). There are at least three forest-dwelling introduced amphibians (Robb 1980) and many invertebrates (G. Hosking, pers.comm.).

Forest birds

In this paper, a forest bird is defined as a species or subspecies whose individuals are found mostly in forest communities throughout their range and life-cycle. This definition covers 51 species or subspecies (Appendix 1), including Blue Duck *Hymenolaimus malacorhynchus*, Kakapo *Strigops habroptilus*, and Weka *Gallirallus australis*. It excludes New Zealand Falcon *Falco novaeseelandiae*, Kea *Nestor notabilis* and Takahe *Notornis mantelli*, as well as seabirds feeding at sea but nesting in forests. Bell (1986) lists 24 (47%) of the 51 taxa as endangered, threatened, rare, or regionally threatened (Appendix 1).

This paper examines the historical and current evidence for the impacts of introduced animals on New Zealand forest birds.

HISTORICAL DECLINES OF FOREST BIRDS AND THEIR CAUSES

Evidence for the causes of historical extinctions or declines in New Zealand is mostly circumstantial, but often compelling.

The Polynesian Period (c. 950-1769 AD)

Polynesian period extinctions of forest birds included all 11 Moa species (genera *Anomalopteryx*, *Megalapteryx*, *Pachyornis*, *Emeus*, *Euryapteryx* and *Dinornis*), the N.Z. Hawk *Circus eylesi*, Haast's Eagle *Harpagornis moorei*, the Snipe-rail *Capirallus karamu*, the North and South Island Adzebills *Aptornis otidiformis* and *A. defossor*, the N.Z. Raven *Corvus moriorum*, the North and South Island Stout-legged Wrens *Pachyplichas jagmi* and *P. yaldwyni*, and the Giant Chatham Island Rail *Diaphorapteryx hawkingi*. The Giant Owlet-nightjar *Megaegotheles novaezealandiae* and the mainland subspecies of the N.Z. snipe *Coenocorypha* sp. were perhaps extinct prior to Polynesian settlement (Holdaway 1989, O.S.N.Z. 1990).

Polynesians cleared about one third of the original New Zealand forest area (Masters et al. 1957, Nicholls 1980). Avian extinctions are attributed largely to this forest habitat destruction and to hunting by humans, although predation by *Rattus exulans* probably played a role in the elimination of smaller birds (Cassels 1984, Trotter & McCulloch 1984, Anderson 1984, Atkinson 1985, 1989, Holdaway 1989, McGlone 1989 but see Craig 1986). The most important evidence is the widespread occurrence of bird remains in middens, the correlation between the abrupt beginning of large-scale avian extinctions and the time of settlement by Polynesians and the absence of alternative explanations for the loss of birds from those forest areas largely unaffected by burning or climatic change. Further indirect evidence is from the known or inferred characteristics of the extinct birds. Large size, flightlessness, fearlessness, food specialisation and low potential chick output would have rendered many species vulnerable to predation by humans or rats, and to the effects of reduced food supply (Cassels 1984, Holdaway 1989).

The European period (after 1769)

Similar evidence explains the new but smaller wave of declines and extinctions of forest birds which followed the arrival of the English navigator Cook in 1769. Forest bird species which became extinct during this time were the Bush Wren *Xenicus longipes*, the Stephen's Island Wren *Traversia lyalli*, the Huia *Heteralocha acutirostris* and the Piopio *Turnagra capensis* (O.S.N.Z. 1990), and many others declined in distribution and abundance.

Cook and subsequent whalers and sealers introduced Norway Rat *Rattus norvegicus*, Mouse *Mus musculus*, Cat *Felis catus*, Pig *Sus scrofa*, Goat *Capra hircus* and perhaps Ship Rat *Rattus rattus* (Wodzicki 1950, Atkinson 1973). Colonists then cleared half of the remaining forest and established a further 26 mammal species (King 1990), 38 birds, 3 amphibians, 20 fish and an unknown but large number of invertebrates. However, not all of these invaded native forests.

It is difficult to separate the past impacts on forest birds of forest clearance, introduced animals, disease, and hunting or collecting by humans. Most authors blame habitat loss and predation, and few mention competition (Appendix 2), although their conclusions are often speculation.

Occasionally, however, separation is possible. For example, the likely time of spread of the Ship Rat in the North Island was more or less coincidental with declines of the Bellbird *Anthornis melanura*, Robin *Petroica australis*, Stitchbird *Notiomystis cincta*, Saddleback *Philesturnus carunculatus*, and Piopio (Atkinson 1973), at least 15 years before the spread of Stoats *Mustela erminea*. In Westland and Fiordland after 1880, Stoats "certainly contributed" (King 1990b) to the demise of Bush Wren, Laughing Owl *Sceloglaux albifacies*, Piopio, Saddleback, Kokako *Callaeas cinerea*, and perhaps Kakapo and Little Spotted Kiwi *Apteryx owenii*. Elsewhere, there were too many competing factors to determine a clear role for Stoat predation.

Islands provide the clearest illustrations of the detrimental impacts of mammals on forest habitat or forest birds. This is particularly so when only one species invaded an island, or when legitimate comparisons can be made between similar islands with different combinations of introduced species. Examples of the former are Ship Rats on Big South Cape Island (Bell 1978), Cats on Stephens Island (Fitzgerald 1990) and feral Goats on Great King Island (Rudge 1990). Similar accounts of impacts due to these species, especially rats, are well-known from other archipelagos (Lever 1985, Atkinson 1985, 1989, Steadman 1989). Compared with rats, Stoats reached few offshore islands and so much less evidence is available from islands to clarify the contribution of Stoats to mainland forest bird declines.

Few of New Zealand's offshore or outlying islands are in a completely pristine state though some, such as Adams and Disappointment in the Auckland group, and the Snares, are nearly so. Despite varying degrees of modification, islands are important refuges for rare and endemic species of many life forms (Daugherty et al. 1990). Saddleback and Stitchbird are well known examples of refugee forest bird species which were once widespread on mainland New Zealand but now survive only on offshore islands.

The most scientifically sound evidence of the effects of particular introduced animal species has come from deliberate manipulation, through the translocation of threatened birds to islands lacking predators and/or competitors, and more recently, the eradication of introduced species from islands. Since 1964, North Island Saddlebacks have been successfully established on several northern offshore islands, away from the Ship and Norway Rats, Cats and Stoats which were probably responsible for their rapid decline on the mainland late last century. However, there are many differences between the North Island mainland and these smaller offshore islands. The success of the translocations cannot alone confirm the hypothesis that introduced predators were responsible for the mainland decline, although it is consistent with it.

Eradications of introduced animals from islands test such hypotheses more effectively, since only one major factor (the abundance of the problem species) is altered. Stitchbirds, Robins and Parakeets *Cyanoramphus novaezelandiae* increased on Little Barrier Island after cats were eradicated (Veitch 1983) and on Kapiti Island numbers of Bellbirds, Robins, Whiteheads *Mohoua albicilla*, Kereru *Hemiphaga novaeseelandiae* and Weka were reported to have increased as possums were removed (T. Lovegrove, unpub. data). Details of translocations and eradications on New Zealand islands are found in Atkinson (1990) and Veitch & Bell (1990) respectively.

PRESENT-DAY INTERACTIONS OF INTRODUCED FAUNA WITH MAINLAND FOREST BIRDS

We suggest that the details of present-day interactions between introduced fauna and mainland forest birds are different from those when the introduced fauna first colonised, for the following reasons:

1. The forest community is different now. Some animal species have acclimatized or invaded successfully while others have become extinct. One example of successful invaders is that of the German and Common Wasps *Vespula germanica* and *V. vulgaris*, which have established in New Zealand since 1945 and now may attain a biomass in South Island beech forest equal to or greater than that of birds, rodents and Stoats combined (Thomas et al. 1990). Also, forest habitats have had up to 12 decades of browse by possums, deer and other introduced mammals. The impact of browsers on forest composition is complex, but is known in detail for some localities (eg Stewart et al. 1987, Nugent 1990, Pekelharing & Batcheler 1990).
2. Current populations of introduced mammals are post-peak. Colonizing mammal populations are frequently irruptive, reaching high peak densities compared with post-peak populations. This is a standard model for ungulate eruptions (Caughley 1977), but it probably applied also to Norway Rats (Moors 1990), House Mice (Murphy & Pickard 1990), Stoats (King 1990b) and feral Pigs (McIlroy 1990), all of which were more abundant when first establishing in New Zealand. The dynamics of New Zealand mammal populations in the current post eruptive phase are complex and so far little understood.
3. Forest birds may have changed their behaviour to cope better with introduced fauna, for example by recognizing mammalian predators and showing alarm behaviour. Robins on Stoat-free Motuara Island did not initially recognize Stoat models as those of an enemy, but Robins trained for five minutes with Stoat models and Robin models and alarm calls responded more strongly than other Robins the following day to the Stoat model (Maloney & McLean 1990).
4. The scale and pace of forest clearance has declined drastically, so that most present forest bird-introduced fauna interactions are happening inside legally protected forests, stable in area. This is in contrast to the historical situation, when forest clearance contributed to all forest bird declines at least in terms of the total bird population size. However some current declines may be a faunal relaxation from past reduction in forest area.

CURRENT CONCERNS FOR FOREST BIRDS

Localised distribution

Ten of the 24 taxa in Appendix 2 were classified as rare or regionally rare, threatened or endangered (Bell 1986) because their distribution was localised, sometimes extremely so, rather than because their populations were declining. They are Little Spotted Kiwi, Black Robin *Petroica traversi*, S.I. Saddleback *Philesturnus carunculatus carunculatus*, Chatham Island Tit *Petroica macrocephala macrocephala*, Black

(Snares) Tit *P. m. dannefaerdi*, Stitchbird, N.I. Saddleback *Philesturnus carunculatus rufusater*, N.I. Robin *Petroica australis longipes*, S.I. Robin *P. a. australis*, and Stewart Island Robin *P. a. rakiura*. Some populations, (e.g. Black Robin) are actually increasing in number but their survival is threatened by chance events such as predator arrival or severe storms on the one or few island(s) on which they occur. Only the Black Tit still has the same distribution as at the time of human arrival in New Zealand; the other nine taxa occur on a remnant of their former range or on safe islands to which they have been translocated. Six species or subspecies are restricted as relicts or refugees to islands lacking Cats, Stoats and Ship Rats.

Declining populations

Of the remaining species in Appendix 2, 12 are feared or known to be declining in numbers, although few robust counts of most of them have been undertaken. Hypotheses for their declines are shown in Appendix 3. As with those given to explain historic declines (Appendix 2), some hypotheses are derived from careful analysis, while others are simply knowledgeable conjecture. Detailed autecological studies of Kakapo, N.I. Kokako *Callaeas cinerea wilsoni*, Brown Kiwi *Apteryx australis*, Blue Duck, Kaka *Nestor meridionalis* and Yellowhead *Mohoua ochrocephala* undertaken since 1980 have helped significantly to clarify the likely causes of their present decline.

