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SYMPOSIUM 21

CO-OPERATIVE BREEDING – A SECOND PHASE

Conveners I. C. R. ROWLEY and G. WOOLFENDEN

SYMPOSIUM 21

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MANIPULATING DISPERSAL OPTIONS IN COOPERATIVELY BREEDING BIRDS: CAN STRIPE-BACKED WRENS COUNT AND DIVIDE?

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ABSTRACT. The conditions that lead to dispersal among males in the Stripe-backed Wren *Campylorhynchus nuchalis* were examined through five experimental removals of breeding males in groups without resident helper males. As most males that obtain a breeding position do so through inheritance on the natal territory, dispersal by males is rare in comparison to females. Only 12% of the possible dispersers (helpers in adjacent territories) responded to breeding vacancies in small groups, a result consistent with the low quality of the position and comparable to the response observed among females in other removal experiments. No first-year males responded and position in the natal queue had no differential effect on response. Three territories failed to attract a replacement and two became defunct. Paradoxically, more females responded to compete against the "widowed" breeding female than males responding to fill the vacancy, and aggression among females comparable to contests for high-quality positions was observed.

Keywords: Stripe-backed Wren, *Campylorhynchus nuchalis*, dispersal, natal philopatry, delayed breeding, field experiments, life-history theory, llanos, Venezuela.

INTRODUCTION

Obtaining a breeding position represents a critical juncture in the life-history of birds. If the quality of territories differs in a population, the potential disperser must discriminate carefully among available options. In cooperatively breeding birds the transition from nonbreeding helper to breeder most often involves a delay past the age of maturity. Natal philopatry is the rule among cooperative species, and mature offspring may not leave the natal territory for up to several years. Considerable debate among researchers has centred on whether the offspring remain on the natal territory because few if any breeding opportunities exist ("habitat saturation") or because they weigh the potential direct and indirect benefits of remaining home versus those of reproductive options elsewhere. The distinction is not merely a semantic one; the issue is whether reproductive delay represents a dispersal constraint or a tactical restraint on the part of the philopatric nonbreeder (e.g. Zack & Ligon 1985).

Stripe-backed Wrens *Campylorhynchus nuchalis* are cooperative breeders that allow a close evaluation of the process of dispersal. Males may obtain breeding status either by remaining at home and inheriting the position or dispersing elsewhere; females must disperse. These wrens are common inhabitants of woodland patches in the llanos of central Venezuela and adjacent Columbia. At Hato Masaguara, near Coroza Pando, Venezuela, these birds have been under continuous study since 1974, and a marked population has been maintained since 1977. The following synopsis of Stripe-backed Wren behaviour and demography is derived from the work of Kerry Rabenold, Haven Wiley, and their colleagues (Rabenold 1984, 1985, 1990, Wiley & Rabenold 1984). Group sizes range from two to 14, with a mean of five. All group

members defend the territory, aid in construction and defense of the communal roost and nest site, and aid in the rearing of young. Stripe-backed Wrens are predominantly monogamous, although recent DNA-fingerprinting evidence indicates that male helpers may occasionally contribute to the paternity of a clutch, but only if the female breeder is unrelated to him (P. and K. Rabenold, pers. comm.). The breeding pair, also called the "principals", exhibit behavioural dominance over other group members, and are easily recognized by their frequent duetting behaviour throughout the year.

Groups of four or more (thus of two or more helpers) produce four-six times more offspring a year than do smaller groups (with one or no helper). Breeder experience and physiognomic aspects of territory quality are overshadowed as determinants of reproductive success by the strong effect of helpers. The strong threshold effect of helpers on reproductive success allows us to categorize the value of reproductive positions to potential dispersers by the number of helpers present.

Natal philopatry is the rule among mature offspring. Females typically delay dispersal by one or two years, occasionally longer. Most disperse within two territories of their natal territory. Males most often remain in the natal territory indefinitely, frequently inheriting breeding status with the demise of their father and older male siblings.

Fully 63% of those males acquiring a breeding position do so on the natal territory. Dispersal to breeding status within two territories' distance accounts for 35% of those obtaining breeding status; only 3% obtain a position further away. A seniority system for priority to breeding position among males exists, and same-aged sibling males appear to establish their position in the queue to breeding status soon after fledging. Incest has never been observed in this species. Females must disperse to obtain a breeding position. Male and female principals' annual survivorship is 63%, annual survivorship for helper males is 76%, and for helper females it is 55%.

In 1985, I, with the help of J. Haydock, began to capture and uniquely colour-band a population of Stripe-backed Wrens adjacent to the long-term study area. By 1988, 98% of wrens in 85 groups were banded and monitored. In 1986 we began a series of breeder-removal experiments in order to examine the dynamics of the dispersal process. By conducting 19 removals of breeding females in both large (4+) and small (2-3) groups we (Zack & Rabenold 1989) showed that (1) more females competed for large groups than did for small groups; (2) intense aggression over several days characterized competition for large group vacancies while aggression was virtually absent in the replacement process for small groups; (3) older females from adjacent territories were most often the winners of vacancies in large territories, yet no clear pattern of the effect of age or proximity emerged among winners in small groups.

Here I present the results of five experimental removals of breeding males. These experiments allow a direct comparison with the results obtained from the experiments with female nonbreeders and reveal the similarities and differences in conditions that trigger dispersal in this species. Additional information on male dispersal comes from the establishment of new groups within the study site.

METHODS

The capturing, colour-banding, sexing, and monitoring of the experimental population of Stripe-backed Wrens are described in Zack & Rabenold (1989). For the time of the experiments described below, virtually all possible contestants for breeding vacancies were colour-banded in 85 groups. Each experimental territory was surrounded by marked birds in a ca. 10 territory radius, or for at least 1500 m in all directions.

As I wished to experimentally examine the conditions that may prompt males to disperse, removals of breeding males were conducted in groups that contained no male helpers. Males in established queues are apparently able to keep outside males from taking over a breeding position, so the only available avenue for male dispersal is when no natal males are present in the target territory. Large groups with no male helpers are virtually absent in the population. The experimental removals created vacancies only in small groups. (The NW territory contained two nonbreeding females, but one of them was known to be a "wanderer" and was rarely present during the day. Such wanderers rarely remain to help during the breeding season (pers. obs.) and so I treated this territory as if it were the reproductive equivalent of a small group.) The male removals were conducted in the dry seasons of 1987 (four experiments: LD, MP, NW, and GL territories) and 1988 (one experiment: MW territory).

Prior to a removal of the breeding male, the territories surrounding the experimental territory were censused. As 97% of males in the long-term study have obtained a breeding position within two territories of their natal territory, the "sphere" of possible replacement males for each experiment was considered from within two territories' distance. A similar assumption underlies the experimental removals of breeding females (Zack and Rabenold 1989), and so also serves as a comparison with the response parameters of females.

The principal males were captured at dawn, soon after roost emergence, by using playbacks of recorded vocalizations on opposite sides of mist nets. The male was then released 5 km away by a field assistant. Other group members caught in the nets were immediately re-released into their territories. The newly "widowed" female was followed until intruders were detected. All intruders were identified and any behavioural interactions, either between the intruder and the "widowed" female, or among intruders, were recorded.

A winner was declared when a replacement male slept with the experimental group. If no males responded, or if responding males left the territory, the territory was monitored from dawn until 1200, and from 1500 to roosting for three consecutive days. After that time the territory was visited periodically, typically once a day for the next week and then once a week throughout the remainder of the study season. Therefore the total number of respondents to each experiment is not known with certainty for those territories not attracting a male within the first three days. However, those territories that failed to attract a male in the first three days never obtained a permanent replacement (below).

To further evaluate male dispersal, the colonisers of newly-formed territories within the study population were monitored. The identity (if previously colour-banded) of founding males was recorded and field notes were examined to identify the males' prior status in their natal group.

RESULTS

Numerical response by males to removals

Overall, only five of the possible 41 (12%) helper males within two territories of the experimental territory responded to the breeding vacancies (Table 1). All five respondents were older males (> 1 yr old), as none of the 12 younger males nearby opted to respond. Only one male competed from further than two territories away. This unbanded male was from outside the study area and so was immigrating from > 2 km away. There was no apparent difference in response by helper males that were “next-in-line” to become breeders in their natal group (3 of 23 (13%) responding) versus those helper males lower in their natal queue (2 of 18 responding (11%)) (Table 1).

TABLE 1 — Actual and possible nonbreeding (helping) male respondents to experimental removals from within two territories distance from experimental territory. Age and position in natal queue are considered separately. Asterisk marks the category of individual that actually dispersed (remained in) to experimentally created breeding position.

Territory	Non-breeding males within two territories (# Responding /# Possible)			
	Age		Position in natal queue	
	> 1 yr	< 1 yr	Top nonbreeder	Lower
LD	2/6	0/5	2/6	0/5
MP	0/5	0/1	0/4	0/2
NW	1/4	0/2	1/3	0/3
GL	1*/8	0/2	0/5	1*/5
MW	1/6	0/2	0/5	1/3
TOTAL	5/29	0/12	3/23	2/18
	5/41		5/41	

Behaviour of responding males

There was considerable variability among males in the timing of first intrusion in the experimental territory, ranging from within 30 min of removal to a delay of five weeks. One experimental vacancy failed to attract any responding males (MP). Responding males immediately flew to the “widowed” females and begin singing duets with them. These duets sounded as fully formed and synchronized to my ear as any long-established pair’s duets did. The newly formed pair would then fly throughout the territory, duetting from conspicuous perches, and occasionally inspected the roost site together. Most responding males would consort with the female by day and return to their natal group to roost each night. Only the unbanded male stayed to roost the first night with the female. The GL replacement male finally “moved in” after 30 days of day-to-day consorting. It is not known whether the sole responding male ever stayed at the final removal (MW), as I left Venezuela 22 days after the start of the experiment. In the LD experiment, the “widowed” female was visited by her brother from an adjacent territory for 50 min, and only five weeks later by an unrelated male. He consorted with her daily for three weeks and then returned to his natal territory permanently.

Two males responded to vacancies that also attracted nonbreeding females (below). One of these males (in the GL experiment) followed and duetted with, at different times, the “widowed” female principal, the experimental group’s helper female, and one of the three intruding females. After five hours of female-female aggression, this male was strongly consorting with the “widowed” principal only. It is not clear whether he had an active role in determining the outcome in the competition among the females. Only one experiment had two males arrive simultaneously (NW) and here the unbanded male chased, briefly, the colour-banded intruder two times. No physical contact was made and the colour-banded male returned to his nearby natal territory within ten minutes.

“Widowed” females without partners

Females that had their breeding partner removed would immediately give contact calls (“WAY” calls) upon their release from the mist nets. In unmanipulated groups, these calls immediately resulted in the joining of the principals and a string of duets. The “widowed” females would give 0-10 of these WAY calls per hour during the morning, and were virtually silent in the afternoons. Two females, at LD and MP, did not obtain mates. Both were observed to desert their territory and “float.” The LD female left her territory beginning the second day after removal of her mate and was only seen back in her territory occasionally after that time. Both females became contestants at experimentally created (female) breeding vacancies in territories elsewhere in the study site. The LD territory was later colonized by a new pair.

Female intruders competing with “widowed” females

One unanticipated result of these removals of breeding males was the response, and fierce competition among, nonbreeding females. These intruding females competed with the “widowed” female, apparently for the territory and its possibility of attracting a new male. In two of these experiments there was intense aggression among the females reminiscent of the aggression observed in contests for large groups described in Zack & Rabenold (1989). None of the nine removals of breeding females in small groups resulted in intense aggression by responding females, most involved no physical contact among respondent females (Zack & Rabenold 1989). Three nonbreeding females competed in the GL and MW experiments (one female was common to both). In both, the females were involved in aggressive chases, head pecking, “spiral tackles” (aerial collisions that result in the birds tumbling to the ground), and long chases. The intense aggression lasted four-six hours. In both cases the “widowed” female held her position and outlasted the outside competition, but only in the GL experiment did she obtain a new male partner. One “floating” female briefly explored the LD territory and flew off. Overall, a total of seven females intruded on the five experiments (one female intruded on two experimental territories). With the exception of an unbanded female of unknown origin outside the study site, four of five of the females were also losing competitors for other experimentally created breeding vacancies.

Males that attempt to establish new territories

On 24 occasions between 1986 and 1988 newly formed pairs (or occasionally larger groupings) attempted to establish a new territory within the study site. Twelve of the 17 groups formed in 1986 and 1987 attempted to breed (two did so successfully), and five of the 17 groups lasted at least a year. Therefore, these new groupings are not necessarily losing propositions — the two successful breeding attempts created large groups. Eleven of the 24 colonizing males were unbanded and hence immigrated from

at least 2 km away. Five of the colour-banded males were either known to be “floaters” (without membership in a group) (N=3), or long distance dispersers within the study site (N=2, moving 1500 m and 4 km). The remaining nine males left their natal territories and moved either to an adjacent space (N=7) or one the equivalent of two territories away (N=2).

Most (N=19) of these founding males were adults (> 1 yr old), as told by eye colour or known directly from colour-banded birds. Three of the five first-year males established territories considerably distant from their natal territory. These first-year males were all over six months of age and physiologically capable of breeding. Of those colonizing males originating from territories on the study site, seven of nine left their position as next-in-line to succeed to the breeding position.

DISCUSSION

The queuing system for priority to breeding positions in Stripe-backed Wrens results in different dispersal tactics for males and females. As the queue for inheritance exists among males only, and close inbreeding is apparently not an option, females must disperse. Dispersing females can obtain high-quality (large group) breeding positions nearby, and older females often do so. The dispersal option for males virtually never allows for competing for high-quality positions. Large groups are invariably composed of one to several helper males (in addition to helper females), and the long-term pattern shows that males cannot disperse to breeding positions where resident males stand to inherit. Vacancies in small groups, or the potential to form new territories with others, remain as dispersal options for both males and females.

The ascent of males in the queue to breeding positions does not seem to involve overt aggression, reflecting the “stability” of the queuing system (Wiley & Rabenold 1984). Females that attempt to disperse to high-quality positions, in contrast, can expect to encounter considerable competition, often lasting several days and occasionally months (Zack & Rabenold 1989). The competition for dispersers of both sexes to breeding positions in small groups does not involve much competition, with the conspicuous exception of those females contesting newly widowed females in small groups.

The overall response among males to the removals was low, and comparable to that of females competing for breeding positions in small groups (Zack & Rabenold 1989). Overall 12% (10/77) of females and 13% (5/41) of males responded to experimental removals in small groups. Response is simply defined as intrusion in the experimental territory, and so it may not imply “intent” to take over the vacancy. The motivational state of the respondents is obviously impossible to know. The overall patterns of response, however, seem to indicate that this simple measure approximates some level of “intent” that is consistent with the response parameters in relation to the value (probable reproductive success) of the breeding position. Response levels among females do differ as a function of the potential reproductive value of the vacancy (Zack & Rabenold 1989), and no males responded to female vacancies. Response among females to large group vacancies invariably resulted in intense aggression, both with other intruding females and with members of the target group. In removals in small groups, response is low and aggression is rare for both sexes; this is consistent with the low value of the reproductive option.

Removals of breeding males in small groups can lead to the dissolution of the territory, as nearby males may not respond to the lone female's calling. By contrast, removals of breeding females in small groups never resulted in the dissolution of the territory. There was always a respondent that would stay, although subsequent mate desertion (followed by yet another replacement) did occur.

No younger males attempted to disperse to experimentally created vacancies, and few young males are involved in the attempted establishment of new territories. This pattern differs from that of young females, who, although they are most often competitively inferior to older females, do compete for both large and small group vacancies (Zack & Rabenold 1989).

There was no clear effect of position in the queue and inclination to attempt dispersal (experimental removals: 13% vs. 11%, respectively), yet 77% of the males that belonged to known groups and attempted to establish a new territory left "first-in-line" positions to do so. But these numbers are somewhat deceiving as males are loathe to leave their natal territories permanently, and those that do, as analysed here, represent an extreme minority. Only one male from the study population filled an experimental vacancy, yet five were created. Approximately 3% of the helping males in the marked population were involved in establishing new territories in any one year, and at least some of these males deserted their attempts and returned to the natal territory. Unbanded males, who must come from at least 2 km distance, account for nearly half of those males attempting to establish new groups. As more than 1/3 of the colour-banded birds involved in new territory establishment were either floaters without a territory or extremely long-distance dispersers, the overriding impression is that most dispersing males are the victims of natal flock dissolution or other source of intra-group problems.

The fundamental difference between male and female Stripe-backed Wrens in acquiring breeding positions is that males primarily rely on persistence and females primarily wait for a high-quality vacancy nearby and engage in intense aggression in attempting to obtain it. The option of joining or creating a new group is always available, yet males, more so than females, are averse to doing so.

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EVOLUTION OF OBLIGATE COOPERATIVE BREEDING IN WHITE-WINGED CHOUGH: A STATISTICAL APPROACH

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ABSTRACT. Many models propose that cooperative breeding is facultative, driven by proximate constraints such as habitat and mate shortages. Without experiment, it may be difficult to demonstrate the nature and effect of a constraint. Some cooperatively breeding species, occurring at low density or sensitive to manipulation, are unsuitable for experimentation. I advocate a "controlled prospective" experimental approach to studying such species, using natural variation combined with statistical modelling. Unassisted pairs of White-winged Choughs *Corcorax melanorhamphos* produce no young; I use statistical techniques to demonstrate the constraining mechanisms. Pairs with one helper also have poor success; only groups of 4 and >4 produce >1 young on average per nesting attempt. Reproductive success increases as more helpers are added. Helpers are essential for nestlings to get sufficient food, and brood sizes are adjusted according to group size through starvation of the youngest nestlings. Coupled with evidence of slow development of foraging skills, these data suggest that the foraging habit of the chough has led to the only case of obligate cooperative breeding so far known among birds.

Keywords: White-winged chough, *Corcorax melanorhamphos*, obligate cooperative breeding, controlled prospective experiment, generalised linear model, foraging skill.

INTRODUCTION

Cooperative breeding, where individuals other than the parents contribute to rearing young, is thought to develop when young individuals are constrained from dispersing and reproducing independently (Brown 1987). The central models propose that cooperative breeding is facultative and driven by proximate constraints, especially habitat and mate shortages (Brown 1978, Koenig & Pitelka 1981, Emlen 1982a). Breeders receiving help often have higher reproductive output than pairs. However the net benefits typically reach an asymptote quickly as the number of helpers increases (Brown 1987), so the per capita reproductive output declines (Koenig & Mumme 1987, Woolfenden & Fitzpatrick 1984). Notable exceptions are Stripe-backed Wrens *Campylorhynchus nuchalis*, White-fronted Bee-eaters *Merops bullockoides*, and Pied Kingfishers *Ceryle rudis*, in which additional helpers continue to enhance reproductive success (Rabenold 1984, Emlen & Wrege 1989, Reyer 1984). There are few direct demonstrations of how the initial reproductive enhancement occurs. Although often cited as a benefit of helping, few workers consider the reproductive enhancement sufficient in isolation to merit delayed dispersal and cooperative breeding.

A common problem in studies of cooperative breeders is the lack of experimental identification of the constraints on dispersal. However, in natural populations, investigative experiments which control extraneous factors are not always possible. Two common reasons are insufficient numbers for manipulation and extreme sensitivity of the study animal. Consequently, when testing hypotheses in such uncontrolled

circumstances, response variables usually depend on many explanatory variables simultaneously. However, the equivalent to experimental design can be achieved through a "controlled prospective" approach. This combines systematic, balanced data collection, recognition of the testing through fitting of appropriate models. Here I present a statistical model of food delivery to White-winged Chough *Corcorax melanorhamphos* nestlings which illustrates a controlled prospective experiment, and identifies a severe constraint on dispersal for young choughs.

METHODS

I studied a population of colour-banded choughs on Black Mountain, Canberra, Australia, 149°15'E, 36°05'S, from 1985 to 1989. Choughs live in permanent cohesive groups of two to fifteen – most are between five and eight (Rowley 1978), and usually initiate nesting in September. For a description of the foraging mode of choughs see Heinsohn (in press). They build a mud nest and lay a clutch of four eggs which typically hatch one day apart. The hatch order imposes a weight hierarchy which is sustained throughout the nestling period. By dyeing nestlings on the back of the head using acrylic paint, I could distinguish individuals from the ground once they were over seven days old. I estimated the quantity of food received by nestlings over 100 minute intervals at least twice per week for the remainder of the nesting period (usually 29 days). Nest trees were climbed four times during this period to weigh nestlings and to time nestling attrition for 29 group breeding efforts. Breeding success was monitored for the years 1986, 1987, and 1988 for 87 group efforts. The timing and probable causes of death were established for 56 marked nestlings for which weight and food data had been collected.

Statistical modelling

Choughs are not suitable for experimental manipulation of group size or clutch size due to extreme sensitivity to disturbance during the breeding season, high levels of uncontrolled egg and nestling mortality, and the scarcity of broods of the same age for exchange of young. Natural variation in group size was used instead. Consequently, the experimental approach taken in this study was controlled prospective; data were collected systematically to enable testing for effects of factors of interest. The statistical approach in this paper is one of generalized linear modelling (GLM, Dobson 1983). In particular, we make repeated use of models combining aspects of multiple linear regression and analysis of covariance. For example, with two explanatory variables, these models take the following forms:

$$E(y) = \mu + e \text{ (null model)}$$

$$E(y) = \beta_0 + \beta_1 x_1 + e \text{ (model 1)}$$

$$E(y) = \beta_0 + \beta_2 x_2 + e \text{ (model 2)}$$

$$E(y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + e \text{ (model 3)}$$

This set of models is the general form for multiple regression with two explanatory variables. The first is the null model where there is no regression and a general mean (μ) explains the variance with error e . Models one to three form a sequence whereby terms (variates x_1 and x_2) are systematically added and deleted from the regression.

Terms are retained in the model if their explanatory power significantly enhances the fit of the regression. Inclusion of all variates denotes the saturated model (model 3; Dobson 1983).

Explanatory power of variables may be enhanced if they are included in the model as covariates (factors) rather than variates. For example, if x_1 is added as a covariate, the saturated form of the regression is given by:

$$E(y) = \beta_0 + r_{1i} + \beta_2 x_2 + e \quad (\text{model 4})$$

where r_{1i} refers to an additive component for each of i levels of the covariate x_1 . Any explanatory variable x can be similarly incorporated into the model as either a variate or covariate. When fitting a variable as a covariate, the improvement of fit over including it as a variate is given by:

$$(RSS_{\text{new}} - RSS_{\text{old}}) / S^2 / df_{\text{new}} - df_{\text{old}}$$

where RSS refers to the residual sum of squares of the old and new models, S^2 is the residual sum of squares of the full model, and df is the degrees of freedom. This yields a variance ratio to be tested on $(df_{\text{new}} - df_{\text{old}})$ and the residual degrees of freedom. The data are assumed to be normally distributed, so if the model is adequate the residuals will show a random scatter. If examination of the residuals shows non-normality, transformations of the y or any of the x variables may be necessary. All algorithms used were provided by the statistical package GENSTAT (Alvey et al. 1980).

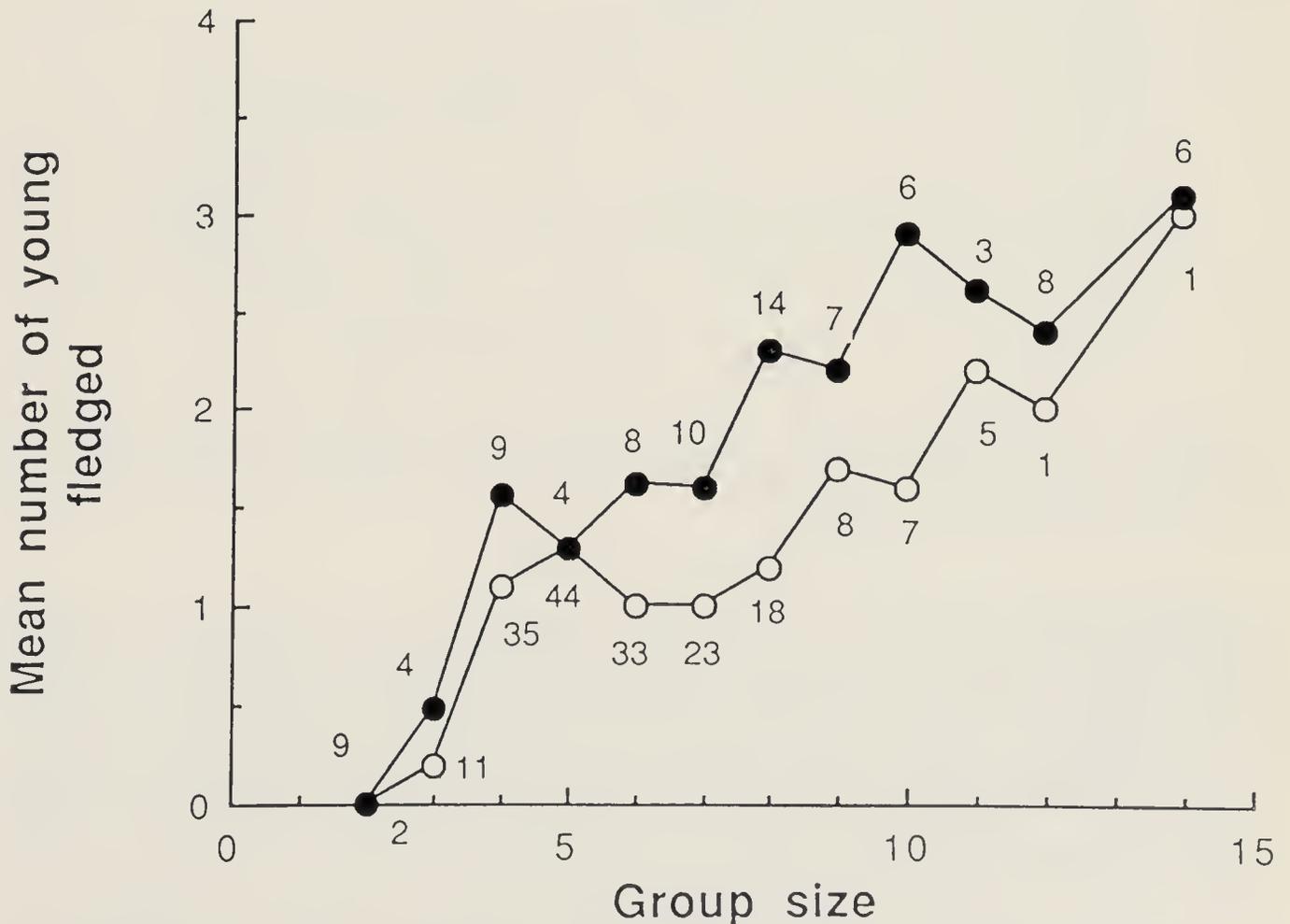


FIGURE 1 - Mean number of young fledged per chough group over varying group sizes. Data were from 87 nesting attempts over four years from 1985 to 1988. Results from this study (closed circles) are compared with those from 186 nesting attempts monitored by Rowley (1978) (open circles). Sample sizes are shown on the graph.

RESULTS

Production of fledglings

The mean numbers of fledglings produced by groups of varying size are plotted in Figure 1 and compared with the results of Rowley's (1978) long-term study. There is a consistent increase in the number of young produced as group size increases. In both this study and Rowley's, unassisted pairs never succeeded in fledging young. Pairs with one helper (trios) also had poor success; only groups of four and above produced greater than one young on average per nesting attempt.

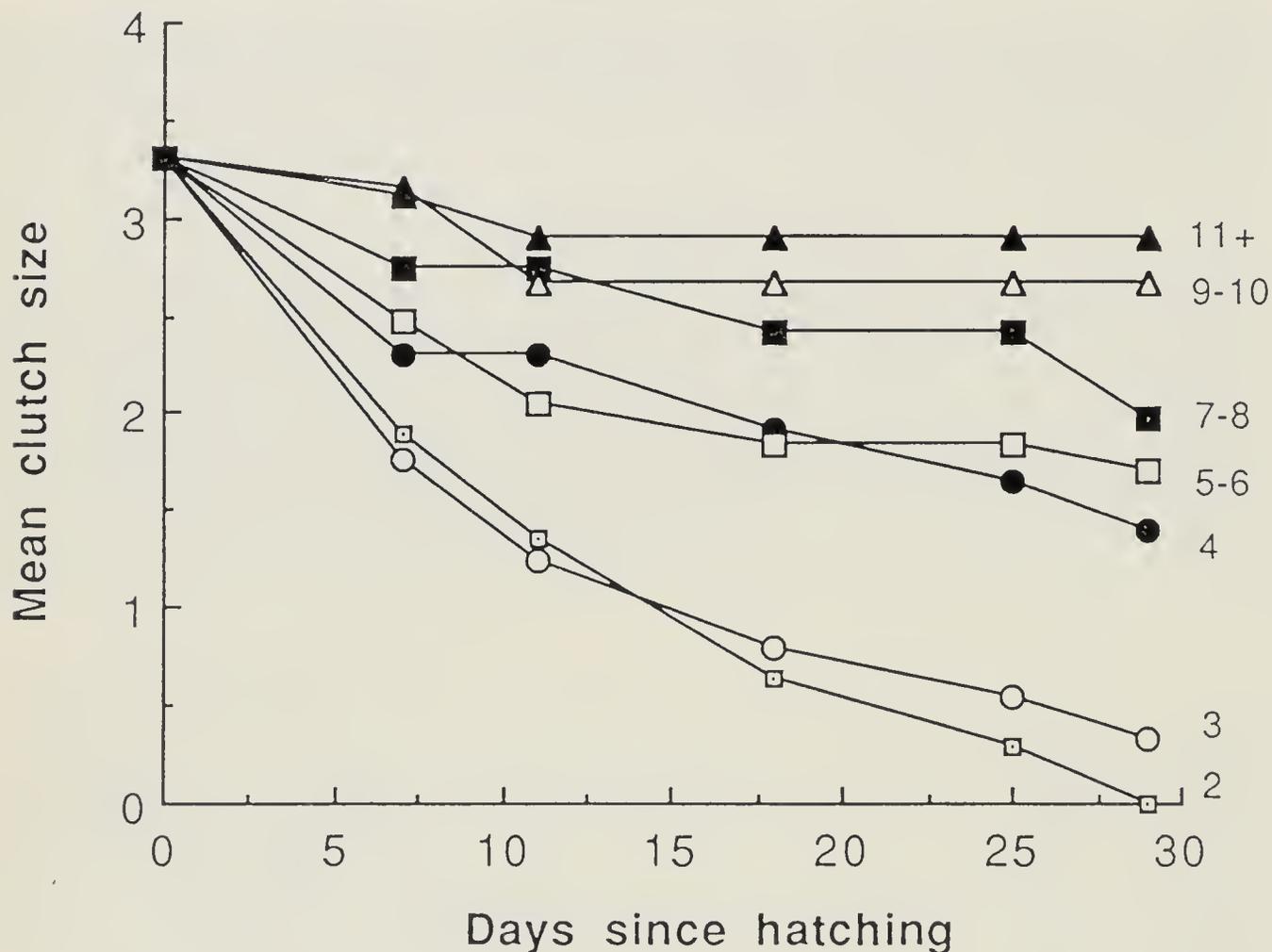


FIGURE 2 - The mean number of nestlings in the brood of groups of various sizes at six times (at hatching, days 7, 11, 18, 25, and at fledging) during the 29 day nesting period. Group sizes are marked on the graph.

Nestling attrition

The mean number of nestlings in the brood of groups of varying size are plotted in Figure 2 for six phases of the 29 day nesting period (at hatching, days 7, 11, 18, 25, and at fledging). Overall, the youngest nestlings in the brood accounted for 43 out of 56 (77%) nestling deaths with the following breakdown for group size (n = number of nests in sample); Group size (GS) = two, 73% of nestling deaths were the youngest in the broods, n = 4; GS = three, 86%, n = 3; GS = four, 83%, n = 4; GS = five/six, 50%, n = 4; GS = seven/eight, 75%, n = 3; GS = nine/ten, 67%, n = 6, GS greater than eleven, 60%, n = 5; Total n = 29. Hatching success was not determined for all nests due to the sensitivity of choughs at this time. However, hatching success is not dependent on group size.

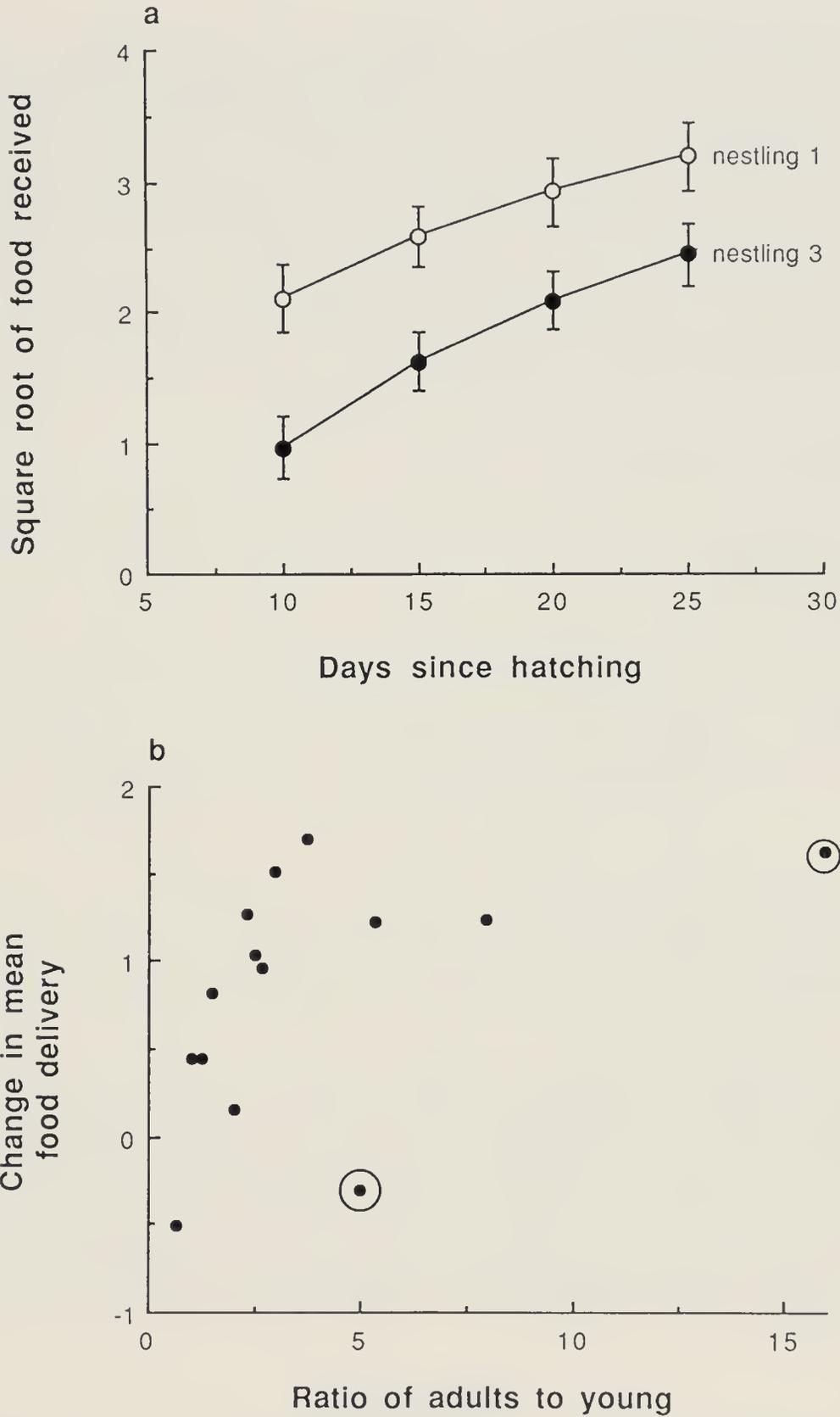


FIGURE 3 - a. Predictions of a statistical model of the square root of food received by nestlings hatched first and third in the brood when ratio of adults to young is held constant at three. The number of food items received per 100 minute interval by individual nestlings was regressed against multiple explanatory variables including days since hatching, ratio of adults to young, hatch order (one to four), and all interactive combinations of these variables. The regression equation is given in the text.

b. The effect of ratio of adults to young on mean food delivery to nestlings. The effects of 14 ratios (r_i) on the mean (intercept) of the multiple regression are plotted. Except for two outliers (circled), food received by nestlings increases linearly with ratio. Most ratios of adults to young in choughs are less than five; in particular, the value for ratio of sixteen to one is very unusual.

Food received by nestlings

The number of food items received per 100 minute interval by individual nestlings was regressed against multiple explanatory variables including ratio of adults to young, days since hatching (of first nestling), hatch order, and all interactive combinations of these variables. Ratio of adults to young was used as a measure of group size which accounted for random variation in clutch size. This value was obtained using the number of nestlings alive at the first observation session (i.e. one week after hatching). For the purposes of this study, adults are all fully grown birds which contributed to feeding young. Ratio of adults to young and hatch order were incorporated as both factors and variates to obtain the best fit. Data for food received by nestlings were Poisson distributed, requiring a square root transformation. The relationship between square root of food received and days since hatching was linearized by taking logarithms of days since hatching.

All variables significantly improved the regression with the following model of best fit and variance ratios:

$$\sqrt{\text{food}} = -0.51 + r_i - 1.05 (\text{nestling}) + 0.96 (\text{log-time}) + 0.21 (\text{nestling.log-time}) \dots 1$$

where $\sqrt{\text{food}}$ = square root of food items received by an individual nestling per 100 minutes

r_i = an additive component for the covariate ratio with 14 increasing ratios of adults to young ($F_{13,284} = 21.3, P < 0.001$)

nestling = the hatch order, one to four, of the nestling within the brood ($F_{1,284} = 178.2, P < 0.001$)

log-time = logarithm of days since hatching ($F_{1,284} = 387.0, P < 0.001$)

nestling.log-time = the interaction between hatch order and log days since hatching ($F_{1,284} = 8.7, P < 0.005$)

The amount of food received by a nestling is therefore negatively dependent on the hatch order, but positively dependent on the ratio of adults to young, the number of days since hatching, and the interaction between hatch order and days since hatching. The trends of equation one are illustrated in Figure 3a by computer predictions generated by GENSTAT. This shows the food rewards received by nestlings one and three in the hatch sequence when ratio of adults to young is held constant. Changes in the mean food delivery caused by 14 values of r_i are shown in Figure 3b.

DISCUSSION

Breeding success increases with each additional helper across group sizes ranging from two to fifteen individuals (Figure 1). This is not a reflection of local conditions as very similar results were obtained by Rowley (1978) at another site 30 km to the north-east. Similarly, choughs occur in low densities and are not territorial (Heinsohn 1988), so production of young is unlikely to reflect varying quality of nesting sites between large and small groups.

The sample size for pairs in Rowley's data ($n=2$) was too small to state conclusively that pairs could not breed without helpers. However, in my study, none of the additional nine pairs without helpers fledged young. Two of these pairs started breeding

with helpers but lost them after the clutch had been laid. Both members in all pairs observed were over four years of age, and thus were competent foragers (Heinsohn et al. 1988). Because individual dispersal in choughs is rare (Rowley 1978), these pairs were probably created due to the death of their helpers; there is no reason to suspect they were lacking in individual ability. Pairs with one helper also have very low success. Mean fledging success increases to above one young per breeding episode when a second helper is present. Because hatching success does not vary with group size, these results reflect processes only occurring during the nestling period. Attrition of nestlings is common in choughs, but in large groups is confined to the first two weeks after hatching (Figure 2). By contrast, small groups lost young throughout the nesting period, and pairs were unable to sustain even a single young.

Statistical modelling showed that the amount of food received by a nestling increases over time but decreases with hatch order, one to four, in the brood (Figure 3a). Across all group sizes, the youngest (and hence smallest) nestling was most likely to die (43 of 56 deaths). Nestlings in groups with lower ratios of adults to young receive less food (Figure 3b). The inability of pairs to raise young appears directly related to their inability to provide sufficient food. An important advantage of fitting models with multiple explanatory variables is recognition of interactions between variables. In nature, independent variables may act in concert to produce an effect, as identified by the interaction between hatch order (nestling) and log-time. Similarly, the presence of outliers in Figure 3b illustrates that apparently continuous variables may have better explanatory power if incorporated as qualitative factors.

These results have a number of important implications. Although pairs of other birds occasionally have quite low success (Rabenold 1984, Monaghan 1989), and some birds virtually always breed in groups (Brown 1987), this is the first direct demonstration of obligate cooperative breeding in birds. My data isolate the probable cause of nestling attrition in small groups as starvation. The hypothesis that extra food from helpers augments growth or survival of nestlings has only been supported by a few studies (Brown 1987). This is the most extreme example of the importance of helper contributions to nestling survival. Further, the results support Lack's (1947) brood reduction hypothesis for the evolution of hatching asynchrony, which argues that asynchrony promotes efficient use of resources when food is scarce. Because food availability is determined by helper number, choughs may be excellent study organisms for further investigation of this hypothesis. Only one other study (Dyer & Fry 1980) has linked survival of later hatched young to helper number, but not to this extreme.

Young individuals may be constrained from dispersing and attempting independent reproduction due to the impossibility of raising young without help (Rabenold 1984). Consequently, dispersal may only be worthwhile if individuals can be sure of finding others with which to form breeding units. Individuals may only benefit from dispersal if they have attained sufficient body condition and age to make dominance within their new breeding groups likely. Individual dispersal in choughs is virtually unknown (Rowley 1978). Instead, groups consisting of parents with multiple cohorts of offspring tend to fragment, often into mother-offspring units, and reform. This usually occurs after the groups have grown very large (over twelve individuals), having been cohesive units for many years (Rowley 1978).

Juvenile choughs require four years to achieve foraging skills (Heinsohn et al. 1988), yet even then adult pairs cannot breed unaided. Collectively, these are the clearest demonstration of the "skill hypothesis" (Lack 1954) for cooperative breeding, and suggest that the evolution of delayed maturity and cooperation in choughs has followed a radically different path to that commonly proposed for facultative cooperative breeders (Woolfenden & Fitzpatrick 1984, Brown 1987, Koenig & Mumme 1987).

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HELPING BEHAVIOUR IN THE FLORIDA SCRUB JAY: NONAPTATION, EXAPTATION, OR ADAPTATION?

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ABSTRACT. Experimental removal of nonbreeding helpers in the cooperatively breeding Florida Scrub Jay *Aphelocoma c. coerulescens* shows that helpers significantly enhance the reproductive success of breeders in two ways. First, by performing sentinel behaviour around nests and mobbing potential predators, helpers reduce predation on nestlings. Second, by feeding dependent young, helpers enhance nestling growth rates and post-fledging survival. Following the terminology suggested by Gould & Vrba (1982), these results indicate that helping behaviour in the Florida Scrub Jay is probably not a selectively neutral *nonaptation*. They do not, however, discriminate between two alternative hypotheses: that helping is an *adaptation* (a trait built by natural selection acting on heritable variation in that trait), or an *exaptation* (a trait that now enhances fitness but that was not built by natural selection for its current role). These findings are discussed in relation to recent critiques of the “functional” approach to the study of helping behaviour.

Keywords: Florida Scrub Jay, *Aphelocoma c. coerulescens*, helping behaviour, cooperative breeding, adaptation, exaptation.

INTRODUCTION

Cooperatively breeding birds are characterized by the presence of helpers: individuals that show parent-like (alloparental) behaviour toward young other than their own genetic offspring. Because it involves apparently altruistic behaviour in the absence of parent-offspring relatedness, helping presents something of an evolutionary paradox. Accordingly, a significant proportion of the literature on cooperatively breeding birds is devoted to the search for adaptive explanations for alloparental behaviour, and an exploration of the possible ways in which individuals might enhance their direct or indirect fitness by acting as helpers (reviewed by Brown 1987).

This adaptive or “functional” approach to the study of helping behaviour, however, has been subjected to some criticism, most recently and notably by Jamieson & Craig (1987) and Jamieson (1989). Their critique has two basic components: (1) *Confounding variables* — Many studies that purport to demonstrate an adaptive or selective value of helping are flawed in that they do not control adequately for the confounding effects of correlated traits. In such cases, it is not clear that helping behaviour per se (the care and provisioning of young other than one’s own offspring) has any selective value independent of the effects of correlated behavioural traits (e.g. delayed dispersal; Jamieson 1989, pp. 400-401); (2) *Evolutionary origin vs. current utility* — Even in cases where helping behaviour appears to be selectively beneficial, its current usefulness does not necessarily constitute evidence of an adaptive evolutionary origin through natural selection (Jamieson 1989, p. 398). This is the well-known fallacy of equating current utility with reasons of historical origin (Williams 1966, Gould & Vrba 1982, Sherman 1988).

A useful way to view the criticisms of Jamieson & Craig is through the terminology suggested by Gould & Vrba (1982). First, because of the problem of correlated traits, Jamieson & Craig suggest that helping behaviour may be selectively inconsequential; that is, it may be a *nonaptation* rather than a selectively beneficial *aptation* (Gould & Vrba 1982). Nonaptive traits may persist in a population because of natural selection acting on correlated characters, developmental or phylogenetic constraints, genetic drift, or other reasons.

The question of whether helping is nonaptive or aptive can be resolved in relatively straightforward fashion through well-controlled experiments. Helping behaviour can be considered to be an aptation if it can be shown that it does produce some measurable phenotypic selective benefit, and that this benefit is not due to the effects of uncontrolled correlated traits.

Depending on their evolutionary origins, however, aptations can be of two types (Gould & Vrba 1982): *adaptations*, characters that are built for their current role by natural selection acting on heritable variation in that character, and *exaptations*, traits that evolved for other reasons (e.g. selection on correlated characters, developmental constraints, etc.) but that now have selective value in an entirely different context.

The distinction between adaptation and exaptation lies at the heart of the second major criticism leveled by Jamieson & Craig. They propose that helping in many cases is a nonaptive or exaptive consequence of group living and the same stimulus-response mechanism responsible for the provisioning of offspring by parents and, in cases of brood parasitism, the feeding of parasites by hosts. Jamieson & Craig in fact advocate "a complete departure from 'increased fitness'-type arguments" to explain helping behaviour (Jamieson & Craig 1987, p. 92).

In this paper I present an experimental analysis of helping behaviour in the cooperatively breeding Florida Scrub Jay *Aphelocoma c. coerulescens* (Woolfenden & Fitzpatrick 1984). I address two questions, each reflecting one of the two major criticisms offered by Jamieson & Craig. First, is helping behaviour in the Florida Scrub Jay aptive or nonaptive? Second, if it is selectively advantageous (aptive), can it be determined whether helping in this species is an evolved adaptation or simply an exaptive consequence of group living?

These questions are particularly pertinent for the Florida Scrub Jay. In this species, breeding pairs that are assisted by nonbreeding helpers have significantly greater reproductive success than do pairs without helpers. However, when potentially confounding variables such as territory quality and prior breeding experience are analytically controlled, the effect of helpers on reproduction is smaller and statistically non-significant (Woolfenden & Fitzpatrick 1984, Table 8.6). Furthermore, the analyses of Woolfenden & Fitzpatrick (1984) indicate that if helpers do enhance reproductive success in the Florida Scrub Jay, they do so primarily by reducing nest predation. This suggests the possibility that the provisioning of nestlings by helpers is in fact a selectively inconsequential nonaptation (Woolfenden & Fitzpatrick 1984, p. 345). These uncertainties regarding the selective value of helping behaviour can be unambiguously resolved only through careful experimentation.

The papers of Jamieson & Craig (1987) and Jamieson (1989) have stimulated considerable debate (e.g., Ligon & Stacey 1989, Koenig & Mumme 1990). Although

important scientific issues lie at the heart of the disagreement, some of the controversy has resulted simply from semantic misunderstandings; biologists are not in general agreement concerning the usage of terms such as "adaptation" and "function" (Gould & Vrba 1982). In order to minimize semantic confusion, I will adhere rigorously to the terminology suggested by Gould & Vrba (1982) and use the terms aptation, exaptation, and adaptation as defined above.

METHODS

The study was performed at Archbold Biological Station in Highlands County, Florida, USA. Archbold has been the site of a long-term study of the demography of the Florida Scrub Jay, and experiments described here were conducted on a colour-banded population of jays adjacent to the main study population of Woolfenden & Fitzpatrick (1984).

Florida Scrub Jays are permanently territorial and permanently monogamous cooperative breeders. About half of all breeding pairs share their territories with 1-5 nonbreeders that are typically offspring of previous breeding seasons. Nonbreeders assist the breeding pair by helping to defend the group territory, feeding nestlings and fledglings, and mobbing potential nest predators. For additional background information, see Woolfenden & Fitzpatrick (1984, 1990).

Prior to the initiation of nesting activities in 1987, eight of 20 families containing one-four nonbreeders (potential helpers) were chosen at random for experimental removal. All nonbreeders from these eight groups were captured in baited traps or mist nets and maintained in captivity until the end of the nesting season, at which time they were released on their original territories. This experiment was repeated in 1988 when four of 13 families containing nonbreeders were randomly selected as experimental groups. During 1988, data were also collected on four groups where "natural" helper removals had occurred. These were families consisting of experienced and previously successful pairs whose nonbreeding helpers disappeared or emigrated immediately prior to the 1988 breeding season. This yielded a total sample of 16 experimental groups and 21 unmanipulated control groups for comparisons of reproductive success and behaviour.

RESULTS

Reproductive success

Experimental removal of nonbreeders significantly reduced the reproductive success of Florida Scrub Jays (Figure 1). Because the experimental approach used in this study controlled for potentially confounding variables such as territory quality or previous breeding experience, this difference between experimental and control groups must be attributed to the removal of nonbreeders. Nonetheless, the data shown in Figure 1 do not allow one to conclude that reproductive output was enhanced because of helping behaviour per se; the increased reproductive success might have resulted merely from the benefits of living in social units rather than from the benefits of helping behaviour itself (Koenig & Mumme 1990). Thus, data on reproductive success alone cannot reject the hypothesis that helping behaviour per se is selectively neutral. An

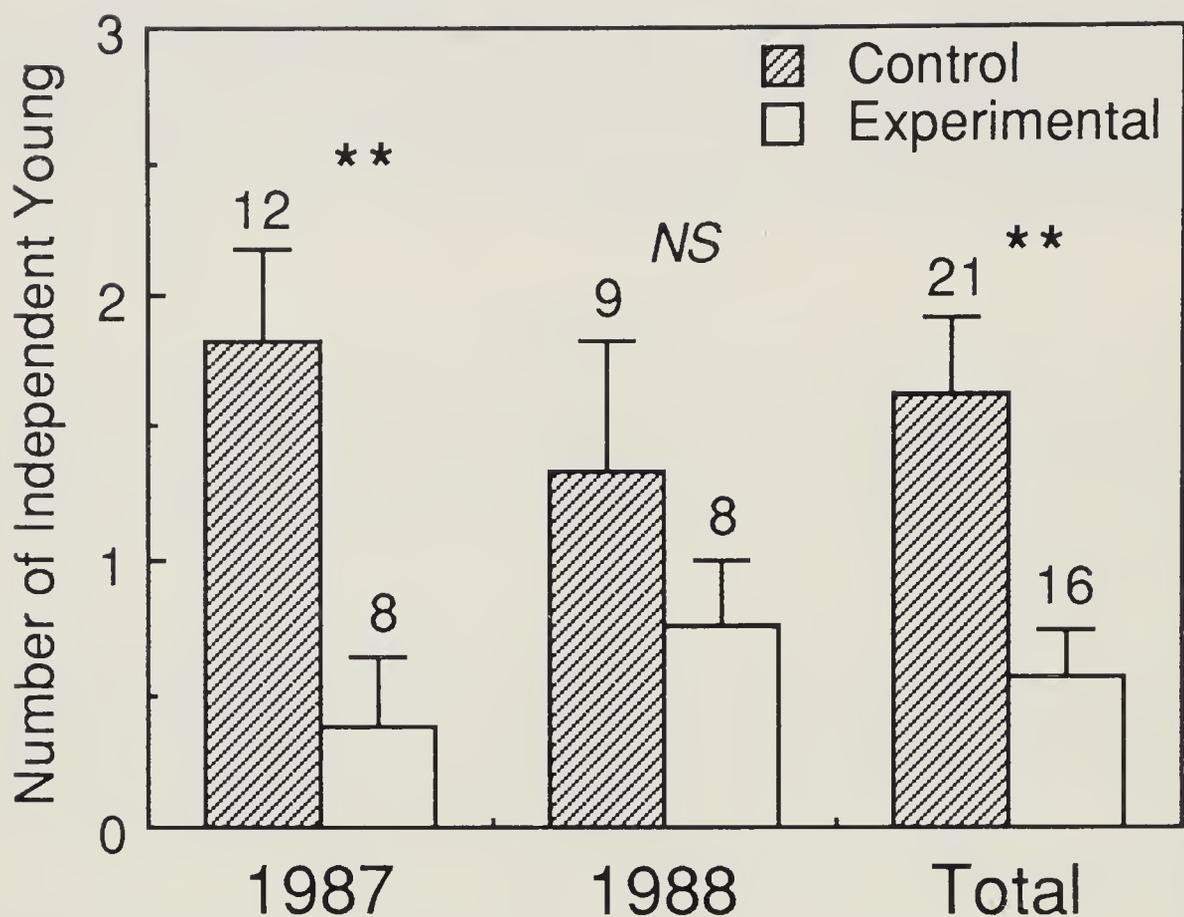


FIGURE 1 - Reproductive success (number of independent offspring produced) in control (helpers present) and experimental (helpers removed) groups of Florida Scrub Jays. Mean, standard error, and sample sizes are shown. ** $P < 0.01$; NS, not significant by one-tailed Mann-Whitney U-Test.

analysis of the mechanism by which nonbreeders increased reproductive success is required (Brown & Brown 1981). Such an analysis, described below, shows that nonbreeding helpers increased reproductive success in two ways: (1) helpers reduced the incidence of predation on nestlings, and (2) helpers enhanced post-fledging survival of juveniles.

Predation on nestlings

Nonbreeding helpers significantly increased fledging success in one year of the two-year study. In 1987, unmanipulated control groups fledged an average of 2.25 young compared with 1.18 young for experimental groups ($P < 0.05$). This difference in fledging success resulted not from differences in the number of nesting attempts, clutch size, hatching success, or nestling starvation, but from differences in predation rates on nestlings; 63.3% of nestlings in experimental groups disappeared as a result of apparent nest predation, compared with 32.5% of nestlings from control groups.

Most predation on Florida Scrub Jay nests occurs during daylight hours (Schaub 1990), and nonbreeding helpers appeared to reduce the incidence of diurnal nest predation in two ways. First, helpers significantly improved "sentinel" behaviour around nests (see McGowan & Woolfenden 1989). At least one adult was observed on sentinel within 20 m of the nest 35.9% of the time in groups with helpers ($n = 8$), compared with 13.8% of the time in groups without helpers ($n = 14$). Second, helpers significantly improved nest defense (Francis et al. 1989); when a live snake was placed near a nest containing young nestlings, groups with helpers mobbed the snake significantly more vigorously than did groups lacking helpers (unpublished data).

Survival of fledglings

During both years of the study, nonbreeders significantly increased the survival of young from fledging to early independence (day 60). Post-fledging survival was 77.3% ($n = 44$) in unmanipulated control groups but only 39.1% ($n = 23$) in experimental groups where nonbreeding helpers had been removed ($P < 0.01$). Although the factors responsible for this difference in post-fledging survival are not entirely clear, the difference appears to be at least partially attributable to the food that young received as nestlings. Ten-day-old nestlings were fed an average of 2.7 ± 0.5 times per hour ($x \pm SD$) when helpers were present ($n = 8$ nests) compared with 1.8 ± 0.5 times per hour when helpers were absent ($n = 14$ nests; one-tailed Mann-Whitney U-Test $P < 0.01$). Although this additional food did not significantly reduce the low incidence of nestling starvation and brood reduction, it did significantly enhance nestling growth rates. By the time they were 11 days old, nestlings that had been fed by the breeding pair and by one or more nonbreeding helpers averaged 5.6 g greater in mass than nestlings attended by the breeders only. Furthermore, 77.8% ($n = 36$) of nestlings that were at or above mean nestling mass on day 11 survived to independence, compared with only 40.7% ($n = 27$) of below-average nestlings (Chi-square $P < 0.01$). Similar results were obtained in a within-brood analysis; within individual broods, larger nestlings were more likely to survive to independence than were their smaller brood-mates.

Relationship of provisioning behaviour to anti-predator behaviour

As described above, nonbreeding helpers enhanced reproductive success in the Florida Scrub Jay by performing anti-predator behaviour around nests (including sentinel behaviour and mobbing of nest predators), and by feeding dependent young. My results also indicate that these two forms of alloparental care are strongly correlated with one another. Nonbreeders that provided little or no food to 10-day-old nestlings spent less than 1% of their daylight hours on sentinel near the nest ($n = 9$ nonbreeders), compared with about 11% for nonbreeders that actively provisioned nestlings ($n = 13$ nonbreeders). Similarly, among nonbreeders that rarely or never fed nestlings, only 20% ($n = 5$) did more than scold from a safe distance when a live snake was placed near a nest containing young nestlings (unpublished data). In contrast, 81% ($n = 16$) of active helpers approached to within striking distance or delivered pecks to a snake placed near the nest. These results indicate that helper contributions to provisioning nestlings, performing sentinel behaviour near nests, and mobbing of potential nest predators should not be viewed as independent traits, but as part of the complex of behaviours that comprise alloparental care.

DISCUSSION

Is helping nonaptive, exaptive, or adaptive?

Experimental removal of nonbreeding helpers indicates that helping behaviour in the Florida Scrub Jay is unlikely to be selectively inconsequential, at least not to the recipient breeders. First, by performing sentinel behaviour around nests and by mobbing potential nest predators, helpers reduce predation on nestlings. Second, by enhancing food delivery to dependent young, helpers increase nestling growth rates and post-fledging survival. The experimental and analytical methods employed in this study indicate that these effects of helpers on reproduction are attributable to alloparental care itself and not to potentially correlated variables such as territory

quality, prior experience of the resident breeders, or incidental beneficial effects of social living.

Thus, Florida Scrub Jay breeders (and their offspring) clearly benefit from the alloparental care that helpers provide. Furthermore, because Florida Scrub Jay helpers nearly always assist close relatives (Woolfenden & Fitzpatrick 1984), alloparental care has selective consequences for the helpers as well; by increasing the reproductive success of nondescendent kin, helpers enhance the indirect component of their inclusive fitness (Brown 1987). Some helpers may also derive more direct benefits from helping. For example, by helping to rear siblings and increasing group size, older male helpers can enhance their prospects of becoming breeders through the process of territorial inheritance and "budding" (Woolfenden & Fitzpatrick 1986).

We can therefore reject the hypothesis that helping behaviour in the Florida Scrub Jay is a selectively inconsequential nonadaptation. Regardless of the reasons "why" helpers might direct alloparental care toward the offspring of nondescendent kin, helping behaviour increases the helper's inclusive fitness (Brown 1987). This conclusion, however, establishes only that helping behaviour is an adaptation, a trait that has current selective utility (Gould & Vrba 1982). It does not tell us whether helping behaviour arose as an evolved adaptation, or merely (as hypothesized by Jamieson & Craig [1987] and Jamieson [1989]) as an exaptive consequence of group living and the same stimulus response mechanism responsible for parental care.

Distinguishing between these adaptive and exaptive alternatives, however, is exceedingly difficult. Although rigorous analyses of developmental, neurophysiological, and phylogenetic aspects of helping behaviour could help resolve this issue (Jamieson 1989), such analyses would probably not produce completely unambiguous results. For example, complex adaptive traits such as helping may in many cases originate via an initial primary exaptation that is subsequently "fine-tuned" by secondary adaptations (Gould & Vrba 1982, Ligon & Stacey 1989, Koenig & Mumme 1990). In such instances, any attempt to classify helping as either exaptive or adaptive would be misleading.

Finally, it should be noted that although the distinction between exaptation and adaptation is important to researchers whose goal is to unravel the evolutionary origins of traits, it is less relevant to evolutionary biologists interested in the potential impact of natural selection acting on existing phenotypic variation (e.g. Lande & Arnold 1983). This point was well recognized by Gould & Vrba (1982), who concluded their paper by emphasizing that the concept of exaptation "is not anti-selectionist . . . The main theme is, after all, cooptability for *fitness* [emphasis theirs]. Exaptations are vital components of any organism's success."

Conclusion: a plea for pluralism

Jamieson & Craig (1987) and Jamieson (1989) provide a useful critique of the "functional" approach to the study of helping behaviour. First, their criticisms reveal that many adaptive explanations that have been advanced for helping lack appropriate scientific rigour and do not explicitly consider nonadaptive or exaptive alternatives. Furthermore, the predominance of adaptive and selective approaches to helping behaviour has meant that our understanding of the phenomenon at other levels of analysis is very limited. The time is now ripe for innovative experimental explorations of the

genetics, development, neurophysiology, and neuroendocrinology of helping behaviour. When combined with careful phylogenetic analyses, such studies will significantly broaden our perspective of helping behaviour beyond its current effect on fitness. The critiques of Jamieson & Craig will be useful to the extent that they encourage this broadening of perspective.

On the other hand, Jamieson & Craig (1987, p. 92) have carried their arguments to the opposite extreme by advocating "a complete departure from 'increased fitness'-type arguments to explain the occurrence of so-called helping behavior." The nonaptive or exaptive explanation that they propose, that helping is a manifestation of the same stimulus-response mechanism responsible for parental care, is a plausible, testable explanation of helping behaviour as a physiological process. But their stimulus-response hypothesis is consistent with other nonaptive, exaptive, and adaptive explanations of helping as well. The specific stimulus-response hypothesis proposed by Jamieson & Craig does not compete with hypotheses concerning evolutionary origins and current utility (Sherman 1988, Koenig & Mumme 1990). Furthermore, if we were to take the path advocated by Jamieson & Craig and ignore the potential selective consequences of helping, we would in effect be abandoning the Darwinian approach to animal behaviour. Because this approach can lead to significant insight and understanding when carefully and rigorously applied (e.g. Alcock 1989), we would be ill-advised to abandon it altogether.

What is needed instead is a more pluralistic approach. It is important to realize that helping behaviour, like all biological problems, can profitably be addressed from multiple perspectives and many different levels of analysis, no one of which is inherently superior to any other (Sherman 1988). In fact, the ideal procedure would be to attack the problem of helping behaviour simultaneously from several different levels of analysis (see, for example, Holekamp & Sherman 1989). Only through rigorous examination of helping from several different levels of analysis will we achieve a thorough understanding of this behaviour.

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INFLUENCE OF TERRITORY QUALITY AND HABITAT SATURATION ON DISPERSAL OPTIONS IN THE SEYCHELLES WARBLER: AN EXPERIMENTAL TEST OF THE HABITAT SATURATION HYPOTHESIS FOR COOPERATIVE BREEDING

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ABSTRACT. As at 1988 the only population of the Seychelles Warbler *Acrocephalus sechellensis* was on Cousin Island (29 ha), where cooperative breeding is common. To enhance the security of this endangered species, 29 warblers were transferred to the unoccupied island Aride (68 ha) in September 1988. This transfer showed that cooperative breeding arises when an ecological constraint, here habitat saturation, inhibits breeding by young birds that would otherwise disperse. All 16 vacancies on Cousin created by removals were filled immediately, some within hours, by previous helping and/or one-year-old birds. All 61 young hatched on Aride left their natal territories when four months old, eight weeks after reaching independence; none has acted as a helper and all birds paired and established territories of their own within one year.

Keywords: Seychelles Warbler, territory quality, habitat saturation, cooperative breeding, lifetime fitness, direct fitness, indirect fitness, dispersal, transfer, vacancy.

INTRODUCTION

The Seychelles Warbler *Acrocephalus sechellensis* Oustalet, 1877, is known only from the Seychelles Islands, where in 1870 it was recorded on Marianne and Cousin Islands, but disappeared from the former with clearance of the forest during the late 19th century, leaving the species restricted entirely to Cousin (29 ha). In 1959 only about 30 birds survived (Crook 1960) and in order to prevent their extinction, Cousin Island was purchased for the International Council for Bird Preservation in 1968, who have managed the island as a nature reserve, increasing suitable habitat for the warbler by allowing native woodland to recover. This has led to a spectacular recovery in numbers, the population rising to nearly 360 birds in 1982 (Bathe & Bathe 1982). Since then, the population has fluctuated around an average of 400 birds, suggesting that this is the maximum carrying capacity of the island and the habitat seems to be saturated.

Cooperative breeding was first observed in 1973, only in a few very rich territories (Diamond 1980), but since 1982 it has been widely observed all over the island, as the population reached its maximum level. It seems that habitat saturation was the main cause of this phenomenon and this paper examines why young warblers stay in their natal territories or disperse, in the light of data obtained from the transfer of 29 individuals from Cousin to the unoccupied Aride Island (68 ha), which is run and owned by the Royal Society for Nature Conservation.

STUDY POPULATION AND METHODS

The data included in this paper were collected between January 1986 and March 1990 as part of a continuing study of Seychelles Warblers. All 115-123 groups (350-400 birds) have been studied since January 1986 on Cousin Island and 13-21 groups (29-90 birds) on Aride Island since the transfer took place in September 1988 (Figure 1). All territories were occupied continuously throughout the study, during which 327 birds were individually colour-ringed, 273 as nestlings.

To follow breeding activity and cooperative breeding all territories both on Cousin and on Aride were checked fortnightly for active nests and presence of colour-ringed birds, the latter to determine the proportion of helpers and breeders that die and those that survive to breed in another territory. A total of three hours' observation of nest-building, incubation and feeding young (the latter every three weeks) was made in each territory.

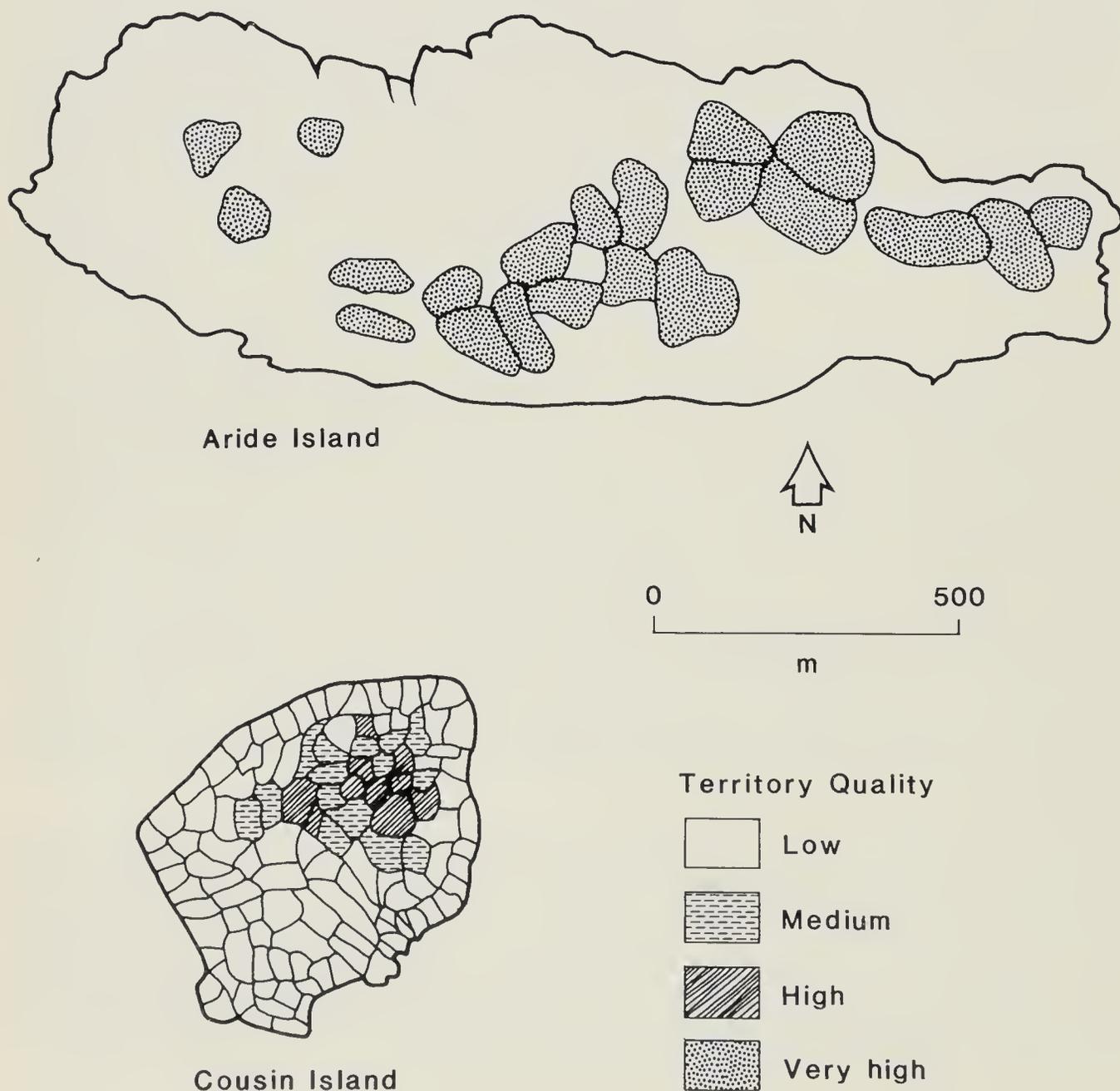


FIGURE 1- Seychelles Warbler territories as at March 1990 on Cousin and Aride Islands (shading indicates: lqt = low, mqt = medium, hqt = high and vhqt = very high quality territories, found only on Aride).

As the Seychelles Warbler is insectivorous, taking 98 % of its insect food from leaves, territory quality (tq) was calculated from three measures: mean yearly territory size (a), mean foliage cover for plant species y (c_y) according to the transect method (Komdeur 1988), and mean insect totals for plant species y per square decimetre leaf area (i_y). Territory quality can be expressed in terms of mean insect number available by the following equation:

$$tq = a \sum_y c_y i_y \quad (1)$$

Territories on Cousin were divided into three categories (Figure 1): low quality territories (abbreviated lqt; $tq = 0-1500$), medium quality territories (mqt; $tq = 1500-3000$), and high quality territories (hqt; $tq = 3000-4500$).

RESULTS

Cooperative breeding in the Seychelles Warbler on Cousin Island

Cooperative breeding is characterised by the presence in a social group of one or more nonbreeding individuals that act as helpers and provide care to young that are not their own offspring. In the Seychelles Warbler such helpers share in virtually all aspects of nesting: nest-building, incubation (only females), feeding nestlings, and tending and defending fledglings during the three month transition to independence (Komdeur 1988). Virtually all helpers are grown offspring of both breeders (98%; $n = 69$). On Cousin groups averaged 2.9 birds, but ranged from two to 12 individuals. Seychelles Warblers also exhibit joint-nesting, a system of nesting in which two or more females (mostly mothers and daughters) lay their eggs in the same nest.

The effect of territory quality and number of helpers on reproductive success on Cousin Island

Seychelles Warbler pairs occupying high quality territories (hqt) fledged more young per year than pairs of lower quality territories, producing an average of 1.6 as many young per year (Table 1). Reproductive success (mean yearly number of fledglings reaching one year old) is even higher in high quality territories, on average 2.8 as high as that in lower quality territories (Table 1).

TABLE 1 - Effect of territory quality on breeding success on Cousin Island (\pm standard deviation). (Numbers in parentheses are bird-years based on colour-ringed individuals; a pair consists of one male and one female.)

terr. qual. cat.	quality	n*	mean no. of young fledged per pair	mean repr. success per pair	mean repr. success per group (V):
low	0-1500	365	0.65 ± 0.12 (286)	0.19 ± 0.12 (286)	0.22 ± 0.13
medium	1500-3000	60	0.84 ± 0.18 (38)	0.51 ± 0.19 (38)	0.85 ± 0.21
high	3000-4500	55	1.21 ± 0.32 (28)	0.98 ± 0.41 (28)	1.27 ± 0.36

* number of territory years

In the Seychelles Warblers, the curve that relates reproductive success in a unit to the number of helpers in the unit shows a step function (Figure 2). One helper added to a pair of warblers occupying low, medium and high quality territories was associated with 1.2, 2.8 and 1.3 as many fledglings as unaided pairs, which corresponds with 0.10, 1.54 and 0.35 additional juveniles per helper respectively. The effect of a helper is more outstanding when considering the mean number of fledglings reaching one year of age: reproductive success of groups with one helper is 1.6, 3.0 and 1.6 as many as that of unaided pairs for lqt, mqt and hqt respectively, which corresponds with 0.12, 1.00 and 0.58 yearlings per helper. A second helper apparently decreased reproductive success of groups occupying lqt and mqt, but produced 2.8 as many yearlings as groups with one helper of hqt. This corresponds with - 0.04, 0.27 and 0.51 yearlings per helper. A third helper was apparently of negative effect on reproductive success of all social units. More helpers can be of negative effect on reproductive success as, due to the joint-nesting system, more young per territory can be produced. A twin or triplet is fed less than a single young and therefore not only weighed less than singles, but also less than adults (mean weight of adult and singles, twin and triplet [at fledging age] is 16.0, 18.0, 14.0 and 10.0 grams respectively). Fewer twins than singles reached independence (12% vs. 26%) and all triplets died before independence (Komdeur 1988).

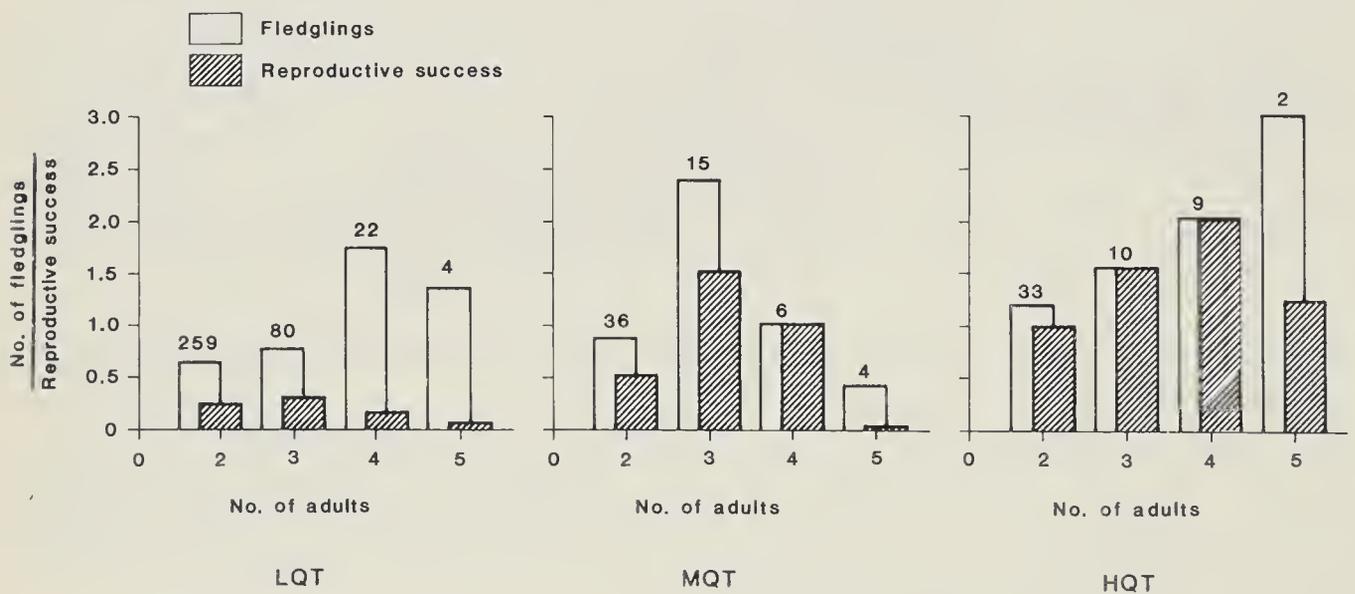


FIGURE 2 - Mean annual production of fledged young and mean reproductive success (= mean number of fledglings reaching one year old) in social units of the Seychelles Warbler in low (lqt), medium (mqt) and high quality (hqt) territories on Cousin Island (number of adults = the breeding pair plus their helpers; n = number of territory years).

Territory quality on Cousin Island and the fitness consequences of dispersal

First year survival (the probability of surviving to one year old) and annual adult survival (the probability of surviving to the next year, starting at one year old) increases with territory quality (Table 2). Both immatures and adults had a higher probability of surviving to the next year if they lived in hqt than if they occupied lower quality territories. Mean adult life expectancy (the length of time after which 50% of the population alive at one year will have died) is therefore also correlated with territory quality (Table 2). Once a warbler has reached one year old it might expect to live for 7.4 years in high quality territories but only 2.7 years in low quality territories.

TABLE 2 - Effect of territory quality on Cousin Island on mean group size, first year and annual adult survival (= the probability of surviving to 1 year old and to the next year starting at age of 1 year old, respectively) and mean adult life expectancy (\pm standard deviation). (For number of territory years see Table 1; number in parentheses are bird years based on colour-ringed individuals.)

terr. qual. cat.	mean group size	first year* survival (s)	annual adult* survival (s)	mean adult life expectancy (z)
low	2.4 \pm 0.21	0.30 (103)	0.76 (156)	2.7
medium	2.9 \pm 0.91	0.67 (23)	0.88 (64)	5.4
high	3.7 \pm 0.93	0.86 (22)	0.91 (48)	7.4

* survival $s = (b/a)^{12/n}$ where: a = number of ringed birds present in year y; b = number of ringed birds still present in year y+1; n = number of months between counts in year y and y year y+1

High quality territories tend to be more continuously occupied than lower quality territories. Of 65 vacancies, 59% were lqt, 30% mqt and only 11% were hqt. Young warblers therefore are not faced simply with the problem of either dispersing or remaining. The options usually are either to fill a vacancy in a low quality territory, where the probability of immediate breeding is higher, or to remain as a non-breeder in a higher quality territory. Because territory quality affects reproductive success as well as survival rates, lifetime payoffs from either dispersing or remaining philopatric have to be considered for each territory category.

The lifetime fitness realised by dispersing and breeding independently in year a (direct component of inclusive fitness) is given by:

$$\sum_{x=a+1}^z p V_x r_{hy} \tag{2}$$

where z is mean adult life expectancy, p is the probability of successful dispersal and establishment as a breeder, V_x is the number of yearlings produced at age x, and r_{hy} is the coefficient of relatedness between helper h (now a breeder) and its own young. Warblers disperse only once; out of 224 ringed adults, only 1% dispersed more than once, and when they fill a vacancy, immediate breeding status is always acquired (n = 65).

Nonbreeding helpers can also gain indirect fitness benefits through the reproduction of relatives. The lifetime fitness realised by helping (indirect component of inclusive fitness) can be estimated as:

$$\sum_{x=a+1}^z (V_n - V_{n-1})_x r_{hby} \tag{3}$$

where $(V_n - V_{n-1})_x$ is the mean increase in yearlings produced per year for each change in group size, weighted by the number of groups of that size observed during the study period, and r_{hby} is the coefficient of relatedness between the helper h and the young (of the breeder b) it helps to rear. In Seychelles Warblers 98% of all helpers (n = 69) were grown offspring of both breeders ($r_{hby} = 0.50$).

Direct fitness benefits (2) together with indirect fitness benefits (3) yield the overall expected lifetime reproductive success. The expected lifetime reproductive success of yearlings that bred immediately and of helpers that delayed breeding for a variable number of years were calculated for each territory category (Table 3). The following assumptions were made:

- All individuals survived to one year old, the point at which Seychelles Warblers decide for the first time whether to disperse or remain in a group (data of Table 3 therefore do not represent mean production of potential breeders in the population, since many died before reaching one year old).
- Group size during breeding was the average for territories of that quality.
- A bird leaving its natal group was always able to breed ($p=1$).
- No breeding status was achieved by the helper within the bird's original group.

TABLE 3 - Expected lifetime inclusive fitness of yearlings in different quality territories on Cousin Island that help for different number of years before breeding (see eq. (2) and (3); Tables 1 and 2).

tq	number of years helping							
	0	1	2	3	4	5	6	7
lqt	0.30	0.22	0.15					
mqt	2.30	2.07	1.95	1.62	1.40	1.17		
hqt	4.70	4.32	3.93	3.55	3.16	2.78	2.39	2.01

A bird that helped for seven years on a high quality territory still produced 6.7 times more offspring equivalents than a bird breeding immediately in a low quality territory (2.01 vs. 0.30) and a bird could help for six years before breeding in a high quality territory and still expect to produce on average the same number of offspring equivalents as a bird that dispersed and bred at one year in a medium quality territory (2.39 vs. 2.30). Because territory quality had a significant effect on both reproductive success and survival, a one year old warbler on Cousin produced more offspring equivalents over its lifetime by remaining in a high quality territory for one or more years as a non-breeding helper and then breeding, than it could by dispersing and breeding immediately in a lower quality territory, even in the absence of habitat saturation ($p=1$). If a vacancy arose on a hqt, a helper should take it immediately (i.e. habitat saturation). If a vacancy arose on a lqt, a young bird on lqt should take the vacancy (i.e. habitat saturation had caused it to stay in its natal territory), but a young bird on good quality territory should remain in its natal territory (i.e. higher lifetime inclusive fitness). This was also shown for Acorn Woodpeckers *Melanerpes formicivorus* (Stacey & Ligon 1987).

Dispersal and occupation of natural vacancies on Cousin Island

As suggested above yearlings on Cousin are more likely to become helpers in high quality natal territories than in territories of lower quality: 92% of yearlings born in hqt became helpers ($n = 31$), 72% in mqt ($n = 18$) and only 29% in lqt ($n = 17$). The effect of territory quality on dispersal decisions was also revealed by comparing the origins of individuals that became breeders in each territory type: 89% of breeders in hqt were born in hqt ($n = 18$); for mqt and lqt this figure was 50% ($n = 22$) and 91% ($n = 23$) respectively. Both analyses indicated that birds acting as helpers in hqt are

more likely to breed eventually in those territories, than are individuals from mqt and lqt and conversely, that birds becoming breeders in lqt were almost always born there.

A transfer of Seychelles Warblers: an experimental test of the habitat saturation hypothesis for cooperative breeding

The transfer of 29 adult Seychelles Warblers to the unoccupied Aride Island (Komdeur et al. 1990) created a two-fold experimental test of the habitat saturation hypothesis for cooperative breeding. As immediate breeding benefits on a given quality territory are greater than helping benefits (Table 3), it was predicted that:

- the vacancies on Cousin, created by removals, should be filled immediately by helpers from neighbouring territories of same or lower quality.
- all young birds produced on Aride that were able to establish new territories of same (or higher) quality on the unoccupied island, should split off from the natal groups immediately after independence (i.e. cooperative breeding should not arise).

OCCUPATION OF VACANCIES ON COUSIN ISLAND. Following the transfer of birds, the vacant places on Cousin were filled immediately, some within hours. The influence of habitat saturation on dispersal follows from the fact that all vacancies ($n = 16$) were filled by previous helping and/or one-year-old birds. Two helping birds on high quality territories stopped feeding twins immediately and moved to the vacant adjacent site of the same quality, within six hours after the removal of original birds. Moreover, territory quality had an effect on dispersal: a vacancy of distinct territory quality, in the presence of an equal proportion of excess birds per territory category, was only filled by a bird from a lower, or same quality territory ($\chi^2 = 26.69$, 4 df, $P < 0.005$).

DISPERSAL OF JUVENILES ON THE UNSATURATED ARIDE ISLAND. The mean age at which Aride juveniles left their natal territories was 17.9 weeks ($n = 61$, $SD \pm 7.0$), eight weeks after reaching independence. Between the time of leaving and pair formation, young were seen wandering all over the island. Unlike young hatched on Aride, Cousin juveniles of highest quality territories (still only a twentieth of Aride territory quality) stayed in their natal territory for on average 2.4 years ($n = 31$, $SD \pm 0.5$). All 61 young hatched on Aride left their natal territories at an early age, none acted as a helper in feeding their parent's younger offspring, and all young were able to establish a territory of the same high quality as their natal territory. It is very clear that habitat saturation is the prominent reason for cooperative breeding on Cousin.

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IMPACT OF CLIMATIC VARIATION ON GALAPAGOS MOCKINGBIRD SOCIAL ORGANIZATION

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ABSTRACT. We studied cooperative breeding of *Nesomimus parvulus* over 13 years (1978-90) across a broad range of climatic conditions. Variation in annual rainfall strongly influenced demography, but had few direct effects on social behavior. Indirect effects were pronounced. The frequencies of polygyny and associated joint nesting decreased with adult sex ratio. Along with density, mate availability determined the proportion of males that bred and, secondarily, the proportion that helped. Sex ratio did not affect the proportion of females that bred, but the proportion helping decreased with availability of males because mate-sharing females most often acted as helpers. Polygyny benefits males but is usually rare because monogamous females have higher reproductive success than females sharing mates. The frequency of plural breeding varied with population age structure. By favoring flexible reproductive behavior, climatic and demographic variation ultimately accounts for the occurrence of polygyny, joint nesting, and plural breeding.

Keywords: Galapagos Mockingbirds, *Nesomimus parvulus*, cooperative breeding, mating systems, sex ratio, demography, El Niño.

INTRODUCTION

In the majority of cooperatively breeding species, most helpers are young non-breeders remaining in their natal groups. Consequently, investigators have focused on environmental and demographic factors that prevent individuals from dispersing and breeding. Why helpers help can be treated as a separate, though interdependent, question (e.g. Curry 1988a).

Despite considerable attention, ecological influences on dispersal and breeding in cooperative systems remain incompletely understood. At least eight different mechanisms have been proposed (Brown 1987: Table 5.1). Emlen (1982) argued that individuals in stable environments would be constrained mainly by the difficulty of acquiring territorial space necessary for breeding, whereas birds in variable environments would be limited by the difficulty of breeding successfully in poor years. Mate shortage (cf. Rowley 1965) could constrain breeding under either regime, especially where extrinsic factors produce sex ratio shifts.

Many environmental and demographic variables are not amenable to experimental study. Their effects nevertheless can be investigated given adequate natural variation. The Galapagos Mockingbird* *Nesomimus parvulus* on Isla Genovesa has provided an excellent opportunity to consider the impact of climatic variation on a territorial cooperative breeder. Our thirteen-year study included two droughts, two wet El Niño events, and eight years with intermediate conditions.

* Common and scientific names follow Swarth (1931)

Previously we documented relationships between climatic variation and mockingbird demography (Curry & Grant 1989). This paper further examines the impact of climatic change on mockingbird social organization. We focus on (1) direct influences of climatic conditions on social behavior, and (2) indirect effects mediated through changes in population structure, especially a shift from an excess of males to an excess of females. Female-biased sex ratios are rare in bird populations, and no previous study of a cooperative breeder has considered whether mate shortage can constrain breeding, and promote helping, by females.

METHODS

Genovesa is a small (17 km²), low island in the extreme northeast of the Galapagos. We color-banded nearly every bird in our 50-ha study area and determined sex from wing measurements and breeding behavior. Most data were collected during the usual breeding season (January-May) and early part (June-August) of the non-breeding season. We measured rainfall daily; annual totals for four years (Figure 1) are minimal estimates because additional rain is known or suspected to have fallen when we were not present.

In each year, we determined the reproductive status of all resident adults (>1 year old) and found and monitored all nests. We identified breeders by courtship behavior, nest building, and egg-laying, and conducted one-hour nest watches at two- or three-day intervals to identify helpers, defined as birds that fed nestlings or fledglings that were not their own offspring. Non-breeders did not invariably act as helpers, and some birds in plural-breeding groups (containing more than one breeding female) both helped and bred (Curry 1988a). Data from 1989 and 1990 were sufficient for estimating population parameters but not for documenting helping behavior or reproductive success.

We studied details of group structure in 1980-87 and in 1990. We classified breeding males as either dominant — including all those in singular-breeding groups, which contained only one nesting pair — or subordinate (Curry 1988b), and as either monogamous or polygynous. We classified breeding females as monogamous or mate-sharers, and categorized the latter as primary and secondary mates, depending on pairing sequence. We usually were unable to follow the fates of individual eggs from joint nests (in which multiple females laid eggs) so we assume contributing females shared parentage of fledglings equally.

Statistical tests were performed using JMP (SAS Institute Inc.). We used rank order correlation (r_s) for tests involving annual rainfall because of this variable's skewed distribution; other statistics are from parametric tests. F values are from two-way ANOVA with year as one factor, except where noted.

RESULTS

Climatic conditions and demography

Annual rainfall varied from 0 to 2408 mm (Figure 1). In most years, rain fell only during the January-April warm/wet season. In El Niño years (1983 and 1987) storms began as early as the preceding November and continued until as late as July. Most plants

were leafless throughout each annual cool/dry season and droughts. New foliage emerged soon after each year's first showers and persisted until a few weeks after the rains ended. Availability of caterpillars, often fed to nestlings, coincided with the presence of fresh vegetation (Grant & Grant 1989).

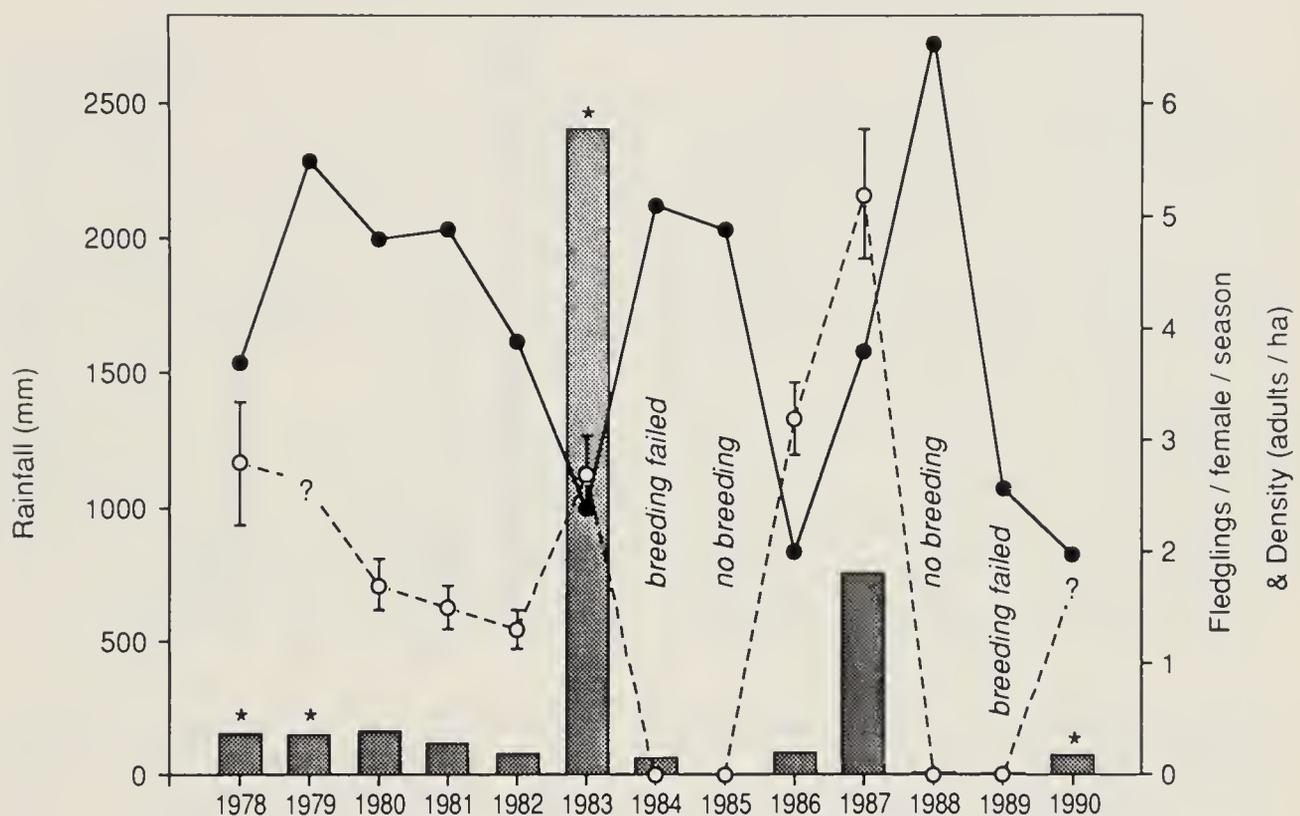


FIGURE 1 - Variation in annual rainfall, natality, and population density. Rainfall values (stippled bars) for four years (asterisks) are minimum estimates. Data on seasonal production of fledglings (open points, $x \pm SE$) in 1979 and 1990 were incomplete. In two drought years (1985 and 1988), no mockingbirds nested. In both 1984 and 1989, few pairs attempted to breed and none were successful. Moderately low adult density (solid points) in 1978 followed a drought in 1977.

Wet years were generally favorable, and dry years poor, for breeding. In most years, nesting began approximately one week after >20 mm of rain had fallen. Duration of breeding varied with rainfall: individual females produced up to six clutches in El Niño years. Natality consequently increased with total rainfall (Figure 1). Three years were extraordinary. In 1984 a moderate amount of rain (57 mm) fell, but most residents did not breed, and no nesting pairs ($N = 8$) produced independent young. In 1989 at least two pairs attempted to nest, though only 7 mm of rain fell; we suspect they failed. In both 1986 and 1989, single pairs began nesting before any rain had fallen. These unusual breeding responses may have been influenced by extreme climatic conditions in the preceding year.

Adult density increased after wet years and declined after droughts, mainly because of variation in natality (Figure 1). Survival was highest under intermediate conditions, dropping during droughts and during an epizootic associated with the 1983 El Niño (Curry & Grant 1989).

Adult sex ratio varied dramatically (Figure 2). Prior to 1983, males outnumbered females because of marginally higher survival. For unknown reasons, more males than females died in the 1982-83 epizootic. Sex ratio then increased following renewed

reproduction and higher survival of males in 1986-89, but an excess of females reemerged in 1990 when they survived better (79%) than males (66%).

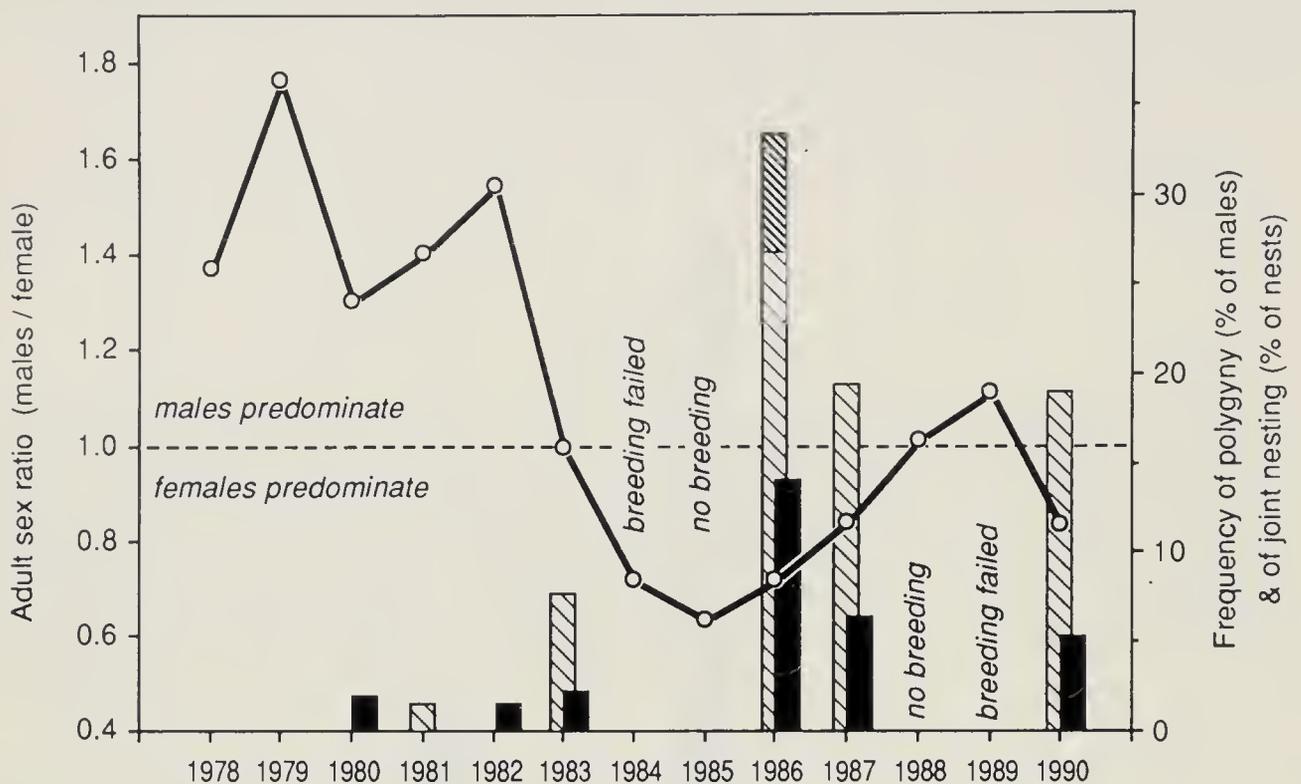


FIGURE 2 - Variation in adult sex ratio and in the frequencies of polygyny and joint nesting. Sex ratio values (open points) for 1988 and 1989 are estimates because the sex of up to 20% of residents was undetermined; sex was known for >95% of residents in other years. Frequency of polygyny is shown as the percentage of breeding males having two (light hatching) or three mates (heavy hatching). Frequency of joint nesting (black bars) is shown as a percentage of each year's nests.

Direct effects

GROUP SIZE AND STRUCTURE. Group size did not vary with annual rainfall ($r_s=0.05$, $N=11$ years, N.S.) but increased with density (Table 1) because the number of groups changed little. The proportion of yearlings dispersing from their natal territories was also independent of rainfall ($r_s=0.38$, $N=7$, N.S.), but decreased with adult density ($r_s=-0.76$, $N=7$, $P<0.05$). The impact of climatic conditions on dispersal and group size therefore appears to have been slight relative to that of competition for territorial vacancies. The frequency of plural breeding increased with annual rainfall ($r_s=0.83$, $N=7$ years, $P<0.05$), but was more strongly associated with variation in population age structure (Table 1 and below).

HELPING BEHAVIOR. Helpers attended 34% of nests ($N=450$). Nearly half (48%) of all helpers ($N=151$ helper-seasons) were non-breeding adult males. Other helpers consisted of 25% breeding males, 9% breeding females, 5% non-breeding females, 9% juvenile males, and 3% juvenile females (Curry & Grant 1990).

Prevailing climatic conditions did not directly influence helping. Neither the proportion of nests attended by helpers, nor the proportion of birds that bred, nor the proportion that helped among birds of either sex varied with annual rainfall (all $r_s<0.50$, $N=8$ years, N.S.; data from the failed 1984 and 1989 breeding seasons are excluded from these and subsequent analyses).

On average, nests attended by helpers produced 19% more fledglings than nests without helpers (Curry & Grant 1989). In a variable environment, climatic conditions might influence the efficacy of help, with helpers providing a larger benefit in poor (dry) years (Orians et al. 1977). However, the change in fledgling production attributable to helpers did not vary with rainfall ($r_s=0.08$, $N=7$ years, N.S.).

Indirect effects

MATING SYSTEM. Adult sex ratio strongly influenced the mating system (Figure 2). In 1978-82, when males outnumbered females, nearly all pairings were monogamous. (Genetic polyandry, however, may result from extra-pair copulations involving dominant males and subordinate females; Curry 1988b). In 1986 and later, when females predominated, polygyny was common, with individual males obtaining up to three mates. The proportion of males mated polygynously thus varied inversely with sex ratio (Table 1).

TABLE 1 - Correlation matrix (Pearson r) for population breeding parameters (N, maximum number of years for which data are available). Significance levels are indicated by ^a, $P<0.05$; ^b, $P<0.01$; ^c, $P<0.005$. (Parameter codes: SR, sex ratio; AD, adult density; pYg, % yearlings; GS, group size; pMB, % males breed; pMH, % males help; pFB, % females breed; pFH, % females help; pMP, % males polygynous; pGP, % groups plural.)

Code	N	AD	pYg	GS	pMB	pMH	pFB	pFH	pMP	pGP
SR	13	.28	-.17	.01	-.96 ^c	.76 ^a	-.45	-.89 ^c	-.90 ^c	-.05
AD	13	.	.65	.84 ^c	-.93 ^c	.88 ^c	-.65	-.61	-.75 ^a	.52
pYg	12		.	.77	-.19	.35	-.72	.51	-.09	.95
GS	11			.	-.77 ^a	.84 ^b	-.66	-.16	-.53	.81 ^a
pMB	9				.	-.87 ^b	.60	.78 ^a	.85 ^c	-.24
pMH	8					.	-.63	-.54	-.81 ^a	.29
pFB	9						.	.11	.23	-.74
pFH	8							.	.84 ^b	.53
pMP	9								.	-.06
pGP	9									.

Mating patterns in turn influenced the mode of nesting. Females laid eggs in separate nests in 98% of plural-breeding groups where they had different, monogamous mates ($N=59$). In contrast, two females laid eggs in a joint nest at least once in 71% of groups that included a polygynous trio ($N=17$; $\chi^2=39.5$, $P<0.001$). Consequently, the frequency of joint nests increased with the frequency of polygyny (Figure 2).

FITNESS CONSEQUENCES. Both mating type and dominance status affected reproductive success. Polygyny was beneficial for breeding males (Table 2). In each of three years, dominant polygynous males produced more fledglings than dominant monogamous

males; both had higher success than monogamous subordinate males. Reproductive success of the two subordinate males that mated polygynously in 1987 was similar to that of dominant males, and higher than that of monogamous subordinate males.

TABLE 2 - Mean number of fledglings produced per season, \pm SE (N, breeders), in relation to sex, dominance status, and type of mating.

Dominance status and mating type	Year		
	1983	1986	1987
MALES			
Dominant			
Monogamous	3.0 \pm 0.47(39)	3.9 \pm 0.53(19)	7.9 \pm 0.88(16)
Polygynous	5.0 \pm 0.58 (3)	5.2 \pm 1.36 (7)	10.0 \pm 0.55 (5)
Subordinate			
Monogamous	2.9 \pm 0.81(10)	3.0 \pm 0.58 (3)	2.3 \pm 0.81(13)
Polygynous	—	—	9.0 \pm 5.00 (2)
Mating type, dominants, $F_{1,83}=4.1$, $P<0.05$; Year, $F_{2,83}=13.1$, $P<0.01$			
Mating type, subordinates (1987 only), $F_{1,13}=6.6$, $P<0.05$			
Dominance status (monogamous only), $F_{1,94}=8.3$, $P<0.01$; Year, $F_{2,94}=4.4$, $P<0.05$			
FEMALES			
Dominant			
Monogamous	2.9 \pm 0.46(41)	4.1 \pm 0.51(18)	7.9 \pm 0.88(16)
1° mate-sharer	3.7 \pm 0.33 (3)	3.1 \pm 0.42 (7)	6.6 \pm 0.70 (5)
2° mate-sharer	1.3 \pm 0.88 (3)	1.6 \pm 0.62 (9)	3.4 \pm 1.13 (5)
Subordinate			
Monogamous	2.3 \pm 0.61(13)	3.0 \pm 0.58 (3)	2.3 \pm 0.81(13)
1° mate-sharer	—	—	4.2 \pm 2.25 (2)
2° mate-sharer	—	—	4.8 \pm 2.75 (2)
Mating type, dominants, $F_{2,98}=6.7$, $P<0.01$; Year, $F_{2,98}=9.4$, $P<0.01$			
Mating type, subordinates (1987 only), $F_{2,16}=0.8$, N.S.			
Dominance status (monogamous only), $F_{1,98}=11.1$, $P<0.01$; Year, $F_{1,98}=6.9$, $P<0.01$			

Mate-sharing did not benefit females (Table 2). Among the mates of dominant males, monogamous females produced significantly more fledglings than did mate-sharing females. Primary females with dominant mates had higher reproductive success than either secondary females ($F_{1,26}=12.9$, $P<0.05$) or females paired monogamously to subordinate males ($F_{1,38}=5.4$, $P<0.05$), principally because of differences in the number of clutches produced per season. Females in the latter two categories had roughly equal success ($F_{1,40}=0.6$, N.S.). Independent of mating type, females with dominant mates produced more fledglings than females with subordinate mates because the former initiated more clutches and more of their eggs hatched (68%, $N=511$ vs. 62%, $N=129$).

Mate-sharing females incurred costs because they often nested jointly. Most joint nests contained 7-8 eggs, with each female contributing 3-4 eggs (modal clutch size for separate nests was 4 eggs). Hatching success in joint nests was poorer (40%, $N=155$ eggs) than in nests where only one female laid (64%, $N=1935$; $\chi^2=33.6$, $P<0.001$). Joint nests consequently produced fewer fledglings per female ($x=0.8$, $N=19$) than separate nests ($x=1.4$, $N=290$; $F_{1,303}=5.6$, $P<0.05$).

BREEDING AND HELPING. The proportions of resident adults that bred and helped in each year varied (Table 1), and associations with sex ratio differed between the sexes. In the absence of polyandry, more non-breeding males were present when females were in short supply. Adult density had an additional influence; sex ratio and density together account for 98% (R^2) of the variation in the proportion of males that bred ($F_{2,6}=156.7$, $P<0.001$). Because non-breeding males most often acted as helpers, the proportion of males helping increased significantly with sex ratio.

The proportion of females that bred did not vary with adult sex ratio (Table 1) because polygyny made it possible for most females to obtain mates. The proportion of females that helped nevertheless decreased with mate availability, as it did for males. Female breeders most often also acted as helpers, especially if they shared mates: 32% of mate-sharing females with a chance to help at another's nest did so ($N=37$) compared with only 1% of monogamously-paired females with such an opportunity ($N=145$; $\chi^2=35.8$, $P<0.001$). The proportion of females helping thus increased with the frequency of polygyny (Table 1). Mate shortage therefore promoted helping by females by forcing them to share mates.

Helping behavior may facilitate joint nesting. In 80% of cases ($N=10$) where one female first acted as a helper at the nest of another female sharing the same male, the two subsequently nested jointly. When neither mate-sharing female first acted as a helper for the other, they less often nested jointly (27%, $N=11$; Fisher's exact test, $P=0.03$).

PLURAL-BREEDING GROUPS. The proportion of groups containing multiple breeding females varied from 14% in 1984 to 76% in 1987. The frequency of plural breeding increased with the proportion of yearlings in the population and, consequently, with group size but did not vary with other parameters (Table 1). Plural groups therefore were not an incidental product of polygyny, but arose when yearlings attempted to breed without establishing independent territories (Curry & Grant 1989).

DISCUSSION

Galapagos Mockingbirds inhabit an extraordinarily variable climatic environment. Nevertheless, reproductive decisions in this territorial species, whose groups fill all available habitat on Genovesa, are influenced principally by indirect effects of changes in population size and structure. Consequently, the social system varies greatly depending on prevailing demographic conditions.

Climatic variation may play a small direct role. Conflict between pairs in plural-breeding groups, for example, appears to be more intense in drier years, possibly because of competition for resources or for helpers (Curry 1988b). Total rainfall may also be an inaccurate index of resource levels. A thorough test of the hypothesis that climatic conditions influence helping by altering breeding costs (Orians et al. 1977, Emlen 1982) would require experimentation or direct measurements of food supplies. We lack these data.

Among demographic variables, mate availability has the strongest influence on mockingbird social organization. Mate shortage increases the pool of male non-breeders

available to act as helpers. This raises the question: Why do dominance interactions prevent polyandry? We hypothesize that young males cannot overcome age-dependent asymmetries in competitive ability, and that dominant males incur negligible costs by imposing a skew in reproductive success (Vehrencamp 1983), because subordinate males have few options in Genovesa's often crowded demographic environment.

Mate shortage also promotes helping by females, by influencing the way in which females must breed rather than the number able to do so. Because females that share mates suffer decreased reproductive success, they mate monogamously if possible. When an excess of males exists, most unpaired females wander in search of mates, rather than staying home and helping (Curry 1988a). Because of Genovesa's unpredictable climatic regime, females gain by breeding whenever conditions are favorable, even if they must pair with a subordinate male to do so (Curry 1988b). When males are in short supply, polygyny becomes the only available route to breeding.

Our results imply that mating decisions are primarily under female control. If males determined mating, polygyny would always occur because the reduced reproductive success of each female is more than offset by their combined fledgling production. Females paired with dominant males, however, should attempt to avoid the costs of mate-sharing. Their resistance may force additional females to pair with subordinate males, if available. When the supply of males is limited, excess females should employ tactics that facilitate polygyny, and to receive support from prospective mates. An unpaired female initially may act as a helper in order to form a social bond with the primary female, and thereby overcome her initial aggression. By laying in a joint nest, the secondary female may also protect her eggs from disruption on the part of the primary female (Curry 1988b). Joint nesting by mockingbirds, however, is not intrinsically advantageous, as in other species where it occurs more often (e.g. Koford et al. 1990).

Though variation in mate availability affects mockingbird breeding, we suggest that the relationship between population density and territory space has an overriding influence on social organization and reproductive strategies (Curry & Grant 1989, 1990). The weak negative correlation between density and breeding by females on Genovesa (Table 1, $P < 0.1$) supports this hypothesis, as does evidence that social organization varies with population density among the four allopatric species of *Nesomimus* (Curry 1989). We predict that under conditions of high density on Genovesa, many females are prevented from breeding, regardless of mate availability. This prediction remains untested because an excess of females and high density co-occurred only once in our study – during a drought year (1985) when no mockingbirds nested.

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SYMPOSIUM 22

MATING AND MATE CHOICE

Conveners N. BURLEY and T. BIRKHEAD

SYMPOSIUM 22

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INTRODUCTORY REMARKS: MATING AND MATE CHOICE

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Sexual selection comprises two parts: inter-sexual selection and intra-sexual selection. The former usually comprises competition between males, and inter-sexual selection usually comprises female choice among males. These two processes determine a male's reproductive success. Any character, such as antlers or spectacular plumage, that enhances mating success constitutes a sexually selected trait.

The intensity of sexual selection is determined largely by the amount that each sex invests in parental care. The sex investing least, usually the male, competes vigorously for the limiting sex (usually the female). The result is generally a greater variance in reproductive success among males than females. Trivers (1972) proposed that males invest less in gametes (spermatozoa) than females do in eggs (ova) and that this results in greater competition among males for females than vice versa. However, since sperm tend to be produced in 'packages', ejaculates or spermatophores, the difference in gamete investment between the sexes is less than was once supposed (Dewsbury 1982). However, there are other important differences between the sexes that usually result in females investing more than males. For example, copulation carries no commitment for a male, but can result in a lengthy pregnancy for a female. This results in the operational sex ratio becoming increasingly male biased as the breeding season progresses. As a result, competition between males for females can be intense.

Sexually selected traits are most apparent among polygamous species, for example, lekking birds, such as the grouse, pheasants and cotingas etc. In these birds males possess extravagant ornaments; brilliant and spectacular plumes which have arisen either as a result of male-male competition, or more likely, as a result of female choice. Among these species males compete vigorously among themselves, and at the same time females are free to choose between the available males.

Sexual selection will increase the variance in male reproductive success, in terms of the number of offspring males father. Sexual selection may also increase the variance in female reproductive success, but only in terms of the quality of offspring they produce. By mating with a preferred male, a female may produce sons with those traits, and enhance her success in that way. Although sexual selection is most obvious in polygamous birds, it also occurs among monogamous species, albeit in a different way (Darwin 1871).

Kirkpatrick et al. (1990) and Moller (in press) have reviewed the ways in which sexual selection can occur among monogamous species. Of the different mechanisms proposed, matings outside the pair bond, extra-pair copulations, have received a considerable amount of attention (Birkhead & Moller, in press). There is now good evidence that paired males increase their reproductive success through extra-pair copulations

and that males differ in their ability to secure extra-pair fertilisations. There is also good evidence that paired females actively seek and solicit extra-pair copulations, particularly from males of better quality than their partner.

The adaptive significance of extra-pair copulation for males is obvious; it can increase the number of offspring they father. The adaptive significance of extra-pair copulation is less obvious. Why should a female pair with one male, only to later seek copulations outside the pair bond? The answer is that many females are unable to pair with the best males in a population, because of ecological and social factors (Moller MS). In addition, the best situation in which to rear offspring might not be where the best males reside (Moller MS). Birkhead & Moller (in press) have suggested that sexual selection in females can occur at a number of different levels: in terms of a choice of initial breeding partner, through subsequent changes in breeding partners and finally through choice of extra-pair copulation partner.

In the present 'chapter' several of these aspects of sexual selection are explored. Davis shows how mate choice occurs in Adelle Penguins *Pygoscelis adeliae* and his study is unusual in showing that this occurs through mate switching rather than extra-pair copulation. Burley examines female choice of extra-pair partners in Zebra Finches *Taeniopygia guttata*, and shows that females prefer to copulate with males with certain features. In the next section Birkhead, Hunter and Pellatt review their sperm competition studies of the Zebra Finch, which show, among other things, that extra-pair copulations both in captivity and the field result in extra-pair fertilizations. Finally, Thornhill considers some methodological and philosophical aspects of the study of sexual selection.

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SPERM COMPETITION IN THE ZEBRA FINCH *TAENIOPYGIA GUTTATA*

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ABSTRACT. Observations of wild Zebra Finches in Australia showed that extra-pair copulations (EPCs) occur; mostly initiated by males, but females also sought EPCs. Males used several paternity guards: frequent pair copulation, close mate-guarding, as well as 'retaliatory' copulations after witnessing EPCs. Despite these paternity guards DNA fingerprinting revealed that 2.4% of offspring (in 8% of broods) were the result of extra-pair fertilizations. Studies of sperm competition in the laboratory using genetic plumage markers showed that for copulations separated by four or more hours last male sperm precedence (70-80%) occurred. Copulations separated by less than two hours resulted in equal paternity, showing that 'retaliatory' copulations devalued EPCs by half, on average. Interspecific variation in the extent of extra-pair paternity is discussed.

Keywords: Zebra Finch, *Taeniopygia guttata*, extra-pair copulation, extra-pair paternity, DNA fingerprinting, sperm competition.

INTRODUCTION

Although most birds are regarded as having a monogamous mating system (Lack 1968), implying an exclusive mating relationship (Wittenberger & Tilson 1980), there is increasingly abundant evidence that matings outside the pair bond occur regularly. Moreover, the recent development of molecular techniques for assigning paternity have demonstrated that extra-pair copulations also result in extra-pair paternity.

Extra-pair matings result in sperm competition, that is, the competition between the sperm of different males to fertilise the egg(s) of a single female (Parker 1970, 1984). In turn, sperm competition results in conflicting selection pressures, on the one hand favouring males that successfully obtain extra-pair fertilizations, but on the other, favouring males that can avoid being cuckolded. Sperm competition results in sexual selection and is generally regarded as a form of male-male, post-copulatory competition. However, recent studies have shown that females are not passive or reluctant participants in extra-pair matings, but actively solicit such matings from particular males, so female choice is also involved (Smith 1988, Moller 1988).

Despite the power of molecular methods such as DNA fingerprinting for assigning paternity, relatively few studies have combined detailed field observations with paternity studies. Moreover, even fewer have considered the causal aspects of sperm competition, such as the mechanism by which copulations translate into offspring.

Since 1985 we have tried to examine a number of aspects of sperm competition in a single species, the Zebra Finch *Taeniopygia guttata*, working both in the field and with captive birds. The aim of this paper is to present an overview of our results to date.

FIELD OBSERVATIONS OF ZEBRA FINCHES

The Zebra Finch is a small (12 g), sexually dimorphic estrildine finch which inhabits the drier parts of Australia (and some of the Lesser Sunda Islands). The Zebra Finch is monogamous and pair members remain together throughout the year. Breeding occurs in loose colonies, and usually occurs after rain. Zebra Finches are short-lived with a high reproductive output. Annual adult survival is less than 10% and birds start breeding as young as 70 days of age.

Observations were made in collaboration with R. Zann, at his study colony of colour-marked birds in Northern Victoria. Extra-pair courtship occurred regularly, and extra-pair copulation also occurred, in some cases initiated by a male, in others by a female. Not surprisingly paired male Zebra Finches have a number of paternity guards: they copulate with their partner frequently, they guard their partner by close following, and they perform retaliatory copulations if they witness their partner being involved in an extra-pair copulation (Birkhead, Clarkson & Zann 1989, Birkhead, Hunter & Pellatt 1989). DNA fingerprinting of wild birds showed that these extra-pair copulations could result in extra-pair paternity, and that overall about 2.4% of offspring were fathered in this way, but that at least 12% of females engaged in extra-pair copulation. The proportion of offspring resulting from extra-pair copulation was not significantly different from that expected from the proportion of all copulations that were extra-pair copulations (Birkhead et al. 1990). Unexpectedly, DNA fingerprinting showed that intraspecific nest parasitism occurred, and was more frequent than extra-pair paternity, and involved at least 30% of all females in the colony.

SPERM COMPETITION EXPERIMENTS WITH CAPTIVE ZEBRA FINCHES

Using genetic plumage markers to assign paternity we performed three sperm competition experiments to determine how copulations translate into offspring.

1. Mate replacement experiment. Extra-pair paternity can arise either through an extra-pair mating, or through rapid mate switching. That is, a female pairs with, and copulates with one male, but then switches mates. Because viable sperm can be stored for long periods (up to 13 days in the Zebra Finch), sperm from the first male could fertilize some eggs (Birkhead et al. 1989). Two males were allowed approximately equal numbers of copulations sequentially with a single female, the second male fertilised the majority of eggs. This result suggested a last male advantage, as occurs in many insects (Gwynne 1984). The second experiment was designed to test this, but at the same time, to test the idea that a single extra-pair copulation could fertilise eggs.

2. Single extra-pair copulation experiment. In this experiment we mimicked the situation in the wild, where a female obtained most copulations from her partner, but a single copulation from another male. The single 'extra-pair' copulation was the final copulation in the sequence before fertilisation. This showed that there was indeed a last male effect, and that a single extra-pair copulation could fertilise a substantial proportion of the clutch. Overall in this experiment the last male fertilised about 80% of the eggs (Birkhead et al. 1988).

3. Retaliatory copulation experiment. This experiment was designed to determine the function of the retaliatory copulations performed by paired males in response to their partner's involvement in an extra-pair copulation. This showed that by copulating immediately after an extra-pair copulation, the paired male reduced the 'value' of the extra-pair copulation by 50% on average (Birkhead unpubl.). In other words the probability of an extra-pair copulation resulting in fertilization was reduced by half by a retaliatory copulation. Experiment 2 had shown that the last male to mate fertilised about 80% of the eggs and this occurred only if there was an interval of four or more hours between copulations. So the best strategy for a male Zebra Finch that witnesses his female's involvement in an extra-pair copulation is first to perform a retaliatory copulation, and second to then copulate with his partner at least four hours later as well. Observations of Zebra Finches in aviaries shows that this is indeed what occurs. Why bother with the retaliatory copulation if one four or more hours later will do nearly as well? The answer to this is that the retaliatory copulation is a kind of insurance in case the female ovulates and fertilizes her next egg within four hours.

LAST MALE SPERM PRECEDENCE

The next question is how is the last male effect achieved? Our results were similar to some of those obtained for chickens using artificial insemination. Considerably more is known about the physiology of sperm utilisation in chickens than it is in the Zebra Finch, so Lessells & Birkhead (1990) built models of sperm competition in chickens in order to identify possible mechanisms in the Zebra Finch. All birds examined so far, including both the chicken and the Zebra Finch, possess sperm storage tubules (SSTs). Sperm are stored here following copulation and prior to fertilization of the ova. Since sperm are released from the SSTs at an exponential rate, last male sperm precedence could arise simply as a consequence of this. If two inseminations occur four (or more) hours apart, by the time second insemination occurs many of the sperm from the first insemination will have been lost from the SSTs. Last male precedence could arise simply because of the exponential rate at which sperm left the SSTs resulting in there being more of the second male's sperm present. However, the model showed that the rate at which sperm were lost from the tubules was too low to account for last male precedence. This indicates that the last male effect was not a passive consequence of sperm movements within the female reproductive tract, but indicates that some other mechanism is involved.

Two such mechanisms have been proposed: displacement and stratification. Poultry biologists have assumed that it is the latter. The sperm storage sites in birds are blind-ending tubules: sperm can get out only one way – the way they came in. It has been assumed therefore that sperm from inseminations made four or more hours apart remain stratified in the tubules and that a last-in first-out system operates. Poultry biologists have also assumed that sperm from inseminations made less than four hours apart mix before entering the tubules; hence the lack of any mating order effect on paternity. However, the models showed that such a mechanism could not account for last male sperm precedence. If stratification is the mechanism the model predicts that the sperm from the last male will eventually be utilised and then the first male's sperm will be 'uncovered' and start to fertilize the eggs. However, there is no evidence for this, either in chickens or in the Zebra Finch.

The stratification hypothesis can also be tested more directly by looking at the arrangement of sperm within the sperm storage tubules. Some stratification does occur, but at too low a level to account for last male sperm precedence (Birkhead & Hunter 1990).

The model indicates that sperm displacement is the most likely mechanism to account for last male precedence, and we are currently investigating this in the Zebra Finch.

CONSEQUENCES OF LAST MALE SPERM PRECEDENCE

Last male sperm precedence means that not all copulations are equal, and if an extra-pair male can obtain the final copulation with a female prior to fertilization he could fertilize a disproportionate number of eggs. In most birds fertilization takes place about 24 hours before an egg is laid. If copulation ceases before the first egg of a clutch is fertilized, one male (either the male partner or an extra-pair male) will fertilize the majority of the clutch if an extra-pair copulation takes place. Someone has to be last! Since females control the timing and success of copulations, they could in theory at least, control the paternity of their offspring.

Several hypotheses have been proposed for why females should engage in extra-pair copulations. (i) A female could be seeking good genes, i.e. a good quality male to father her offspring, or (ii) a female could be seeking to increase the genetic diversity of her brood. In the first of these the female would want all her offspring to be fathered by a particular male, in the second, only a proportion. For females seeking good genes, last male sperm precedence would be advantageous. They could simply arrange for the best quality male to obtain the final insemination. On the other hand for a female attempting to increase the genetic diversity of her offspring, this might be a problem. One way round this problem would be to continue copulating throughout the period that eggs are fertilized. This is exactly what occurs in the polyandrous Dunnock *Prunella modularis*, where it has been shown that it is in the female's interest to have multiple paternity of her offspring (Davies 1983, Burke et al. 1989). Some of the remarkable diversity in the copulation patterns of birds (Birkhead et al. 1987) might be explicable in these terms.

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MATE CHOICE AND SEXUAL DIMORPHISM IN PENGUINS

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ABSTRACT. Female choice in monomorphic, monogamous species has long posed a theoretical problem, as there would seem to be little opportunity for intersexual selection to produce asymmetries in mating success for males with favoured traits. Penguins are obliged to be monogamous breeders, and they are monomorphic save for a slight sexual size dimorphism. I show empirically from a study of Adélie Penguins that females do choose males, and that they do so on the basis of (i) whether they have bred successfully with a male in either of the two previous breeding seasons, or (ii) the proximity of the male's nest to their previous season's nest site. These preferences account for the rapid mate switching that occurs during the courtship period. Female choice may contribute to the degree of sexual size dimorphism in species of penguins where males endure lengthy fasts and a male's ability to fast is related to its body size. However, mate choice for conditional traits (i.e. traits perceived differently by each female, such as learned calls or relative positions of nest sites) could occur without the elaboration of secondary sexual traits, as they are not tied to an underlying genotype. Preferences may exist because of conditioning (repeated reinforcement) to traits like calls and nest sites.

Keywords: Mate choice, female choice, sexual dimorphism, monomorphic, monogamy, penguins, Adélie Penguins, rapid mate switching, conditional traits, conditioning.

INTRODUCTION

Mate choice is theoretically inconsequential for sexual selection in monogamous, monomorphic species. This is because: (i) in monogamous species there is little opportunity for intersexual selection to produce asymmetries in male mating success, as individuals pair only once and nearly all individuals pair, and (ii) a lack of morphological secondary sexual characteristics, by definition, provides no evidence for sexual selection.

Penguins are an ideal group in which to evaluate possible effects of mate choice in such species as, firstly, biparental care and, therefore, monogamy, is essential to rear offspring successfully; and secondly, their external morphology is identical (with none of the variations in plumage patterns, colouration or ornamentation characteristic of classical sexually selected species of birds) apart from slight differences in size (Davis & Speirs 1990). Previous demonstrations of mate choice in "monomorphic" birds have involved species in which the sexes differ in the intensity of their colouration (Burley 1981, Johnson 1988).

In this paper I analyse the mating patterns of Adélie Penguins *Pygoscelis adeliae* for evidence of mate choice, and address whether sexual dimorphism in penguins is likely to result from mate choice.

COULD SIZE DIMORPHISM IN PENGUINS RESULT FROM MATE CHOICE?

For mate choice to be of consequence in a monogamous species, individuals with favoured traits must pair first and experience greater reproductive success through:

(i) an advantage to breeding early, such as minimizing predation risk or fledging chicks before conditions deteriorate at the end of the season, (ii) gaining extra-pair copulations, (iii) being of superior genetic quality, such that the progeny experience higher survival and reproductive success, or (iv) providing higher quality parental care.

In Adélie Penguins, large males do pair first (Davis & Speirs 1990). This in itself provides no evidence for size-based selection, as the largest males tend to arrive first at the rookery at the beginning of the breeding season (Ainley & Emison 1972) and time of breeding correlates with time of arrival (Davis & Speirs 1990). Neither is fledging success higher for the broods of early breeders (Davis & McCaffrey 1986, Davis & Speirs 1990).

Extra-pair copulations are common in that up to a third of males and females copulate with more than one partner in a single season. However, these "extra" copulations result not from paired males copulating with other females or being cuckolded by other males, but from the breaking of partnerships and the subsequent reforming of new ones. They are not so much "extra-pair" copulations as they are "serial-pair" copulations that ensue from rapid mate switching; though they may still result in some males rearing chicks they did not sire (Davis & Speirs 1990). Female Adélies, then, take new mates only from single unattached males and they do not participate in sneaky copulations when paired. This suggests that females are mating for more than just "good genes" (since if that were the case, there would be no disadvantage to copulating with paired males or while paired), and that it is the male's potential to give parental care that is important (i.e. they are mating only with partners that are free to participate in the incubation of the eggs and the feeding of the chicks).

MATING PATTERNS

I examined mating patterns in a colony of Adélie Penguins at Cape Bird, Ross Island, Antarctica, during two courtship periods. The study area and methods are described in detail elsewhere (Davis 1988, Davis & Speirs 1990).

Patterns of courtship were followed for 18 females in 1986 and 15 in 1987, from their arrival at the colony until they were finally paired with a partner with which they subsequently shared incubation duties (defined as their "mate" for that season). Fourteen females were common to both seasons. However, as the observed patterns in each season were similar when analysed separately, data from both seasons were pooled.

The mating pattern of *all* females can be described by a model that predicts all instances of rapid mate switching as well as the male with which a female eventually shares incubation duties. The model describes the females' behaviour in terms of a series of conditional responses to the situation they find when they arrive at their colony (Figure 1). (A previous model of mating patterns in Adélie Penguins [Davis & Speirs 1990] predicted only the male with which a female shared incubation duties, and it did not take into account the past breeding success of the birds.) These conditional responses can be mimicked by a few simple "rules of thumb". These are:

- (i) Return to the previous season's nest site.
- (ii) If last season's mate is there *and* you were "successful" with him in either of the last two seasons, pair with him again, even if it means driving out another female if he already has a partner.

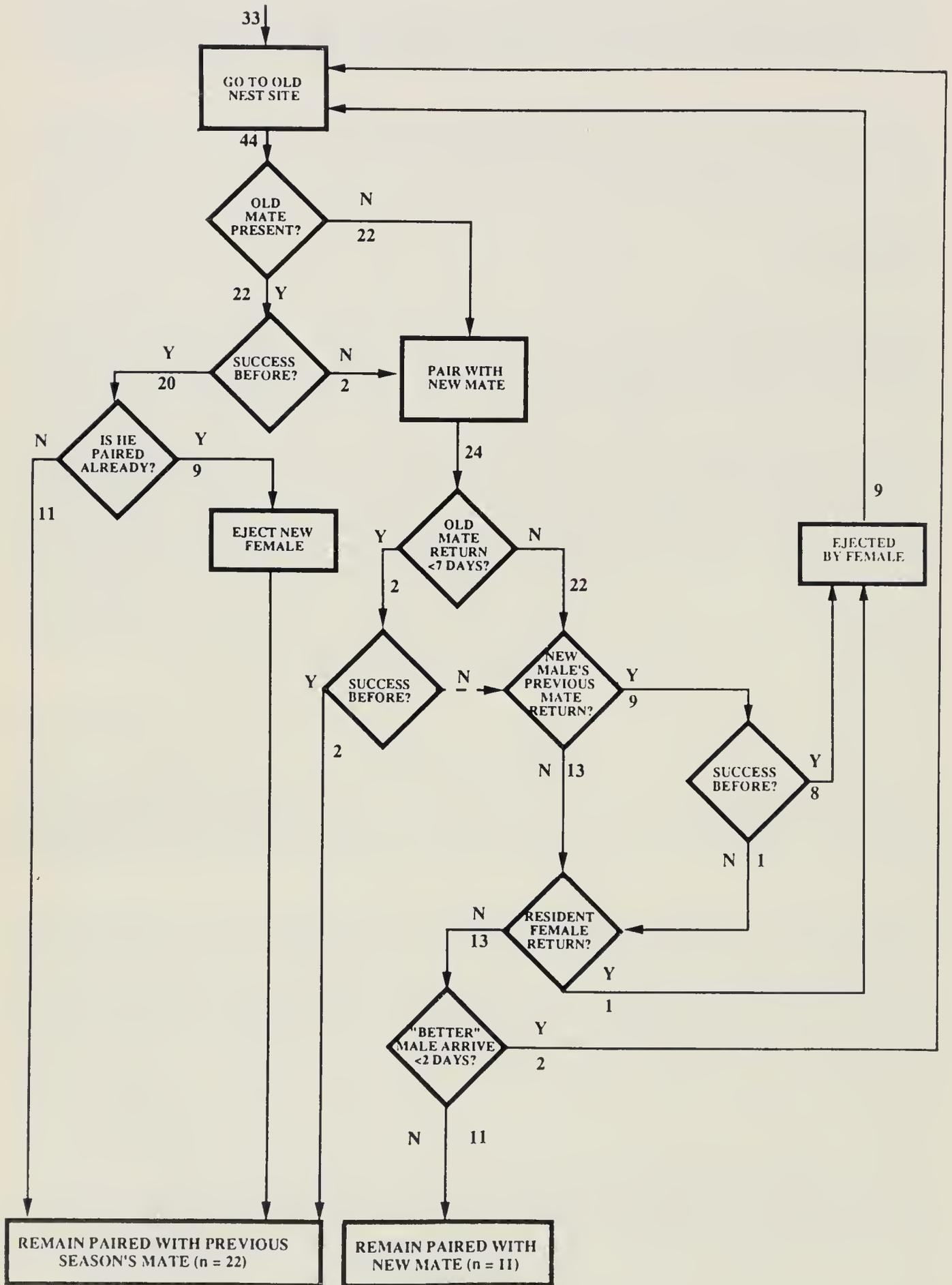


FIGURE 1 - Mating patterns of female Adélie Penguins returning to their colony to breed in 1986 and 1987. Mating decisions are represented as diamonds, while squares indicate outcomes. Key: Y = yes, N = no, numbers = numbers of females.

- (iii) Otherwise, choose a new male, but if your previous mate returns within seven days and you were successful with him in either of the last two seasons, leave the new male for him.
- (iv) Leave the new male also if he was successful in either of the last two seasons with his previous mate and she returns to the colony subsequently (as she will drive you out) *or* if within two days a “better”² male arrives at the colony.

This implies that female Adélie Penguins exercise choice, whereas males are passive pawns in the mating game: they remain on their nest and try to court any female until paired. The nest site is the focal point for reuniting with a previous mate or beginning the search for a new one. Females place a high priority on renewing previously successful partnerships, fighting for previous mates that have proven their parental investment capabilities. Asynchrony of arrival is likely to break previously successful partnerships when the male is late, suggesting that the strength of a new pair bond develops with time spent together; but not when the female is late, underlining the determination of females to reunite with their previously successful mates.

ON WHAT BASIS ARE FEMALES CHOOSING MALES?

As females paired and copulated with only unattached males (except former mates with whom they were successful), it was possible in this study to evaluate parameters of choice by comparing the characteristics of unpaired males available in the colony *at the time* each female arrived and paired with her first partner. (N.B. Females paired typically within minutes of arrival at the colony, and all did so within 12 hours.) Here I consider only females taking new partners. Expected values are calculated on the basis of the proportion of males available in each category, and the significance between observed and expected pairings is tested with a Goodness of Fit Test (χ^2 statistic). Sample sizes vary because I include only those instances where a female had a choice between at least one male of each category.

Nest location

Central nests are twice as likely to fledge chicks as peripheral nests because of reduced predation risk from South Polar Skuas (Davis & McCaffrey 1986). In 12 instances where females had at least one nest of each category available: females did not display any preference for males in central nests ($\chi^2 = 1.00$, $df = 1$, $P > 0.3$) (Figure 2a).

Familiarity

Available males consisted of those which had bred in the colony previously and were familiar to females (as all females had bred in the colony previously also) and new recruits (males attempting to breed in the colony for the first time). The latter were unfamiliar to the females and were probably also less experienced and younger, as

¹ “Successful” is defined as the pair having successfully completed incubation. During the incubation period incubating males endure lengthy fasts in the absence of their foraging mates, and an ability to withstand such fasts is a major factor in their breeding success (Davis & McCaffrey 1986).

² A “better” male is one that is closer to the previous nest site.

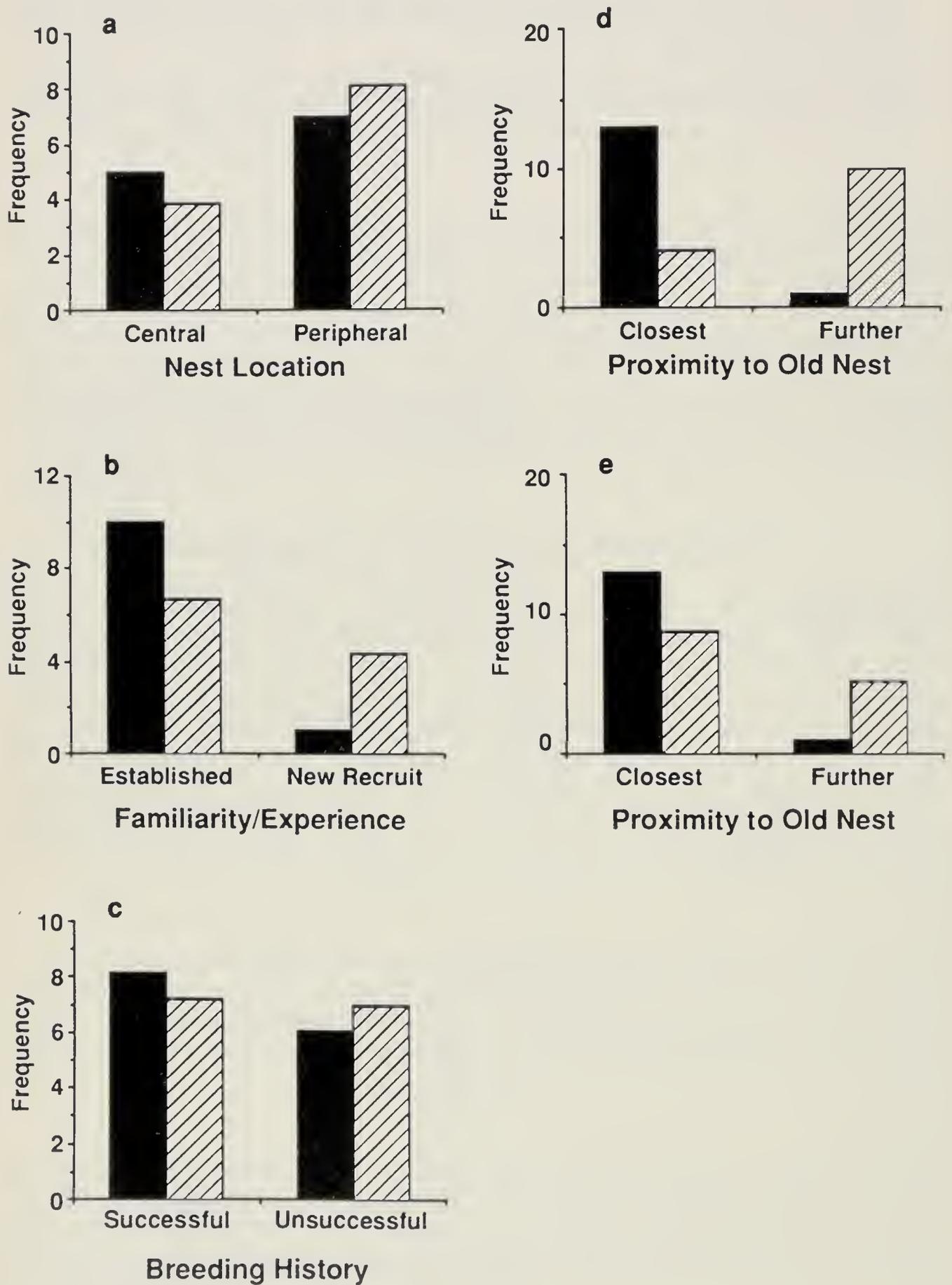


FIGURE 2 - Actual (black bars) and expected (hatched bars) numbers of males in each category chosen by females given (a) location of the male's nest, (b) familiarity to the female, (c) the male's previous season's breeding history, (d) the male's proximity to the female's old nest site, and (e) the male's proximity to the female's old nest site using expected values derived from the random model (see text).

established males are strongly philopatric and tend not to move colonies, or even nest sites, between seasons (Penney 1968, Spurr 1975, Ainley et al. 1983, Davis 1988, Trivelpiece & Trivelpiece 1990). In 11 instances where females had available at least one familiar and one unfamiliar male, females showed no significant preference for familiar males ($\chi^2 = 2.98$, $df = 1$, $P = 0.08$), albeit, a tendency to prefer familiar males may have been apparent given a larger sample size as only one female mated with a new recruit (Figure 2b).

Breeding history

While females exhibit a preference for their own previously successful mates (Figure 1), no preference was apparent ($\chi^2 = 0.04$, $df = 1$, $P > 0.8$) for other males in the colony that had successfully completed incubation the previous season (i.e. proven their parental investment capabilities) compared with males that had not (Figure 2c). Females may be unable to assess a male's previous breeding history, and preference for their own previously successful mates may be based not on an assessment of their prowess as parental investors, but instead be a simple response that occurs because of the repeated reinforcement of the pairbond that occurs during chick rearing (Rowley 1983).

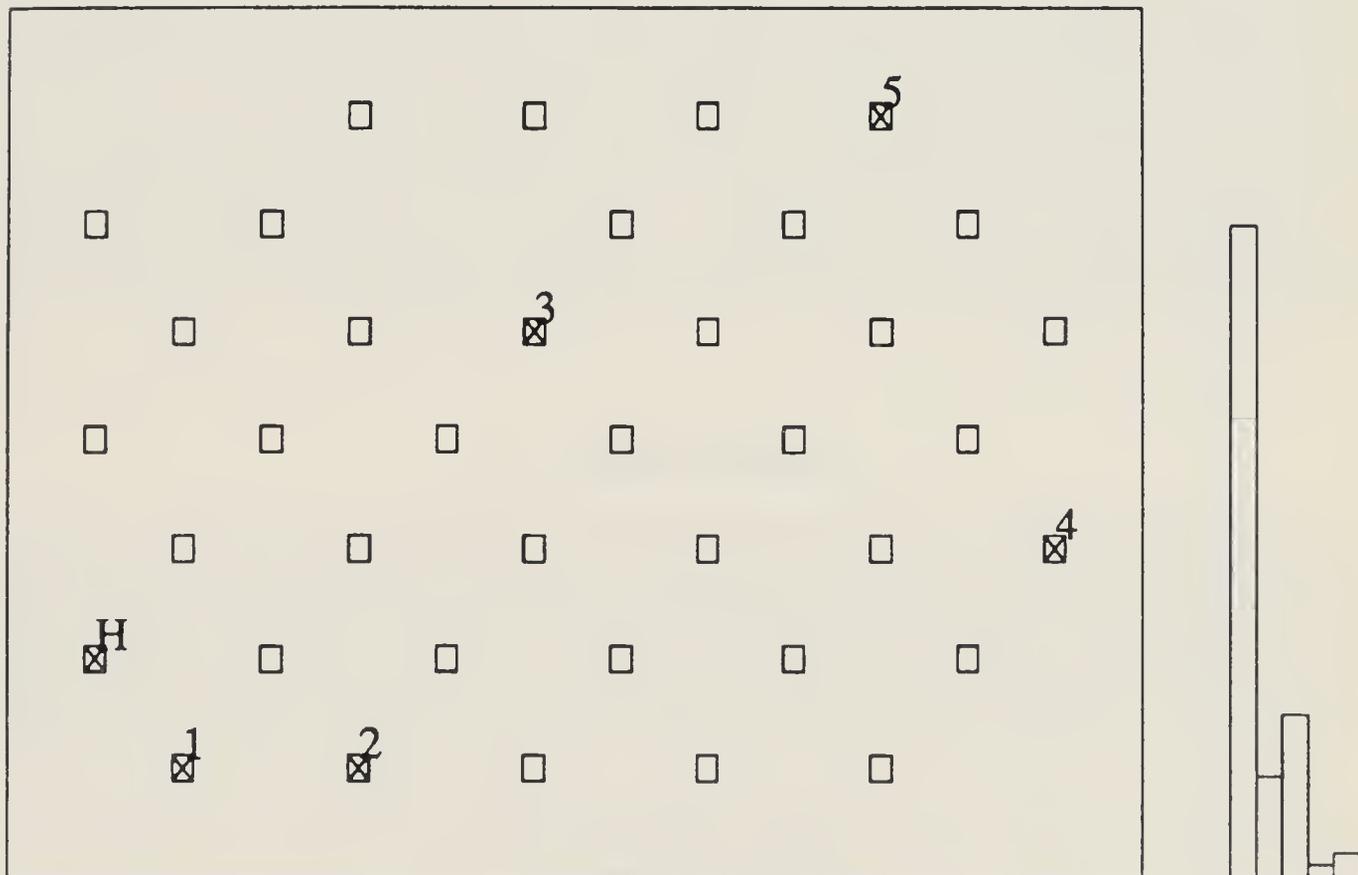


FIGURE 3 - An example of the probabilities of pairing with each available male generated using a random model that assumes for each female that she starts from her previous season's nest site (H), moves randomly and pairs with the first available male she encounters. Nests in the colony are shown as squares, and nests with available males (i.e. unpaired males) are marked with crosses and numbered in ascending order the greater their distance from H. Five hundred simulations of the model were run for each female. The relative probabilities of pairing with each male for this female are shown at right, with nests 1 to 5 represented from left to right.

Frequency of ecstatic calls

Male penguins exhibit a sex-specific behaviour and call during the courtship period known as the ecstatic display (Sladen 1958, Jouventin 1982). Female penguins could potentially choose mates based on the frequency of this call. Males selected by females had ecstatic calls with a lower weighted average frequency than males that failed to pair at all (Davis & Speirs 1990). However, if the ratio of the number of times a male was chosen over the number of times it was available is used as a measure of its probability of being chosen, then males with calls of the lowest fundamental frequency (that component of the call most likely to correlate with body size) were not more likely to be chosen by new partners (i.e. females other than their previous partner) ($r = 0.01$, $df = 16$, $P > 0.9$).

Proximity to old nest site

Females were significantly more likely to choose males in nest sites closest to their previous year's nest than would be expected on the basis of the proportion of such males available ($\chi^2 = 24.71$, $df = 1$, $P < 0.001$) (Figure 2d). However, if females return to their old nest site before starting to look for a male, then males at close nest sites are likely to be picked even if the females exhibit no choice. To determine whether females were actively choosing to mate with males in close proximity to their old nest, I calculated expected probabilities each female had of mating with each of the males available at the time she arrived at the colony by running 500 simulations of a random model. Under this model, the female started from her old nest and moved randomly through the colony, mating with the first unpaired male that she encountered. The null model assumed that the female was unaware of the other males in the colony as she moved around, which biased it towards high expected probabilities for mating with nearest males (Figure 3). Even so, females were even more likely to mate with the closest males than would be expected if they moved randomly from the nest and exhibited no choice ($\chi^2 = 4.29$, $df = 1$, $P < 0.05$) (Figure 2e).

CONCLUSION

Female Adélie Penguins have mating preferences and exhibit mate choice. Females select males on the basis of proven paternal investment abilities by preferring to mate with males that have previously incubated successfully throughout their absences while foraging, or by taking males near to their previous nest, which gives them the opportunity of returning to their previous partner should he turn up later. The latter, combined with a willingness to fight for previously successful partners even if they are already paired, contributes to the high level of rapid mate switching that occurs during the courtship period in this species. A similar process seems to occur in Fiordland Crested Penguins (Davis, McLean & Murie unpublished observations) and Magellanic Penguins (Boersma pers. comm.), and it may well be a general feature of the mating system of penguins.

Two proximate mechanisms to explain apparent female preferences for previously successful mates have been put forward (Davis 1988). One, that unsuccessful pairs fail to reunite because they are more inclined to arrive asynchronously at the colony the following season, is inadequate as late females will reunite with males if they have been successful previously. Further, given that pairs reunite if successful in only one of the last two breeding seasons, this suggests a durable form of mate recognition.

This is likely to occur through conditioning to the "loud mutual" calls which are used for mate recognition and which accompany nest relief (Speirs & Davis in press). Frequent exposure to loud mutual calls occurs during chick rearing when nest reliefs occur approximately daily, and it is this repeated reinforcement of the pairbond which seems important for mate fidelity between seasons (Rowley 1983). In contrast, pairs are together for only two or three brief nest reliefs during the incubation period (Davis & Miller 1990), and pairs that fail during incubation miss out on the exposure to each other's calls that occurs during chick rearing.

Choosing previously successful mates might select for large size if large-sized males are more successful. This effect is likely to be strongest in those species where males fast longest during incubation, assuming that fat reserves are limiting and that larger males have larger reserves, and might explain a considerable amount of the interspecific variation in sexual size dimorphism in penguins (Davis & Speirs 1990). However, even in the least dimorphic species with the shortest fasting periods, a preference for previously successful mates is high (e.g. Richdale 1957), suggesting that it may occur through conditioning to a mate's call. Further, female Adélie Penguins exhibit choice for males in close proximity to their previous nest site, and it seems that females of other species of penguin may behave similarly. Both of the latter are examples of choice for conditional traits (i.e. ones that will be perceived differently by each female, such as call learnt and relative nest location). I suggest that mate choice can occur in a monomorphic, monogamous species without the elaboration of secondary sexual characteristics (see Bateson 1983 p. ix) as long as the trait being selected is a conditional one, and therefore, not tied to an underlying genotype. Whether selection of previously successful males or males close to old nest sites is adaptive, in that it selects for better parental care or facilitates reuniting with such care, respectively, or whether it is merely a consequence of conditioning to mates or nest sites, is a moot point.

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THE SIGNIFICANCE OF MALE COLORATION FOR MATE CHOICE IN THE PIED FLYCATCHER

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ABSTRACT. The importance of female choice for the evolution of male secondary sexual characteristics is controversial. We performed two field and one laboratory experiment, using the Pied Flycatcher *Ficedula hypoleuca*, to test the female choice aspect of sexual selection. Observational data suggest a slight preference for dark males by females but in field experiments when we presented males with territories at random sites (= no choice of a territory) or altered male colour of concurrently arriving males, we found no preference for darker ones. Similarly, estradiol-treated females did not show a preference for black or brown males in the laboratory. Thus, there is very little support for the idea that female choice has been an important mechanism in the evolution of sexual dichromatism in the Pied Flycatcher.

TELEONOMY AND THE STUDY OF SEXUAL SELECTION

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ABSTRACT. The disciplined application of the adaptationist program is essential for understanding how sexual selection actually has operated during the evolutionary history of life and for understanding the nature of selection responsible for the evolution of mate choice mechanisms. However, much of the current research in sexual selection is focused on measuring sexual selection, generating correlations between reproductive success and variation in traits that are assumed to be important in sexual selection, and determining the traits' heritabilities, rather than on the analysis of the functional design of secondary sexual characteristics and mate choice. Results from a study of the sexual selection system of the Red Jungle Fowl *Gallus gallus spadiceus* illustrate the utility of teleonomy in the study of sexual selection.

Keywords: Adaptation, evolutionary psychology, Red Jungle Fowl, sexual selection, teleonomy.

TELEONOMY

Natural selection and sexual selection are the only known processes that can produce adaptations, the complex, purposefully designed features of organisms. But biologists understand to a far greater extent how natural selection works over the long haul of evolution to produce adaptation than how sexual selection works during long-term evolution to produce complex phenotypic features such as the peacock's tail, the cock's comb or the song of male cicadas. This limited knowledge of how sexual selection operates in long-term evolution, including the limited knowledge about the role of female mate choice in evolution, is a major gap in human understanding of life.

That secondary sexual traits and choice of mates are important in sexual selection was discovered by Darwin (1874). Ghiselin (1969) has summarized the vast and diverse evidence that Darwin pulled together to demonstrate that secondary sexual characters are the result of selection in the context of competition for mates, and that female mate choice was important in the evolution of male ornamental traits and courtship behavior. Darwin did not, however, answer the question of how sexual selection worked during long-term evolution in designing male ornamental features. Nor did he answer the question of the evolutionary function of mate choice. Darwin (loc. cit.) provided a hypothesis about how sexual selection may have worked in long-term evolution, and other hypotheses have been proposed since Darwin, including hypotheses about the evolution of mate choice (Fisher 1958, Zahavi 1975, Hamilton & Zuk 1982, Kodric-Brown & Brown 1984).

The central problems of sexual selection are the elucidation of (a) the way sexual selection actually has operated in evolutionary history to bring about secondary sexual traits and (b) the nature of selection during evolutionary history that is responsible for mate choice. Thus, it is essential to distinguish procedures that can provide direct evidence about the workings of selection in evolutionary history from those that cannot.

The method of teleonomy (as it was called by Pittendrigh 1958) — the modern study of adaptation as outlined by Williams (1966) — has been too often ignored in studies of sexual selection but is essential for understanding the central problems of sexual selection. Teleonomy focuses on the purposeful design of adaptations and thereby illuminates the kind of directional selection responsible for adaptation. Only directional cumulative selection can make phenotypic design, and thus the understanding of the purposeful design of an adaptation reveals the kind of selection responsible for the design. Research on sexual selection that does not focus on characterizing the design of secondary sexual traits or of mate choice cannot in itself yield evidence bearing on the central problems of sexual selection.

Sexual selection is now receiving a great deal of attention from evolutionary biologists (Bradbury & Andersson 1987). Some popular methods of analyzing traits of potential importance in sexual selection do not focus on phenotypic design and therefore do not actually address the central problems of sexual selection directly. These indirect methods of analyzing phenotypic design focus on microevolution and on characterizing current selection, as opposed to long-term outcomes of evolution by selection. Microevolutionary questions pertaining to sexual selection are addressed by studies involving artificial selection; tallies of changes in gene frequencies in populations; and measures of the genetic parameters (heritabilities and genetic correlations) of populations (Thornhill 1990, also see Bradbury & Andersson 1987). It is impossible to infer directly the process of long-term historical evolution from knowledge about microevolution or current selection (see Thornhill 1990, also Williams 1985, Grafen 1988, Symons in press). Results from studies of microevolution that demonstrate or falsify a particular microevolutionary process cannot be viewed logically as evidence for or against the same process in evolutionary history. Furthermore, it does not follow that because an adaptation is the product of selection in the past, the adaptation must be currently adaptive. Indeed, there is no reason to expect that an adaptation of interest will be currently under selection, and regardless of how strong a form of current selection on an adaptation may be, that form of selection may have had nothing to do with the production of the adaptation during evolutionary history.

At best the study of current selection and microevolutionary aspects of sexual selection may lead to new hypotheses about processes that may have been important in evolutionary history. However, any kind of observation made on the living world may lead to a significant hypothesis about evolution in the past, and thus analyses of microevolution and current selection have no special significance or priority in regard to generating creative hypotheses about evolutionary history.

I am not saying that studies of microevolutionary processes and current selection do not have value. They provide knowledge that we do not have and therefore they are important, and, as mentioned, they may lead to hypotheses about long-term evolution in the past. I am saying that results from studies of microevolution and current selection cannot yield direct evidence of how the evolutionary process actually worked during evolutionary history.

CHARACTERISTICS OF ADAPTATIONS

Adaptations are characterized by low phenotypic variance. Adaptations typically are species-typical traits. Of course, a species-typical adaptation may only occur in one

sex or one life-history stage. Even in the case of multiple adaptations to a single ecological domain within a sex or life-history stage of a species, each adaptation is widespread throughout the species. A phenotypic feature that is highly variable among individuals within a population is not a candidate adaptation, because adaptations are the product of long-term evolution by selection in the past, which inevitably reduces phenotypic variation in the adaptation.

Phenotypic analysis in studies of sexual selection should focus on the design of psychological adaptations that regulate mating decisions and secondary sexual traits rather than entirely on analysis of morphology or behavior. Psychological design is important to study because psychological analysis forces attention on phenotypic invariance and thus is likely to lead to identification of adaptations (see Symons 1987, Tooby & Cosmides 1990). Morphology and behavior are facultative manifestations of species-typical, essentially invariant psychological adaptations, and their study can illuminate psychological design.

Psychological adaptations are information-processing mechanisms that have evolved as solutions to information processing problems in evolutionary history. The design of a psychological adaptation is the environmental information that the adaptation has evolved to process. It is the design of the evolved information-processing mechanisms in the sexual domain that will precisely illuminate the way selection has acted during evolutionary history to produce secondary sexual characteristics and female choice.

Adaptations also are characterized by low genetic variance. First, adaptations should exhibit low heritabilities, because of selection in the past. Second, adaptations are genetically encoded by many genes but yet are inherited as species-typical traits; as emphasized by Tooby & Cosmides (1990), this means that adaptations will necessarily have low heritability. Sexual reproduction recombines in offspring different genes from the two parents; it therefore destroys gene combinations that are variable among interbreeding individuals. As Tooby & Cosmides (1990, p. 17) put it, "Complex adaptations necessarily require many genes to regulate their development, and sexual recombination makes it improbable that all the necessary genes for a complex adaptation would be together at once in the same individual, if genes coding for complex adaptations varied substantially between individuals."

Moreover, adaptations are expected to be domain-specific in functional design as opposed to being general-purpose. Adaptations are phenotypic solutions to environmental problems that had significant and consistent effects on fitness over long periods of evolutionary history. Environmental problems that affect fitness and thus give rise to selection are always specific and not general problems (e.g. finding food of proper nutritional content, or a mate of high reproductive value), and thus special-purpose phenotypic design is the outcome of the long-term process of evolution by selection (see Symons 1987).

RED JUNGLE FOWL

The jungle fowl study attempted to discover the functional design of the psychological adaptation controlling the ornamentation of roosters and the functional design of hens' mate choice. The psychological adaptation controlling the great variation in the

expression of ornaments of roosters (both within and between individuals) contains in its design the evidence about how sexual selection actually worked in the evolutionary history of jungle fowl. The design features of the psychology of hens' mate choice — i.e. the kind of information processed by hens in mate choice — are the data that precisely identify how selection worked on female mating decisions in the evolutionary history of jungle fowl.

Results of mate choice experiments with Red Jungle Fowl were as follows:

- A. Hens preferred males with large combs/colorful combs, red eyes and certain ornamental feather colors in both of two sets of mate choice trials conducted in different years using different males and females in each year (Zuk et al. 1990b, in press b).
- B. In separate mate choice trials associated with an experiment in which a roundworm parasite *Ascaridia galli* was given to some rooster chicks but not others, hens generally preferred the same ornaments as the hens in A (Zuk et al. 1990a).
- A. and B. indicate that female choice is consistent and that the pattern of hens' mate preference is species-typical.
- C. The parasitized and control roosters in the parasite experiment were distinguishable at adulthood on the basis of all male characters on which hens base mate choice (see A), but not on the basis of other male characters such as bill size, which are unrelated to female mate choice in jungle fowl. Thus, during the period of male development, the male features that hens look at in mate assessment are most sensitive to the effects of roundworms.

The jungle fowl research reveals that variation in the ornaments of roosters — the features that hens assess in mating decisions — reflects a male's ability to deal with parasites (Ligon et al. 1990, Zuk et al. 1990a, in press a). Variation in ornamentation of roosters, both within and between individuals, is regulated by testosterone. The results of the jungle fowl research imply that testosterone production is controlled by a sex-specific, species-typical psychological adaptation of roosters that is designed to process information about a male's health in such a way that each male's allocation to ornamentation is adaptive for his own personal situation (Ligon et al. 1990, Zuk et al. in press a). Clearly the ornaments of jungle fowl are not designed as arbitrary indicators of male sexual attractiveness, as predicted by what might be called the arbitrary sexual selection hypothesis (Darwin 1874, Fisher 1958, O'Donald 1980, Lande 1981, Kirkpatrick 1982).

Not only do the results suggest that jungle fowl ornaments evolved as a result of sexual selection generated by host parasite coevolution (Hamilton & Zuk 1982), they also indicate that hens' mate choice evolved in the manner expected under the parasite hypothesis of sexual selection. Female mate choice is focused on male features that are most sensitive to parasites, and hens prefer to mate with males whose ornamental features show limited effects of parasitism (Zuk et al. 1990a, b, in press a, b). Female mating decisions in jungle fowl imply the existence of psychological mechanisms in hens that are designed to detect and motivate mating with males who can cope with parasites.

Results from quantitative genetic analysis reveal that neither the ornaments of roosters nor female preference of ornaments is heritable (Thornhill unpubl.). This result supports the interpretation that the processing of information about the effects of parasites on male ornaments by hens during mate choice is a species-typical aspect of hens' psychology.

In identifying and characterizing the evolutionary function of adaptation, it is essential to show that a phenotypic feature of interest is designed to accomplish a specific purpose, because it is evidence for the existence of special-purpose phenotypic design that can eliminate interpretations that the feature is an incidental effect of another adaptation. The results of the jungle fowl research indicate that the mechanism of female mate preference in jungle fowl that my colleagues and I have discovered almost certainly is not an incidental effect of the following candidate adaptations: (a) an adaptation to optimally inbreed/outbreed, (b) an adaptation to find foods of certain colors, (c) an adaptation to mate with dominant males, (d) an adaptation to mate with older males, (e) an adaptation to avoid heterospecific matings. Thus, the psychological mechanisms of hens that leads them to prefer as mates roosters that show in their ornaments reduced effects of parasites may be specially designed to process information about the effects of parasites on ornaments and regulate hens' mating behavior accordingly.

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EXTRA-PAIR COPULATION AND ATTRACTIVENESS IN ZEBRA FINCHES

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ABSTRACT. In the monogamous and sexually dichromatic Zebra Finch *Taeniopygia guttata*, females prefer as mates males having very red bills. Red male bill color is associated with participation in unforced extra-pair copulations (UEPCs), but not in forced extra-pair copulations or courtships in which no mountings took place. Hence male attractiveness contributes to success in obtaining UEPCs. The low incidence of UEPCs, combined with a tendency for females to engage in UEPCs with males whose bills are redder than their mate's, suggest that females participate in them for their own benefit. For both sexes, reproductive success (RS) achieved within the pair bond is associated with participation in extra-pair activities, implying a lack of tradeoff between within pair RS and effort spent in extra-pair activities.

Keywords: Sexual selection, attractiveness, extra-pair copulation, Zebra Finches, *Taeniopygia guttata*.

INTRODUCTION

The incidence and dynamics of extra-pair courtship and copulation in pair-bonding species are relatively unstudied, but are critically important to an understanding of the evolution of mating systems and paternal care (Trivers 1972), gene flow and population structure (Gowaty 1985), and for assessing the validity of currently used estimates of fitness. This is particularly true for birds, a class typified by sociographic monogamy and substantial male parental investment (PI).

Extra-pair copulation (EPC) is generally viewed as a male reproductive strategy, the obvious benefit of which is the production of offspring without PI. Extra-pair solicitation in pair-bonding avian species is typically a secondary tactic engaged in by paired males rather than an alternative tactic pursued by unpaired males (Ford 1983). Males of many avian families pursue both forced extra-pair copulations (FEPCs) and unforced extra-pair copulations (UEPCs), though the relative effort and success of these are generally unknown.

Several possible costs and benefits of EPCs to females have been envisioned, but these — especially benefits — are largely unstudied. Suggested benefits (reviewed by Westneat et al. 1990) include increased genetic variability of progeny, procurement of superior genes, and insurance against mate infertility. Possible costs include mate abandonment or reduction of PI by mate, increased intrabrood competition, and, for FEPCs, risk of injury or death (McKinney et al. 1983). Resistance to FEPC attempts is usually considered evidence that FEPCs are costly to females.

Here we explore the incidence of extra-pair courtship and copulation as they relate to bill color and other phenotypic traits in a captive population of Zebra Finches *Taeniopygia guttata*. Bill color was selected as the primary focus of this study because mating preferences for this highly variable and sexually dichromatic trait are well

established (Burley & Coopersmith 1987). We ask whether attractiveness influences participation in extra-pair courtship and copulation by members of either sex.

THE STUDY SPECIES

Zebra Finches are monogamous Australian estrildines with strong pair bonds that can endure for several years, both in nature (Zann pers. comm.) and in captivity (Butterfield 1970, Burley 1986). Both sexes participate in all phases of parental care, males providing about 40% of the care (Burley 1988).

Zebra Finches are sexually dichromatic. Males have several plumage markings (throat stripes, black breast bands, gold cheek patches, and white-flecked chestnut flank markings) that females typically lack. Bill color varies from orange to bright red, shows high repeatability within individuals (Burley unpubl.), and is somewhat heritable (Price unpubl.). On average, female bill color is less red than that of males, but there is considerable overlap between the sexes in phenotypic expression. Previous research (Burley & Coopersmith 1987) has established that females prefer males with the reddest bill colors. Males, by contrast, do not prefer red-billed females. Instead, they are most attracted to females toward the orange end of the continuum. On the basis of these findings we expected that females would more commonly engage in UEPCs with males having red bills.

METHODS

A breeding population was established that consisted of wild-type, adult, never-mated finches. Founders were selected on the basis of bill color: for each sex, 15 birds were selected from each phenotypic extreme of an available pool of 92 males and 72 females.

Opportunities for close inbreeding were minimal. Phenotypic measurements (bill color, breast band size, cheek patch size, flank patch size, and tarsus-metatarsus length) were made prior to the release of the founders into a 50 m³ aviary. Bill color was scored using the Munsell system (Burley & Coopersmith 1987, Burley unpubl.). Birds were assigned unique combinations of colored and numbered metal bands using colors which do not affect mate preferences. As an added precaution, color band combinations were changed several times throughout the course of the study.

Upon release, birds were free to select mates and reproduce for a 19-month span. During this interval, social parentage was established by observations of birds engaged in parental activities. Offspring were removed from the aviary at independence. Resources needed for reproduction were supplied in abundance. (See Burley 1986 for avicultural details.)

Observations of courtship and copulations were made during the last half of the experiment, primarily via all-accounts sampling. In this procedure, one or two observers watched courtship and copulatory behaviors from a darkened observation room and recorded all behaviors involving birds whose color band combinations could be clearly seen. Events were scored as courtship only (male observed singing in

characteristic courtship posture and oriented towards a female - Morris 1954), courtship followed by FEPC/FEPC attempt, or courtship followed by UEPC/UEPC attempt. Forced extra-pair copulations and attempted copulations were scored when females responded to mounting males by pecking or by moving rapidly away. Extra-pair copulations were scored as unforced when females showed no resistance or actively solicited copulation (Morris 1954). Because it is difficult to determine whether or not copulation attempts succeeded, no distinction is made here between successful and unsuccessful attempts.

RESULTS

We examined the number of extra-pair courtships and copulations observed for 20 individuals of each sex that survived through the observation period using stepwise regression procedures. Independent variables for females included bill color, tarsus length and reproductive success (RS — number of offspring surviving to independence). Additional variables included for males were breast band size, cheek patch area and number of spotted flank feathers. Separate analyses were conducted for which the dependent variable was participation in courtship, UEPCs, FEPCs, and for total courtship and copulatory activity (excluding within-pair courtship). We report the “best” statistical model based on the Cp statistic (SAS 1985).

TABLE 1 - Stepwise regressions of extra-pair interactions and male phenotypes. Total = total number of observed extra-pair courtships, FEPCs and UEPCs; court only = courtships which were not followed by copulation attempts; FEPC = forced extra-pair copulations; UEPC = unforced extra-pair copulations. Probability values in parentheses.

	Total	Court Only	FEPC	UEPC
Bill color	—	—	—	b = +0.0908 (.042)
Breast band size	b = +0.8026 (.009)	b = +0.7419 (.004)	—	b = +0.0717 (.038)
Cheek patch size	—	—	—	—
Flank patch size	—	—	b = +0.1512 (.116)	—
Tarsus length	b = +54.7468 (.022)	b = +45.0585 (.022)	—	b = +3.5256 (.173)
RS	b = +0.2333 (.027)	b = +0.1900 (.028)	—	b = +0.0216 (.083)
	<hr/> R ² = 0.5474 (.004)	<hr/> R ² = 0.5757 (.003)	<hr/> R ² = 0.1313 (.116)	<hr/> R ² = 0.5603 (.011)

A total of 37 FEPCs, 7 UEPCs, and 140 courtships not leading to attempted copulation were observed. For males, significant models were obtained in three of four analyses (Table 1). Bill color contributed to only one of these models, namely male tendency to engage in UEPCs. The direction was as predicted; in fact, males from the red end of the continuum participated in all seven unforced extra-pair mountings (binomial $P = 0.015$). There was, however, no tendency for red-billed males to court disproportionately often.

Males with high within-pair RS participated in courtship and unforced extra-pair activities at high frequency, but RS patterns did not predict participation in FEPCs. Males with large breast bands tended to court and participate in UEPCs and total extra-pair activities, but not in FEPCs.

For females, significant models were obtained for courtship and for total extra-pair activities (Table 2). Within-pair RS of females was the sole predictor in both these models. The model for UEPCs approached significance; in addition to RS, bill color contributed to the best model, with orange-billed females tending to participate disproportionately often.

TABLE 2 - Stepwise regressions of extra-pair interactions and female phenotypes. Legend as in Table 1.

	Total	Court Only	FEPC	UEPC
Bill color	–	–	–	b = -0.0428 (.161)
Tarsus length	–	–	b = +6.7920 (.259)	
RS	b = +0.1714 (.016)	b = +0.1358 (.020)	–	b = +0.017 (.109)
	$R^2 = 0.2571$ (.016)	$R^2 = 0.2428$ (.020)	$R^2 = 0.0632$ (.259)	$R^2 = 0.2458$ (.069)

If females selectively participate in UEPCs in order to obtain good genes for bill color, we can expect that females will copulate with males whose bill colors are redder than those of their mates, while females involved in FEPCs should not show this trend. The average difference of bill scores between mate and copulatory partners of 12 females involved in FEPCs was 0.31 bill color units (mates' bills being slightly redder). For seven of these females, the average difference scores favored their mates, while for five, copulatory partners had higher average scores. By contrast, four females observed in UEPCs were involved in six copulations, all with males having bills redder than those of the females' mates. A fifth female copulated with a male whose bill color score was identical to that of her mate; both her mate and EPC partner had the maximum score observed. The average difference score for the mates and copulatory partners of these five females was 2.51 units. The difference between UEPCs and FEPCs in female tendency to copulate with males whose bills were redder than those of their mates is significant ($P = 0.041$) by a one-tailed Fisher 2 x 3 exact test.

DISCUSSION

Male bill color influences participation in unforced extra-pair copulatory activities, but does not influence participation in courtship or FEPC. Moreover, females tend to engage in UEPCs with males whose bill colors are redder than those of their mates. These results suggest that attractive males obtain greater fitness benefits from EPCs than do unattractive males. DNA fingerprinting is under way to determine the correspondence between EPCs and extra-pair fertilizations.