Competition from introduced animals for food has been hypothesized as contributing to the decline of four taxa. They are N.I. Kokako, N.I. Kaka *Nestor meridionalis septentrionalis*, S.I. Kaka *N. m. meridionalis* and Stewart Island Weka *Gallirallus australis scotti* (Appendix 2). In the northern South Island the major competitors of the S.I. Kaka are two introduced wasp species of the genus *Vespula*, which consume most of the autumn supply of honeydew on which the Kaka depend. However, Possums *Trichosurus vulpecula* have reduced or eliminated alternative foods to which the Kaka may otherwise turn (Beggs & Wilson in press).

Eight of the forest birds in Appendix 2 are suggested to be declining for more than one reason. Factors causing decline of forest birds are probably additive in a historical sense as well as in the sense of operating concurrently. Atkinson (1989) proposed a model describing the relationship between alien animals and habitat loss, as two factors causing extinctions. He suggested that the cumulative effect of the introduction of a series of alien animal species may be to finally reduce the population density of a native animal to the point where its habitat requirement exceeds that available, and so extinction follows. The cause of the extinction could be deemed to be the alien species which finally pushed the native species to the point from which recovery was impossible, but this would be an oversimplification, disregarding the sequential impacts of earlier introductions.

N.I. Kokako is a declining forest passerine for which both predation and competition have been invoked as causes of the decline. Research on this species provides an example of one attempt to determine causes. Two research approaches have been taken to clarify the relative importance of the two factors. The first is to look at Kokako breeding attempts and their outcomes on the mainland (Rotoehu Forest, Bay of Plenty) where many introduced animal species are present. The proportion of the population which attempts to breed, and the outcome of those attempts, will provide important clues to the cause of decline. If most pairs do not attempt to breed, the Kokako may be in poor condition due to reduced food abundance or quality. If most

pairs attempt to breed but their clutches are lost to predation, predators may be the more serious threat. These data should then be compared to those from Little Barrier Island, when funding permits. No mammalian browsers or predators except *Rattus exulans* occur on Little Barrier, and study of this translocated Kokako population should reveal how natural populations behave. This approach indirectly tests the hypothesis that predators and/or competitors limit Kokako populations, by gathering data which may or may not support the hypothesis. The second research approach is to test the hypothesis directly, by experimentally reducing the numbers of mammalian browsers and predators at three mainland sites, to see if Kokako numbers increase. This "research-by-management" initiative is underway at Kaharoa, near Rotorua; at Mapara in the King Country, and at Waipoua Forest in Northland. The two approaches are complementary. Predation and competition may be impacting simultaneously on Kokako breeding success, or the importance of each may vary from year to year.

Manipulative experimental designs are increasingly used to determine the cause(s) of decline of other forest birds. Current Kaka research aims to test the competition hypothesis by providing supplementary food to Kaka (P. Wilson, pers. comm.). Predators are being experimentally removed to assess their impact on Parakeets and Yellowheads in the Eglinton Valley in Fiordland in 1990/91. Parakeet and Yellowhead breeding success is being assessed in a 30 ha forest area which is intensively trapped for Stoats, and in another 30 ha area where no trapping is to be undertaken (G. Elliott, pers. comm.).

CONCLUSIONS

Most mainland forest bird studies have done little more than confirm that introduced fauna are strongly implicated in current declines. However, this outcome is consistent with historic evidence, especially from islands, that introduced animals have reduced or eliminated many forest bird populations. Several manipulative experiments are planned or underway which will directly test hypotheses that introduced browsers and predators limit mainland forest bird populations. These should yield robust evidence which will contrast with the largely circumstantial evidence pertaining to historical declines.

Introduced fauna, especially predators, are still regarded as the most frequent proximate cause of current forest bird declines. However, we can readily see cases, such as in the Chatham Islands, where habitat degradation is a crucial additional problem. We dispute the suggestion by King (1984, p.190) that "... the processes of nature are repopulating New Zealand with birds that are able to live with predators, while the rest are either adapting or have already gone". If current concern for the taxa listed in Appendix 3 is justified, then at least twelve endemic forest bird species or subspecies have yet neither adapted nor gone, but are declining.

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APPENDIX 1

New Zealand forest birds and their conservation status (Bell 1986).

SPECIES	CONSERVATION STATUS (Bell 1986)
Brown Kiwi (3 subsp.)	
NI Brown Kiwi	threatened
SI Brown Kiwi	threatened
Stewart Is Brown Kiwi	
Little Spotted Kiwi	endangered
Great Spotted Kiwi	
Blue Duck	threatened
Weka (4 subsp.)	
NI Weka	
Western Weka	
Buff Weka	
Stewart Is Weka	regionally threatened
New Zealand Pigeon (2 subsp.)	
NZ Pigeon	
Chatham Is Pigeon	endangered
Kakapo	endangered
Kaka (2 subsp.)	
NI Kaka	threatened
SI Kaka	regionally threatened
Red-crowned Parakeet (2 subsp.)	
Red-crowned Parakeet	regionally threatened
Chatham Is Red-crowned Parakeet	
Yellow-crowned Parakeet (2 subsp.)	
Yellow-crowned Parakeet	
Chatham Is Yellow-crowned Parakeet	
Shining Cuckoo	
Long-tailed Cuckoo	rare
Morepork	
Rifleman (2 subsp.)	
NI Rifleman	
SI Rifleman	
Brown Creeper	
Whitehead	
Yellowhead	threatened
Grey Warbler	
Chatham Is Warbler	
Fantail (3 subsp.)	
NI Fantail	
SI Fantail	
Chatham Is Fantail	
Tit (5 subsp.)	
Pied Tit	
Yellow-breasted Tit	
Chatham Is Tit	threatened
Black Tit	threatened
Auckland Is Tit	
Robin (3 subsp.)	
NI Robin	regionally threatened
SI Robin	regionally threatened
Stewart Is Robin	regionally threatened

SPECIES	CONSERVATION STATUS (Bell 1986)
Black Robin	endangered
Silvereye	
Stitchbird	rare
Bellbird (2 subsp.)	
Three Kings Bellbird	
Bellbird	
Tui (2 subsp.)	
Tui	
Chatham Is Tui	rare
Saddleback (2 subsp.)	
NI Saddleback	rare
SI Saddleback	endangered
Kokako (2 subsp.)	
NI Kokako	endangered
SI Kokako	endangered

APPENDIX 2

Perceived causes of historic declines of endangered, threatened and rare New Zealand forest birds.

SPECIES/SUBSPECES	PERCEIVED CAUSE(S) OF HISTORIC DECLINE
ENDANGERED*	
Little Spotted Kiwi	Habitat loss, predation, hunting (Oliver 1955)
Chatham Island Pigeon	Habitat loss, predation, hunting (Mills & Williams 1979, Bell 1986)
Kakapo	Habitat loss, predation, collecting (Oliver 1955)
Black Robin	Habitat loss, predation (Oliver 1955, Merton 1990)
S.I. Saddleback	Habitat loss, predation, collecting (Oliver 1955)
N.I. Kokako	Habitat loss, predation, competition (Oliver 1955, Williams 1976, Leathwick et al. 1983)
S.I. Kokako	Habitat loss, predation, collecting (Oliver 1955, Clout & Hay 1981)
THREATENED	
N.I. Brown Kiwi	Habitat loss, predation, hunting (Reid 1985)
S.I. Brown Kiwi	Habitat loss, predation, hunting (Reid 1985)
Blue Duck	Forest clearance, river siltation (Mills & Williams 1979)
N.I. Kaka	Habitat loss, predation (Moynihan 1985)
Yellowhead	Habitat loss, predation? disease? (Gaze 1985)
Chatham Island Tit	Habitat destruction (Oliver 1955)
Black (Snare) Tit	No decline
RARE	
Long-tailed Cuckoo	Habitat destruction (Oliver 1955)
Stitchbird	Habitat loss, predation, collectors, disease? (Oliver 1955, Atkinson 1973, G. Rasch unpub. data)
Chatham Island Tui	Habitat destruction (Bell 1986)
N.I. Saddleback	Habitat loss, predation (Oliver 1955, Atkinson 1973)

REGIONALLY THREATENED

Stewart Island Weka	Predation, competition (Beauchamp 1987, Bell 1986)
S.I. Kaka	Habitat loss (Oliver 1955)
Red-crowned Parakeet	Habitat loss, shooting, predation (Oliver 1955)
N.I. Robin	Habitat loss, predation (Oliver 1955)
S.I. Robin	Habitat loss, predation (Oliver 1955)
Stewart Island Robin	Predation (Oliver 1955)

* after Bell 1986

APPENDIX 3

Perceived causes of current declines of endangered, threatened and rare New Zealand forest birds.

SPECIES/SUBSPECIES	PERCEIVED CAUSE(S) OF CURRENT DECLINE
ENDANGERED*	
Chatham Island Pigeon	Habitat loss, predation (Bell 1986, Bellingham 1988)
Kakapo	Predation on Stewart Is. (R. Powlesland unpub.)
N.I. Kokako	Predation, competition (J.R. Hay, J. Innes unpub.)
S.I. Kokako	Predation? (Clout & Hay 1981)
THREATENED	
N.I. Brown Kiwi	Chick predation, gin trapping, predation by dogs (McLennan 1988, Taborsky 1988)
S.I. Brown Kiwi	Predation, gin trapping (R. Colbourne unpub.)
Blue Duck	Population fragmentation, floods, predation, habitat loss (M. Williams unpub.)
N.I. Kaka	Predation, competition (Moorhouse in press)
Yellowhead	Predation by Stoats (G. Elliott & C. O'Donnell unpub.)
RARE	
Chatham Island Tui	Habitat destruction (Bell 1986)
REGIONALLY THREATENED	
Stewart Island Weka	Predation, competition (Beauchamp 1987, Bell 1986)
S.I. Kaka	Competition with wasps & Possums, predation (Beggs & Wilson in press)
Red-crowned Parakeet	Predation, esp. by Cats & Stoats (Taylor 1985)
* after Bell 1986	

EFFECTS OF BRUSHTAIL POSSUM CONTROL OPERATIONS ON NON-TARGET BIRD POPULATIONS

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ABSTRACT. The Brushtail Possum *Trichosurus vulpecula*, a herbivorous Australian marsupial, is a serious pest of forest and farmland in New Zealand. Possum numbers are periodically controlled, mainly by aerial distribution of baits containing Compound 1080, ground-based trapping, or cyanide poisoning. Poisoning with 1080 kills more non-target birds per hectare than commercial trapping or cyanide poisoning, but is also potentially more beneficial to bird populations because it causes a greater reduction in Possum populations, and hence a greater improvement in the condition of the habitat. There is no evidence that Possum control operations have any detrimental effects on population survival of the more common bird species present in Possum areas.