The finding that male breast band size predicts courtship and success in UEPCs is somewhat surprising, since females lack mate preferences for breast band size (Coopersmith & Burley unpubl.). Moreover, breast band size is not correlated with bill color (Price & Burley unpubl.). The social significance of breast band size remains obscure. Preferences for flank markings and tarsus length (an indicator of body size) have not been measured. In this experiment, male tarsus length was negatively correlated with within-pair RS (Price & Burley unpubl.).

Female bill color contributes to the best UEPC model, with orange-billed females tending to engage in unforced extra-pair activities. The opportunity for a significant female bill color effect was weakened by the tendency of red-billed females to die (Price & Burley unpubl.); as a result, only six of the 20 females included in this behavior sample came from the red end of the continuum. Mating patterns were weakly negatively assortative for bill color (Price & Burley unpubl.), so the tendency of orange-billed females to engage in UEPCs cannot be explained by lack of attractiveness of their mates. Further work is needed to establish whether attractive females do indeed participate uncommonly often in UEPCs.

Birds of both sexes that participate in extra-pair courtships and UEPCs tend to have high within-pair RS. Individuals capable of high RS should be preferred as mates. Others may assess their capability through a complex set of phenotypic cues or, in a colonial species, through direct observation of reproductive performance. According to the differential allocation hypothesis (Burley 1986), individuals of both sexes that are desirable as mates incur lower parental care duties than do unattractive ones. Such birds may spend more time away from the nest, having more time in which to court or be courted. If this were the explanation for the association between RS and courtship and UEPCs, one would also expect a similar pattern for FEPCs. Such a pattern was not found here.

An alternative explanation also assumes that birds with high RS are attractive: attractive males may profit more from extra-pair courtship and engage in it more commonly, while attractive females are courted more often. This explanation is deficient because a similar trend does not occur for bill color, a trait for which variable attractiveness is well established. Bill color is correlated with RS in both sexes, however (Price & Burley unpubl.); perhaps RS is a better indicator of attractiveness than is bill color alone.

Regardless of the reason for the association between RS and extra-pair activities, there is an important implication of this result: there is no tradeoff between RS obtained within the pair bond and effort devoted to seeking RS through extra-pair courtship. Such a tradeoff is predicted by the principle of allocation (Williams 1966).

The low proportion of unforced EPCs (16%), the finding that only 5% of extra-pair courtships result in UEPCs, and the distinct differences in phenotypic traits of males involved in UEPCs versus FEPCs, do not support the contention (Halliday & Arnold 1987) that the tendency of females to engage in EPCs evolved as a correlated response to selection on males. Rather it appears that UEPCs are advantageous to females as well as to males.

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CONCLUDING REMARKS: MATING AND MATE CHOICE

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This symposium illustrates some of the range of approaches currently taken by researchers studying mate choice — from Lloyd Davis's efforts to infer mating preferences from mating patterns observed in nature to Tim Birkhead's models of sperm competition. Birkhead and Hunter reported here on their investigations of extra-pair paternity in the Zebra Finch and have shown a significant last-male advantage. They also suggest that females are in control of mating and paternity of their offspring. The work by myself and Don Price showing greater success of attractive red-billed males in unforced extra-pair copulations certainly gives credence to the notion of female choice of copulatory partners. However, in our study only 16 % of EPCs were unforced, indicating that females are hardly in "control". Also, within-pair copulations were much less frequent than EPCs in our study. Although rates of extra-pair fertilization in Zebra Finches are relatively low based on studies from Birkhead's group and from mine, the frequent attempts of males of this gregarious species to obtain EPCs through force should have a significant influence on social organization and pairbond dynamics.

I hope that detailed investigation of the mechanisms of sperm storage and sperm utilization, as well as sperm morphology, will continue, perhaps using Zebra Finches and chickens as models of birds with very different social organizations. Such study would provide insight into the potential range of evolved strategies of sperm competition in birds.

Davis has investigated mate choice in Adélie Penguins, which are sexually indistinguishable by plumage, but are size-dimorphic. He has found strong female preferences for previous partners and known nesting sites. For these traits, female choice is not directional — i.e. there is no consistently preferred male phenotype. Davis's results provide a reminder that sexual dimorphism does not always evolve through sexual selection and suggest that constraints may limit the evolution of sexually selected traits.

Certainly the most provocative paper in the symposium is Randy Thornhill's. He argues that the current focus on the microevolutionary process — especially on heritability of traits and fitness measurements — does not yield direct evidence regarding the causes of evolutionary patterns we observe because cumulative directional selection, which is the force responsible for producing adaptation, eliminates heritable variation. Hence any genetic variability we witness is relatively unimportant. By this equilibrium view, constraints on adaptive evolution are trivial. I would like to point out that, while there may be no heritable variation for secondary sexual traits in junglefowl, there is heritable variation in Zebra Finch bill colour, as well as strong mate choice

for bill colour by both sexes. Moreover, recent research indicates that such variation is maintained by the constraint of a genetic correlation between the sexes.

Thornhill's approach implies that, while the investigation of process cannot accurately predict or reveal resulting pattern, nevertheless process can be accurately inferred from pattern — i.e. that we can understand the process of sexual selection by elucidating functional design. I cannot accept the contention that process is evident from pattern while pattern is not revealed from process. While I agree to a considerable extent with Thornhill's view that phylogeny recapitulates psychology, I view these two approaches as necessary and complementary, that neither is sufficient by itself to understand the subtleties of evolution. In sum, then, researchers assembled here today represent a range of philosophical as well as methodological approaches to the study of avian mating behaviour.

SYMPOSIUM 23

**FEEDING ECOLOGY OF ANTARCTIC AND
SUB-ANTARCTIC SEABIRDS**

Convener M. J. IMBER

SYMPOSIUM 23

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INTRODUCTORY REMARKS: FEEDING ECOLOGY OF ANTARCTIC AND SUB-ANTARCTIC SEABIRDS

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Of the original five speakers found for this symposium, we have regrettably lost two who were unable to raise sufficient funds: Vincent Ridoux was to have talked about the Crozet Islands, until recently a blind spot in our knowledge of this subject, and John Cooper was to have presented a review of studies at the Prince Edward Islands. Fortunately Allen Place agreed to convert a paper, first submitted as a contributed paper, for presentation here on digestion by chitinase.

When I began studying seabird feeding ecology 20 years ago, the literature often gave the impression that seabirds are land birds that sometimes go to sea. It is gratifying that many studies now are, directly or indirectly, of birds at sea; as they really are – birds that sometimes visit land. One of our speakers is going to talk about birds that spend most of their lives in, or on, the sea – penguins and shags.

CHITIN DIGESTION AND ASSIMILATION BY SEABIRDS

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ABSTRACT. Seabirds such as those that feed on crustaceans in the Southern Ocean would benefit greatly from an ability to tap the considerable energy and carbon/nitrogen source represented by the exoskeletons of their prey. We have estimated chitin assimilation efficiencies for Sooty Albatrosses *Phoebetria fusca*, White-chinned Petrels *Procellaria aequinoctialis*, Leach's Storm Petrels *Oceanodroma leucorhoa* and Rockhopper *Euyptes chrysocome*, Gentoo *Pygoscelis papua* and King *Aptenodytes patagonicus* penguins fed meals of Antarctic krill *Euphausia superba*. These seabird species are apparently able to assimilate a substantial proportion (34.5 - 85%) of the chitin that they ingest. We also have obtained preliminary estimates of chitinase activity in the Sooty Albatross and Leach's Storm Petrel. Activity was found in the proventricular mucosa and contents but not in the intestinal mucosa. Absorption of the chitin building block, N-acetyl-D-glucosamine, is half as efficient as absorption of glucose in Leach's Storm Petrel chicks.

Keywords: Sooty Albatross, White-chinned Petrel, Leach's Storm Petrel, Rockhopper Penguin, Gentoo Penguin, King Penguin, chitin assimilation efficiency, chitinase activity, N-acetyl-D-glucosamine absorption, glucose absorption.

INTRODUCTION

The chitin in crustacean exoskeletons represents a substantial source of potential energy for marine predators (Anderson et al. 1978, Rehbein et al. 1986). Estimates of krill biomass, for example, range from 80 to 500 million metric tons (Sahrhage & Steinberg 1975), some 0.6 to 3.4 million tons of which comprise chitin. With the premise that the ability to digest chitinous crustacean exoskeletons is of considerable selective advantage to opportunistic marine predators, we investigated the degradation of chitin and subsequent assimilation of the products of chitinolysis in the guts of six seabird species with widely different natural diets (Jackson et al. *subm.*). We also review the evidence for chemical digestion of chitin in these species and other birds.

Most forms of chitin (a (1 - 4)- β -linked homopolymer of N-acetyl-D-glucosamine) are tough, highly hydrophobic, insoluble in most ordinary solvents, and relatively inert to biodegradation (Pangburn et al. 1984, Gooday 1990). The ability to degrade chitin involves the action of two enzymes, chitinase (E.C. 3.2.1.14 - mucopolysaccharide) and chitobiase (β -N-acetyl-D-glucosaminidase, E.C. 3.2.1.30) (Jeuniaux 1961). Chitinase hydrolyses chitin to the repeating subunit chitobiose, the β -1,4 linked dimer of N-acetyl-D-glucosamine (NAG), and chitobiase hydrolyses the dimer to NAG.

RESULTS

Chitin balance

Chitin digestion was investigated in Leach's Storm Petrel *Oceanodroma leucorhoa* chicks, Sooty Albatross *Phoebetria fusca* adults and fledglings, White-chinned Petrel *Procellaria aequinoctialis* fledglings, and Rockhopper *Eudyptes chrysocome*, Gentoo *Pygoscelis papua* and King *Aptenodytes patagonicus* penguin adults. Five birds of each species and age class were used. We determined the chitin content of dried, homogenized food and fecal samples by the method of Horwitz et al. (1975), or of Clarke (1980), and expressed apparent chitin utilization efficiencies as percentages of the original quantity of chitin ingested. Chitin utilization efficiency ranged from 35 to 85% in the six species studied. These values are similar to published chitin assimilation efficiencies of 57% in passerines and 24-32% in Domestic Hens *Gallus domesticus* (Jeuniaux & Cornelius 1978, see Figure 1), but are lower than values of up to 92% given by Hirano et al. (1984) for domestic chicks and hens.

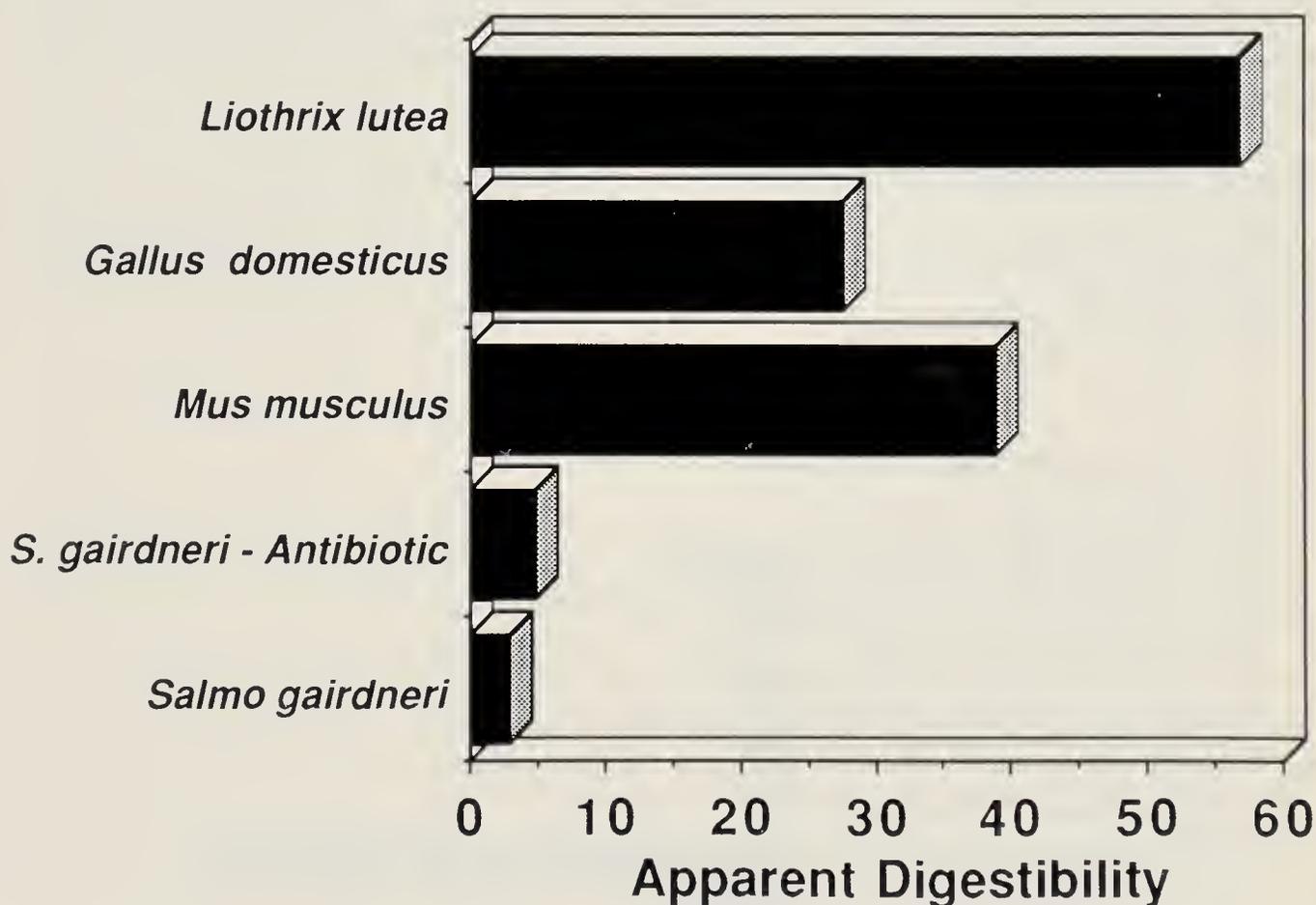


FIGURE 1 - Apparent chitin digestibilities in Japanese Nightingales *Liothrix lutea*, Domestic Hens *Gallus domesticus*, House Mice *Mus musculus* and Rainbow Trout *Salmo gairdneri*. After Jeuniaux & Cornelius (1978) and Lindsay et al. (1984).

In vivo chitinolysis in Leach's Storm Petrel chicks

We used a double-isotope technique to measure hydrolysis of chitin in Leach's Storm Petrel chicks. By feeding a homogenized krill meal to which had been added tritiated chitin and carbon-14 labelled polyethylene glycol ("PEG", a non-absorbable aqueous marker with M.W. 4000), we avoided over-estimation of chitin digestibility resulting from retention of undigested chitin in the birds' guts.

Post-ingestion sampling of proventricular contents by intubation indicates that average rates of proventricular chitinolysis are between 17 and 33 $\mu\text{mol NAG/hr/ml}$ of proventricular liquid. Hydrolysis is slower in birds fed larger krill meals. One ml of proventricular liquid contains sufficient chitinase activity to completely hydrolyse the ingested chitin (240 to 489 mg) to chitobiose in 24 hours. Between 76% and 88% of the total dose of the PEG-4000 aqueous marker was recovered in excreta after 24 hours, and tritiated chitin is recovered in the feces at between 40% and 50% of the ingested quantity after the same period. These apparent digestibilities for radio-labelled chitin are comparable to those obtained in the chitin balance study using the crude fiber measurement with unlabelled chitin.

Assimilation of the products of chitinolysis by Leach's Storm Petrel chicks

N-acetyl glucosamine (NAG) and D-glucosamine absorption efficiencies were estimated both using an isotope ratio technique, and by measuring total isotope recovery. The first method was used in birds fed the tritiated monosaccharide of interest (either N-acetyl glucosamine or D-glucosamine) plus ^{14}C -labelled polyethylene glycol in a carrier meal of either Avian ringer solution or homogenized whole krill. Secondly, we measured total isotope recovery of ^{14}C -glucose, and of the above two tritiated monosaccharides, in accumulated feces.

Absorption efficiency values of NAG estimated by the marker ratio method and by radio-isotope recovery methods are similar, between 39% and 46%. Absorption efficiencies of D-glucosamine were 12.5%. In contrast, 90% of ingested D-glucose is absorbed.

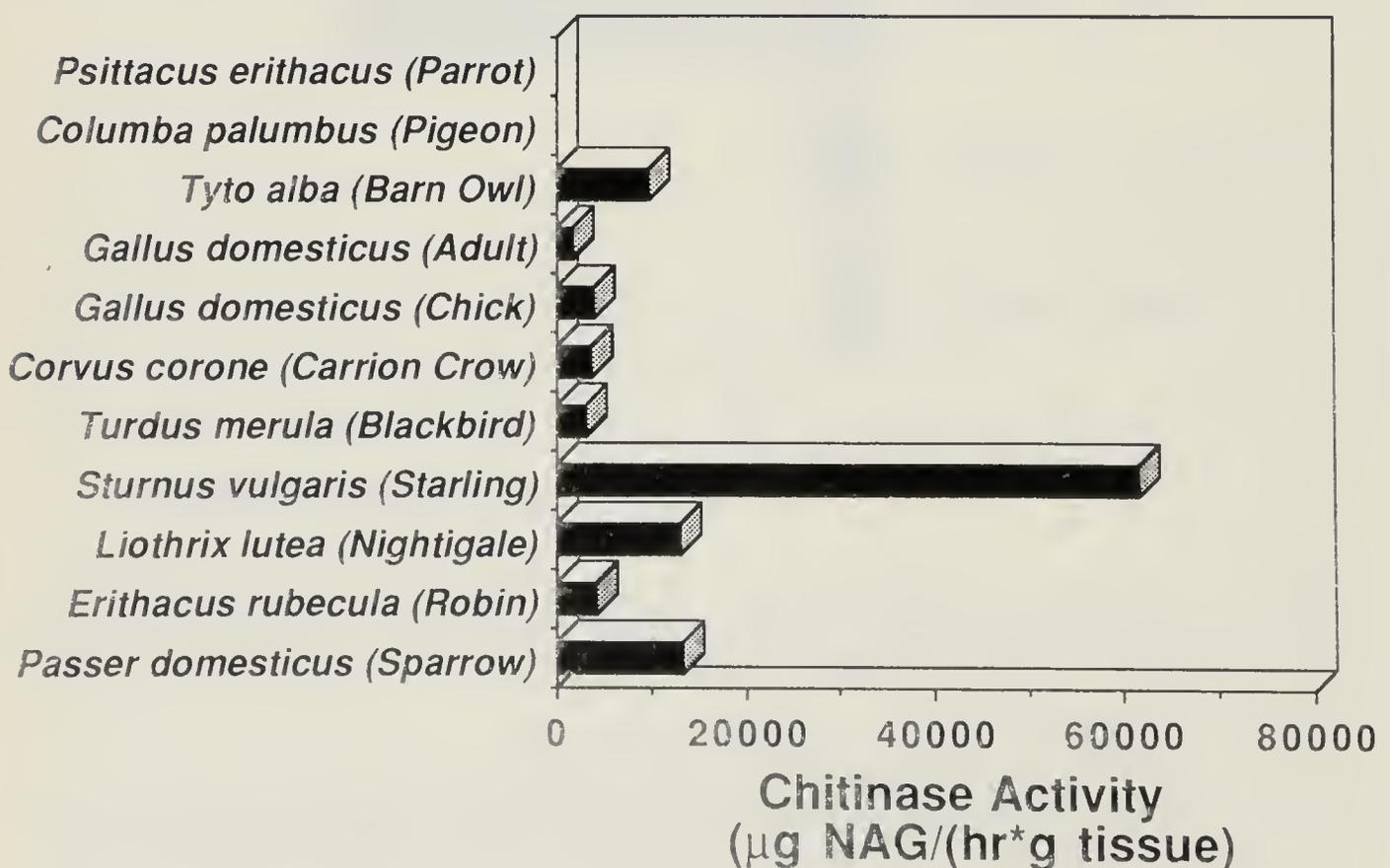


FIGURE 2 - Chitinase activities ($\mu\text{g NAG}$ produced per gram of tissue per hour) in eight species of terrestrial birds. After Jeuniaux & Cornelius (1978).

DISCUSSION

Chitinolytic enzyme activity

The occurrence of chitinase in vertebrate digestive systems has been reviewed by Jeuniaux (1963) and more recently by Jeuniaux & Cornelius (1978), who reported gastric chitinase activity in eight species of partially insectivorous terrestrial birds (Figure 2). Chitinase activity was detected in the regurgitated pellets of a further seven raptor species by Leprince et al. (1979).

Endogenous chitinase synthesis by vertebrates was first reported by Jeuniaux (1961), and has since been documented in marine fish (e.g. Okutani 1966, Rehbein et al. 1986, Seiderer et al. 1987) and in terrestrial mammals (Cornelius et al. 1975).

The main source of avian chitinase is the mucosa of the proventriculus, with chitinase activity levels decreasing progressively from the gizzard and intestinal lumen contents to the intestinal mucosa (Jeuniaux 1963). These chitinases have an optimum pH of 4.7 - 5.4, retaining considerable activity at lower pH values, but showing a sharp decrease in activity above pH 6. Chitinase activity levels in the gastric mucosae of the six seabirds in the present study are within the range of the levels reported by Jeuniaux & Cornelius (1978), whereas no chitinase activity was discernible in samples of the intestinal mucosa of the White-chinned Petrel and Sooty Albatross (Jackson et al. *subm.*). In view of the fact that many invertebrates are able to synthesise chitinolytic enzymes (Jeuniaux 1971), it seems likely that synthesis of chitinase is a primitive retained characteristic widespread among high-latitude seabirds because of the advantages it confers on opportunistic marine predators feeding in waters rich in crustacea.

Why digest chitin?

The seabirds we studied are able to hydrolyse a substantial proportion of the chitin that they ingest. Chitin itself is probably not an important energy source for seabirds, because crustaceans such as krill contain only a small proportion of chitin (between 2.1% and 2.9%, dry mass, Clarke 1980, this study)¹. Even assuming that chitin has the same energy value (17.9 kJ.g⁻¹ dry mass, Karasov *in press*) as whole krill, an overestimate, seabirds able to digest and fully assimilate 40% - 90% of ingested chitin would derive a maximum of between 1.2% and 2.7% of their total energy gain from the chitin fraction of each meal. Furthermore, our data on absorption of NAG and D-glucosamine suggest that intestinal absorption of the products of chitinolysis is far from complete in at least one planktivorous species, further reducing the potential energetic value of chitin to seabirds. The major benefit of chitinolysis to seabirds is thus probably facilitation of digestion of soft prey tissues within the exoskeletons of crustacean prey.

As a dietary supplement, chitin improves utilization efficiency of whey in Domestic Hens (Sprenen et al. 1984), apparently by enhancing intestinal growth of lactase-producing *Bifidiobacteria* spp. Despite the benefits of chitin digestion, absorption of the

¹ Cephalopod "beaks" are proteinaceous, with a small chitin component (6-12.3% by mass, Hunt & Nixon 1981). The small amount of energy residing in the chitin fraction of accumulated beaks in seabird stomachs may be unavailable to the birds in the absence of an appropriate protease.

products of this digestion may carry a cost. Chitin and chitosan supplements in the diets of juvenile Domestic Hens (Hirano et al. 1984) and Rainbow Trout *Salmo gairdneri* appear to inhibit growth (Lindsay et al. 1984). In the light of our data, which suggest surprisingly low absorption efficiencies of the products of chitinolysis, D-glucosamine in particular, the inhibitory influence of chitin breakdown products on the growth of juvenile seabirds warrants further investigation.

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FOOD RESOURCE UTILIZATION BY SEABIRDS BREEDING IN PRYDZ BAY, ANTARCTICA

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ABSTRACT. Prydz Bay supports nine seabird species that breed on the Princess Elizabeth Land coast: two penguins, six Procellariiformes and one skua. Information on their diet is reviewed. Apart from the scavenging South Polar Skua *Catharacta maccormicki* and Southern Giant Petrel *Macronectes giganteus*, three diet types were distinguished. First, the Emperor Penguin *Aptenodytes forsteri* ate almost exclusively fish; secondly, the Adelie Penguin *Pygoscelis adeliae*, Cape Petrel *Daption capense*, and Wilson's Storm Petrel *Oceanites oceanicus* consumed at least 60% euphausiid, the remainder largely fish; and thirdly, a diet of greater than 60% fish, the rest euphausiids, was taken by the Southern Fulmar *Fulmarus glacialisoides*, Antarctic Petrel *Thalassoica antarctica* and Snow Petrel *Pagodroma nivea*. Seasonal fluctuation in composition of Adelie Penguin, Cape Petrel and Southern Fulmar diet suggested either fluctuating foraging ranges or movement of *Euphausia superba* inshore during summer months. Annual fluctuation in diet composition was correlated with seabird reproductive success. When *E. crystallorophias* dominated the euphausiid component of Adelie Penguin diet, reproductive success was high; when *E. superba* was scarce in Prydz Bay, Antarctic Petrel and Southern Fulmar productivity was low.

Keywords: Penguins, petrels, diets, krill, fish, Antarctica.

INTRODUCTION

Many early Antarctic seabird diet studies were of populations breeding in the Atlantic sector of the Southern Ocean. These studies indicated the importance of Antarctic krill *Euphausia superba* to many species. Some relied on it almost exclusively. This situation reflects the relative abundance of this euphausiid there. Circumpolar surveys of relative krill abundance have identified the Scotia Sea and Atlantic sector as the richest area for krill in the Southern Ocean. Elsewhere there is significantly less krill, and seabird diets studied have been more varied.

Nine species of bird that rely either directly or indirectly on marine resources breed in Prydz Bay. Two scavenging/predatory birds, the South Polar Skua *Catharacta maccormicki* and the Southern Giant Petrel *Macronectes giganteus* inhabit the region. Though the skua consistently consumes at least some Adelie Penguins, it adapts its diet to whatever is the closest colony of nesting seabirds (Green 1986a, Norman & Ward 1990). Approximately 20 pairs of Southern Giant Petrels nest at Hawker Island (Johnstone et al. 1973). The birds here range throughout the Vestfold Hills and Rauer Islands, scavenging and predating at seabird colonies, particularly of the Adelie Penguin, and at Weddell seal *Leptonychotes weddellii* and elephant seal *Mirounga leonina* haulout sites (Green 1986b). These two species are not considered further in this account.

About 2000-3000 pairs of Emperor Penguins *Aptenodytes forsteri* breed at Amanda Bay (Cracknell 1986), and an estimated 325,000 pairs of Adelie Penguins *Pygoscelis*

adeliae breed within the Prydz Bay area (Whitehead & Johnstone 1990). Approximately 17,000 pairs of Southern Fulmar *Fulmarus glacialisoides* and 2400 pairs of Antarctic Petrel *Thalassoica antarctica* breed at the Rauer and Svenner Islands (Green & Johnstone 1986, Woehler and Johnstone in press). An estimated 1600 pairs of Cape Petrels *Daption capense* nest at the Vestfold Hills and Svenner Islands (Woehler & Johnstone in press), and an unknown number of Snow Petrels *Pagodroma nivea* and Wilson's Storm Petrels *Oceanites oceanicus* also breed throughout the region.

This paper synthesizes the results from recent diet studies of each of these species.

SEABIRD DIETS

Dietary composition

Few prey taxa are consumed by Prydz Bay seabirds, indicative of the lack of diversity in the Antarctic macro-zooplankton and pelagic fish faunas. The three most important prey species in terms of mass are *E. superba* and *E. crystallophias* and the pelagic schooling nototheniid fish, *Pleuragramma antarcticum* (Tables 1 and 2). The myctophid fish *Electrona antarctica* is important to some of the species (Table 2). *E. crystallophias* and *P. antarcticum* typify the continental shelf fauna (Thomas & Green 1988, Hubold 1985), while *E. superba* and *E. antarctica* are more commonly associated with waters near the shelf-break and beyond (Hosie et al. 1988, Williams & McEldowney in press).

Despite the lack of prey diversity there are some obvious differences in seabird diets. Three obvious groupings of diet type are distinguishable.

First, there is only one diet that consists almost entirely of fish, that of the Emperor Penguin. Cephalopods contribute a minor component (Table 1).

The second diet type is that represented by the Adelie Penguin, Cape Petrel and Wilson's Storm Petrel, consisting of in excess of 60% euphausiid, the remainder comprising mostly fish. The Cape Petrel and Wilson's Storm Petrel may be segregated from the Adelie Penguin diet to an extent by the consumption of some *P. antarctica*, in addition to *P. antarcticum* (Tables 1 and 2). Further, *E. crystallophias* dominates the euphausiid component of the Wilson's Storm Petrel diet by almost 2:1 (by mass) over *E. superba*. In both the Cape Petrel and Adelie Penguin, on average, this ratio is reversed (Table 1).

The third diet type consists of greater than 60% fish, the remainder being mostly euphausiid: represented by Antarctic Petrels, Southern Fulmars and Snow Petrels. Snow Petrel diet may be distinguished from the other two in that the majority of fish consumed were *E. antarctica*, not *P. antarcticum*, and most euphausiids were *E. crystallophias*. The euphausiid component of Antarctic Petrel and Southern Fulmar diet was exclusively *E. superba* (Tables 1 and 2).

The food resources of the Emperor Penguin may be further differentiated from the other seabirds by prey size. They seem to consume smaller *P. antarcticum* than the other species, all of which eat similar-sized fish (Table 3). This probably shows

TABLE 1 – Percentage composition by mass, and frequency of occurrence (in parentheses), of the major prey taxa in the diets of seabirds breeding in Prydz Bay.

	Euph's. combined	<i>E. superba</i>	<i>E. cryst.</i>	Fish	Amphs.	Cephs.	Ref.
Adelie Penguin							
1982/83 Post Hatch		25(80)	42(84)	32(88)	1(79)		1
1983/84 Pre Hatch		6(14)	46(46)	3(20)	39(94)		1
1983/84 Post Hatch		77(100)	18(84)	5(80)	0.1(16)		2
1984/85 Pre Hatch		5(10)	6(14)	4(18)	58(70)		2
1984/85 Post Hatch		66(90)	13(45)	20(90)	0.5(40)		2
Emperor Penguin							
1984	(1)			(96)	(30)	(3)	3
1986	0.1(6)			97(86)	0.3(41)	3(36)	4
Cape Petrel							
1983/84	76(77)	?(47)	?(5)	23(38)			5
1987/88		85(95)	0(0)	14(77)	0.5(5)	0.5(5)	6
1989/90		37(35)	39(52)	19(62)	2(17)	2(21)	7
Antarctic Petrel							
1982/83		(100)	(0)	(6)	(0)	(18)	8
1987/88		22(83)	0(0)	78(98)	0(0)	0(0)	6
Southern Fulmar							
1987/88		36(97)	0(0)	63(100)	0.2(9)	0.4(9)	6
Snow Petrel							
1989/90		6(22)	28(66)	65(94)	0.8(6)	0.3(6)	7
Wilson's Storm Petrel							
1989/90		25(46)	42(73)	28(78)	5(42)	0.02(2)	7

References: (1) Puddicombe & Johnstone (1988), (2) Green & Johnstone (1988), (3) Green (1986c), (4) Gales et al. (1990), (5) Green (1986d), (6) Arnould & Whitehead (in press), (7) Hodum & Whitehead (unpublished data), (8) Montague (1984)

differing-sized *P. antarcticum* are available to Emperor Penguins over their winter breeding months, or in the deep water that they can exploit.

Adelie Penguins and Cape Petrels consume similar-sized prey: *P. antarcticum* and, in the only year when stomach samples of both were collected concurrently (1983/84), *E. superba* and *E. crystallophias* (Tables 3 & 4).

Though Wilson's Storm Petrel also consumed similar-sized euphausiids, its fish diet consisted of post-larval / juvenile individuals, not the sub-adult / adult fish consumed by all other species (Tables 3 - 5).

Antarctic Petrel, Southern Fulmar and Snow Petrel seem to consume largely overlapping size-ranges of *P. antarcticum*, though in the year when Antarctic Petrel and Southern Fulmar diet was studied concurrently (1987/88), Southern Fulmars ate larger

TABLE 2 – Percentage composition by numbers of the taxa comprising the fish component of diets of Prydz Bay seabirds.

	<i>P. antarcticum</i>	<i>Trematomus/ Pagothenia</i>	Channichthyids	<i>F. antarctica</i>	Ref.
Adelie Penguin	36*	21*	17*	0*	1
Emperor Penguin	95	5	0	0	2
	95	2	2	0	3
Cape Petrel	0	100	0	0	4
	100	0	0	0	5
	64	0	0	36	6
Antarctic Petrel	100	0	0	0	7
	100	0	0	0	5
Southern Fulmar	100	0	0	0	5
Snow Petrel	37	0	0	63	6
Wilson's Storm Petrel	?50	0	0	?50	6

* Frequency of occurrence data only - Percentage composition by number data not available

References: (1) Puddicombe & Johnstone (1988), (2) Green (1986c), (3) Gales et (1990), (4) Green (1986d), (5) Arnould & Whitehead (in press), (6) Hodum & Whitehead (unpublished data), (7) Montague (1984)

P. antarcticum, perhaps suggesting a partitioning of food resources. No difference existed in the size of *E. superba* consumed by these two species, and no data exist on the size of euphausiid consumed by Snow Petrels (Tables 3 - 5).

That seabirds breeding in Prydz Bay take *E. crystallophias*, *P. antarcticum* and *E. antarctica* in similar or greater proportions to *E. superba* has prompted the suggestion that the latter is of reduced importance here to these seabird predators (Williams 1988) compared with the South Atlantic, where some of these seabirds eat *E. superba* almost exclusively. However, the only report of stomach contents from birds sampled at sea off Prydz Bay found that *E. superba* constituted almost 100% of the prey items (Montague 1984). This may indicate that *E. superba* is the staple prey for many seabirds during oceanic stages of their life-cycles: non-breeding individuals during summer, and the entire populations outside the breeding season. Sampling at sea during these periods would resolve this possibility.

Based on the current knowledge of prey distributions, the almost exclusive reliance of Emperor Penguins on *P. antarcticum* suggests that they are largely restricted to the waters of the continental shelf; the occurrence of *E. superba* in the diets of Adelie Penguins, Cape Petrels, Wilson's Storm Petrels, Antarctic Petrels and Southern Fulmars would suggest that they range to the continental shelf-break on foraging trips;

and the high incidence of *E. antarctica* in Snow Petrels' diet perhaps suggests that they range beyond the continental shelf. The incidence of *E. crystallophias* in the diet of Adelie Penguins, Wilson's Storm Petrels and Snow Petrels however, indicates a substantial amount of foraging over the continental shelf – perhaps on their way to or from the shelf-break.

TABLE 3 – Standard lengths (mm) of *P. antarcticum* consumed by Prydz Bay seabirds.

	<i>P. antarcticum</i> Standard length (mm)				Dates	Ref.
	x	sd	Range	n		
Emperor Penguin	129.5	23.8	72.3 - 182.6	21	Aug - Oct 84	1
	101.0	10.3	69.6 - 134.9	194	Aug - Oct 86	2
Adelie Penguin	139.1	16.5		17	83/84 & 84/85	3
Cape Petrel	144.5	12.1		3	18 Jan - 12 Feb 88	4
	148.1	11.2	125.2 - 158.1	7	3 Feb - 22 Feb 90	5
Antarctic Petrel	160.0	160.0		2	16 Dec 82	6
	125.4	35.2		143	16 Jan - 12 Feb 88	4
Southern Fulmar	142.1	33.4		104	26 Jan - 12 Feb 88	4
Snow Petrel	142.4	23.1	99.1 - 162.0	6	7 Feb - 20 Feb 90	5

In Wilson's Storm Petrel samples only one nototheniid juvenile was identified.

References: (1) Green (1986c), (2) Gales et al. (1990), (3) Green & Johnstone (1988), (4) Arnould & Whitehead (in press), (5) Hodum & Whitehead (unpublished data), (6) Montague (1984)

The most difficult species pair in which to detect food resource segregation is the Antarctic Petrel and Southern Fulmar. An investigation of these birds' foraging ranges and feeding methods would be valuable.

Seasonal fluctuations

Repeated serial sampling shows seasonal variation in the diets of Adelie Penguins (Green & Johnstone 1988), Emperor Penguins (Green 1986, Gales et al. 1990), and Cape Petrels, Antarctic Petrels and Southern Fulmars (Arnould & Whitehead in press).

Adelie Penguin diet is dominated by *E. crystallophias* and amphipods prior to hatching, with *E. superba* and *P. antarcticum* becoming important during the chick-rearing period (Table 1).

During the winter chick-rearing of the Emperor Penguin, *P. antarcticum* becomes increasingly important over the benthic *Trematomus / Pagothenia*, and crustaceans are also more frequently brought ashore (Green 1986, Gales et al. 1990).

TABLE 4 – Body lengths (mm) of *E. superba* consumed by Prydz Bay seabirds.

	<i>E. superba</i> Body length (mm)				Dates	Ref.
	x	sd	Range	n		
Adelie Penguin	40.6	7.9	20.3 - 56.9	262	82/83 Post & 83/84 Pre Hatch	1
	40.1	4.3	-	448	83/84 Post Hatch	2
	40.7	4.7	-	8	84/85 Pre Hatch	2
	36.6	4.6	-	137	84/85 Post Hatch	2
Cape Petrel	41.7	5.4	23.2 - 52.6	93	26 Jan - 20 Feb 84	3
	46.6	4.3	-	99	18 Jan - 12 Feb 88	4
	46.2	2.7	40.5 - 49.3	13	3 Feb - 22 Feb 90	5
Antarctic Petrel	47.7	2.7	41 - 55	47	16 Dec 82	6
	46.6	4.1	-	102	16 Jan - 12 Feb 88	4
Southern Fulmar	47.0	3.8	-	176	26 Jan - 12 Feb 88	4
Wilson's Storm Petrel	46.4	3.5	42.9 - 49.9	3	4 Feb - 19 Feb 90	5

References: (1) Puddicombe & Johnstone (1988), (2) Green & Johnstone (1988), (3) Green (1986d), (4) Arnould & Whitehead (in press), (5) Hodum & Whitehead (unpublished data), (6) Montague (1984)

TABLE 5 – Body lengths (mm) of *E. crystallophias* consumed by Prydz Bay seabirds.

	<i>E. crystallophias</i> Body length (mm)				Dates	Ref.
	x	sd	Range	n		
Adelie Penguin	27.4	1.8	21.1 - 34.2	343	82/83 Post & 83/84 Pre Hatch	1
	28.3	1.8	-	284	83/84 Post Hatch	2
	26.3	2.1	-	57	84/85 Post Hatch	2
Cape Petrel	25.5	1.4	23.9 - 26.4	3	26 Jan - 20 Feb 84	3
	25.9	2.9	20.0 - 30.9	69	3 Feb - 22 Feb 90	4
Wilson's Storm Petrel	26.6	3.0	20.1 - 32.9	50	4 Feb - 19 Feb 90	4

References: (1) Puddicombe & Johnstone (1988), (2) Green & Johnstone (1988), (3) Green (1986d), (4) Hodum & Whitehead (unpublished data)

During the chick-rearing of both Cape Petrels and Southern Fulmars, *P. antarcticum* declines in importance concomitant with increase of *E. superba*. For Antarctic Petrels, the reverse was reported (Arnould & Whitehead in press).

These seasonal trends reflect fluctuating seabird foraging ranges while breeding, fluctuating prey distributions, changing prey preferences, or some combination of these. Further research on these aspects is needed.

Assessing seasonal fluctuation in diet may provide an indirect measure of seasonal fluctuation of prey distribution or behaviour, if foraging ranges are constant and the extent to which prey consumption reflects availability does not alter seasonally. Accordingly, Adelie Penguins may forage further offshore during chick-rearing than during incubation. This seems unlikely: the small weight of *E. crystallophias* brought ashore during incubation probably represents the most recent items consumed en route to the colony from more distant foraging grounds, from which few identifiable items remain, as foraging trips were relatively lengthy, there being no need to regularly bring back food to the chick.

Increased amounts of *P. antarcticum* in Emperor Penguin stomach contents may suggest a greater concentration of effort over deeper shelf waters later in chick-rearing, compared with more local foraging in relatively shallow waters earlier.

The contrasting patterns of seasonality in diet composition of Cape Petrels and Southern Fulmars, compared with Antarctic Petrels, may suggest different foraging locations. Perhaps Cape Petrels and Southern Fulmars forage increasingly offshore as chicks grow, while Antarctic Petrels forage increasingly nearer shore.

Alternatively, if constant foraging ranges are assumed, *E. superba* may move inshore over the continental shelf during chick-rearing of these species, and more of the Prydz Bay *E. superba* population may come within foraging range of Adelie Penguins, Cape Petrels and Southern Fulmars. This would support the contrasting view that Antarctic Petrels forage further offshore than Southern Fulmars.

Clearly, there are three distinct areas requiring work if this spectrum of possible predator-prey interactions is to be resolved. First, an examination of the seasonal dynamics of prey distribution and behaviour; secondly, elucidation of the seasonal details of seabird foraging ranges; and thirdly, experimental manipulations enabling an assessment of the extent to which chick-solicitation of food influences prey selection.

Annual fluctuations

The only species for which data enable annual comparisons of diet to be made are the Adelie Penguin and Cape Petrel (Table 1). For the three years for which published data exist, there is a three-fold variation in the proportions of *E. superba* and *E. crystallophias* in the post-hatching diet of Adelie Penguins. In 1983/84, when the proportion of *E. superba* was greatest, the contribution of fish was very low (Table 1).

Similarly, difference in the proportions of *E. superba* and *E. crystallophias* in the diet of Cape Petrels is the most striking feature of an annual comparison. In 1987/88 all were *E. superba*, but in 1989/90 equal proportions of these species were consumed (Table 1).

An annual comparison of prey sizes indicates that *E. superba* is the only species which has exhibited varying size distribution. In 1984/85, the mean length of *E.*

superba consumed by Adelie Penguins was 4 mm less than the mean size of the two previous years. And in 1983/84, *E. superba* consumed by Cape Petrels was between 4 mm and 5 mm smaller on average than in two recent years (Table 4). These differences probably reflect varying annual age/size structure of the local *E. superba* population. Further monitoring of the prey size structure of seabird diets may be useful in detecting anomalous events or long-term changes in the age structure of prey populations.

Annual fluctuation in species composition of diets probably also reflects varying annual food availability; as ideal food preferences probably remain constant, and foraging ranges probably vary only as a response to fluctuation in prey abundances. This is supported by the positive correlation between Adelie Penguin reproductive success and proportion of *E. crystallophias* in their post-hatching diet (Green & Johnstone 1988). They hypothesised that in years when the neritically occurring *E. crystallophias* was abundant, chicks would have been fed more frequently, with subsequently improved fledging success. Additionally, Antarctic Petrel and Southern Fulmar chick productivity was very low in 1985/86, a year when *E. superba*, an important diet constituent, was of reduced abundance in Prydz Bay (Whitehead et al. 1990).

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DIETARY SEGREGATION AMONG THE SEABIRD COMMUNITY AT SUB-ANTARCTIC CROZET ISLANDS

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ABSTRACT. The diets of the whole seabird community were investigated at subantarctic Crozet Islands (750 stomach contents from 27 species). The samples were collected by regurgitation and/or stomach flushing according to species and then analysed by occurrence, number, reconstituted biomass and body length of each prey taxon identified to the lowest possible level. In accordance with the diversity of planktonic and micronektonic organisms in Crozet Island waters and adjacent water masses a broad spectrum of prey was found in seabird diets and the specific diets generally widely overlapped either in terms of prey species or prey body length. In order to find out other characteristics upon which the seabirds could efficiently segregate, all prey taxa were clustered according to various features considered as the most important clues allowing the birds to identify an organism as a potential prey regardless of any taxonomic relationship (i.e. body length, velocity, swarming behaviour, colour and photophore patterns). The various prey profiles thus defined fit the different foraging and feeding methods encountered in the Crozet Island seabird community. Fine segregation between closely related seabird species appears to be achieved mainly through different foraging areas as evidenced by both at-sea observations and the occurrence of various prey species diagnostic of different latitudinal and/or bathymetric regions.

DIVING PATTERNS AND PROCESSES IN EPIPELAGIC AND BENTHIC FORAGING SUB-ANTARCTIC SEABIRDS

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ABSTRACT. We contrast the depth, duration and pattern of diving in the epipelagic foraging Gentoo Penguin *Pygoscelis papua* and the benthic-foraging Blue-eyed Shag *Phalacrocorax atriceps*. The daily foraging period was 8 hours in both species, but Gentoos spent 50% of this time diving compared to 20% by Shags. Shags had longer surface intervals between dives than Gentoos, with a higher incidence of extended (>15 min) surface intervals. Dive depth was bimodal with deep (>31 m) and shallow (<20 m) dives accounting for 71% and 25% of time spent diving in Gentoos, and 90% and 9% in Shags. Deep dives averaged 80 m in both species, but were more variable in Gentoos (31-158 m) than Shags (34-116 m). Gentoos made four times more total dives per hour than Shags and twice as many deep dives per hour. We discuss these differences in relation to foraging strategy and the distribution and type of prey obtained.

Keywords: Gentoo Penguin, *Pygoscelis papua*, Blue-eyed Shag, *Phalacrocorax atriceps*, diving behaviour, foraging strategy, diet.

INTRODUCTION

Until recently, studies on the foraging behaviour of pelagic seabirds have relied chiefly on indirect sources of data, e.g. diet studies, colony attendance patterns, or on the few anecdotal observations of birds feeding at sea. In the last few years, with the development of small devices for recording the activity of free-ranging birds, it has become possible to measure directly various dive parameters (e.g. depth, duration) and to obtain continuous records of the pattern and profile of foraging activity. So far, however, there have been no published studies analysing continuous records of diving behaviour over consecutive days. Few other studies have attempted to examine the functional organisation of diving behaviour in relation to a species' ecological adaptations and constraints, and there have been no inter-species comparisons made from this perspective.

In this paper we compare and contrast the at-sea activity patterns, and depth, duration and pattern of diving, in two sub-Antarctic seabirds, the Gentoo Penguin *Pygoscelis papua* and the Blue-eyed Shag *Phalacrocorax atriceps*. Both are sedentary species with similar breeding chronologies, and both forage close inshore using pursuit diving, returning to the breeding colony daily. They differ in that Gentoos are flightless, highly specialised divers which use wing propulsion under-water, whereas Shags fly (presumably resulting in less extreme specialisation for diving) and use foot propulsion under-water. Detailed intra-specific analysis of the diving data appear elsewhere (Croxall et al. in press, Williams et al. submitted); in this paper we focus on inter-specific differences in foraging and diving behaviour.

METHODS

Diving behaviour was studied using time-depth recorders (TDRs) in the 1988-89 austral summer at Bird Island, South Georgia (54°00'S, 38°02'W). Two types of TDR were deployed on Gentoo Penguins and Blue-eyed Shags engaged in chick-rearing. Those deployed on two Gentoos (one male, one female) and two (male) Shags were mechanical, continuously-sampling devices developed by the National Institute of Polar Research, Japan. Full details of these and the data analysis procedure used are given in Naito et al. (1989); they measured 25 mm (diameter) by 85 mm (length) and weighed 73 g in air (2.7% of Shag mass). TDRs deployed on the other seven Gentoos (four males, three females) were micro-electronic devices, with a 15 second sampling interval, from Wildlife Computers (Woodinville, Washington, USA). These measured 100 mm (length) by 35 mm (width) by 16 mm (height), and weighed 90 g in air (1.5% of Gentoo mass). Both devices were attached to the bird's back feathers using quick-set epoxy resin. They recorded date, time, dive number, depth, duration and the duration of the surface interval between successive dives. These data were only recorded for dives where the minimum depth attained exceeded 1.9 m. Due to the different sampling systems in the two recorder types there were some differences in the number of shallow dives recorded, but not the total time spent in shallow dives (see Williams et al. in prep.). However, the difference between recorder types was insignificant compared with the inter-species differences, so data from both devices were pooled for Gentoo Penguins.

Both species foraged exclusively diurnally (Figure 1), daylength being 15.5-19 hours during the deployment period. Our initial unit of analysis, therefore, was the daily foraging period, defined as the time between the first and last dive in a day. The pattern of activity within this foraging period was examined by identifying dive bouts using estimated bout-ending criteria (BEC). For Gentoo Penguins, surface interval survivorship curves (Gentry & Kooyman 1986) indicated an inflexion point at an average of 10 minutes (range 8-14 minutes), so this was used as the BEC. For Shags, this method gave an average BEC of 15 minutes (range 12-17 minutes). Various statistics were then recalculated using dive bout as the unit of analysis. Foraging periods (or bouts) were only included in the analysis if they contained more than three or 20 dives for Shags and Gentoos respectively.

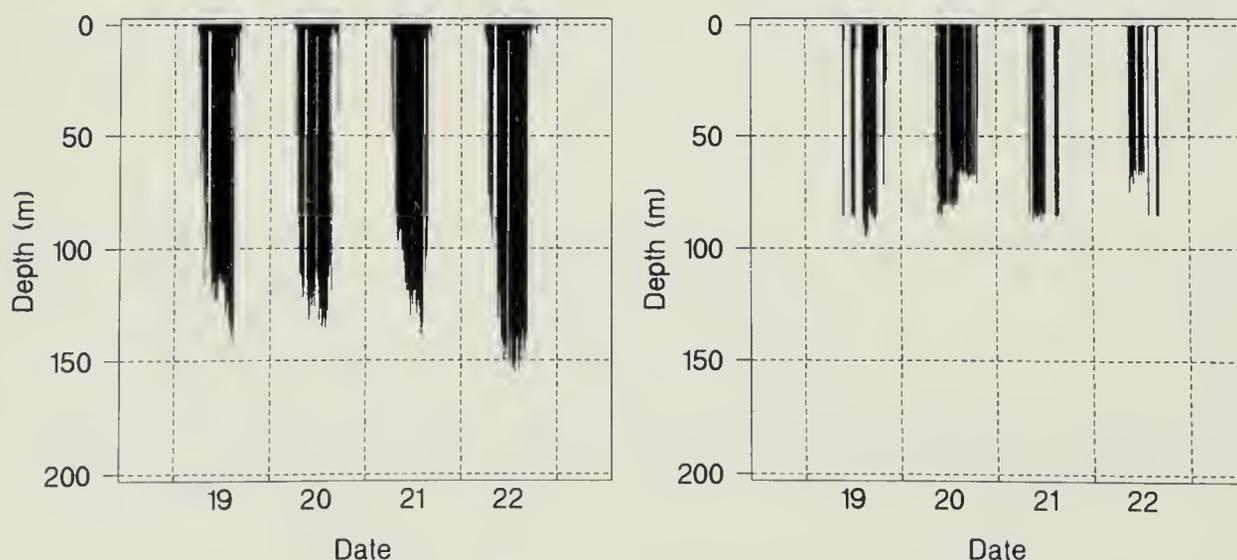


FIGURE 1 – Part of the diving record for an individual Gentoo Penguin (left) and a Blue-eyed Shag (right).

RESULTS

Data were obtained for 92 foraging periods for Gentoo Penguins, representing 15841 dives (97% of all dives recorded), and 14 foraging periods for Blue-eyed Shags, representing 651 dives (94% of all dives recorded). The mean duration of foraging periods was not significantly different for the two species but Gentoo Penguins made, on average, almost four times as many dives per foraging period, and four times as many dives per hour, compared with Blue-eyed Shags (Table 1). Consequently, although both species spent about 33% of each day at sea (42-52% of available daylight hours), i.e. potentially foraging, Gentoos spent 50% (range 7-80%) of the foraging period diving (in dives which exceeded 2 metres) compared with only 20% (range 13-26%) in Shags (Table 1).

TABLE 1 – Foraging period duration, number and frequency of dives and proportion of foraging period spent diving (in dives which exceeded 2 metres) for Gentoo Penguins and Blue-eyed Shags. Values are mean \pm s.d. with range in parentheses, and Student's *t* statistic and probability.

Parameter	Gentoo Penguin	Blue-eyed Shag	<i>t</i>	P
Foraging period duration (h)	8.8 \pm 4.2 (1.1 - 18.8)	8.6 \pm 2.1 (5.8 - 12.8)	0.26	NS
Total no. dives per period	171 \pm 88 (25 - 461)	47 \pm 21 (21 - 80)	11.52	<0.001
Dive frequency (dives/h)	20.4 \pm 6.5 (7.8 - 48.6)	5.3 \pm 1.7 (3.1 - 8.1)	18.80	<0.001
Proportion (%) of period spent diving	50 \pm 13 (7 - 80)	20 \pm 4 (13 - 26)	17.67	<0.001

The distribution of dive depths was strongly bimodal for both species (Figure 2) and dives were therefore classified as deep (>31 metres), intermediate (21-30 metres) or shallow (<20 metres), and each category analysed separately. There was no difference in the mean depth of each dive category between species (Table 2). However, there was much greater variation in the depth of deep dives in Gentoo Penguins compared with Shags (Figure 2), with the coefficients of variation being 29.7% and 10.7% respectively. Maximum dive depth was 116 m for Shags and 158 m for Gentoos. Gentoo Penguins made a significantly greater number of both deep and shallow dives per hour, and spent a greater proportion of each foraging trip in deep and shallow dives, than did Shags (Table 2). The proportion of total diving time (in dives which exceeded 2 m) spent in deep and shallow diving was 71% and 25% respectively for Gentoo Penguins and 90% and 9% respectively for Blue-eyed Shags. Deep dives were of significantly longer duration, and intermediate dives of shorter duration, in Blue-eyed Shags compared with Gentoos, and surface intervals between dives were significantly longer in Shags (Table 2).

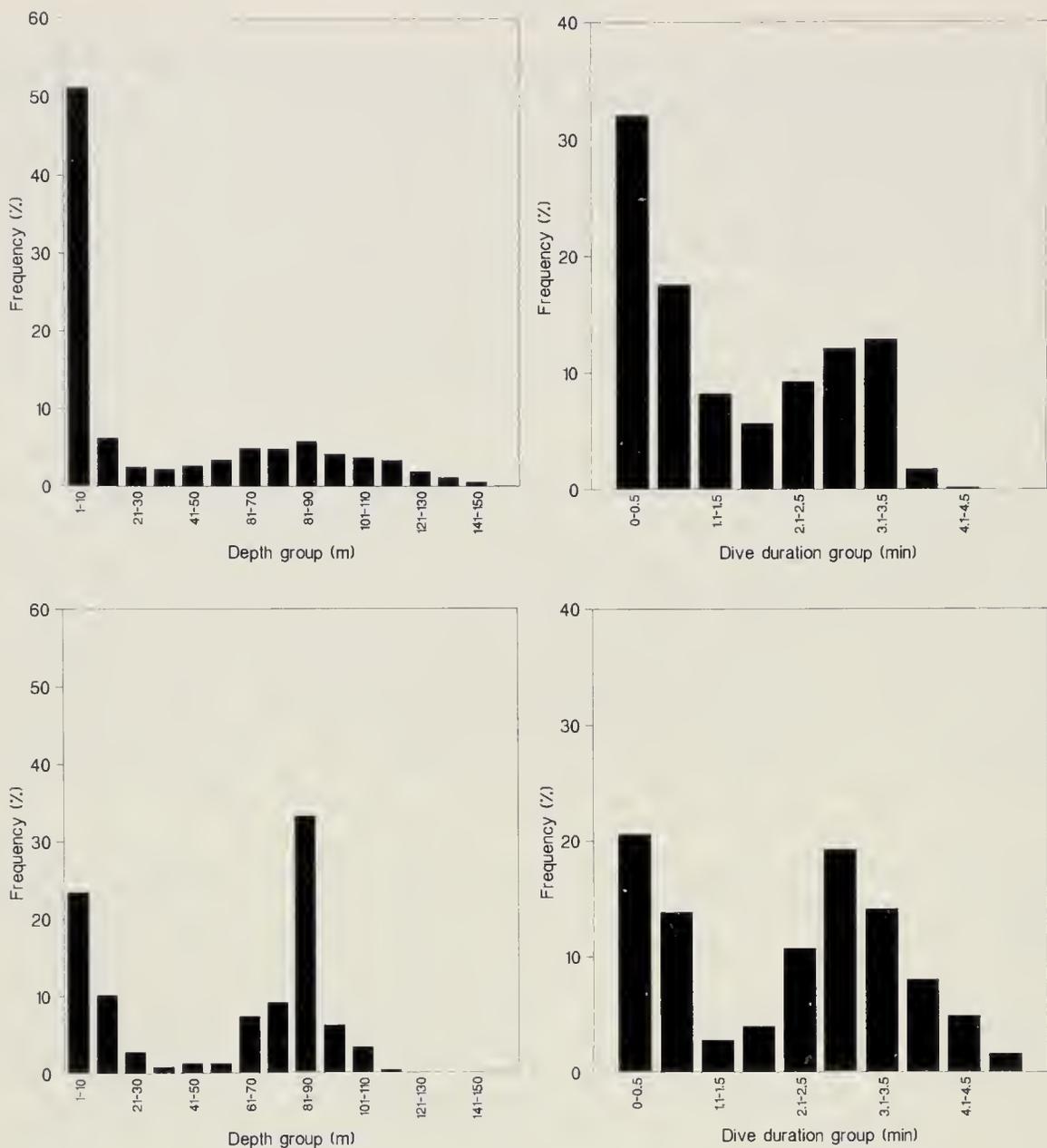


FIGURE 2 – Frequency distribution of dive depth and duration in Gentoo Penguins (above) and Blue-eyed Shags (below).

The profile of the dives could be ascertained from the continuously-sampling Japanese recorders. In Blue-eyed Shags, 98% of deep dives had recognisable bottom time (defined as time spent at or near maximum depth), and this accounted on average for half of the dive duration. In Gentoo Penguins only 6% of deep dives had recognisable bottom time. Shallow dives lacked bottom time in both species.

Blue-eyed Shags had a greater number of surface intervals which exceeded the bout-ending criteria, and consequently had more, and shorter, diving bouts per foraging period compared with Gentoo Penguins (Table 3). Of 92 foraging periods for Gentoo Penguins, 48 (52%) consisted of only one bout of more than 20 dives (i.e. there was no surface interval exceeding 10 minutes). Conversely, for Shags all 14 foraging periods consisted of two or more dive bouts. Gentoos spent 87% of the foraging period within dive bouts (defined as total time minus all surface intervals > BEC), compared with 60% for Shags. Within dive bouts Gentoo Penguins made almost ten times as many dives per bout and more than twice as many dives per hour, compared with Shags (Table 3).

TABLE 2 – Frequency (dives/h) of deep (>31 metre), intermediate (21-30 m) and shallow (<20 m) dives by Gentoo Penguins and Blue-eyed Shags, proportion (%) of foraging period spent in each depth category and depth, duration, surface interval between dives for each category. Values are mean \pm s.d.

Species	Parameter	Dive category		
		Deep	Intermediate	Shallow
Gentoo (N=15841)	Dives/h	8.3 \pm 3.7**	0.8 \pm 1.8	12.5 \pm 8.3**
	% period	36.1 \pm 15.9**	1.6 \pm 2.9	12.1 \pm 8.8**
	Depth	78.7 \pm 23.4	25.2 \pm 2.2	6.0 \pm 2.4
	Duration	2.7 \pm 0.4*	1.6 \pm 0.4*	0.7 \pm 0.2
	Interval	1.5 \pm 0.7**	1.5 \pm 2.4	1.7 \pm 1.9*
Shag (N=651)	Dives/h	3.5 \pm 0.7	0.1 \pm 0.2	1.7 \pm 1.2
	% period	17.9 \pm 4.0	0.4 \pm 0.4	1.7 \pm 1.2
	Depth	84.3 \pm 9.0	25.6 \pm 0.8	7.6 \pm 3.5
	Duration	3.1 \pm 0.6	0.9 \pm 0.4	0.6 \pm 0
	Interval	9.6 \pm 3.7	8.6 \pm 8.9	17.3 \pm 24.8

Asterisk indicates significantly different from Shag (t-test): * = $p < 0.05$, ** = $p < 0.01$

TABLE 3 – Numbers and duration of bouts of diving by Gentoo Penguins and Blue-eyed Shags, and number and frequency of dives in bouts. Values are mean \pm s.d. with range in parentheses, and Student's-t statistic and probability.

Parameter	Gentoo Penguin	Blue-eyed Shag	t	P
No. foraging periods	92	14		
No. bouts/period	1.7 \pm 0.8 (0 - 4)	3.8 \pm 1.0 (2 - 6)	8.74	<0.01
Total duration of bouts per period (h)	7.4 \pm 3.3 (1.0 - 15.5)	4.8 \pm 1.1 (3.3 - 7.7)	2.89	<0.01
% of daily diving period in bouts	87.1 \pm 15.7 (32.1 - 100)	60.3 \pm 12.1 (39.8 - 79.5)	6.05	<0.01
Mean duration of bouts (h)	4.2 \pm 2.8 (0.6 - 15.1)	1.3 \pm 0.2 (0.2 - 4.0)	7.59	<0.01
Mean number of dives per bout	97.6 \pm 70.3 (20 - 460)	11.0 \pm 2.8 (3 - 48)	9.00	<0.01
Mean dive frequency (dives/h) in bouts	24.0 \pm 6.7 (4.7 - 52.5)	9.7 \pm 3.0 (4.4 - 22.5)	15.08	<0.01

DISCUSSION

Both Gentoo Penguins and Blue-eyed Shags had daily foraging periods of similar duration, about eight hours, but there were large differences in diving effort within this at-sea period. Shags had longer surface intervals between dives and spent only 20% of the foraging period diving (in dives exceeding 2 m) compared with 50% for Gentoos. Consequently Shags had a much lower dive frequency, both of deep and shallow dives, within both foraging periods and dive bouts. Despite this apparent lower diving effort, Blue-eyed Shags have a shorter chick-rearing period and achieve a relatively greater chick growth rate and a higher provisioning rate (energy equivalent of food delivered per offspring) than Gentoo Penguins (Table 4). We suggest that this is due to differences in foraging strategy and the distribution and type of prey taken.

TABLE 4 – Comparison of chick growth and provisioning rates in Gentoo Penguins and Blue-eyed Shags

Parameter	Gentoo Penguin	Blue-eyed Shag
Adult mass (g)	5900	2750
Brood size	2	2.5
Fledging period - absolute (d)	80	55
- scaled ¹	3.95	3.46
Growth rate - g/day	85	57
- g/g/day	0.016	0.024
Fledging wt. as % of adult weight	98	91
Provisioning rate ² – absolute (W)	42.2	34.7
- relative	2.7	3.8

¹ After Pennycuick et al. (1984)

² [(energy density of delivered food x meal size)/interval (time) between meals], after Croxall & Briggs (in press)

At South Georgia, Gentoo Penguins feed predominantly on Antarctic krill *Euphausia superba*, a pelagic species which occurs mainly at depths of 80-120 m (but sometimes up to 20 m) during daylight hours (Everson 1983), and where adults weigh about 1 g (Croxall et al. 1988). Blue-eyed Shags, throughout their range, feed mainly on benthic nototheniid fish, with some benthic octopus and crustaceans (Shaw 1984, Espitalier-Noel et al. 1988). About half (by weight) of the Shag's diet consists of large fish (c.60 g) and half of small fish (c.2 g). The daily energy requirement of Gentoo Penguins and Blue-eyed Shags during chick-rearing is 3708 kJ.d⁻¹ (Croxall et al. 1988) and 2574 kJ.g⁻¹ (Bernstein & Maxson 1985) respectively. With a calorific content of fish and krill of 4.76 kJ.d⁻¹ (Dunn 1975) and 4.6 kJ.g⁻¹ (Clarke 1984) respectively, and an assimilation efficiency of 0.75 (Wiens 1984), this gives a daily requirement of 1080 g of krill for Gentoos and 721 g of fish for Shags. For the average mass of the most frequent prey given above, Gentoo Penguins therefore have to obtain 1080 individual prey and Blue-eyed Shags 180 small and six large individual prey per daily foraging trip. In the present study, Gentoo Penguins made on average 170 dives, and spent 4.4 hours diving, in each foraging period. Assuming they obtained prey on each

dive (see below) they would need to capture six krill per dive and four krill per minute. Blue-eyed Shags made 47 dives, and spent 1.7 hours diving, per foraging period, and would require a prey capture rate of four fish per dive and two fish per minute. Blue-eyed Shags therefore need to catch prey at a lower rate, mainly due to the larger size of the individual prey they consume.

The assumption that prey are caught on every dive brings us to a consideration of the function of deep and shallow dives. Shallow diving could have three possible functions: travelling, searching and occasional foraging on prey visible from the surface. The average duration of shallow dives we recorded (0.7 minutes) is similar to the 0.8 minute dives which Trivelpiece et al. (1986) called 'underwater swimming' and which they suggested was the primary method of travelling used by penguins. However, Trivelpiece et al. (1986) also described shallow, horizontal dives which they suggested were searching dives. Together with underwater swimming these shallow dives accounted for 48% of the Gentoo's total foraging time in their study. Although we have been unable to distinguish different types of shallow dives in this study, shallow dives only accounted for 13% of the foraging period in Gentoo Penguins. If shallow dives have a searching function, then species such as Gentoos, which exploit pelagic prey with a highly variable and therefore less predictable vertical distribution, would be expected to benefit more from exploratory dives and should spend more time in shallow dives. Conversely, benthic-foragers, such as the Blue-eyed Shag, exploit prey which has a highly predictable vertical distribution (on or near the sea bed), and they will not increase the probability of encountering prey by making shallow exploratory dives. This is supported by the results of this study: Gentoo penguins spent 25% of the total diving time in shallow dives, compared with only 9% in Blue-eyed Shags. This difference in the potential vertical distribution of prey would also explain why there is much greater variation in the depth of deep dives made by Gentoo Penguins compared with Blue-eyed Shags.

If the function of the majority of shallow dives in both species is either travelling or searching then only deep dives will be foraging dives. Gentoo Penguins and Blue-eyed Shags made on average 73 and 30 deep dives per foraging period (from Table 2). Assuming a daily requirement of 1080 and 186 individual prey respectively, this gives prey capture rates of 15 per deep dive for Gentoos and six per deep dive for Shags. Both species must therefore be capable of handling and consuming prey without returning to the surface (cf. Wilson & Wilson 1988).

A major part of the foraging period in both species consisted of time spent at the surface, i.e. not diving, and this was greater in Shags (80% of the foraging trip) than in Gentoos (50%). We have no data on the activity of either species during these surface intervals. However, Shags have wettable plumage compared with the highly modified, waterproof plumage of Gentoo Penguins. Shags may therefore need to spend more time preening and drying their feathers between dives to prevent them becoming waterlogged (cf. Bernstein & Maxson 1982). Also, chick-feeding frequency per adult for Blue-eyed Shags is 3-6 per day (Shaw 1984) compared with once per day for Gentoo Penguins (Williams & Rothery in press). It is therefore likely that at least during the longer surface intervals Shags were returning to the colony to feed chicks. Gentoo Penguins spent 50% of each foraging trip on the surface (or in dives of less than two metres) in the present study. In Trivelpiece et al.'s (1986) study, Gentoos were recorded as resting on the surface for only 3% of the foraging period,

with 'porpoising' and 'underwater swimming' (that is, travelling) accounting for 5% and 31% of the foraging period respectively. This suggests that travelling dives in Gentoo Penguins may largely be restricted to the top two metres of the water column.

Finally, we want briefly to consider the results presented in this paper in relation to physiological adaptations for diving. Kooyman (1989) reviewed diving behaviour in birds and concluded that dive depths and durations reported for smaller penguins posed no problems in terms of the birds' physiology, in contrast to diving in the larger King *Aptenodytes patagonicus* and Emperor *A. forsteri* Penguins. In fact, this study has shown that the diving ability of Gentoo Penguins, relative to body size, is comparable to that of the larger penguins. Gentoo Penguins made 11% of all dives to depths greater than 100 metres and 36% of dives lasted in excess of 2.5 minutes, greater than the estimated aerobic diving limit of the similar sized Humboldt Penguin, *Spheniscus humboldti* (Kooyman & Davis 1987). The smaller Blue-eyed Shag has perhaps an even more remarkable diving ability: 10% of dives exceeded 100 metres and 48 % had durations longer than 2.5 minutes. The physiological adaptations that allow birds to make frequent, prolonged, deep dives is still unknown (Kooyman 1989), but clearly such adaptations must be more widespread amongst pelagic seabirds than previously thought.

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FEEDING ECOLOGY OF ANTARCTIC AND SUB-ANTARCTIC PROCELLARIIFORMES

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ABSTRACT. The foods and feeding ecology of Antarctic and subantarctic procellariiforms are reviewed using published information and new data mainly from the New Zealand/Australian subantarctic. New data are presented for Royal Albatross *Diomedea epomophora*, Grey-headed Albatross *D. chrysostoma*, Light-mantled Sooty Albatross *Phoebetria palpebrata*, Mottled Petrel *Pterodroma inexpectata* and Atlantic Petrel *P. incerta*. For several species, virtually nothing is known. There are few specialists.

Keywords: Procellariiformes, Antarctic, subantarctic, foods, Cephalopoda, fish, Crustacea.

INTRODUCTION

In this paper I use unpublished data on the diets of various procellariiforms obtained mainly in the New Zealand subantarctic together with published information to review procellariiform feeding ecology in the Antarctic and subantarctic. It is not my intention to duplicate the work of recent reviewers (Prince & Morgan 1987, Croxall & Prince 1987) so I shall consider only the main foods in the diets – generally those constituting about 15% or more of the biomass.

METHODS

New data are from Royal Albatross *Diomedea epomophora* regurgitations obtained from the Chatham Islands and Taiaroa Head breeding colonies by C.J.R. Robertson and co-workers; Grey-headed Albatross *D. chrysostoma* stomach contents from Campbell Island collected for the National Museum of New Zealand; Light-mantled Sooty Albatross *Phoebetria palpebrata* regurgitations collected at Macquarie Island by K.R. Kerry and co-workers, and at Campbell Island by New Zealand Meteorological Service staff; regurgitations of Mottled Petrel *Pterodroma inexpectata* chicks from Codfish Island, southern New Zealand, collected by J.A. West and myself; and Atlantic Petrel *P. incerta* regurgitations collected by me at Gough Island.

I identified cephalopods by their beaks, fish by their otoliths and crustaceans by their exoskeletons, largely using material identified in my previous studies of diets of marine vertebrates. Biomasses of cephalopods consumed were determined from measurements of their beaks using the formulae given by Clarke (1986).

RESULTS

For Royal Albatrosses at the Chatham Islands (Table 1) cephalopods form a major part of the diet, though it is likely that fish are also important, as for Wandering

Albatrosses *D. exulans* (Croxall et al. 1988). When digested, fish leave no persistent remains comparable to squid beaks, so fish are usually under-represented in regurgitations. Because of their low masses, *Pyrosoma* (Tunicates) and crustaceans form a smaller part of the diet. The carrion was penguin feathers. The large onychoteuthid squid *Moroteuthopsis ingens* (ca. 3.7 kg) was of major importance, though *Histioteuthis* species were most frequent in the diet. All beaks of *M. ingens* were from adult squid. The distribution of this squid with two centres, one around southern New Zealand and the other off southernmost South America, closely reflects the range of Royal Albatrosses (Robertson & Kinsky 1972). Possibly this albatross specialises in exploiting the New Zealand population of *M. ingens* when breeding, and the South American population in the pre-breeding and contranuptial years.

Gough Island in the South Atlantic is, like Chatham Islands, at the subtropical convergence. The great albatross breeding there is, however, the Wanderer, not the Royal. The main cephalopods in the diet of Gough Island Wandering Albatrosses were *Histioteuthis* species (27% of biomass), *M. ingens* (15%) and *Architeuthis* sp. (13%) (Imber in press). Thus Wanderers rather than Royals breed at the Gough-Tristan group, probably because of a sparse population of *M. ingens* there; and that apparently related to the very limited area of shallow seas around that archipelago.

TABLE 1 – The food of Royal Albatrosses *Diomedea epomophora* at Chatham Islands and Taiaroa Head.

	CHATHAM IS. 32	TAIAROA HEAD 19
CEPHALOPODA	% of biomass of cephalopods	% of biomass of cephalopods
<i>Moroteuthopsis ingens</i>	80	16
<i>Histioteuthis</i> spp.	7	1
<i>Architeuthis</i> sp.	5	–
<i>Nototodarus</i> spp.	tr	28
<i>Octopus maorum</i>	tr	52
Other	7	3
OTHER FOODS	% frequency of occurrence	% frequency of occurrence
Fish	19	16
<i>Pyrosoma</i> sp.	68	22
Crustacea*	19	32
Carrion	6	–

* *Munida*, Isopoda, *Lepas*

The cephalopod diet of Royal Albatrosses at Taiaroa Head is dominated by *Octopus* and *Nototodarus* (Table 1). There seems no way that albatrosses can acquire *Octopus* other than by commensalism, with seals and/or with fishing boats (e.g. in crayfishing). Even the capture of *Nototodarus* may be through attendance at trawlers operating off that coast between Banks Peninsula and Auckland Islands. The dearth

of pelagic squid in the diet (*Histioteuthis*, *Architeuthis*, other species) also shows that they are feeding over the continental shelf and slope, where trawlers, crayfishers, seals and *Moroteuthopsis ingens* are to be found. Thus this small colony may be dependent on such commensalism.

TABLE 2 – Cephalopods taken by Grey-headed Albatrosses *Diomedea chrysostoma* at South Georgia*, Campbell Island and Prince Edward Islands† (% of biomass of cephalopods).

	SOUTH GEORGIA	CAMPBELL IS.	PRINCE EDWARD IS.
Number of samples	100+	5	18
CEPHALOPODA			
<i>Kondakovia longimana</i>	11	17	67
<i>Moroteuthis knipovitch</i>	1	–	23
<i>Histioteuthis</i> spp.	tr	5	tr
<i>Martialia hyadesi</i>	71	74	
<i>Galiteuthis glacialis</i>	7	1	tr
Others	10	3	10

* Rodhouse et al. 1990; † Brooke & Klages 1986

The food of Wandering Albatrosses (Imber in litt., Croxall et al. 1988) comprises a considerable variety of mainly pelagic cephalopods and fish. Except at Gough Island, Onychoteuthidae were the preponderant cephalopods eaten at most colonies, with *Kondakovia longimana* the main species and three other onychoteuthids also important, though histioteuthids and cranchiids were more frequently taken at most colonies. There was strong evidence of commensalism with the Falkland Islands fishery by South Georgian Wanderers.

Grey-headed Albatrosses have a diet which varies circumpolarly (Table 2). At South Georgia and Campbell Island they mainly take the ommastrephid squid *Martialia hyadesi* but at Prince Edward Islands, where ommastrephids are absent, they largely take two onychoteuthids: *Kondakovia* and the locally abundant *Moroteuthis knipovitchi*. Smaller proportions of fish, crustaceans and lampreys are taken.

Black-browed Albatrosses *D. melanophrys* at South Georgia have a diet in which *Euphausia superba* (38% by mass) and fish (39%) outweigh squid (21%), but at the Falkland Islands, cephalopods (57%) and fish (41%) are the main items (Thompson 1989a). Little is known of their diet elsewhere.

The diet of Buller's Albatross *D. bulleri* contains a large proportion of ommastrephid squids (*Nototodarus* spp.) plus other cephalopods, fish and crustaceans (West & Imber 1986). There is little or no quantitative information on the diets of other small

TABLE 3 – The food of Light-mantled Sooty Albatrosses *Phoebastria palpebrata* at Macquarie and Campbell Islands, Prince Edward Islands* and South Georgia†.

	MACQUARIE & CAMPBELL IS.	PRINCE EDWARD IS.	SOUTH GEORGIA
Number of samples	34	14	37+
CEPHALOPODA	% of biomass of cephalopods	% of biomass of cephalopods	% of biomass of cephalopods
<i>Kondakovia longimana</i>	21	40	14
<i>Moroteuthis knipovitchi</i>	-	9	3
<i>Psychroteuthis</i> spp.	23	9	47
<i>Alluroteuthis antarcticus</i>	15	21	2
<i>Martialia hyadesi</i>	23	-	5
<i>Galiteuthis glacialis</i>	11	7	22
Others	7	14	7
OTHER FOODS	Occurrence		% of total biomass
<i>Euphausia superba</i>	-		36
Prawns and mysids	✓		4
Myctophidae	-		12
Other fish	✓		2

* Imber & Berruti 1981; † Thomas 1982; Prince & Morgan 1987

southern albatrosses (mollymawks): the three *D. cauta* subspecies or *D. chlororhynchos*.

The food of Light-mantled Sooty Albatrosses (Table 3) is quite variable from colony to colony but shows that this species feeds closer to Antarctica than any other albatross because of the prevalence of *Psychroteuthis* and *Alluroteuthis* squids. In contrast the cephalopod diet of Sooty Albatrosses *Phoebetria fusca* at Prince Edward Islands comprised 61% (by mass) *Kondakovia* but less than 1% *Psychroteuthis* and only 5.5% *Alluroteuthis* (Imber & Berruti 1981, further analysed here). This shows the more northerly feeding range of *P. fusca*.

Like albatrosses, *Procellaria* petrels feed by surface seizing, occasionally diving. There is little quantitative information on the food of Grey Petrels *P. cinerea*, though histioteuthid and cranchiid squids were prevalent in three samples (pers. obs.). The diet of White-chinned Petrels *P. aequinoctialis* comprises cephalopods, fish, crustaceans and tunicates. In the New Zealand region histioteuthid and cranchiid squids were the main cephalopods eaten (Imber 1976) but at South Georgia cranchiids, *Martialia* and *Kondakovia* were prevalent (Prince & Morgan 1987).

Subantarctic shearwaters (*Puffinus* spp.) and diving petrels (*Pelecanoides* spp.) are distinct in that they obtain virtually all their food underwater and in daylight. Like penguins, they pursue sub-surface prey after diving from the surface or from a shallow-angled plunge. Euphausiids are the main prey (Table 4). Only diving petrels have been recorded taking copepods whereas shearwaters also take quantities of small shoaling fish (e.g. *Engraulis* and *Scomberesox*) and juvenile ommastrephid squid (*Nototodarus* in Australasia). The absence of breeding shearwaters at Indian Ocean subantarctic archipelagoes may be partly due to the lack of such fish and squid there. This is particularly likely to be so at the Prince Edward Islands.

TABLE 4 – The foods of subantarctic shearwaters and diving petrels.

Prey	SHEARWATERS			DIVING PETRELS		
	Sooty	Short-tailed*	Little	Common SG†	NZ	South Georgian†
Euphausiidae	++	+++	++	15	+++	76
Copepoda	-	-	-	68	-	20
Other Crustacea	+	+	-	17	+	4
Ommastrephidae	++	++ or +	++	-	-	-
Small fish	+ or ++	+ or ++	+	-	-	-

+ 1 to 20% of biomass, ++ 20 to 50% of biomass, +++ 50% or more of biomass.

* Skira 1986, Montague et al. 1986

† Payne & Prince 1979: % by volume

The diets of fulmars, which feed by surface seizing or dipping, are dominated by euphausiids during the breeding season but are probably more variable between species at other times, when it is difficult to obtain samples. *Euphausia superba* is most often taken, though *E. crystallorophias* may be taken near Antarctic coasts. This is so for Cape Pigeons *Daption capense* (Beck 1969, Croxall & Prince 1987), Snow

TABLE 5 — The foods of prions *Pachytila* spp. and the Blue Petrel *Halobaena caerulea* (% by weight)†.

Species	Prions						Blue Petrel	
	Fairy	Fulmar	Thin-Billed	Antarctic	Salvin's	Broad-Billed	Chatham	SG
Locality	NZ	SG	Heard Chatham	Falkland	SG	Crozet	Chatham	SG
Euphausiidae	92	79	-	23	52	14	+	40
Amphipoda	+	14	++	41	+	55	20	+
Copepoda	-	+	-	-	29	15	70	tr
Other Crustacea	+	tr	++*	19	tr	+	tr	+
Fish	+	+	+	+	10	+	+	50

tr trace (less than 1%), + minor item, ++ major item

* *Lepas*

† Data from Ealey 1954, Harper 1976, Prince 1980, Imber 1981, Thompson 1989b, Bretagnolle et al. 1990, Prince & Copestake 1990

TABLE 6 – The foods of subantarctic gadfly petrels *Pterodroma* spp. and the Kerguelen Petrel *Lugensa brevirostris* (% by weight).

	Kerguelen*	Mottled	Soft-Plumaged*	White-Headed	Atlantic	Great-Winged*
Number of samples	22	69	13	8	13	31
CEPHALOPODA						
<i>Gonatus antarcticus</i>	36	4	22	13	25	17
<i>Histioteuthis</i> spp.	5	6	9	31	21	19
Other spp.	29	10	58	41	23	53
FISH						
Myctophidae	6	39	1	8	9	3
Other spp.	-	3	-	-	9	1
CRUSTACEA	24	30	10	7	12	6
TUNICATA	-	8	-	tr	-	-

* Data mainly from Schramm 1986; identifications revised herein

Petrels *Pagodroma nivea* (Maher 1962, Brown 1966, Griffiths 1983, Croxall & Prince 1987), Antarctic Petrels *Thalassoica antarctica* (Bierman & Voous 1950, Griffiths 1983, Montague 1984) and Antarctic Fulmars *Fulmarus glacialisoides* (Bierman & Voous 1950). *Euphausia superba* also forms up to 22% of food fed to Giant Petrel *Macronectes* spp. chicks at South Georgia in some years (Hunter 1983), and is important in food of young *M. giganteus* chicks at South Orkney Islands (Conroy 1972). Carrion (mainly penguin, seal and petrel) is, however, the predominant food of both species at Macquarie Island (Johnstone 1977) and South Georgia (Hunter 1983), and of *M. giganteus* at South Orkney Islands (Conroy 1972).

The diets of prions *Pachyptila* species (really little fulmars) and Blue Petrels *Halobaena caerulea* show a predominance of crustacean zooplankton (Table 5) taken by dipping, pattering or hydroplaning. However, Blue Petrels take many small fish, and most of these are probably myctophids (Prince 1980). The three narrow-billed prions mainly eat euphausiids and amphipods, but Chatham fulmar prions seem to have evolved their massive bills for tearing barnacles off floating objects. The three wider-billed prions show increasing specialisation towards exploiting copepods, supplemented by small amphipods, by filter-feeding.

Most subantarctic gadfly petrels *Pterodroma* spp. and Kerguelen Petrels *Lugensa brevirostris* have diets in which Cephalopoda are important (Table 6). However, fish and crustaceans are frequently taken and are underestimated where allowance is not made for the indigestibility of cephalopod beaks (Furness et al. 1984). They feed by surface plunging or dipping, mainly at night. Clearly the Mottled Petrel has a high fish component in its diet, as does its North Pacific relative, the Bonin Petrel *P. hypoleuca* (Harrison et al. 1983). Although the fish and crustacean fraction of other species' diets may have been underestimated, they do not take fish as frequently as do Mottled Petrels. Kerguelen Petrels have a higher proportion of crustaceans and fish in the diet than sympatric gadfly petrels do (Schramm 1986), but further research is needed to show to what extent this difference enables the chick-rearing period of Kerguelen Petrels to be 63% of the duration of that of similar-sized *Pterodroma* species.

Southern storm petrels (Oceanitidae) feed while hopping along the surface. There is no information for the Black-bellied *Fregetta tropica*. Of the two others (Table 7), the Grey-backed Storm Petrel is a specialist, taking barnacle larvae, while Wilson's is a more general predator of larger zooplankton. Grey-backed probably feed by day, searching for floating objects such as wood or algae that attract the 2-3 mm long barnacle larvae as they prepare to settle and metamorphose; also home for the isopod *Idotea metallica* (Naylor 1957), another prey item.

DISCUSSION

Procellariiformes thus attack the marine food chain at three levels. Zooplankton and small nekton are preyed on by shearwaters, diving petrels, fulmarine petrels, prions, Blue Petrel and storm petrels. Predation may be sub-surface by day (shearwaters, diving petrels) or at the surface at any time, perhaps especially crepuscularly (the others). Larger marine life (nekton), particularly mesopelagic forms, are attacked or scavenged at the surface by albatrosses, *Procellaria*, fulmarine petrels and gadfly petrels. Nocturnal feeding is particularly indicated for this group. Hunting at night by

albatrosses, from the evidence of activity recorders (Prince & Morgan 1987) and transmitters (Jouventin & Weimerskirch 1990), seems to be surface based, but hunting on the wing is likely by gadfly petrels and smaller fulmarines. Commensalism (with cetaceans, seals, humans) can be important to some albatrosses, *Procellaria* (Enticott 1986) and fulmarines. At the third level, giant petrels are scavengers and predators of procellariiforms themselves.

TABLE 7 – The foods of Antarctic and subantarctic storm petrels: Wilson's *Oceanites oceanicus* and Greybacked *O. nereis*. No data available for Black-bellied *Fregetta tropica*.

	Wilson's ¹	Grey-backed ²
Euphausiidae	37	7
Amphipoda	30	7
Cirripedia*	tr	85
Fish	28 †	tr
Other items	4	tr

* Juvenile stages of barnacles, *Lepas australis*

† Mainly lantern-fish, Myctophidae

¹ Croxall et al. 1988

² Imber 1981

Finally, a comment on the prevalence of cephalopod predators among southern seabirds. Both in terms of the number of available families, and the number of available species per family, there are significantly more cephalopod prey in the southern oceans than in the northern.

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CONCLUDING REMARKS: FEEDING ECOLOGY OF ANTARCTIC AND SUB-ANTARCTIC SEABIRDS

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These four papers show the different aspects of seabird feeding ecology studies today. The use of activity and diving recorders and of transmitters is going to yield further stimulating information. However, there is still very much basic information to be gathered - some species are essentially unstudied in regard to their foods. We still know very little about diets outside the breeding seasons; how much, if at all, do they differ from those of breeders, about which we know most? Solving this is a challenge with no sign of an easy solution.

We look forward to the results of research on the feeding ranges of seabirds other than albatrosses particularly as transmitter power to mass ratio increases. The frequency, or otherwise, of nocturnal feeding will also become better known. To what extent is crepuscular feeding important? Given the midnight sinking of plankton and nekton, even nocturnal feeders are likely to concentrate their activity in the first and last few hours of darkness.

The matter of what proportion of cephalopods in seabird diets is taken as moribund (probably post-spawning) animals that have floated to the surface, as opposed to active animals preyed on at the surface, is another interesting debate awaiting further resolution.

Physiological studies associated with seabird feeding and digestion are another ripe field. How is it that stomachs of non-breeders at colonies, and of most birds caught at sea, are virtually empty, yet adults feeding chicks can bring large volumes of food back to their young from great distances? What is the physiology associated with, and the purpose of, the helicoidal intestines of gadfly petrels?

One of the purposes of studying seabird feeding ecology is to better understand conflicts between seabirds and fisheries. Whether we shall in most cases be able to predict imminent problems for seabirds from over-exploitation of their food resources is debatable. A fisheries manager recently described the problems inherent in his task. He compared fish stocks assessment to using a helicopter hovering above a thick cloud sheet, and lowering a grab-hook or drop-net on a rope, to census the sheep population of New Zealand. Given this, it is likely that we shall often be on the defensive in endeavouring to influence the decisions of fisheries managers, regarding levels of exploitation of stocks common to birds and humans. Usually we have to wait until the effects on seabirds become evident *ad nauseam* before action is taken.

Within the last 25 years we have seen the adverse effects on seabirds of over-exploitation of anchovies off the west coast of South America and of sand-eels around the

Shetland Islands. Imminent problems for Gulf of California seabirds, from massive commercial exploitation of small fish, were told at the ICBP meeting in Hamilton recently.

In the New Zealand region the main current concern (apart from incidental by-catch problems) is the squid fishery for *Nototodarus*. This is taken by many seabirds - particularly penguins, shearwaters and albatrosses, as well as fur seals. Little blue penguins and shearwaters take juveniles of it, but also a wide range of other prey. Albatrosses can compensate for adverse effects of the fishery by taking offal and lost catch at trawlers. The main concern is for Yellow-eyed penguins, currently in decline for several reasons, including starvation last breeding season. Small *Nototodarus*, larger than taken by shearwaters and little blue penguins, form a fair proportion of their prey.

As yet there is no exploitation in the New Zealand region of small fish. Long may this remain so.

We have seen great advances in knowledge of seabird feeding ecology in the last 20 years. I look forward to the next IOC symposium on this subject: sure to reflect fascinating advances.

SYMPOSIUM 24

**MECHANISMS OF INTERSPECIFIC
COMPETITION**

Conveners A. A. DHONDT and R. V. ALATALO

SYMPOSIUM 24

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INTRODUCTORY REMARKS: MECHANISMS OF INTERSPECIFIC COMPETITION

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Competition is a biological interaction between individuals or populations for a limiting resource, resulting in a reduced fitness of all parties involved. Evidence for its existence can either be provided by changes in population size (numerical response) or by a niche shift. Its existence is also accepted as proven if an effect can be demonstrated on population processes (Dhondt 1989). This approach is relevant when one is interested in the question 'Does interspecific competition occur?' It does not answer the question 'How or for what resources, or by which behaviour does competition actually take place?'

Many studies on competition between species stop once they have demonstrated its existence. This can be explained by the fact that the rigorous demonstration of the existence of interspecific competition is no easy task. However, it is only then that the problem really becomes interesting: which resources are limiting? What behavioural responses are associated with competition?

In this symposium we have tried to bring together a number of examples of studies that have gone beyond the first question whether competition between different species takes place at all. In these studies researchers tried to identify the resources for which competition occurs, the behavioural mechanisms involved, or ways to measure the possible existence of interspecific competition. Most contributions have used field experiments to contribute to these problems.

FORAGING NICHEs IN NORTH EUROPEAN TITS (PARIDAE): INTERSPECIFIC COMPETITION AND OTHER FACTORS

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ABSTRACT. Interspecific competition restricts the choice of foraging sites, and experiments indicate that both interference between species and exploitation of common resources are involved in niche shifts. Risk of predation is higher on exterior tree parts, and socially dominant species seem to avoid predation by foraging in the interior parts. There is a high correlation between the abundance of food and the number of guild members foraging in each tree part, even if exterior tree parts are used relatively less. Many species hoard food which may have consequences on choice of foraging sites. Tit species living in coniferous forest have more slender bills than tits in deciduous habitat, and the species smallest in size forage in exterior tree parts. These morphological requirements restrict the foraging niche of each population, even though the morphology may change between populations, for instance in response to the change in the presence of competing species.

Keywords: *Parus*, *Regulus*, *Certhia*, *Sitta*, interspecific competition, predation, ecomorphology, niche.

INTRODUCTION

In the last decade very little attention has been paid to the study of avian communities or guild organization. The earlier hopes of explaining community structure in terms of interspecific competition have not come true. The frustration arose from the use of superficial community data such as species lists and from the emphasis on the mere testing of the presence of interspecific competition. In future it will be necessary to concentrate on detailed studies of the individuals and populations within the guilds with a broad theoretical framework that includes also other factors than competition.

We have an ongoing research project on the organization of North European *Parus* communities, and in this paper we will review our findings of the factors that explain the choice of foraging niches by each species. The foraging niche is here defined to include the tree species and sites in trees used for foraging as well as the diet.

THE GUILD

Seven species of the genus *Parus* are common in Fennoscandia (Table 1). The community is richest in Southern and Central Sweden and Southern Norway with all but the northerly distributed Siberian Tit present. Three species mainly live in deciduous forests, while others are mostly confined to coniferous habitats. Within each habitat the species are segregated in the choice of tree portions where they forage on arthropods. Five of the species regularly hoard seeds, and they do so in particular in autumn presumably to be used later during the long winter with snow-cover (Haftorn 1956). The Goldcrest is a common participant in the mixed species winter flocks of tits in coniferous habitats, and they eat only arthropods. The Common Treecreeper

is a specialist on foraging on arthropods on tree trunks. The Nuthatch is southerly distributed in deciduous habitats and it commonly hoards seeds and nuts.

TABLE 1 - The species of the genus *Parus* and ecologically related wintering species in Northern Europe. Habitats are deciduous (Dec.) and coniferous (Con.), and foraging niches in trees refer to horizontal position on branches (Int. = interior, Ext. = exterior). The species names are according to Howard & Moore (1980).

Name	Abbreviation	Habitat	Niche in tree	Distribution	Hoarding
Great Tit <i>Parus major</i>	Gr	Dec.	In	Wide	No
Blue Tit <i>Parus caeruleus</i>	Bl	Dec.	Out	South	No
Marsh Tit <i>Parus palustris</i>	Ma	Dec.	Middle	South	Yes
Willow Tit <i>Parus montanus</i>	Wi	Con.	In, Wide	Wide	Yes
Siberian Tit <i>Parus cinctus</i>	Si	Con.	Wide	North	Yes
Coal Tit <i>Parus ater</i>	Co	Con.	Out	South	Yes
Crested Tit <i>Parus cristatus</i>	Cr	Con.	Middle	Wide	Yes
Goldcrest <i>Regulus regulus</i>	Gc	Con.	Out	Wide	No
Long-tailed Tit <i>Aegithalos caudatus</i>	Lt	Dec.	Out	South	No
Treecreeper <i>Certhia familiaris</i>	Tc	Wide	Trunk	Wide	No
European Nuthatch <i>Sitta europaea</i>	Nh	Dec.	In	South	Yes

INTERSPECIFIC COMPETITION

In the absence of some species the remaining species do partly fill the vacant foraging niches (Alatalo et al. 1986). It is the morphologically most similar species to the one absent that is likely to have the niche shift. This supports the idea that interspecific competition restricts the use of foraging sites.

We reduced Crested and Willow Tit numbers in three flocks to mimic the situation on the island of Gotland with only the Coal Tit and Goldcrest present (Alatalo et al. 1985).

The remaining species moved to inner tree parts. One could argue that the shift would be due to increased risk of predation in smaller flocks, since inner tree parts are safer from predation (see Ekman 1986, 1987). However, in another experiment we removed Coal Tits and Goldcrests in three flocks, and Willow and Crested Tits increased the use of exterior tree parts. Therefore we find interspecific competition over limited food as the most likely explanation for these niche shifts. In future, it is necessary to expand the removal experiments to include monitoring food abundance and survival or condition of the birds.

Socially subdominant species (Coal Tit, Goldcrest) may influence the foraging site choice of the dominant species. Hence, exploitation of common food resources is likely to be influential, but interference by the dominant species may strengthen the competitive effect. In an aviary the subdominant Coal Tits responded to the presence of the dominant Willow Tits, while Willow Tits were indifferent (Alatalo & Moreno 1987).

RISK OF PREDATION

Ekman (1986, 1987) suggested that the risk of predation by Pygmy Owls *Glaucidium passerinum* is higher for tits foraging in exterior and lower tree parts. This idea is supported by a comparison of five different areas in Northern Europe and Russia (J. Suhonen, M. Halonen & T. Mappes, unpubl.). Coal Tits and Goldcrests, the specialists of the exterior tree parts, were over-represented in the food caches of Pygmy Owls. In contrast, Willow and Crested Tits that forage in inner tree parts were always under-represented compared with their local abundances. Predation risk by Pygmy Owls varies greatly with the availability of voles that have four year population cycles. In Central Finland, Willow and Crested Tits changed to forage in the inner tree parts after the vole populations had crashed and owls started to hunt tits (J. Suhonen, unpubl.).

Predation risk and interspecific competition act as complementary factors in determining the foraging niches (see also Szekely et al. 1989). The heavier species are socially dominant over the lighter ones (Hogstad 1978, Morse 1978), although there may be exceptions related to sex and age dependency in dominance (Ekman & Askenmo 1984, Hogstad 1989). In the coniferous forest flocks the Crested Tit usually dominates Willow Tits followed by Coal Tit and Goldcrest. It seems that Crested Tits and also Willow Tits take up the foraging sites where predation risk is smallest, while the two smaller species exploit the risky exterior tree parts. However, the choice of foraging sites cannot be understood solely in terms of avoiding predation. If food were not limiting at all, one would expect all the species to seek into the safer inner tree parts. Furthermore, the experimental removal of the two smaller species resulted in Crested and Willow Tits increasing the use of exterior tree parts (Alatalo et al. 1987).

It is likely that avoidance of predation by joining in mixed species flocks has a positive effect on survival of all the species. This cooperation is likely to be outweighed by competition over food if the species are ecologically similar. However, for species with distinct foraging niches, like the Common Treecreeper, it may well be that there

is a net benefit of the presence of other species. Furthermore, in Willow Tit flocks in Central Norway the presence of adult individuals enhanced the survival of yearlings (Hogstad 1989). It will be interesting to study the degrees in which cooperative avoidance of predation and competition may balance each other as contradictory interactions between populations. It will also be crucial to study the foraging site selection of each individual in the mixed species flocks, an approach that has been very useful in understanding the organization of Willow Tit flocks (see Ekman & Askenmo 1984, Ekman 1987, Hogstad 1989).

FOOD AVAILABILITY

Experiments with addition of food during winter have demonstrated that tits are food limited during winter (Jansson et al. 1981). We estimated the distribution of food within trees in spruce forests of Central Sweden (J. Suhonen, R.V. Alatalo, A. Carlson & J. Höglund unpubl.). First, we wanted to test how closely the guild uses the different parts of trees in relation to the abundance of the arthropod food. The correlation was quite good suggesting that in that sense the guild is rather saturated. The foraging niches, species composition, and numbers of individuals are largely determined by the availability of food.

However, there were also exceptions to the idea that food availability determines the foraging site selection of tits. There were relatively more arthropods per individual bird in the exterior tree parts, where the subdominant species are foraging. This suggests again that predation risk influences the choice of foraging sites, the dominant species choosing to forage in inner tree parts with less food but smaller risk of predation.

HOARDING BEHAVIOUR

The habit of tits to hoard food in autumn for use later in the winter (Haftorn 1956, Pravosudov 1987, Suhonen & Alatalo 1991) may have important effects on the choice of foraging niches. It may be economical to hoard in the same sites in trees where the individuals are also searching for other food during winter. It may also be that some sites are more suitable for hoarding (see Petit et al. 1989) thus influencing the choice of foraging sites.

Tits can remember their caches at least over periods of a few days (Sherry et al. 1981), and maybe they can do so for the much longer periods necessary to find the caches later in winter. Alternatively or additionally the caches are found by using certain types of sites for hoarding and by looking later for similar types of sites. Crested and Coal Tits usually only partly hide their caches suggesting that other individuals, also individuals of other species may find the caches. Crested and Willow Tits differed more in their hoarding sites than they did in their foraging sites (Suhonen & Alatalo 1991). Also the studies by Haftorn (1956) in Norway show the trend that Crested Tits avoid hoarding in the sites where other species are foraging. Interspecific kleptoparasitism may restrict the use of hoarding sites and consequently as a correlated response it might also influence the choice of foraging sites.

MORPHOLOGICAL CONSTRAINTS

The choice of the foraging sites is constrained by the morphological characteristics of the individuals. In bird populations the between individual variation in morphology is relatively small, even if there may be sexual differences related to niche segregation, for instance in the Great Tit (Ebenmann 1986, Gosler 1987). In Coal Tits on the island of Gotland also the morphological variation within sex and age groups was correlated with the foraging site choice (Gustafsson 1988). The correlations may reflect different morphological adaptations causing differences in the optimal foraging sites, but it is possible that intraspecific social interactions may at least partially be responsible for the correlations. Bill length may be variable even within individuals in a way that makes bill shape suitable for the food available in each season, as exemplified by the study of Gosler (1987) in the Great Tit.

The tit species inhabiting coniferous habitats have more slender bills than those inhabiting deciduous habitats (Figure 1). Snow (1954) verified the same pattern even for different Coal Tit populations living in the two types of habitats. The stronger bills in deciduous habitats may be related to the use of seeds and nuts that are harder to break than the small seeds of conifers. Marsh Tits having a blunter bill than Willow Tits were quicker in opening sunflower seeds (Alatalo et al. 1983). Great Tits with the largest bill are even quicker, while the Crested and Coal Tits with their slender bills have the longest handling times (unpubl. obs.).

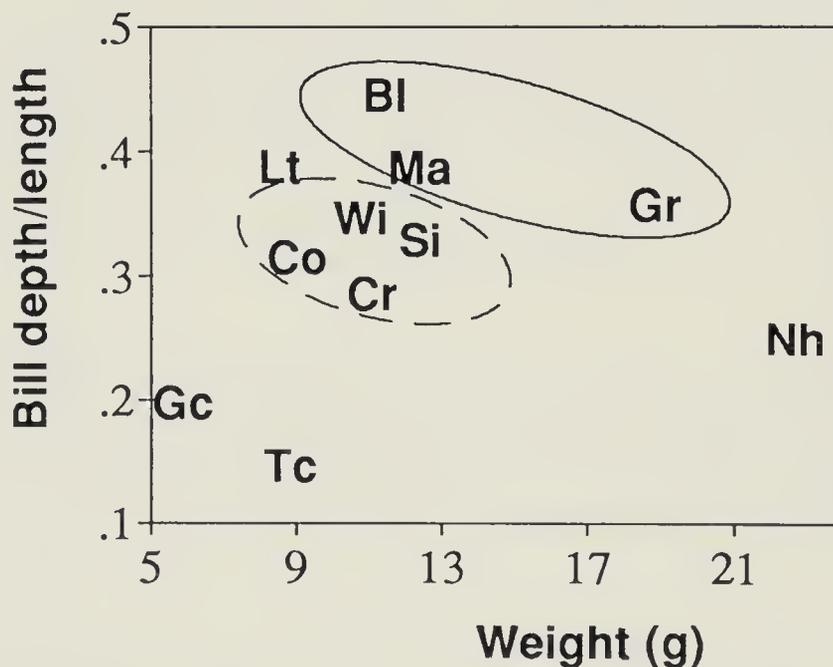


FIGURE 1 - The morphology of tits and the associated species in Northern Europe (based on Alatalo et al. 1983). The species abbreviations are given in Table 1, and the ellipses indicate the deciduous (solid) and coniferous habitat (broken) species of tits.

The other ecomorphological pattern is that the smallest species tend to forage in exterior tree parts while the heavier species use the inner parts (Alatalo 1982, Figure 1). One factor that may explain this trend is the social dominance of the heaviest species and the relative safety of inner tree parts from predation. It may also be that heavier species are less efficient in using the exterior tree parts that demand energetically more expensive searching methods of hanging and hovering (Alatalo & Moreno 1987). Doubly-labelled water technique revealed that the smallest coniferous

forest tit, the Coal Tit, used as much or somewhat more energy than the two heavier tit species (Moreno et al. 1988). It seems that Coal Tits had to use more energy for activities related to food-searching in winter.

In English deciduous forest the average size of arthropods in the diet increases from smaller to heavier tit species (Betts 1955). However, in northern coniferous forests the sizes of the arthropods in the stomachs of Goldcrests and Willow Tits were similar (R.V. Alatalo, A. Carlsson, J. Höglund, J. Suhonen, unpubl.). It seems that in winter the food items are so small that even for the smallest bird species it pays to take the largest items. According to the marginal value theorem the predator should employ a threshold in terms of the energy gain under which the food items should be rejected. It may well be that such a threshold operates only for the small items, all species accepting even the largest items. When comparing the size distribution of arthropods in trees with the diet, it was clear that both species avoided the very small items. Carlsson (1991) compared Coal, Willow and Great Tits in aviary feeding on mealworm pieces of different size. The heavier the bird the more efficient it was in using each food item. However, there were no clear differences in the size of the optimum food items and the three species showed surprisingly similar preferences with respect to food size. While size differences between tit species may not be very critical in determining size of the suitable arthropod food in winter, it may well be so in summer when larger items such as larvae are available. Likewise, the size of a tit together with its bill shape may be crucial for handling hard seeds. Furthermore, size is important in determining the social position of the species in mixed species flocks.

EVOLUTIONARY CHANGES

While morphology constrains the possibility of each population to use different types of foraging sites, evolutionary changes between populations are possible. It has been questioned whether such morphological changes are genetically determined or caused by environmental effects directly. Alatalo & Gustafsson (1988) switched Coal Tit eggs between the island of Gotland and the Swedish mainland. The island population is about 6 % larger in tarsus length, and the experiment revealed that this difference has a genetic background.

The Coal Tits on the island of Gotland are free from competition with the Crested and Willow Tits which have not reached the isolated island. The lack of interspecific competition has allowed Coal Tits to move inwards in trees, to increase highly in numbers and to become larger in size. The same pattern has been verified on all the islands around the Southern Swedish mainland, indicating that a similar evolutionary change has taken place independently several times (U. M. Norberg & R. A. Norberg, in prep.). A similar case of evolutionary change in the absence of competitors has been suggested for the Blue Tits on the Canary Isles (Grant 1979).

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INTERSPECIFIC RELATIONS BETWEEN THE COLLARED FLYCATCHER *FICEDULA ALBICOLLIS* AND THE PIED FLYCATCHER *F. HYPOLEUCA*

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ABSTRACT. The Collared Flycatcher (CF) and the Pied Flycatcher (PF) hybridize frequently on the island of Gotland in the Baltic. Although there is no reduction in the breeding success of heterospecific pairs, hybrids have highly reduced fertility. Females are infertile while 25 % of the males produce offspring. Data suggests that CF males are socially dominant to PF males. Interspecific competition for nest holes is intense and PF mainly breed in the less preferred coniferous habitats. PF males have a longer time interval between arrival and pairing than CF males, which clearly affects their reproductive success. The proportion of PF males involved in mixed pairs is higher in deciduous than coniferous forests. In a recently colonized coniferous forest the numbers of PF decreased over time due to increasing numbers of CF. It has been suggested that CF males are less aggressive towards brown than black PF males. This idea was supported by (1) observational studies of the distribution of brown vs. black PF males in relation to habitat and CF males and (2) a field experiment where brown PF males were accepted to occupy a nest box closer to the CF male than were black PF males.

Keywords: *Ficedula albicollis*, *Ficedula hypoleuca*, hybridization, interspecific competition, population dynamics, mate acquisition, plumage variation.

INTRODUCTION

The mechanisms of interspecific competition that determine population dynamic patterns are of fundamental importance, not only for understanding population distribution and variation in numbers but also for understanding the evolution of species specific morphology and behaviour. This paper argues for the importance in incorporating population dynamics with other biological fields, such as evolutionary genetics and behavioural ecology and, also, the importance of performing such research both at the individual and the population levels.

The direct link between these subdisciplines is that behavioural ecology is the study of relationships between fitness and behaviour and other variables, including population density, N , where fitness of a phenotype is defined as the rate of increase per individual $(1/N) \cdot dN/dt$. But the dynamics of a population depend on its rate of change dN/dt in relation to N and other variables. Therefore, a behaviour study which relates fitness to behaviour and density necessarily provides the information needed to calculate the rate of change of the population in relation to its density, and, thus, the population dynamics (Smith & Sibley 1985). Furthermore any study, within the context of evolutionary biology, of phenotypic variation and its change over time, inevitably needs information of its genetic background.

The above relates to the assumption that all individuals are identical. If we take into account individual differences it is possible to calculate this effect on population dynamics (Charlesworth 1980). By investigating the fitness of observed behaviour of a particular category of individuals in relation to possible alternatives, one can test

whether observed behaviour maximizes fitness given the constraints imposed by environment and individual phenotypes (Charlesworth 1980). Thus an integrated approach can reveal the mechanisms that limit population increase or enforce population decrease and therefore has the potential to explain differences in dynamics between populations.

In this paper we will analyse and discuss mechanisms of interspecific competition between two closely related *Ficedula* spp, the Collared Flycatcher *F. albicollis* and the Pied Flycatcher *F. hypoleuca*. These two species hybridize in areas of sympatry in east and central Europe and on the islands of Gotland and Öland in the Baltic (e.g. Löhrl 1955, Alerstam et al. 1978, Alatalo et al. 1982, 1990, Wallin 1986).

Our aim is to make a first step towards understanding the underlying mechanisms of the dynamics of these species when occurring in sympatry. We will in a stepwise procedure demonstrate the fitness consequences for Pied Flycatchers breeding in sympatry with Collared Flycatchers and its effects for the population dynamics. Furthermore we will discuss a possible consequence of this interaction, namely the evolution of plumage variation in the Pied Flycatcher.

METHODS

We collected data of Pied and Collared Flycatchers in several nest box plots on the island of Gotland (57° 10'N, 18° 20'E) in 1980-1990 (for details see Pärt & Gustafsson 1989). About 80-90% of all flycatchers on Gotland are Collared (Gustafsson & Högström 1981), but Collared Flycatchers are much more predominant in deciduous woodlands (>95%), than in mixed and coniferous forests (Gustafsson & Högström 1981, Alatalo et al. 1982). For this reason, to describe the population dynamics, we only use data from one of our study plots which is mainly made up of coniferous forest (see Pärt & Gustafsson 1989). However, for some comparisons we also use data from our deciduous plots.

Parents were caught on the nest during incubation (females only) or when feeding their nestlings. For each nest we recorded several breeding parameters such as the date of egg-laying, clutch size and number of fledged young. We also took morphological measurements, aged the birds, and classified them into Collared, Pied or Hybrid Flycatchers (for details see Alatalo et al. 1990). About 80% of the birds were previously ringed by us. In 1989 we recorded arrival date of males and females in a few plots by daily checking the plots between 4.00 am and 3.00 pm for newly arrived males and females. During that season we also recorded the number of males that failed to acquire females. All statistical tests are two-tailed.

RESULTS AND DISCUSSION

The population dynamics of the two species in our coniferous plot are shown in Figure 1. Initially both populations had low numbers but increased dramatically after the first year. The number of Collared Flycatchers (males+females) increased between 1980 and 1990 (regression $Y=3.46X-229$, $F=5.02$, $P=0.052$) whereas the number of Pied Flycatchers significantly decreased from 1981 (regression $Y=-1.25X+120$,

$F=7.58$, $P=0.025$). Interestingly, except for the first two years, the two population curves seem to be antagonistic. In 1987 when the numbers of Collared Flycatchers decreased due to severe weather conditions during spring the number of Pied Flycatchers increased. The decline in the Pied Flycatcher population was not due to a year effect since a multiple regression with year and number of Collared Flycatcher pairs as independent effects ($F=21.3$, $P<0.001$) revealed that the number of Pied Flycatchers was not affected by year (partial $F=2.5$, $P>0.15$) but by the number of Collared Flycatchers (partial $F=22.1$, $P<0.001$). The effect of the number of Collared Flycatcher pairs on the proportion of Pied Flycatcher pairs is shown in Figure 2. What are the mechanisms of this interaction that causes the decline in the population of the Pied Flycatcher?

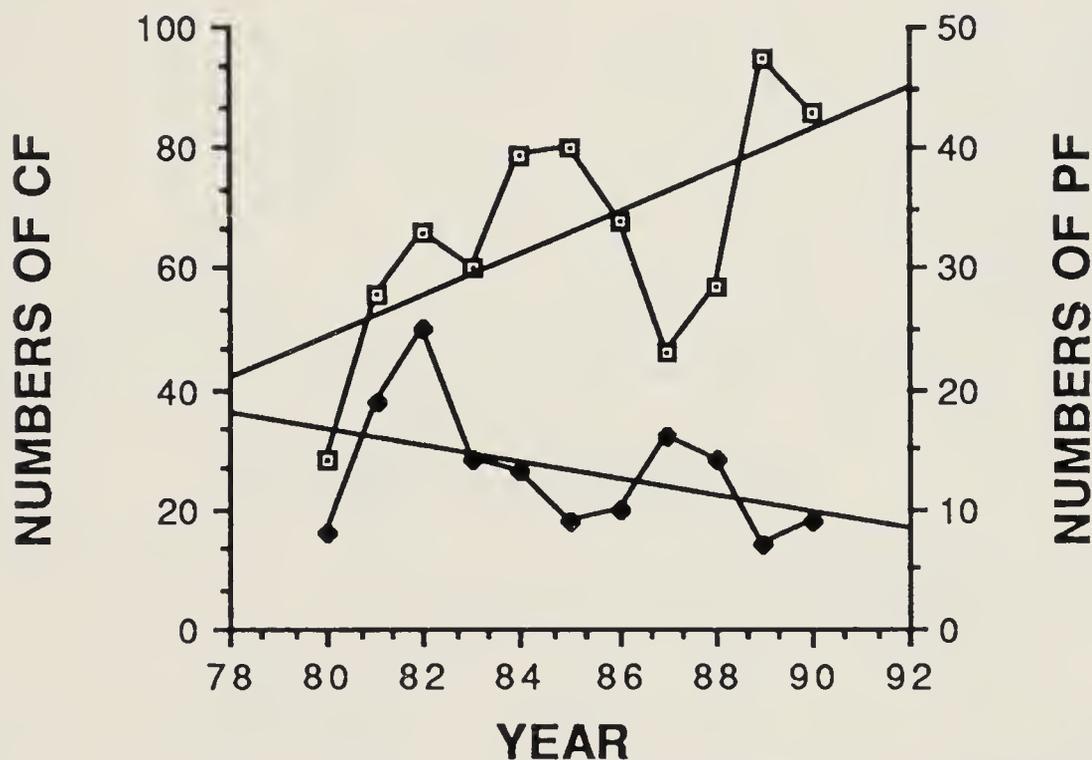


FIGURE 1 – The number of breeding males and females of Pied and Collared Flycatchers in the coniferous plot during the study period.

Interspecific competition and dominance

There is intense competition for nest boxes (Gustafsson 1988) and Collared Flycatchers have been suggested to be dominant over Pied Flycatchers. For example, Collared Flycatchers have been seen to evict Pied Flycatchers from nest boxes (Löhrl 1955). Collared Flycatchers also are somewhat larger than Pied Flycatchers (Alatalo et al. 1990). Although the Pied Flycatchers on the mainland of Sweden prefer deciduous to coniferous forests, in sympatry Collared Flycatchers seem to more or less monopolize the preferred deciduous forest (Alerstam et al. 1978, Alatalo et al. 1982). In our study the proportion of Pied Flycatchers (v Collared Flycatchers) breeding in deciduous forests v coniferous forests were 3.5% and 20.7% respectively ($P<0.05$, G-test).

Interspecific competition and mate acquisition

There was a significantly higher proportion of Pied Flycatchers involved in interspecific (mixed) pairings in the deciduous than in coniferous forest (36.2% and 18.3% respectively, $P<0.05$, G test). This could probably be attributed to differences in relative abundance between the habitats. Furthermore, in the coniferous habitat the frequency of

Pied Flycatchers that ended up in mixed pairs increased with increasing number of Collared Flycatchers (Figure 3).

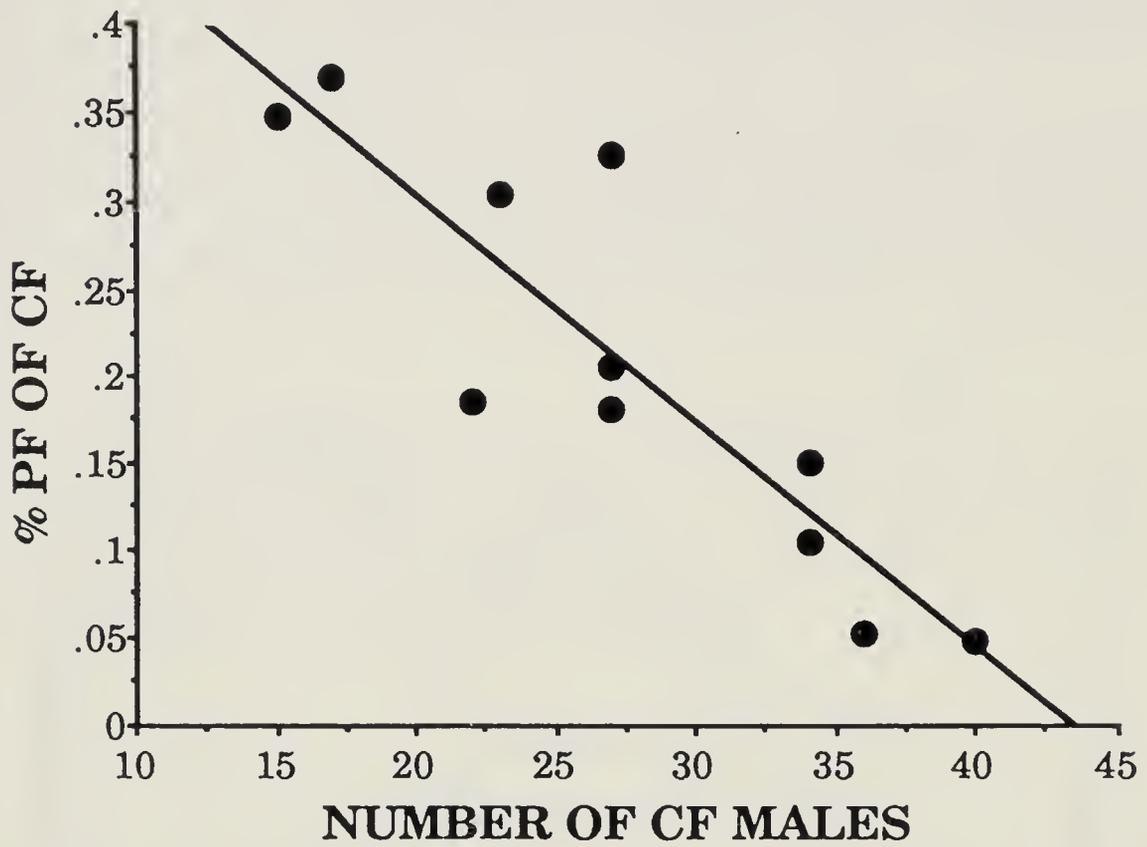


FIGURE 2 – The relationship between the number of Collared Flycatcher males and the proportion of Pied Flycatchers. Data from the coniferous plot.

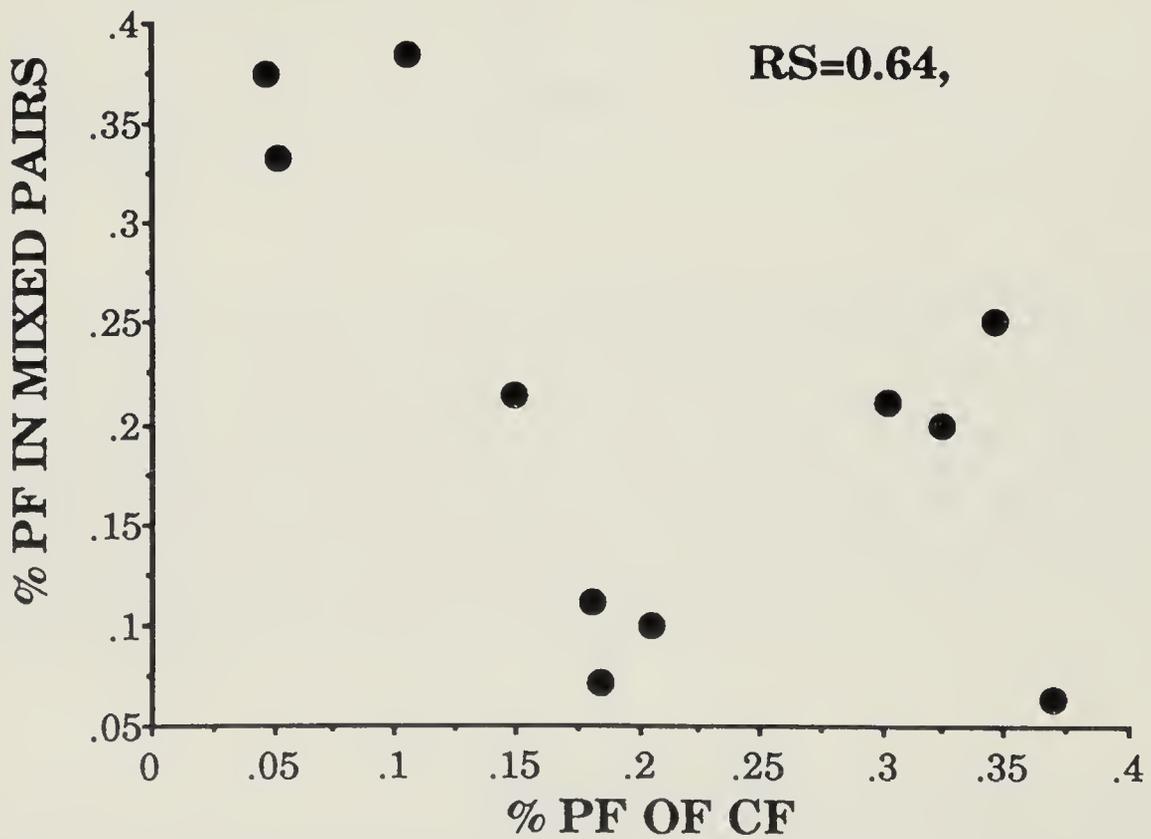
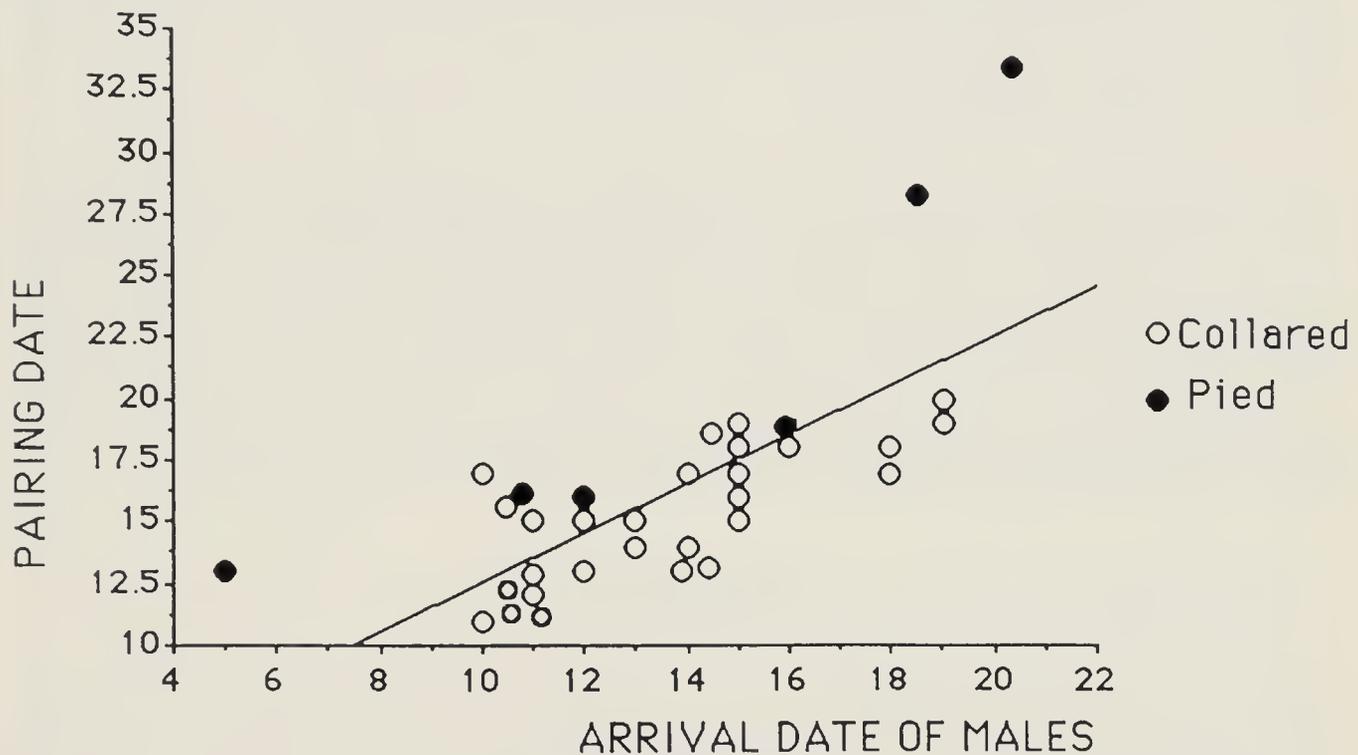


FIGURE 3 – The relationship between the number of Collared Flycatchers and the proportion of Pied Flycatchers involved in mixed pairs in the coniferous plot.

The data on male arrival and pairing date collected in the coniferous forest in 1989 revealed two interesting results. First, arrival dates of Pied Flycatcher males did not differ from Collared Flycatcher males (16.1, $n=11$ and 14.3, $n=29$, respectively, $P>0.25$, t -test). However, Pied Flycatchers had problems in acquiring mates. On average Pied Flycatcher males had to wait for a longer time than Collared Flycatcher males before they were chosen by a female (Figure 4, t -test of residuals, $P<0.001$). Second, a higher proportion of Pied Flycatcher males (5 out of 11) than Collared Flycatcher males (2 out of 58) failed to attract a female (G -test, $P<0.001$).



Although there are many mixed pairs, pair formation is significantly species assortative (Alatalo et al. 1990). Apparently perfect species recognition seems to be a process which takes time to evolve, even when hybrid fitness is highly reduced.

Röskaft et al. (1986) suggested that the variation in male colour in the Pied Flycatcher has evolved in sympatry with Collared Flycatchers. The phenotypic variation of male plumage in relation to distribution of Collared Flycatchers supports this view. The selective advantage should be that Collared Flycatcher males are less aggressive towards brown than black Pied Flycatcher males (Röskaft et al. 1986, Kral et al. 1988). This mechanism should allow brown males to occupy high quality nest holes close to a Collared Flycatcher nest.

We have three pieces of evidence that support this view. First, male Pied Flycatchers are more brown in coniferous than deciduous woodlands when age is controlled for (unpublished data). Second, in the deciduous plots, Pied Flycatcher males breeding inside "among" the Collared Flycatchers were browner than males that occupied edge boxes (unpublished data). Third, an experiment where a nest box defended by a Pied Flycatcher male was gradually moved towards a nest box defended by a Collared Flycatcher male showed that brown males were accepted to occupy a nest box closer to the Collared Flycatcher male than black males (unpublished data).

CONCLUSION

It seems clear that Pied Flycatchers, when occurring in sympatry with Collared Flycatchers, have a fitness disadvantage, the mechanism being multifactorial. Pied Flycatchers are relegated to less preferred habitat and they have problems in finding a mate, which leads to a later breeding and a higher risk of being unmated. However, most importantly a large proportion of the population is involved in interspecific pairing. This hybridization has severe consequences since hybrids have highly reduced fertility. Since the frequency of hybridization increases as the relative abundance of Pied Flycatchers decreases, we would expect the Pied Flycatcher population to go extinct. Thus, the maintenance of the population of Pied Flycatchers is probably dependent on immigration from other populations. These mechanisms of "competition" probably are important for the evolution of male plumage variation in the Pied Flycatcher.

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DEMOGRAPHIC, BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES OF WINTERING CAROLINA CHICKADEES *PARUS CAROLINENSIS* TO THE REMOVAL OF A DOMINANT CONGENER, THE TUFTED TITMOUSE *P. BICOLOR*: A PROGRESS REPORT

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ABSTRACT. In an ongoing experiment in the American Midwest, we are removing Tufted Titmice *Parus bicolor* at the beginning of winter from isolated woodlots occupied by Carolina Chickadees *P. carolinensis*, leaving other woodlots as controls. In the one winter's work accomplished to date in this system where supplementary food, roosting boxes and movement into or out of the study sites have been eliminated, chickadees in the absence of titmice were more intraspecifically social. Pairs of chickadees foraged together more often, on average, and individuals reduced the amount of time they spent solitary. We have found no significant difference in within-winter survivorship between control and experimental treatments, nor have we found any difference in nutritional condition between controls and experimentals, as indexed by the daily growth of a rectrix we induced the chickadees to grow during the winter. Although further records are to be collected, at this point in the experiment we have no conclusive evidence that interspecific competition affects fitness in this *Parus* assemblage.

Keywords: Carolina Chickadee, interspecific competition, *Parus bicolor*, *Parus carolinensis*, ptilochronology, removal experiment, social coherence, survivorship, Tufted Titmouse.

INTRODUCTION

Controversy continues over the importance that interspecific competition for limited resources has for the fitness of individual animals, the density of populations, and the structure of communities (Diamond & Case 1986, Hairston 1989). While generally de-emphasising interspecific competition as a strong and continual selective agent, Wiens (1986, p.171) pointed to relatively closed systems such as islands and relatively sedentary populations, "e.g., some *Parus* assemblages" (tits*, titmice and chickadees) as cases where interspecific competition is "clearly important". Here, we present a progress report on an ongoing project evaluating the hypothesis that within-winter interspecific competition exists within the genus *Parus*.

We predicted that if the presence of a socially dominant parid species reduces the fitness of socially subordinate congeners during the non-breeding season, then Carolina Chickadees in island woodlots from which Tufted Titmice have been removed at the start of the winter: 1) have higher within-winter survivorship; 2) exhibit niche shifts toward the niche of the removed titmouse; 3) grow induced feathers more rapidly, indicating they are in better nutritional condition. Based on one winter's research (1989-90), we relate progress in testing predictions 1 and 3, and present a preliminary assessment of monospecific flocking responses. Improvements over previous

* Common and scientific names of North American and European species follow American Ornithologists' Union (1983) and Voous (1977), respectively.

studies are: 1) the use of closed systems, island woodlots surrounded by tilled fields that are essentially impermeable to parid movements during the winter; 2) the use of study areas known to be free of uncontrolled artificial sources of food; 3) the use of study areas devoid of artificial roosting/nesting boxes; 4) the measurement of survivorship within the winter season; 5) the measurement of intraspecific sociality in the presence and absence of the potential competitor species; 6) the use of a new measure of fitness, the feather growth bar index of nutritional condition, in the presence and absence of the potential interspecific competitor.

We are removing all Tufted Titmice *Parus bicolor* from experimental woodlots, leaving the Carolina Chickadee *P. carolinensis* as the only parid. The removal of Tufted Titmice could cause, as a behavioural response, a change in the monospecific flock size of Carolina Chickadees. Mixed-species foraging group theory (e.g. Barnard & Thompson 1985, Grubb 1987) would predict that in order to maintain vigilance for predators, chickadees in the absence of titmice should form larger conspecific flocks.

Birds regenerate a lost feather, or one plucked by a researcher. Grubb (1989) coined the term, ptilochronology, to describe the procedure we are using to monitor the nutritional condition of free-ranging birds by determining the width of daily growth bars on a feather they have been induced to regenerate.

METHODS

Our project is being replicated in 30-40 ha island woodlots in central Ohio. The seasonal protocol begins in November when all birds in each woodlot are mistnetted at feeders, measured, weighed, colour-streamered and have their outermost right (R6) rectrix plucked and stored in an individual glassine envelope. During each winter of the project, Tufted Titmice captured in the experimental woodlot are transported 50 km and released. Following the capture period, all food is removed from both the control and experimental woodlot. In the beginning of March, after the surviving chickadees have fully grown the induced feather, but before any pre-breeding influx of juveniles from outside the island woodlot has occurred, we replenish the feeders and recapture all birds to obtain the induced R6 rectrix.

In order to draw the widest possible inferences, we will eventually use the numbers of woodlots as sample sizes in testing predicted responses of chickadees to the removal of titmice (Hurlbert 1984). However, to date we have results for only one experimental woodlot, one within-year control and one within-woodlot control. Thus, for this progress report we will use the numbers of birds in control and experimental groups as our sample sizes. Also, after more records are in hand we will work up the analysis by age and sex category. Here, we lump these categories within treatment groups.

In our system of island woodlots, there is no immigration or emigration of chickadees during the winter. Since we know the fate of every bird, we determine within-winter survivorship by dividing the number of marked birds present at the second trapping period by the number caught and streamered during the first trapping period. We evaluate intraspecific social responses to the removal of the congener by determining dyadic coherence (Smith & Van Buskirk 1988) for the chickadees. For each bird,

we calculate the mean of its dyadic coherences with all other chickadees, and its maximum dyadic coherence with just one other chickadee. We compared average values of mean and maximum dyadic coherence between control and experimental treatments. For each chickadee, we also calculate the proportion of all censuses in which it is recorded as being away from all conspecifics. We use this last measure to compare the tendency for chickadees to be conspecifically solitary floaters in the presence and absence of titmice. Analyses of coherence and tendency to be solitary are confined to birds sighted at least five times over the course of a winter.

Finally, we calculate a standard growth bar index (Grubb 1989) to provide information about the nutritional condition of each control and experimental chickadee, controlled for the absolute size of the bird.

RESULTS

During the winter of 1989-90, 7 of 11 (63.6%) and 28 of 36 (77.8%) chickadees survived in the experimental and lumped control woodlots, respectively. This difference was not significant (Chi-square test, $P = 0.347$).

The average coherence \pm SE between pairs of chickadees in the experimental woodlot (0.55 ± 0.09 ; $N=8$) was significantly greater than in the lumped control woodlots (0.23 ± 0.01 ; $N=30$; t-test on angular-transformed values; $P = 0.01$). Similarly maximum dyadic coherence \pm SE was significantly higher (t-test on angular-transformed values; $P < 0.0001$) in the experimental woodlot (0.88 ± 0.03 ; $N=8$) than in the lumped control sites (0.50 ± 0.03 ; $N=30$).

The average proportion of sightings \pm SE when an individual chickadee was alone was significantly lower (0.12 ± 0.04 ; $N=8$) in the absence of titmice than in their presence (0.25 ± 0.02 ; $N=25$; t-test on angular-transformed values; $P = 0.02$).

Finally, the mean daily feather growth index of nutritional condition \pm SE of chickadees in the absence of titmice (0.687 ± 0.280 ; $N=6$) was greater than the same index of nutritional condition of chickadees in the presence of titmice (0.645 ± 0.002 ; $N=30$), but the difference was not significant (t-test on angular-transformed values; $P = 0.14$). In this comparison, β , the probability of accepting the null hypothesis when it was false (type II error), was 0.72. The difference in the feather growth bar index between control and experimental groups was greater for males than for females, but a two-way ANOVA was not significant.

DISCUSSION

Removing titmice was not associated with a significant increase in survivorship of Carolina Chickadees. Our experimental (64%) and control (78%) values of within-winter survivorship are similar to those reported for other species of parids known to be wintering in the absence of artificial food (Jansson et al. 1981, Brittingham & Temple 1988, Desrochers et al. 1988).

Our results from the first winter's study suggest that Carolina Chickadees become more intraspecifically social when a dominant congener, the Tufted Titmouse, is

removed from their habitat. Pairs of birds occupying the same flock home range (Cimprich & Grubb, unpubl.) tended to forage together more often, and "floaters" tended to reduce the amount of time they spent solitary). Both of these reactions to the loss of heterospecific flock mates support current theory for the adaptiveness of mixed-species flocking (e.g. Grubb 1987).

Comparison of daily feather growth suggested that the nutritional condition of chickadees may be affected by the presence or absence of the congeneric titmouse. Because α was as small as 0.14 and β was as large as 0.72, the lack of a statistically significant difference between control and experimental treatments may have been a function of the small sample sizes.

In conclusion, Carolina Chickadees became more intraspecifically social in the absence of Tufted Titmice. However, at this point in a within-season experiment that eliminates roosting boxes, supplementary food and movement into or out of the study sites, we have no conclusive evidence that interspecific competition in one particular *Parus* assemblage is "clearly important" in reducing fitness.

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PROTECTED WINTER ROOSTING SITES AS A LIMITING RESOURCE FOR BLUE TITS

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ABSTRACT. During winter tits roost in cavities if suitable holes are available. The breeding density of Blue Tits increases about 1.5 times when large-holed boxes are replaced by small-holed ones, showing that interspecific competition between Great and Blue Tits reduces Blue Tit breeding density. By manipulating Great Tit density and the availability of protected roosting sites for Blue Tits independently we can show that only the latter factor contributes to the increase in Blue Tit breeding numbers. Our data, therefore, suggest that interspecific competition between Great and Blue Tits in winter is for roosting sites but not for food.

Keywords: Blue Tit, field experiments, Great Tit, interspecific competition, *Parus caeruleus*, *Parus major*, roosting behaviour.

INTRODUCTION

Blue Tit *Parus caeruleus* and Great Tit *P. major* are secondary cavity breeders that readily accept nestboxes for breeding. They form an interesting species pair since, in W. Europe, the preferred habitat of both species is mature oakwood and they compete interspecifically both for food and for cavities (Dhondt 1977, 1989, Dhondt & Eyckerman 1980a, Minot 1981, Minot & Perrins 1986).

Outside the breeding season tits always sleep alone in a hole. Cavities are used for roosting at night during two periods: in small numbers during summer when moulting (Winkel & Winkel 1973, pers. obs.); in larger numbers from October to March (Dhondt 1970, Kluyver 1957, Schmidt 1976, Schmidt et al. 1984, 1985, Winkel & Winkel 1973). If the diameter of the entrance hole of the nestboxes is 32 mm, the vast majority of roosting birds are Great Tits, and Blue Tits are found only in small numbers (Dhondt & Eyckerman 1980a, Winkel & Hudde 1988). When Great Tits are excluded from the nestboxes by reducing the entrance-hole-diameter to 26 mm, many more Blue Tits are found roosting in winter, and this is followed by an important increase in their breeding density (Dhondt & Eyckerman 1980a). Dhondt & Eyckerman (1980a) gave no information on: (i) the number of Blue Tits roosting in winter in a situation with both nestbox types; (ii) roosting behaviour of Blue Tits in the absence of Great Tits. We will here present observations relative to both problems.

A problem with the experiment which Dhondt & Eyckerman (1980a) performed is that two conditions were changed simultaneously: (i) the type of nestbox available to tits was changed from only large-holed (diameter of entrance hole 32 mm) to only small-holed (diameter 26 mm), and (ii) the density of Great Tits was lowered by the removal of the large-holed nestboxes. Dhondt & Eyckerman (1980a) concluded that the increase in Blue Tit breeding density following the experimental change in nestbox configuration was the result of a reduction in interspecific competition between Blue and Great Tit. This competition would in part be the result of interactions over roosting

sites, in part be a direct result of a change in numbers because of competition over food. Experiments to test the hypothesis of food competition in winter have given contradictory results. Krebs (1971) found an effect in one winter, Källander (1981) found no effect in two winters.

We have, therefore, manipulated nestbox configuration and Great Tit density independently.

The hypotheses to be tested to explain the increase in Blue Tit breeding density are:

- H1. The increase in Blue Tit breeding density is only caused by a reduction in Great Tit density in the previous winter;
 H2. The increase in Blue Tit breeding density is only caused by the provision of small-holed nestboxes in the previous winter;
 H3. The increase in Blue Tit breeding density is caused both by a reduction in Great Tit density and by the provision of small-holed nestboxes in the previous winter.

Great Tit density, both in winter and in the breeding season, is influenced by the availability of large-holed nestboxes. It is therefore possible to manipulate Great Tit density and roosting site availability for Blue Tits independently as shown in Table 1. In Table 2 relative Blue Tit densities are shown which are predicted by the three hypotheses.

TABLE 1 – Effect of nestbox configuration on the importance of interspecific competition for resources available to Blue Tits. It is assumed that an increase in Great Tit density results in an increase in winter competition for food and that when small-holed nestboxes are present competition for roosting sites is reduced.

Nestbox configuration	Great Tit density	Availability of protected roosting sites for Blue Tits
L (only large-holed)	high	no
LS (both types)	high	yes
S (only small-holed)	low	yes

TABLE 2 – Blue Tit breeding densities predicted by the three hypotheses in plots with different nestbox configurations. (For more details see text.)

Hypothesis	Nestbox Configuration		
	L	LS	S
H1	Low	Low	High
H2	Low	High	High
H3	Low	Medium	High

MATERIAL AND METHODS

The three nestbox configurations (L, LS and S) were replicated near Antwerp (N. Belgium), and 50 km further SW near Ghent. The Antwerp plots are in or close to a

large wooded estate. The Ghent plots are isolated habitat islands. The replicates were not simultaneous, but data on Blue Tit density are available for a minimum of 5 breeding seasons in each plot. Information on plots used and study period in each plot is summarised in Table 3. In all plots there was a surplus of nestboxes.

We have analysed the data using a two-way analysis of variance on mean breeding density (to avoid pseudo-replication) with nestbox configuration as one factor and area as the second. As concerns data on number of roosting Blue Tits in the different nestbox configurations we will only present data from the Antwerp study sites. The nestbox configuration in Plot T was changed after five breeding seasons. We will therefore compare the number of individuals roosting in Plot T in 4 winters (1979-80 to 1983-84; only large-holed boxes, period A) with that in another 4 winters (1983-84 to 1986-87; only small-holed nestboxes, period B) and this in comparison to the numbers found in Plots C and B in the same periods.

TABLE 3 – Study plots and periods.

Nestboxes	Area and Period	
	Ghent	Antwerp
S	Gontrode (n = 7) (1977-80,82-84)	Plot C (n=11) (1980-1990)
SL	Maaltepark (n=8) (1979-86)	Plot B (n=11) (1980-1990)
L	Zevegem (n=15) (1964-1978)	Plot T (n=5) (1979-1983)

n : number of breeding seasons

More details on the study plots can be found in Dhondt & Hublé (1968) and in Dhondt & Eyckerman (1980b) for the Ghent plots; in Dhondt et al. (1982) and Dhondt (1987) for the Antwerp plots.

In some winters or plots only two winter evening visits were made. In order to make the results comparable we will use the observations only from the first December visit and the first February visit of each study plot. If the presence of a different nestbox configuration has an effect on the number of roosting individuals, and since we have changed the experimental setup after 4 years, we should find a significant interaction term when comparing the number of individuals found roosting between plots and periods.

RESULTS

Breeding density

The average breeding densities are shown in Table 4. Table 5 gives the results of the ANOVA. The nestbox configuration has a significant effect on breeding density. Density is also significantly higher in Antwerp than in Ghent. In both areas the study plots that contain small-holed nestboxes, either alone or with large-holed boxes, have a breeding density of Blue Tits that is 1.4 to 1.7 times higher than the plots that contain no small-holed boxes. The breeding density in the Antwerp plots is about 1.7 times higher than in the Ghent plots.

TABLE 4 – Average Blue Tit breeding density (pairs/ha) in each study plot.

Plot name	Area	Nestbox Configuration	n years	Mean	Standard Deviation
Zevegem	Ghent	L	15	1.02	0.208
Maaltepark	Ghent	LS	8	1.71	0.270
Gontrode	Ghent	S	7	1.51	0.313
Plot T	Antwerp	L	5	1.83	0.390
Plot B	Antwerp	LS	11	2.72	0.578
Plot C	Antwerp	S	11	2.58	0.359
Overall			57	1.88	0.762

TABLE 5 – Two-way analysis of variance of Blue Tit mean breeding density per area and nestbox configuration. Densities differ significantly between experimental nestbox configurations and between the Ghent and Antwerp study plots. Since only one value (the average) is used per cell no interaction term can be calculated. In a similar analysis, using all values for each plot, both main effects were significant but the interaction term was not.

Source of Variation	Sum of Squares	DF	Mean Square	F	P
Area	1.398	1	1.398	161.986	.006
Nestbox configuration	.696	2	.348	40.329	.024
Explained	2.094	3	.698		
Residual	.017	2	.009		
Total	2.111	5	.422		

A comparison of the results in Table 4 with the predictions under the different hypotheses in Table 2, shows that hypotheses 1 and 3 must be rejected, and that therefore hypothesis 2 is accepted. The Blue Tit breeding density in the areas where both nestbox types are mixed is in fact higher than in the area with only small-holed nestboxes. For hypotheses 1 or 3 to be true the breeding density in the plot with both box types had to be lower than in the plots with only small-holed nestboxes. It should be noted that the differences between only small-holed and both types are not statistically significant: at Ghent we have 5 years with breeding densities both in Maaltepark (LS) and Gontrode (S). A paired t-test yields $t = 2.743$, 4 df, $P > 0.05$. At Antwerp we have 11 paired values: $t = 0.684$ NS; combined data: $n = 16$, $t = 1.43$, $df = 15$, $P > 0.10$).

Roosting behaviour

The average number of individuals found roosting in winter does not change between the two 4 year periods in Plots B and C, where the nestbox configuration remains unchanged, but increases sixfold in Plot T when small-holed boxes replace large-holed ones. The averages differ between plots and periods, but also show a significant interaction term (Table 6). When only small-holed boxes are available in Plot T (period B) the number of individuals roosting reached a level similar to that found in Plot C in the entire study period, and higher than in Plot B in which both nestbox types are present.

TABLE 6 – Mean number of individuals found roosting per ha in two evening winter visits. Period A covers the 4 winters 1979-80 to 1982-83; period B the next 4 winters. In Plot T the nestbox configuration was changed from only large-holed boxes in period A to only small-holed boxes in period B. In both other plots the nestbox configuration remained unchanged: only small-holed boxes in Plot C; both types in Plot B. Note the significant interaction term in the ANOVA, caused by the change in experimental nestbox configuration in Plot T.

Period	n	Plot B		Plot C		Plot T	
		mean	s.e.	mean	s.e.	mean	s.e.
A	4	1.30	.360	2.15	.262	0.37	.072
B	4	1.35	.443	2.59	.443	2.38	.503
A+B	8	1.32	.233	2.37	.252	1.37	.446

ANOVA	Sum of squares	df	Mean square	F	P
Main effects	9.734	3	3.2446	6.267	.004
Plot	5.559	2	2.7794	5.369	.015
Period	4.175	1	4.1750	8.064	.011
Interaction	4.243	2	2.1216	4.098	.034
Residual	9.319	18	0.5177		
Total	23.296	23			

TABLE 7 – Proportion of Blue Tits breeding in two successive seasons that use nestboxes for roosting in the intervening winter (1979-1986).

Plot	Males		Females	
	n	%roosting	n	%roosting
C	106	61.3	127	45.7
B	63	39.7	68	25.0
T _a	25	16.0	31	6.5
T _b	37	48.7	39	18.0

3-way G-test	area effect	sex effect
all plots	46.394 (3) **	16.407 (1) **
T _a v. T _b	9.395 (1) **	9.452 (1) **
T _a v. B	10.172 (1) **	4.382 (1) *
T _b v. B	0.011 (1) NS	10.079 (1) **
T _b v. C	10.211 (1) **	11.993 (1) **

n = number of individuals found breeding in two successive seasons.

The bottom half of the table contains G-values followed, in brackets, by the number of degrees of freedom.

** : P < 0.01; * : P < 0.05

In Table 7 it is shown that the proportion of Blue Tits presumed to be present during winter in the plot, because they were found breeding in that plot in two successive years, is also influenced by the nestbox types present. What is important in that

analysis is that the proportion of roosting breeders increases about threefold in Plot T when nestbox type is changed from large- to small-holed, and this for both sexes.

The data certainly confirm that the provision of small-holed nestboxes at Antwerp, as previously at Ghent, results in more Blue Tits roosting in a nestbox at night, and is followed by an increase in the breeding density.

As concerns the roosting behaviour of Blue Tits in the absence or presence of Great Tits in constant aviary conditions the recent experiments by Kempenaers & Dhondt (1991) gave following results:

- Single Blue Tits offered 2 boxes of each type significantly preferred large-holed nestboxes.
- When a Great Tit was added to the aviary Blue Tits significantly switched to small-holed nestboxes, although no behavioural interactions could be observed.
- The proportion of Blue Tits using a large-holed nestbox in an aviary in which a Great Tit was also present was higher than the proportion of Blue Tits found roosting in large-holed boxes in the field.

DISCUSSION

The results clearly show that Blue Tit breeding density in a study plot in which small-holed boxes are provided increases by about half compared with a plot in which only large-holed boxes are present. This increase occurs regardless of the density of Great Tits, as Blue Tit breeding density does not differ if small-holed boxes are the only type present, or if they are combined with large-holed nestboxes, and therefore supports hypothesis 2. This result therefore suggests, as did Källander's (1981) experiments, that winter competition for food plays only a very limited role in the Blue Tit/ Great Tit interaction. Although unlikely, it cannot be excluded that the provision of artificial food during winter close to the study areas has influenced interactions over food and overwinter survival and hence breeding densities and that the conclusions drawn here are influenced by it.

Why is it that the provision of small-holed nestboxes has such a dramatic effect? Kempenaers & Dhondt (1991) have shown in aviary experiments that a Blue Tit offered a choice of large- and small-holed nestboxes for roosting prefers the large-holed boxes when alone, but the small-holed boxes when together with a Great Tit. Great Tits, therefore, exclude Blue Tits from potential roosting sites when they can use them. A behavioural mechanism results in the exclusion of Blue Tits from roosting sites. The presence of small-holed nestboxes, which Great Tits cannot enter, is sufficient to cause a clear increase in Blue Tit breeding density. The population processes causing this increase are an increase in adult annual survival and an increase in local recruitment (Dhondt 1989). We therefore think that the presence of protected roosting sites for Blue Tits in winter makes the habitat more attractive (less dispersal of juveniles) and increases habitat quality (higher adult survival).

There are, however, still unexplained area and possible plot effects. Thus the breeding densities of Blue Tits at Ghent are lower than at Antwerp in all study plots. This is true also for Great Tits (own observations) and will be further explored elsewhere.

Furthermore the effects of nestbox type available on the number of individuals roosting and on the proportion of breeders found roosting are not exactly the same in all plots. Thus the density of roosting tits is lower in Plot B (both types) than in plots C and T (second period) with small-holed boxes only, although breeding densities are the same in all three. Is this a plot effect, caused for example by more natural cavities suitable for roosting being present in Plot B, or is this an experimental effect? Results from more different study plots are needed to sort out the effects of nestbox configuration and those of the plot itself.

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POPULATION DYNAMICS OF LAND BIRD POPULATIONS ON OAHU, HAWAII: FIFTY YEARS OF INTRODUCTIONS AND COMPETITION

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ABSTRACT. Data from the annual Christmas Bird Count between 1939 and 1989, around Honolulu, on the island of Oahu during late December, were analyzed to discover the annual rates of change and possible competitive interactions of introduced and native land bird species. Both total number of species and total number of individuals increased over the period. The proportion of species that were rare dropped, rose, and dropped again during the 50-year period, probably as a result of new introductions. Two species held steady, while 12 increased (about 9 linearly and 3 logarithmically). The higher rates of increase were 10-25% per year. Six species declined, but no well-established species became extinct. Negative correlations between population sizes indicated possible competition between the Japanese White-eye *Zosterops japonicus* and the native Apapane *Himatione sanguinea* and Elepaio *Chasiempis sandwichensis*, and between the Red-billed Leiothrix *Leiothrix lutea* and White-rumped Shama *Copsychus malabaricus*.

Keywords: Introduced birds, Hawaii, bird populations, extinction, population dynamics.

INTRODUCTION

The Oahu Christmas Bird Count, part of a nation-wide effort of standard censusing conducted in early winter, provided a unique opportunity for a study of populations of introduced birds; the Hawaiian avifauna has been liberally enriched by human introductions of birds (Berger 1981, Long 1981). During late December from 1939 to 1989, missing only 1941-1943, observers counted birds in 15-mile (24-km) radius circles in the city, suburbs, and forested mountains around Honolulu.

In her excellent compendium of Christmas Count data from North America, Root (1988) describes the usefulness of the data, when proper correction for observer effort is applied. Butcher et al. (1990) also examined the data and found it very useful for trends over large geographical areas. The Oahu Christmas Count data have been analyzed previously by Ralph (1980) and Williams (1987), but not in the detail presented here. To my knowledge no analysis has been conducted, however, of any other count over so many years.

The 50 years of data analyzed here contribute to a topic for which, as Hutchinson (1978:29) states "A very few cases are known where species have been introduced into, or have invaded, isolated areas and have been studied effectively." Among these few cases were Ring-necked Pheasants *Phasianus colchicus* in British Columbia (Einarsen 1942, 1945), and Collared Turtle-Dove *Streptopelia decaocto* in Britain and Ireland (Hudson 1965, 1972).

METHODS

These data were taken from the annual count in a 15 mile (24 km) circle. Birds are recorded primarily during daylight hours on a predetermined day. Observers are divided into "parties" which spend time in various habitats recording all individuals of all species seen or heard. The number of birds seen by all observers in all areas combined was divided by the total number of hours spent counting by the separate parties (party-hours), as recommended by Bock & Root (1981), and followed by all investigators since.

Between 1964 and 1971 observers made a conscious effort to count Common Myna *Acridotheres tristis* and Zebra Dove *Geopelia striata* in evening roosts. Through the courtesy of R.L. Pyle in obtaining original field forms, and from accounts published in *Elepaio*, the journal of the Hawaii Audubon Society, I have been able to determine which observers counted at roosts and to estimate the number seen at each roost. I have subtracted these birds from the total for those years to make years comparable.

During 1949-1953 the data included counts from the Poamoho Trail, a remote area of largely native forest in the Waianae Mountains, actually outside of today's count circle of 24 km. This area was excluded after 1953 as other native forests were covered. Since this was the only area of native forest covered during this earlier period, I felt it best to include these data, as did Williams (1987).

The land bird species used in this analysis were those which I felt have actually established breeding populations. I included in most analyses only those species with more than 250 individuals counted, all years combined. Several rare but persistent species, such as the Lavender Waxbill *Estrilda caerulescens*, which was more common in the 1960s and 1970s, were not included in many analyses. The waxbill has persisted in low numbers, or has been continuously reintroduced, since then. The Rock Dove *Columba livia* was excluded from analyses because in early years it was not counted by observers. The first two years of the Yellow-fronted Canary *Serinus mozambicus* were also not included in analyses, as they were probably a flock of introduced birds. I have omitted cordon-bleus *Uraeginthus* spp. and waxbills *Estrilda* spp. except the Lavender Waxbill since many observers have found them difficult to identify as to species.

Analytical methods

RATE OF POPULATION CHANGE. The measure of population change (Table 1) was the least squares regression using year as the independent variable and number of birds per party-hour as the dependent variable. Because zero has no logarithm, 1.0 was added to the birds per party-hour in all years for those species with no detections of birds in some years. A regression model was calculated using both untransformed and logarithmically transformed data. Year equalled 1 on the first year the species was detected on a census, excluding the canary, as mentioned above. The various R^2 values shown in Table 1 estimate the amount of variation in the bird population size explained by years. A relatively high R^2 value would indicate a population with relatively low between-year variation. Such a population might be less responsive to environmental variation, showing, for instance, a consistent growth during the study. A relatively low value could indicate a species fluctuating from year-to-year. In expanding or contracting populations, the slope of the line (β) can be considered to be the rate of population increase of the species if the change is linear. The values allow the

TABLE 1 - Population changes of birds on Oahu, Hawaii, between 1939 and 1989 as calculated by: a regression analysis (the R^2 value, y-intercept, and slope (β) of normal and the natural logarithm of the number of birds per party-hour); the years included in the model; and the type of food taken.

Species	Regression of population change						Foraging mode ^a	
	Non-transformed		Natural logarithm		Years	R^2		
	R^2	y-int,	β	y-int.			β	
Unchanging population								
Japanese Bush-Warbler	0.009	0.252	0.005	0.058	-2.007	0.042	71-89	I
Northern Cardinal	0.005	2.322	-0.004	0.018	0.555	0.005	40-89	G
House Finch	0.482	0.382	0.069	0.454	-0.754	0.046	39-89	G
Expanding population								
Zebra Dove	0.623	-1.398	0.807	0.673	1.646	0.042	39-89	G
Spotted Dove	0.659	0.073	0.285	0.643	0.539	0.046	39-89	G
Red-vented Bulbul	0.919	-3.461	0.939	0.847	-1.931	0.262	68-89	I,F
Red-whiskered Bulbul	0.645	-0.965	0.179	0.791	-3.849	0.242	67-89	I,F
White-rumped Shama	0.629	-0.237	0.064	0.683	-2.107	0.084	54-89	I,F
Common Myna	0.424	7.121	0.531	0.473	2.000	0.032	39-89	I,F
Japanese White-eye	0.414	2.448	0.148	0.453	0.998	0.027	39-89	I,F,N
Red-crested Cardinal	0.633	-0.272	0.093	0.698	-1.342	0.064	40-89	G
Yellow-fronted Canary	0.659	-0.031	0.012	0.767	-3.870	0.109	67-89	G
House Sparrow	0.184	4.671	0.264	0.374	1.136	0.038	39-89	G
Java Sparrow	0.654	-1.880	0.432	0.831	-2.169	0.223	69-89	G
Contracting								
Elepaio	0.331	2.586	-0.059	0.447	1.167	-0.023	39-89	I
Northern Mockingbird	0.068	0.178	-0.002	0.042	-1.987	-0.014	57-89	I,F
Red-billed Leiothrix	0.302	4.493	-0.100	0.421	1.690	-0.036	40-89	F
Amakihi	0.191	2.211	-0.032	0.155	0.557	-0.018	39-89	I,N
Apapane	0.220	9.590	-0.213	0.362	1.889	-0.056	39-89	N,I
Nutmeg Mannikin	0.153	11.053	-0.143	0.097	2.143	-0.015	39-89	G

^a Foraging mode is: G = granivore; I = insectivore; F = frugivore; and N = nectarivore (based on Berger 1981; Ralph, in press).

separation between populations expanding: at higher rates of increase with a high value of β ; and those expanding at lower rates, due either to the influence of limiting factors or lower intrinsic rates of increase.

TESTS FOR COMPETITION. To test for possible competition between species, I used the simple premise that if one species is affecting another, their populations could show corresponding negative statistical relations. I divided birds into granivores, nectarivores, frugivores, and insectivores (Table 1), under the assumption that negative correlations on a population basis would not likely occur between species with widely different foraging niches.

I used the General Linear Model Procedure of SAS (SAS Institute 1985), specifically the partial sums of squares (Type III sums of squares), whereby I performed a least squares regression of the number of birds per party-hour per year of a given species with all other species of similar foraging niche. The first analysis included using all species in a foraging group as multiple regression predictors for one of the component species. While many had significant positive associations, a few negative interactions were significant in this analysis. Such an analysis, however, includes many numerical interactions. I then regressed separately each species pair. I included only those species having negative slopes from the first analysis. That is, I included only those species in which the addition of individuals of one species was significantly correlated with the loss of individuals of another, as calculated by the Student's t value (and associated P value), for testing the null hypothesis that the slope equalled zero. A very small P value leads to the conclusion that the independent variable contributed significantly to the model. If all significance disappeared when the species were analyzed separately, without the influence of other species, then I considered the previous negative relationship to be spurious.

RESULTS

Population characteristics

TOTAL NUMBER OF SPECIES. The total number of species recorded by year (Figure 1) was 15-20 species in the early years. In the late 1960s a surge of newly introduced species started to appear in the counts, and the number has reached 25-30 species recently. Only three or four in any one year were native Hawaiian species; all others have been introduced by humans.

TOTAL NUMBER OF INDIVIDUALS RECORDED BY YEARS. The number of individuals of all species recorded per party-hour has gradually increased over the past 50 years (Figure 2). The number during the 1940s through the late 1960s was variable, but usually 30-100 birds per party-hour. Since then, the average has increased, with only one year below 80 birds per party-hour, reaching an average in the 1980s of about 150 birds (a regression of: $R^2 = 0.775$; $P < 0.0001$). This pattern of increasing numbers of birds was maintained even when I removed the rarest species from the analysis, removing the possibility that the increase was solely due to an influx of rare species. To do this, I deleted from the analysis all species with a total of less than 250 individuals recorded over the 50 year period. The average number of individuals still increased, indicating that not only the rare species were increasing, as they established themselves, but also the commoner species were becoming more abundant. This pattern of increase could result from an increase in observer ability, an increase in overall bird density, or both.

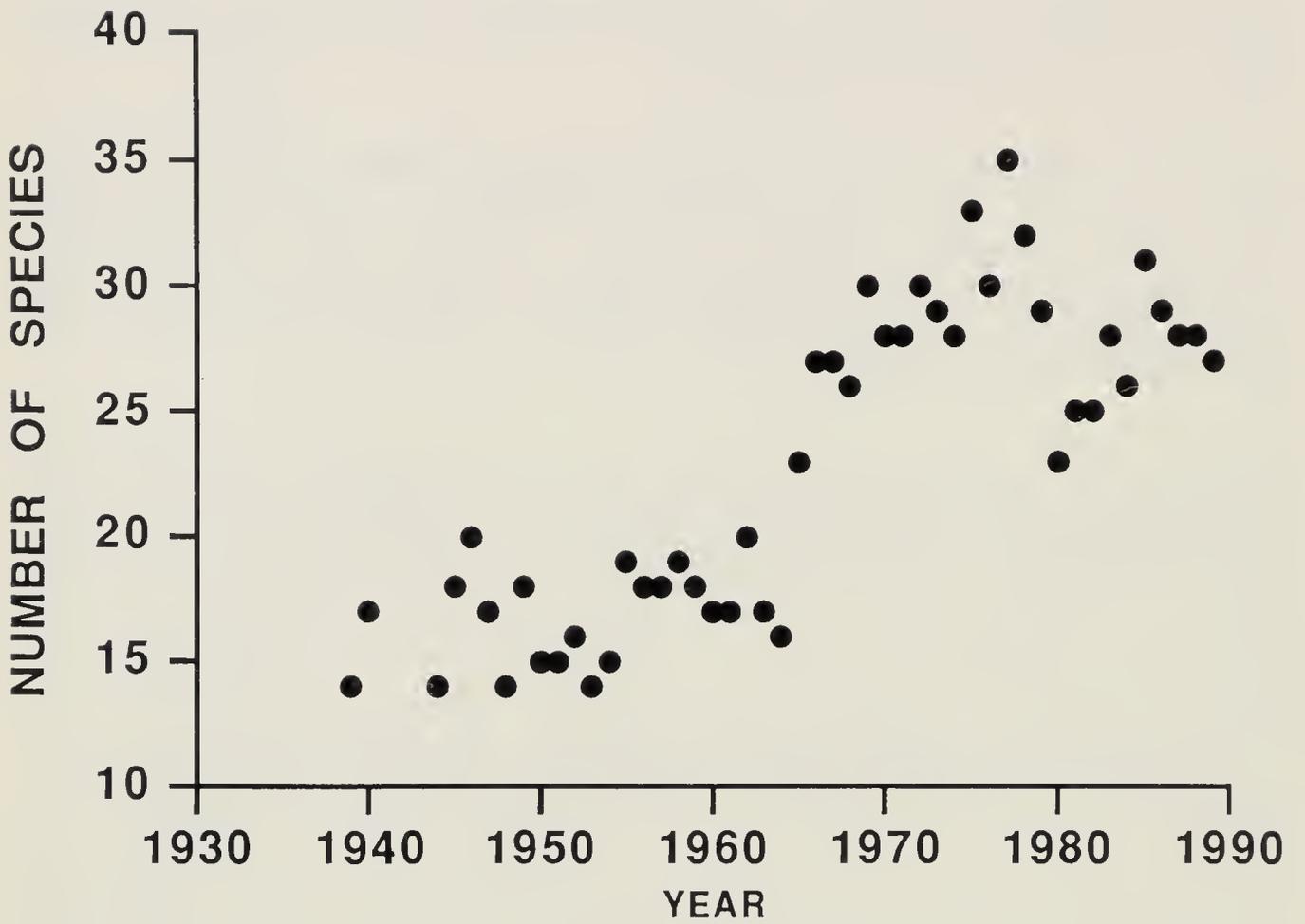


FIGURE 1 - Number of species recorded in each year on the Oahu Christmas Count.

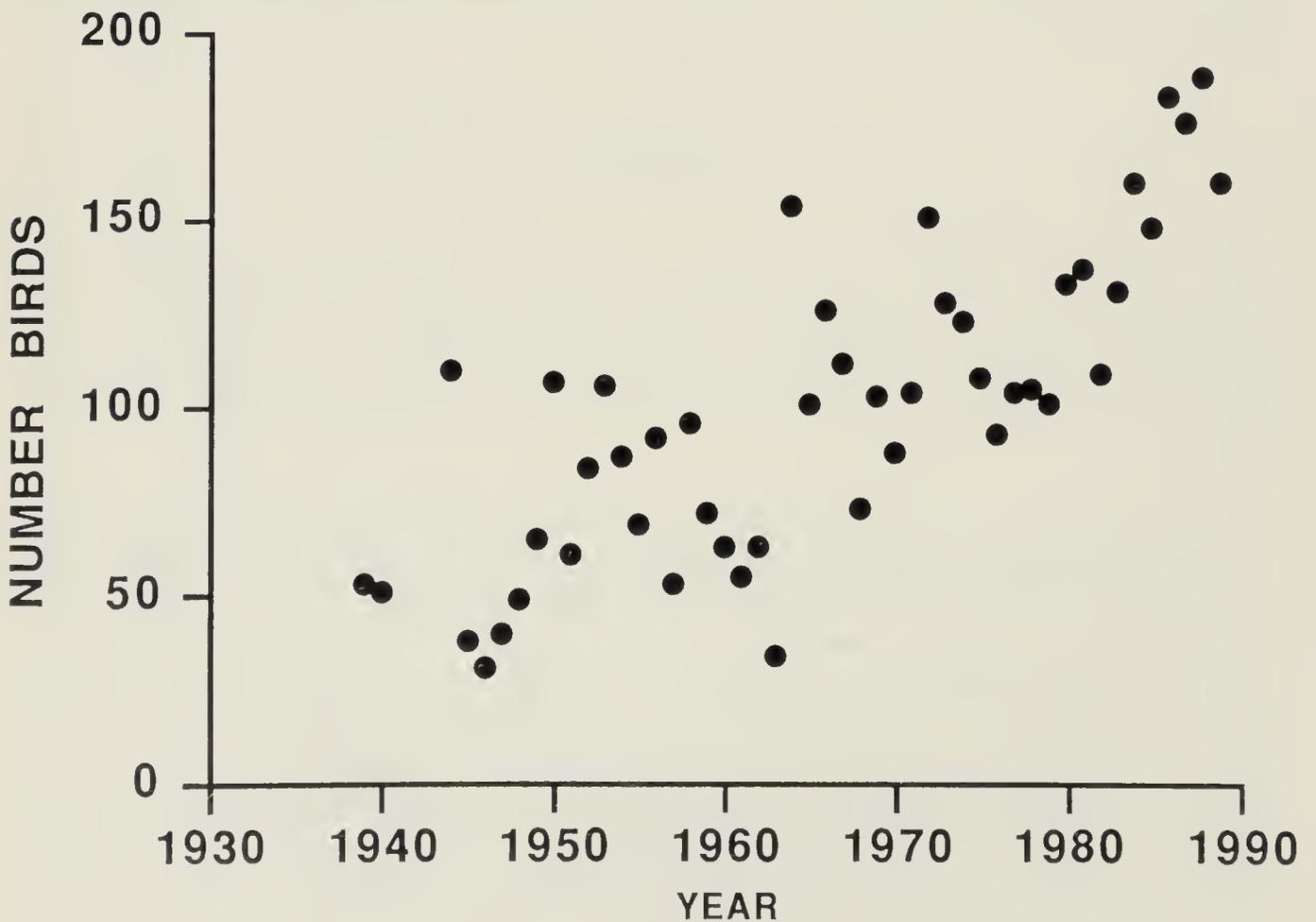


FIGURE 2 - Total number of individuals per party-hour of all species combined seen each year.