Keywords: Brushtail Possums, control, trapping, cyanide, sodium monofluoroacetate, baits, poisoning of non-target species, birds, New Zealand.

INTRODUCTION

The Brushtail Possum *Trichosurus vulpecula*, a herbivorous Australian marsupial, was introduced into New Zealand in the mid nineteenth century to establish a fur industry (Pracy 1974). However, as Possums spread and their numbers increased they became pests. Selective browsing by Possums has locally eliminated or reduced the availability of certain flowering and fruiting species that are important food plants for forest birds (Kean & Pracy 1949, Pracy & Kean 1949, Fitzgerald 1976, Fitzgerald & Wardle 1979, Leathwick et al. 1983). Possums also damage crops (Spurr & Jolly 1981) and have been implicated in the transference of bovine tuberculosis on farmland bordering forests (Coleman 1988).

The first official control campaign against Possums in the late 1940s used traps and cyanide poison. Today these methods are used mainly by fur hunters. In 1988, an estimated 9000 commercial and 41 000 non-commercial Possum hunters, using traps and/or cyanide, killed about 1.9 million Possums (G. Nugent 1989 unpublished Forest Research Institute contract report). The area of forest hunted for Possums varies but probably exceeds 5 million ha when fur prices are high. The reduction in Possum numbers as a result of commercial hunting perhaps averages 40% (Brockie 1982, D.R. Morgan & B. Warburton 1987 unpublished FRI contract report). Intensive hunting however, can result in eradication of Possums, as on Kapiti Island (Cowan et al. 1985).

Since the late 1950s, baits containing Compound 1080 (sodium monofluoroacetate) have also been used to control Possum numbers. The baits are usually chopped carrots or pollard pellets, distributed from either the ground or air. The area of forest covered by 1080 poison averages less than 50 000 ha annually (rough estimate), perhaps 1% of the area covered by traps and cyanide. The reduction in Possum numbers after aerial 1080 poisoning operations averages about 70% of populations near car-

rying capacity (Morgan et al. 1986). In many areas, Possum control has been sufficient to limit dieback of common forest trees (Pekelharing & Batcheler 1990) and allow regeneration and increased flowering and fruiting of some plant species (I.A.E. Atkinson 1985 unpublished DSIR Botany Division report). However, Possum control needs to be on-going to maintain such improvements in habitat conditions.

Possum control operations are assumed to be beneficial to birds because they improve the condition of the habitat and reduce competition for food. However, concern has been expressed that Possum control operations could be detrimental if birds are killed as an indirect consequence. This paper reviews research into these concerns.

SPECIES AND NUMBERS OF BIRDS KILLED

Trapping

Thirteen native and five introduced land bird species have been caught in Possum traps (Table 1). In surveys of 53 trappers in 1936 and 59 trappers in 1946, more than 1200 birds were reported caught (i.e., about 12 birds per trapper per year); 90% of these were introduced Blackbirds and Song Thrushes (Wodzicki 1950; see Table 1 for scientific names of birds). The most commonly caught native species were the Kiwi, Weka, Morepork, and Harrier. In the 1946 survey, 61 native birds were reported killed. When related to hunting effort, this represents about one native bird caught per trapper per year (trap nights unknown) or one native bird per 529 Possums caught. These figures are probably underestimates because not all birds caught would have been reported. In an intensive trapping operation on Kapiti Island, 52 native birds (mainly New Zealand Pigeons, Moreporks, and Weka) were killed in 2 years (approximately one native bird killed per 11 000 trap nights, per 73 ha/year, or per 365 Possums caught) (Cowan et al. 1985). In a carefully monitored trial at Pureora Forest in 1987, eight trappers caught one native bird (a Fantail) in about five weeks, equivalent to one native bird caught per 3872 trap nights, per 1434 ha, or per 646 Possums caught (D.R. Morgan & B. Warburton 1987 unpublished FRI contract report).

TABLE 1 - Bird species found dead after Possum control operations using traps, cyanide, and 1080 (+ species found dead; - species not found dead; o species not exposed).

BIRD SPECIES		FOUND DEAD AFTER OPERATIONS USING		
Common name	Scientific name	Traps	Cyanide	1080
Native species				
Robin	<i>Petroica australis</i>	+	+	+
Tomtit	<i>Petroica macrocephala</i>	+	+	+
Weka	<i>Gallirallus australis</i>	+	+	+
Kiwi (3 sp.)	<i>Apteryx</i> sp.	+	+	-
Fantail	<i>Rhipidura fuliginosa</i>	+	-	+
Harrier	<i>Circus approximans</i>	+	-	+
Kaka	<i>Nestor meridionalis</i>	+	-	+
Kea	<i>Nestor notabilis</i>	+	-	+
Morepork	<i>Ninox novaeseelandiae</i>	+	-	+
Pigeon	<i>Hemiphaga novaeseelandiae</i>	+	-	+

TABLE 1 – Continued

BIRD SPECIES		FOUND DEAD AFTER OPERATIONS USING		
Common name	Scientific name	Traps	Cyanide	1080
Pipit	<i>Anthus novaeseelandiae</i>	+	-	+
Silvereye	<i>Zosterops lateralis</i>	-	+	+
Kokako	<i>Callaeas cinerea</i>	+	-	-
Parakeet (2 sp.)	<i>Cyanoramphus</i> sp.	+	-	-
Bellbird	<i>Anthornis melanura</i>	-	-	+
Grey Warbler	<i>Gerygone igata</i>	-	-	+
Pukeko	<i>Porphyrio porphyrio</i>	-	-	+
Rifleman	<i>Acanthisitta chloris</i>	-	-	+
Whitehead	<i>Mohoua albicilla</i>	-	-	+
Tui	<i>Prothemadera novaeseelandiae</i>	-	+	-
Brown Creeper	<i>Mohoua novaeseelandiae</i>	-	-	-
Falcon	<i>Falco novaeseelandiae</i>	-	-	-
Fernbird	<i>Bowdleria punctata</i>	-	-	-
Kingfisher	<i>Halcyon sancta</i>	-	-	-
Rock Wren	<i>Xenicus gilviventris</i>	-	-	-
Saddleback	<i>Philesturnus carunculatus</i>	-	-	-
Stitchbird	<i>Notiomystis cincta</i>	-	-	-
Welcome Swallow	<i>Hirundo tahitica</i>	-	-	-
Yellowhead	<i>Mohoua ochrocephala</i>	-	-	-
Takahe	<i>Porphyrio mantelli</i>	-	-	0
Kakapo	<i>Strigops habroptilus</i>	+	0 ?	0 *
Introduced species				
Blackbird	<i>Turdus merula</i>	+	+	+
Song Thrush	<i>Turdus philomelos</i>	+	-	+
Californian Quail	<i>Lophortyx californica</i>	+	-	+
Magpie	<i>Gymnorhina tibicen</i>	+	-	+
Chaffinch	<i>Fringilla coelebs</i>	-	-	+
Goldfinch	<i>Carduelis carduelis</i>	-	-	+
Greenfinch	<i>Carduelis chloris</i>	-	-	+
Hedge Sparrow	<i>Prunella modularis</i>	-	-	+
House Sparrow	<i>Passer domesticus</i>	-	-	+
Redpoll	<i>Carduelis flammea</i>	-	-	+
Skylark	<i>Alauda arvensis</i>	-	-	+
Yellowhammer	<i>Emberiza citrinella</i>	-	-	+
Little Owl	<i>Athene noctua</i>	+	-	-
Starling	<i>Sturnus vulgaris</i>	-	+	-

Sources of information: Wodzicki 1950; Pracy 1956, 1958 unpublished NZFS reports; Batcheler 1978; Harrison 1978a, b; Spurr 1979; Warburton 1982; Reid 1983, 1985, 1986; Cowan et al. 1985; Morgan & Warburton 1987 unpublished FRI contract report; Morgan 1988 unpublished FRI contract report. Scientific names of birds after Turbott 1990. * Kakapo have been exposed to 1080 in fish baits for Cat control.

The native bird most at risk from trapping is the Kiwi. In a 1984 survey, 66 Possum trappers reported 141 Kiwi caught in traps (Reid 1985, 1986). This represents about one Kiwi caught per three trapper years (trap nights unknown), or one per 3940 Possums trapped. However, only about 40% of trapped Kiwi die. The commonly used Lanes-Ace gin trap catches no more birds than alternative trap types (Warburton 1982).

Cyanide poisoning

Fewer landbird species have been reported killed by cyanide than by trapping (Table 1). Also, smaller numbers of individual birds have been killed by cyanide than caught in traps. The most commonly poisoned native bird species have been Weka and Kiwi. For example, in 1947-48, extensive use of cyanide in Poverty Bay killed many thousands of Possums, but only a small number of native birds, mainly Weka (L.T. Pracy 1958 unpublished New Zealand Forest Service report). In 1984, 66 hunters reported 37 Kiwi poisoned by cyanide, about a quarter the number caught in traps, equivalent to one Kiwi poisoned per 10 hunter years or per 14 430 Possums poisoned (Reid 1985, 1986).

1080 poisoning

The list of landbird species found dead after 1080 poisoning operations is greater than for trapping (Table 1). About 90% of the birds poisoned by 1080 have been introduced Blackbirds and Chaffinches. Trials in 1956-58 with non-toxic baits of the types used for 1080 poisoning (chopped carrot and pollard pellets) showed that the Robin and Weka were the native species most likely to take baits (L.T. Pracy 1958 unpublished NZFS report). However, searches for dead birds after 1080 poisoning operations in exotic conifer plantations in the central North Island in 1976-77 found a wide range of native bird species had been killed, mostly small insectivorous passerines (Tom-tits, Robins, Whiteheads, Grey Warblers, Riflemen, Fantails, and Silvereyes). Weka were not present in the search areas. Most dead birds were found after operations using unscreened carrot bait that had a high percentage of small pieces or "chaff" (Harrison 1978a,b). This indicates that most birds, even insectivorous species, were probably poisoned directly as a result of eating baits. Insectivorous species are known to feed on fruit, especially in winter when poisoning operations take place. However, some birds may have died from secondary poisoning; e.g., dead Moreporks may have eaten sublethally poisoned mice (Spurr 1979). Systematic searches for dead birds have not been made in native forest.

Modifications to 1080 poisoning operations have been made as a result of research to reduce the number of birds killed. For example, baits are dyed green because green-coloured food was shown to be unattractive to many species of birds (L.T. Pracy 1958 unpublished NZFS report, Caithness & Williams 1971). Use of lures such as raspberry has been banned because they were found to be attractive to birds. Since 1977, carrot baits have been screened through a 16-mm grid to remove the small pieces because this reduced bird deaths by 50%, to one dead native bird per 12 ha (Harrison 1978a,b). The use of pollard baits has reduced bird deaths even further, to one dead native bird per 35 ha (Harrison 1978a,b). These figures are minimums because not all dead birds would have been found. Since 1983, cinnamon has been added to baits, primarily to mask the smell of 1080 to Possums, but also to repel birds (Udy & Pracy 1981, Pracy et al. 1982, Morgan et al. 1986). Application rates of baits have been reduced from more than 30 kg/ha to less than 10 kg/ha in recent years, reducing potential bird-bait encounters. However, reducing the toxic loading of baits probably would not reduce bird deaths because, even at the lowest loading effective against Possums, baits contain more than enough 1080 to kill small forest birds.

Finds of dead birds give no indication of the effect of Possum control operations on bird populations. Poisoning and trapping may be additional causes of mortality or may simply be replacing other causes of mortality such as winter starvation.

FIGURE 1 - Numbers of Robins counted in poison (dark hatch) and non-poison (light hatch) areas before and after eight 1080 poisoning operations in (a) Whirinaki Forest and (b-h) Kaingaroa Forest, 1978 (operations c, e, and g used Wanganui No.7 pollard baits, the others used screened carrot). Vertical lines indicate the 95% least significant intervals (L.S.I.).

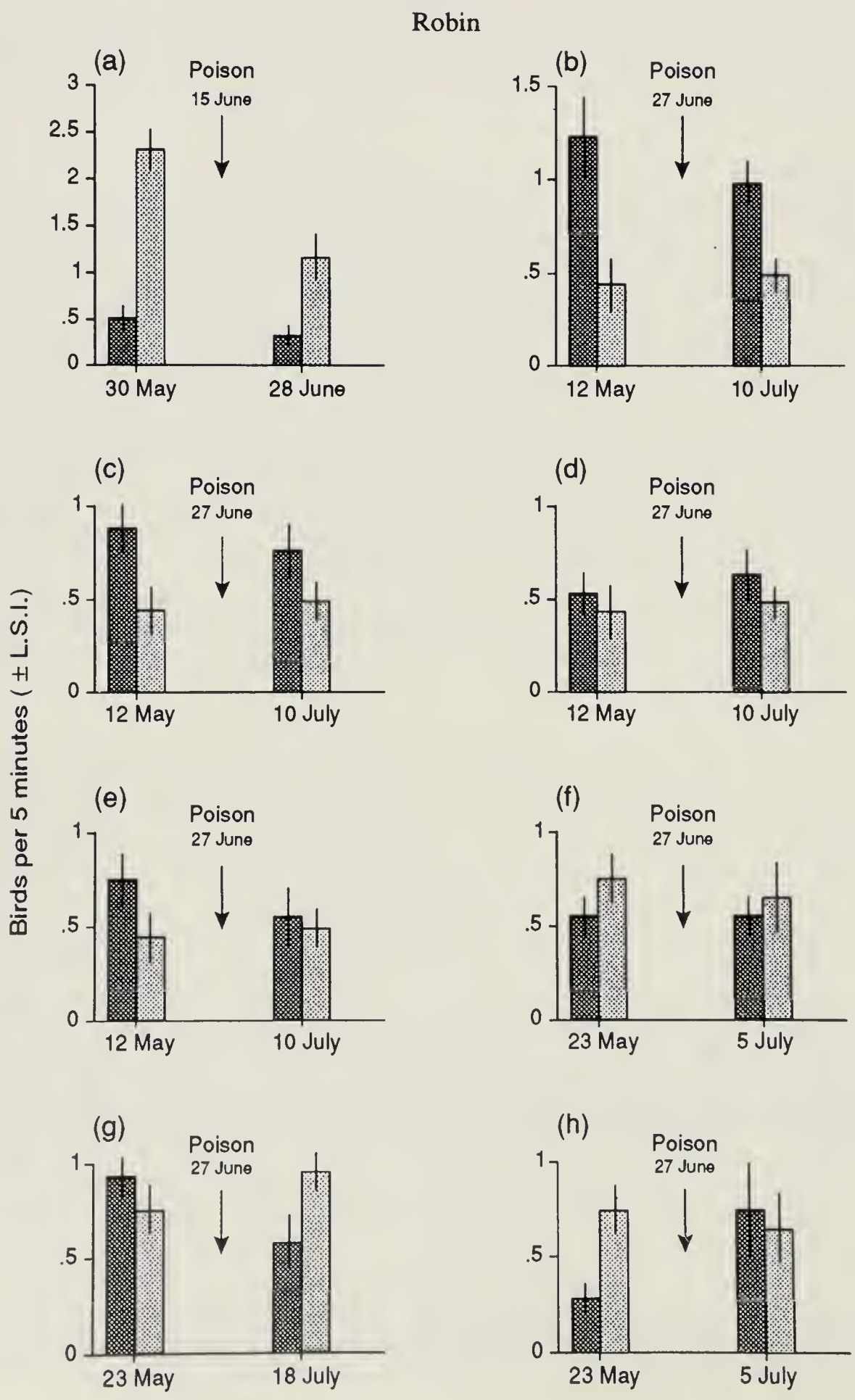
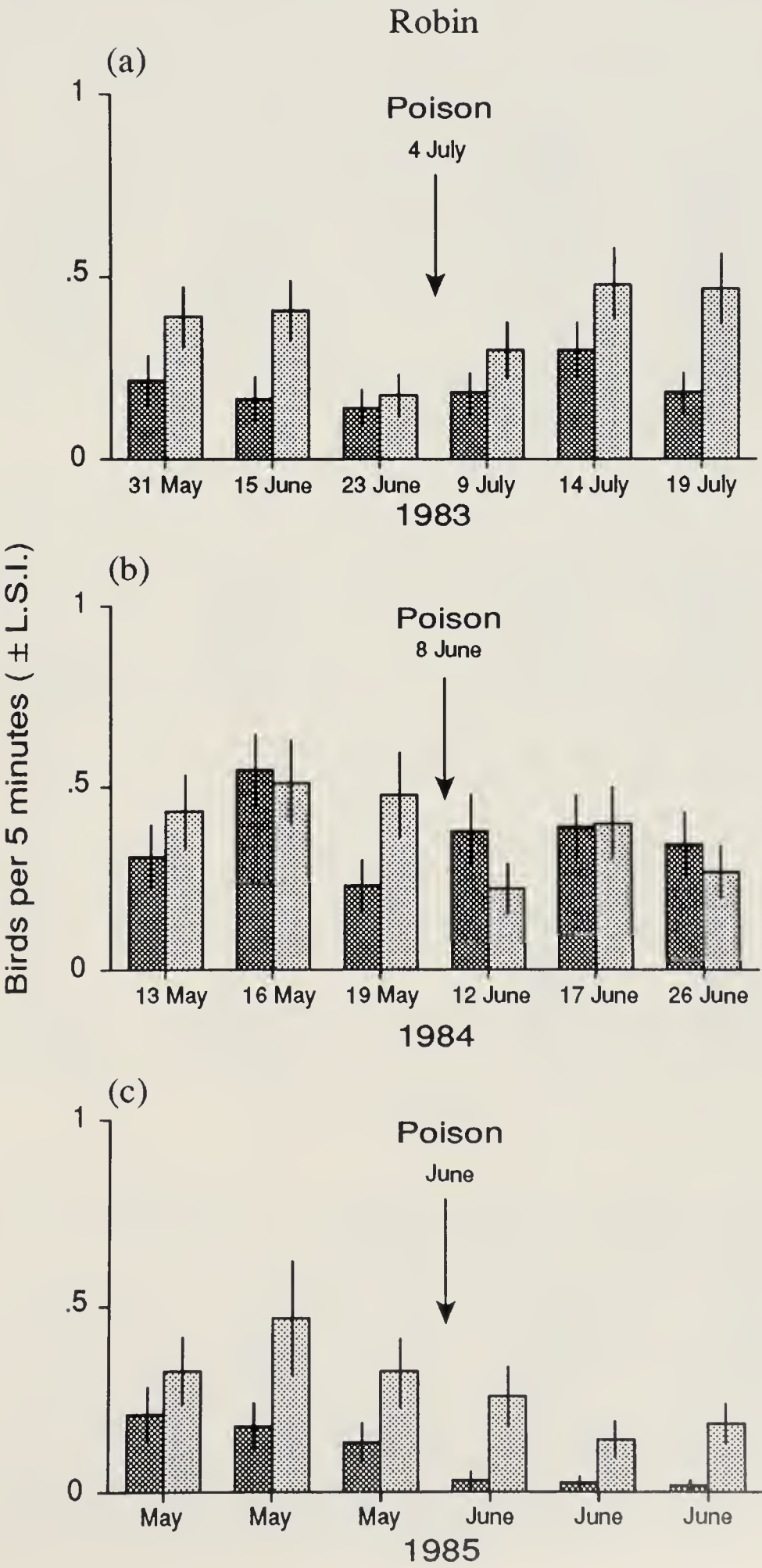


FIGURE 2 - Numbers of Robins counted in poison (dark hatch) and non-poison (light hatch) areas before and after three 1080 poisoning operations in Pureora Forest in (a) 1983, (b) 1984, and (c) 1985 (the first two operations used Mapua pollard baits, the last used screened carrot). Key as in Figure 1.



EFFECTS OF DEATHS ON BIRD POPULATIONS

Between 1978 and 1979, I monitored bird population survival by making 5-minute counts (after Dawson & Bull 1975) of birds heard or seen in poison and equivalent non-poison areas, before and after 15 trial aerial 1080 poisoning operations in both introduced conifer plantations and native forest in the central North Island (Forest Research Institute 1981). Ten trials used toxic screened carrot and five used toxic Wanganui No.7 pollard baits. The numbers of birds in most poison areas did not change after poisoning in relation to the numbers of birds in non-poison areas. Where bird numbers did change, the changes were divided almost equally between increases and decreases. For example, Robins (one of the species commonly found dead after 1080 poisoning operations) were present in eight trials, and in six the population trends in the poison and non-poison areas were similar (Figure 1a-f). However, in one trial using toxic Wanganui No.7 pollard baits (Figure 1g) Robin numbers in the poison area decreased, and in another using toxic carrot baits (Figure 1h) they increased after poisoning. Overall, neither toxic screened carrot nor toxic Wanganui No.7 pollard baits had any effect on bird numbers.