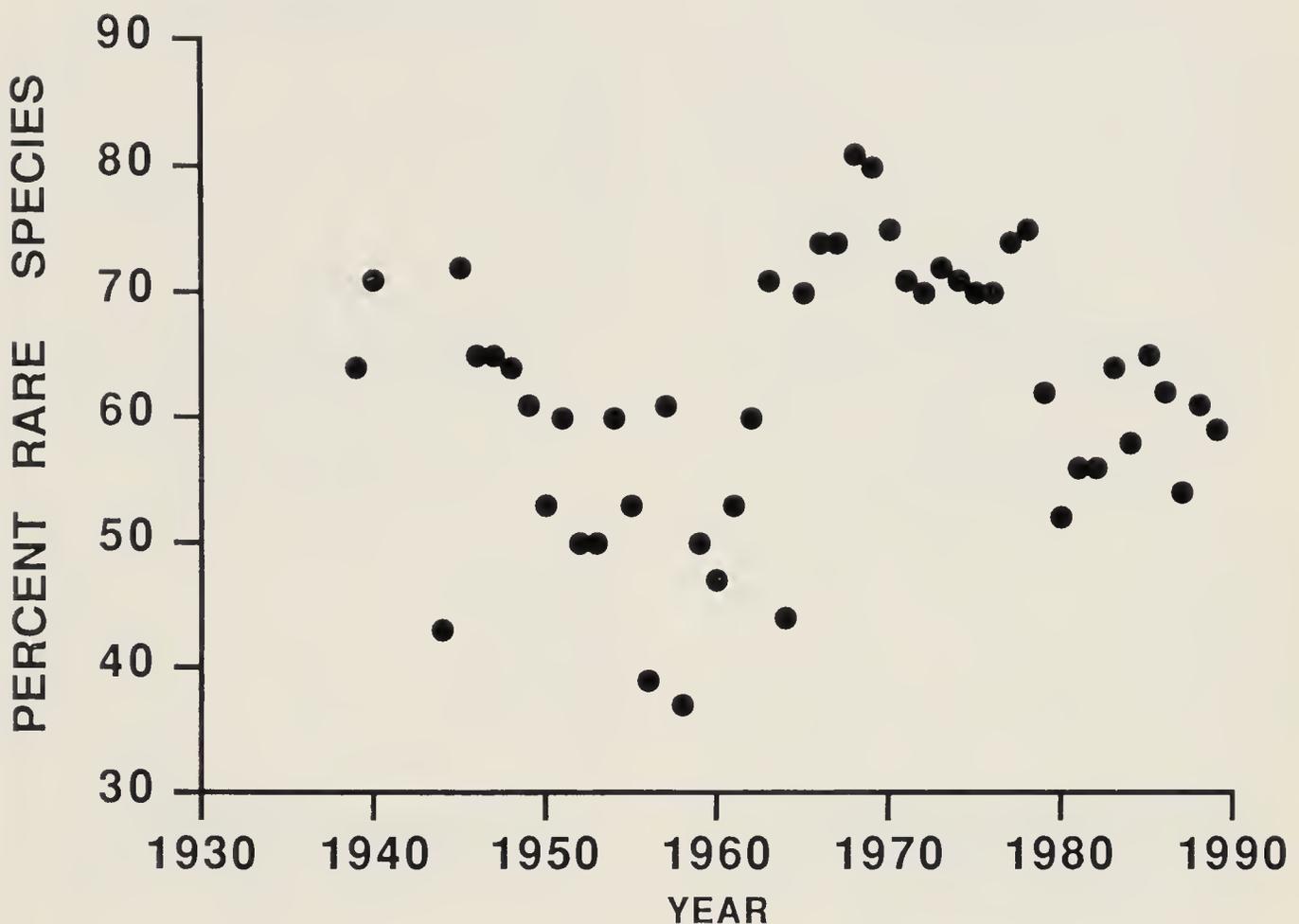


FIGURE 3 - Percent of rarer species (those with less than 2.5 individuals per party-hour) in each year.

NUMBER OF INDIVIDUALS/SPECIES. The least common species, defined here as those numbering less than 2.5 birds per party-hour in any one year (Figure 3), made up 64% of all species recorded from 1939 through the 1940s. During the 1950s this average dropped to 51%, as more species became more common. During the 1960s observers recorded a sharp increase in the number of newly introduced species, perforce in small numbers. The result was a marked increase in the percentage of rare birds, to 68% overall, and to about 80% in the last two years of the decade. Through the 1980s the proportion of rare birds again declined, as perhaps the community matured, to an average of 71% in the '70s and 59% in the '80s. Looking at it from another perspective, the average number of individuals per species per party-hour was significantly higher in the 1980s (mean = 5.6) and the 1950s (4.8), than in other decades (60s: 3.9; 70s: 3.6; and 40s: 3.1) by a Waller-Duncan multiple range test ($T = 2.08$, $df = 1086$).

Population changes

UNCHANGING POPULATIONS. Two species, the Japanese Bush-Warbler *Cettia diphone* and Northern Cardinal *Cardinalis cardinalis*, had constant populations (Table 1; Figure 4). The only change in the cardinal was a diminishing of the variance later in the period. The bush-warbler was unusual, in that it first appeared in counts in 1971 and remained fairly constant. Most species, once established, had a marked and constant increase in population. This cryptic species, usually detected only by voice, may have been overlooked in earlier counts.

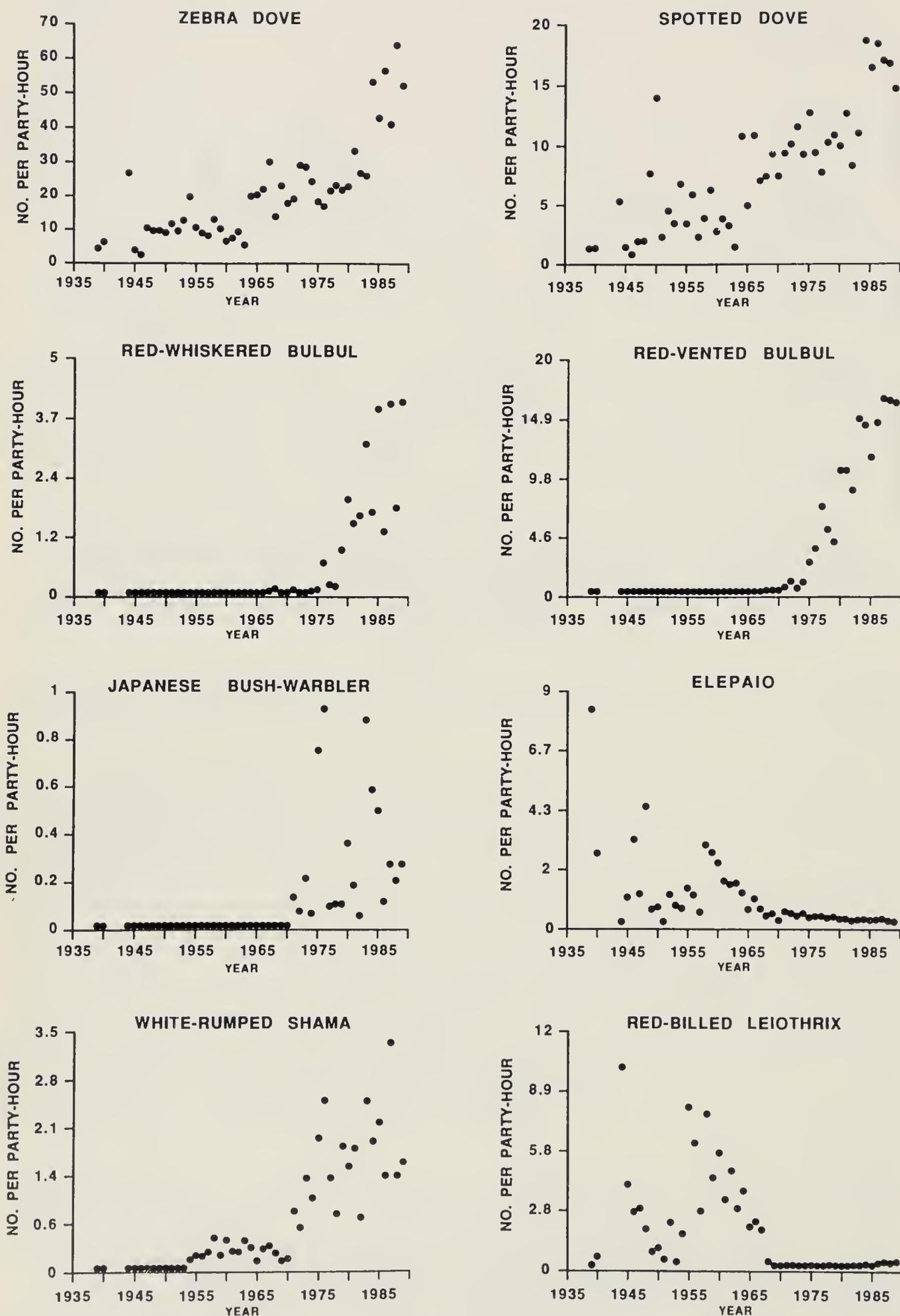


FIGURE 4 - Number of birds per party-hour detected of various species in the Honolulu Christmas Count between 1939 and 1989.

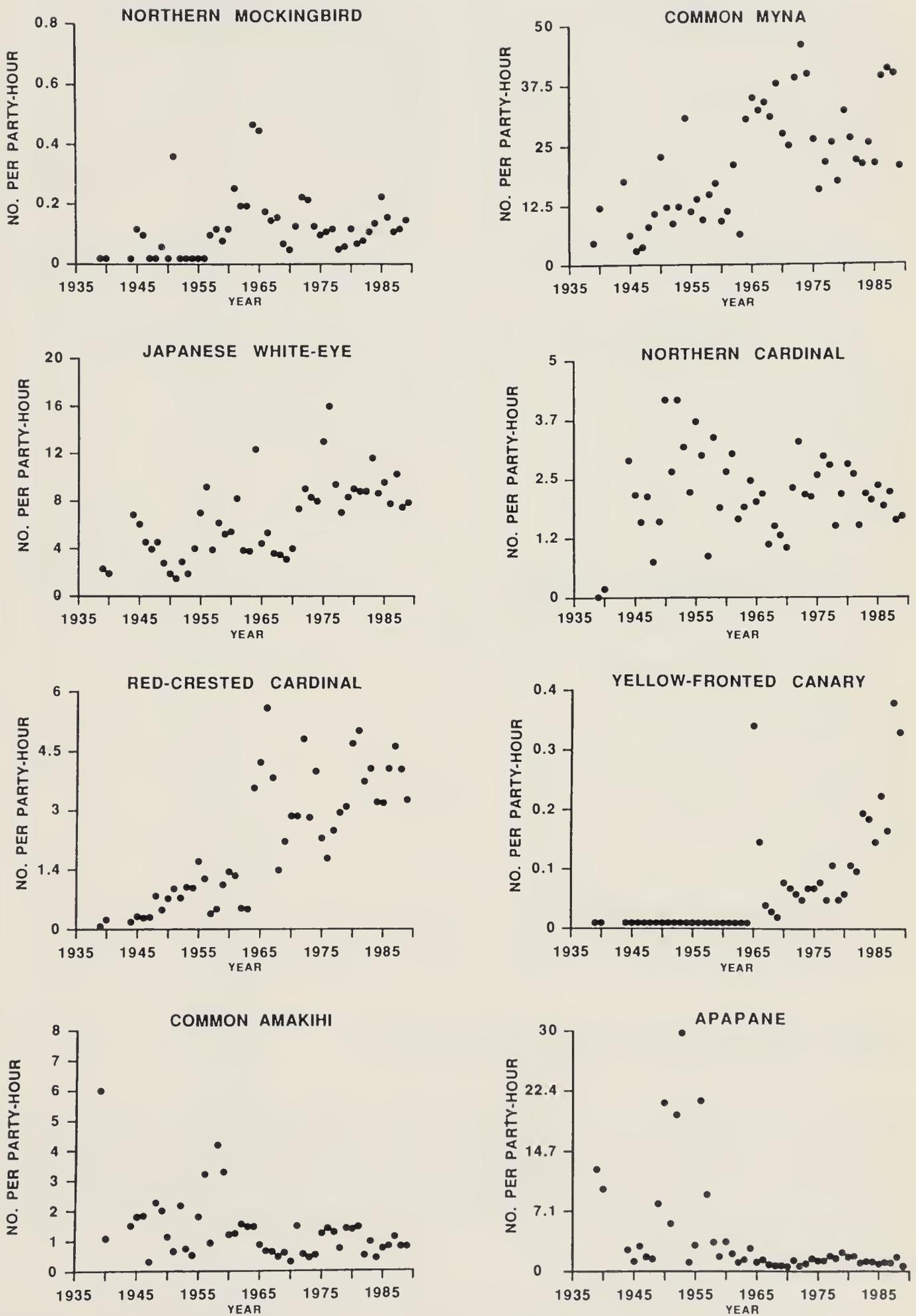


FIGURE 4 - Number of birds per party-hour detected of various species in the Honolulu Christmas Count between 1939 and 1989 (continued).

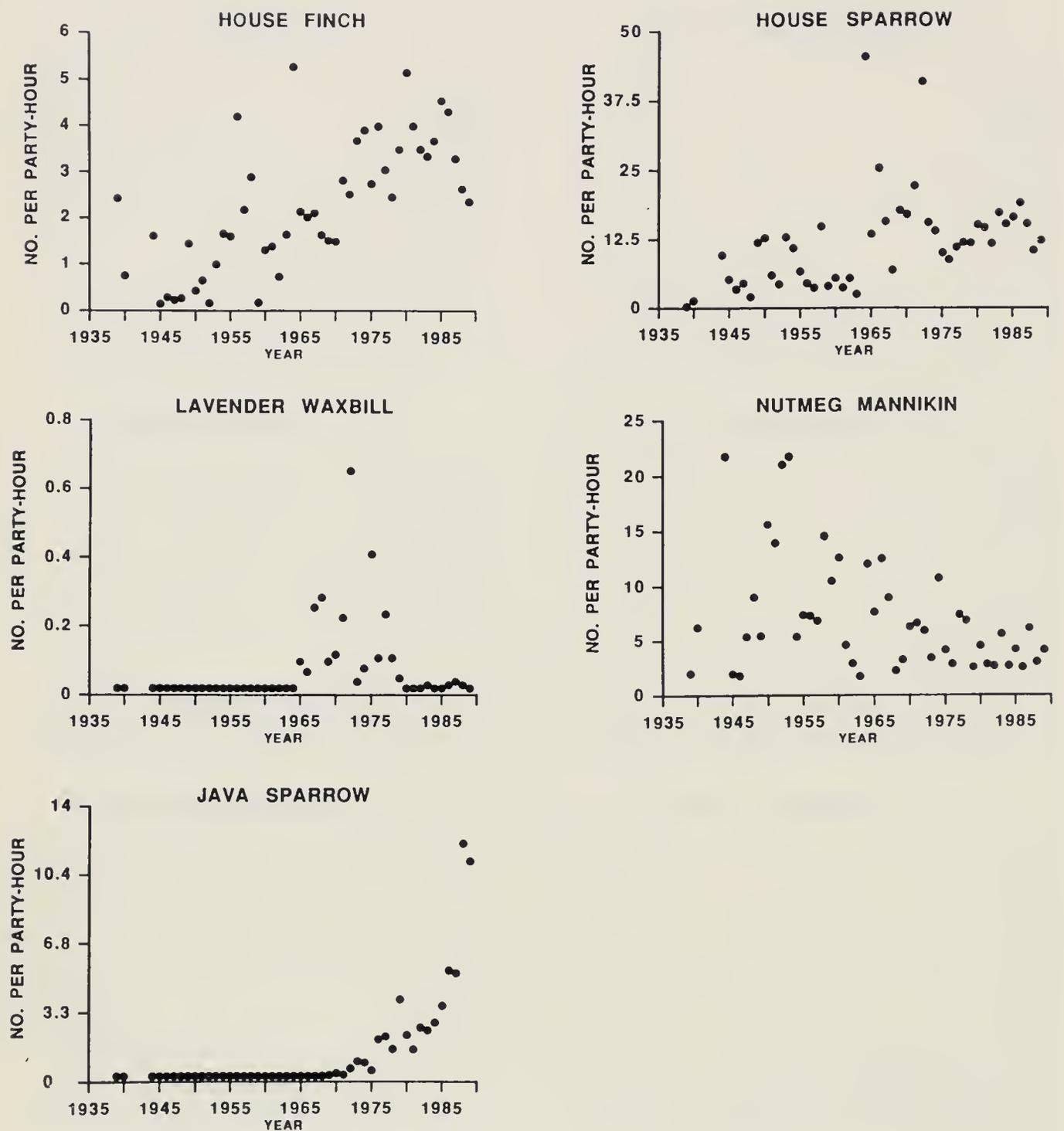


FIGURE 4 - Number of birds per party-hour detected of various species in the Honolulu Christmas Count between 1939 and 1989 (continued).

EXPANDING POPULATIONS. Several species showed rapid population increases, usually shortly after introduction. In many species with expanding populations, a large amount of their variation (R^2) could be explained by the passage of time. Of these expanding species, only the House Sparrow *Passer domesticus*, Japanese White-eye *Zosterops japonicus*, and Common Myna (Table 1), all long-time, abundant inhabitants of Oahu, had a R^2 lower than 60%.

The species with the highest values of R^2 , and the most rapid growth (β), the ones possibly under the least environmental resistance, from density dependent factors, were all introduced in the 1960s (the Red-whiskered *Pycnonotus jocosus*, and Red-vented *P. cafer*, bulbuls; Yellow-fronted Canary; and Java Sparrow *Padda oryzivora*).

TABLE 2 - Results of a multiple regression analysis between species having negative interactions, showing: (1) the slope of the negative interaction (Estimated Value), and the significance of it, and (2) the results of an overall model, with the amount of variation explained (R^2), and the significance of the model.

Dependent vs. Independent Species	Estim. value	T	P	Overall Model		
				F-value	P	R ²
Japanese White-eye v Apapane v Elepaio	-0.168 -0.606	-2.49 -2.03	0.016 0.048	6.43	0.0035	0.222
Apapane v Japanese White-eye	-0.770	-2.86	0.006	8.19	0.0063	0.151
Elepaio v Japanese White-eye	-0.152	-2.45	0.018	5.98	0.0183	0.115
Red billed Leiothrix v White-rumped Shama	-1.299	-3.31	0.002	10.98	0.0018	0.193

Except for the Red-vented Bulbul, these species also had the higher R^2 values with the logarithmic transformation of their numbers, possibly indicating populations still in their expansion phases, and not having encountered significant environmental resistance. Red-vented Bulbul may have reached a point of environmental resistance, with the population increase in recent years being slowed, and is best described by a logistic equation. In future years, other species could begin to show this phenomenon, apparently undocumented in the vertebrate literature.

Eight species showed steadily, but not rapidly, increasing populations with a growth rate (β) of 2-8% in the logarithmic models, thus possibly interacting against a variety of limiting factors. These species were all equally well described (R^2) by a simple linear model with either transformed or untransformed population data; in the range of 35-70% of the variation was explained. They included the Zebra and Spotted *Streptopelia chinensis* doves, White-rumped Shama *Copsychus malabaricus*, Common Myna, Japanese White-eye, Red-crested Cardinal *Paroaria coronata*, House Finch *Carpodacus mexicanus* and House Sparrow.

CONTRACTING POPULATIONS. Of the six species which declined during the period but did not become extinct, three were native: the Elepaio *Chasiempis sandwichensis*, Apapane *Himatione sanguinea*, and Common Amakihi *Hemignathus virens*. Of the natives, the Apapane had the most precipitous decline (β), about 5% per year by the logarithmic transformation. In the Elepaio, Red-billed Leiothrix *Leiothrix lutea*, and Apapane, the amount of variation explained (R^2) was 35-45%, at the lower end of those increasing species mentioned above that were possibly interacting against density dependent limiting factors. All three have declined to very low levels in recent years. The other three species Japanese Bush-Warbler, Common Amakihi, and Nutmeg Mannikin *Lonchura punctulata* had very little of their variation explained by the year variable, and their populations are probably responding to other, non-annual factors. The Northern Mockingbird's *Mimus polyglottos* population has declined only slightly.

EXTINCTIONS. To date, only two species have apparently become extirpated from the count area after establishing small populations: the Saffron Finch *Sicalis flaveola* and Pin-tailed Whydah *Vidua macroura* were last recorded about 1980. The Lavender Waxbill has declined to very low numbers after a few years of modest populations. It is unlikely that any of these species ever reached sufficient numbers to influence other species.

Interspecific interactions

The vast majority of interactions were positive and significant, as most introduced species increased their populations more or less in concert. Of the nine species in the granivore group, none interacted negatively with another. Interspecific competition seems unlikely. Three species in the insectivore group, however, had significant negative interactions (Table 2). These interactions included the very abundant and pervasive Japanese White-eye, and two native species, the Elepaio and Apapane. These models explained a relatively small (12-22%), but statistically significant, amount of the variation among those species. Both the Apapane and white-eye also feed on nectar.

In the group I considered to be frugivores, most members also taking considerable amounts of insects, the interaction between the two introduced species, the Red-billed Leiothrix and the White-rumped Shama, was significantly negative. The shama was present in moderate numbers from 1954 to 1970, then expanded rapidly. It was during the 1950s and early 1960s that the leiothrix population declined.

DISCUSSION

I used the data from the Oahu counts as a tool for the documentation of the arrival, spread, and changes in population which may indicate interspecific interactions at the population level of introduced birds, despite being taken by many observers, or perhaps in part because of it. The data apparently give the first approximation of population sizes from an entire community of species introduced into an isolated area that Hutchinson (1978) sought. As such, they give some insight into the natural potential for growth of some species. Of course, the real potential will depend upon many parameters not studied here such as clutch size, longevity, and fertility, but the range of values presented by this study was instructive.

The rates of increase of introduced birds differed. Some were high, possibly indicating species introduced into environments with relatively few constraints to population increase. Others increased at a slower rate, possibly as a result of interactions with various components of the environment, perhaps including competitors. The consistency of the increase, as measured by the R^2 value, indicated that newly introduced birds had a more consistent rate of increase than well-established species.

At the same time, the count documented the decline of some native birds and species from earlier introductions. There is circumstantial evidence that competition was involved with some of these changes, as the populations of some species with similar foraging niches were negatively correlated. In addition, the rate of decline of some species was similar to the rate of increase of some expanding species, perhaps suggesting a connection between the species or to common environmental factors.

The increasing number of individuals detected per party-hour during the study could indicate a gradual maturation or succession of the avian community. This maturation could be influenced by the introduction of more species, perhaps buffering the community against change. In addition, maturation might involve those species previously introduced having time to work out competition and niche exploitation patterns to fully utilize the relatively newly-colonized environment. While it is possible that observer efficiency increased as well, there is only the case of the Japanese Bush-warbler to support this.

Community maturation is also possibly the cause of the change in the distribution of the number of individuals per party-hour of the rarer species. It appeared that the community went through two cycles of this aspect of maturation during the study.

Robert Pyle (pers. comm.) has raised the possibility that increasing effort over the years in non-forested areas may have artificially deflated abundances of native birds and inflated abundances of birds of residential and park areas. However, Williams (1987) found no significant decline in percent of party hours in mountain forests

between 1967 and 1985. Further analysis may show that is involved to some extent, although I suspect it would be minor.

The interspecific interactions on a population scale were mostly positive associations; species pairs and groups responding in common to generally favorable or unfavorable environmental conditions. However, the Japanese White-eye, which has long been postulated as having a negative impact upon native birds, showed a slight, but significant, statistical effect upon two native species, the Elepaio and the Apapane. The white-eye was introduced in 1929 to Oahu (Caum 1933), and today is found abundantly everywhere from the dry, arid coasts to the wettest interior forests. Scott et al. (1986) also found slight, but significant negative interactions in habitat preference between the white-eye and two species, the Elepaio and the Liwi *Vestiaria coccinea* (the Liwi is very uncommon on Oahu). In another analysis (Mountainspring & Scott 1985), they found more negative interactions between native/introduced species pairs (37% of interactions), than between either native/native (8%), or introduced/introduced (0%) pairs. From these two separate lines of evidence, then, the case for the white-eye's involvement in competitive interactions seems likely.

The other negative interaction I found was between two introduced species. One, the Red-billed Leiothrix, had inexplicably declined during the study. The other, the White-rumped Shama, was introduced in 1940 (Harpham 1953), became common enough to be recorded on the count in 1954, and had a significant negative interaction with the leiothrix in my study. Lending credence to the possibility of these two species being in competition is the situation on Kauai Island. There, the shama has also been introduced, and the leiothrix, formerly abundant, is now virtually absent (Scott et al. 1986). On Hawaii Island, by contrast, the leiothrix is still abundant, and the shama has not been introduced (S. Conant, pers. comm.).

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SYMPOSIUM 25

**THE GENERALITY OF COMMUNITY CONCEPTS
IN AVIAN ECOLOGY**

Conveners J. A. WIENS and O. JÄRVINEN

SYMPOSIUM 25

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OLLI JÄRVINEN: A REMEMBRANCE

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Olli Järvinen, who was to have convened this symposium with me, died suddenly the week before the congress opened. Olli was a valued professional colleague and a close personal friend, and his loss affects us, and our discipline, deeply.

Olli intended to speak here on the multiple factors influencing the dynamics of Northern European bird communities. This work of Olli and his colleagues and students changed the way we view communities. It built firmly on a base of solid quantitative observations and a rich tradition of careful field studies in Finland that began early this century. Olli made all of us aware of the central position of Finnish ornithology in the development of avian community ecology.

Olli combined the rigor of a scientist with the sensitivity of an artist. What emerged was a rare blend of thoughtful and innovative work. Through all of it ran a stream of excitement and joy, and optimism. As simple models of community structure have become increasingly irrelevant to the complexity of Nature, many ecologists have given up hope of answering questions about communities. Olli recognised that the pathway to understanding community structure would be a long and difficult one, but he anticipated what fun it would be to travel it. He has left that challenge for us, and we should embrace it with the joy and enthusiasm that Olli would have.

A BASIS FOR DEVELOPING BROADER GENERALIZATIONS OF BIRD COMMUNITY STRUCTURE AND SPECIES CO-OCCURRENCE

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ABSTRACT. Despite more than 30 years of intensive investigation of bird community structure and species co-occurrence patterns, few broad generalizations have emerged. Five major problems may explain this paucity of generalizations: (1) most studies have been too narrowly focused on birds or specific habitat types; (2) life cycle stages, especially nestlings and eggs, have received inadequate attention; (3) alternative and simultaneous selective forces such as competition, predation and physical factors have seldom been included together; (4) there has been a bias toward studies in the historically disrupted temperate zones; and (5) studies have been predominantly short term. By using these problems to identify the most suitable characteristics for test assemblages of bird species and by designing tests of species co-occurrence across latitudinal gradients, the next stage of avian community structure studies can maximize the probability of revealing emergent generalizations.

Keywords: Community structure, history, latitudinal gradient, life cycle stages, multiple selective factors.

INTRODUCTION

Ecological communities can be defined as sets of co-occurring species that exhibit measurable interactions. A prime goal of community structure studies has been the identification of predictable patterns and broad generalizations. Except for one or two broad biogeographical patterns, however, this goal has been difficult to attain.

From past studies, five major and often interdependent problems for studies of species co-occurrence can be identified. My goal here is to use these problems to develop a philosophical basis against which future hypotheses of avian ecological communities can be framed. This framework involves a different approach from that taken by the majority of previous workers. It requires a careful experimental or comparative design and prudent selection of the test species to overcome the inherent complexities of interactions among multiple and simultaneous factors.

Problems of co-occurrence studies

HABITAT AND TAXON CHAUVINISM. Naturally co-occurring species have been defined in many ways, but even the most unambiguous definitions do not include all potentially interacting species. In response to this often complex situation and as a first step in understanding communities, many studies of co-occurrence focus on a single habitat or taxon. Examples of communities defined in terms of only bird species are many, and they have provided considerable insight. With this insight, however, it has become obvious that insects, mammals, amphibians, and other organisms potentially interact with birds in many places, and that more accurate predictions and generalizations may emerge by including a broader spectrum of taxa in the definition of the community (Fenton & Fleming 1976, Reichman 1979, Wright 1979, Gill et al. 1982, Terborgh 1986, Jordano 1987, Herrera 1989).

Examples in which generalizations derived for one habitat do not hold in another habitat are also numerous. Virtually all ecology texts include the well-known relation between foliage height diversity and bird species diversity (MacArthur & MacArthur 1961). Apparently this relation is valid for many temperate-zone forested habitats, but it has virtually no predictive powers in tropical lowland forests or semi-arid scrublands around the world (Pearson 1975, 1982).

EXCLUSION OF SEASONAL AND LIFE CYCLE STAGES. Most co-occurrence studies concentrate, often exclusively, on the most obvious or easily studied stages. For birds the focus is usually on adult stages on breeding grounds, although recent studies have begun to speculate about the significance of wintering area effects on migratory and resident birds (Keast & Morton 1980). Egg and nestling stages have also received more attention than previously (Slagsvold 1984, Ydenberg 1989).

From these and similar studies, it has become apparent that factors directed at one stage can have significant effects on other stages. Adult characters can influence offspring survival (Amundsen & Stokland 1990) and characters of the offspring can influence the survival and eventual composition of adult communities (Schaffner 1990, Simons & Martin 1990).

Wintering populations are often exposed to totally different selective factors that necessitate different behavior and community interactions than found on the breeding grounds (Morton 1971, Baker & Baker 1973, Rogers 1987, DuBowy 1988). Even resident birds in tropical habitats show considerable differences in community structure from season to season (Beals 1970, Fogden 1972, Bell 1980). In a more subtle time frame, much of the structure of a community of birds can be influenced by their interactions during a relatively short but critical period. In some tropical forests, the majority of the bird biomass concentrates at lower vertical vegetation strata for a few hours each mid-day. The primary selection for characters that allow co-occurrence may only be observable and measurable for this short period each day, yet this period may determine patterns of community structure for the entire day, season, and year (Pearson 1971).

ALTERNATIVE AND SIMULTANEOUS SELECTIVE FORCES IGNORED. Three categories of ecological factors are generally considered to explain most patterns of co-occurrence: (1) predation (including parasitism and disease) (Smith 1977, Blake & Karr 1987, George 1987, Lima 1987, Desrochers 1989, Metcalf 1989, Rudolph et al. 1990, Moller 1990); (2) competition (Hulsman 1981, Nudds & Bowlby 1984, Torok 1987, Martin 1987, Pulliam & Dunning 1987, Benkman 1988, Brittingham & Temple 1988, Brawn & Balda 1988, Dhondt 1989); and (3) physical factors (Willis 1976, Collins et al. 1980, Montevecchi et al. 1984, Karr & Freemark 1983, Hennemann 1985, Root 1988, Weathers et al. 1990). Although most ecologists (e. g., Schoener 1983, Strong 1983) will admit that all three of these factors are operative to some degree in all communities, conceptual and logistical complexities have forced most workers in this area to concentrate on only one of these factors, or rarely two (Martin 1985, Schluter 1988, Kotler & Holt 1989, Szekely et al. 1989). For example, interspecific competition predominates in studies of bird communities while predation, especially on adults, and physical factors are extremely uncommon.

Justification for this type of simplification is often based on the assumption that, in general, individuals are only weakly influenced (low selective advantage detectable in evolutionary time over many generations) by predation and physical factors. The single strong factor of competition (high selective advantage detectable in ecological time within one or two generations) is then the only one that tends to be tested. For instance, in over 5000 h of observation in tropical rain forests around the world, I have observed actual predation on adult birds nine times, and only three of those bouts were successful. I could easily be tempted to exclude predation on adult birds as a significant factor in patterns of co-occurrence on the basis of its being such a rare phenomenon. However, distinctive anti-predator characteristics such as mobbing, hawk alarm calls, freezing in position, camouflage and flocking have obvious impact on community structure but may need only one predator attack (most of which are unsuccessful) every two or three generations to maintain the characteristic. The rarity of an event can not then be used as a justification for its exclusion in development of hypotheses and experimental design.

Whatever the source of bias, experience from single-factor design indicates that this type of community structure analysis is not warranted. These analyses are either narrowly applicable to specific habitats or taxa, or they may actually be misleading for understanding some aspects of co-occurrence (Holt 1977, Hilborn & Stearns 1982, Pearson 1986).

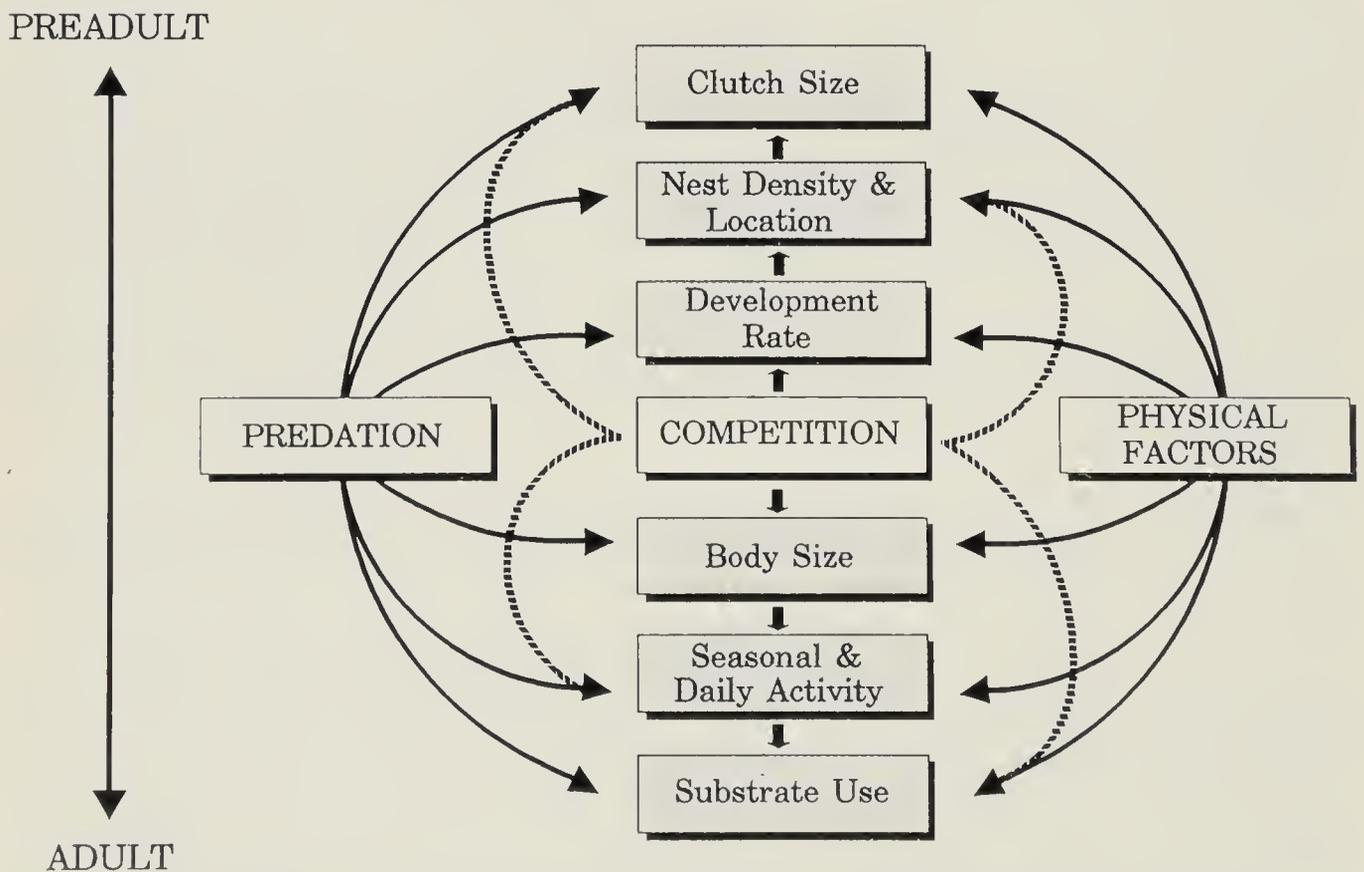


FIGURE 1 – The multiple effect of predation, competition, and physical factors on birds. These effects are reflected in structural, behavioral and physiological characters, and each arrow indicates a test or observation needed to establish a relationship. Many of the effects directed at one stage of the life cycle can have significant effects on other stages.

The simultaneous interaction of all these factors is bound to be difficult to test, but the results are likely to have more predictive power than single factor analyses. The interactions can be multiplicative or even counter selective (Figure 1). For instance, nest

density and location may be strongly influenced by nest predation (Emlen & Demong 1975) but simultaneously and perhaps in the opposite direction by competition for food to feed the young or thermoregulatory aspects of the nest site (Ricklefs 1975). Evidence for counter selection can provide much insight into the relative importance of multiple selective factors and under what conditions one selective factor tends to "win out" over others in these counter selective bouts.

HISTORICAL BIAS TOWARD TEMPERATE-ZONE STUDIES. Because of the preponderance of temperate-based ecologists, the perceived complexity of tropical habitats and the added expense of travel, few studies of bird communities have been conducted in the tropics. For instance, of the 164 studies dealing with tests of competition cited by Schoener (1983), fewer than 10% were from tropical sites. Arguments against tropical studies usually include the paucity of natural history background available. In addition, there is often an implicit assumption that the temperate-zone communities are somehow "normal" and tropical communities are aberrant.

Several lines of evidence indicate that studies of tropical communities should be emphasized. Both tropical and temperate zones have undergone dramatic changes in recent geological time (Haffer 1969). Although based on incomplete evidence and subject to various interpretations, the Quaternary glacial periods and resultant dry climate probably caused tropical areas to break up into moist, isolated islands of forest surrounded by scrub vegetation and grasslands. These isolated forest islands enhanced speciation so that during interglacial periods, when precipitation increased and the forest islands expanded to reconnect, the net result was a continuous forest with more species and more potential interactions and selection for adaptations enhancing co-occurrence (Prance 1982).

In marked contrast, north-temperate areas were subjected by glaciation to cataclysmic changes in habitat in which the severity of the climate (temperature, continentality and drought), extent of geographical displacement of species, community composition in refugia, and small population sizes all led to high probabilities of species extinction. In addition, selection was evidently skewed toward characters that enhanced dispersal and colonization rather than co-occurrence (Davis 1983).

Although the geological and biogeographical evidence is complex and difficult to generalize, it appears that most temperate taxa have tropical ancestors (Stenseth 1984). Dobzhansky (1950) argued that plants and animals originated in the tropics. Special adaptations to biotic and abiotic factors made possible the dispersal of some of these tropical forms into temperate zones. Tropical forms are thus likely to exhibit ancestral tendencies of community structure. The temperate zone forms can be considered different in that they developed specializations that enabled them to escape the tropics. Most modern ornithologists, for instance, now consider migrant birds to be generally tropical birds that come to the temperate zone for a short period to nest and then return to their tropical home to spend most of the year (Keast & Morton 1980).

The study of temperate-zone bird communities alone is thus less likely to distinguish many patterns of co-occurrence not because the communities are unstructured or abnormal, but because there are fewer opportunities for species interactions, historical factors are complex, and it is difficult to test incomplete or fragmented patterns.

Few studies have taken historical factors into account in designing experiments on community structure and interpreting present-day patterns of bird species co-occurrence (Terborgh 1973, Diamond 1984, Finch 1989, Murphy 1989). This historical component has been shown in some cases to have far more predictive powers concerning bird community structure than any of numerous alternative ecological theories (Pearson 1977, 1982). Future studies of bird communities must incorporate historical components into the hypotheses.

PAUCITY OF LONG TERM-STUDIES. The degree and unpredictability of annual fluctuations in weather, resources, and population levels in many temperate zone habitats may have irregularly significant influences on species co-occurrence. Important aspects of adaptations for co-occurrence may only be apparent and testable at concomitantly irregular periods, frequently separated by many years (Wiens & Rotenberry 1980). Studies of tropical forests indicate that these supposedly more consistent habitats also show considerable annual variance in population levels. As more and more organisms are studied in detail, this high year to year variance appears to be common (Wolda 1978, Pearson & Derr 1986). Studies of many years are necessary in both tropical and temperate habitats.

Co-occurrence studies: a solution

If these impediments to developing valid generalizations of bird species co-occurrence are genuine and significant, a major part of the solution lies in developing hypotheses and experimental designs that incorporate: (1) all significantly interacting taxa, (2) comparisons of distinct habitats, (3) all life cycle and seasonal stages, (4) tests of simultaneous and multiple selective factors, (5) historical factors, and (6) sufficiently long periods to include year to year changes.

Clines and latitudinal gradients provide a basis for conducting such comprehensive tests. Studies to successfully identify further emergent generalizations are suggested by the numerous examples of abiotic (cosmic rays, electric fields and temperature) and biotic (physiological characteristics, genetic organization, reproductive strategy and species richness) factors that show a consistent latitudinal organization. By studying communities along such a gradient, predictable similarities and dissimilarities can be determined within the context of a continuum. Instead of basing a search for generalizations on one extreme end of the continuum, the ends can be more logically understood within the context of their probable origin.

For instance, because disruption of south-temperate zones was far less cataclysmic than in equivalent northern latitudes (Darlington 1965), studies of species co-occurrence both north and south from tropical areas should reveal different types and more gradual changes toward the south. Many characteristics of communities can be tested in this manner and their significance determined by how abruptly or gradually they are altered or eliminated along the continuum.

Three decades of community-structure studies have yielded few generalizations, but they have provided a basis upon which future studies of birds can point the way to emergent generalizations. With the difficulties involved in funding and logistics, many future studies will use small teams of collaborating investigators gathering data in a quantitatively comparable way over many geographical sites. The long-term study can best be handled by a single individual or a core of investigators directing a series of

graduate and post-doctoral studies over many years (e.g., Holmes et al. 1979) that have a common, unifying hypothesis and goal.

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THE DYNAMICS OF BIRD COMMUNITIES OF EUCALYPT FORESTS AND WOODLANDS IN SOUTH-EASTERN AUSTRALIA

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ABSTRACT. Australian woodlands and forests are evergreen, and not strongly seasonal in climate and food resources. Their birds tend to be sedentary, have low adult mortality, small clutches, long breeding seasons and low breeding success, indicating that they are close to the carrying capacity of their environment. Experimental evidence suggests that birds deplete nectar and insects. In addition many species display delayed dispersal and breed cooperatively. Many communities are dominated by honeyeaters (Meliphagidae). In habitats poor in nutrients, insects and insectivorous birds are scarce, whereas aggressive nectarivorous honeyeaters are abundant. In richer woodlands, honeyeaters that rely on insects and sugary exudates are common. They attack and harass other insectivores, often virtually excluding them. Environmental changes that reduce reproductive success may cause populations to decline at a rate that is not noticeable during short-term studies. Species could thus disappear locally without warning. Also subtle changes to habitats could lead to their domination by one or a few species, with consequent loss of diversity.

Keywords: Bird communities, eucalypts, honeyeaters, competition, nectar, insects.

INTRODUCTION

Australian forests and their bird communities have evolved independently from those of the rest of the world. Consequently they provide an opportunity to test the generality of community concepts that have been developed in the Northern Hemisphere. The types and numbers of birds that can be present are very much determined by the availability of resources (Gilmore 1985). Which particular species are actually present in a locality may result more from subtle interactions between temporal and spatial patterns of availability of food, shelter and nesting sites, competition, predation and weather. In this paper we look at the structure of bird communities in eucalypt forests and woodlands in relation to the resources available to them and the impact of competitors and predators.

The genus *Eucalyptus* dominates most woodland and forest communities in Australia. Eucalypts are tough-leaved evergreens providing a wide range of resources for birds. The flowers of many species produce substantial quantities of nectar consumed by honeyeaters and lorikeets. The seeds provide food for parrots. A great diversity of insects consume foliage or other parts of eucalypts and these are eaten by several guilds of insectivorous birds. As foliage is available year-round, and in temperate regions new leaves may be produced over nine months, leaf-eating insects are usually available. Many eucalypts have decorticating bark, which provides refuges for insects, especially resting ones during winter (Noske 1982). The ground also provides arthropods among fallen litter. In south-eastern Australia there is a seasonal change in the abundance of insects, especially larger ones (Woinarski & Cullen 1984, Bell 1985, Recher et al. 1983, Ford, Huddy & Bell 1990, Recher et al. 1990), though this is probably less marked than in the temperate forests of the Northern Hemisphere. Other plants in eucalypt woodland and forest produce nectar and seeds, and foraging sites

for shrub-feeding and ground-feeding birds. Fleshy fruits are scarce though parasitic mistletoes and some understorey plants produce them and fleshy galls are also eaten.

THE BIRD COMMUNITY

Holmes and Recher (1986) found nine foraging guilds of birds in eucalypt forest and woodland compared with only four in the forests of the north-eastern United States. We present the numbers of species in each of 10 guilds in two regions in southern and northern New South Wales in Table 1 (from Recher et al. 1985, Ford et al. 1986). We have modified the guilds of Holmes and Recher 1986, by adding frugivores (only present in the northern site), adding an insectivore/nectarivore guild to include the more insectivorous honeyeaters and the Silvereye, and combining the various ground gleaning species. Few data exist of a comparable nature from forests in the Northern Hemisphere. The data of Holmes et al. (1979) from the north-eastern USA has been added to the Table. We have also presented data from California and Mexico (Landres & MacMahon 1983, Avery & van Riper 1989) and from Spain by Zamora and Camacho (1984) and Herrera (1980) from Spain, on the main food guilds (Table 2). These studies were carried out in evergreen oak woodland, the Northern Hemisphere habitat that perhaps most resembles eucalypt woodland and forest. Such analyses are fraught with difficulties, because people use different categories, include different portions of the avifauna and differed in the time of year they covered. Nevertheless we believe such a comparison should be attempted.

TABLE 1 – Numbers of bird species belonging to each foraging guild from two studies in eucalypt woodland and forest and five studies in the Northern Hemisphere.

	Recher et al. s NSW	Ford et al. n NSW	Holmes et al. ne USA
Frugivore/Insectivore	0	1	0
Granivore	2	2	0
Nectarivore-Insectivore	3	5	0
Insectivore/Nectar etc.	7	5	1
Hawker/Snatcher	5	6	3
Foliage gleaner	2	4	3
Foliage snatcher	4	4	4
Bark feeder	5	4	5
Ground gleaner	9	6	7
Ground pouncer	4	3	0
Total	41	40	23

TABLE 2 – Number of species in each main food guild in Australia and in five Northern Hemisphere sites of comparable vegetation (- indicates not studied).

	Australia	N. America	Spain
Fruit	0-1	-	9-10
Seeds	2	10	4-7
Nectar	3 - 5	0-1	0
Insects	32- 36	10-15	16- 21

Australian bird communities show some differences from Northern Hemisphere ones. Only one species takes a substantial amount of fruit - the Mistletoebird *Dicaeum hirundinaceum* though other frugivores occur when an understorey containing rainforest plants is present (Milledge & Recher 1985). Parrots consume seeds from trees and, along with pigeons, from the ground, with finches specialising on grass seeds. Nectar-feeders are often common and diverse, with some species depending on nectar as a major supplier of energy, whereas others use nectar as an adjunct to other resources (Pyke 1980). Carbohydrate foods such as honeydew, lerp (scale insect covers) and manna (leaf exudates) are used to a remarkable degree by honeyeaters and small insectivores (Paton 1980, Woinarski 1984, 1985a). Insectivores separate into aerial feeders, foliage gleaners and snatchers, bark and ground foragers, though some species combine more than one substrate (Recher et al. 1985, Ford et al. 1986). Unusual foraging modes are shown by the Crested Shrike-tit *Falcunculus frontatus* which crunches up hanging bark in search of insects, and the Yellow-tailed Black-Cockatoo *Calyptorhynchus funereus* which chews into eucalypt branches in search of large insect larvae (McInnes & Carne 1978) and breaks up the extremely hard fruits of *Banksia* and *Hakea*.

Birds show various responses to seasonal and year-to-year changes in abundance of insects. The aerial feeders and snatchers, whose food probably declines most markedly in autumn, are often fully migratory in south-eastern Australia (Table 3). Many of the gleaners are sedentary or locally mobile. Pardalotes, which consume small foliage insects and exudates, are somewhat nomadic, apparently concentrating where food is abundant (Woinarski 1985a). Seasonal changing of foraging substrate is an alternative to migration. The Flame Robin *P. phoenicea* pursues much aerial prey in summer, migrating to lower altitudes in winter, whereas the Scarlet Robin *P. multicolor* is sedentary increasing the amount of ground-pouncing (Robinson 1990). The Buff-rumped Thornbill *Acanthiza reguloides* also increases its ground-feeding in winter (Bell 1985, Recher 1989, Ford et al. 1990).

TABLE 3 – Numbers of species in each guild that are resident (R), summer (S) or winter visitors (W) in four sites in south-eastern Australia - Bombala, from Recher et al. 1983, Brindabella Ranges from Tidemann et al. 1988, Blue Mountains from Hardy & Farrell 1990, and Armidale from Ford et al. 1986 & pers. obs.

	Bombala 800m 37°S			Brindabella 1050m 35°20'S			Blue Mtns 250m 33°40'S			Armidale 1000m 30°30'S		
	R	S	W	R	S	W	R	S	W	R	S	W
	Granivores	2	0	0	0	2	0	5	0	0	8	0
Nect./Insect.	2	1	0	1	1	0	2	1	0	0	4	1
Insect./Nect.	0	3	0	1	4	0	0	3	2	3	0	3
Aerial	0	4	0	0	2	0	1	1	0	2	8	0
Fol./Bark Gl.	8	2	0	6	0	0	5	0	0	8	0	0
Fol./Bark Sn.	1	4	0	1	4	1	1	4	1	0	6	2
Ground Gl.	10	0	0	4	1	0	9	0	0	13	1	0
Ground Pounce	2	2	0	1	2	0	4	2	0	6	4	0
Total	25	16	0	14	16	1	27	11	3	40	23	6

IMPORTANCE OF INTERSPECIFIC COMPETITION

Interspecific competition has been assumed to play a role in the structure of bird communities, either by determining the presence or absence of a species or affecting its abundance or foraging niche. Evidence for competition has been gathered in numerous ways and, ranging from weakest to strongest, includes: resource partitioning; niche expansion in the absence of potential competitors; interspecific aggression (interference); depletion of common resources used by more than one species (exploitation) and by changes in the abundance or behaviour of a species following experimental removal of a potential competitor. Evidence of all these types has been gained from studies in eucalypt woodlands or forests in south-eastern Australia.

Studies comparing the foraging behaviour of congeners have shown the familiar pattern of resource partitioning found in North American warblers and European tits (MacArthur 1958, Hartley 1953, Cody 1974). The thornbills *Acanthiza* provide a particularly good example (Bell 1985, Woinarski 1985, Recher 1989, Bell & Ford 1990). As many as five species may occur in an area. The Yellow-rumped Thornbill *A. chrysorrhoa* feeds on the ground in open areas, the Buff-rumped Thornbill feeds on foliage, bark and on the ground in the forest, whereas the Brown Thornbill *A. pusilla* is a shrub specialist. Both the Striated *A. lineata* and Yellow Thornbill *A. nana* glean foliage in the canopy and subcanopy. Usually they occupy different habitats, but where they are together *nana* feeds somewhat higher than *lineata*, which often hang-gleans to reach insects on the end of long leaves (Recher 1989). Two other warblers may also be present in eucalypt woodland: the White-throated Warbler *Gerygone olivacea* is more of a snatcher than the thornbills, whereas the Weebill *Smicronis brevirostris* hovers at outer foliage. The robins *Petroica*, fantails *Rhipidura* and whistlers *Pachycephala* partition resources by different habitat or foraging sites, or by seasonal changes in occupancy (Fleming 1980, Robinson 1990, Cameron 1985, Bridges 1980). Differences between sympatric pardalotes are often more subtle (Woinarski 1988).

There are numerous cases of ecological release in the absence of potential competitors. The Tasmanian Strong-billed Honeyeater *Melithreptus validirostris* has become a bark specialist in the absence of treecreepers (Keast 1968). The Purple-gaped Honeyeater *Lichenostomus cratitius* occupies a range of habitats on Kangaroo Island in the absence of several congeners (Ford & Paton 1976). Several small insectivores and honeyeaters that do not occupy forest in eastern Australia, occur in this habitat in southwestern Australia where the typical species are absent (Keast 1976). This suggests that congeners may be held apart by mutual aggression or avoidance where their preferred habitats abut. Chan (1990) found that this seemed to be the case with White-plumed and Fuscous Honeyeaters (*Lichenostomus penicillatus* and *L. fuscus*). The former occupies riverine woodland, the latter adjoining eucalypt woodland, with much interspecific chasing at the boundary. Where only one species is present it occupies both habitats.

The nectarivorous honeyeaters are notoriously aggressive to each other. Large species like wattlebirds *Anthochaera* and friarbirds *Philemon* dominate rich patches, whereas middle-sized species, such as New Holland Honeyeaters *Phylidonyris novaehollandiae*, defend other rich areas of nectar and exudates (Ford & Paton 1982, Paton 1985). Smaller or less aggressive species may use thinly dispersed flowers

(Eastern Spinebill *Acanthorhynchus tenuirostris* - Ford & Paton 1982). A similar hierarchy apparently exists among birds feeding on exudates and insects. Miners dominate rich areas (Dow 1977, Wykes 1985), while other aggressive, social species like Yellow-tufted *Lichenostomus melanops* and Fuscous Honeyeaters, defend other favourable areas (Wykes 1985, Dunkerley 1989). Less aggressive species either specialise on a particular resource (White-eared Honeyeater *L. leucotis* on bark exudates; Ford & Paton 1976), or move in search of localised rich, undefended patches (pardalotes, Yellow-faced Honeyeater *L. chrysops*; Woinarski 1984, Wykes 1985). Among insectivores, the Scarlet and Flame Robin are interspecifically territorial (Loyn 1980, Robinson 1989).

Evidence for food-depletion comes from both nectarivores and insectivores. In south-eastern Australia, a common pattern of nectar availability is that it is scarce in summer and autumn, increasing in winter and spring (Ford 1979, Paton 1985, Ford & Paton 1982, Pyke 1983, Armstrong 1990). Scarcity is caused by lack of flowers, lack of moisture and, particularly, consumption by birds and other flower visitors. Depletion of insects is harder to show, but A. Smith (unpub.) and G. Dunkerley and L. Bridges (unpub.) found that insect numbers increased in enclosed branches compared with control branches. They attributed this to depletion by birds and small mammals.

Removal experiments are difficult to carry out with birds, as many species are sufficiently mobile that vacancies can be filled rapidly. Loyn et al. (1983) removed Bell Miners *Manorina melanophrys* from a colony in Victoria. Within a few days numbers of other honeyeaters and insectivores had increased significantly. At the same time numbers of insects declined.

Curiously, several factors point to a scarcity of food being an infrequent event, whether or not it is exacerbated by interspecific competition. Starvation of young birds in nests seems to be a rare phenomenon (Woinarski 1989), despite the fact that breeding seasons are long (Wyndham 1986). Time budgets suggest that birds do not spend much more time foraging in autumn and winter than in spring and summer (Haylock & Lill 1988, Ford 1989). Delayed dispersal, cooperative breeding and low adult mortality all indicate a fairly equable environment (Woinarski 1985b, Ford et al. 1988). However there can be considerable year-to-year variation in insects and nectar. Birds respond to periods of scarcity by nomadic movements or by delaying or even forgoing breeding.

THE ROLE OF PREDATION

Predation is almost invariably the major cause of nest failure, and for many species only 20-40% of nests give rise to young (Rowley 1965, Marchant 1974, 1984, Dow 1978, Smith & Robinson 1978, Clarke 1988, Nias 1986, Bell & Ford 1986, McFarland 1986, Woinarski 1989, Robinson 1990, Armstrong 1990). There are numerous native mammalian, reptilian and avian nest predators in Australia, including tiger cats *Dasyurus*, snakes, goannas *Varanus* and many corvids. To these have been added feral cats and foxes. It is hard to tell if the current low breeding success is the same as the pre-European level. Nesting success in North America and Europe is frequently around 50% (summarised in Ford 1989), but again it is hard to know how this has been affected by changes in habitats and nest predators.

Cuckoos are common in eucalypt forest and woodland, with 10 species being brood parasites of a wide variety of passerines (Brooker & Brooker 1989). On occasion cuckoos can account for a high proportion of nest failures (Rowley in Brooker & Brooker 1989).

CLIMATE AND FIRE

The weather can also affect population sizes, either directly or through food or other resources. Emphasis is usually placed on heat or drought in Australia (McGilp 1932) and in eucalypt woodland drought can reduce the abundance of arthropods (Bell 1985), with consequential changes in foraging behaviour of insectivorous birds (Bell & Ford 1990). Populations declined during a severe drought in an isolated patch of woodland, but possibly due to a failure to produce offspring, rather than an increase in adult mortality (Bell & Ford 1986). In another site Smith (1989) found that the combined effects of drought and fire led to birds contracting into moister gullies, without major population declines. However, at least along the Great Dividing Range, cold weather may be a more important cause of periodic mortality. Bell (1983) found that more thornbills disappeared in winter, especially during cold, windy weather, than at any other time. This was perhaps because energy demands were high at a time when foraging was difficult. Low, overnight temperatures can reduce nectar production, resulting in temporary, local population declines of honeyeaters (Ford 1990).

Fire is another environmental hazard experienced by birds in eucalypt woodland and forests (Recher, Allen & Gowing 1985). It can kill species directly, but often the effect is one of slightly increased adult mortality and decreased reproductive success over several years (Rowley & Brooker 1987). Recovery is often rapid, with some species becoming more abundant in the few years after the fire (Christensen et al. 1985).

If production of young is low, due to predation or climate, then populations of many bird species could be below the density at which intra- or inter-specific competition are important. Alternatively the brunt of competition may be borne by immature birds attempting to gain access to a breeding population. As many of these birds are transient, or occupy a floating underworld, it is difficult to follow their fate.

RELEVANCE TO CONSERVATION

Two hundred years of European colonisation have brought dramatic changes to eucalypt woodlands and forests and the bird communities inhabiting them (Recher & Lim 1990). Forests have been logged for timber, and more recently declared national parks. Eucalypt woodland has been extensively cleared and fragmented, and degraded by grazing, loss of understorey, decline in tree health and invasion by exotic species. It is under-represented in conserved areas. Degradation leads to a simplification of the bird community, as it becomes progressively dominated by large aggressive birds, such as Noisy Miners *Manorina melanocephala* and Grey Butcherbirds *Cracticus torquatus* (Loyn 1987, Ford & Bell 1982). Even in areas where much native vegetation remains, subtle changes have taken place. Typically the richest patches have been cleared for agriculture (Lunney & Leary 1988). These usually have eucalypts of the subgenus *Symphomyrtus* rather than *Monocalyptus*. The former grow on

better soil, have more insects and a richer bird community (Recher 1985). Nomadic and migratory species may depend on a succession of these rich patches. Their loss or domination by Noisy Miners could be the cause of the decline of the endangered Regent Honeyeater *Xanthomyza phrygia* (Franklin et al. 1989). Other species may be declining insidiously, due to a decreased breeding success, caused by structural changes to their habitat, plus an increase in nest predators. Loyn (1987) found a negative correlation between species diversity on remnants of woodland and time since fragmentation.

Whereas these changes may deny ecologists the chance of assessing what naturally determined the structure of bird communities in eucalypt woodlands and forests, we have to face the altered conditions if we are to maintain the rich diversity of birds that have adapted to these habitats. Our thesis is that the types and species of birds in an area are dependent on the spatial patchiness of soil richness and associated vegetation and the temporal variation in climate and its effects on resources such as nectar and insects. This variation in time and space is perhaps different from that in Northern Hemisphere ecosystems which have more regular seasonal patterns and more even fertility. Nest predation and interspecific competition for rich patches or ephemeral resources may be more prevalent than in Europe and North America. Both of these may have a considerable influence on the species that actually occur in an area.

It seems prudent to assume that bird communities are structured in the way that we currently believe they do, when we design management plans for the future. It is obvious that a knowledge of the dynamics of community structure, however incomplete, is essential if we are to conserve the entire suite of species living in eucalypt woodlands and forests. As has often proved to be the case, the conditions and driving forces could be subtly different in Australia from those in other temperate regions.

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GENERALISING FROM THE DYNAMICS OF NORTHERN EUROPEAN BIRD COMMUNITIES

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ABSTRACT. The remarkable flux of numbers and expansions and contractions of ranges in northern European bird populations since 1850 were previously attributed to the climatic amelioration in north-western Europe, but recent work shows that species-specific, human-caused habitat changes have played the key role. Other factors of importance have been protection, persecution and pollutants. The short-term dynamics seem more clearly related to fluctuations in food resources and unusual weather conditions. But how general are the northern European patterns? How much are they affected by the peculiarities of the geological history (the whole region was glaciated during the most recent Ice Age), or by the pronounced seasonality of the region? How much can be attributed to the peculiarities of the spatial scale and history of the human impact on the environment? Are northern coniferous forests somehow ecologically peculiar from the avian point of view? Such questions will be discussed using comparative data from other regions.

DYNAMICS OF GUILD STRUCTURE AMONG AVIAN PREDATORS: COMPETITION OR OPPORTUNISM?

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ABSTRACT. Does guild structure of predatory birds at top trophic levels reflect competition, with or without the addition of migrants? We examined the dynamics of guild composition of predatory birds (raptors) in three seasonal environments: Auco, Chile (no migrants), Donana, Spain (some migrants), and Washtenaw County, Michigan, USA (many migrants). Guild structure remained surprisingly stable from non-breeding to breeding seasons in both Chile and Spain, despite seasonality in prey abundance at both sites, and the arrival of three migrants in Spain. Guild structure in Michigan shifted seasonally, reflecting increased prey diversity in the breeding season. Nevertheless, there was no obvious displacement of residents' diets by migrants, which either joined existing guilds or specialized on seasonally abundant prey. Overall, raptor diets appeared to reflect species-specific preferences intersecting with basic prey availability, resulting in a guild structure not obviously affected by competition.

Keywords: Guilds, competition, opportunism, Falconiformes, Strigiformes, residents, migrants, Chile, Spain, United States.

INTRODUCTION

Assemblages of avian consumers need not always reflect competitive processes. Competition that is intense only during occasional "ecological crunches" in resource levels may be insufficient to impose recognizable pattern (Wiens 1977), although seasonal fluctuations could still induce predictable shifts in niche relationships among consumers (Schoener 1982). The relationship between fluctuating resource levels and niche relationships becomes more complex when communities are composed of both migrant and resident populations. Do niche relationships of resident consumer populations change in connection with seasonal influxes of migrants? Or, are migrants superimposed, in resource-rich seasons, on residents that maintain more or less consistent relationships among themselves? Predatory birds in the orders Falconiformes and Strigiformes (diurnal and nocturnal raptors) constitute ideal model assemblages for examining these questions. Raptors are often assumed to be limited by their prey resources, and their food habits can be examined at very detailed levels of resolution. Furthermore, assemblages exist both with and without migratory members.

Some previous studies on the trophic guild structure of raptors have disputed the role of interspecific competition in shaping these predatory assemblages, proposing that they are simply groupings of species that opportunistically exploit superabundant prey (e.g. Jaksic & Braker 1983). These studies, though, are weakened by relying on static pictures of average conditions of prey levels and on niche descriptors that pool data from different regions over extended time spans.

Here, we examine whether three raptor assemblages that exist in seasonal environments exhibit seasonal shifts in guild structure in the absence (Chile) or presence (Spain, United States) of migrant populations. We evaluate evidence for patterns

reflecting competition versus opportunism. Finally, we discuss the role of biogeographical idiosyncrasies in the dynamics of raptor assemblages.

MATERIALS AND METHODS

Chile

Our study site is the Reserva Nacional Las Chinchillas, at Auco (31°30'S; 71°06'W), 300 km north of Santiago. The area is semi-desert, with thorn scrub vegetation (Jimenez & Jaksic 1989). Common species of raptors at the study site are listed in the Appendix.

We sampled regurgitated pellets at known roosts, nests, and perches monthly throughout 1988 and part of 1989. In the laboratory, pellets were dissected and their contents identified to species (vertebrate prey) or family level (invertebrates). Information from pellet collections was pooled into two biological seasons: non-breeding (from 1 March to 31 August) and breeding (from 1 September to 28 February). Mammalian prey densities were somewhat higher during the non-breeding season, but avian and reptilian prey were the reverse (Jaksic, Jimenez & Feinsinger, unpublished data).

Spain and Michigan

In two other sites, food habits of local raptors had previously been sorted by season: Reserva Biologica de Donana, Huelva Province, Spain (Kufner 1986), and Superior Township, Washtenaw County, Michigan, USA (Craighead & Craighead 1956). In Spain, shifts in prey density from breeding to non-breeding season apparently resembled those in Chile. Craighead & Craighead (1956) provided crude estimates for mammalian and avian prey abundance.

Assessment of trophic guild structure

Predator diets from the three study sites were analyzed quantitatively using three metrics: (1) Diet breadth (= diet diversity) was computed as $B = 1/\sum(p_i^2)$, where p_i is the relative occurrence of prey category i in a given predator's diet. This index reflects population-wide use of resources regardless of their relative availability (Feinsinger et al. 1981). We computed diet breadth using only broad prey categories (mammals, birds, reptiles, amphibians, fish, terrestrial and aerial invertebrates, aquatic invertebrates) that require different foraging techniques and/or capture methods on the part of raptors. (2) Diet overlap (= diet similarity) of Pianka (1973) was computed as $Ov = \sum p_i q_i / [\sum(p_i^2)(\sum(q_i^2))]^{0.5}$, where p_i is the relative occurrence of prey category i in one predator's diet, and q_i is its relative occurrence in another predator's diet. Here we used the highest possible taxonomic resolution of prey in all cases. (3) Trophic clusters. Using entries in the diet similarity matrices for calculating Ov , we applied the unweighted pair-group clustering method with arithmetic averaging (UPGMA, Sneath & Sokal 1973). We arbitrarily set a threshold at 70% diet similarity to assign predators to trophic guilds.

RESULTS

Chile

During the non-breeding season of 1988, the raptors formed three trophic guilds (Figure 1): (a) Omnivorous guild. The Burrowing Owl and the Ferruginous Pygmy Owl

consumed primarily mammals and insects. (b) Mammalivorous hawk guild. The Red-backed Hawk and the Black-chested Eagle consumed primarily Darwin's Leaf-eared Mouse *Phyllotis darwini* but ate some reptiles as well. (c) Mammalivorous owl guild. The Great Horned Owl and the Common Barn Owl ate only mammals, primarily Darwin's Leaf-eared Mouse. Two species were isolated in the cluster analysis: The Harris' Hawk, primarily consuming the Degu Fence Rat *Octodon degus* and secondarily Darwin's Leaf-eared Mouse, and the American Kestrel, whose primary prey was birds.

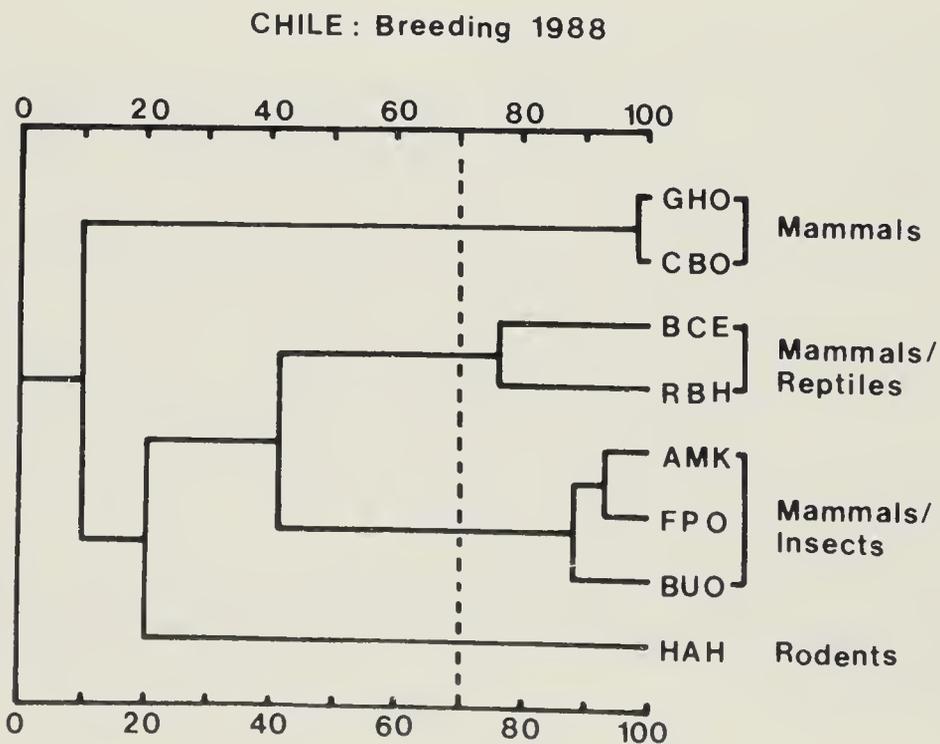
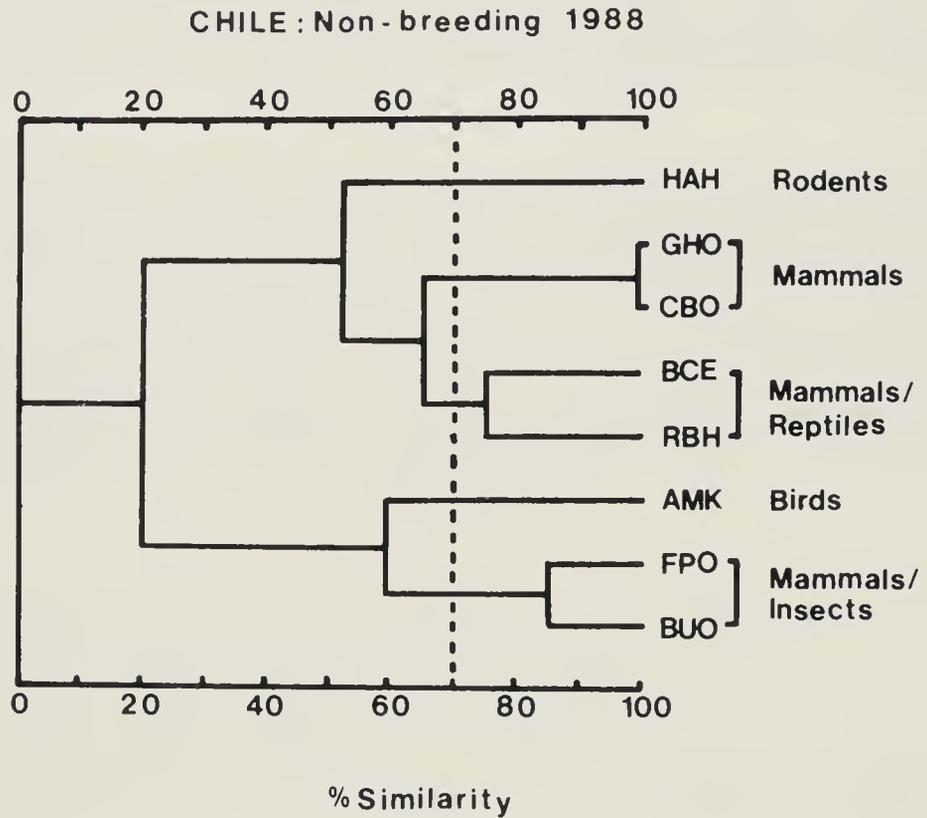


FIGURE 1 – Guild structure of raptors in Auco, Chile, resulting from UPGMA cluster analysis. Dashed vertical line here and in the following figures indicates the arbitrary criterion of guilds at > 70% diet similarity. Data collected by the authors. Abbreviations as in Appendix.

During the breeding season of 1988, the same species occurred at the site and formed the same guild pattern, with only slight modifications: (a) In the omnivorous guild, the Burrowing Owl increased slightly its relative consumption of mammals, whereas the Ferruginous Pygmy Owl became somewhat more insectivorous. The American Kestrel joined this guild by becoming strongly insectivorous. (b) In the mammalivorous hawk guild, the Red-backed Hawk increased its consumption of reptiles and its primary prey became the Degu Fence Rat, while the Black-chested Eagle increased its consumption of birds. (c) In the mammalivorous owl guild, diets of the Great Horned Owl and the Common Barn Owl remained the same. Harris' Hawk, now isolated in the cluster analysis, still ate the Degu Fence Rat but increased its consumption of birds. Thus, of the few seasonal changes in guild structure, most involved raptors that presumably keyed in on abundant alternate prey such as birds and reptiles.

On average, the level of diet similarity at which guilds formed in the cluster analysis did not move up or down between non-breeding and breeding seasons (Mann-Whitney U-test; $P > 0.10$). There was no trend for diet breadths to change between non-breeding and breeding seasons (Wilcoxon signed-ranks test; $P = 0.10$).

Spain

During the non-breeding season, two trophic guilds occurred: (a) Mammalivorous/avivorous guild. The Red Kite and the Imperial Eagle ate mainly mammals and birds. (b) Omnivorous guild. The Little Owl and the Eurasian Tawny Owl ate large numbers of insects, although the Eurasian Tawny Owl also ate some vertebrates. One species, the Common Barn Owl, remained alone in the cluster analysis because of its strictly mammalivorous food habits.

During the breeding season three species, the Black Kite, Old World Kestrel, and Eurasian Buzzard, immigrated into the locality, changing the guild membership observed during the non-breeding season: (a) Mammalivorous/avivorous guild. The Eurasian Buzzard joined the resident Red Kite and Imperial Eagle. All ate primarily mammals and birds, with reptiles as secondary prey. (b) Omnivorous guild. The Black Kite and the Old World Kestrel joined the resident Little Owl and Eurasian Tawny Owl. All ate large numbers of insects (the Little Owl almost exclusively so), together with some vertebrates. The Common Barn Owl remained a mammalivorous specialist. In summary, three species migrated into the area to breed, but the nature of guilds remained essentially unchanged.

As in Chile, on average the level of diet similarity at which guilds formed did not change between non-breeding and breeding seasons (Mann-Whitney U-test; $P > 0.10$), and diet breadths remained the same (Mann-Whitney U-test for all species, $P > 0.10$; Wilcoxon signed-ranks test for year-round residents only, $P = 0.20$). Thus, the scenario in Spain resembles that of Chile, except for the migration of raptor species that bred in the Spanish site but left in the autumn.

Michigan

During the non-breeding season of 1942, all raptors belonged to a single cluster of mammal eaters. Two groups with slightly different specialties occurred: The Great Horned Owl and Eastern Screech Owl, whose primary prey were the white-footed mice *Peromyscus* spp., versus the Red-tailed Hawk, Red-shouldered Hawk, Rough-

legged Hawk, Short-eared Owl, Common Long-eared Owl, American Kestrel, and Northern Harrier, whose primary prey was the meadow mouse *Microtus pennsylvanicus*.

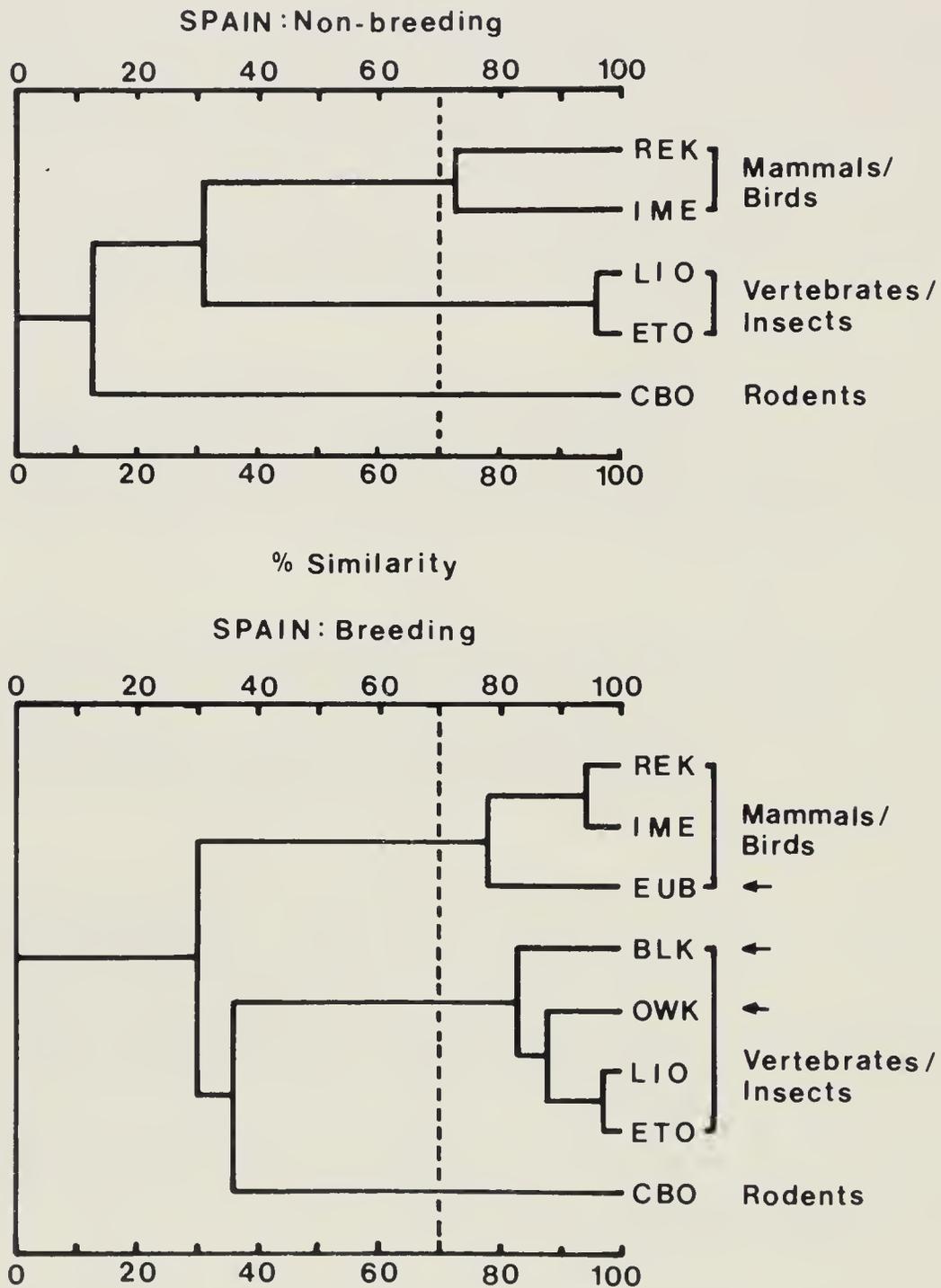


FIGURE 2 – Guild structure of raptors in Donana, Spain. Data from Kufner (1986). Abbreviations as in Appendix.

During the breeding season, a complex exchange of species occurred and the guilds prevailing during the nonbreeding season dissociated. Rough-legged Hawks, Short-eared Owls, and American Kestrels emigrated, while Cooper's Hawks and Common Barn Owls immigrated. The mammalivorous guild shrunk to the Eastern Screech Owl (which started eating insects also) and Common Long-eared Owl, but these were now joined by the Common Barn Owl. Three previous members of this guild, the Great Horned Owl, Red-tailed Hawk, and Northern Harrier, formed a distinct mammalivorous/aviorous guild, greatly increasing their consumption of birds at the expense of mammals. Another ex-mammalivore, the Red-shouldered Hawk, became

more omnivorous than the previous three species by eating snakes in addition. The second of the two immigrants, the Cooper's Hawk, ate almost exclusively birds.

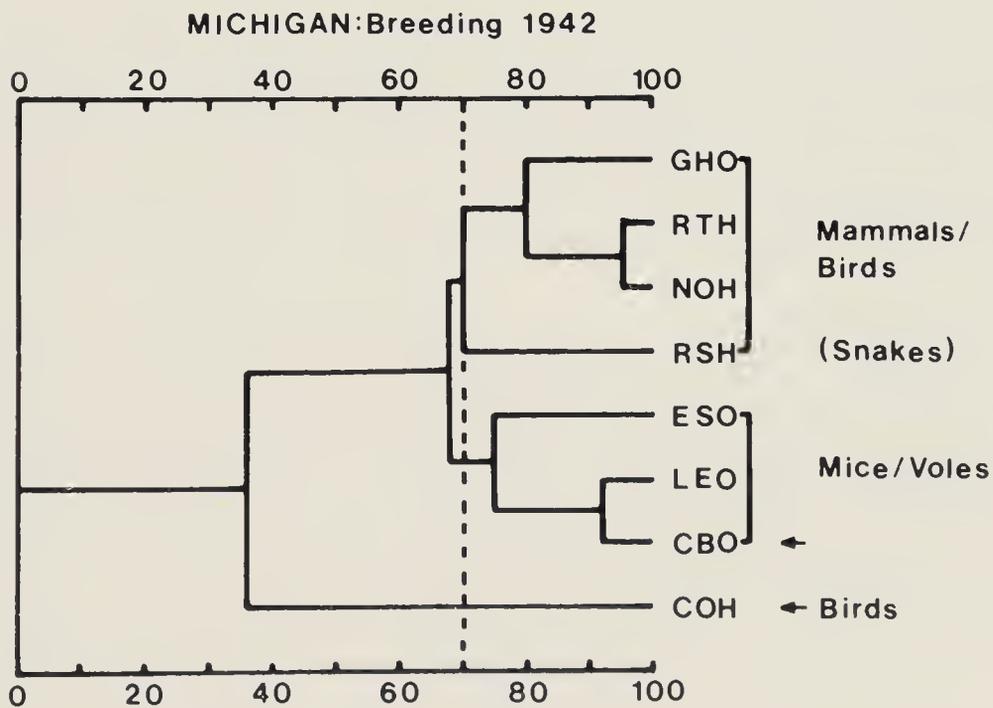
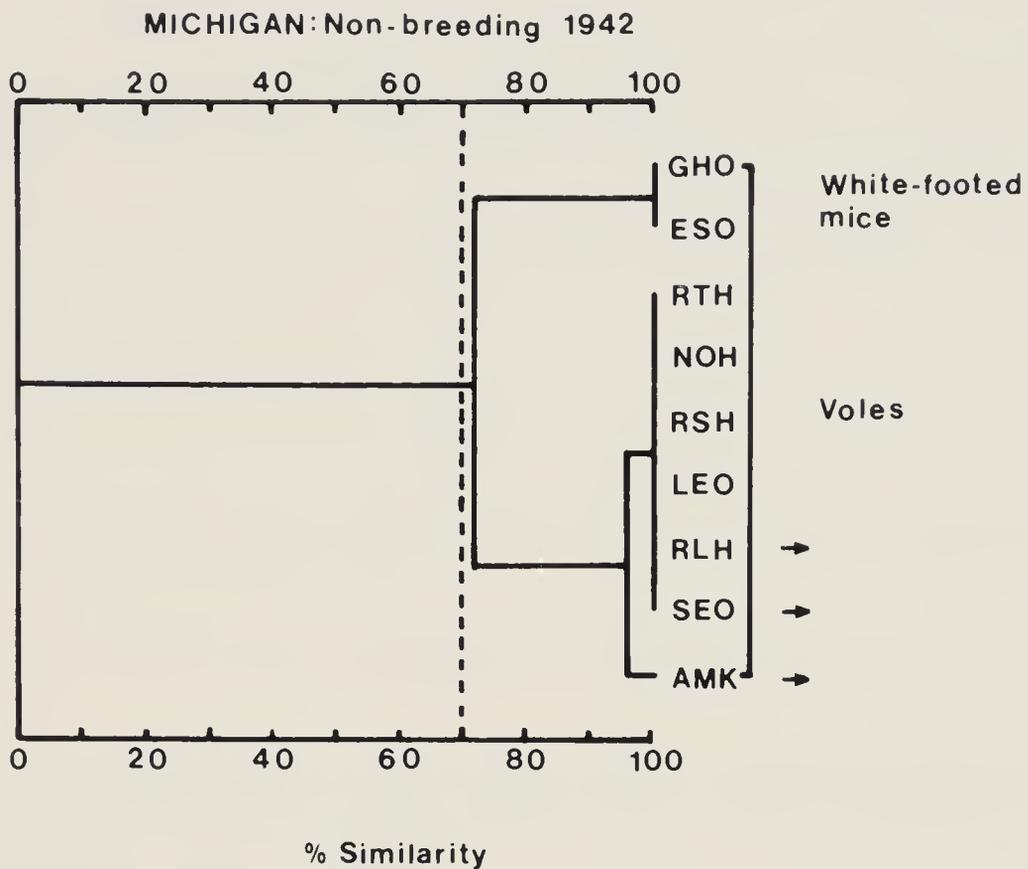


FIGURE 3 – Guild structure of raptors in Michigan, USA. Data from Craighead & Craighead (1956). Abbreviations as in Appendix.

On average, levels of diet similarity at which guilds formed were higher during the non-breeding season than during the breeding season (Mann-Whitney U-test; $P < 0.005$). Diet breadths were higher during the breeding season than during the non-breeding season, when all species were considered (Mann-Whitney U-test; $P < 0.005$) or when only year-round residents were considered (Wilcoxon signed-ranks test, $P = 0.01$).

DISCUSSION

The three localities represent a gradient in dynamics of guild structure. Chile demonstrated the least dynamic assemblage, even though the climate there is highly seasonal. The same species were present throughout the year, and guild structure did not vary. Minor changes in diet between the non-breeding and breeding seasons were not sufficient to shift node values of similarities or diet breadths, even though shifts occurred in the prey resource base (Jaksic, Jimenez & Feinsinger, unpublished data). The situation in Spain was intermediate. Guild structure remained quite stable throughout the year, even to the values of node levels. Guild membership changed because of an influx of migrants that bred in the locality during the prey-rich season, but no significant shifts among residents resulted. The most dynamic changes in guild structure between seasons occurred in Michigan. During the non-breeding season, raptors concentrated on specific resources, forming tight trophic guilds. During the breeding season, guilds broke down through species emigration and by the remaining guild members using more diverse prey. Immigrants also contributed to changes in guild membership. There was no evidence, however, that immigrants caused lateral displacements in the diets of residents; rather, residents broadened breeding-season diets in an apparently opportunistic response to a broader array of available prey (Craighead & Craighead 1956).