Between 1983 and 1985, bird populations were assessed before and after three aerial 1080 poisoning operations in different parts of Pureora Forest, two using Mapua pollard baits and one using carrot. Birds of all species present were counted three times during the month before and after the poison operations to give a measure of the natural variation in numbers over time. The numbers of some species changed significantly during this time, but not only in the poison areas, nor necessarily coincident with the poison operations. For example, in 1983 (Figure 2a), Robin numbers in the poison area were similar before and after poisoning, but in the non-poison area they decreased during the month before poisoning then increased after poisoning. In 1984 (Figure 2b), Robin numbers in the poison area decreased between the second and third pre-poison counts, then increased after poisoning. In 1985 (Figure 2c), Robin numbers started declining before poisoning and declined in both poison and non-poison areas. Similar changes occurred in the counts of 20 other bird species. None of these changes could be attributed to 1080 poisoning (see also A. Warren 1984 unpublished NZFS report, B. Calder & F. Deuss 1985 unpublished NZFS report).

Bird populations were also monitored before and after aerial 1080 poisoning operations using screened carrot bait in Westland National Park in 1983 and 1986 (E.B. Spurr 1988 unpublished FRI contract report). Poisoning had no measurable effect on any of the 12 most common bird species monitored.

The bird species most likely to be exposed to 1080 poisoning operations have now been monitored 11-20 times (Table 2). There is no evidence that such operations are having a significant detrimental effect on population survival of any of these species. Other species at risk during 1080 poisoning operations have been less adequately monitored (Table 2). However, the results which are available indicate that these species also are not being adversely affected. For example, Kokako populations have been monitored during six 1080 poisoning operations that used Mapua and Wanganui No.7 pollard baits in the central North Island between 1986 and 1988 (J. Innes & D. Williams 1990 unpublished FRI contract report). Of 83 Kokako located before poisoning, 82 were relocated after poisoning. The missing Kokako may have been poisoned, died by chance, or moved away naturally. No dead bird was found. Innes & Williams concluded that there was little risk to Kokako from current 1080 poisoning operations

using Wanganui No.7 and Mapua pollard baits. However, Kokako have not been monitored during operations using carrot bait.

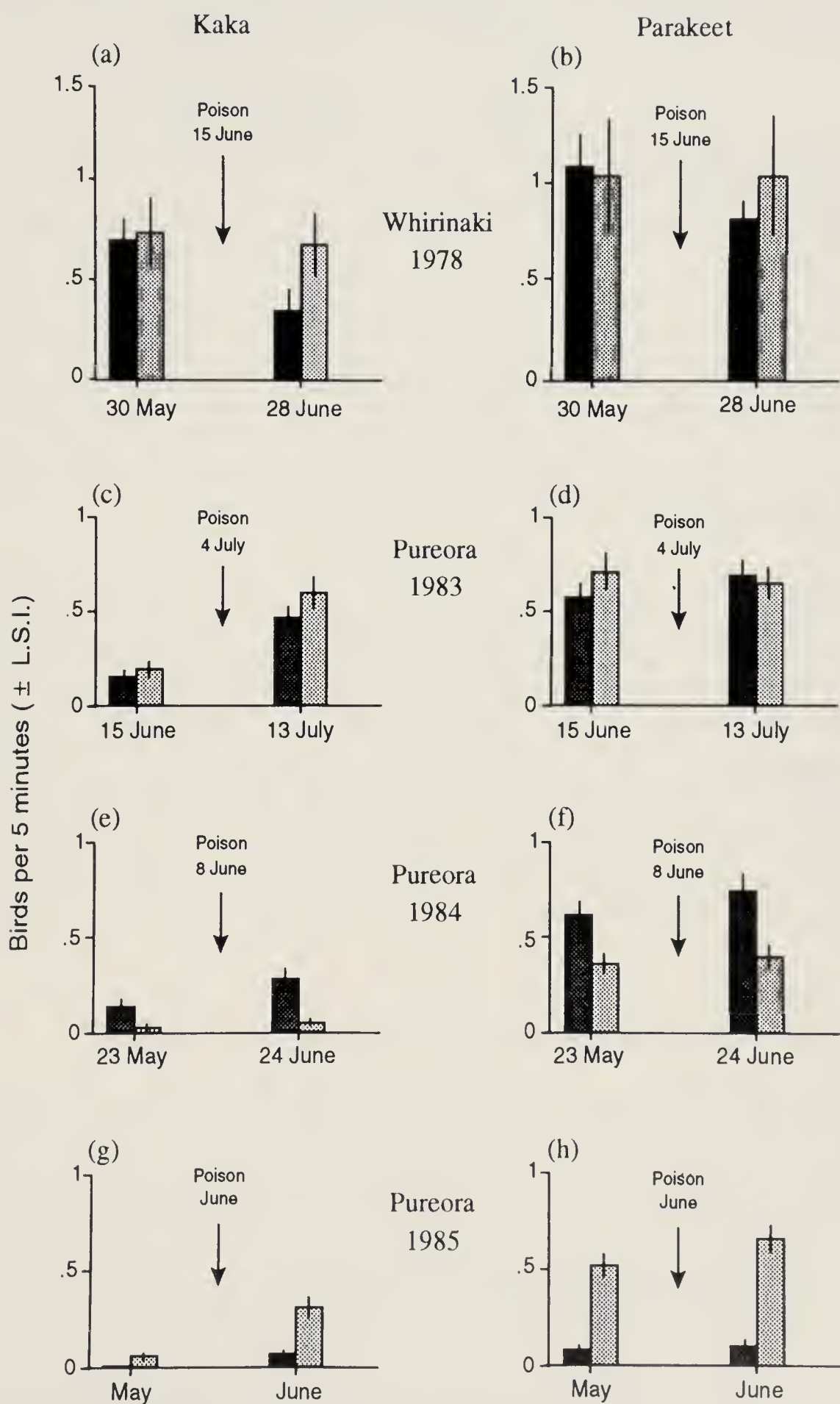


FIGURE 3 - Numbers of Kaka and Parakeets in poison (dark hatch) and non-poison (light hatch) areas before and after four 1080 poisoning operations in (a-b) Whirinaki Forest 1978, and (c-h) Pureora Forest 1983-1985. Key as in Figure 1.

TABLE 2 - Number of Possum control operations using carrot, Wanganui No.7, and Mapua baits containing 1080 in which native bird populations have been monitored.

BIRD SPECIES	NUMBER OF OPERATIONS MONITORED USING			
	Carrot Bait	Wanganui No.7 Bait	Mapua Bait	Total
Adequately monitored				
Fantail +	13	5	2	20
Grey Warbler +	13	5	2	20
Silvereye +	13	5	2	20
Tomtit +	13	5	2	20
Whitehead +	11	5	2	18
Bellbird +	9	2	2	13
Rifleman +	9	2	2	13
Pigeon +	8	2	2	12
Robin +	6	3	2	11
Tui	7	2	2	11
Inadequately monitored				
Kokako	0	3	3	6
Kaka +	2	0	2	4
Parakeet	2	0	2	4
Brown Creeper	2	0	0	2
Kea +	2	0	0	2
Falcon	0	0	1	1
Weka +	1	0	0	1
Not monitored				
Fernbird				
Harrier +				
Kingfisher				
Kiwi				
Morepork +				
Pipit				
Pukeko				
Rock Wren				
Saddleback				
Stitchbird				
Welcome Swallow				
Yellowhead				
Not exposed to 1080				
Kakapo *				
Takahe				

+ species found dead after 1080 poisoning operations (see Table 1).
* exposed to 1080 in fish baits for Cat control but not in baits for Possum control.

Kaka and Parakeets have been monitored in four 1080 operations (Figure 3), two using screened carrot (Whirinaki in 1978 and Pureora in 1985) and two using Mapua pollard baits (Pureora in 1983 and 1984). Although bird numbers changed significantly over time, sometimes coinciding with the poison operations, there was no evidence

that the changes after poisoning were any different to changes before poisoning. For example, Kaka numbers decreased in the Whirinaki poison area after poisoning, but increased after poisoning at Pureora in 1984 (Figure 3). Without further information on Kaka behaviour and movements, I can only conclude that poisoning was not responsible for these changes.

Falcon territories were mapped before and after the 1080 poisoning operation at Pureora Forest in 1984 (B. Calder & F. Deuss 1985 unpublished NZFS report). The single territory in the poison area was still occupied after poisoning (presumably by the same birds). However, the risk to Falcons from 1080 poisoning operations has not yet been adequately assessed.

Bird species inadequately monitored or not monitored at all include rarer species seldom exposed to Possum control operations (e.g., Saddleback, Stitchbird, Takahe, and Yellowhead). The safety of Possum control operations for some bird species does not mean safety for all. Rarer species do not have the same reproductive or dispersal capabilities as more common species, and consequently not the same ability to withstand reductions in numbers (Spurr 1979). Research on rare species will be essential if Possum control operations are contemplated in areas where they occur.

There have been two studies of the effects of Possum trapping and cyanide poisoning on bird populations. First, populations of 18 bird species were monitored during a combined trapping and cyanide poisoning operation in Charleston Forest in 1978 (E.B. Spurr 1978 unpublished FRI report). Most species did not change in abundance, but Weka numbers decreased and Fantail and Tomtit numbers increased one week after the operation. Because two species increased in abundance and the trial was unreplicated it cannot be concluded that Weka numbers decreased as a result of trapping and cyanide poisoning. No birds were found dead. Second, Kokako numbers were monitored during a combined trapping and cyanide poisoning operation in Mapara Forest in 1988 (J. Innes & D. Williams 1990 unpublished FRI contract report). The 41 Kokako located before the operation were relocated afterwards. No Kokako were found dead, although one Harrier was (D.R. Morgan 1988 unpublished FRI contract report).

BENEFICIAL EFFECTS ON BIRD POPULATIONS

Evidence for the beneficial effects of Possum control on bird populations is mainly circumstantial (see Introduction). The only specific evidence for an increase in bird numbers after Possum control has come from Kapiti Island (2000 ha), where bird numbers, especially New Zealand Pigeon, Tui, Bellbird, Whitehead, Robin, and Weka, steadily increased from 1982 to 1986, coinciding with the trapping of about 20 000 Possums (T. Lovegrove 1986 unpublished NZFS report). However, bird populations probably need monitoring for 10 years before and after control operations to demonstrate that changes in numbers are real (Veitch & Bell 1990). To date, funding has not been available for this sort of research.

The benefits of Possum control operations for birds may include reduction in predation as well as improvement in food supply and shelter. For example, large numbers of rats are sometimes caught in traps set for Possums (Wodzicki 1950, Reid 1983,

1985, 1986, D.R. Morgan & B. Warburton 1987 unpublished FRI contract report, D.R. Morgan 1988 unpublished FRI contract report). Cats, Stoats, and other pests may also be caught in Possum traps. In one operation, more than 90% of the rats present in the area were killed by aerial 1080 poisoning for Possum control (B. Warburton 1989 unpublished FRI contract report). These secondary benefits are probably short-lived but may relieve predation pressure for a breeding season.

Overall, the potential benefits of Possum control to bird populations outweigh the detrimental effects of the loss of a few individuals (see also Cowan et al. 1985, Reid 1986). Aerial 1080 poisoning of Possums is probably more beneficial to birds than commercial trapping or cyanide poisoning because it can be applied to inaccessible country and can reduce Possum populations to a level where some recovery of the habitat is possible if the reduction is sustained.

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ARE SMALL POPULATIONS VIABLE?

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ABSTRACT. Many of New Zealand's rare birds persist in small populations. Some are natural remnants, others result from translocating small numbers of founding individuals onto islands that can support only populations of tens or hundreds of birds. Conventional theory from continental and presumed outbreeding populations argues for the establishment of a large population. In contrast New Zealand birds have a history of small population sizes with considerable inbreeding. Therefore, the current practice of establishing many sometimes small and geographically spread populations is arguably both the best theoretical and practical solution for the long term conservation of New Zealand's rare birds.

Keywords: Small populations, inbreeding, translocations, New Zealand birds.

INTRODUCTION

In addition to the three major islands, New Zealand includes more than 700 islands many of which support land birds (Towns et al. 1990). Since human colonization over 1000 years ago, and rapidly accelerated after European colonization 150 years ago, forest and swamp habitats have been reduced to less than 20% of their previous extent (Anderson 1977, Ogden & Caithness 1982). The introduction of 58 mammals (King 1990) including rats, mice, mustelids, dogs and cats have further eliminated or reduced bird populations. With the exception of a few large offshore islands which are still forested and lack mammalian predators, most land birds are now found at low densities in remnants of habitat, or at higher densities on small offshore islands.

The large number of islands and the extreme fragmentation of mainland habitats has meant that small, largely isolated sub-populations are a feature of New Zealand bird populations. At one extreme, some populations, for example Forbes' Parakeet *Cyanoramphus auriceps* and Black Robin *Petroica traversi* on Little Mangere Island (Flack 1973, Taylor 1975), Bellbirds *Anthornis melanura* on Tiritiri Matangi Island (Craig unpublished), and Campbell Island Teal *Anas aucklandica nesiotis* on Dent Island (Robertson 1976) have probably persisted with less than 20 pairs for a century or more. At the other extreme, some populations have persisted with 1000s - 10,000s of individuals in large areas of little modified habitat (e.g. Fantail *Rhipidura fuliginosa*, Bellbird and Grey Warbler *Gerygone igata* in forests of Westland).

SPECIES TRANSLOCATIONS

Habitat destruction and introduced mammals have impacted on some bird species more than others. Some have become extinct while others are now restricted to small relict localized populations. The response of conservation authorities (Wildlife Service and now Department of Conservation) has been to translocate birds to predator-free offshore islands (Williams 1977), an approach started last century, but

increasingly common since the early 1960s (Atkinson 1990). Species translocations have been highly variable involving as few as five birds to as many as 386 birds being transferred onto islands ranging from 4 ha (Merton 1973) to 3000 ha. The majority of transfers (77%) have been successful, and surprisingly (see Griffith et al. 1989) establishment of a self-sustaining population is unrelated to the number of founders (Craig & Reed unpublished data).

The initial rationale of transfers was largely pragmatic. The number of birds transferred and the choice of destination was dictated by time, weather, and a shortage of islands with similar vegetation and no predators. Intuition, (probability theory) that many were better than one, led to multiple transfers with founder members usually exceeding 15. However, in the absence of genetical theory being applied to conservation, logistical reasons dictated that some transfers were made from populations newly derived from the survivors of previous translocations.

In the 1970's realization that some species were represented by a single small population led to translocation trials with more common species. Flack (1973) working on the Black Robin population that then numbered less than 20 birds trialed island transfers using as few as five South Island Robins *Petroica australis*. In the 1980's some managers and scientists adopted the 50/500 rule (Frankel 1980, Simberloff 1988, Soule, 1980, 1987). This saw calls for populations of at least 500 individuals (e.g. Williams 1986, Crouchley 1990) and the evaluation of islands as likely transfer release sites according to their size and ability to support a population of at least 500 individuals (J. Jolly unpublished letters to Hauraki Gulf Maritime Park Board). With the 1990's, the collation of behavioural and genetics studies for many New Zealand birds, along with closer evaluation of the underlying theory, is now explaining the success and justifying the practice, of establishing many small populations as a viable conservation strategy.

SINGLE LARGE OR SEVERAL SMALL POPULATIONS?

Ideas of the relative value of a single large population in one reserve versus several small populations in isolated or semi-isolated reserves vary, as do the supporting data. The apparent conflict must cause total confusion for most conservation managers. Recommendations (IUCN 1980) derived from island biogeographic theory (e.g. MacArthur & Wilson 1967) argued for a single large population rather than several small ones, although this applied more to species assemblages in habitat fragments than to a single species (see Dawson 1984, Simberloff 1988). Field observations show that several small reserves or islands can maintain higher species numbers than a single large reserve of the same area (Simberloff & Abele 1982, Soule & Simberloff 1986). Likewise, from a genetical viewpoint, multiple populations can maintain greater variability than a single population (e.g. Kimura & Crow 1963, Wright 1969, Chesser 1983, Broeklen, W.J. 1986, Gilpin 1987, Lacy 1987, Shaffer 1987) and can guard against purely chance extinctions (e.g. Quinn & Hastings 1987) caused by random stochastic events.

The loss of population genetic variability, due to genetic drift and inbreeding whether in a single large or several small populations, is also seen as a major conservation problem (c.f. Frankel & Soule 1981, Schonewald-Cox et al. 1983, Soule 1987,

Simberloff 1988 and references therein). While Shaffer (1987) argues that demographic factors are likely to be more important in extinctions than genetic considerations, the large field of effective population size and viability analysis relates extinction chances primarily to genetic influences. Such analyses assume that natural selection is less important than genetic drift, and that populations are outbred, therefore, levels of inbreeding greater than 1-3% (Soule 1983) are deleterious. Hence, they assume that animals mating patterns are naturally close to random, relative to their genetic characteristics (e.g. see Lande & Barrowclough 1987, Simberloff 1988).

Numerous workers have questioned these assumptions (e.g. Beardmore 1983, Shields 1982, Craig & Jamieson 1988, Simberloff 1988) but few have suggested that conservation managers can afford to or indeed should ignore effective population sizes and viability analyses. For New Zealand forest and swamp birds, the assumptions of viability analyses are so at variance with what we know about mating patterns that we should ignore the theory. At best the theory refers to animals of large land masses that, as part of their annual life cycles, migrate in large groupings. Emotive ideas that “no-one likes inbreeding” (Simberloff 1988 p. 500) or that we need to avoid “vicious circles of inbreeding” (Soule 1987 p. 180) need to be replaced with our knowledge of the full range of what birds actually do.

INBREEDING IN NEW ZEALAND BIRDS

The small size of many New Zealand island and relict populations suggests that inbreeding has long been part of the mating systems of New Zealand birds. Studies of banded birds (e.g. Craig 1979, Craig & Douglas 1986, Craig & Jamieson 1988, Williams in press, Stewart 1980, B. Gill, pers. comm., I.G. McLean, pers. comm.) have demonstrated that many of our species retain year-round residence of a localized home range or territory and that young settle near their natal area. Where known (Table 1) levels of inbreeding far exceed the 1-3% level suggested by Soule (1983) as the maximum allowable before loss of genetic variability occurs with consequent deleterious effects.

TABLE 1 – Known levels of close inbreeding among New Zealand birds

Black Robin <i>Petroica traversi</i>	: 2 island populations derived from one female (Merton 1990)
Pukeko <i>Porphyrio porphyrio</i>	: ≥ 70% (Craig & Jamieson 1988)
Saddleback <i>Philesturnus carunculatus</i>	: > 8% pairings where $r \geq 0.25$ (Craig & Jenkins unpublished data)
Tui <i>Prothemadera novaeseelandiae</i>	: > 14% pairings (Stewart 1980, Bergquist pers. comm.)
Blue Duck <i>Hymenolaimus malacorhynchos</i>	: > 15% pairings (Williams in press) > 50% DNA fingerprinting (Triggs et al. in press)

HOW SHOULD WE MANAGE RARE NEW ZEALAND BIRDS?

The presence of predatory and grazing mammals on the mainland of New Zealand means that small islands offer the best protective habitat for many of our rare birds (e.g. Towns et al. 1990). The size of islands with suitable habitat and without mammals varies markedly. At best, some could only support very small populations of birds.

The establishment of many populations has wide support in the literature (see above). If, in addition, we accept that a level of inbreeding is within the normal range of mating systems, the main question becomes what size of population, and how many populations are needed for the effective long term conservation of rare species? The empirical results of Pimm et al. (1988) for British islands, and the known persistence of small populations of some New Zealand birds (see above) suggest that populations as low as 7-10 pairs have at least medium term viability. With the exception of South Island Saddleback on Betsy Island, most island populations of New Zealand birds already exceed, or will exceed, this number. Where possible one sub-population should be planned for hundreds.

The larger the number of populations the better, both in terms of demographic and genetic stochasticity (e.g. Lacy 1987, Shaffer 1987, Simberloff 1988). Current practice in New Zealand shows an initial move to a minimum of two or three populations per species, although some have already proceeded to nine or more populations (Table 2).

TABLE 2 – Number of island populations of rare New Zealand birds

Species	No. of Island Populations	Further Planned	Mainland Population	No. of Failed Transfers ¹
South Island Saddleback	9	✓	No	3
North Island Saddleback	9	✓	No	2
Kokako	1	?	Yes	–
Little Spotted Kiwi	5*	✓	No	?
Black Robin	2	✓	No	–
Stitchbird	4*	✓	No	?
Kakapo	2*	?	No	–
Takahe	3	✓	Yes	–
Brown Teal	5	?	Yes	?
Shore Plover	1	✓	No	1
Chatham Island Pigeon	2	✓	No	1
Forbes' Parakeet	2	?	No	–

* Some populations recently established and success requires future confirmation.

¹ Only transfers since 1960 considered.