The lack of migratory dynamics in the Chilean raptor assemblage results from geography. Chile is enclosed by important barriers to raptor migration: the open ocean to the west and south, the high Andes to the east, and the Atacama desert to the north. No large pool of migrants exists at higher latitudes, simply because the area to the south is small. Most raptor migration within the country is short range, effected by only fractions of the populations (Jaksic & Jimenez 1986). In contrast, the North American continent poses no unsurmountable obstacles to raptor migration, and to the north of Michigan lies a vast region providing a large pool of seasonal migrants. Spain is in the middle of the important European-Saharan corridor of raptor migration through the Gibraltar Strait, with large pools of potential migrants at higher latitudes.

Stability of trophic guild structure in terms of prey use is evident in both Chile and Spain. In both regions, many raptors appear to rely on mammals as staple prey during the non-breeding season, whereas during the breeding season they broaden their diets only slightly by exploiting alternate prey that are increasingly available (in terms both of numbers and activity), such as reptiles and birds, but without ceasing predation on mammals. Given these sites' geographical position at about 30° latitude, subjected to the moderating influence of the ocean and without snow, prey fluctuations may not be as pronounced as those in the truly continental, higher latitude setting of Michigan. Complete data are not currently available on seasonal changes in prey in these localities. Nevertheless, an indirect test of this hypothesis could be performed by studying guild dynamics in, for example, California, whose geographic and climatic features are more similar to those in central Chile and southern Spain than they are to Michigan. We expect that California guild structure should be less dynamic than that in Michigan.

A general picture emerges from scrutinizing guild dynamics under fluctuating levels of prey resources at these sites. In no case does niche separation increase under conditions of presumably limiting resources (the non-breeding seasons). Either there

are no significant changes in levels of diet similarity (Chile and Spain), or the changes go in the opposite direction (Michigan) expected for competition-structured assemblages. We propose the following scenario: (1) During lean seasons, raptors emigrate from areas where resources become scarce, or alternatively, they converge upon the few resources that can be exploited. (2) During resource-rich seasons, raptors immigrate back into the same areas and/or opportunistically exploit a more varied supply of prey resources as these become available. Yet the immigrants, where these occur, do not appear to displace residents' diets in any discernible way, nor does emigration result in "competitive release" among the residents. If competition occurs among raptors in these assemblages through their common use of prey, it has no obvious links to diet shifts.

ACKNOWLEDGMENTS

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APPENDIX

Raptor species found in the three study sites and their residence status. Scientific and vernacular nomenclature after Amadon et al. (1988).

- A) CHILE. Residents: *Buteo polyosoma* (Red-backed Hawk, RBH); *Falco sparverius* (American Kestrel, AMK); *Geranoaetus melanoleucus* (Black-chested Eagle, BCE); *Parabuteo unicinctus* (Harris' Hawk, HAH); *Athene cunicularia* (Burrowing Owl, BUO); *Bubo virginianus* (Great Horned Owl, GHO); *Glaucidium brasilianum* (Ferruginous Pygmy Owl, FPO); *Tyto alba* (Common Barn Owl, CBO).

- B) SPAIN. Residents: *Aquila heliaca* (Imperial Eagle, IME); *Milvus milvus* (Red Kite, REK); *Athene noctua* (Little Owl, LIO); *Strix aluco* (Eurasian Tawny Owl, ETO); *Tyto alba* (Common Barn Owl, CBO). Breeding visitors: *Buteo buteo* (Eurasian Buzzard, EUB); *Falco tinnunculus* (Old World Kestrel, OWK); *Milvus migrans* (Black Kite, BLK).
- C) MICHIGAN. Residents: *Buteo jamaicensis* (Red-tailed Hawk, RTH); *Buteo lineatus* (Red-shouldered Hawk, RSH); *Circus cyaneus* (Northern Harrier, NOH); *Asio otus* (Common Long-eared Owl, LEO); *Bubo virginianus* (Great Horned Owl, GHO); *Otus asio* (Eastern Screech Owl, ESO). Breeding visitors: *Accipiter cooperii* (Cooper's Hawk, COH); *Tyto alba* (Common Barn Owl, CBO). Wintering visitors: *Buteo lagopus* (Rough-legged Hawk, RLH); *Falco sparverius* (American Kestrel, AMK); *Asio flammeus* (Short-eared Owl, SEO).

TROPICAL RAIN FOREST BIRD COMMUNITIES: EMERGING PATTERNS AND PROCESSES OF ORGANIZATION

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ABSTRACT. Marked constraints in primary rain forests may be responsible for the rarity of many species, which is a typical feature of the structure of these bird communities and a major factor facilitating species coexistence. Natural disturbances and habitat heterogeneity, low availability, patchy distribution or seasonality of food resources, interspecific competition, and high predation pressure may be the most prominent constraints. These allow the maintenance of a high species diversity. The form and degree of rarity and its ecological correlates vary widely among species and localities. Whatever the species composition and richness (ecological and historical origins), there are striking convergences in the evolution of bird community structure along habitat successions in both temperate and tropical forests, notably in the relative proportion of dominant and rare species. Most divergent interpretations about the organizing process may come from the comparison of forests with different levels of disturbance, maturity, history or productivity.

Keywords: Bird community, rain forest, structure, organisation, constraints.

INTRODUCTION

Tropical rain forest communities have reached the highest degree of complexity in terrestrial ecosystems, in terms of number of coexisting species and interspecific interactions. Yet almost all our knowledge and theoretical framework about bird community organization come from the poorer temperate avifaunas. Do the latter exhibit similar structure, less evolved but easier to study, or are the organization "rules" different from those in the tropics?

The origin of the higher diversity of tropical communities has been classically explained by supposed rates of speciation and extinction, climatic stability and predictability, spatial heterogeneity, foliage complexity, stable productivity, plant taxonomic diversity and associated variety of food resources, niche specialization, competition and predation (Pearson 1975, Pianka 1978, Terborgh 1985, Diamond 1988, Ashton 1989, Gentry 1989, Wiens 1989). Historical factors, such as time for speciation or colonization and Pleistocene refugia (Haffer 1974), have probably shaped the existing regional species pools from which are drawn the actual communities, each of them accommodating only a subset of the available pool. My goal is to understand the factors explaining the degrees of species packing and the maintenance of diversity, without considering their origin or the rates of speciation and extinction acting on a longer time scale. I shall concentrate on primary equatorial rain forests to present a general framework of hypotheses, drawn from personal investigations and published data, about the organization and functioning of these species-rich communities. The similarities between comparable stages of forest succession in temperate and tropical areas will be emphasized.

METHODS

Comparative analyses of the species composition and structure of bird communities have been conducted from 1981 to 1989 in eight main localities, widely spaced within 80,000 km² of unbroken primary forest in French Guiana, northern Amazonia (Thiollay 1986, 1988a). To check the general relevance of the major conclusions, primary rain forest communities have also been more briefly surveyed since 1968 in Mexico, West Africa, Madagascar, Nepal, Borneo and Java, as well as a mature temperate forest in France for comparison (Thiollay in press). Some studies were limited to particular guilds (e.g. foliage insectivores, diurnal raptors). The census methods were mainly derived from a point count technique (20-minute counts on regularly spaced 0.25 ha plots), complemented by line transect counts and mistnetting. Other published accounts of rainforest bird communities are analyzed in the fine study of Terborgh et al. (1990). Their general conclusions are similar to those obtained in French Guiana and differences mainly come from different census methods, plot sizes and characteristics of study sites.

OBSERVED PATTERNS OF COMMUNITY STRUCTURE

The following structural trends were found in every primary rain forest bird community studied (Thiollay 1980 to 1988a and in press):

- Little more than 1 % of the species are really abundant and widespread. An additional 10-15 % of species reach moderate levels of abundance. Together they account for 40-50 % of all individual birds.
- All other species are rare, patchily distributed, or have low densities. They account for most of the alpha diversity.
- The distribution of species abundance is truncated noncanonical lognormal; the biological significance of this distribution is not clear.
- The above structure is usually similar within particular guilds, families, or habitats.
- There are frequent species distributional gaps at all scales and significant differences in specific abundances or species composition between the bird communities of rather close and structurally similar forest areas.
- Some species exhibit seasonal nomadic movements (frugivores) or habitat shifts (insectivores), but most species appear sedentary.
- The total density of birds in rain forests is usually not higher than that found in temperate forests, especially when corrected for the larger vegetation volume. So the average species density is much lower in the tropics and the higher species packing mainly becomes prominent when the sample area increases.
- Spatial distribution is partly correlated with microhabitat distribution and species diversity is substantially accounted for by habitat heterogeneity. In Guiana, 44 % of forest species are associated with natural disturbances (treefall gaps, edges, river banks, second growth, emergent trees, swamps) and still others with army ants, rocky outcrops, etc. The most widespread (> 50 % of the total area) and mature of the six forest types is the only habitat for a mere 25 % of the species.
- Species niches are densely packed over the full range of resources and widely overlapping, as if the number of species was higher than the number of available resource categories.
- There is a roughly equal trend among species toward niche specialization and generalism.

- The habitat niche of some species may vary markedly between localities.
- There are instances of both coexistence of closely similar species and interspecific exclusion or replacement.
- Because of low densities and patchy distributions, species often seem more spatially juxtaposed than superimposed; a complete mapping of territories or areas of occupancy however gives a high species overlap and thus a high point diversity or degree of actual coexistence (Terborgh et al. 1990).
- There are many specifically distinct ecological correlates of rarity, and rare species are found among almost every guild, trophic category, size class, or habitat type.
- Complex social structures, permanent pair bonds and commensal, mutualistic or parasitic interactions are prominent features in tropical forest bird communities.
- Most species, especially in mature understory, seem to have surprisingly low reproductive rates, long periods of juvenile dependence, high survival rates at the adult stage, delayed reproduction, and other demographic attributes of K selection. However, species of upper canopy, gaps, edges and second growth may exhibit more r-selected traits.
- Interannual variability of rainfall often results in marked between-year variations of at least the timing or output of reproduction in many birds. This may affect the relationships and competitive interactions between species and, consequently, community organization.

Overall, multiple mechanisms of species coexistence are apparent: patchy distribution of small territories, overlap of large home ranges, temporary species grouping on abundant food sources (e.g. fruiting trees, army ants), itinerant exploitation by mixed flocks (foliage insectivores), niche shifts according to local competitors, subordinate species with marginal foraging behavior (Willis 1981) or interspecific territoriality. These factors require thorough investigation; they may be key factors in the persistence of species-rich assemblages.

The structure of bird communities in primary rain forests bears many similarities to that of mature, broad-leaved, temperate forests (Thiollay in press, Tomialojc et al. 1984). The high proportion and patchy distribution of rare species, many of them associated with natural openings and successional stages, are especially prominent, and contrast with the patterns found in managed or younger, more homogeneous, forests in both temperate and tropical areas.

The dynamics of community structure along successional gradients (latitude, altitude, disturbance) also reveal basic convergences. From young regrowth to oldest stages, the proportion of dominant species tends to decrease while rare species increase. Conversely, any shift toward secondary forest or habitat disturbance often results in a higher proportion of abundant species and a decline in the number and abundance of less common taxa, leading to a reduction of both species richness and diversity. A similar trend is apparent when hunting pressure, logging, or fragmentation are involved (Thiollay 1985a, b, in prep.). When the forest is opened, some species, previously rare in the primary forest become abundant, while many species from closed understory decrease or disappear. The communities of most tropical successions so far investigated exhibit similar general patterns of evolution, although more detailed studies may reveal minor differences. This also seems to hold for temperate bird communities though true primary forests, the reference stage, are now rarely available.

ECOLOGICAL CONSTRAINTS AND ORGANIZATION PROCESSES

Suggested processes of species enrichment and maintenance of diversity in tropical communities include both equilibrium and nonequilibrium hypotheses (Wiens 1984, Ashton 1989). Widely accepted assumptions involve long evolutionary time, climatic stability, and abundance or variety of food resources and foraging sites in tropical forests. These are thought to provide ample opportunities for specialization, and niche segregation, and thus species coexistence. However, a different picture emerges from field experience in rain forests and studies of their bird communities. In short, the relatively low populations of most species may be a fundamental determinant of species coexistence, and may originate from a wide array of major constraints.

The view that mature rain forest acts as a constraining ecosystem, thereby producing higher species diversity, is supported by the inverse relationship between habitat productivity or resource levels and both plant and animal species richness in terrestrial as well as aquatic ecosystems (Tilman 1982, Goulding et al. 1988, Owen 1988, Ashton 1989, Bourliere & Harmelin-Vivien 1989). Species richness may increase with habitat productivity at low levels of productivity, but thereafter, when resources are not limiting, species richness is depressed by an increase in species dominance (Abramsky & Rosenweig 1984). There are many aspects of rarity such as low density, patchy distribution, subordinate behavior, narrow specialization, or ephemeral colonization of disturbed patches. Since the presence of rare species often seems unpredictable, interspecific competition and niche specificity must be low among most of them. Thus, little density dependence and primarily nonequilibrium phenomena should be expected.

Four non exclusive types of constraints are apparent in tropical forests. Their relative importance is likely to differ widely among species and communities.

Low food availability

Many life-history traits, and foraging behaviors and the limited foraging success of rain forest birds suggest that food resources may be often irregular in space and time or available with difficulty, at least in primary forest understory (Thiollay 1988b). Strong and multiple antipredator defences, high prey diversity, and patchy or unpredictable distribution, low density, and low productivity or standing biomass of most prey species are chronic constraints. Marked seasonal and interannual fluctuations of both insect and fruit production are common in tropical forests (Willis 1976, Leigh et al. 1982, Sabatier 1985, Boinski & Fowler 1989). These fluctuations produce seasonal breeding, movements, and dynamics in forest bird populations (Fogden 1972, Greenberg 1981). A relatively short daylight period, the high frequency of rains, and midday heat and high anti-predator vigilance also limit daily food intake.

Habitat heterogeneity

Natural disturbances (e.g. treefall gaps, watercourses) and associated patch dynamics are largely responsible for rain forest bird diversity (Schemske & Brokaw 1981, Thiollay in press). Populations are fragmented and inter-specific relationships are disrupted by the mosaic of habitats, promoting a higher species richness through the maintenance of gap specialists or other fugitive species and the limitation of dominant species (Holt 1984, Sousa 1984, Denslow 1985).

Interspecific competition

Possible diffuse or direct interspecific competition is suggested by negative correlations in the abundance of some congeneric coexisting species, cases of interspecific territoriality, mutually exclusive occurrence of similar species between localities and habitat shifts associated with the presence or absence of a congener (Diamond 1980, Terborgh 1985, Thiollay 1986, 1988a). However, the actual influence of interspecific competition has been repeatedly questioned (Strong et al. 1984). Direct evidence of effective competition remains untested and striking instances of association between related species are also known. Low availability of many prey species and dietary opportunism often limit the pressure of predators, thus preventing competitive exploitation and facilitating co-existence of competitors (Hanski 1983).

Predation pressure

There is much circumstantial evidence of a high predation rate, at least on broods (Skutch 1985) by a wide variety of predators. Besides mammals and reptiles, 10 % of the bird species in the primary forest community of French Guiana are regular predators of vertebrates. The multiple and highly evolved antipredator adaptations among animals are indicative of a constant predation threat, which shapes life-history strategies and behaviors, and may strongly influence the dynamics of bird populations. Predation may limit the size, distribution, or resource exploitation patterns of many species, thus favoring the maintenance of other marginal species (Glasser 1979). By holding prey populations below the level of food limitation, predation pressure may reduce the abundance of many species and thereby facilitate their coexistence. Indeed, predation and competition can interact to structure communities in several ways (Kotler & Holt 1989) and may provide alternative explanations for observed patterns of resource partitioning as well as for the trend toward niche generalism.

Interspecific coexistence, which is the basis of community structure and diversity, may be mediated by the complex interaction of not only competition and predation but also spatial, seasonal, or interannual variations in resource abundance and the resulting variability of niche adaptation and diet or habitat selection. The relative importance of these pressures remains to be assessed, but there is circumstantial evidence that they may be more convergent between temperate and tropical mature forests than between primary and secondary stages within any succession.

CONCLUSION

Several factors are classically put forward to explain the high diversity and the organization of tropical communities. Without minimizing their possible influence (although they have never been accurately measured), I have stressed the often underestimated importance of strong environmental constraints in the supposedly stable and resource-unlimited tropical forests. These constraints may be responsible for the rarity, niche patterns, and dynamics of many species. They may fragment, over-disperse, or reduce the size of populations, thus facilitating the coexistence of an increased number of species. This maintenance of a high species packing by a limitation of dominance of most species, may in turn intensify biotic interactions, further increasing the opportunities for coexistence and strengthening species richness. Indeed, these hypotheses, drawn from empirical observations, remain to be tested.

High predation rates and competitive or parasitic interactions are mostly inferred from casual observations or the mere number of coexisting species. They also remain to be fully assessed. Such biotic constraints are likely to play an important role, but are also likely to be lessened by the overall rarity of species. Patchiness, seasonality, limited abundance, and low accessibility of most food resources are other constraints so far underestimated in primary rain forests and which must be investigated. Productivity is spread over a longer period in the tropics and there is evidence that the breeding season food levels differ less from non breeding levels in tropical than in temperate forests (Thiollay 1988b). The often-quoted consequence is that rain forest communities may be permanently saturated with resident species; under more seasonal conditions, however the smaller proportion of residents is kept below the maximum population level, allowing a large, temporary influx of migrants.

Habitat heterogeneity increases beta diversity but it is also a limiting factor for many populations. Vegetation heterogeneity is produced by environmental variability in space and time due not only to soil, relief, and microclimate heterogeneity but also to local disturbances. Among these factors, frequent and spatially unpredictable treefall gaps are a prominent feature of primary forests and a critical determinant of community diversity. Disturbed patches may interrupt species interactions and decrease the risks of competitive exclusion, thus enhancing species coexistence (Chesson 1986). The lack of such gaps in more homogeneous temperate or tropical forests may be a major cause of their lower richness. However, to maintain these gap species and at the same time to prevent them from becoming dominant, the spatial and temporal distribution of successional patches has to remain within limited proportions. This has led to the concept of intermediate disturbance (Connell 1978, Abugov 1982, Buckley 1983) and explains why logging of primary forest, which at first creates more gaps, has such a negative impact on species richness (Thiollay in prep.). Finally, there is empirical evidence that biotic constraints and both the complexity and intensity of species interactions increase along successions toward the richest, mature rain forest. This would support the mechanism of community organization outlined above.

The occurrence of at least as many broad generalists as narrow-niched specialists is interpreted as a means to cope with limited resources and interspecific competition. Habitat heterogeneity and environmental instability may set a limit to the degree of specialization and favor the evolution of generalists. The selection of localized habitats by half the forest species in Guiana contributes to their rarity and to the persistence of competitively inferior taxa. Sometimes several of them may be able to exploit a similar resource without apparent competition.

Any prediction about the evolution of a rain forest community must take into account the existence of populations with different sensitivity, reactions and dynamics. These range from K-selected species of closed understory, which are highly sensitive to disturbance, to r-selected generalist edge species that quickly thrive in new openings. Among canopy birds alone, every kind of response may be found to disturbance such as logging (Thiollay in prep.), from the disappearance of species that require dense continuous canopy, to the persistence of species tolerant of openings, and to the increase of some of those species primarily associated with tree tops, gaps, or edges. What is constantly changing is dominance interactions, but this measure of interference is difficult to define. A numerically dominant species may share an abundant resource with other species without intense interference, whereas a rarer species is expected to be functionally dominant when it monopolizes a scarce resource.

Rain forest bird communities display the attributes of so-called equilibrium communities, as far as life-history traits, species interactions, rates of disturbance and patch dynamics are sufficiently known so that changes may be predictable (Wiens 1984, Giller & Gee 1987). Yet the complexity of interactions between so many little-known species, the stochastic occurrence of extrinsic abiotic factors, and the weight of past adaptations or evolutionary history are such that a well understood order is still out of reach and the role of chance cannot be dismissed. Moreover, the position of each species or community subset along the equilibrium-nonequilibrium continuum may be different. The now questioned relationship (Strong et al. 1984) between complexity, equilibrium, saturation and stability of communities is not supported by the sensitivity of most rain forest bird populations to disturbance (Thiollay 1985b).

A search for generalizations is promising. After the confusing effect of species number and historical evolution are removed, common patterns of organization may be found between mature temperate and mature tropical forests (Thiollay in press). Similar community patterns, environmental constraints and causal processes have been found in coral reefs (Bourliere & Harmelin-Vivien 1989) and Amazonian river fishes (Goulding et al. 1988). Conversely there are many differences between communities along successional or elevational gradients within the tropics (Thiollay 1980, 1985a) that match nicely the trends observed along a tropical-temperate gradient. Most divergent interpretations of community patterns may come from the comparison of forest ecosystems at different stages of maturity, environmental conditions, disturbance levels, management, or historical evolution and from the study of taxonomic categories with different ecological attributes. Small vs. large study areas and short vs. long-term investigations may also lead to dissimilar conclusions. Organization rules are probably similar. Only the relative importance of organizing forces are likely to differ between habitats, species and latitudes.

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SYMPOSIUM 26

LONG-TERM POPULATION STUDIES OF BIRDS

Conveners C. M. PERRINS and J. A. MILLS

SYMPOSIUM 26

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INTRODUCTORY REMARKS: LONG-TERM POPULATION STUDIES OF BIRDS

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The number of long-term population studies of birds is still relatively small; most still come from Europe and North America and more are needed from elsewhere. In particular, there is a shortage of studies from the tropics and also for certain groups of birds, such as long-distance migrants. Here we present five studies, which span some of the range of features of population studies.

One is of a southern hemisphere gull, the Red-billed Gull, which has a diet of plankton and suffers periodic food failures during the breeding season - a feature probably not uncommon in seabirds, though still poorly documented and its effects on populations poorly understood.

The two passerine studies described also show periodic declines, one as a result of winter cold and hence - presumably - food shortage, the other at least partly as a result of nest predation. The latter is of particular interest since the authors show that, at least in this species, losses of nests on the breeding grounds may be of greater concern than losses in winter quarters; this contrasts with the view that these species may be declining as a result of habitat loss in winter quarters. Again, the frequency of "poor years" is likely to be crucial to the understanding of such populations, yet very long periods of study are necessary to gather such information - even longer if we are to see whether the frequency of poor years is changing.

Korpimäki's paper on Tengmalm's Owl deals with a population whose individuals encounter good and poor years on a fairly regular basis and shows how the reproductive success of individuals varies in relation to the stage of the cycle of the food supply at which these individuals enter the breeding population.

The fifth paper, on Mute Swans, deals with a different aspect of population dynamics. There are several concurrent population studies of this species and they show rather different life-cycle parameters in different areas. This paper stresses the point that we should not rely on the findings of a single study of a species to give us the only possible set of parameters for that species.

Hence, in combination, we believe that these papers show us that the need for long-term studies is, if anything, greater than ever. It may be important to establish the frequency of "poor years" and whether this frequency is changing. Also, we need to know more about populations in a range of habitats or areas before we can fully understand the factors affecting populations.

LONG TERM POPULATION STUDIES: THE MUTE SWAN

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ABSTRACT. The Mute Swan *Cygnus olor* is a well-known European bird and, in the last 20 years or so, there have been a number of population studies, both in Europe and of introduced birds in North-eastern United States. The populations were very depressed after World War II, but, due to protection are now increasing rapidly in many areas. The demographic characteristics of this species differ markedly in different areas; most are strongly territorial, others nest colonially. Survival of nests and survival of both young birds prior to breeding and breeding birds differ markedly between areas. In some populations, a significant proportion of the adults fail to breed in any year. The differences between these study areas are contrasted and compared. The Mute Swan seems able to maintain its numbers over a remarkable demographic range.

Keywords: Mute Swan, populations, demography.

INTRODUCTION

The Mute Swan *Cygnus olor* (Gm) is a large bird, weighing from 8-12 kg when mature. It is widespread in Europe and in recent years, due largely to protection, has been increasing rapidly and expanding its range. Since the early 1960s, it has been the subject of a number of detailed studies, some lasting a generation (some 8 - 10 years) or longer, and a number of shorter-term investigations. The majority of these studies have been made in Western Europe, especially Britain.

None of these studies is fully comprehensive, but, collectively, they enable us to build up a good picture of the life cycle of Mute Swan populations and to see how different parameters affect population dynamics. In this paper we look in detail at our studies in the Oxford area and compare these with some other studies, chosen for particular characteristics. The length of each investigation and the ability to look at most stages of the life-cycle have been our major reasons for selection, but we have included some shorter term or less comprehensive studies where they either refer to a population in particularly interesting circumstances or provide a useful contrast, from a different region, to another of these studies.

The majority of study sites are in mixtures of rural, sub-urban and urban habitats where the birds breed in the normal territorial fashion. However, at Abbotsbury, UK, and Roskilde, Denmark, the swans nest colonially: the population in the Hebrides, off the west coast of Scotland, is geographically more isolated than are most of the others which are not closed, but have extensive immigration and emigration.

In the first section of this paper we compare the demographics of the different populations. We have adopted a method similar to the "Balance per pair per year" (BPA) calculations given in Bacon (1980a, b), Birkhead (1982) and Birkhead & Perrins (1986). The method used by Bart, Earnst & Bacon (1991), following discussions at the

Third International Swan Symposium, is simpler to use, but, provided the necessary data are available, the BPA is more reliable. We discuss factors likely to cause the observed differences in performance between these key study areas, supplementing this discussion with pertinent information from other populations.

Although in theory, the Mute Swan is easy to see and count, biases arise as a result of movements and we discuss difficulties in estimating the parameters and likely limitations of such a general comparison. These considerations highlight aspects of the swans' ecology that are important in determining population dynamics, but are difficult to study. In the final section we discuss the importance of the different parameters to changes in numbers within populations.

COMPARATIVE DEMOGRAPHY

The BPA method and that used by Bart et al. (1991) both require the estimation of four parameters of production and survival for a population. The parameters are:

- P_1 Proportion of "adults" breeding;
- P_2 Average clutch-size;
- P_3 Survival from laying to "adulthood";
- P_4 Proportion of adults surviving each year.

The product of the first three terms (with the clutch size divided by two) is the production per adult to the adult population (=recruitment): one minus the fourth term is the adult mortality (=losses); in a stable population recruits must replace adult losses, so these two derived values should be about equal:-

$$P_1 \times P_2 / 2 \times P_3 = (1 - P_4) \quad (1)$$

The main difference between the two methods concern the definition of P_1 . Bart et al. (1991) define "adult" as any birds in the population which are aged four or more. This has the advantage that age of first breeding does not have to be established; it is defined as being four. However, it has the disadvantage that it is necessary to calculate the proportion of the population which is four years old or older and, in some cases, this has produced rather unrealistically high estimates which, in turn, results in very low estimates of the proportion of breeders.

Here we define as "adult" a bird which is known to have made a nesting attempt. Non-breeders are birds which have not bred in a given year, but are known to have done so in an earlier year. Using such a definition requires the modification of the P_3 term to be a variable length, from egg to mean age of first breeding. Since age of first breeding varies between populations, it is important to make such an adjustment where known. The parameters used by Bart et al. are easier to collect and are especially useful for population studies where the birds are surveyed from the air or where the age distribution (including age at first breeding) of the birds is not easily available. However, in the case of the Mute Swans where more detailed information is becoming available, the BPA system seems often more appropriate to the published data.

There is a further problem with defining an "adult" as being of a standard age. This is that one would expect the proportion of "adults" breeding to decline with

increasing density, simply because birds may start breeding later under such conditions. Available data suggest this may be so. For example, in the 1960s, when the Oxford population was high, there were a number of older birds in the urban flocks which had apparently not tried (or had tried and failed) to obtain a breeding territory. In the lower populations of the 1980s it was rare to see a four-year-old bird in the flocks.

Since few natural populations change at more than a few per cent per year, Bart et al. (1991) assume these parameters to be in balance; this enabled them to estimate any missing parameter given the other three. This technique is useful when comparing populations for which certain data are not readily available. However, in the studies we report here (for which all four parameters can be estimated) we would expect approximate equality to hold if the population had indeed been stable. This has not always been the case. But where the population has changed, we usually have an estimate of the rate of change from independent census data. Where equation (1) does not hold for a stable population we deduce that one or more of the estimation procedures which we (or other workers) have been obliged to use, were not accurate.

The parameters are tabulated in Tables 1 to 3. Values in square brackets denote either indirect estimates or direct observations of samples that are either small or thought not to be fully representative.

Proportion of “adults” breeding

The proportion of a Mute Swan population which breeds varies considerably. Plainly any calculations about balance of the survival of juveniles to breeding and the mortality of adults, is considerably affected if adult Mute Swans (i.e. birds which have bred in previous years) have years when they fail to breed.

In our experience, the proportion of adults (using our definition) which do not breed in any year is not a major feature in the demography of Mute Swans. It is difficult to calculate accurately since some pairs which the observers may have thought did not nest may have had a nesting attempt which quickly failed without it being observed. Even so, it is our impression that few birds fall into this category. The commonest cause of non-breeding occurs when a bird loses its mate close to the breeding season and fails to establish a firm pair bond with the new partner in time to breed.

While the early work of Perrins & Reynolds (1967) and of Minton (1968) showed that birds which bred in one year and survived to the next had a high probability of nesting in the second year, these probabilities are now known to vary considerably; in particular, colonially breeding birds may have a higher chance of not breeding. Perrins & Ogilvie (1981) suggest that only 82% of the Abbotsbury birds bred after breeding the previous year, while the figure for Roskilde may be as low as 24% (Bacon & Andersen-Harild 1989). The latter authors also estimate a figure as low as 66% for the non-colonial Kobenhavn birds.

Average clutch-size

The calculations used below require only average clutch-size. In Table 1 we include information on hatching and fledging success, as many studies report these in some detail; brood-size at fledging is also given. Nearly all the average clutches are between 5.5 and 6.5 eggs. It is of some interest that the three more northerly studies

(above 55° lat.) are below 6.0, in line with the trend for swan species (Bart et al. 1991), but more data are needed to investigate this (especially from more northern and southern sites). Clutches at the two colonial sites are notably low (4.8, 5.2) .

TABLE 1 – Clutch-size and nesting success in different populations of the Mute Swan. For each population, column: (a) gives the mean clutch-size; (b) the percentage of eggs which hatch; (c) the percentage of hatchlings which fledge (the cygnets reach the flying stage about September in most European populations); (d) is the product of (b) and (c); (e) is the mean brood-size at fledging (this is not available for Abbotsbury where most young are hand-raised).

Site	C/S (a)	%H (b)	%F (c)	cx (d)	B/S (e)
Lower Thames	6.8	69	58	40	2.76
Oxford	6.8	75	67	50	3.42
Stafford	6.6	52	75	40	2.56
Hebrides	5.88	60	40	24	1.44
Abbotsbury	4.8	62	64	40	–
Roskilde	5.2	54	37	20	0.9
Kobenhavn	5.6	82	54	44	2.6
Chesapeake	6.2	49	82	40	2.2

Survival from hatching to adulthood

Although it is possible to calculate the parameters used later in this paper without knowing the details of the nesting cycle, in many cases the studies of Mute Swans are sufficiently detailed to allow us to break them down into their component parts, and this provides useful additional information.

SURVIVAL FROM HATCHING TO FLEDGING. Hatching success (the number of eggs which become cygnets, including nests which fail completely) varies from 49% to 82%, a considerable range (excluding 25% for Rhode Island where management deliberately controls hatching rate). Hatching success is higher at the Abbotsbury colony (62%) than the Roskilde colony (54%) where aggression between pairs leads to the destruction of many clutches. Hatching success is also low in Stafford, where human vandalism is a common cause of loss.

The percentage of hatchlings fledging varies from 37% to 85%, an even larger range than for egg survival. The lower survivals (Roskilde 37%, Hebrides 40%) are probably caused by less nutritious food for the growing cygnets, exacerbated in some years by inclement weather (see Andersen-Harild 1981 & Spray 1981 for details); within the Hebrides the fledging success on the richer eutrophic lochs was higher than on brackish lochs (mean brood-size at fledging 3.0 and 1.46 respectively).

Overall success from eggs to fledging varies from 20% to 60% (excluding the controlled population on Rhode Island). It is lowest in Roskilde and Hebrides (20% & 24% respectively) and highest in Groningen (60%). At the other sites, which are more consistently mixtures of rural and suburban regions, egg to fledging survival varies from 44% to 55%. The long-established colony at Abbotsbury achieves twice the rearing success of the colony at Roskilde, but this difference is in part due to many of the cygnets being hand-raised in pens, which greatly increases their chances of survival compared with those which are “free-living”.

TABLE 2 – Survival of Mute Swans at different ages. The two data-sets for Oxford relate to different time periods, the 1960s and the 1980s. The columns show: (a) the proportion of eggs producing fledglings (also column d of Table 1); (b,c,d,e) the survivals of first, second, third and fourth year birds; (f) the cumulative product of the five columns; (g) the adult survival rate, assuming that the average age of first breeding is four in all populations. The survival rates quoted from different studies for first year birds are not always strictly comparable since they may not always be for a full year. The bottom row shows the survival rates for the whole of Britain, where immigration and emigration are negligible, calculated from national ringing data (Perrins 1991)

Site	E-F (a)	S.1y (b)	S.2y (c)	S.3y (d)	S.4y (e)	Tot (f)	S.Ad (g)
Lower Thames	.40	.39	.69	.69	.70	.052	.77
Oxford 1	.21	.67	.67	.75	.75	.053	.82
Oxford 2	.50	.37	.49	.67	.75	.045	.87
Stafford	.40	.44	.68	.65	.75	.059	.74
Hebrides	.24	.58	.75	.75	.75	.058	.90
Abbotsbury	.40	.70	.90	.90	.90	.204	.94
Roskilde	.20	.68	.86	.74	.87	.075	.88
Kobenhavn	.44	.45	.68	.87	.86	.101	.86
Chesapeake	.40	.84	.90	.95	.95	.273	.95
British Ringing	–	.66	.72	.76	.82	–	–

SURVIVAL FROM LAYING TO ADULTHOOD. Survival from laying to fledging is discussed above, and the overall estimates from Table 1 are repeated as column (a) of Table 2 which also gives estimated survivals for the first four years of life, and for “breeding adults”. The published first-year survivals vary between 37% and 70% for the different study areas, but these are based on different methods of estimation. Two sources of information are available: records of ringed birds found dead and re-sightings of marked individuals seen alive. Recoveries at death give small samples of the older age groups and are subject to well-known biases in analysis. Re-sightings of marked immatures can be confounded by dispersal and the loss of plastic rings: juveniles are known to disperse further and then return closer to breed (Coleman & Minton 1979, 1980); this may partly explain the low survivals for Lower Thames and Oxford in Table 2. Other values also need interpreting with caution.

First-year survival rates are variable, and vary within study areas depending on winter severity and the cygnets' weights at fledging: first-year survivals of particular cohorts can probably vary between 10% and 90% (Andersen-Harild 1981, Perrins & Ogilvie 1981). As a rule of thumb, typical first-year survivals are probably between 40% and 70% depending on site and season. Survivals in years two, three and four are higher, starting at around 60% and rising to 80% or more – the same as for breeding adults. The precise survivals vary by some 10% about these typical values, depending on area and circumstance. Using the above yardstick, annual survivals of first, second and third year swans are high for Abbotsbury and Chesapeake.

The mortality data are consistent with Perrins' (1991) finding that fledged cygnets from Stafford survive better than those from Oxford, although the low fledging success in Staffordshire gives the overall advantage to the Oxford population.

Combining the information on all phases from egg to adulthood provides the information needed for P_3 . Overall survival, from egg to breeding varies from 6% to 29% between areas. Chesapeake and Abbotsbury are the highest with 29% and 23% respectively, followed by Oxford and Kobenhavn with about 15% each. The other figures are in the region 5% to 10%.

Bart et al. (1991) take the production per pair and multiply that by the survival rates for the next three years to obtain the number alive in the spring of their fourth year. Actually, since the number fledging per pair is taken in about September, the interval between fledging and the spring of the fourth year is three and a half, not three years. Hence, the Bart et al. calculation of the number of survivors to breeding age should be reduced by a further winter's mortality, important since winter mortality is higher than summer (Perrins 1990). In practice, this potential error is counterbalanced, at least to some extent, by the proportion of the population which breed at age three and so have a higher survival to breeding than that calculated by Bart et al. However, in the case of populations, such as that in the Hebrides, where the age of first breeding is more than four, the error will be greater.

Adult survival

The survival rates of breeding adults are more straightforward to estimate in many circumstances due to the high chances of re-sighting breeding adults. The main reason for this is that they tend to remain faithful to their nesting territories and do not move very far. Also, available data indicate that adult mortalities "stabilise" with age, so bulked estimates can be made on the increased samples sizes.

The reported rates are given in the right hand column of Table 2 (to aid comparison with rates for younger age groups): they are typically in the range from 80 to 94%. In general the estimates given by records at death and re-sightings of live swans are quite close. On this basis a "typical" adult survival of 85% ($\pm 5\%$ S.D.) would seem reasonable. Only Abbotsbury and Chesapeake are above 90%. Present estimates for Lower Thames and Stafford are below 80% (77 and 74%): however, both have been higher in the past.

Adult survival also depends on the paired and breeding status of the "adult" birds in the Stafford area (Minton 1968). It is likely that some of the differences in mortality between swans which differ in breeding status are caused by varying risks to collisions with over-head power cables (Minton 1968, Perrins & Sears in press). Paired and breeding birds fly less and, in particular, they fly much less in novel surroundings. Mute Swans may thus show decreased mortality associated with breeding, especially in industrialised countryside where the risks are higher. Bart et al. (1991), commenting on the differences in adult mortality between the migratory northern swan species and the more sedentary, southern Mute Swan, also discussed deaths from cable collisions as a potential alternative explanation to latitude.

Synthesis: Production and losses compared

Table 3 presents the parameters for each of the study areas concerned. Each study area is described very briefly below, with a few key references, and the balance figures, given in Table 3, are commented upon. These show how strikingly the populations differ in the way in which their current populations are maintained. It must be stressed that some of the parameters are not wholly reliable; some may have been

estimated over different years than others. In particular, the proportion of adults which fail to breed is usually very poorly known and these values are little more than guesses for some populations.

TABLE 3 – The balance of numbers in different populations of the Mute Swan. The two data-sets for Oxford relate to different time periods, the 1960s and the 1980s. The columns show: (a) the survival of eggs per nest (divided by 2 to compare with individuals) multiplied by the survival of eggs to four years (ie Table 1, column (a) divided by two x Table 2, column (f)); (b) the proportion of the adults which breed; (c) the annual adult mortality; (d) the difference between the two. See text for further explanation.

Site	Prod. (a)	%Bd (b)	Ad.Mt (c)	Balance (d)
Lower Thames	.052	.9	.23	-.071
Oxford 1960s	.053	.9	.18	-.018
Oxford 1980s	.045	.9	.13	.009
Stafford	.058	.9	.26	-.087
Hebrides	.059	.7	.10	.021
Abbotsbury	.204	.8	.06	.330
Roskilde	.076	.3	.12	-.061
Kobenhavn	.101	.7	.14	.057
Chesapeake	.273	.8	.05	.542

LOWER THAMES. The River Thames for some 100 km above London (Birkhead 1982, Sears 1990).

The recent balance of -0.07 per annum (1983-89) is reasonable for a population beginning to recover from lead poisoning (Sears 1990). The former value of -0.25 (1980-84) is probably too low, but is in the right direction for a population undergoing serious decline due to lead poisoning (Birkhead & Perrins 1986). The actual decline may have been less than this value implies because of appreciable immigration. This population also had an unusually high proportion of swans breeding in their third year, which means that the actual balance per annum would be less low than that calculated using the definition of an adult as being four years old.

OXFORD. The River Thames above the Lower Thames study area, plus some tributaries (Perrins & Reynolds 1967, Bacon 1980, plus references to Lower Thames).

All the more reliable "balance" values are close to the expected 0.0 for a stable population. The estimates for 1980-84 vary from +0.15, when mortalities from 1960-66 are used, to -0.05 when those for 1983-89 are used. The actual population decreased in the late sixties and increased in the early eighties, so that these figures are not inconsistent.

STAFFORD. An area of the English Midlands centred on Staffordshire (Minton 1968, Coleman et al. 1990).

The net change is -0.087, though this depends on which of the range of adult mortalities is chosen. Using the present average of 74%, would lead to the popula-

tion halving in eight years (in a closed population): indeed breeding numbers did halve from 70 to 35 pairs between 1960 and 1985 (Coleman pers comm; see Birkhead & Perrins 1986).

HEBRIDES. A population on islands off the west coast of Scotland (Spray 1991).

This population is approximately stable, so the calculated 0.021 is too high. However, the population was not studied for a long period and it is known that the age of first breeding is very high compared with that of any other British population; only one out of a possible 25 birds bred at age four.

ABBOTSBURY. The only British colony of Mute Swans. On the Fleet, a brackish water lagoon behind a shingle bank in Dorset (Perrins & Ogilvie 1981).

Spring counts of the Fleet and Radipole lake show this population increased from around 480 in 1969 to 545 in 1980 and has remained around this value. An estimate of change of 0.33 is therefore much too high. It is strongly dependent on the high survival rate of the chicks. However, in eight years chick survival varied from 38% to 92% and so the mean for any run of years may not be typical of others.

ROSKILDE. A Danish colony, nesting in brackish water (Bacon & Andersen-Harild 1989).

The calculated values of -0.061 is probably reasonable, and is largely due to the very low proportion of adults breeding. The colony is known to depend on immigration for its continued existence, so would obviously be decreasing if there were no immigration.

KOBENHAVN. A Danish territorial population (Bacon & Andersen-Harild 1989).

This population has been stable in size for some years, and our calculated value of about 0.057 seems a little high. There will be a slight negative bias in our estimates due to emigrants breeding outside the study area, especially as this population (and other adjacent territorial ones) contributes immigrants to the (otherwise non-sustainable) colonies in the region.

CHESAPEAKE BAY. An introduced population of Mute Swans in the United States which is expanding very rapidly (Reese 1980).

The age structure of the rapidly expanding population changed markedly during the study (Reese 1980). The actual population almost exactly doubled in five years, between 1974-1979. Our estimates seem much too high, suggesting that the survival rates may have been over-estimated in this population. Modified calculations, more closely tailored to the Chesapeake circumstances give balances between 0.11 and 0.25: these refined estimates exactly bracket the observed rate of population increase.

DIFFICULTIES OF ESTIMATING P_1 TO P_4

The factors would be a concise summary of the state of a closed population around equilibrium. If all their four factors could be reliably estimated they should provide an accurate, though less useful, summary of populations that are increasing or

decreasing. In practice, only two of the studies we report here (Hebrides, Chesapeake) are sufficiently closed for population counts to be completely comparable with the estimates of survival. Several are complicated by recent changes in total (study area) population size and all factors have appreciable estimation problems. These estimation problems are exacerbated by likely density dependent relationships and interactions between the factors themselves.

- (i) Clutch-size seems rather consistent and, at least compared with other elements of their demography, its variations seem unimportant in the Mute Swan. Two factors will cause local clutch-size to vary. First, where there are unusually higher proportions of young breeders, as in expanding populations (e.g. Chesapeake), these may have low clutch-size and have rather poor nesting success. Further, in a given study area, the better breeding habitats tend to be occupied at low density and, as the population increases, the poorer sites are filled progressively with a concomitant drop in clutch-size and or nesting success; hence the low density population achieves a higher breeding success.
- (ii) The proportion of hatched cygnets that fledge changes slightly with clutch-size and date of laying (Bloch 1970, Walter et al. 1991, Beekman 1991).
- (iii) Proportions surviving their first winter depend on autumn weights (Perrins & Ogilvie 1981, Andersen-Harild 1981). The social structure of swan flocks in winter (Scott 1978, 1988, Earnst & Bart 1991, Lessells 1975) gives a competitive advantage to pairs, families and older, larger, more dominant birds. In circumstances where winter severity reduces first year survival (which seem frequent for Mute Swans) it is therefore very likely that age-dependent survival will vary with population density, and especially so in the "immature" period (although this remains to be clearly demonstrated).
- (iv) Estimating adult survival rates has problems similar to those for immatures, except that the re-sighting data are generally much more reliable for breeding adults, given their high fidelity to the same territory in successive years. However, "adult" survival is known to vary with breeding status, and in some areas the probability of a breeding pair nesting again in the following years is not high. This may affect estimates of adult survival rates as these are unlikely to be independent of the probability of re-nesting.

We can indicate the nature of the summary and illustrate the formula with typical values taken from Table 3.

$$\text{Change} = [(\text{clutch}/2) * (\% \text{ "adults" breeding}) * (\% \text{ survive to "adult"})] - (\text{breeder mortality})$$

$$\begin{aligned} \text{Typically:} &= [(6.0/2) * 0.3 * 0.2] - [0.15] \\ &= 0.18 - 0.15 \\ &= + 0.03 \\ & (= 0.0 \text{ for stable population}) \end{aligned}$$

We can next expand this to include the egg to fledging stage, to illustrate the relative effects of early survival versus juvenile survival, using two sets of typical (low and high) values from Table 3.

Expanded:

$$= 3.0 * 0.3 * [\text{egg to fledge} * \text{Fledge to adult}] - 0.15$$

or
$$3.0 * 0.3 * [\text{egg to fledge} * S_j^{(Ya-1)}] - 0.15$$

where S_j is juvenile survival, Ya is "adult" age.

The following gives the likely range of the parameters (clutch-size seems fairly consistent)

Low:
$$\begin{aligned} &= 3.0 * 0.3 * [0.25 * 0.5^3] - 0.15 \\ &= 3.0 * 0.3 * [0.25 * 0.125] - 0.15 \\ &= 3.0 * 0.3 * [0.03] - 0.15 \\ &= 0.03 - 0.15 \\ &= - 0.12 \end{aligned}$$

Such a population would halve in 5 to 6 years.

High:
$$\begin{aligned} &= 3.0 * 0.4 * [0.50 * 0.7^3] - 0.15 \\ &= 3.0 * 0.4 * [0.50 * 0.343] - 0.15 \\ &= 3.0 * 0.4 * [0.17] - 0.15 \\ &= 0.21 - 0.15 \\ &= + 0.06 \end{aligned}$$

Such a population would double in 12 years.

Survival from egg to fledging and in the first winter (first winter survivals vary most) is very important; 50% survivals in both these periods, followed by two years "juvenile" survival S_j at 70% ($.5 * .5 * .7 * .7 = 0.12$) would depress population increase rate as much as 90% survivals in these periods followed by five years of delayed maturity with S_j at 70% ($.9 * .9 * .7^5 = 0.14$). Algebraically the equation is sensitive to the "adult" age, Ya ; but if Ya is quite small and S_j is large, the power effect of Ya becomes small. Some of the effects of these variations can be seen in Figure 1.

Figure 1 is only a very approximate guide to part of the story. The starting point of each line (1.0) assumes that brood-size at fledging is 2.0 (1.0 per adult). Further reductions would need to be made if either 1) the brood-size was lower than this, as is the case in the Hebrides and the colonial populations or 2) a proportion of the adults fail to breed. Both Abbotsbury and Chesapeake Bay have high juvenile survival rates, but Abbotsbury has a low number of cygnets per brood (and probably a substantial number of non-breeding adults) and hence is not as out of balance as this figure might suggest, whereas the population at Chesapeake Bay has been increasing very rapidly. In the other population with high juvenile survival rates, the Hebrides, there is both low brood-size at fledging and a late age of first breeding.

All the survival rates given in Table 2 are based on detailed local studies where the estimates of survival might be under-estimates if there was substantial emigration. However, Perrins (1990) calculated the survival rates of young Mute Swans from the British ringing data where emigration should not pose any problems. These calculated annual survival rates for Britain are also shown in Figure 1 and Table 2.

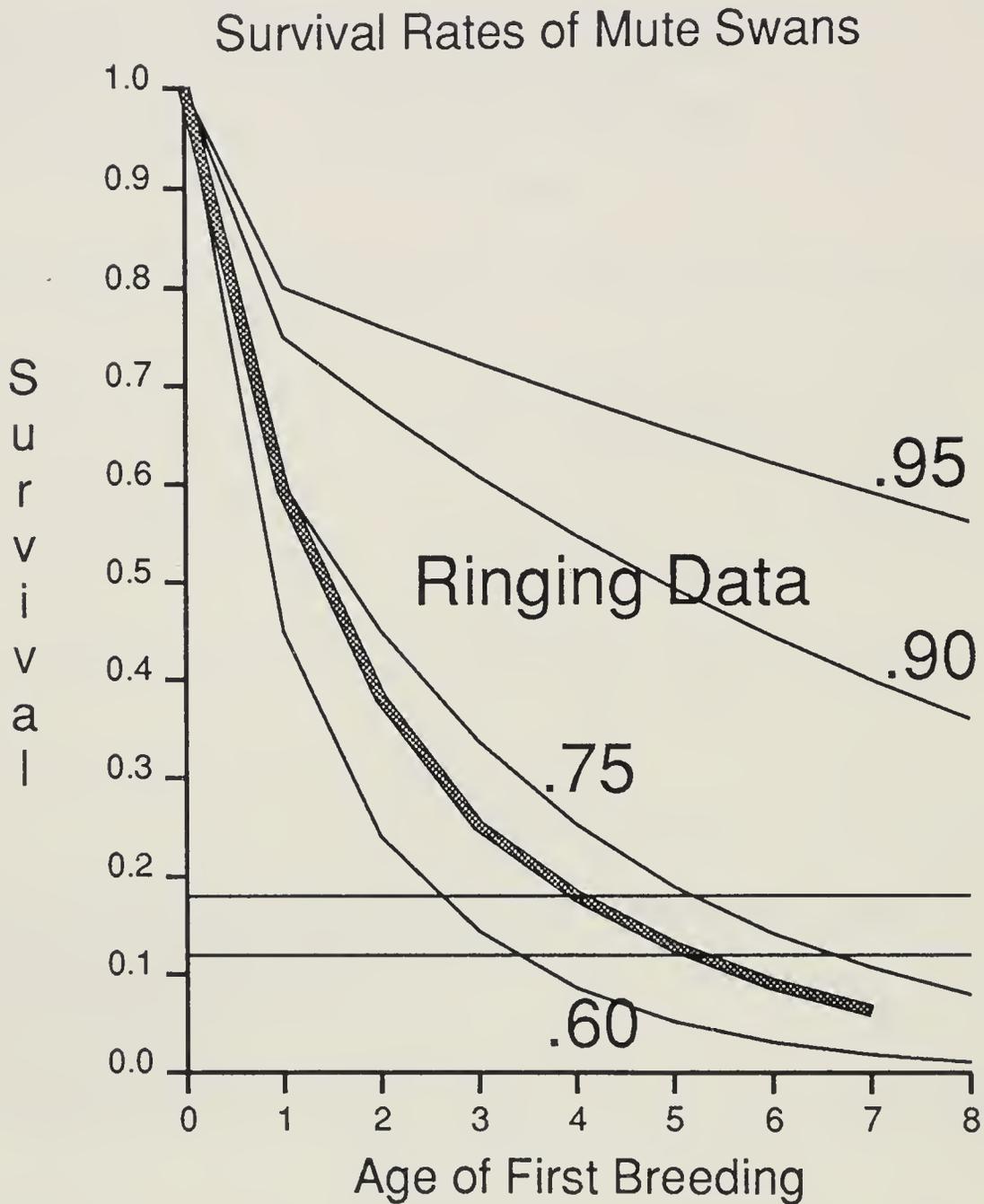


FIGURE 1 – Survival rates of young Mute Swans in relation to age from fledging. The figure shows four possible patterns of survival rate; in each case survival was estimated as 15% lower than that shown for the first years and then constant thereafter (i.e. the top curve assumes 80% survival in the first year and then 95% in each of the following years). The thicker line is calculated from the British ringing data (Perrins 1991). Each curve is for an individual chick, so that the figure omits variation in the proportion of the adults which breed or the mean brood-size of different populations. The horizontal lines show the inverse of the normal range of adult mortality. No population could survive if, at a given age of first breeding, the cygnet survival curve falls below the line for adult survival, unless the starting value was above 1.0 fledged chicks/breeder (or 2.0 in column (e) of Table 1).

DISCUSSION

Demographic patterns in space and time

The demographic patterns of different populations vary to a considerable degree; some idea of this variation can be seen in the tables. It appears possible for

populations to maintain themselves with quite different demographic structures. It must, however, be stressed that the amount of immigration and emigration occurring in some of these populations is not known, and that such movements may be enabling certain populations to appear stable when in fact they would not be so in isolation.

Nevertheless most populations seem to be able to persist with annual adult survival rates of some 85% or even 82% whereas adults at Abbotsbury, Chesapeake and in the Hebrides have annual adult survival rates of nearer to 95%. The degree of difference is more striking if looked at in terms of average longevity; a bird with an annual survival rate of 85% has a median life expectancy of just over six years whereas one with a 95% survival rate has a median life expectancy of 19.5 years, more than three times as long.

Not surprisingly, those populations with the lower adult survival rates have a higher egg-to-adult survival rate than is the case with the populations at Abbotsbury and in the Hebrides where productivity is low. This suggests that there may be an element of density dependent regulation in the populations, with young birds finding it harder to survive and enter the breeding populations where adult survival is high than where it is low.

The curves in Figure 1 show where some of the variations in demographic character of populations had the greatest effect on potential population change. As discussed above, one area where density dependent effects are likely to be manifest is that of age of first breeding (or even the proportion of adults which breed each year after they have once started to breed). Except for the few colonial populations, Mute Swans are fiercely territorial, requiring large, exclusive areas for breeding. As a population increases, there will be great competition for suitable sites until many birds are unable to obtain a site and will be forced to remain longer in one of the non-breeding flocks. In the Oxford area, prior to the decline in the population in the late 1960s, there were large flocks in a number of places along the River Thames and, although there is no good quantitative evidence, there was a strong impression that many birds remained in these flocks until the age of four or older and that, with the decline in the size of the flocks, the age of first breeding also declined. In accord with this, both Minton (1968) and Mathiasson (1973) record birds of eight years and older which were known never to have bred.

The future

Mute Swan populations are increasing rapidly in many parts of Europe (see papers in Sears & Bacon 1991) and are also expanding their range into areas which, at least in the recent past, have been devoid of swans. Almost all such increases seem to stem from increased protection over its range. Much of lowland Britain has been an exception to this upwards trend; here, until recently, there has been a marked decline due largely to lead poisoning (Birkhead & Perrins 1986). Now that the main source of the poisoning, lead fishing weights, has been removed, these populations have responded rapidly and are now increasing. Hence it seems appropriate to consider what the future holds for this species.

In many areas of the UK the increases probably stem mainly from both an increase in nesting success and an improved survival rate of the fledglings. Assuming that this situation continues to hold, there seems to be no reason to suppose that the

populations will not continue to increase rapidly; many other species of waterfowl, including in Britain, the Canada Goose *Branta canadensis*, have been increasing rapidly in recent times and show no signs of slowing down. Nevertheless, as the population increases, the nesting success of the Mute Swan can be expected to decline for the reasons given above.

In Britain therefore, the Mute Swan may increase markedly in the next few decades. Such an increase may, however, be expected to slow down at an earlier stage than the increase of the Canada Goose since the goose will breed at very high densities compared with the highly territorial Mute Swan. Nevertheless, the Mute Swan will increase for some time. Numbers may be expected to increase until there is no longer space for further breeding pairs, at which time the flocks will continue to increase (with a concomitant rise in the age of first breeding). Numbers will level off only when production of the pairs no longer exceeds the mortality in both breeding pairs and non-breeding flocks.

Other factors will affect this picture. The steady developments of the river banks in many areas will both reduce nesting sites and feeding areas. The complaints by farmers of agricultural damage will increase as the birds are concentrated on fewer suitable grazing areas. As populations increase, non-breeding birds will have to fly further and explore greater areas in their search for a breeding territory; this will increase their chances of being killed by flying into over-head cables.

In some parts of Britain at least, such large - and to the human population unacceptable - levels of swan populations have occurred in the past. In the late 1920s and 1930s, the populations on the River Thames reached levels which were thought to be unacceptable. For many years efforts were made to reduce the population by lowering the nesting success. This was done mainly by reducing all clutches along the main part of the river to two eggs; in many years some 150 eggs were removed. The success of this operation seemed to be negligible. Whether this was due to a high proportion of nests being missed, to immigration from outside the river or to improved survival of the remaining cygnets is unknown. Whatever the explanation, the numbers continued to increase until, in the late 1920s and the 1930s, large numbers of fully-grown birds were culled. The public relations problems of such an action are unlikely to be as acceptable today as they were then. Nevertheless, such large populations wintering on lowland rivers with poor food supply in late winter are likely to starve unless fed by the public. If they are fed, then they are likely to survive and increase still further!

In almost all areas, the Mute Swan now lives in a very man-made habitat and hence is living in areas which are largely un-natural. It is of interest to speculate what the natural demographic pattern of this species would have been. In many areas such as the inland rivers and lakes of western Europe, the species could have doubtless survived well during the late summer period. However, it is doubtful whether it could have survived in these areas in the late winter when the aquatic vegetation died down. The river margins would have been well-covered with reeds or woodland so that there would have been no opportunity to come ashore and graze as many Mute Swans do on farmland today. Almost certainly therefore they would have had to have been migrants - as are many of the birds in northern and eastern Europe today. Many of the birds need not have undertaken long-distance migrations, but they would have had

to go to coastal marshes or estuaries for food. Further, nest predation would presumably have been higher from larger populations of wild animals such as wolf, boar and bear. Survival of cygnets in the early period after hatching may have been poor owing to poor food supply at this time. Hence we suggest that the demography of the birds would have been more like those on the Hebrides, with lower productivity, but higher adult survival rates than those which are found over most of Western Europe today.

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DETERMINANTS OF ABUNDANCE IN AN ISLAND SONG SPARROW POPULATION

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ABSTRACT. We studied the dynamics of a resident and permanently territorial population of Song Sparrows *Melospiza melodia* on Mandarte Island, B.C., Canada, from 1974 to 1990. Breeding populations on the 6 ha island fluctuated from 4 to 72 females. This instability was mainly a function of two population crashes in winter. The more severe of these declines occurred during unusually severe weather in February 1989. The cause of the other crash was unknown. Between episodes of high mortality, the population behaved much more predictably, and was regulated jointly by low reproductive success, and by high juvenile mortality. Annual reproductive success was regulated by several proximate mechanisms, including the rate of nest failure and the abundance of food. Regulation in winter was related to both age and sex. Adult survival in winter was unrelated to population density, but juveniles, particularly females, survived poorly at high densities, apparently because of competition for breeding territories. There were more nonbreeding male "floaters" in spring at high densities. There were very few non-breeding females. Breeding immigrants to the population were infrequent, but many more birds visited the island without settling. Song Sparrow populations on neighbouring islands differed in their dynamics.

INTRODUCTION

Long-term studies are necessary to answer many questions about the population biology of long-lived organisms, and certain questions about the population biology of shorter-lived ones (Franklin 1989, Likens 1989, Taylor 1989).

While some key questions about populations of short-lived birds can be answered without long-term study (e.g. Krebs 1971, Dhondt 1979, Reyer 1990), questions about the stability of populations (Pimm & Redfearn 1988) require data on rare but ecologically-significant events. These data can only be obtained in long-term studies. Most bird populations are characterised by high short-term stability in numbers of breeders (examples in Perrins & Birkhead 1983). However, in several long-term studies of bird populations (Kikkawa 1977, Gibbs & Grant 1987, Koenig & Mumme 1987, Wolfenden & Fitzpatrick 1990, Curry & Grant 1989), periods of stability have been followed by episodes of high adult and/or juvenile mortality. Small insectivorous birds breeding at high latitudes sometimes exhibit less stable dynamics (Graber & Graber 1979, Perrins & Birkhead 1983 (Fig. 7.11), Beier & Rudemo 1985), as do some subtropical species (e.g. Kikkawa 1977). In this paper, we discuss the determination of abundance in a resident insular population of a short-lived bird, the Song Sparrow *Melospiza melodia* (Emberizidae), and the mechanisms responsible for changes in numbers. This population exhibits an unstable and very simple demography. Immigration is virtually absent, and reproductive and survival rates vary through time under the influence of local events.

Previous reports of the dynamics of this population have stressed the regulation of reproduction by food limitation (Arcese & Smith 1988, Hochachka et al. 1989) and the catastrophic effects of bad weather on winter survival (Tompa 1964, 1971, C.M. Rogers et al. unpublished). In this article, we summarise past findings and report new data on annual variation in reproductive and immigration rates, and on the recovery of the population from two severe population crashes. We also comment on when insights were gained during the 20 years that the population has been studied.

METHODS

Mandarte Island is a small (6 ha) and isolated shrubcovered rock in the Gulf Island archipelago, between southern Vancouver Island and the Continental mainland of North America. Mandarte lies on the western edge of the 5 km wide Haro Strait, about 1.3 km from the nearest land, Halibut Island, which also supports a population of Song Sparrows.

Study of the population was begun by Frank Tompa in 1959. Tompa (1964) gives a detailed description of the study site and its vegetation. He marked all adult birds individually, mapped their territories intensively, and followed the survival of individuals throughout the year.

We followed Tompa's monitoring methods, but also studied reproductive success of individuals in detail (Nol & Smith 1987, Smith 1988, Arcese & Smith 1988, Hochachka et al. 1989, Hochachka 1990). Our methods have been described in detail by Smith (1981), Arcese (1989b) and Arcese et al. (unpublished). In brief, we follow the reproduction of all individuals intensively and mark all locally-born individuals with unique combinations of coloured leg bands. Immigrants are trapped with mist nets, and cohorts of independent young are trapped and their morphological characters measured each autumn. Censuses of breeding birds are made approximately weekly during the breeding season, and about monthly during the non-breeding season.

There was an 11-year gap in data collection from the end of Tompa's study in 1963 to the onset of our work in 1974; there was also a short break in our study in 1979-80. During this winter, no censuses were conducted, and only a spring census and some banding were done early in 1980. Intensive monitoring resumed in August 1980. Since 1988, small populations of Song Sparrows on nine other islands near Mandarte have been monitored by similar methods.

Song Sparrows on Mandarte were parasitized by Brown-headed Cowbirds in most years for 1975 to 1990. Cowbirds are recent immigrants to the Pacific Northwest, and were absent during Tompa's study from 1959-1963. Cowbird eggs and nestlings were noted when they appeared in the nests of Song Sparrows, and their fates were followed.

RESULTS

Population trends and overall stability

The breeding population in spring (April 30) fluctuated strongly (up to 10-fold) around a long-term median of 46.5 breeding females (Figure 1). Spring populations were high

in 1963, at the end of Tompa's 4-year study, in 1979, and in 1985. Two major periods of catastrophic mortality occurred when numbers fell sharply to very low levels in 1980 and in 1989.

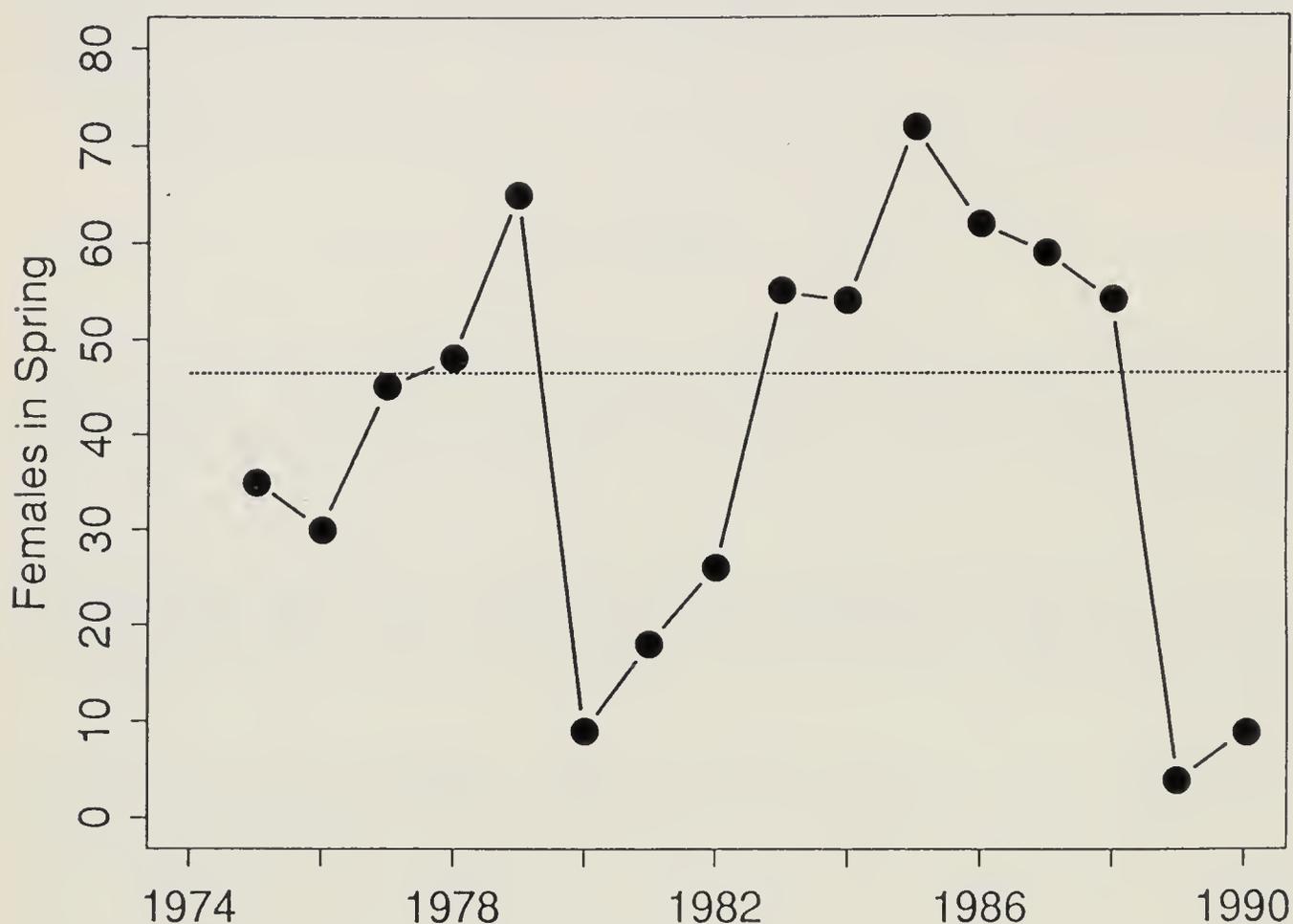


FIGURE 1 – Numbers of breeding female Song Sparrows on Mandarte Island in spring from 1975-1990. The dotted line indicates the median density (46.5 females).

In years without population crashes, populations did not change strongly from year to year (Figure 1), but changed predictably in relation to population density in the previous year (Arcese et al. unpublished). On average, numbers increased from below, and remained stable above, the median density. Thus, the population exhibited moderately stable year-to-year changes in numbers, but unstable long-term dynamics, because of infrequent but severe periods of catastrophic mortality.

Annual variation in reproductive rates

Reproductive rates covaried closely and negatively with population density in 13 of the 15 years for which data were available (Figure 2). The remaining 2 years, 1975 and 1990, particularly 1990, were conspicuous outliers from this relationship. Reproductive success was very poor in 1975, the first year of our study, despite a fairly low population density (36 breeding females). This spring was cold, with a late onset to breeding, and parasitism by Brown-headed Cowbirds was frequent. In 1990, per-capita reproductive success was unusually high. Indeed, the *mean* value for the nine breeding females (one of which died after raising one brood) was close to the previous *maximum* for any individual female in the 15 previous years for which data were available. The unusually high average breeding success in 1990 was probably caused by the low breeding density, warm spring weather, and by a near absence of brood parasitism by cowbirds. The principal cause of low annual reproductive success

across years was a high rate of nest failure, which in turn was positively related to the the rate of cowbird parasitism within the Mandarte population (Arcese et al., unpublished). The frequency of brood parasitism by cowbirds was also closely correlated with differences in reproductive success between Mandarte and populations on the continental mainland near Vancouver, where breeding success was very low (unpublished data).

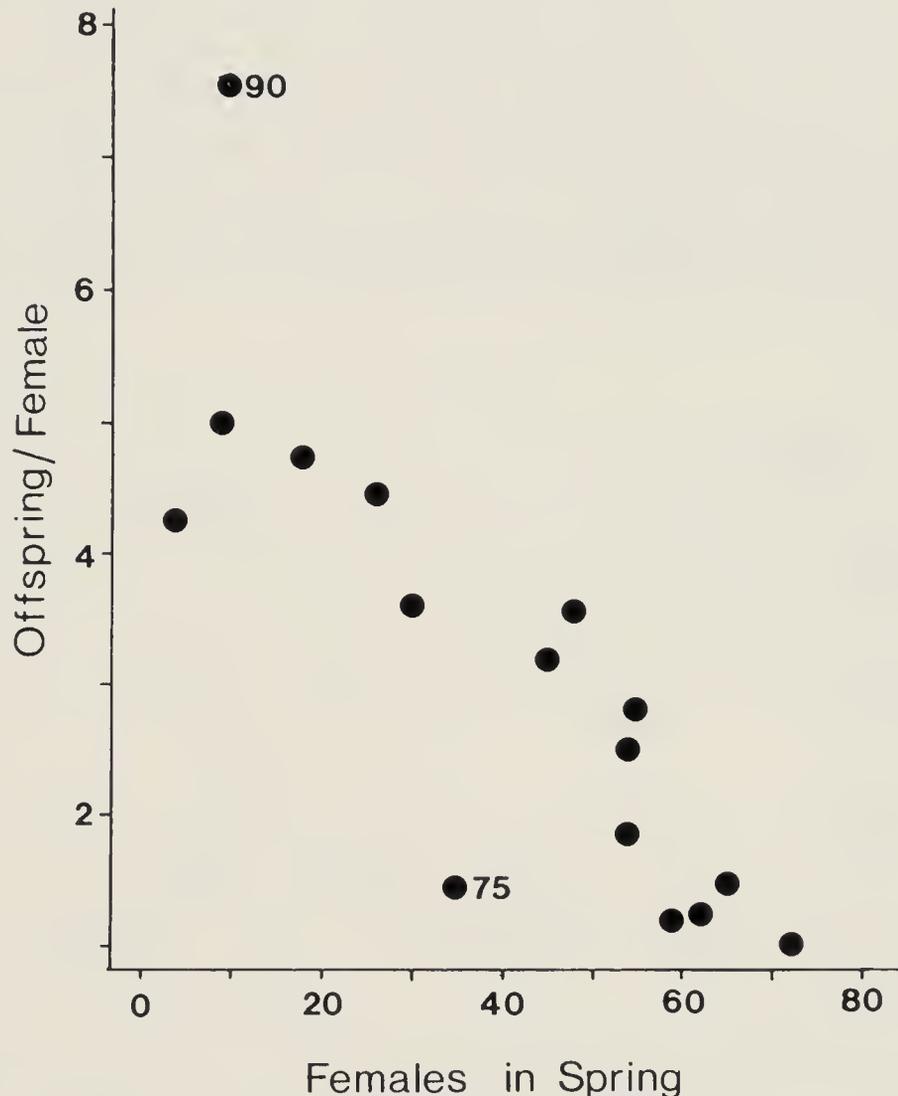


FIGURE 2 – Production of independent offspring in relation to breeding density of Song Sparrows on Mandarte Island. Note the presence of two strong outlying data points in 1975 and 1990.

Long-term variation in winter survival

Survival varied strongly with age class and season in winter, but varied little during the breeding season. The survival of adults was density-independent and relatively high for a small temperate passerine ($x = 0.69 \pm 0.03$) for 12 winters without population crashes, but dipped to only 0.14 and 0.07 in the winters of 1979-1980 and 1988-1989 respectively. Survival of juveniles to breeding age varied considerably from year to year (0.29-0.72) in non-crash winters, and was very low (0.14 and 0.03) in the two winters when population crashes occurred. Survival to breeding age was strongly and negatively related to adult density in the autumn in birds of both sex, but in most years there were some non-breeding floater males, particularly at higher densities. Nearly all surviving females bred, even at high densities, although the onset of breeding was delayed among late-settling birds. Females formed breeding trios with already-mated males in years when there were more surviving breeders than territorial males (Arcese 1989a).

Annual variation in immigration rates

Only a few avian populations (e.g. McCleery & Perrins 1985) have been studied in sufficient detail to assess the role of immigration versus local recruitment in recoveries from periods of low numbers.

The number of immigrants that bred each year on Mandarte was always low (mean 1.2, $n=14$ years, range 0-3), and did not peak in the years after the two crashes. Most immigrants (13 of 16) were females. In 1980, 24 of the 25 breeding birds that survived the 85% mortality of the 1979-80 winter, were hatched locally. In 1989, one of the 12 breeders was a previously-banded immigrant from a site 7 km distant. The low number of immigrants did not occur because Mandarte is too distant from other land for potential immigrants to reach it. Each year, we banded new birds on the island in the late summer, autumn, and winter. Immigration rates were particularly high in 1987-88 and 1989-90, and did not vary closely with local density over all years ($r = 0.23$, $n = 13$, Figure 3).

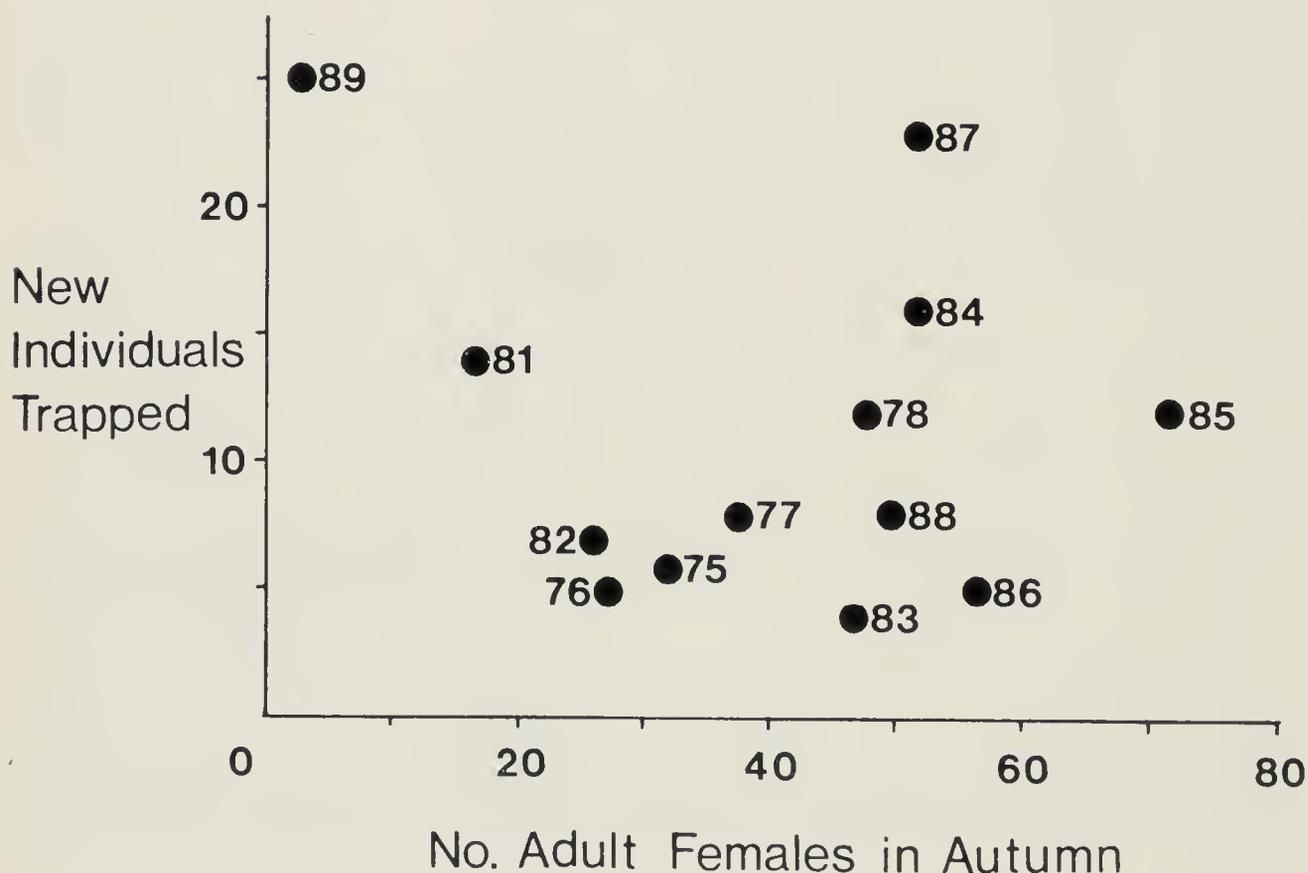


FIGURE 3 – Annual numbers of unbanded Song Sparrows trapped on Mandarte Island, B.C. in relation to the number of adult females alive on August 30 each year. All unbanded birds were assumed to be immigrants, as all locally-hatched birds were banded as nestlings, save in 1980. There was also no trapping in the autumn of 1979.

Origins of new recruits after population crashes

As recruitment rates of immigrants to the breeding population were very low, and apparently independent of population density, recovery from the two periods of low numbers was almost entirely through successful breeding by the few local survivors from the population crashes. Following the crash in 1988-89, only one immigrant bred, and this bird disappeared after a single nesting attempt. Average reproductive success of three locally-hatched females was high in 1989, and even higher in 1990, when nine females bred. We are less certain of the roles of local recruitment and immigration after the crash of 1979-80. As most young that hatched in 1980 were not

banded as nestlings, we could not distinguish local recruits from immigrants. No immigrants bred in 1982, when female numbers were still low (Figure 1). The low numbers of immigrants during periods of low density are puzzling, since other evidence (Smith et al. in press) suggests that territoriality regulates recruitment of locally-hatched juveniles in the non-breeding season.

DISCUSSION

As some of our results have recently been discussed elsewhere (Arcese & Smith 1988, Arcese 1989b, Smith et al. in press, C.M. Rogers et al. unpublished, Arcese et al. unpublished), we focus on two issues here: a) the rate at which new information accrues about episodic events during long-term studies; and b) the influence of local dynamics and dispersal in the determination of numbers in insular populations.

Episodic influences on population dynamics.

After the first four years of our study, and the previous four years of study by Tompa (1964, 1971), the population of Song Sparrows on Mandarte seemed to be fairly stable. Tompa, however, described an episode of high adult mortality in a spring snow-storm in 1962 that led to an eventual increase in the number of breeders (Tompa 1971). The first major population crash occurred in the 5th year of our study, in the winter of 1979-80, and was followed 9 years later by a second similar event in 1989. The second sudden crash was probably due to an episode of very cold weather and high winds (C.M. Rogers et al. unpublished).

Thus, three periods of catastrophic mortality were detected during 20 years of study between 1959 and 1990. The least severe episode had only a moderate, and immediate, effect on the number of breeders, but the other two episodes dominated the long-term dynamics of the population. Following each severe crash, the population grew rapidly, free from the effects of high density. As in the Great Tit (McCleery & Perrins 1985, Clobert et al. 1988), the number of new birds arriving each winter varied considerably from year to year. In the Song Sparrow, however, few immigrants bred, while many immigrant Great Tits did so in some years. One possible difference between the two studies is that some unmarked Song Sparrows arriving on Mandarte may have been migrants on passage or winter visitors, and not prospective immigrants. Three recaptured birds seemed to be migrants in transit, from their dates of capture and recapture in subsequent autumns, and the absence of other sightings of them. We could not, however, estimate the proportion of migrants among newly-trapped birds.

The two periods of catastrophic mortality not only dominated changes in numbers, but they also facilitated the detection of regulating mechanisms. The strong density dependence in seasonal production of young (Figure 2), and in juvenile survival, could only have been detected because of the greatly enhanced survival and reproductive rates seen at well below the median population density. In addition to the two episodes of poor survival, we noted an episode of exceptionally high reproductive success in 1990. Although this was an extreme event, we do not yet know if it will have a long-term impact on numbers.

Thus, episodic but rare population events had a major impact on our understanding of the dynamics of the Mandarte Island population of Song Sparrows. Such knowledge would have been impossible to obtain without long-term study. Because of the rarity of such episodic events, and their local causes, it is difficult to generalize on either their frequency or severity, in this or other studies (Gibbs & Grant 1987, Koenig & Mumme 1987, Curry & Grant 1989). A better understanding may, however, be possible in populations like the Silvereyes *Zosterops lateralis* of Heron Island (Kikkawa 1977), where cyclonic summer storms cause more frequent episodes of high mortality.

Metapopulation dynamics and long-term population studies

In most long-term population studies, the samples of individuals studied are only part of a larger set of conspecifics living in contiguous habitats nearby. Song Sparrows on Mandarte Island are part of a metapopulation inhabiting coastal islands and fragmented habitats on the large Vancouver Island nearby. Populations inhabiting highly modified habitats, like Great Tits in Sweden (Dhondt 1979) or England (Clobert et al. 1988), are likewise parts of a metapopulation in woods separated by agricultural land. In both these species, individuals move regularly among habitat patches or islands. In the Great Tit, such movements play a key role in the stability of the population (McCleery & Perrins 1985). In the Song Sparrow, movements are common among very close islands (unpublished data), but rare for the isolated Mandarte Island, which causes it to have locally-driven dynamics.

If catastrophic mortality dominates population dynamics, as it seems to in this and some other studies (Kikkawa 1977, Perrins & Birkhead 1983, Figure 7.11, Gibbs & Grant 1987), it is of interest to know the spatial scale at which high mortality occurs. Droughts, like those noted by Gibbs & Grant, are likely to show a high degree of spatial correlation in their effects on a metapopulation, while storms (Kikkawa 1977, this study) might have much more local effects. We found only 5% of adult Song Sparrows on Mandarte Island survived the winter of 1988-89, while 61% of adults on nearby islands within 8 km did so. Such a low degree of spatial correlation can have a strong stabilising effect on the whole metapopulation (Harrison & Quinn 1989). In most long-term studies, including this one, little has been known about the performance of neighbouring populations, or about the source/sink relationships (Pulliam 1988) between the study population and others. Gathering such information at a broad spatial scale is a formidable challenge facing future long-term population studies.

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LIFETIME PRODUCTION IN THE RED-BILLED GULL

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ABSTRACT. Data from a 26 year study of a population of Red-billed Gulls at Kaikoura, New Zealand, have been analysed to examine lifetime breeding success. The population has an excess of females resulting from a higher survival rate of females than males. Females have a longer deferment of maturity and breed less frequently than males. Approximately 77% of the fledglings died before they bred and of those which bred only 18% produced 50% of the fledged young for the next generation. Frequency of breeding, longevity and laying date were the most important sources of variation in lifetime fledging success.

Keywords: Red-billed Gull, *Larus novaehollandiae scopulinus*, age, breeding, survival, retention of mate, lifetime reproductive rates, female-female pairings.

INTRODUCTION

Major advances in avian population and evolutionary biology have been made over the last six years from long-term studies that have been able to calculate lifetime reproductive success (Woolfenden & Fitzpatrick 1984, Coulson & Thomas 1985, Newton 1985, Hotker 1988), and studies reported in recent books edited by Clutton-Brock (1988) and Newton (1989a). The value of lifetime productivity combines two key measures of individual performance, namely survival and success in breeding, into a single overall measure of performance (Newton 1989b). Hence it is one of the best available measures of biological fitness.

In a previous paper (Mills 1989) the lifetime breeding success of individual Red-billed Gulls *Larus novaehollandiae scopulinus* was calculated over a 12 year period (1975-1986). The present study extends that analysis by incorporating larger samples resulting from additional field study. As background to appraising the differences in lifetime performance of males and females this paper also describes the demographic characteristics of the population.

The population at Kaikoura Peninsula, the third largest breeding colony in New Zealand, has been studied annually since 1964. The Red-billed Gull is a monogamous coastal breeder and during the breeding season feeds predominantly in the inshore region on planktonic euphausiids. Breeding occurs in large colonies at high densities, and clutches of one to three eggs are laid. The bird is highly philopatric and searches at nearby and distant colonies have revealed that less than 1% of Kaikoura birds emigrate (Mills 1973).

METHODS

Nestlings were banded for 32 consecutive years (1958-89) and in total over 80,000 have been marked. In addition, 4408 adults and 1078 chicks have been individually colour-banded for detailed study.

Each year nests of colour-banded gulls were marked, the identity of both partners and the fate of the eggs or brood were determined, and the nestlings banded. An individual was considered to have bred when it or its partner laid an egg and to have died if it was not sighted for two years. The measure of lifetime productivity was the number of chicks that an individual fledged.

The present analysis covers the period from 1967-68 to 1988-89. Over this 22-year period fledging success was monitored in all but four seasons (1969-70, 1972-73, 1973-74 and 1974-75). Because of the missing data, lifetime analyses have been confined to birds which commenced breeding and completed their lifespans between 1975-76 and 1988-89.

RESULTS

Demographic characteristics of the Kaikoura population

NON-BREEDING AND BREEDING COMPONENT. The Red-billed Gull population at Kaikoura has a large non-breeding component. On average, 6000 pairs nest annually and in 1983-84 when 5888 pairs nested the total adult population was estimated by capture-recapture analysis to be $23,192 \pm \text{SE } 1674$ individuals (Mills 1989). Hence non-breeders made up approximately half the population. Most of the non-breeders were females. Annually approximately only 51% of the available adult females in the population breed in contrast to 86% of the males (Mills 1989).

ADULT SURVIVORSHIP. An unequal sex ratio resulted from females having a higher annual survival rate ($89.4\% \pm \text{SE } 2.6$) than males ($84.4\% \pm \text{SE } 2.9$). For both sexes survivorship decreased with age but the differential survivorship was maintained in all age groups.

The excess of females causes differences in the individual performance of the sexes. Females have a longer deferment of maturity than males, only 63% commencing breeding by the fourth year compared to 96% of the males by that age (Mills 1989). It also impacts on the frequency of breeding with some females having long periods of non-breeding, in some cases up to 16 years. The shortage of males results in some females forming female-female pairings and these associations make up approximately 6% of the pair-bonds.

Proportion of fledged chicks that survive to breed

For 6310 nesting attempts monitored between 1967 and 1981, 33% of the 11,821 eggs laid produced fledged young but only 7% gave rise to young which survived to breed. Overall 77% of the fledged young died before breeding. In different years the number that died as immatures varied from 69 to 94%.

Lifetime reproductive rates

For birds which commenced breeding for the first time between 1975 and 1988 I was able to calculate the lifetime reproductive rate for 131 females and 177 males. The age distribution of these individuals covers a wide range of lifespans. The maximum age for which lifetime data was available was 16 years for both sexes but some individuals can live to 29 years of age and so the measures of lifetime reproduction presented will be under-estimated.

There was considerable variation in the number of fledglings produced, ranging from 0 to 10 for males and 0 to 12 for females (Figure 1). The mean number was 2.1 for males and 1.7 for females.

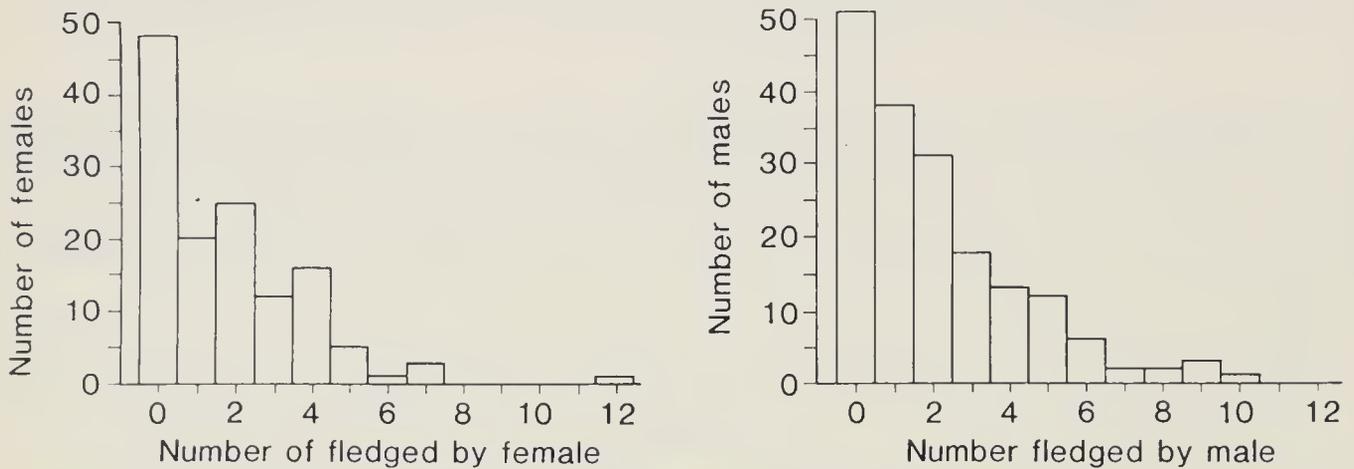


FIGURE 1 – Lifetime fledging success of 131 females and 177 males.

Of those which bred, 37% of females and 29% of males produced no fledglings during their lives. Overall 18% of the females and males which bred produced 50% of all fledglings.

Factors affecting lifetime reproductive rate

LIFESPAN AND FREQUENCY OF BREEDING. The number of years an individual lived accounted for 23% of the variance in lifetime production of fledglings by females and 50% for males.

Eight females and two males survived for nine or more years but failed to fledge a chick (Figure 2). Over their lifespan females bred on average 2.1 (SD 1.6) and males 2.7 (SD 2.7) times. The number of seasons a bird bred accounted for the greatest amount of variance in lifetime fledging success, 41% for females and 60% for males.

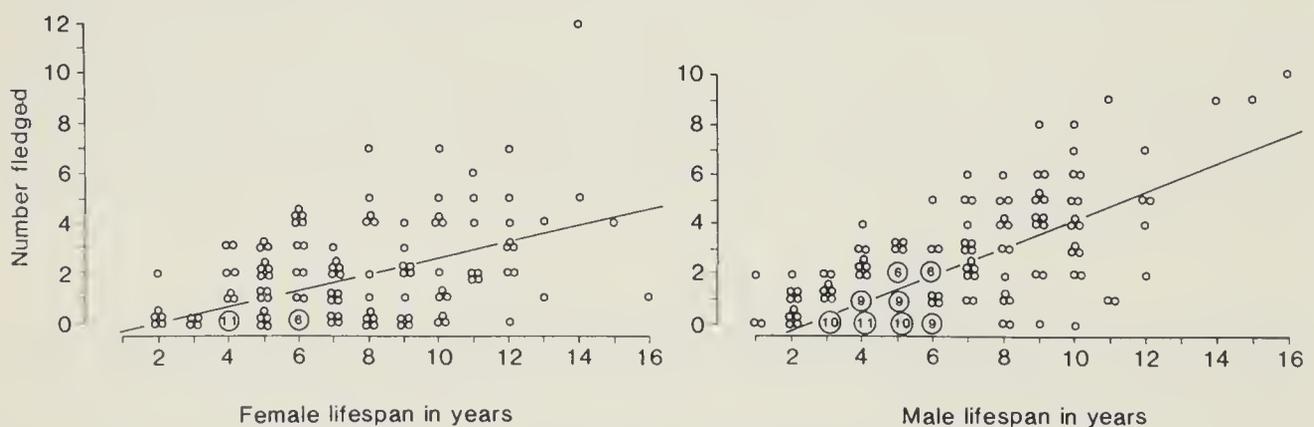


FIGURE 2 – Lifetime fledging success in relation to lifespan.

PAIR-BOND RETENTION AND BODY WEIGHT. An average of 39% of the females and 30% of the males had only one breeding partner during their lives. In contrast for those that changed mates the maximum number of different mates a bird had in its lifetime was seven for both males and females. The effect of pair-bond stability on lifetime production was assessed on individuals that had bred for five or more years but it contributed little (0.7-1.0%) to lifetime fledgling production.

Similarly body weight contributed only 2% of the variation for females and less than 1% for males.

TIMING OF LAYING. Egg laying can extend over four months but in general the earliest breeders are the most productive (Mills 1973). The mean lifetime laying date of the first clutch of the season contributed 22% of the variability of fledgling production for females and 12% for males.

FEMALE-FEMALE PAIRINGS AND LIFETIME PRODUCTION. The surplus of females of breeding age in the population leads to the formation of female-female pairings which make up approximately 6% of the pair-bonds. Of the 131 females which had bred and completed their lifespans, 21% had been paired to another female at least once during their reproductive careers. Overall 10% of the females bred exclusively in female-female pairings and another 11% were involved in male-female and female-female pairings during their reproductive lives.

As a result of males seeking extra-pair copulations, approximately a third of the eggs laid in female-female pairings hatch.

Females involved in female-female pairings had a lower lifetime reproductive rate than those which bred only in male-female pairings (Table 1). Females which bred exclusively in same sex pairings produced less than half as many chicks in their lifetimes as those which bred only in heterosexual pairings. Females which were bisexual during their life produced 14% fewer chicks than females in exclusively male-female pairings (Table 1).

TABLE 1 – Lifetime fledging success of females in differing breeding relationships.

Pair-bond status	No. females	Mean no. fledged in lifetime	No fledged/ pair/season bred
Exclusively female/female	13	0.85	0.39
Bisexual females	14	1.64	0.36
Exclusively male/female	104	1.91	0.64

DISCUSSION

These analyses show that the majority of individuals died before they bred and of those which did breed relatively few individuals maintained the population from one generation to the next. This has also been found in other species for which lifetime production has been calculated (see Newton 1989c for review). After fledging an average of 77% of Red-billed Gulls died before breeding. Assuming post-fledging survival is the same for both sexes a total of 86% of the fledged females and 84% of the fledged males were unproductive. For other species, the proportion of non-contributing individuals ranged from 62-87% of all fledglings (Newton 1989c).

Of the Red-billed Gulls which attempted to breed, 18% of females and males produced 50% of the fledged young for the next generation. Thus only 3% of fledgling females and males from one generation produced 50% of the fledged young for the next generation. In other species the proportion has been found to range from 3-9% (Newton 1989c).

In terms of egg production, 93% of Red-billed Gull eggs failed to give rise to young which survived to breed.

The total number of fledglings produced by an individual varied considerably with most individuals producing small numbers of young and comparatively few producing many fledglings. Females had greater variability in lifetime production than males (Mills 1989) because females were recruited into the breeding population at a later age and bred less frequently. The number of seasons a bird bred in its lifetime accounted for more variability in lifetime production of fledglings than lifespan. Another factor which contributed to the higher variability of fledgling success of females was the formation of female-female pairings. Female lifetime production was less in individuals that formed female-female pairings. Pair-bond retention did not contribute significantly to lifetime fledging success and the same was found in the Kittiwake (Coulson 1988).

Extra-pair copulations means that some males will be fathering additional offspring at little cost to themselves. Further research needs to identify the success of this mixed reproductive strategy and the characteristics of the birds involved. Its advantages are not only confined to males. Females also increase their chance of raising young by forming female-female pairings instead of remaining unpaired. In many of these pairings both females lay eggs. The intriguing aspect is why are there only about 6% female-female pair-bonds when 49% of the females fail to breed each year.

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LIFETIME REPRODUCTIVE SUCCESS OF MALE TENGMALM'S OWLS

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ABSTRACT. I examined the lifetime reproductive success (LRS) of male Tengmalm's Owls in western Finland where vole abundance fluctuates cyclically among years. Males were site-tenacious after their first breeding attempt. The productivity of 141 males, all of which started to breed during 1979-87, was studied up to 1990. They spent between 1 and 7 years (mean 1.5 yr) as breeders and raised from 0 to 26 fledglings (mean 5.4) during their lifetime. Offspring survival from egg to fledgling stage was the most important component of LRS, followed by the lifespan and clutch size. 21% of males reared 50% of all fledglings produced by the population. The lifetime number of fledglings produced by males was highly significantly correlated with their lifetime contribution of known recruits to the breeding population. The age of first breeding did not affect LRS, but polygynous males produced twice as many fledglings as monogynous ones. Among environmental factors, vole supply was the most important determinant of LRS: males entering the breeding population in the low and increase phases of the vole cycle gained larger LRS than males recruiting in the peak and decrease phases. As the breeding lifespan of polygynous males was longer than that of monogynous ones and as there was no negative relationship between the brood size and the duration of breeding life, no evidence of reproductive costs could be obtained. Superior males may easily compensate for the large parental investment by increasing their food intake without risking their future survival.

INTRODUCTION

Studies on lifetime reproductive success (LRS) have become very popular, for the following reasons – see Clutton-Brock (1988) and Newton (1989) for reviews. First, LRS is a better approximation of fitness than other known measures, if fitness is defined as the contribution of an individual's genotype to subsequent generations proportional to that of other individuals in the same population (see e.g. Endler 1986). Second, LRS studies may better help to understand the conflict between reproduction and survival, known as the cost of reproduction (e.g. Williams 1966, Bell & Koufopanou 1986). Third, longitudinal studies provide a better estimate of between-individual variation in breeding success than do cross-sectional ones based on data mostly collected over short periods and from individuals of unknown histories (Newton 1989).

Birds of prey are unique in the sense that males invest substantially more in offspring than do females (see e.g. Wijnandts 1984, Masman et al. 1988). The female incubates the eggs and broods the young, whereas the male provides for the family from prior to the egg-laying to the late nestling stage (e.g. Newton 1979, Korpimaki 1981).

The LRS of females has been studied in five predatory bird species, the Sparrowhawk *Accipiter nisus* (Newton 1985, 1989), the Tawny Owl *Strix aluco* (Wallin 1988), the Osprey *Pandion haliaetus* (Postupalsky 1989), the Screech Owl *Otus asio* (Gehlbach 1989) and the Ural Owl *Strix uralensis* (Saurola 1989). However, data on the LRS of male birds of prey are scarce, because males are much more difficult to trap than are females.

Tengmalm's Owl *Aegolius funereus* is the most numerous predatory bird in Fennoscandian coniferous forests (Merikallio 1958, Ulfstrand & Hogstedt 1976). The owls feed mainly on *Microtus* and *Clethrionomys* voles (e.g. Sulkava & Sulkava 1971, Korpimaki 1981, 1986a, 1988a). Fennoscandian voles show 3-4-year population cycles with the most pronounced and regular fluctuations in the north (e.g. Kalela 1962, Hansson & Henttonen 1985). Tengmalm's Owls originally bred in natural cavities, but because these cavities are in short supply in forests of commercial use, they readily accept nest-boxes, which considerably facilitates population studies. Here I present LRS data from 141 individually marked male Tengmalm's Owls, and I discuss factors that may affect their LRS.

MATERIAL AND METHODS

Study area and population

This paper is based on the ongoing study in the Kauhava region (ca. 63°N, 23°E), western Finland. The study area covered 1300 km² and contained from 355 (1979) to 530 (1988-90) nest-boxes and known natural cavities suitable for Tengmalm's Owls. Details on the study area, and the methods used for finding nests and for determining laying dates, clutch sizes and brood sizes have been described in earlier papers (Korpimaki 1981, 1987a, 1988a,b,c).

I ranked territory quality by grading a total of 133 territories according to the number of times breeding was attempted between 1977 and 1986: from 0 (no breeding attempts) to 5 (breeding attempts in 5-9 years) (Korpimaki 1988b). Based on the additional data collected during 1987-89, I was able to grade 28 more territories.

I trapped (ringed or retrapped) females at 560 nests (in 1976-90) and males at 438 nests (in 1979-90) early in the nestling period. Owls were weighed to the nearest gram and their wing and tail lengths were measured to the nearest mm. From 1981 onwards, owls were aged based on the moult pattern of primary feathers (Glutz von Blotzheim & Bauer 1980, Lagerstrom & Korpimaki 1988). Three age classes were differentiated: 1-year, 2-year and older owls.

Spring and autumn abundances of small mammals in the four main habitat types were assessed annually by snap-trapping in May and in September. Trap nights totalled 21,564 in the western part of the study area during 1977-89 and 29,860 in the central part during 1973-89 (see Korpimaki 1981, 1986b, Korpimaki & Norrdahl 1989 for further details).

Data on lifetime productivity

Ringed and retrapping data on breeding Tengmalm's Owls revealed that females disperse up to at least 500 km between successive reproductive seasons (Korpimaki et al. 1987), whereas males move only up to 5 km between successive seasons (Korpimaki 1987b and unpubl.). The site-tenacity of adult males allows determination of their LRS, but the mobility of adult females does not.

All males doing their reproductive debut during 1979-87 in the study area were included in the analyses of LRS, provided that there was sufficient information on their later breeding histories. However, the males whose brood sizes were manipulated

during 1985-86 (see Korpimaki 1987a, 1988c) were excluded. LRS was calculated under the assumption that the male trapped at a nest was the father of all the nestlings. This may not be true for all the nests, as two males were trapped at one nest in 1989, which may indicate multiple paternity. These two males were not, in any case, included in the analyses of LRS, as they entered the population in 1989. Males that were not retrapped for two or more years (including at least one good vole year) were counted as dead, although they may possibly have moved from the study area. But this proportion was small, as there are no movements > 5 km inside the study area and no ringed males were recovered outside the area (Korpimaki 1987b, unpubl.). As males readily enter traps only during the early nestling period, the males associated with nesting attempts that failed early in the season remained unknown. This underestimates the number of breeding attempts, but does not affect the lifetime productivity.

Only three (out of 82) of the males entering the breeding population during 1985-87 were still alive in 1990, but in earlier years some owls bred for up to seven years. Thus, the breeding lifespans of males included in the analyses were not biased towards short-lived individuals. Some males occupying territories near the limit of the study area may sometimes have bred outside the area, which underestimates their LRS.

RESULTS

Variation in lifetime productivity

LRS is the number of breeding attempts multiplied by the mean brood size. The number of breedings is dependent on the age of first breeding and the duration of breeding life (which together constitute the lifespan), as well as on the number of females per breeding season. Some 10-20% of males are polygynous in good vole years (Korpimaki 1989, 1990). The mean brood size is in turn affected by the mean clutch size of all the partners of males, and by breeding success (measured by the percentage of eggs that produce fledglings).

TABLE 1 – Morphological and breeding characteristics in 141 male Tengmalm's Owls of known lifetime young production.

	Mean	S.D.	N	Median	Min.	Max.
Wing length (mm)	170.3	3.4	141	170	163	177
Tail length (mm)	103.1	5.1	141	103	92	120
Body mass (g)	109.4	8.3	141	109	92	132
Lifespan (yr)	3.5	1.2	125	3	2	8*
Breeding lifespan (yr)	1.5	1.0	141	1	1	7*
Breeding attempts	1.6	1.2	141	1	1	9**
LRS (no. of eggs)	9.2	6.9	141	6	2	51
LRS (no. of fledglings)	5.2	4.5	141	4	0	26
Clutch size	5.7	1.1	141	6	2	8
Brood size	3.3	1.8	141	3	0	7

* The age of first breeding in 16 males was unknown. ** A nest with eggs was taken as a breeding attempt.

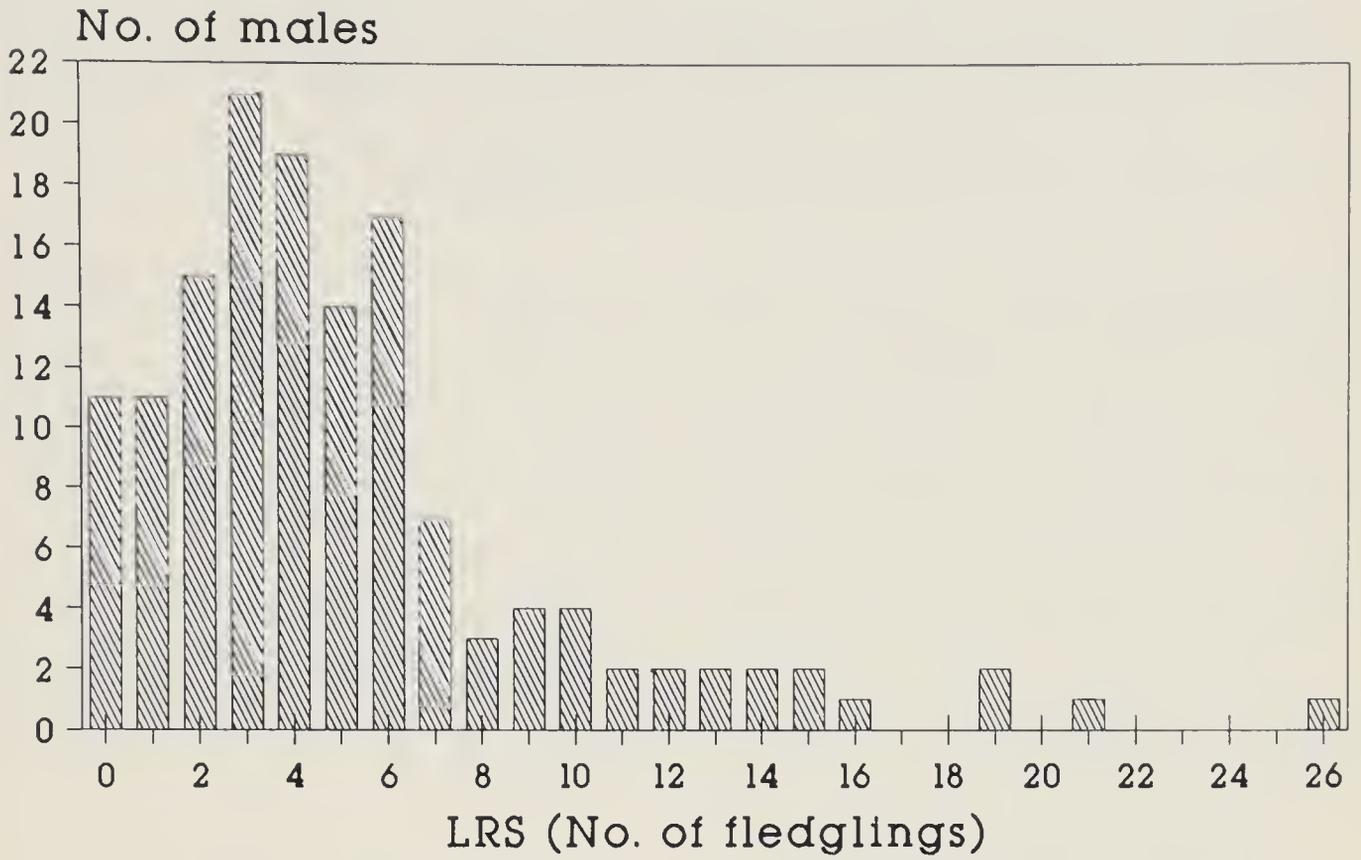


FIGURE 1 – The distribution of lifetime reproductive success (as measured by the number of fledglings) in 141 male Tengmalm's Owls.

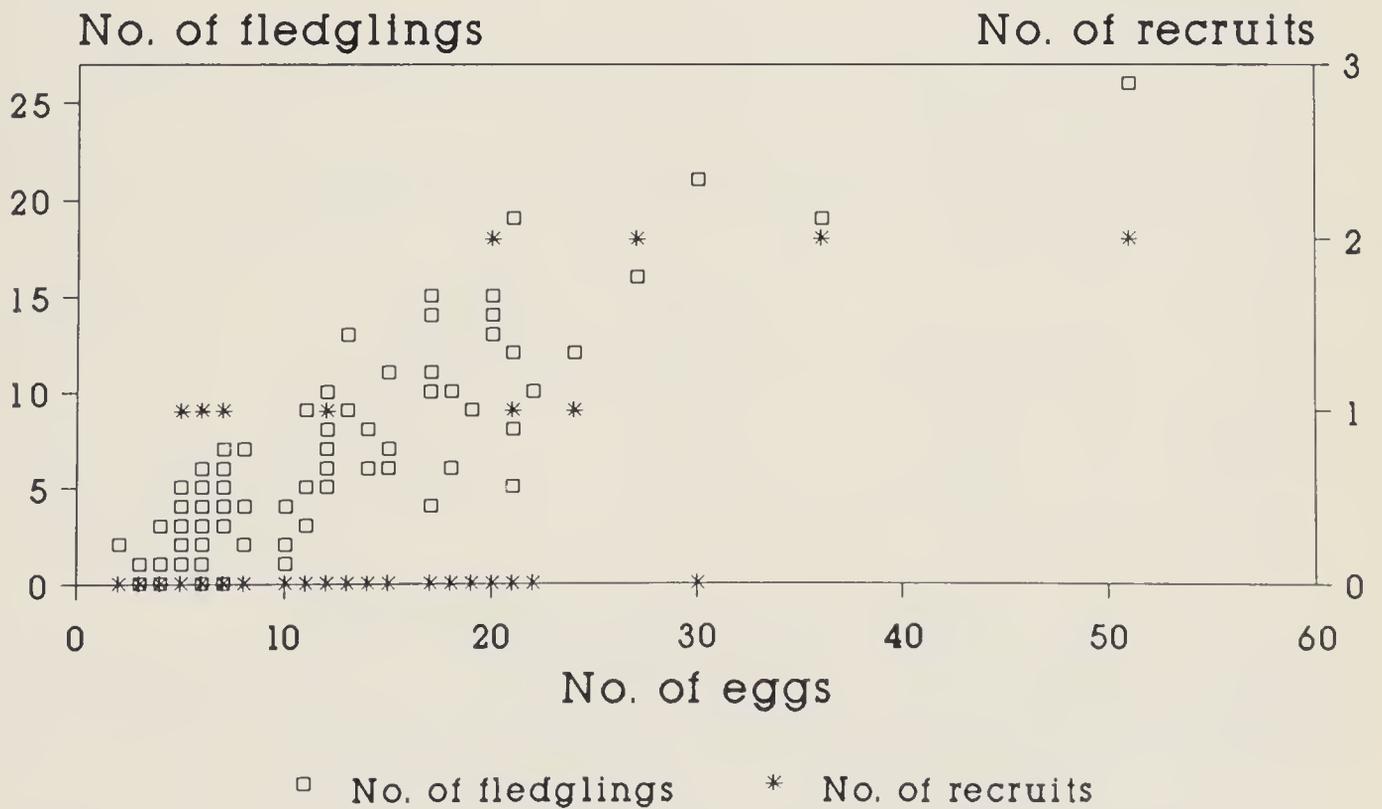


FIGURE 2 – The lifetime number of fledglings and recruits plotted against the pooled number of eggs produced by all the partners of males. Spearman rank correlation = 0.72, $P < 0.001$ for the number of fledglings and 0.30, $P < 0.001$ for the number of recruits.

141 males spent on average of 1.5 years (range 1-7) as breeders and reared on average of 5.2 fledglings (0-26) during their lifetimes (Table 1); 8% (11 out of 141) of males failed to produce any young (Figure 1), despite attempting to breed. Because broods normally contain between two and six young, and most owls bred only once, the lifetime productivity peaked at 2-6 young. A few males, however, were much more productive, which skewed the distribution of LRS (Figure 1).

The lifetime fledgling production of males was highly significantly correlated with the pooled number of eggs laid by all their partners (Figure 2). However, the lifetime contribution of recruits to the breeding population would be a better estimate of fitness. Of the 732 fledglings produced by the study males, only 15 (2%) were later retrapped as breeders inside (8 males and 5 females) or outside (1 male and 1 female) the study area. A majority of the remaining survivors probably dispersed from the area, as juveniles usually show long-distance natal dispersal (Korpimäki et al. 1987). Nevertheless, the number of recruits produced by individual males was closely dependent on their lifetime production of fledglings (Figure 2; Spearman rank correlation, $r_s = 0.31$, $df = 128$, $P < 0.001$; excluding males that did not raise any young). Males that reared < 5 fledglings during their lifetimes produced no recruits, whereas only males that raised > 20 fledglings produced two recruits. Accordingly, the lifetime production of fledglings is a reliable estimate of fitness in this species.

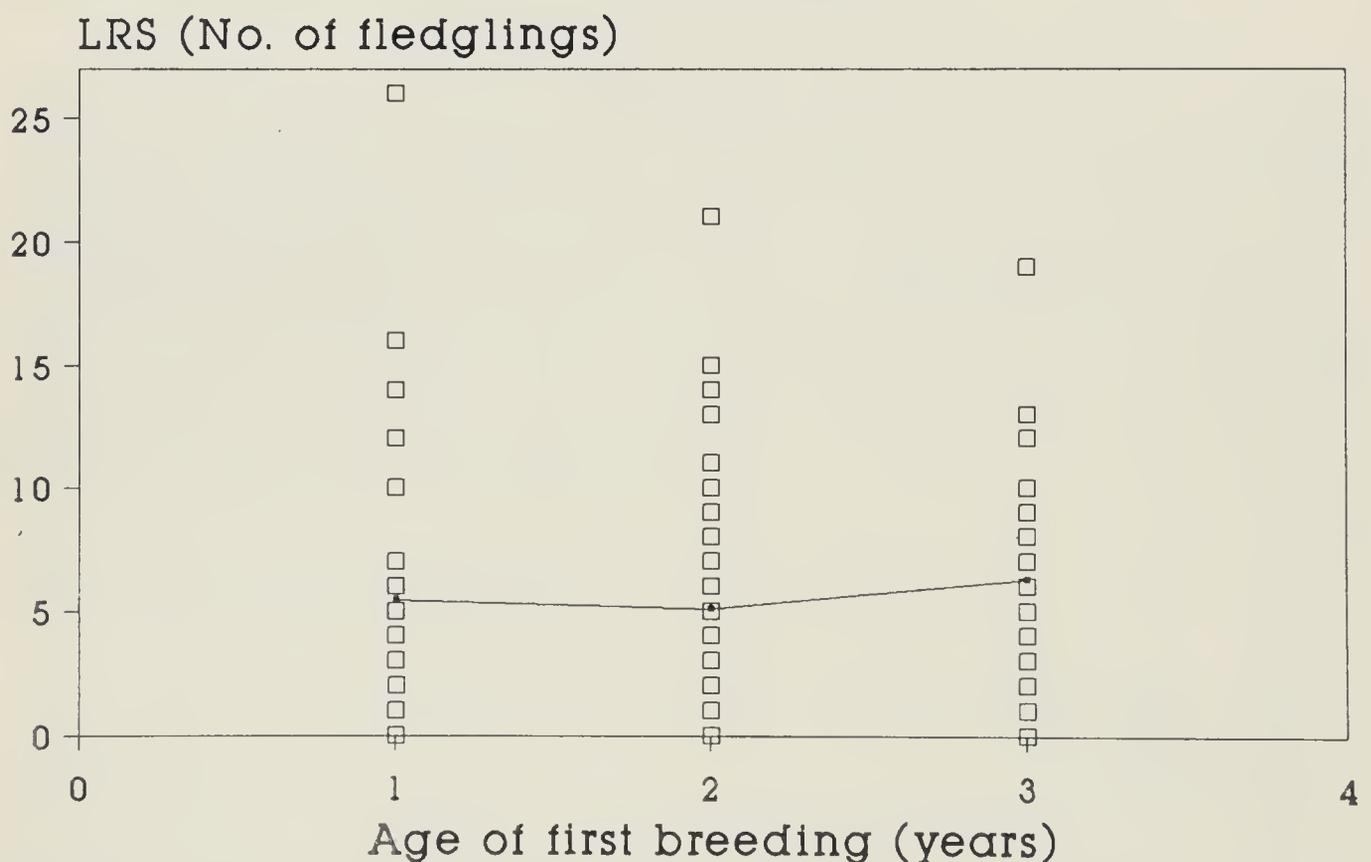


FIGURE 3 – The lifetime number of fledglings produced by males that recruited to the breeding population at different ages. The line shows the average LRS.

Factors affecting lifetime production of young

25% of males entered the breeding population as yearlings, 51% as 2-year old and 24% as >3 -year old. There was no difference in the lifetime productivity among all males, whether they first bred at age 1, 2 or >3 years (Figure 3; Kruskal-Wallis-test, $H = 0.27$, N.S.). In contrast, the duration of breeding life was positively correlated with LRS (Figure 4; $r_s = 0.68$, $P < 0.001$). If males bred for at least two years, they raised

at least some fledglings, and if reproductive life lasted for at least four years males produced > 10 fledglings. There was no relationship between the breeding lifespan of males and their mean breeding characters in individual attempts ($r_s = 0.00$ for clutch size, $r_s = 0.04$ for brood size, and $r_s = 0.01$ for breeding success).

LRS (No. of fledglings)

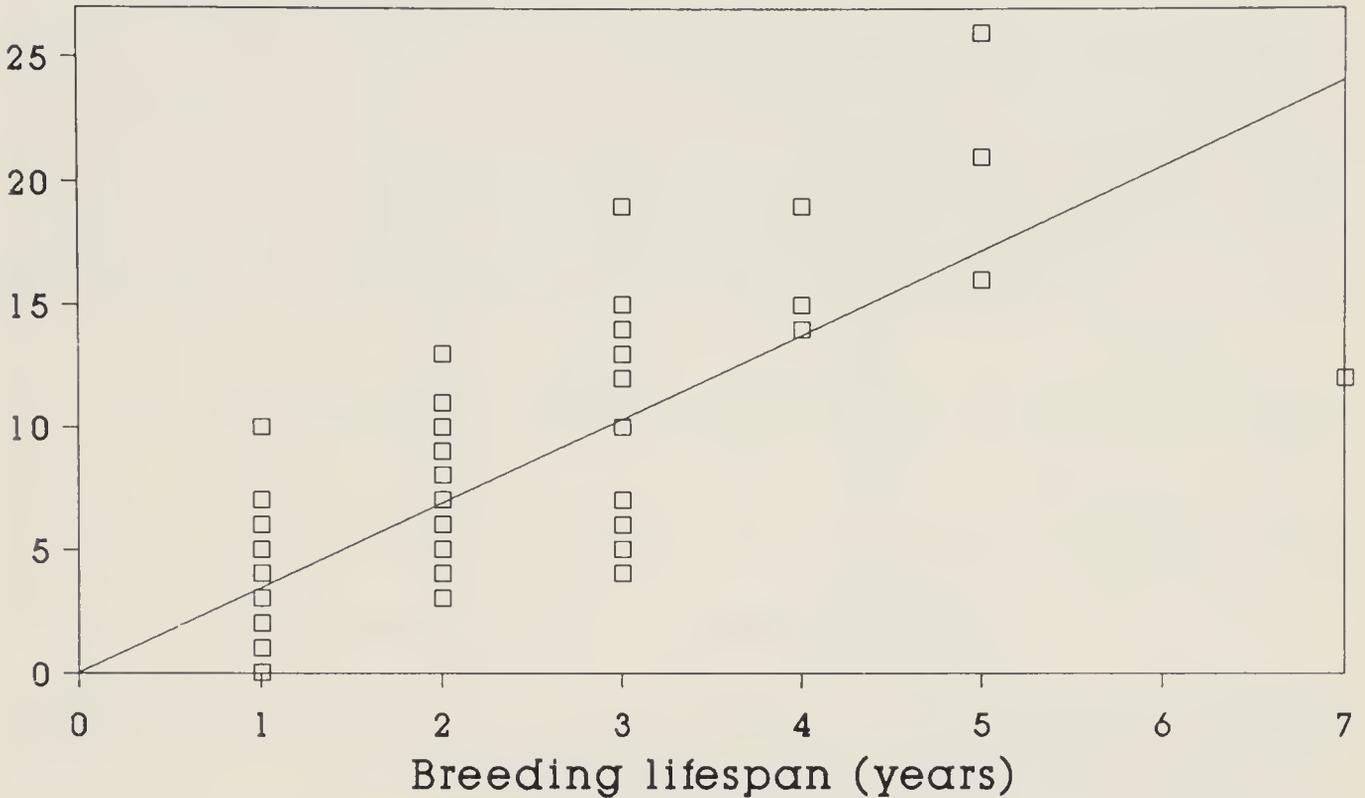


FIGURE 4 – The correlation between the lifetime number of fledglings and the duration of the breeding life. Spearman rank correlation = 0.68, $P < 0.001$.

TABLE 2 – Multiple regression of lifetime production of fledglings on lifespan, mean clutch size per breeding attempt and breeding success. LRS and lifespan were log-transformed, as their distributions were not normal.

Independent variable	Regression coefficient	Standard error	t	P <
Lifespan	0.444	0.048	9.3	0.001
Clutch size	0.045	0.016	2.8	0.01
Breeding success	0.0069	0.0006	12.4	0.001

F = 101.5, df = 121, $P < 0.001$

Some males (17 out of 141) were trapped at two (15) or three (2) nests in at least one year and were thus defined as polygynous. Polygyny occurred only in increase and peak vole years (Korpimaki 1989, 1990). The LRS was significantly positively related to the mean number of females per season ($r_s = 0.27$, $P < 0.01$). Polygynous males produced about twice as many fledglings as monogynous ones (Figure 5; mean±S.D.: 9.1 ± 6.6 vs. 4.7 ± 3.6 ; Mann-Whitney U-test (two-tailed), $z = 3.34$, $P < 0.001$). Their breeding lifespan was also longer than that of monogynous males (2.1 ± 1.2 vs. 1.4 ± 1.0 ; $z = 2.84$, $P < 0.01$).

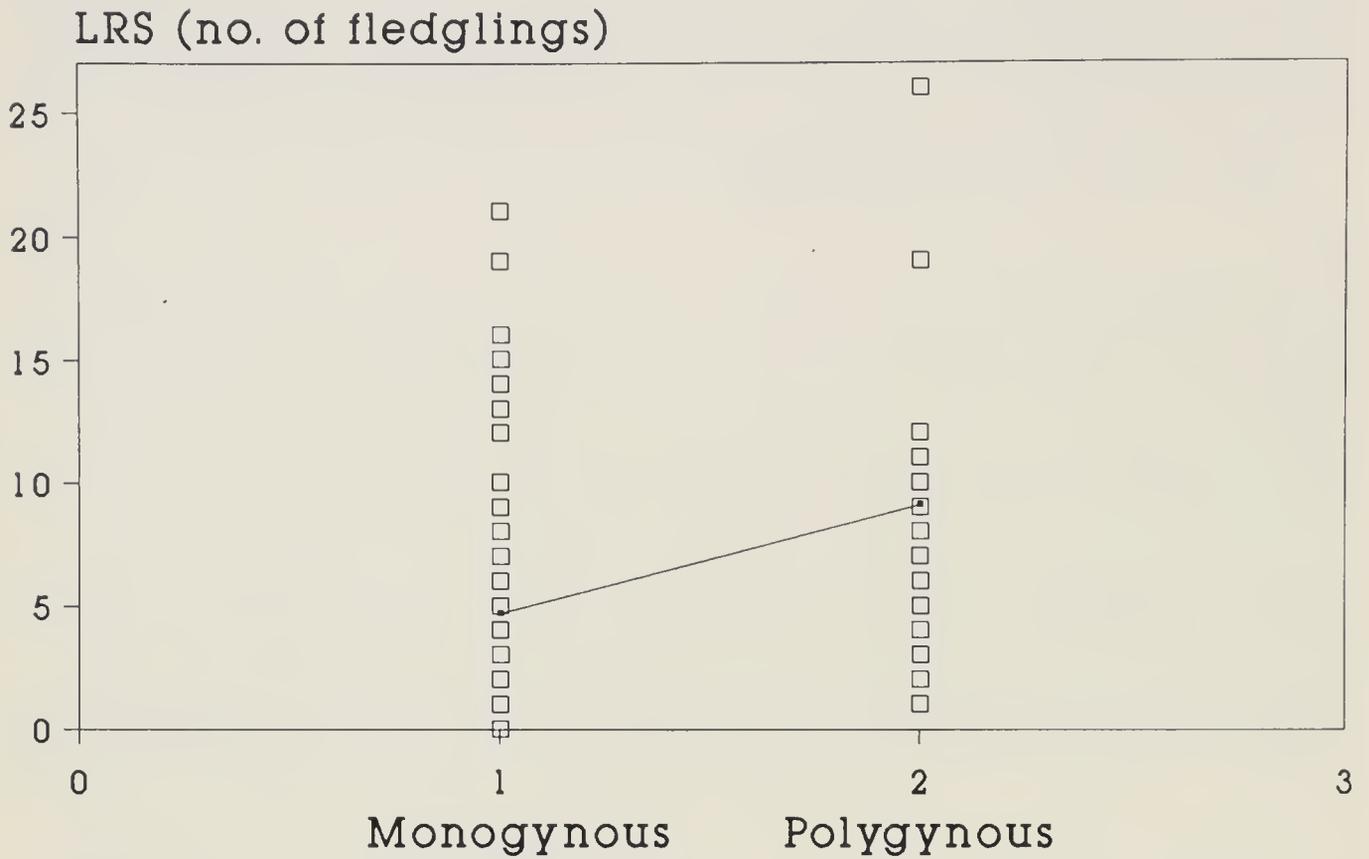


FIGURE 5 – The lifetime number of fledglings produced by monogynous and polygynous males. Males were defined as polygynous, if they were trapped at two or more nests in the same breeding season. The line shows the mean LRS.

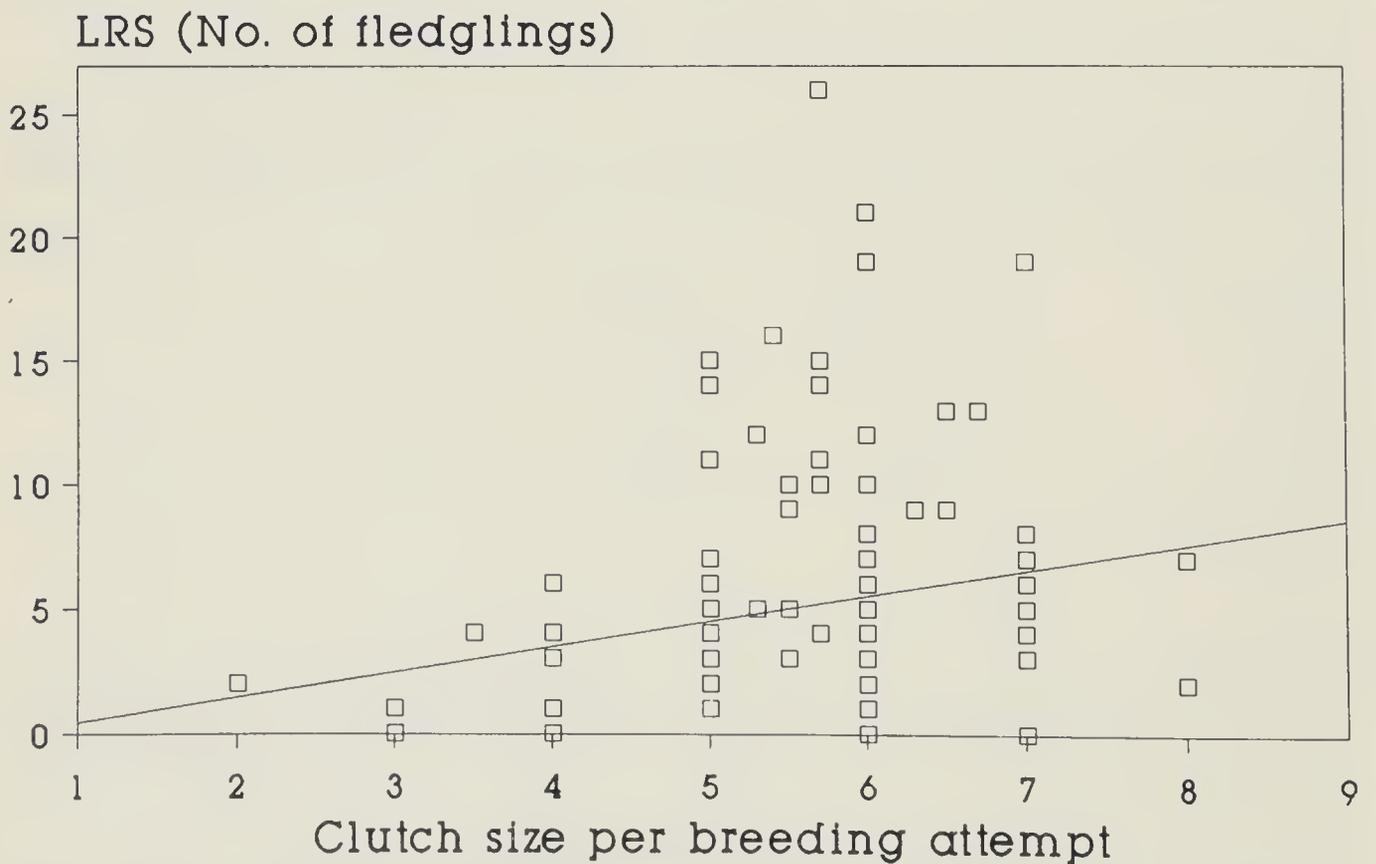


FIGURE 6 – The lifetime productivity of males plotted against the mean size of all clutches produced by all partners of a particular male. Spearman rank correlation = 0.31, $P < 0.001$.

The mean size of all clutches produced by all partners of a particular male also affected LRS so that males who fathered large clutches produced more fledglings than males who fathered small ones (Figure 6; $r_s = 0.31$, $P < 0.001$). In addition, LRS was positively dependent on the success of males in rearing young to the fledgling stage in individual breeding attempts (Figure 7; $r_s = 0.65$, $P < 0.001$).

Which factors were most important in explaining the variance in lifetime production? A multiple regression analysis revealed that lifespan, clutch size and breeding success explained 71% of the variance in LRS (Table 2). Breeding success contributed most to the variance, followed by lifespan and clutch size. I examined how well the model fits the data by computing residuals and by testing their distribution using an approximate Wilk-Shapiro statistic (Shapiro & Wilk 1965). The distribution of residuals did not show evidence of non-normality (approx. Wilk-Shapiro 0.99).



FIGURE 7 – The lifetime number of fledglings produced by males plotted against their mean breeding success ((100 x brood size) per clutch size) in individual nesting attempts. Spearman rank correlation = 0.65, $P < 0.001$.

Breeding habitats of Tengmalm's Owls vary both in space and time (see below), and these variations may affect LRS. There were marked differences in the habitat composition between different sites of the study area. High-quality territories had lower proportions of poor pine forest and marshland and relatively more farmland and spruce forest (Korpimaki 1988b). Although the ranking of territories was not independent of the LRS (see Material and Methods), there were no obvious differences in LRS among males occupying different grades of territories (Figure 8). With respect to the most important components of LRS, males lived longer on good territories than on poor ones ($r_s = 0.26$, $P < 0.01$), but there were no territory-related differences in the brood size ($r_s = -0.15$, N.S.)

Habitat quality varies markedly in time due to the population fluctuations of the staple prey. The 3-4-year vole cycle is typical of the study area. The breeding seasons were classified into the following phases on the basis of the snap-trapping data: 1) In the decrease phase (1979), vole densities decreased throughout the owls' breeding season and were low during the next winter; 2) In the low phase (1980-81, 1984 and 1987), voles were scarce during the breeding period, but started to recover in late summer and in the next winter; 3) In the increase phase (1982 and 1985), voles rapidly increased in the course of the breeding season and peaked in the next autumn and winter; 4) In the peak phase (1983 and 1986), vole abundance was still good during the early breeding period, but deteriorated in the late summer and was moderate or poor during the next winter. In the 3-year cycle, voles crashed from peak numbers in spring to low densities in the following autumn (see Korpimäki & Lagerström 1988, Korpimäki & Hakkarainen 1990 for details).

LRS (No. of fledglings)



FIGURE 8 – The lifetime number of fledglings produced by males occupying different territory grades. The line shows the mean LRS. Kruskal-Wallis test, $H = 1.57$, N.S.

TABLE 3 – The duration of the breeding life (years) and the number of fledglings produced by male Tengmalm's Owls doing their first breeding attempt in the different phases of the vole cycle.

Phase of the cycle	Breeding lifespan		Brood size		N
	Mean	S.D.	Mean	S.D.	
Decrease	1.7	1.7	2.6	1.1	13
Low	1.9	1.1	2.7	1.2	23
Increase	1.5	0.8	4.2	1.7	44
Peak	1.3	0.8	2.9	2.0	61

The phase of the vole cycle during the first breeding attempt of males affected LRS significantly (Figure 9). LRS was largest in males that entered the breeding population in the increase phase, followed by males recruiting in the low, peak and decrease phases. However, vole abundance affected differently the breeding lifespan and the brood size. The breeding lifespan was longest in males that first bred in the low phase, followed by those recruiting in the increase, decrease and peak phases (Table 3; Kruskal-Wallis-test, $H = 9.39$, $P < 0.05$). The mean brood size was largest in the increase phase and decreased through the peak phase to the low and decrease phases (Table 3; $H = 16.62$, $P < 0.001$).

LRS (No. of fledglings)

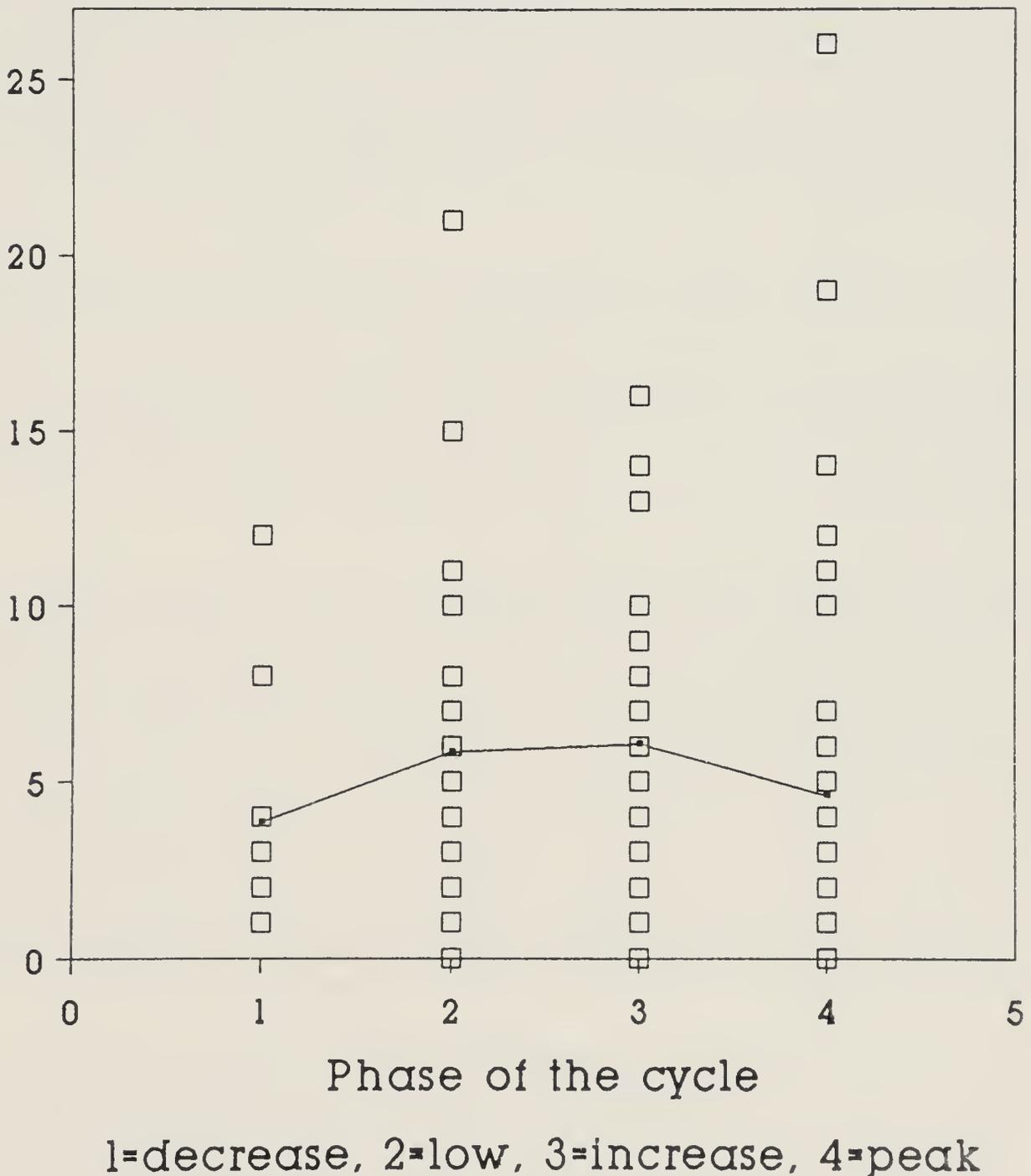


FIGURE 9 – The lifetime number of fledglings produced by males that entered the breeding population in different phases of the vole cycle. The line shows the mean LRS. Kruskal-Wallis test, $H = 12.59$, $P < 0.01$.

DISCUSSION

Fluctuating food supply determines LRS

The temporal variation in habitat quality due to fluctuating vole supply was the most important environmental determinant of LRS in male Tengmalm's Owls. As vole cycles are fairly predictable in time, we (Korpimaki & Lagerstrom 1988) have suggested that males should invest more in offspring in the increase phase of the cycle than in the peak phase, as the first-year survival of their young is highest at that time. In this work, I observed that LRS of males entering the population in the low and increase phases of the cycle is larger than those entering in the decrease and peak phases. It may be so that recruitment in the low phase is more adaptive than in the increase phase, as then the offspring of males have good possibilities to enter the breeding population in the increase phase and the second generation in turn in the peak phase. It is the contribution of an individual genotype relative to that of other genotypes to subsequent generations that matters in terms of fitness (e.g. Endler 1986, Newton 1989). However, gaining this "optimal" strategy is unlikely, as only > 2-year old males are able to reproduce in the low phase (Korpimaki 1987c). In addition, the birth year of an owlet is a chance event.

The spatial variation in habitat quality did not have obvious effects on LRS, although in the earlier data the males on good territories performed better in individual attempts than did males on poor territories (Korpimaki 1988b). In the present data, the breeding lifespan was also longer on high-quality territories than on low-quality ones. I do not have any other explanation for this disagreement than that the grades of territories changed through time, as vole cycles are not identical. Female Sparrowhawks gained larger LRS on good territories than on poor ones (Newton 1985).

Inter-individual variation in the productivity

Newton's (1989) generalizations from the individual variation in LRS of birds also held for male Tengmalm's Owls that take a larger share of parental care than do females. (1) 8% of males attempting to reproduce failed to rear any fledglings, but this percentage may be an underestimate, as I was not able to identify males whose nests failed in the egg stage. (2) LRS of males varied widely, and 21% (31 out of 141) of males produced 50% of all the fledglings in the population. (3) Considering a large share of fledglings that died before the first breeding (78%, E. Korpimaki unpubl.), 5% of young fledged in one year produced 50% of fledglings in the next generation. In female Sparrowhawks and Ural Owls these proportions were similar (20-23% and 5-6%; Newton 1989, Saurola 1989), although these species are monogamous. It is expected (Clutton-Brock 1988) that inter-individual variance in LRS would be larger in males and in polygynous species than in females and in monogynous species.

In most bird species studied so far, lifespan has been the major component of LRS (Newton 1989, but see Wallin 1988). In contrast, calculations of LRS for male Tengmalm's Owls showed that offspring survival, from egg to fledgling stage, was more important. My result was not unexpected, as the breeding lifespan of most males was shorter than the vole cycle (most males bred only once) and their breeding success varied largely, depending on the vole supply (Korpimaki 1981, 1987a). In addition, fluctuating food conditions also affect the first-year survival of young (Korpimaki & Lagerstrom 1988). Accordingly, individuals that happened to breed in a year with an increasing vole population had better survival of eggs and recruitment of young. I suggest, therefore, that if it was possible to measure LRS by the number of recruits,

rather than by the number of fledglings, lifespan would be even less important to the variance in LRS than the present data indicate. However, the duration of breeding life in highly productive males was longer than the vole cycle so that one cannot underestimate the importance of the lifespan to the fitness. The number of eggs fathered by males (i.e. clutch size) had only minor effects on LRS, as the limiting factor in breeding success seemed to be how many young the males were able to feed.

No evidence of reproductive costs

Orians (1969) argued that polygyny should always be advantageous to males, and, indeed, LRS of polygynous males in three passerine species was larger than that of monogynous ones (Gustafsson 1989, Sternberg 1989, Orians & Beletsky 1989). However, the males of these species provide no parental care for their young, or, at most, very little. Thus, it is not unexpected that they can increase their LRS by fathering as many eggs as possible. Polygyny in Tengmalm's Owls is limited by the dependence of the young on males providing enough food (Korpimäki 1989, 1990). Although polygynous males fed two or three families in one season, this large feeding effort did not decrease their future survival (i.e. there was no evidence of reproductive costs). These males were probably of high quality, as there was no difference in the mean territory grade between monogynous and polygynous males (3.5 ± 1.4 vs. 3.4 ± 1.2). This indicates that harem females may get good genes to their offspring.

A negative relationship between the major fitness components (reproduction and survival) is the basis of prevailing life-history theory (e.g. Williams 1966, Stearns 1976, Bell & Koufopanou 1986 with references). However, I did not find evidence that a high reproductive effort (as measured by the clutch or brood size) of male Tengmalm's Owls reduced survival (as measured by duration of breeding life). In addition, experimental reduction or enlargement of newly-hatched broods did not decrease future survival or reproductive success in males (Korpimäki 1988c unpubl.). Thus, a trade-off between reproduction and survival played a minimal role in the life of male Tengmalm's Owls. Superior males may easily compensate for the large parental investment by increasing their food intake so that they do not risk their future survival or reproductive potential. This idea is consistent with the compensation hypothesis of Tuomi et al. (1983), which predicts a weaker negative relationship between reproduction and survival than does the trade-off hypothesis.

My results, however, contrast with those obtained from Tawny Owls, in which both females and males that raised large broods seemed to suffer from a reduced survival (Wallin 1988), though correlations between present fecundity and future survival tell us little about the costs of breeding (Partridge & Harvey 1985). In addition, I question why long-lived Tawny Owls (maximum lifespan 17 yr, Saurola 1988) invest "too" much in one breeding attempt and thus reduce their residual reproductive value, as short-lived male Tengmalm's Owls (8 yr) do not do so. Natural selection should counteract the apparently maladaptive behaviour of Tawny Owls.

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POPULATION AGE STRUCTURE OF LONG-DISTANCE MIGRATORY PASSERINE BIRDS: VARIATION IN TIME AND SPACE

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ABSTRACT. Long-term demographic studies of American Redstarts *Setophaga ruticilla* in the Hubbard Brook Experimental Forest, New Hampshire, USA, illustrate the large spatial scale necessary to identify causes of population variation. Redstart age structure fluctuated dramatically from year to year (16.5-54% yearling males in 180 ha study area). Total males declined by 50% from 1981-1990, and in most years yearlings comprised fewer than 30% — the minimum value expected in a hypothetical steady-state population — suggesting that recruitment was insufficient to maintain population levels. This temporal demographic variation resulted from spatially widespread processes: (1) ratios of yearling:older males varied least on the largest-scale (64 ha) replicate subplots studied; (2) most yearling recruits could not have been produced locally; and (3) immigration of new older males was substantial in some years. These results are discussed in the context of population regulation in habitat mosaic landscapes, such as observed in both breeding and wintering areas.

Keywords: Age-structure, American Redstart, demography, density dependence, longevity, migrant, population regulation, scale, *Setophaga ruticilla*, survival.

INTRODUCTION

Most studies of the population dynamics and population regulation of passerine birds have been conducted with year-round resident species in the temperate zone, such as the Great Tit *Parus major* (e.g. Kluijver 1951, Perrins 1965, 1980, Dhondt 1971, Krebs 1971, O'Connor 1980, Minot 1981, Clobert et al. 1988), Willow Tit *P. montanus* (Ekman 1984a, b, Ekman & Askenmo 1981, 1986), and European Nuthatch *Sitta europaea* (Nilsson 1987). Much of the success of these studies derives from their long-term measurement of demographic parameters, i.e. age-specific reproduction and mortality, in relation to season, population density, competitors, and other ecological circumstances.

By contrast, the ecological factors influencing the demography of long-distance migratory species are relatively poorly known. Reasons for this are diverse, but include the global spatial scales over which many migrants travel annually, and their often opportunistic responses to unpredictable environments and resources (e.g. Gauthreaux 1981, Cox 1985, Sherry 1990, Martin & Karr 1990 — but see Morton & Greenberg 1989). Although several demographic studies of migratory passerines are available (e.g. Mayfield 1960, Nolan 1978, Ketterson & Nolan 1982), their population dynamics remain poorly understood, a fact made all the more unfortunate by recent population declines in a variety of North American migrant birds (e.g. Terborgh 1989, Robbins et al. 1989, Askins et al. 1990).

As Berryman (1987) noted, "One of the main problems in obtaining and interpreting population data is that of scale; i.e. what is the correct spatio-temporal scale in which

to view the subject population?" For migratory bird populations long time-scale studies are crucial, as suggested by the large annual variability we have observed in population abundances and their food supplies in a north temperate forest (Holmes et al. 1986, Rodenhouse 1986, Holmes & Sherry 1988, Holmes et al. this volume), as well as in their reproductive success (Sherry & Holmes 1991) and survival (Holmes & Sherry 1991). Variability in bird abundances among habitats (Sherry & Holmes 1985) also suggests the need to examine spatial variability of demographic variables.

Here we consider temporal and spatial variation in the age-structure of a migratory passerine species (*Setophaga ruticilla*, Parulinae) in order to illustrate the scale and some of the ecological determinants of the population changes observed. Redstarts are suitable for this type of study because yearling males, which look like females, can be distinguished from older males easily in the field (Rohwer et al. 1983). Patterns in age structure variation can then provide clues to the underlying ecological influences. In this paper we ask (1) How variable are redstart abundance and age structure annually? (2) How does observed age structure compare to that expected on theoretical grounds? And, (3) at how large a spatial scale must population processes be considered in order to identify the important ecological processes involved? We briefly discuss pitfalls of measuring population age ratios, review the ecological bases for the demographic patterns observed, and discuss implications of our results for understanding population regulation of long-distance migratory birds.

STUDY AREA

These studies were conducted on a 180 ha area of continuous northern hardwoods and mixed deciduous-coniferous forest, within extensively forested stands of the Hubbard Brook Experimental Forest, which is located within the White Mountain National Forest, New Hampshire, USA. Trees are dominated by Sugar Maple *Acer saccharum*, American Beech *Fagus grandifolia* and Yellow Birch *Betula alleghaniensis*, with occasional White Ash *Fraxinus americana*, Hemlock *Tsuga canadensis*, Red Spruce *Picea rubra*, Balsam Fir *Abies balsamea*, Red and Striped Maples *A. rubrum* and *A. pensylvanicum* respectively, and Paper Birch *B. papyrifera*. The vegetation and avifauna of this area are described more fully elsewhere (Sherry & Holmes 1985, 1991).

Embedded within the 180 ha area is a 10 ha census plot on which intensive bird population monitoring has been conducted since 1969 (Holmes & Sturges 1975, Holmes et al. 1986, Sherry & Holmes 1985). This plot is dominated by deciduous tree species.

METHODS

Redstarts were censused using modified territory-mapping methods (Holmes & Sturges 1975) during the peak breeding period (first three weeks of June), 1981-1990, on the 180 ha study area (see Sherry & Holmes 1991 for details of censusing methods).

Survival and longevity

Parameters used to develop a model for the proportions of male redstarts that should be yearlings (or older males), i.e. average annual mortality and maximum observed

longevity of redstarts at Hubbard Brook. These data came from a mark-recapture study of redstarts on the 10 ha plot, and they are statistically independent, because of when they were collected (1969-79), of the demographic data considered in the present study. Birds were captured in 12 m long mist nets, one of which was placed at each intersection of a 50 m grid throughout the 10 ha study area. Nets were opened from approximately 0600-0700 until 1400-1500 (EDT), 1-2 days per week, during the nest-building through early fledgling periods of the breeding cycle (roughly early June until mid July). Methods were comparable each year, and effort was nearly so.

Scale of age-specific habitat selection

To determine what plot size was necessary to characterize redstart population age-structure, we looked at how variable the ratios of number of yearling:older male territories were in different-sized quadrats within the entire study area. We omitted from this analysis data collected in 1981, because a large percentage of males were not aged that year (26% — see Figure 1). The number of yearling or older male territories contained within a quadrat was defined as the number of territory centers of that age class contained within, or on the line of, that quadrat area; and a particular territory could be assigned to only one quadrat. Variability in these ratios among quadrats was quantified with Whitaker's (1975) coefficient of fluctuation (CF), which is a logarithmic analog of the coefficient of variation, based on logarithms of ratios, in our case. We added 0.1 to each abundance value (i.e. to both numerator and denominator) because logarithms of zero are undefined.

To look at these CFs as a function of spatial scale within our study area, we first chose the easternmost 128 ha area because it contained on average a higher density of redstarts, and in the latter years contained the only redstarts. This area was then halved, yielding two quadrats of 64 ha, each of which was then halved again, and so on, without reference to either bird or vegetation distribution patterns. The result was one quadrat of 128 ha, two of 64 ha, four of 32 ha, eight of 16 ha, 16 of 8 ha, and 32 of 4 ha. To calculate yearling:older male ratios for each spatial scale and each year, we counted territory centers of each age class of male redstart occurring within quadrats of each size.

To determine whether the observed CFs exceeded those expected from random distributions of yearling and older male territories among the quadrats, we simulated distributions of yearling:older male ratios expected under the null hypothesis of no patchiness in age-specific distributions. For data from each year and for each of the five spatial scales, we randomly assigned each territory present in that data set to an older or yearling male, subject to two constraints: (1) the total number of yearlings and older males in the random data sets were identical to the actual values, and (2) the total number of territories (yearling + older male) per quadrat in the random data set matched the total number of territories in the actual data for each of the different quadrats at a particular spatial scale. For each data set we then repeated the random assignment of territories 99 times, which, in addition to the one actual value, gave a frequency distribution of 100 CFs. The 95% confidence interval for these randomly generated CFs was the inclusive set of the 95 smallest values, against which we compared the actual value (this is a one-tailed procedure, since we were concerned with the null hypothesis that observed ratios did not exceed random values). We rejected the null hypothesis, i.e. that the yearling:older male ratios did not fluctuate more than would be expected by chance, if the observed CF fell above the 95% confidence interval.

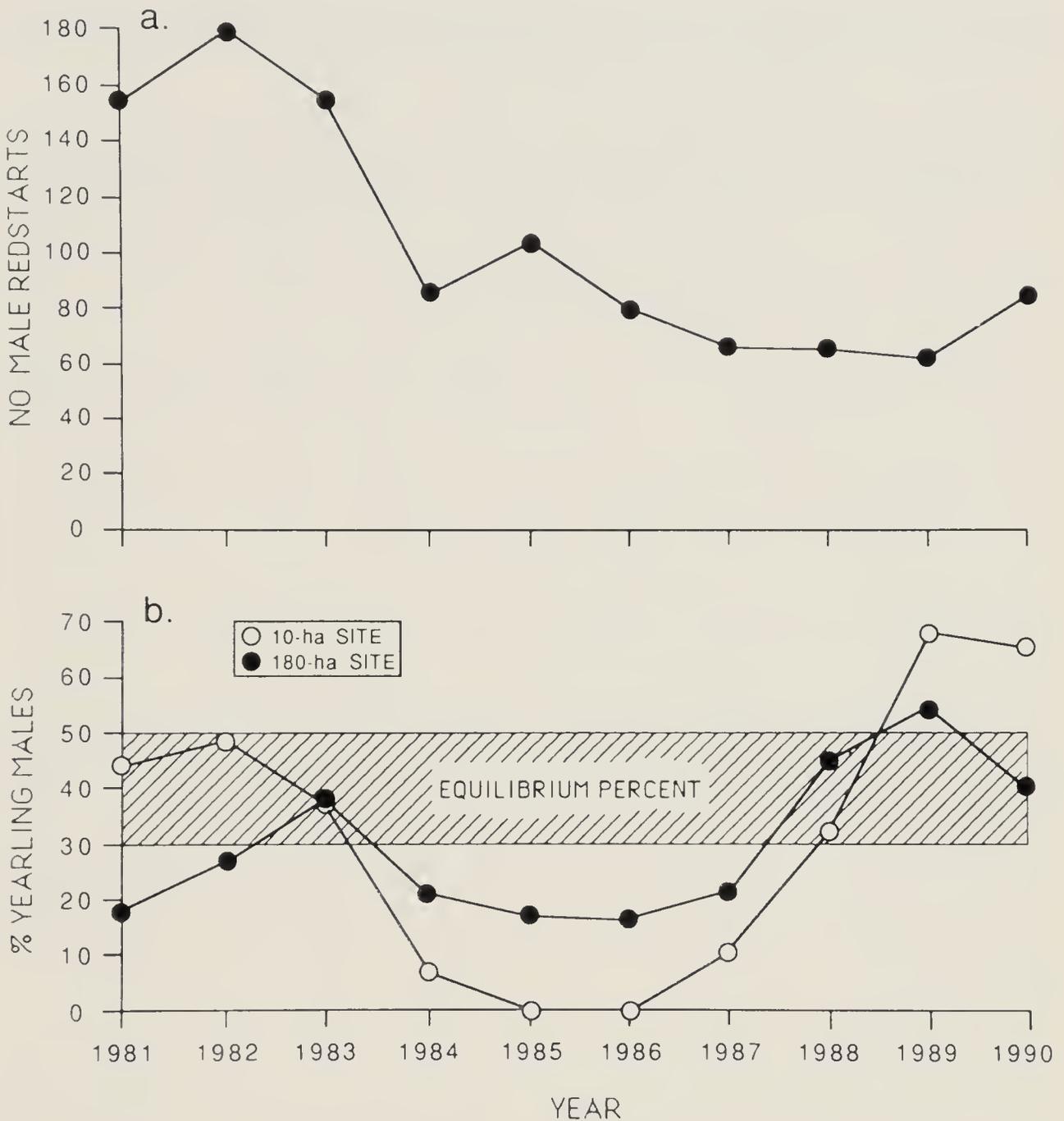


FIGURE 1 – Abundance and male population age structure of American Redstarts in Hubbard Brook Experimental Forest study sites during decade 1981-1990. a) Total male (territory) abundance on 180 ha site. b) Percentages of total males that were yearlings on 10 ha site (empty circles) and on 180 ha site (solid circles). Cross-hatched region designated “equilibrium percent” refers to the percentage of the males expected to be yearlings according to equations 1 and 2, for annual survival values ranging from 50-70% (see text). Percentages of total males aged within 180 ha area, in 1981-1990, respectively, were 74, 85, 92, 99, 94, 98, 100, 100, 100, 100.

RESULTS AND DISCUSSION

Temporal population variability

During the period 1981-1990 male redstart abundances fluctuated between 63 and 180 individuals on the 180 ha study area, with a net decline of about 50%, and only three years of small increases (Figure 1a). The population structure also varied, from

0 to 70% yearling males on the 10 ha area and 16.5 to 54% on the 180 ha area (Figure 1b). Generally fewer than 30% yearling males on the 180 ha area, except in four years with relatively large cohorts (1983 and 1988-1990).

The significance of this 30% figure can be seen from a model of expected age structure in a hypothetical population with the same average annual survival rate and longevity of redstarts. We make four assumptions to characterize this ideal population: (1) All ecological conditions influencing the population, including weather, nest predation, and food abundance remain constant. (2) The probability of surviving from one age to the next (= S) is constant, once birds reach one year of age (Ricklefs 1973; but see Botkin & Miller 1974, Nedelman et al. 1987, Loery et al. 1987). We make this assumption here because our mark-and-recapture data were approximated by a negative exponential relationship, i.e. a nearly constant proportion of birds disappeared between each age interval as indicated by a linear decline in $\log N$ with age (Figure 2). The average proportion of males surviving each year, based on this equation, is the ratio of the number in year t to the number in year $t-1 = e^{-0.74} = 47.7\%$, where e is the base of natural logarithms. The assumption that all age classes survived equally from one year to the next is probably unreasonable, but one which is made here to model a hypothetical constant population, against which to compare the actual one. (3) Neither population size nor age distribution changes from year to year. This assumption was clearly violated (Figure 1), but the assumption is made here, again, to model a hypothetical constant population. And (4) dispersal is unimportant, either because it is infrequent or because immigration and emigration are identical within an age class.

If we start out with a relative frequency of 1.0 for yearling males in the population, then from our assumptions the number of two-year-old males each year is S , three-year-old males is S^2 , four-year-old males is S^3 , and so on, and the ratio of yearling: older males is then

$$1 / (S + S^2 + S^3 + \dots + S^\infty)$$

Addition of 1 to the denominator yields a standard geometrical progression, which simplifies to $(1 - S)^{-1}$, and resubtraction of 1 from the denominator (outside parentheses) gives

$$1 / [(1 - S)^{-1} - 1], \text{ or } (1 - S) / S. \quad (1a)$$

Redstarts banded at Hubbard Brook have lived at least seven years (Figure 2), so a more realistic expression than (1a) for the yearling:older male ratio is

$$1 / (S + S^2 + S^3 + \dots + S^6) \quad (1b)$$

The percentage of total males that are yearlings is then

$$(r / (1 + r)) \cdot 100, \quad (2)$$

where r is the ratio of yearling:older males. The percentages of total males that are yearlings, resulting from these expressions, and plotted as a function of S (Figure 3), did not differ appreciably in the two models, except at values of S greater than about 0.6.

If a reasonable value of S for Hubbard Brook male redstarts lies between 0.48 (the measured proportion of birds returning each year, Figure 2; see also Holmes & Sherry 1991) and, say, 0.70 (to account for the fact that we underestimate true survival, because some birds undoubtedly emigrate from the site each year — T.W. Sherry, unpubl. data, see also Roberts 1971, Nichols 1981), then from Figure 3, at least 30%, and perhaps as many as 50%, of total males ought to be yearlings on average, in our hypothetical redstart population.

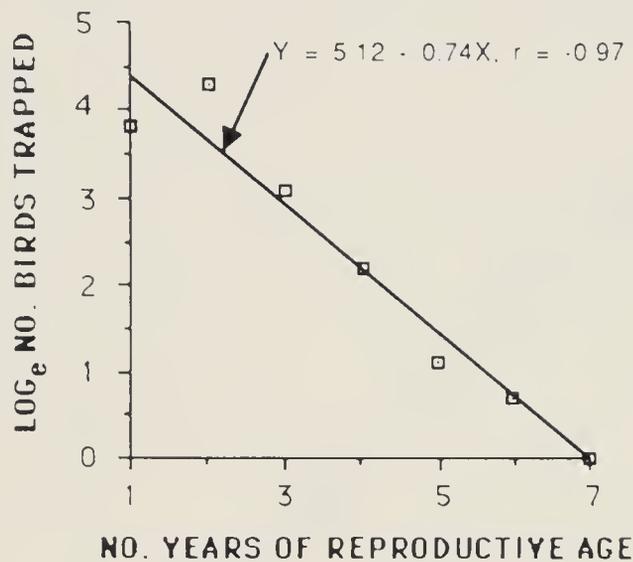


FIGURE 2 – Age-specific survival of male American Redstarts captured with mist nets and banded on a 10 ha site in the Hubbard Brook Experimental Forest, New Hampshire, between 1969 and 1979. The equation shown is the least-squares regression. The reason for more two-year old than yearling males was that birds first captured in their two-year-and older (definitive male) plumage were added to the two-year-old pool of birds.

The significance of the fact that we observed fewer yearlings than 30% of total males most years (Figure 1) is that according to the model (Figure 3) such a population should have been declining, as was indeed the case (Figure 1). A decline in the redstart population after 1983 corresponded with lower recruitment of yearling males, which comprised only about 20% of the males in the years 1984-1987; and an increase between 1989 and 1990 followed several years of relatively high yearling recruitment (Figure 1b; see also Sherry & Holmes 1991). Thus our percentages of yearling males observed in the 180 ha area were at least close to those one would expect in a large hypothetical population with the observed average population characteristics of redstarts. Nolan (1978) obtained estimates of 65% and 35% for annual survival and percentage of yearlings, respectively, in a population of another long-distance migrant, the Prairie Warbler *Dendroica discolor* — values in close agreement with our model (Figure 3).

We have reported elsewhere (Sherry & Holmes 1991) that nesting success appears to explain most variation (60%) in redstart recruitment. Redstart nesting success was largely a function of nest depredation rate, but also of food abundance, since in at least one year starvation of nestlings caused as many nests to be abandoned by adults as depredation. Food abundance during the breeding season also influences the reproductive success of foliage gleaners at Hubbard Brook as well as their abundance the following year (Holmes et al. 1986, Rodenhouse 1986).

To conclude this section on temporal variation, redstart total male abundance as well as age structure varied markedly between 1981 and 1990 (Figure 1), suggesting the existence of a cohort-effect, in which high recruitment of young into the breeding population occurred only in some years (Figure 1). In most years yearling recruitment was insufficient to maintain the population, which thus declined, because of several years of heavy nest predation and one year of high nestling starvation. Such long-term studies are crucial to establish the range of variation in population parameters, to estimate the frequency of important ecological events, and to seek ecological causes of population changes.

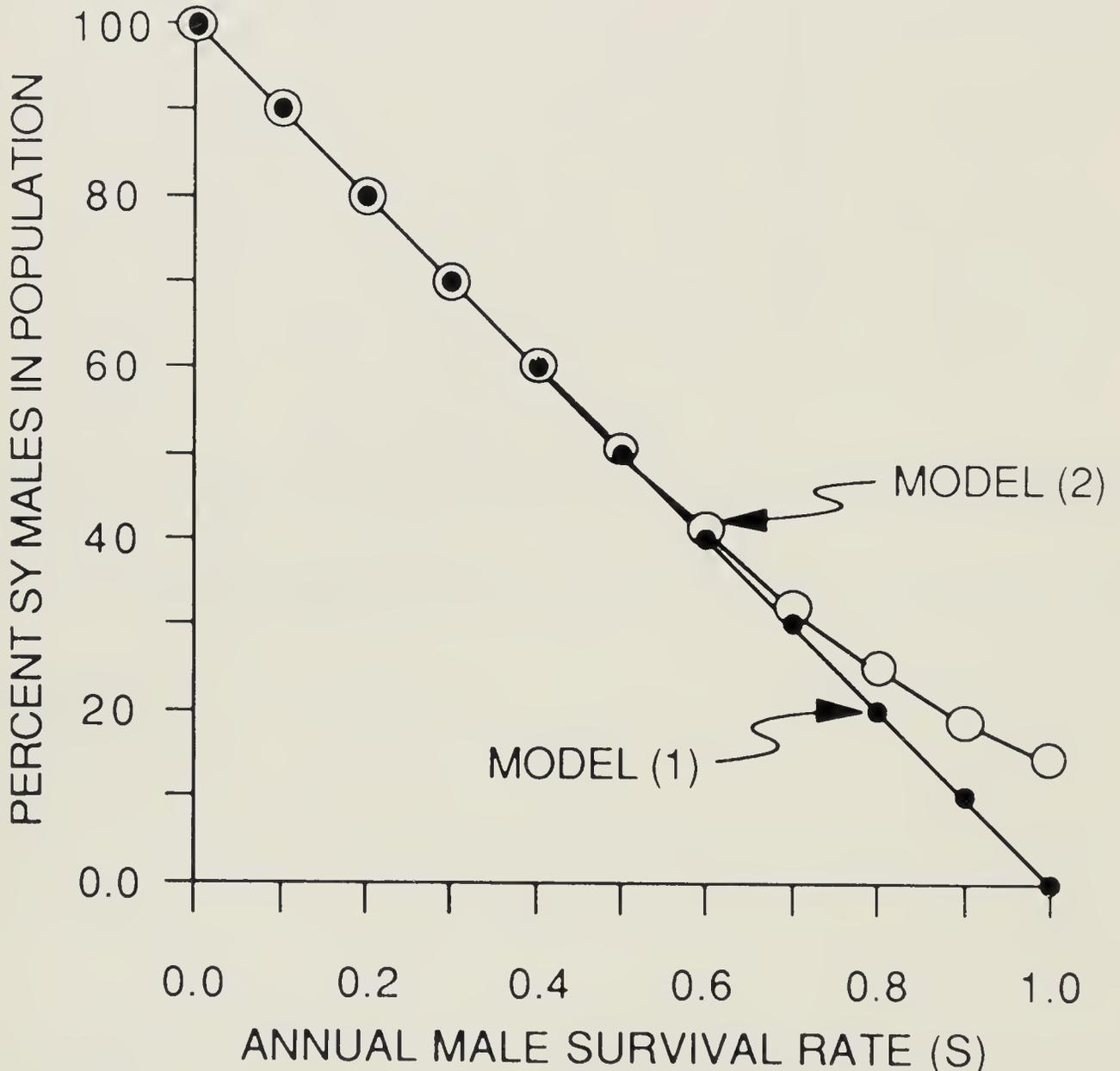


FIGURE 3 – Percent yearling males expected in total redstart population according to two related models described in text, as a function of the average annual survival rate of all males (yearling and two years and older). Model (1) assumes infinitely long lifetimes; model (2) assumes maximum longevity of 7 years.

Spatial scale of population variation

Comparison of redstart age structure on our 10 ha and 180 ha study sites within years (Figure 1b) suggested the possibility that small areas, containing few territories, provide erroneous age structure estimates. The percent of yearlings on this particular 10 ha area covaried with, but usually differed substantially from, that on the 180 ha area (Figure 1b).

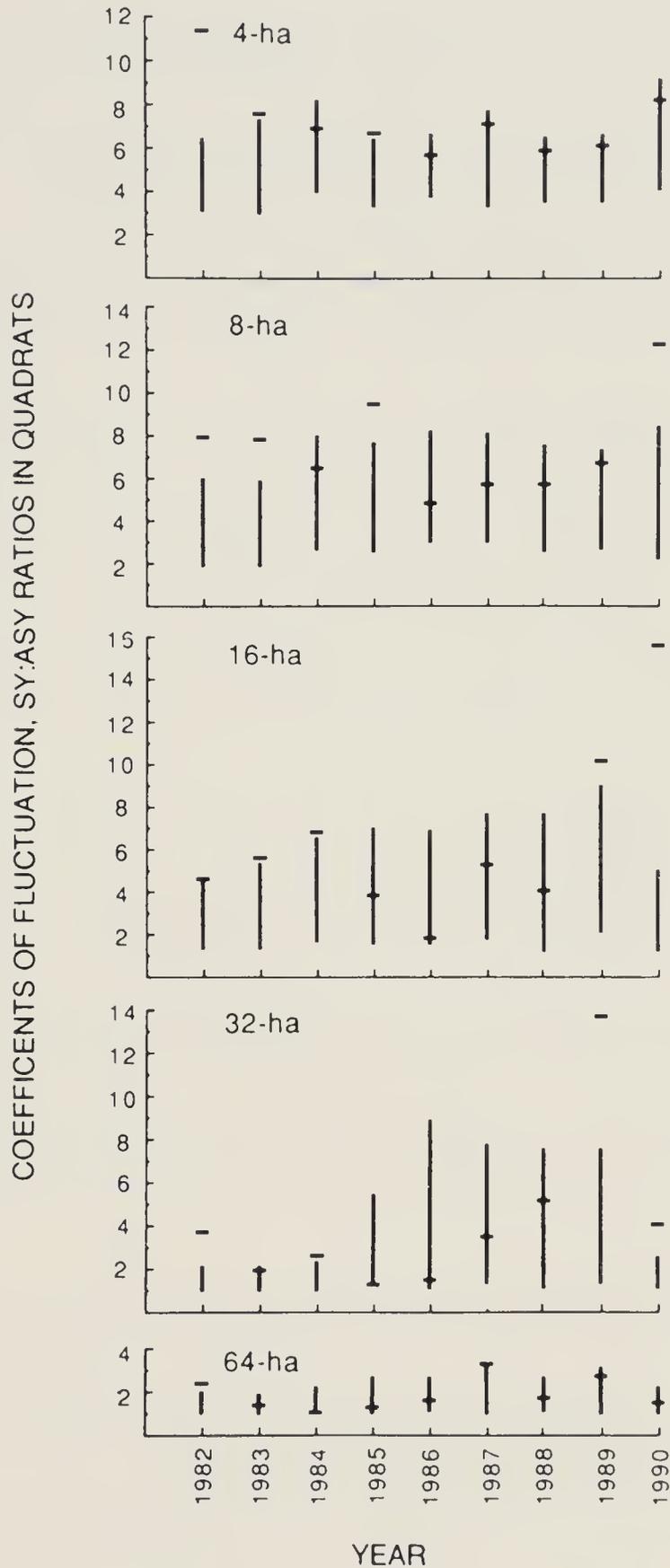


FIGURE 4 – Observed coefficients of fluctuation (CFs — horizontal bars) of the ratio of American Redstart yearling:older male abundances among quadrats, and 95% confidence intervals for randomly generated CFs (vertical bars) for each of five scales of analysis (4, 8, 16, 32, and 64 ha corresponding with 32, 16, 8, 4, and 2 plots per scale, respectively). Bars for observed CFs touch 95% confidence interval bars for all cases in which observed value fell within this interval. Each 95% confidence interval is given by the lower 95% of values calculated in the Monte-Carlo simulation for that year and spatial scale, since the null hypothesis under consideration was that actual ratios of yearling:older male redstart abundances among quadrats was not greater than random ratios (see text).