Theoretical ideas vary as to whether populations should be kept isolated or whether limited gene flow should be allowed through direct management. Many authors argue that even limited movement of individuals between populations can maintain higher levels of heterozygosity and retain more rare alleles in each population than without

interpopulation movements (e.g. Allendorf 1983, Allendorf & Phelps 1981, Boecklen 1986, Lacy 1987, Lande & Barrowclough 1987, Foose 1983, Selander 1983). However, the complete isolation of individual populations will ensure a still higher total level of heterozygosity, even more rare alleles among the populations, and ensure against the spread of disease even though levels of heterozygosity may be low in some populations (e.g. Lacy 1987, Chesser 1983, Beardmore 1983). Maintaining separation also allows local genetic adaptation to occur whereas migration encourages a view of freeze-frame preservation of a past genetic structure that may be independent of present habitat (Carson 1983).

New Zealand conservation practice has kept island populations largely separate. The only intentional movement of birds has been soon after a translocation to counter the chance death of one member of a few founding pairs (e.g. Takahe).

A final consideration is the number of birds translocated to establish a new population. As Nei et al. (1975) and Rowell (1983) suggest, as few as five founders will carry 90% of the source population alleles, whereas 20 individuals, or more, are preferable to ensure high levels of allelic variation (e.g. Lacy 1987, Lande & Barrowclough 1987). To date, all releases of New Zealand birds have been of five or more and greater than 75% have involved 20 or more individuals (Craig & Reed unpublished).

Other genetic ideas, such as the need to equalise the contribution of founding members (e.g. Frankel & Soule 1981, Foose 1983) may be reasonable for captive populations, but is counter to natural patterns and potentially can act against selection (Carson 1983). As yet, no attempt has been made to counter even the extreme departures from equal contribution of founders (Craig unpublished) amongst New Zealand's translocated bird populations.

CONCLUSIONS

Most population conservation models assume that animal populations are outbred. New Zealand birds do not meet this assumption in that most are site attached year round, young remain in the natal area and where known, levels of inbreeding are high. Inbreeding has been poorly understood and ignored by New Zealand conservation managers even in small populations established from markedly uneven contributions of founding individuals, as well as in populations established from as few as five individuals or less (three effective individuals in the case of Black Robin, Merton 1990). The likely deleterious effects of genetic drift and of chance demographic events have been countered by the establishment of a number of fully isolated populations. The wide geographic spread of some of these populations is a sure protection from environmental catastrophes such as fire, earthquake, volcanic activity or cyclones. Conservation managers in other island nations may similarly benefit by re-evaluating the assumptions and accepted interpretations of conservation theory. The assumption that mating systems are universally based on outbreeding needs to be evaluated in terms of ecological reality.

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THEORY REALLY MATTERS: HIDDEN ASSUMPTIONS IN THE CONCEPT OF “HABITAT REQUIREMENTS”

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ABSTRACT. In New Zealand conservation research considerable effort and resources are devoted to determining the habitat requirements of endangered birds. While the concept of “habitat requirements” may seem quite atheoretical we argue that research on habitat requirements contains several problematic assumptions. Such research implicitly assumes that the current habits of birds are optimal (the adaptationist fallacy), it assumes that current ecological factors are vastly more important than historical factors (the ahistorical fallacy), and it assumes that a species’ requirements are fixed (the fallacy of genetic determinism). These fallacies are illustrated with examples from research on New Zealand birds. The positive implications of abandoning the concept of habitat requirements, for a broader approach that utilises the plasticity and social transmission of avian behaviour, are discussed.

Keywords: Habitat requirements, ecological theory, adaptationism, genetic determinism, social traditions.

WHY WORRY ABOUT THEORY?

In a world where the practical concerns of avian species conservation are so immediate and so important it may seem like a dangerous academic game to pause and ask, “what are the theoretical assumptions underlying our current conservation practices?” This is particularly likely to be the case with a concept like “habitat requirements”. The use of this term is so ingrained in current conservation practice that it seems completely uncontroversial and almost atheoretical. And yet, it is precisely in questioning practices that seem so straightforward and obvious that they entail no assumptions, that theory can be most valuable. By revealing hidden assumptions theoretical analyses can open up alternative, previously unthought of approaches, to avian conservation. What we aim to do in this paper is to analyse some assumptions underlying the concept of habitat requirements and to suggest some other options for conservation research.

THE IMPORTANCE OF HABITAT REQUIREMENTS

Research on the habitat requirements of endangered species is a major aspect of conservation research both in New Zealand and overseas. For example, in the 1988 and 1989 issues of the journal *Biological Conservation* approximately 86% of the papers on animal ecology were broadly related to the question on habitat requirements. Within New Zealand over 50% of the species listed in the Wildlife Service’s 1981 research priorities (Crawley 1981) had a declared or implied study of habitat requirements. More recently in the Department of Conservation’s research project summaries (Napper 1988, 1989) approximately 46% of the wildlife projects were broadly related to the question of habitat requirements. Such research usually takes the form

of documenting the distribution and abundance of a species, analysing the ecological correlates of the species' distribution and abundance and studying things like its habitat and diet preferences. The implicit justification for this research seems to be that uncovering where a species is currently located and what it currently does will provide us with the answers to important management questions like, "what are the most important habitats to conserve?", "where could the species be transferred to?", and "how should the current habitat be managed?". What problematic assumptions could possibly lie behind such important research? We think that there are at least three potentially problematic assumptions underlying this kind of research - an adaptationist assumption, an ahistorical assumption, and an assumption of genetic determinism.

THE ADAPTATIONIST ASSUMPTION

Within evolutionary theory in the last decade or so, there has been a sustained critique from biologists like Gould and Lewontin of the idea that all aspects of an organism's phenotype are optimally adapted to its environment (see Gould & Lewontin 1979, Lewontin 1983, Gray 1987). They have emphasized the importance of nonadaptive processes such as genetic drift, evolutionary lag and phylogenetic and developmental constraints, all of which mean that many aspects of an organism's phenotype are unlikely to be perfectly adapted to its environment. Gould and Lewontin have also argued that much of what goes under the name of adaptive explanation is not really rigorous science but rather the spinning of plausible and entertaining but untestable "just-so stories".

Although these ideas in evolutionary theory may seem a long way removed from research on the habitat requirements of endangered birds, this is not the case. In much of the research on habitat requirements there is a strong presumption that the habitat and diet preferences of the species being studied are the best of the available options - they are optimal. If the assumption of optimal behaviour is doubtful for many healthy species then it should certainly be questionable for endangered species.

An example of this adaptationist approach can be seen in the research on the habitat requirements of New Zealand's endemic flightless rail, the Takahe *Porphyrio mantelli*. In a series of papers Mills and colleagues (Mills et al. 1978, 1984, 1988) have argued that Takahe possess a combination of behavioural and morphological features that are specific adaptations to an alpine tussock environment. The behavioural features include a very restrictive predominantly tussock diet, "eating the most nutritious part of the plant (the basal meristematic portion and the seeds); switching from species to species to take advantage of seasonal changes in plant chemistry of each species; and selecting the most nutritious individuals of a particular plant species. The morphological features are the large size of the bird and the possession of a powerful beak, which are necessary to pull out and cut the tussock tillers" (Mills et al. 1984, p. 60). Mills et al. acknowledge that Takahe might be able to survive in other habitats but imply that these habitats would be suboptimal. The management implications of this adaptationist perspective are obvious, "Our research shows that the species is adapted to life in the alpine zone and so the major thrust of future management of Takahe must be aimed at preserving them in that environment (Mills et al. 1984, pp. 67-68). This approach has recently been adopted by the Department of Conservation in its 'Takahe Recovery Plan' (Crouchley 1990).

Although this is not the place for a detailed critique of the Takahe research (see Beauchamp & Worthy 1988), we would caution against the automatic conclusion that the current habitat and diet preferences of any species, let alone a relict population facing extinction, are the best possible. The recent success of Takahe released on Kapiti, Mana and Maud Islands (where they feed on pasture grasses and fern rhizomes) illustrates that there may always be habitats and diets outside the currently utilised range that the species can do better on.

THE AHISTORICAL ASSUMPTION

In contrast to the adaptationist view that all features of an organism are optimally fitted to its current environment there has been a growing emphasis in recent evolutionary theory on the fact that many traits are legacies of phylogenetic history (see Gould & Lewontin 1979, Maynard Smith et al. 1985, Gray 1989). For a variety of developmental and genetic reasons once certain features are fixed in a lineage they may persist regardless of their current utility. In research on habitat requirements the focus is typically on just the current environment and current habits of a species. Phylogenetic history is generally ignored. In the case of the Takahe the behavioural and morphological features Mills et al. have claimed are adaptations to life in an alpine tussock environment may well be legacies of history. The Pukeko *Porphyrio porphyrio melanotus*, a close relative of the Takahe, feeds in a similar highly selective manner on pasture grasses, fern rhizomes and *Typha* shoots in its swampy environment. Many other gallinules forage selectively on the meristems of uprooted monocotyledons. This suggests that this type of foraging might be a primitive feature of the group. Beauchamp and Worthy (1988) have also pointed out that several other species of large flightless gallinules are found in habitats other than alpine tussock. Although this brief consideration of the comparative evidence is not a rigorous phylogenetic analysis, it suggests that far from being adapted to alpine tussock foraging the behaviour and morphology of the Takahe are merely ancestral traits that have persisted in the gallinule lineage over a range of environments.

Another way in which considerations of history may alter the conclusions drawn from studies of current habitat use is through an analysis of the historical distribution of a species. Once again the Takahe study illustrates this rather well. (It may seem that we are unfairly singling out the Takahe research for analysis. We hope this is not the case. The Takahe research simply provides a very good example of a great deal of research on habitat requirements that is done in New Zealand. It is easier to analyse than most programmes of research because its authors have published many papers explicitly outlining the rationale for their work). Although the Takahe is currently restricted to a small population in the Murchison mountains in Fiordland, it was once widely distributed throughout New Zealand. Evidence from subfossils in caves, dunes and swamp sites and bones in Maori middens indicates that Takahe were found from North Cape to Bluff (Mills et al. 1984). There has been some debate about this evidence. While Mills et al. (1984, 1988) claim this widespread distribution was only possible because of the widespread availability of tussock in the Pleistocene glacial periods, the growing consensus seems to be that the Takahe were found in both tussock and forest environments (Beauchamp & Worthy 1988, Atkinson 1991). Thus historical considerations can suggest that the range of suitable habitats is wider than just those currently utilised. If Takahe were in New Zealand prior to the Pleistocene ice

ages, as Beauchamp and Worthy suggest is possible, then they “must have been able to survive in temperate climates during which alpine grasslands were not widespread (Beauchamp & Worthy 1988, p. 109). Indeed, in Buller’s “A History of the Birds of New Zealand” Buller reports that both local Maori and an early European explorer (“Mr Gibson, who is a really good careful observer . . .”) saw Takahe in swampy habitat (Turbott 1967, p. 166).

GENETIC DETERMINISM

Implicit in the concept of habitat requirements is the idea that these requirements are fixed, genetically determined traits. They are not variable nor flexible. This denial of the possibility of variability and plasticity is at odds with modern studies of behavioural development. Most researchers now accept that the old idea of innate, or genetically determined, behaviour is a misleading view of behavioural development (see Bateson 1983). Instead, current researchers stress that all phenotypes are the product of an interaction between an organism and its environment. From this view the constancy of development is due to the constancy of patterns of interaction rather than a genetic blueprint (Oyama 1985). Thus if you change these patterns of interaction, by changing the environment experienced by the organism, then the resulting phenotype can often be changed. There is an enormous amount of evidence for the potential variability and plasticity of traits typically studied in research on habitat requirements. A species’ habitat preferences, diet preferences, feeding methods, digestive enzymes, gut morphology and microfauna, and even feeding morphology can all change as a consequence of exposure to different habitats or diets (see Table 1).

TABLE 1 - Habitat and foraging plasticity

Variables	References
Habitat selection	Gluck (1984)
Diet preference	Rabinowitch (1965), Kuo (1967)
Specialist/generalist	Gray (1981)
Feeding methods	Padilla (1935), Norton-Griffiths (1968)
Prey capture success	Polsky (1977), Caro (1980a,b), Brandt (1984)
Digestive enzymes	Grossman, Greengard & Ivy (1943), Brattsten, Wilkinson & Eisner (1977), Ahmad (1983), Terrier (1984)
Gut micro-organisms	Smith (1965), Abe & Iriki (1978)
Gut length	Miller (1975), Kenwood & Sibly (1977), Al-Jaborae (1979)
Morphology	Greenwood (1965), Moore (1965), Bouvier & Hylander (1981), Beecher, Corruccini & Freeman (1983), Hulscher (1991)

TABLE 2 - Social traditions

Type	Reference
Feeding methods	Fisher & Hinde (1949), Norton-Griffiths (1968), Galef (1985)
Habitat preferences	Klopfer & Hailman (1965)
Migration routes	Van Denburgh (1914), Helfman & Schultz (1984)
Home ranges & territories	Carrick (1963), Jolly (1972), Woolfenden & Fitzpatrick (1978)
Nest sites	Temple (1977), Harris & Murie (1984)

One of the obvious consequences of this developmental plasticity is that there may often be habitats and diets outside a species' current, or even historical range, in which the species could survive quite happily. The effects of habitat imprinting and early exposure to a limited diet may, however, mean that the species apparently prefers a suboptimal habitat or a suboptimal diet. If it is never exposed to alternative habitats or diets, or if this exposure is after a sensitive period in early development, then it may never recognise nor prefer additional habitats or diets.

Temple (1977) has noted that there is a more positive flip side to this potential developmental plasticity. He noted that not only can habitat preferences, diet preferences, nest site preferences and migration routes be changed, many of these changes can be passed on to future generations through social traditions (see Table 2). He suggested a potential management practice that is quite contrary to the idea of rigid habitat requirements. He suggested that if all existing habitat was under threat, or if that habitat had been modified to the point of no longer being habitable, then it may be possible to change the species' behaviour by altering its social traditions to fit the new environment.

Research currently being conducted by Tim Lovegrove on the social transmission of roost site preferences in Saddlebacks *Philesturnus carunculatus* provides an excellent example of this. Saddleback parents naturally take their juvenile offspring to potential roost sites (holes in trees or dense vegetation). Over several weeks the juveniles learn to use these sites and subsequently return to them unaccompanied. Unfortunately, birds at these sites are often vulnerable to predation from Stoats, rats and feral Cats. Tim Lovegrove has been able to use the social transmission of roost site preferences to imprint juveniles onto predator-safe artificial roost boxes.

There are numerous possibilities for the careful modification of the social traditions of other endangered New Zealand avian species. For example, the Black Stilt *Himantopus novaezelandiae*, frequently nests on dry shingle river beds on the east coast of the South Island of New Zealand. This means that their nests are vulnerable to both predation and flooding. By imprinting some chicks on nest sites in a safer environment it may be possible to develop a population that continues to nest in this safe environment.

Obviously this kind of manipulation raises some difficult questions about the desirability of changing a species' seemingly "natural" behaviour. However, as Temple (1977)

remarks, "faced with the choice of either allowing a bird to become extinct or manipulating its niche, I think most would vote for the latter" (p. 42). Perhaps we should also remember that the natural state of nature is not just of stasis but also change and variability. Some of the most spectacular successes in New Zealand avian conservation have been achieved by going against what was "natural" (e.g. the fostering of Chatham Island Black Robins by Tomtits).

CONCLUSION

The necessity to be brief has meant that many of the arguments we have presented have been simplified and abbreviated. In conclusion we would like to attempt to be very clear about what exactly we are, and are not, saying. We are not saying that these assumptions in research on habitat requirements are unique to New Zealand. We believe they are widespread throughout the world. We are not saying that research on habitat and diet preferences is of no value, but rather we are saying that this work should not be over-interpreted nor over-emphasised. Habitat and diet use, along with historical analyses, can show the range of behaviour known for a species and allow a continuation of innovative management practices that will see endangered birds returned to past ranges, rather than locked into existing refuges. And we are not saying that all features of bird behaviour are infinitely plastic and socially transmitted. Instead, we are saying that the assumption that the current habitats and diets of endangered birds are optimal is questionable. We are saying that the phylogenetic and biogeographic history of the bird being studied should be considered as well as its current behaviour. We are saying that sometimes it might be useful to utilise the plasticity and social traditions in avian behaviour as a tool in conservation. And above all else we are saying that we need to consider the theoretical assumptions underlying current conservation practices.

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CONCLUDING REMARKS: INTEGRATING NEW ZEALAND CONSERVATION

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From this symposium, we hope that you have gained a deeper appreciation of the diversity of problems which must be tackled in New Zealand conservation. However, let us again consider the goal that we are trying to achieve. Ultimately, this can be stated as the conservation of New Zealand avifauna for both present and future generations. Proximally, this can be restated as the maximisation of the success of the project which each of us is involved with. Integrated conservation allows this to happen by ensuring that we have a structure in which we can collect and interpret meaningful information.

Let us strive to understand the system we are dealing with and the processes we are hoping to manipulate. To do this, let us search for causal relationships rather than be content with simple correlations. Let us understand the full variability, and therefore the plasticity of the system, as this will allow us to continue to develop innovative management techniques.

New Zealand has a proud record of innovative conservation management and research. However, let us again return to the notion that conservation is applied science which has, therefore, a limited timeframe to solve each problem. Let us not forget that political, social and economic considerations are equally important components of conservation, otherwise we risk having the real decisions taken from us, regardless of how good the science is. Let us strive to ensure that the various conservation options can be identified and that the best conservation decisions can be made. Only then will we maximise the chance of success for our ultimate goal, and achieve a truly integrated conservation endeavour.

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BALL G F	984	BULL P C	62
BALL R M	514	BURGESS E C	2353
BAPTISTA L F	1243	BURLEY N T	1367
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BARROWCLOUGH G F	493	BURNS M D	2257
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BATESON P	1054	CADIOU B	1641
BAVERSTOCK P R	591	CALDER W A	800
BAVERSTOCK P R	611	CAPPARELLA A P	307
BEASON R C	1803	CAREY C	263
BEASON R C	1813	CAREY C	800
BEASON R C	1845	CARPENTER F L	1156
BEISSINGER S R	1727	CARPENTER F L	1188
BELL B D	5	CASSIDY A L E V	1514
BELL B D	65	CATTERALL C P	1204
BELL B D	193	CAWTHORN M	1229
BERKHOUDT H	897	CHAMBERS G K	554
BERRUTI A	2246	CHANDOLA-SAKLANI A	2030
BERTHOLD P	780	CHEREL Y	2177
BIEBACH H	773	CHRISTIDIS L	359
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CICERO C	600	ELZANOWSKI A	1938
CIMPRICH D A	1432	EMMERTON J	1837
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CLOUT M N	1617	ERIKSTAD K E	2272
COCKREM J F	2092	ESCALANTE-PLIEGO P	333
COLLIER K J	860	ESTRELLA R R	1641
COLLINS B G	1139	EVANS P R	2197
COLLINS B G	1166	EVANS P R	2228
COOKE F	1666	EVANS P R	2236
COOPER A	554	EVANS R M	1734
COULSON J C	2365	FAITH D P	404
CRAIG J L	231	FEDUCCIA A	1930
CRAIG J L	2513	FEINSINGER P	1480
CRAIG J L	2546	FEINSINGER P	1605
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CROXALL J P	1393	FORD H A	1470
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DAUGHERTY C H	525	FURNESS R W	1678
DAVIDSON N C	2228	FURNESS R W	2239
DAVIS L S	1352	FURNESS R W	2241
DENNISON M D	504	GASTON A J	2306
DE LAET J	1436	GEE G F	2403
DERRICKSON S R	2402	GELTER H P	592
DHONDT A A	1417	GENTLE M J	1915
DHONDT A A	1436	GERSTBERGER R	2114
DRENT R	761	GNAM R S	673
DROGE D L	932	GOLDSMITH A R	2063
DUMBELL G S	2513	GOSLOW G E JR	701
DUMBELL G S	2561	GOSLOW G E JR	716
DUNNET G M	1639	GOSLOW G E JR	748
DYER A B	1061	GOSS-CUSTARD J D	2199
EADIE J M	1031	GOTO M	2015
EBIHARA S	2015	GOUDIE R I	811
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GRIFFIN J M	1273	JAMES F C	2469
GROSCOLAS R	2177	JAMES H F	420
GRUBB T C JR.....	1432	JÄRVINEN O	1479
GUSTAFSSON L	1425	JENKINS P F	1262
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HASKELL M	860	KEAST A	419
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HOLMES R T	1542	KING J R	2186
HOLMES R T	1559	KLINKE R	1805
HOMBERGER D	398	KLOMP N I	1678
HORNE J F M	468	KOMDEUR J	1325
HOWE R W	903	KOOYMAN G L	1887
HUGHES M R	2138	KORF H-W	2006
HULSCHER J B	889	KORPIMAKI E	1528
HUMMEL D	701	KREIG M	611
HUMMEL D	730	KRUIJT J	1068
HUMMEL D	748	LAL P	2030
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JACKSON S	1378	LOVVORN J R	1868

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LYON B E	1023	MUMME R L	1317
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MENCH J A	1905	OWEN M	1105
MERTON D	2514	PAABO S	554
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TIEBOUT H M III	1605	WILLSON M F	1630
TRIGGS S J	525	WILSON A C	554
TRIGGS S J	860	WILSON A C	628
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WENZEL B M	1820	ZIEGENFUS C	1229
WETTON J H	2435	ZINK R M	591
WHITEHEAD M D	1384	ZINK R M	629
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