To ascertain how large an area was needed to characterize redstart age-structure within a particular season we determined ratios of yearling:older male abundances in quadrats of different sizes. Our results indicate that these ratios fluctuated least among the largest quadrats, since CFs were on average smaller for larger quadrat sizes (Figure 4). These ratios tended to approach an asymptote of "1" for CFs, namely an absence of variation among quadrats, most frequently at the larger scales of 32-64 ha, except in 1982 when more than 64 ha were necessary to characterize the population's age-structure (Figure 4). More importantly, actual CFs exceeded 95% confidence intervals for random coefficients more often at the smaller scales (Figure 4). Specifically, actual CFs exceeded 95% confidence intervals for random coefficients during three years at the 4 ha scale (1982, 1983, 1985), four years at each of the 8 ha, 16 ha, and 32 ha scales, and just one year at the 64 ha scale (1982). In 1982 the actual CF was greater than random ones at all scales except 16 ha (Figure 4). In the mid 1980s (1984-1987), a period when yearlings were relatively infrequent (Figure 1b), CFs tended to be well within the 95% confidence interval for random values, even though these coefficients were still large, especially at smaller scales (Figure 4). We emphasize that CFs need not approach 1 even at the 64 ha scale (one cannot calculate CFs at any greater scale with our data): For example, if all yearlings had been in one 64 ha plot and all older males in the other, the CF would have been close to 7000 (using 1982 total frequencies of yearling and older males)!

These analyses of spatial scale indicate that within our study area a quadrat of at least 64 ha was necessary to characterize the ratio of yearling:older male redstarts in most years. In some years (1982, probably 1987) a greater area was needed. Our 180 ha study area was therefore almost certainly large enough to estimate reliably the regional male redstart age structure in most, if not all, years. Published estimates of redstart age structure, by contrast, are all questionable due to inadequately small or otherwise inappropriate samples. Ficken & Ficken (1967) found "surprisingly small" proportions of yearling males, averaging 12% in the three deciduous habitats with "large" sample sizes (59, 48, and 34 total males). Howe (1974) observed two habitats in which yearling males comprised 0%-7% of total males, based on similarly small samples. Our results suggest that these low proportions of yearling males are simply artifacts of small study areas, which probably included just preferred habitat from which yearling males were largely excluded by older males (see Sherry & Holmes 1989). Spellman et al. (1987) characterized their redstart study population as having 35% yearling males, but gave no information on number of males, size or characteristics of study area, number of years of study, or variation in age ratios. Rohwer et al. (1980) concluded that American Redstart life-history traits vary geographically, based on their observation that yearling males comprised 25% ($n=71$) and 42% ($n=64$) of museum specimens collected east and west of the Rocky Mountains, respectively. Our results suggest that any such fixed ratio is illusory, unless replicable over large areas and long time periods, because redstarts rarely, if ever, reach a stable age distribution in natural populations.

Spatial variation in redstart age ratios results from variation in habitat quality in a floristically patchy (mosaic) landscape (Morse 1973, Sherry & Holmes 1985). Redstarts compete for territories, and older males are able both to exclude yearlings from mutually preferred habitat, and, at least in some cases, to displace yearlings from already established territories (Sherry & Holmes 1989). Older males have tended year-after-year to avoid settling on parts of our Hubbard Brook study area with higher

proportions of coniferous trees (Sherry & Holmes, unpubl. data), and have also tended more than yearlings to avoid aggregations of pugnacious and socially dominant Least Flycatchers *Empidonax minimus* (Sherry & Holmes 1988). Moreover, yearling male territories have in many years been segregated from patches of older males' territories, forming yearling territory aggregations, the locations of which have changed more from year-to-year than those of older males (Sherry & Holmes, unpubl. data). It is precisely this patchiness in the age-specific distribution of redstart territories that leads to the high coefficients of fluctuation of male age-ratios in space, especially in the years 1983 and 1989-90 (Figures 1 and 4). The ultimate ecological reasons for the habitat preferences or aversions we have observed are under study.

A large spatial scale is necessary to study redstart population demography, if only to characterize the age structure of the population (Figure 4) for the reasons just discussed. Two other lines of evidence emphasize the need for a large spatial area in which to estimate population parameters. First, as we noted elsewhere (Sherry & Holmes 1991; see also Nolan 1978), most yearlings recruited into our study area could not have been produced there, since only 0.6% (1 of 161) nestlings banded in our study area returned there to breed. This suggests that yearlings colonizing our study area have come from a large (but unknown) region surrounding our study area. Second, the redstart population under study is "open", in the sense that many new, older individuals have established territories there each year that were not present in previous years. In most years we have banded all male redstarts on our study area (see legend of Figure 1), yet each year a relatively large number of new, unmated older males established territories on the study plot (59, 48, 40, 36, 20, and 61%, in the years 1985-1990, respectively). We do not know who these males were, except that they were probably individuals that moved from nearby areas onto our study area. Such lack of site tenacity may be due to mating or nesting failure in the previous season or the opportunity to occupy higher quality sites (Sherry & Holmes 1989). Such an influx of new birds, which have resided at least one previous season in breeding regions, onto our study area suggests, again, that ecological circumstances in a large region well beyond its boundaries influence annual abundance, not to mention age structure there (see Sherry & Holmes 1991 for further arguments on scale of population processes).

The area needed to characterize population parameters must in general depend, at least in part, on the scale at which vegetation or other critical habitat characteristics are patchily distributed. Results from the present study suggest that an appropriate study area must include a range of good and poor habitats among which socially unequal groups of individuals have become sorted, and ideally should include replicates of both good and poor habitat patches. Other authors recognize the importance of spatial scale to studies of vertebrate habitat selection (e.g. Karr & Freemark 1983, Morris 1987, Wiens et al. 1987) and population dynamics (e.g. Slade & Balph 1974, Pulliam 1988), yet few studies of migratory birds have been conducted at a large enough scale to obtain demonstrably reliable estimates of population parameters. Our studies indicate that reliable estimates of abundances (e.g. Holmes & Sherry 1988) and age structure (this study), are possible and often apply to a broad region surrounding the study area, increasing our ability to generalize beyond such studies. For example, the high correlation between nesting success one year and yearling recruitment the next (Sherry & Holmes 1991) implies that our measurements of both nest success and yearling recruitment apply to a much broader region than our study area, as discussed above.

Population regulation of migratory birds

We do not understand, for any migratory bird species, what factors regulate or limit their populations. We can, however, outline some of the likely factors involved (Figure 5). The annual cycle of migratory birds consists of at least two sets of habitat-selection events, one in spring and one in winter, to emphasize the importance of large spatial scale factors operating on birds occupying habitat mosaics. In addition, habitats occupied during migration may also be important, although data on this phase of the annual cycle will be very difficult to obtain.

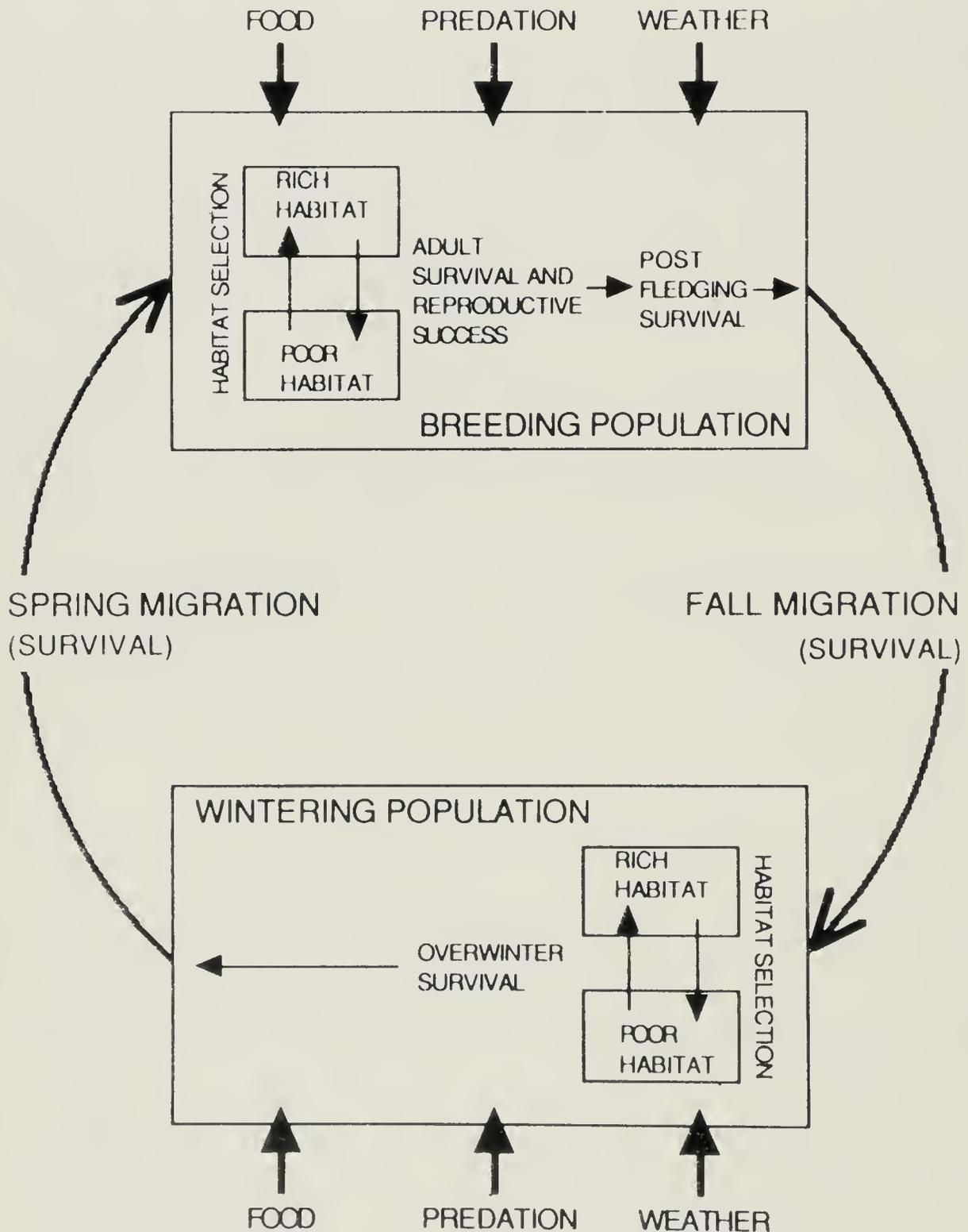


FIGURE 5 – Simplified scheme for important population processes in migratory birds. Following each migration, birds face the problem of selecting new habitat (including the decision of whether to stay with the same habitat as occupied in previous year), often from a mosaic of habitat patches.

Our demographic data on redstarts at Hubbard Brook indicate the importance of breeding season habitat selection: Intraspecific competition mediated via territorial behavior tends to segregate the two age classes, yearlings and older males, into relatively preferred and less preferred habitat patches, respectively. Redstart patterns of habitat selection are indeed strongly dependent on population density, with expansion of both yearlings and older males into less preferred habitats in proportion to density (Sherry & Holmes, manuscript). However, we do not yet know how reproduction and survival vary with density either within or between habitats. Recent study of European Jays *Garrulus glandarius* suggests that with despotic habitat selection, increased expansion of a population into less preferred habitats automatically regulates the population via declining average per capita reproductive success (Andren 1990). We expect that such a mechanism of population regulation operates in redstarts as well, because of their despotic habitat selection, lower reproductive (mating) success in yearlings than older males probably as a consequence of the habitat occupancy patterns (Sherry & Holmes 1989), and strong aversion for coniferous habitats (Morse 1973, Sherry and Holmes manuscript) as though fitness components decline when breeding is attempted in habitat with more coniferous trees.

Populations of many other migratory warbler species may be regulated similarly as they expand into relatively non-preferred habitats, given the often pronounced breeding habitat specificity of these species and their widespread intraspecific competition for preferred habitat (Morse 1989). Both migratory and resident species studied in Europe may be regulated similarly whenever populations expand into less preferred habitat at higher overall population abundance (O'Connor 1985, 1986).

At present few data exist demonstrating competition in migrant birds during the winter (Greenberg 1986), but habitat segregation is widespread. Wintering redstarts compete for habitat in a manner suggesting that suitable sites in which to survive may be in short supply, and could thus limit populations via declining survival when wintering populations expand into less preferred habitat (Figure 5). Although redstart males appear not to be segregated by age into different habitats during winter (A. Sliwa & T.W. Sherry, unpubl. data), the redstart sexes are strongly segregated (Lopez Ornat & Greenberg 1990, A. Sliwa & T.W. Sherry, unpubl. data).

Competition for limited resources in winter is implicated in redstarts by their strong territoriality throughout winter (Holmes et al. 1989), and by the reoccupation by yearling males and females of areas from which territorial older males have been removed experimentally (T.W. Sherry & R.T. Holmes unpubl. data). The sexes of migratory birds are frequently segregated by habitat (Lynch et al. 1985, Lopez Ornat & Greenberg 1990, Wunderle 1991) and geography (e.g. Gudmundsson 1988), although present competition may not be the proximate reason for the patterns in all cases (Morton 1990).

To determine the relative importance of various ecological factors that could influence population demography (Figure 5), and whether these are more important in summer, winter, migration, or a combination of these annual cycle phases, will require measurement of demographic parameters at large spatial scales involving replicated habitat patches. More long-term population studies at several localities and scales throughout the annual cycle are needed to provide such information.

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SYMPOSIUM 27

**FOOD LIMITATION IN BREEDING TERRESTRIAL
BIRD POPULATIONS**

Conveners K. G. SMITH and H. F. RECHER

SYMPOSIUM 27

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NUMERICAL AND DEMOGRAPHIC RESPONSES OF TEMPERATE FOREST BIRDS TO ANNUAL FLUCTUATIONS IN THEIR FOOD RESOURCES

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ABSTRACT. Results of a long-term study of breeding birds in a north temperate deciduous forest in New Hampshire, USA, suggested that bird densities fluctuate in response to changes in abundances of defoliating Lepidoptera larvae (caterpillars). To test this hypothesis more explicitly, we measured bird and caterpillar abundances on four replicate plots over five seasons, and found that bird abundances were significantly correlated with caterpillar biomass in the previous summers, suggesting an effect of food in the previous year on bird reproduction and/or survival. To test the latter, we studied reproductive performance and demography of a common understory, leaf-gleaning warbler (*Dendroica caerulescens*) in years with varying food levels. Reproductive success of this species was positively and significantly related to caterpillar biomass, even though these prey were fluctuating at endemic, not outbreak, densities. Multiple lines of evidence thus indicate that food (caterpillar) abundance influences reproductive success and probably survival of these temperate forest birds, which in turn affect subsequent population levels.

Keywords: Bird reproductive performance, defoliating Lepidoptera larvae, *Dendroica caerulescens*, food limitation, forest passerines, Hubbard Brook, neotropical migrant birds.

INTRODUCTION

Most passerines that breed in temperate zone forests feed extensively on insects, especially during the breeding season. MacArthur (1959) noted that many bird species in North America, especially those that migrate long distances to winter in the tropics, were largely dependent on Lepidoptera larvae (i.e. caterpillars) for food during the breeding period and that this food resource was characterized by periodic irruptions providing superabundant food in some years followed by seasons of relative food scarcity. Although studies have documented that forest birds respond both numerically and functionally to periodic irruptions in their prey populations (e.g. Kendeigh 1947, Morris et al. 1958, MacArthur 1958, Zach & Falls 1975, Morse 1978, Crawford & Jennings 1989), few have examined the influence of insect food resources on abundance, recruitment, and other characteristics of forest bird populations, or even the extent to which food might be limiting (Martin 1987). Indeed, it has practically become dogma that food for temperate-zone birds during breeding is rarely, or at most infrequently, limiting (Fretwell 1972, 1986, Wiens 1977).

Since 1969, we have monitored bird and insect populations in a northern hardwoods forest within the Hubbard Brook Experimental Forest in central New Hampshire, USA. Bird populations in this study area have varied from >200 individuals per 10 ha in 1970-71 to a low of <90 per 10 ha in 1987 (Holmes et al. 1986, Holmes & Sherry 1988, and unpublished data). Peak numbers in the early 1970s coincided with an irruption of a defoliating caterpillar, *Heterocampa guttivita* (Lepidoptera: Notodontidae).

This species again was found in outbreak phase in other parts of New Hampshire in 1980-81, but not within the Hubbard Brook valley. The only other defoliator irruptions at Hubbard Brook in the last 22 years were of two inchworm species (Lepidoptera: Geometridae) in 1982-1983 (Holmes et al. 1986, Rodenhouse 1986). Neither of these had any detectable impact on bird numbers, probably due to small sizes of the caterpillars involved and to the fact they were only available for a short time during the summer (Holmes et al. 1986, Holmes & Sherry 1988). Such infrequent and apparently unpredictable occurrences of defoliator outbreaks in northern hardwoods forests led us to propose that periods of abundant food may, in fact, be infrequent and that long periods between outbreaks might be times when food is potentially limiting for birds in temperate forests (Holmes et al. 1986, Holmes 1988).

To test more explicitly the hypothesis that food, especially caterpillars, may be limiting for temperate forest passerines, we expanded our research in 1986 to monitor bird and caterpillar abundances on four replicate plots, one of which was our long-term Hubbard Brook study area. We also intensified demographic studies of a common, foliage-gleaning paruline warbler (Black-throated Blue Warbler *Dendroica caerulescens*) to examine the effects of food and other factors on its reproductive ecology and survival. In this paper, we consider the correlative associations between bird and caterpillar abundances on these four study sites over a five-year period, 1986-1990, and the reproductive performance of *D. caerulescens* on one site over a series of years with varying food levels.

STUDY AREA AND METHODS

This research was conducted in the Hubbard Brook Experimental Forest and other nearby parts of the White Mountain National Forest in central New Hampshire, USA. Prior to 1986, our efforts were focused on and around the 10 ha study area described by Holmes & Sturges (1975) and Holmes et al. (1986). In 1986, we enlarged this plot to 20 ha, to allow us to estimate more accurately abundances of less common species. Also in 1986, we established three replicate 20 ha plots in nearby sections of the National Forest: (1) on the slope of Mt. Moosilauke, 8 km N of Hubbard Brook, (2) on Stinson Mountain, 13 km SW of Hubbard Brook, and (3) near Russell Crag, 11 km NE of Hubbard Brook. These four sites were located on different mountain systems separated by intervening valleys, roads and/or human development. They were chosen to be similar with respect to elevation (500-600 m a.s.l.), aspect (south-southeast), vegetative cover (northern hardwoods, see Holmes et al. 1986 for description), and land-use history (all had been selectively logged 70-80 years previously). In addition, each had at least one permanent stream with additional intermittent drainages, and was located within unfragmented, relatively homogeneous northern hardwoods forest.

Bird populations were censused intensively on each study plot, with standardized methods in use at Hubbard Brook since 1969 (Holmes & Sturges 1975, Holmes et al. 1986). These involved timed censuses, territory mapping, nest locations and observations of individual birds, all of which, when combined, allowed for quantitative estimates of numbers of individual birds of each species occupying the census area. These estimates took into account territories occurring partly on and partly off the study area, as well as unpaired males (although not of unpaired females or floaters,

if, in fact, any occurred). Bird density estimates are given as numbers of adult birds (males plus females) per 10 ha.

Defoliating caterpillars, mostly Lepidoptera larvae, but also a few sawflies (Hymenoptera: Symphyta), were censused by a visual inspection method (Holmes and Schultz 1988) at two week intervals from late May through mid July. Five censuses were made each year, except for 1987 when there were four. For each census, we visually searched 4000 leaves and the associated stems on each of two tree species (American beech, *Fagus grandifolia*, and sugar maple, *Acer saccharum*), and counted, identified (to family), and measured body lengths of all caterpillars encountered. Each census consisted of two 50-leaf sampling units on sapling or lower branch foliage of each tree species at each of 40 grid intersection points, 50 m apart on each census plot. Caterpillar biomass was estimated using a length-dry weight regression for caterpillars from this forest (J.C. Schultz & R.T. Holmes, unpubl. data, Rodenhouse 1986). Data are expressed as both mean numbers and biomass (in mg) of caterpillars per 1000 leaves.

For demographic and reproductive data, Black-throated Blue Warblers were studied on an 80 ha study area, which included and surrounded the long-term census plot at Hubbard Brook. Individual birds were caught, color-banded, and their breeding activities followed through each season. All nesting efforts of the 20-25 pairs occupying the study plot were recorded each year, including clutch sizes, fledging success, fledging mass (at day 6 of the nestling period), and frequencies of late season clutches and of second-brooding.

RESULTS

Numerical responses of birds to changing food levels

During summers of 1986 to 1990, mean caterpillar abundances for all four plots combined ranged from 2.4 to 4.1 per 1000 leaves, and mean caterpillar biomass varied from 6.4 to 17.9 mg/1000 leaves (Figure 1). These values are low compared to outbreak years at Hubbard Brook (20-40 caterpillars, with cumulative biomasses of >80 mg, per 1000 leaves; Rodenhouse 1986). Thus, caterpillar abundances during this study represented endemic or non-outbreak levels. Even so, caterpillar numbers and biomass did vary significantly between years (Kruskal-Wallis test, $H = 9.73$ and 10.08 , respectively, $df = 4$, $P < 0.05$). Both numbers and biomass of caterpillars generally increased from 1986 through 1989 and then declined in 1990 (Figure 1).

Because foliage-gleaning species (mostly warblers, vireos, grosbeaks, tanagers, see species list in Holmes et al. 1986) feed extensively on caterpillars (Robinson & Holmes 1982) and because they dominate community patterns by their numerical abundance (Holmes et al. 1986), we considered their population changes in most detail. Mean numbers of individuals of (1) just those bird species that take prey primarily from foliage, (2) the three most common foliage gleaners (*D. caerulescens*, *D. virens*, and *Vireo olivaceus*), and as a consequence (3) total birds on the four study plots decreased slightly from 1986 to 1987 and then increased through 1990 (Figure 1). The same general patterns occurred on each individual plot (R.T. Holmes unpubl. data).

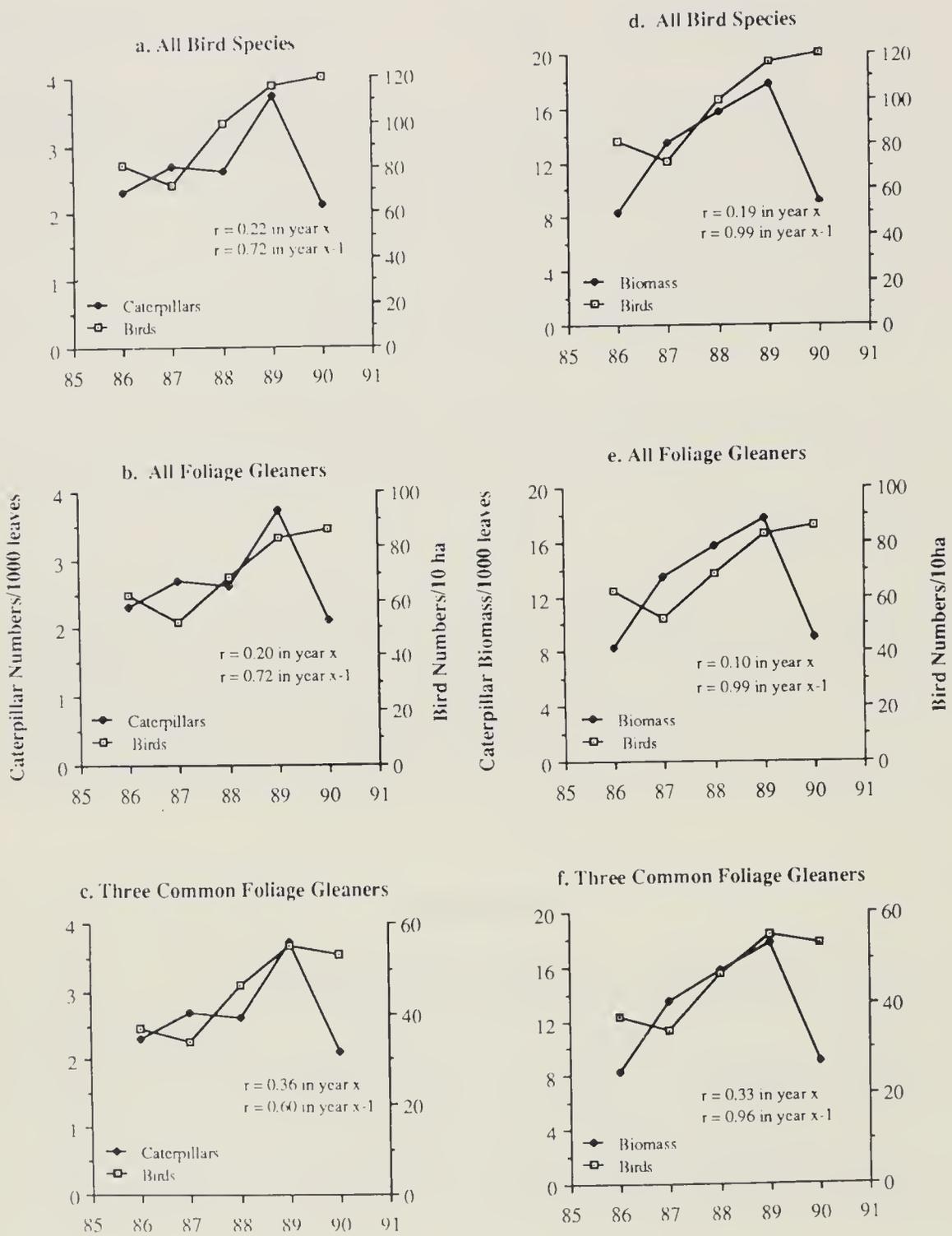


FIGURE 1 – Annual trends in the numbers and biomass of caterpillars and (a,d) combined abundances of all bird species, (b,e) all foliage-gleaning species ($n = 11-12$, see list in Holmes et al. 1986), and (c,f) the three most common foliage gleaners (*Vireo olivaceus*, *Dendroica caerulescens*, *D. virens*). Values are means for four replicate plots in each year of study 1986-1990. Correlation coefficients (r) are given for relationships between bird and caterpillar numbers in the same years (year x) and between bird numbers in one year and caterpillar numbers and biomass in the previous summer (year $x-1$).

Trends in numerical abundances of these three groups of bird species were weakly correlated ($r = 0.20-0.36$) with mean numbers of caterpillars present in the same years. However, when bird densities were compared to caterpillar numbers in previous summers, this association was measurably strengthened ($r = 0.60-0.72$, Figure 1). The same pattern of low or no correlations in the same years held for bird abundance with caterpillar biomass ($r = 0.10-0.33$), but these increased to statistically

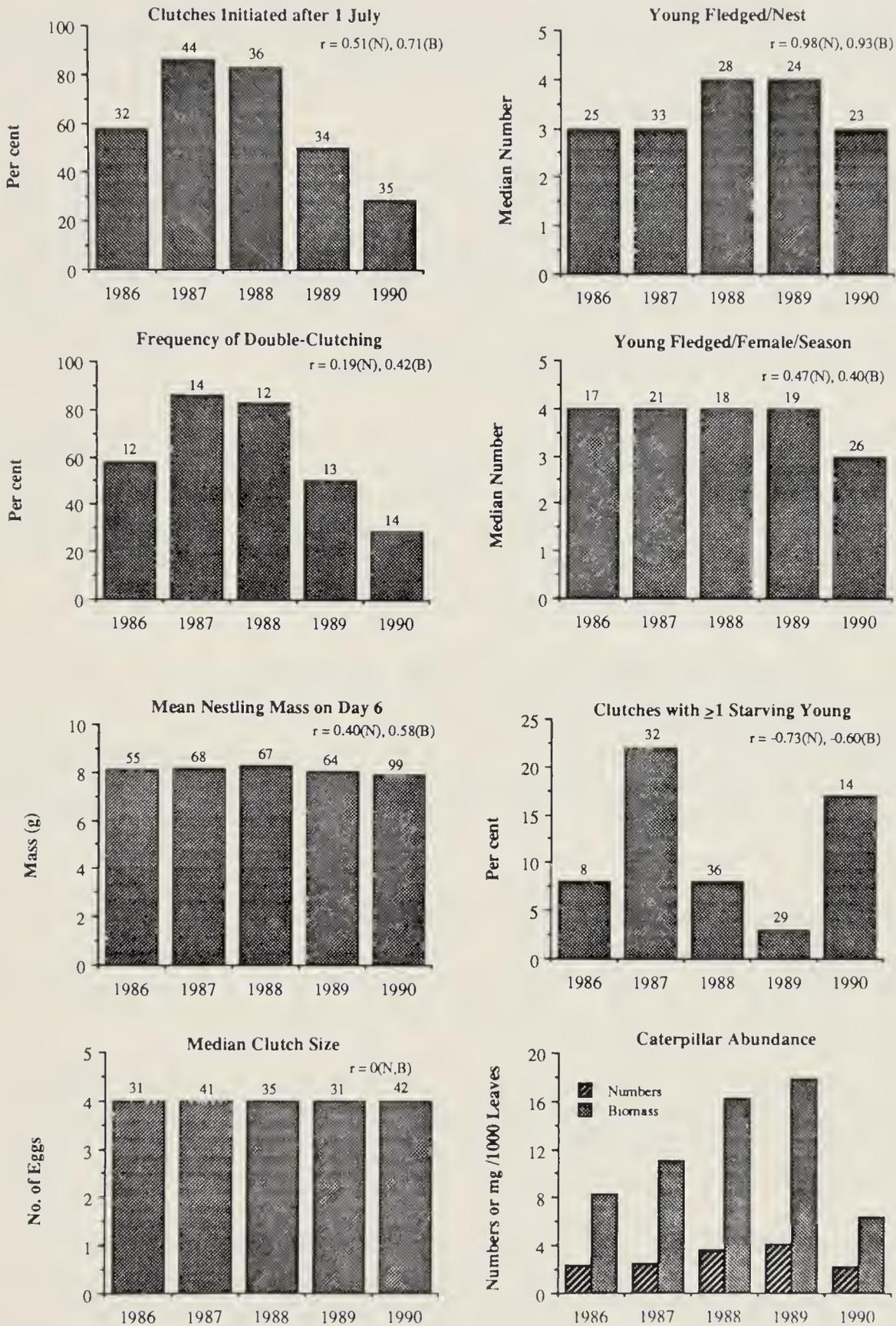


FIGURE 2 – Reproductive performance of *Dendroica caerulescens* and caterpillar abundance (numbers and biomass) on the Hubbard Brook study area, 1986-1990. Explanations: mass of nestlings on day 6 (hatch = day 0), as an index of fledging weight; double clutching based on the % of pairs laying a second clutch after having successfully fledged young from a previous nest; and clutches with >1 starved nestlings, as an indicator of starvation levels. Numbers above each column indicate numbers of nests sampled, except for nestling mass in which case n = number of individual nestlings. Correlation coefficients (r) are given for each measured reproductive parameter with caterpillar numbers (N) and biomass (B).

significant levels ($r = 0.96-0.99$, $P < 0.05$, $df = 2$) when bird numbers were correlated with caterpillar biomass the previous season (Figure 1). These results indicate that years with greater food (caterpillar) resource abundance are followed by years with higher bird population densities.

Demographic responses to changing food levels at Hubbard Brook

Findings above suggest that the number of birds in one season may be influenced in some way by caterpillar abundance the previous summer. One possible causal mechanism is that food supply may affect bird reproductive output and/or survivorship, especially of newly fledged young. To explore this at the population level, we examined the reproductive ecology of *D. caerulescens* in relation to annual differences in caterpillar abundance on the Hubbard Brook study area.

Like the various groups of species shown in Figure 1, the change in abundance of *D. caerulescens* on the Hubbard Brook study area was also strongly and significantly correlated with caterpillar numbers and biomass present the previous summer ($r = 0.99$ and 0.94 , respectively, $P < 0.05$, $df = 2$), but not at all with caterpillar numbers or biomass in the same year ($r = 0.06$ and -0.07). Thus, *D. caerulescens* provided an appropriate species to examine for the mechanism proposed above.

Between 1986 and 1990, caterpillar numbers and biomass on the Hubbard Brook study area increased through 1989 and then declined sharply in 1990 (Figure 2). Among the reproductive variables of *D. caerulescens* we measured, only median clutch size did not vary among years (Figure 2). Of the other parameters measured, the mean number of young fledged per nest was positively and significantly correlated ($P < 0.05$, $df = 3$) with both caterpillar numbers and biomass (Figure 2), while the frequency of pairs laying a second clutch after successfully completing the first, percentage of nests initiated after 1 July, and number of young fledged per pair per season also were positively correlated with caterpillar abundance but not significantly so (Figure 2). Some parameters, especially late-season nests and double clutching, are indicators of increased nesting efforts, and reflect effects of nest predation, weather events, and other factors, as well as differences in food levels.

Percentage of clutches that had one or more young die of starvation ranged from 3-22% (Figure 2), and were negatively correlated with caterpillar numbers ($r = -0.73$) and biomass ($r = -0.60$). Although not statistically significant, these trends indicate that starvation increased in years when caterpillar abundance was low.

For an overall index to annual reproductive success of *D. caerulescens*, which could be related to caterpillar biomass, we multiplied values from Figure 2 for (1) clutch size (median), (2) fledging success (mean number of young fledged per nest/median clutch size), (3) frequency of second brooding ($1 + \% \text{ second brood attempts}$), (4) frequency of starvation ($1 - \% \text{ nests with } >1 \text{ starved young}$), and (5) fledging mass (relativized as actual mass/heaviest mass recorded during the 5-year study). This composite index was positively and significantly related to mean annual caterpillar biomass (Figure 3), indicating that *D. caerulescens* had higher reproductive success in years with greater caterpillar abundances.

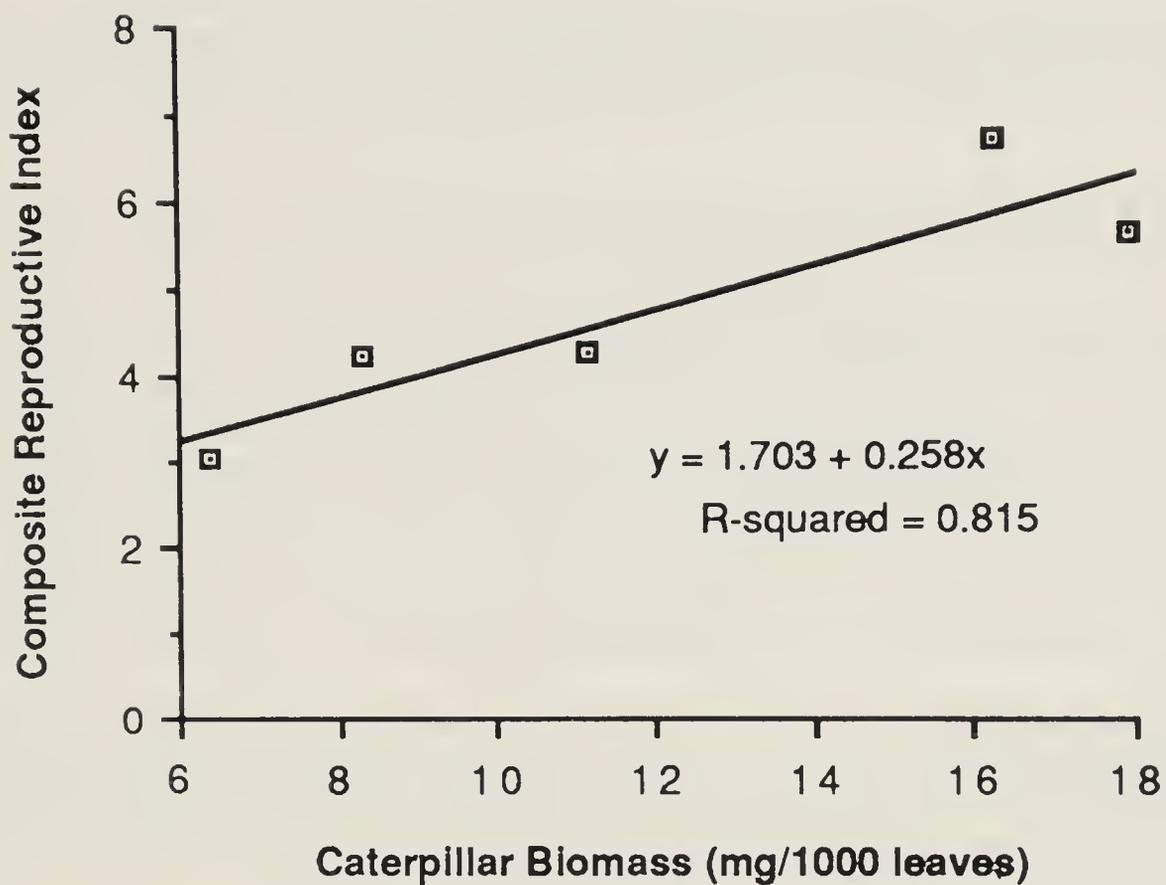


FIGURE 3 – Relationship between annual reproductive success of *Dendroica caerulescens*, as estimated by a composite reproductive index (see text), and mean annual caterpillar biomass on the Hubbard Brook study area, 1986-1990.

DISCUSSION AND CONCLUSIONS

These results support the hypothesis that bird populations in temperate deciduous forests are affected by changes in food abundance during the breeding period. Correlative associations between caterpillar numbers one year and bird numbers the next were found even during a period of relatively stable and low caterpillar abundances, i.e. in the absence of a major defoliator outbreak or irruption. Furthermore, reproductive performance of *D. caerulescens* was significantly correlated with caterpillar biomass (see Figures 2 and 3). These correlations are particularly significant since this species provisions its young primarily with caterpillars when they are available (T.W. Sherry and R.T. Holmes, unpubl. data). Additional evidence of a connection between reproductive success and subsequent population levels in temperate breeding passerines comes from a related study at Hubbard Brook, in which annual recruitment of yearling male American Redstarts *Setophaga ruticilla* was found to be strongly and significantly correlated to redstart fledging success the previous summer (Sherry & Holmes 1991). In that case, factors that affected nesting success were primarily nest predation but also food abundance.

Several limitations to the present study need to be mentioned, all of which would tend to weaken the relationship between caterpillar abundance and bird population responses. First, although caterpillars are important prey for these bird species, especially when adult birds are feeding nestlings and fledglings, they are not the only prey taken. Beetles, flies, spiders, adult moths, and other arthropods are also commonly

taken as food, and may comprise 50-90% of the prey of these species during mid summer (Robinson & Holmes 1982). These other food items may supplement caterpillars in some years and in some parts of the summer season (see Rodenhouse 1986).

Second, the spatial and temporal scales at which these relationships were examined need to be considered. Defoliator irruptions in temperate forests appear to be patchily and unpredictably distributed in time and space (Holmes 1988). Since birds are capable of dispersing widely, one might expect less variability in their population changes across a landscape than in that of their prey. If so, bird populations might fluctuate more synchronously on a regional scale (Holmes & Sherry 1988), while caterpillar abundances would vary more on a local level. In fact, this variability in food abundance was the primary motivation for conducting the present study on replicate plots, a procedure all too rare in avian population studies. Nonetheless, our results indicate that samples from even four replicate sites may still not adequately represent changes in food abundance for these forest birds, especially its local spatial variability.

Third, small sample sizes (5 years or data points per correlation) make the strength of the observed correlations all the more impressive. Single deviant observations can strongly influence significance of such correlation coefficients. More data over a longer series of years, especially some with outbreak densities of caterpillars, will be needed to test more definitively the generality of our findings.

Fourth, there are many other factors that affect bird abundances and reproductive success. Most obvious are mortality factors, especially those operating during migration or in winter, and nest predation (Martin, this symposium). Although we have little data on such mortality, we do know that nest predation within our study areas at Hubbard Brook is highly variable both within and between seasons (Rodenhouse 1986, Reitsma et al. 1990, Sherry & Holmes 1991). This variability may mask or mitigate effects of food shortage (Rodenhouse 1986).

Since the occurrence and operation of any combination of the four factors described would be expected to weaken a correlation between caterpillar (food) and bird population abundance, the fact that we found relatively strong correlations provides, we believe, compelling evidence of chronic food limitation for birds during breeding. If low caterpillar abundance results in lower reproductive output of breeding birds, by inference then, food may be limiting (Martin 1987). The extent, frequency, and importance of such food limitation for these forest bird populations, however, has yet to be determined. From a 1982-1985 study of *D. caerulescens* at Hubbard Brook, Rodenhouse (1986) concluded that food was an important factor limiting annual breeding productivity in two of the four years of his study. From our extension of his data here through 1990, it appears that food was important in about five of 9 years, but perhaps most severely in one year (1984). In the latter year, starving nestlings were documented in 48% of *D. caerulescens* broods, double clutching did not occur, and nestling weights on day 6 averaged 7.59 g (Rodenhouse 1986), the lowest of any year for which we have data (see Figure 2). Also, in 1984, nestling starvation was frequent for other species breeding at Hubbard Brook (Sherry & Holmes 1991).

Our correlative findings therefore indicate that food resources in summer, and specifically caterpillars, influenced bird reproductive success and probably survival, and, thus, are at least one important factor influencing abundances of these species in their north temperate breeding habitat. More definitive tests of food limitation and evalua-

tions of the relative importance of food, nest predation and other factors on reproductive success, recruitment, and survivorship will require long-term demographic studies, coupled with experimental manipulations of food resources, bird brood sizes, and perhaps even nest-predator populations.

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TEMPORAL AND SPATIAL VARIATION IN THE ABUNDANCE OF EUCALYPT CANOPY INVERTEBRATES: THE RESPONSE OF FOREST BIRDS

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ABSTRACT. Numbers and kinds of invertebrates in the canopies of Australian eucalypt forests differ among tree species, with season, and from year to year. Birds respond to invertebrate abundances by selecting between trees according to the abundance, kinds and sizes of invertebrates found on each species. Carbohydrate-dependent species forage preferentially on trees with an abundance of lerp, an energy-rich secretion produced by psyllid (Hemiptera) insects. In eastern Australia, the selection, by foraging birds, of tree species with abundant lerp is greatest during the cooler months when invertebrates are least abundant and energy demands the greatest. In Western Australia, where seasonal changes in invertebrate numbers are less pronounced, birds also select trees with large numbers of invertebrates and respond to psyllid outbreaks by foraging on those trees with the most abundant lerp.

Keywords: Eucalypt forests, canopy invertebrates, lerp, forest birds, avian food resources.

INTRODUCTION

Eucalypt forests are fluctuating environments with significant temporal and spatial variation in avian food resources (e.g., Recher et al. 1983, Bell & Ford 1990, Ford et al. 1990). These variations occur in response to seasonal climatic patterns, to annual differences in weather, to soil nutrients and moisture, and to the effects of fire (Ford & Recher 1991). Resources therefore differ in kind and abundance at local, regional and continental levels from season to season, and from year to year. Many of the patterns of food availability are imposed by erratic and largely unpredictable variations in rainfall.

Birds respond to patterns of food abundance by seasonal migration and by aggregating opportunistically in areas of high food abundance. Such movements result in seasonal and annual changes in the relative abundance of bird species and the composition of avian communities (Recher et al. 1980, 1983). Although avian species richness is correlated with the structural complexity of the vegetation (Recher 1969, Recher et al. 1980, in press), soil nutrients and moisture also affect patterns of species diversity and differences in species composition (Gilmore 1985, Recher 1985, Braithwaite et al. 1989). Presumably the effect of differences in soil nutrients and moisture on avian communities is expressed through the kinds and abundances of food resources that can be sustained by the vegetation. Productivity of food resources may be high, low, consistent or variable, according to the annual availability of nutrients and moisture. Each combination (e.g. low and variable productivity, low and consistent productivity) should sustain a different community of birds.

The response of birds to spatial patterns of food abundance, the effects of temporal variation in the kinds and abundances of food on reproductive success, and the relationship between productivity and community structure are largely unknown for

Australian avifaunas. Since 1985, two of us (HFR, JDM) have studied the distribution and abundance of eucalypt canopy invertebrates (Majer & Recher 1988, Majer et al. 1989). In this paper we present information on the temporal and spatial patterns of canopy invertebrate communities in eastern and Western Australia and discuss them in relation to the foraging behaviour of birds. We then consider the ways in which patterns of food abundance have affected the evolution of the Australian avifauna.

METHODS AND DATA ANALYSIS

Canopy invertebrates were sampled seasonally using chemical fogging at Scheyville near Sydney in eastern Australia from January 1987 to January 1988 and at Karragullen near Perth in Western Australia from April 1987 to January 1989. Two species of eucalypts were sampled at each site: Ironbark *Eucalyptus crebra* and Box *E. mollucana* at Scheyville, and Marri *E. calophylla* and Jarrah *E. marginata* at Karragullen. For site details and a description of sampling methods see Recher (1989) and Majer et al. (1990).

Bird foraging data were collected by HFR using the procedures described by Recher and GebSKI (1990). Data from individual species are combined into foraging guilds using those described in Holmes and Recher (1986) and Ford et al. (1986). Foraging data were recorded for Australian warblers (Acanthizidae) at Scheyville during 1984 and 1985, and for all species of birds in 1987. Foraging data were obtained at Karragullen for Australian warblers in 1986 and for all birds in September 1987, January 1989 and November 1989. Bird names follow CSIRO (1969).

Differences in the use of eucalypt species by foraging birds was tested using Pearson Chi Square. Unless otherwise indicated significance was accepted at $P < 0.01$.

RESULTS

Canopy invertebrates

In eastern Australia, numbers of invertebrates were greater for all seasons on Ironbark than Box (Table 1a). However, the biomass of invertebrates was greater on Box than Ironbark during spring 1987 and summer 1988, but less during summer, autumn and winter in 1987 (Table 1b). In Western Australia, the numbers of invertebrates were relatively similar on Marri and Jarrah for six of the eight samples analysed. On one occasion (spring 1988) they were greater on Marri and once (summer 1989) they were greater on Jarrah (Table 1a). For five sampling periods (autumn and winter '87, summer '87, spring '88, summer '89) invertebrate biomass was greater on Marri than Jarrah. On two occasions (winter '87, spring '88) the greater biomass was due to a small number of large sawfly (Pergidae) larvae and once (summer 88/89) to a few large moth (Lepidoptera) larvae. After excluding large insects, invertebrate numbers and biomass were generally greater on Ironbark and Box than on Marri and Jarrah (Table 1a,b). Foliage nutrients (N,P,K) were significantly greater for Ironbark than Box and for Marri than Jarrah (Majer & Recher unpubl.). Ironbark and Box had greater nitrogen and phosphorus levels than Marri and Jarrah, but less potassium.

At Scheyville, the numbers and biomass of canopy invertebrates on Box tended to be higher during spring and summer than autumn and winter (Table 1a,b). On Ironbark,

invertebrate biomass was lowest in autumn and winter. Numbers of invertebrates on Ironbark were lowest in winter, but also showed a pronounced difference between years with the summer and autumn of 1987 having higher numbers than spring and the summer of 1988 (Table 1a). Much of the seasonal increase in invertebrate numbers on Ironbark was by psyllid insects (Hemiptera) (Majer & Recher unpubl.). Psyllids produce lerp, an energy-rich carbohydrate used by many birds.

TABLE 1 – Abundance of canopy invertebrates.

Tree species	Season									
	1987			1988				1989		
	S	A	W	S	S	A	W	S	S	
A. NUMBERS¹										
Jarrah	-	20	23	22	12	10	32	19	49	
Marri	-	24	21	20	15	11	35	27	20	
Ironbark	111	114	64	75	69	-	-	-	-	
Box	65	52	48	53	61	-	-	-	-	
B. BIOMASS² (x100)										
Jarrah	-	15	42	54	20	13	33	9	45	
Marri	-	26	768*	22	72	13	17	133*	180**	
Ironbark	85	48	61	121	56	-	-	-	-	
Box	50	26	15	280	84	-	-	-	-	

¹ mean number/0.5 m² net (N = 200 nets)

² mean g/tree (10 x 0.5 m² nets) (N = 20 trees)

* includes sawfly larvae

** includes moth larvae

TABLE 2 – Percentage of prey-attacks on Ironbark and Box by different foraging guilds at Scheyville, eastern Australia, during 1987.

Foraging guild	Season			
	Spring	Summer	Autumn	Winter
A. Lerp-eaters				
Ironbark (44) ¹	70	67	84	78
Box (56)	30	33	16	22
(N)	(411)	(294)	(405)	(375)
B. Insect-eaters				
Ironbark (44) ¹	45	72	72	68
Box (56)	55	28	28	32
(N)	(275)	(47)	(118)	(95)

* ** significantly different within each foraging guild, Pearson Chi-square, $P < 0.001$

¹ The percentage of foliage shared between the two eucalypts studied on each site is shown in parentheses.

There was no obvious seasonal pattern of invertebrate abundance or biomass in Western Australia on either tree species, although some groups of insects, including psyllids, had seasonal peaks of abundance (Majer & Recher unpubl.). However, there may be a trend towards lower numbers and reduced biomass during summer and autumn when it is dry in Western Australia, and higher numbers and greater biomass in autumn and spring when it is moist.

Use of tree species

In eastern Australia, birds generally selected Ironbark over Box as foraging substrates (Table 2). Same birds (e.g., honeyeaters, silvereyes, pardalotes) feed extensively on energy-rich carbohydrates (lerp, manna, honeydew) found on eucalypt foliage and twigs and preferred Ironbark at all seasons. Birds (e.g., flycatchers, whistlers, robins) that seldom take carbohydrates selected Ironbark as a foraging substrate during summer, autumn and winter. During spring these birds foraged on both species in about equal proportions to the amount of foliage of each species (Table 2) ($P = 0.65$).

In Western Australia, Marri was selected over Jarrah significantly more often in January 1989 (Pearson Chi Square, 94.815, $P < 0.001$), than in November 1989 (4.376, $P = 0.036$) or September 1987 (6.357, $P = 0.012$) (Table 3a). The small number of insectivores at Karragullen prevented a separate analysis of carbohydrate and noncarbohydrate dependent guilds for the Western Australian data.

The Striated Pardalote, *Pardalotus substriatus* was the most abundant lerp-eating species on the Karragullen plot. During September 1987 and January 1989, it foraged significantly more often on Marri than Jarrah, but in November 1989 Striated Pardalotes foraged on Marri and Jarrah in about the same proportion as the amount of foliage of each species ($P = 0.65$) (Table 3b).

TABLE 3 – Percentage of prey-attacks on Jarrah and Marri at Karragullen, Western Australia, by foliage-foraging birds.

Tree species ¹	Sep '87	Month/year	
		Jan '89	Nov '89
A. All species			
Jarrah (89)	79	55	83
Marri (11)	21	45	17
(N)	(149)	(341)	(309)
B. Striated Pardalote			
Jarrah (89)	60	47	91
Marri (11)	40	53	9
(N)	(48)	(118)	(110)

¹ The percentage of foliage shared between the two eucalypts studied on each site is shown in parentheses.

TABLE 4 – Selection of tree species by Australian Warbler (Acanthizidae) in Eastern and Western Australia as the percentage of prey-attacks.

A. EASTERN AUSTRALIA		Tree species¹	
Bird species (N)		Ironbark (44)	Box (56)
White-throated Warbler (349)		55	45
Little Thornbill (1404)		73	27
Striated Thornbill (1492)		69	31
Weebill (1136)		91	9
B. WESTERN AUSTRALIA		Tree species¹	
Bird species (N)		Marri (11)	Jarraah (89)
Western Warbler (154)		34	66
Western Thornbill (189)		25	75
Broad-tailed Thornbill (257)		21	79

¹ The percentage of foliage shared between the two eucalypts studied on each site is shown in parentheses.

Australian warblers

On both plots, Australian warblers were among the most abundant species (Recher unpubl.). Species differed in their use of foraging substrates, foraging behaviour and foraging height range (Recher 1989, unpubl.). They probably also differed in the kinds of prey taken. In eastern Australia, Little *Acanthiza nana* and Striated *A. lineata* Thornbills and the Weebill *Smicrornis brevirostris* frequently fed on lerp, whereas the White-throated Warbler *Gerygone olivacea* did not (Recher unpubl.).

At Scheyville both thornbills and the Weebill foraged significantly more often on Ironbark than Box (Table 4a). Although the White-throated Warbler foraged significantly less often on Ironbark and more often on Box than the thornbills or the Weebill, it also used Ironbark significantly more often than Box. Weebills foraged significantly more often on Ironbark and less on Box than either Little or Striated Thornbills.

Western Warbler *G. fusca*, Broad-tailed Thornbill *A. apicalis*, and Western Thornbill *A. inornata* foraged significantly more often on Marri than on Jarraah relative to the proportion of foliage of the two eucalypts (Table 4b). There were no significant differences ($P = 0.07$) between the Western Warbler and the thornbills in their use of the foliage of the two eucalypts.

DISCUSSION

Birds foraged more often on trees with high foliage nutrient levels; in eastern Australia, Ironbark was used more often than Box, and Marri more than Jarraah in Western Australia. Canopy invertebrates were consistently more abundant on Ironbark than Box, but Marri and Jarraah appear to have had similar abundances of invertebrates. The preference for Ironbark and Marri is probably related to the greater abundance of lerp-forming psyllid inserts on these two species (Majer & Recher unpubl.).

When invertebrate numbers and biomass increased, birds were less selective in their choice of tree species (Tables 2 & 3). At Scheyville most species increased their use of Box and decreased their use of Ironbark during the spring and summer (Table 2). This may reflect the increased numbers of invertebrates overall and the need for breeding birds to forage for insects, as distinct from carbohydrates, thereby diminishing the distinction between Box and Ironbark as foraging substrates. We also have data suggesting that Box may have had larger sized insects on average than Ironbark during the warmer months (Majer & Recher unpubl.). This may have made Box more attractive to breeding birds. During winter when energy demands are high and requirements for protein are probably lower, birds forage for energy-rich carbohydrates and select for trees where lerp is present, despite the lesser amount of lerp than in spring and summer.

Seasonal changes in invertebrate abundance were more pronounced at Scheyville than at Karragullen (Table 1a,b). However, the Western Australian plot had more frequent irruptions of insects (e.g., sawflies, moths) which greatly increased invertebrate biomass for brief periods (Table 1b). There were also increases in psyllid insects with regular, brief outbreaks on Marri and on occasion, on Jarrah (HFR pers. obs.). These outbreaks did not coincide with sampling periods and are absent from the invertebrate samples. The preference for Marri by Striated Pardalotes in September 1987 and January 1989 and for Jarrah in November 1989 (Table 3b) is due to the large amounts of lerp on these species when foraging data were collected (Recher pers obs).

The relationship between foliage nutrients and psyllid insects is a significant aspect in the ecology of eucalypt forest avifaunas. The most abundant birds in eucalypt ecosystems are carbohydrate-dependent species; honeyeaters, silveryeyes, pardalotes, and Australian warblers, such as Weebill and Striated Thornbill. They also comprise a significant proportion of the species present in any community. As pointed out by Recher (1985), the richest and most abundant eucalypt forest avifaunas are associated with nutrient-rich soils and abundant moisture. Recently, Braithwaite et al. (1989) showed a correlation between foliage calcium levels and bird species richness in forests of southeastern New South Wales. They related high calcium levels to high forest primary productivity, probably indicating abundant invertebrate and carbohydrate food resources for birds.

In general eucalypt forests growing on nutrient-rich soils and with abundant moisture are more productive and sustain richer and more abundant avian communities (Braithwaite et al. 1989, Recher 1985, Recher et al. in press). This is illustrated by the comparative richness of the avifaunas at Scheyville and Karragullen. Between 1984 and 1988, 66 species of birds were recorded nesting at Scheyville, while only 36 species nested at Karragullen between 1986 and 1989 (Recher unpubl.). Numbers of birds were also much greater at Scheyville than at Karragullen.

In eucalypt forests there may be long periods of reduced production of invertebrates interspersed with outbreaks of psyllids and other insects. These temporal patterns are associated with several features of Australian environments. These include: 1. *low soil fertility* - requiring periods of time for vegetation to accumulate energy reserves to flower or for abundant insect populations to develop; 2. *low seasonality* - long periods of leaf production and abscission, also affecting productivity; 3. *climatic variation* - significant annual differences in rainfall affecting both primary productivity and the abundance of invertebrates; 4. *fire* - which releases nutrients and stimulates

vegetative growth and associated invertebrate populations; 5. *temporal and spatial patchiness of eucalypt blossoming* – which results from the above, but may also be synchronized within a species population to attract pollinators, facilitate outcrossing, and satiate seed predators.

The avifauna has responded to these conditions by: 1. occurring at low densities; 2. moving locally and aggregating at patches of forest rich in food; 3. being long-lived; 4. having potentially long breeding seasons; 5. having small clutch sizes; 6. group living and feeding; 7. breeding co-operatively.

Bird species richness therefore differs significantly between years and from place to place within the same forest type on poorer and drier soils (for an example see Recher et al. 1980), while remaining uniformly high in forests on rich soils receiving regular rain. Such variations are primarily associated with carbohydrate dependent species including those (e.g. honeyeaters, lorikeets) which feed on nectar and those (e.g. pardalotes, honeyeaters) which depend on alternative carbohydrates, such as lerp and manna, as well as arthropods. The abundance and kinds of food resources in eucalypt forest not only influence where birds forage, but determine overall community structure and richness.

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FOOD LIMITATION IN TROPICAL BIRD POPULATIONS

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ABSTRACT. Food resources in tropical ecosystems often are considered abundant, diversified, seasonally stable and, consequently, unlimiting, at least when compared to spring in temperate and boreal areas. However, several well-documented examples show that permanently low levels or strong fluctuations of food availability may affect both timing of breeding, clutch size, breeding success, territory size or seasonal movements in tropical birds. Granivorous, frugivorous, as well as large carnivorous bird species, have been found to be limited by food in a variety of habitats ranging from Mexican deserts to West African savannas and neotropical rain forests. The distinction between prey accessibility and actual prey density is emphasized. It also is suggested that low food availability may be one constraint explaining low clutch size and rarity of many species, and, hence, the structure of bird communities in tropical forests.

Keywords: Food supply, birds, tropical forests, savannas, breeding, seasonal movements.

INTRODUCTION

Food is one of the most widespread and important factors limiting bird populations. Conversely, food supply is often considered greater and more permanent, and, hence, unlikely to be limiting, in tropical than in temperate areas. Empirical observations suggest that food availability may be limiting in the tropics, even in the seemingly richest rain forests. Yet, no experiment has provided compelling evidence of unambiguous food limitation in the tropics.

Much discussion, refinements, experimental testing and field evidence (see Thiollay 1988b) have confirmed Lack's hypothesis (1968) on the prominence of food supply on clutch size determination, even if seasonality, predation rate, phylogeny, nest size or adjustment to mortality also play a role (Murray 1985). Prey availability may be a constraint at all stages of the breeding cycle, from pair bond and egg formation to the survival of independent young. However, whether food supply is really limiting, probably depends on the period and habitat type considered. From wet primary forests to deserts, tropical areas undergo increasing, and sometimes dramatic, seasonal changes and interannual fluctuations, which may lead to divergent conclusions about the effect of food supply on bird populations.

My goal is not to resolve a conflicting body of data (see Lima 1987, Martin 1987) but to review briefly some selected studies from a wide range of habitats, latitudes, continents and guilds that suggest food limitation occurs in tropical bird populations. This review is intended to draw attention to the possible and widespread influence of food level on foraging behavior, productivity and dynamic of breeding tropical populations.

FORAGING SUCCESS, BREEDING SEASONS AND CLUTCH SIZE IN RAIN FORESTS

Breeding birds in tropical forests do not experience the high spring flush of insect food and lengthening of daylight observed in the temperate zone (Morse 1989). During the short temperate breeding season, food also may become more abundant than at any time in lower latitudes (Hails 1982). Thus, tropical bird populations may be much closer to the maximum carrying capacity of their habitat at all times, although some temperate populations may be at saturation during the breeding season (Monkkonen 1990).

Yet, marked seasonal fluctuations of food supply occur in the tropics, even in the most humid and stable primary forests. Productivity of both leaves, fruits and arthropods, from the litter to the canopy, can vary considerably as can the bird populations themselves (Karr 1976, Willis 1976, Greenberg 1981, Sabatier 1985, Boinski & Fowler 1989). In some cases, seasonality of insect food determines timing of breeding cycles, even among understory frugivores (Levey 1988). Seasonal changes also are probably responsible for the well-defined breeding seasons observed in most tropical forest species (Fogden 1972, Thiollay & Tostain unpubl.), although tropical breeding seasons are often spread over a longer period than are temperate seasons. Further, a greater seasonality of reproduction has been reported in canopy birds than in those of understory (Loiselle 1988), and severe dry or rainy seasons occasionally will cause famines (Leigh et al. 1983) or large scale movements (pers. obs.), especially among large frugivores (such as Tucans *Ramphastos* sp., pers. obs. in French Guiana).

The mean standing biomass or annual production of arthropods is not much higher in tropical forests than in temperate forests in spring (Janzen 1973, Penny & Arias 1982, Erwin 1983, Owen 1983). Particularly outbreaks of caterpillars, a rich prey base in temperate forests, are rare in rain forests (Thiollay 1988b). The high number of morphologically and behaviourally different prey species, their often spectacular antipredator defenses, their patchy distribution in space and time and heavy rains are additional factors limiting food availability in tropical forests. Food limitation in understory rain forest birds is inferred from high proportion of daily time spent foraging (Marcotullio & Gill 1985), low rates of prey delivery to nestlings (Skutch 1976), reduced growth rates (Ricklefs 1976, Martin 1987), starvation of young (Dyrce 1985), and long post-fledging dependence (Tostain pers. comm.).

Foraging behavior and success may be an indicator of food availability (Hutto 1990). Even when corrected for prey size and bird body size, success rate of actively-foraging small foliage gleaner insectivores in an Amazonian rain forest was found to be four to six times lower than that of similar species in a temperate forest (Thiollay 1988b). The variance of this attack rate, indicating the patchiness of prey distribution, also was higher in tropical than in temperate forests. Rain forest birds also made more frequent use of concealed prey and costly foraging techniques. Thus, both density, detectability, accessibility and distribution predictability of prey may be lower in tropical than in temperate forest ecosystems, at least for small insectivores. This constraint may limit the ability to raise more young and may determine, in part, the lower clutch sizes of tropical forest birds (two eggs for many passerines, compared with four to eight eggs for their temperate counterparts). Seemingly, Beissinger (1990) has shown that brood size is limited by food supply in a neotropical wetlands' raptor. Lower food availability also may be a major constraint contributing to the rarity of

many species, and hence, structure of tropical forest breeding bird communities. However, Skutch (1976) questioned that clutch size may be limited by food supply and offered anecdotic examples of the ability of some neotropical birds to rear more young than the usual brood. Predator avoidance, heat stress, low energetic needs, or metabolic rate also can interfere with prey availability. Tropical bird populations, in forest understory, also may be socially regulated at a level below limits set by food resources (Greenberg & Gradwohl 1986).

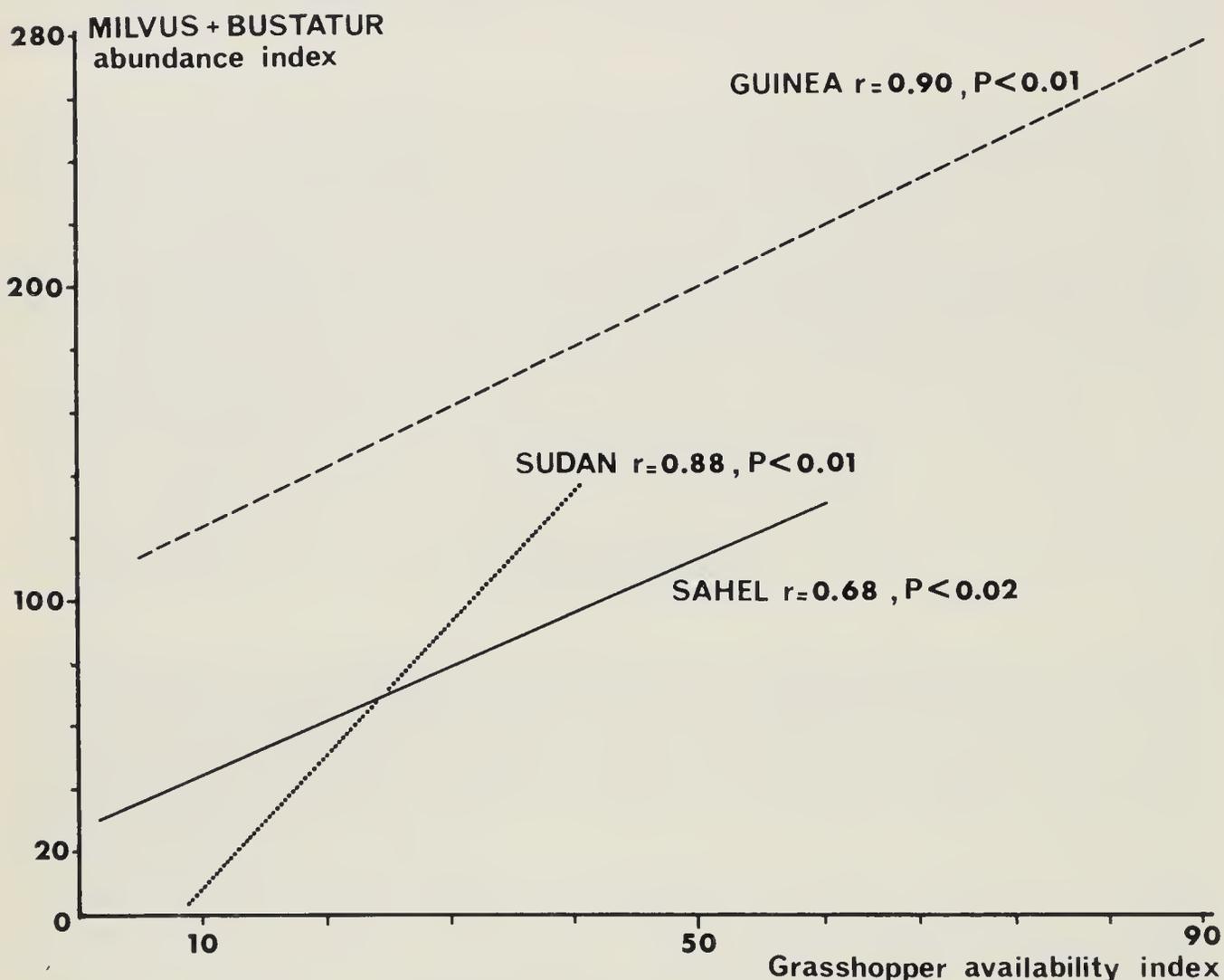


FIGURE 1- Positive correlation between monthly abundance of the two main locust-eating, seasonally migrant, Ethiopian raptors (Black Kite, *Milvus migrans* and Grasshopper Buzard, *Bustatur rufipennis*) and the relative density of their critical food source through the three main vegetation belts (Sahelian, Sudanese and Guinean zones). Both indices were obtained along the same sample transects in all months where at least some migrants were present in the area. Bird abundance was derived from roadside counts. Prey availability was estimated by counting grasshoppers along 100 m lines, which is sensitive to density, accessibility and conspicuousness (see Thiollay 1978).

FOOD AVAILABILITY, HABITAT USE AND SEASONAL MOVEMENTS IN AFRICAN SAVANNAS

Mean clutch sizes are reputed to be higher in savannas than in tropical forests (Lack & Moreau 1965), probably because of greater seasonality and availability of food resources during the shorter breeding season. It has been shown that a small granivore (*Lagonosticta*) can successfully rear its brood when it is enlarged by eggs of the para-

sitic *Hypochoera* (Morel 1967), suggesting that food availability was not the factor limiting clutch size.

A major impact of rainfall fluctuations in African savannas is to shift seasonally the areas of optimal food availability. Within West African savannas, 24 species of Ethiopian diurnal raptor species make latitudinal movements associated with seasonal variations in food supply (Thiollay 1978). Six species undertake long distance migrations on a regular basis. Timing and extent of those northward movements are closely correlated with the onset of rains (Figure 1) and the consequent flush of major prey (e.g. locusts, caterpillars, termites). The rapidly declining availability of food at the beginning of the dry season triggers southward movements of raptors into moist savannas, which reach their maximum food production at that time. According mainly to diet and foraging behavior, each species (or population) breeds within the period and latitudinal range where food availability is optimal. The duration of the species' presence in respective areas also is adjusted to availability of their main food supply. In the Red-billed Quelea *Quelea quelea* sudden population declines occur at the onset of rains when grass seeds germinated, and thus, became unavailable to this granivorous bird. Faced with such a temporary food shortage, a southward migration occurred at a time when starving birds were numerous among the population (Ward 1965).

Detailed studies on hunting behavior, foraging success and reproduction of mostly insectivorous raptors and rollers in a dense Guinean savanna (Thiollay 1976, 1985, Thiollay & Clobert 1990) emphasized the great difference between prey density and actual prey availability, where accessibility and detectability of food items were more important than their true abundance. Each predator exhibited morphological and behavioral characteristics that resulted in particular foraging patterns, patch use, habitat selection, and prey choice. These features of foraging behavior are related to vegetation structure (height and density of the grass cover) which changes considerably over the seasons. Thus, ability to breed, or simply to stay, in an area was a trade-off between dynamics of prey populations and seasonal changes in vegetation cover through a cost-benefit interaction between hunting method, energy expense and success rate.

FEEDING RATES, ENERGY BUDGETS, BREEDING SUCCESS AND FOOD SUPPLY IN OPEN HABITATS

Circumstantial evidence of food limitation in tropical birds also comes from a variety of other situations. Within a dense breeding population of Fish Eagles *Haliaeetus vocifer* in Uganda, energetic cost of activities associated with breeding (e.g. territorial defense, hunting, food delivery to young) increased the total daily energy expenditure of an average adult rearing one and two young by 19 % and 30 %, respectively, over a nonbreeding adult (Thiollay 1981a). The energy gained from food consumption increased correspondingly by only about 8 % and 5 %. Thus, the net daily energy budget, which was positive for a non-breeding adult, was just balanced when one young/pair was fed and became negative when broods of two (maximum clutch size) were involved (Table 1). The additional fish prey necessary for brood rearing was obtained by an increase in the most energy demanding hunting method (searching in flight rather than perch hunting). Reyer & Westerterp (1985) also showed that growth

of young Pied Kingfishers *Ceryle rudis* was below the maximum rate because parents could not increase their energy expenditures.

TABLE 1 - Daily energy budget of average adult Fish Eagles in Uganda during the nestling stage (Thiollay 1981a). Individual birds in each brood size categories were followed during 12 to 24 full daily activity periods (12 h). Males were more active than females.

	Brood size of observed pairs		
	0	1	2
Fishing flights + prey deliveries (min./12 h)	8	30	41
Territorial flights and social behaviors (min./12 h)	31	71	88
Maintenance activities + perch hunting + surveillance (min./12 h)	681	619	591
Mean number of captures/day/adult	0.68	1.20	1.51
Ratio total energy lost in 24 h/energy gained from fish consumed	0.91	0.99	1.13

Strong differences in diet and foraging behavior between habitats in American Kestrels *Falco sparverius* of a Sonoran desert (Mexico) were correlated with prey availability and energy budgets of foraging birds (Thiollay 1984). Breeding occurred only in habitats where hunting was the most energetically profitable and where relatively large vertebrate prey were available the year round. Likewise, in a Chihuahuan desert (Mexico), two sympatric hawks (*Buteo jamaicensis* and *B. swainsoni*) segregated their respective breeding and hunting habitats according to the particular prey resources on which they were most successful (Thiollay 1981b). The low breeding success of an island population of Peregrine Falcon in Tunisia (Thiollay 1988c) was mostly attributable to a lack of the most profitable prey (dove-sized migrant birds). The reliance on smaller and more difficult to catch passerines led to deficits in daily energy budgets and frequently to starvation of young.

The influence of food limitation on territory size, timing of breeding, clutch size, growth rate of nestlings and fledging success of Galapagos Darwin's Finches (*Geospiza*) has been repeatedly documented (Schluter 1984, Grant 1985, Price 1985). The succession of droughts and rainy years provided convincing natural experiments on the role of abundance and quality of food supply to these granivorous or insectivorous birds. Similar conclusions have been drawn from studies of a small Australian insectivore (Catterall et al. 1982) and a Hawaiian nectarivore (Riper 1984).

DISCUSSION

The idea that food may limit reproductive success may not be obvious from studies of temperate or boreal ecosystems. In these areas, food supply increases dramatically in spring and bird populations, reduced by seasonal shortages, barely reach a saturation level, even with the influx of migrants. Here I have demonstrated that, in various tropical habitats on several continents, food levels could influence markedly both

population density and reproduction of many species. Prey availability is not always high in the tropics where seasonal fluctuations are relatively lower, but more irregular, than in temperate areas.

Tropical birds also may incur at least greater time limitation than temperate birds due to the shorter daylight period. Despite energy demands of tropical birds that may be lower than that of their temperate counterparts because of reduced thermoregulatory requirement, lower metabolism and slower growth rates (Bryant & Hails 1983), many tropical birds are apparently unable to increase significantly their activity level or foraging success. In some cases (see Thiollay 1981a), it would be probably too costly for them to rear more young than they do, due to limited food availability.

Because of vegetation structure and multiple highly-evolved antipredator adaptations of the prey, a greater difference may exist in the tropics between actual prey abundance and accessibility of food items than in the temperate areas. This may promote either narrower specializations or broader generalism that both result in a reduction of the prey base really exploited. These two opposite options are equally adaptive strategies and are equally marked trends observed among tropical rain forest birds (Thiollay 1988a). There is also a considerable disparity between food productivity or prey availability within the tropics, between open habitats and forests, between young secondary forest and old growth, and between gaps or upper canopy and closed understory. The former are usually more seasonal and productive (both in terms of insects and fruits), while the latter are darker, more stable and populations may be more permanently saturated.

Any generalization must be cautious and the degree of food limitation must vary widely within both tropical and temperate latitudes among habitats and seasons. There are suggestions that food availability limit reproductive success of at least some tropical birds, but still no evidence suggesting that it may be more important or more frequent in the tropics than in the temperate zone.

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NATURAL FLUCTUATIONS IN FOOD SUPPLIES - EFFECTS ON BREEDING RESULTS IN EUROPEAN BIRDS

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INTRODUCTION

Individual animals bridge time by reproducing, thereby perpetuating their genes into future generations. Since reproduction is energetically costly, animals have to employ a number of tactics such as exploiting favourable seasons, habitats, nest-sites, and other organisms, which in turn are modified/manipulated through an array of behaviours. The resulting life-history patterns, moulded by natural selection to maximize fitness, are determined by many limiting factors, of which food is a general and decisive one (Lack 1954). This is particularly obvious in birds, which typically must secure sufficient food supplies, not only for mating and egg-laying, but also for rearing their young, which attain full size before becoming independent.

There is now ample experimental evidence for the limiting effect of food on birds' reproductive success (Murphy & Haukioja 1986), so here I shall not consider such work. Instead, I shall give examples of studies in which natural food levels and reproductive variables have been measured and see how they interact. It could rightly be argued that experimental studies are scientifically sounder than correlational analyses, but it could also be said that experiments sometimes are difficult to evaluate due to problems with scales, replication, design, and side-effects, respectively. Also, it is of interest to see how universal the expected positive correlation between food supplies and reproductive success is in nature. Finally, I believe correlational studies, carried out formally or in the mind, have a right in themselves by generating new ideas to be tested and by structuring the many variables a biologist encounters (Clutton-Brock & Harvey 1984).

In this paper I shall restrict myself to European work on the relations between food abundance and reproductive output. Undoubtedly much important information has been published in languages I don't understand and/or in journals I have had no access to, so my surveillance is far from exhaustive. Further, I shall only consider papers in which food levels have been directly measured along any kind of quantitative scale, from a nominal (poor/rich) to a ratio one. Since ornithologists tend to think of birds in taxonomic entities, I have chosen to give the data for separate orders.

RESULTS

Divers (Gaviformes)

One of the examples for which there is a negative relation between food abundance and production of young is provided by Eriksson (1986), studying Black-throated Divers *Gavia arctica*. He found a negative correlation between abundance of small

fish and number of "large" chicks in 24 lakes (Figure 1). Neither did water transparency correlate with chick production, so Eriksson suggested that lakes with low densities of fish might have richer supplies of aquatic insects (due to relaxed predation by fish), another important food for young divers.

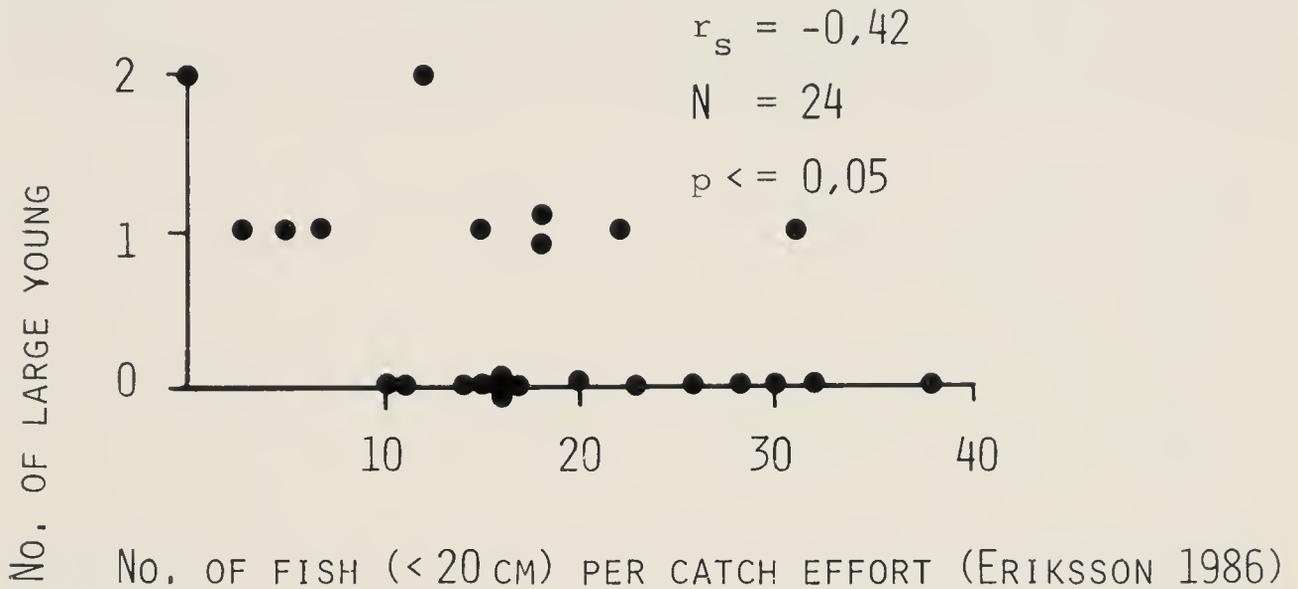


FIGURE 1 - Fledging success ("large" chicks) of Black-throated Diver in relation to abundance of small (20 cm) fish. ($r = - 0.42$; $P < 0.05$.) From Eriksson 1986.

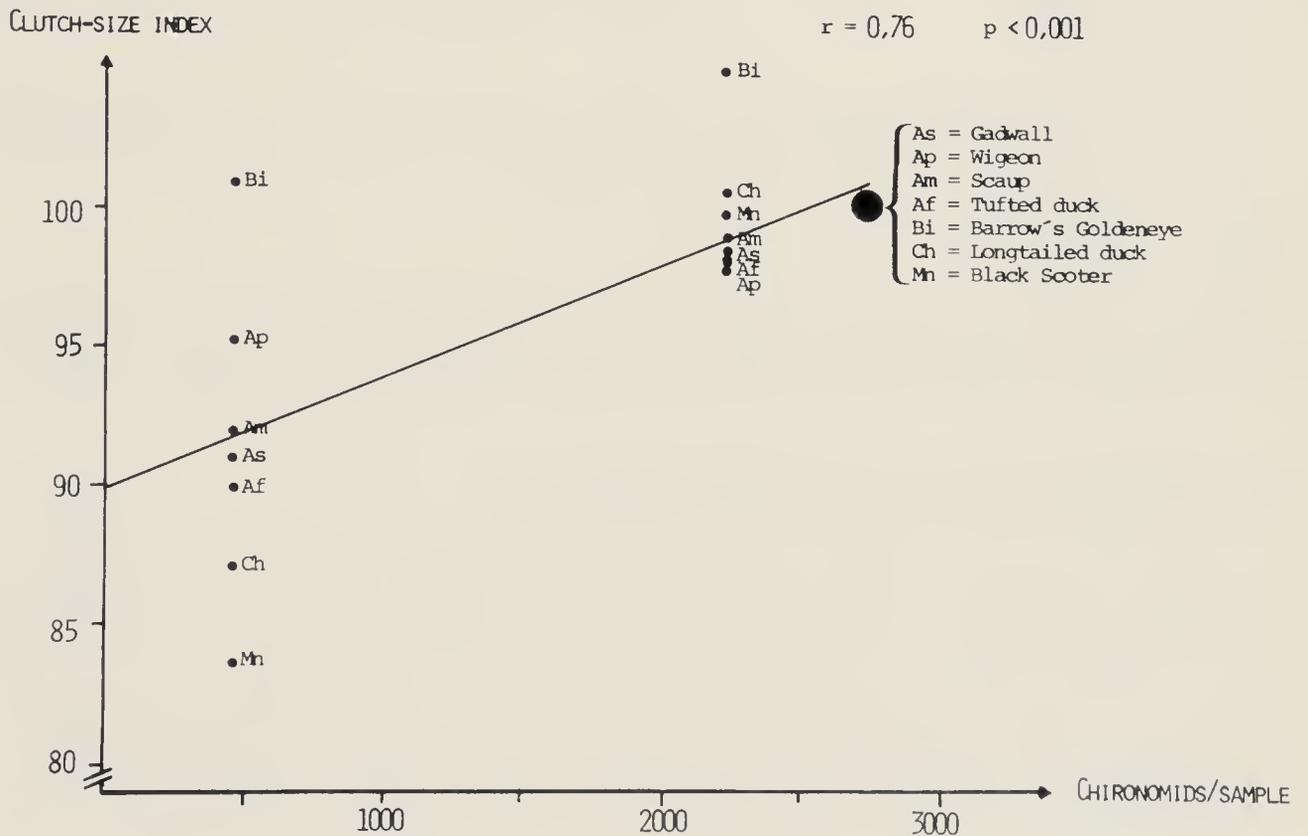


FIGURE 2 - Clutch-size index (1968 = 100) in relation to abundance (4 samples at each of 8 stations/year) of Chironomid larvae for Icelandic ducks (after Bengtson 1971). ($r = 0.76$; $P < 0.001$.)

Ducks (Anseriformes)

Bengtson (1971) measured density of Chironomid larvae, main food of ducks in Lake Myvatn, Iceland, and related this variable to breeding performance in eight species of ducks. In one of the three years density was only some 20 % of normal, which made the ducks lay smaller clutches (Figure 2). The Red-breasted Merganser *Mergus serrator*, a fish-eater, did not respond to the shortage of insects. None of the species responded by laying later, and clutch-size reduction seemed to be related to the importance of animal matter in the diet. Overall, the response by the birds seemed to be moderate, with a reduction in clutch-size at 10 % following a 75 % reduction in food supplies.

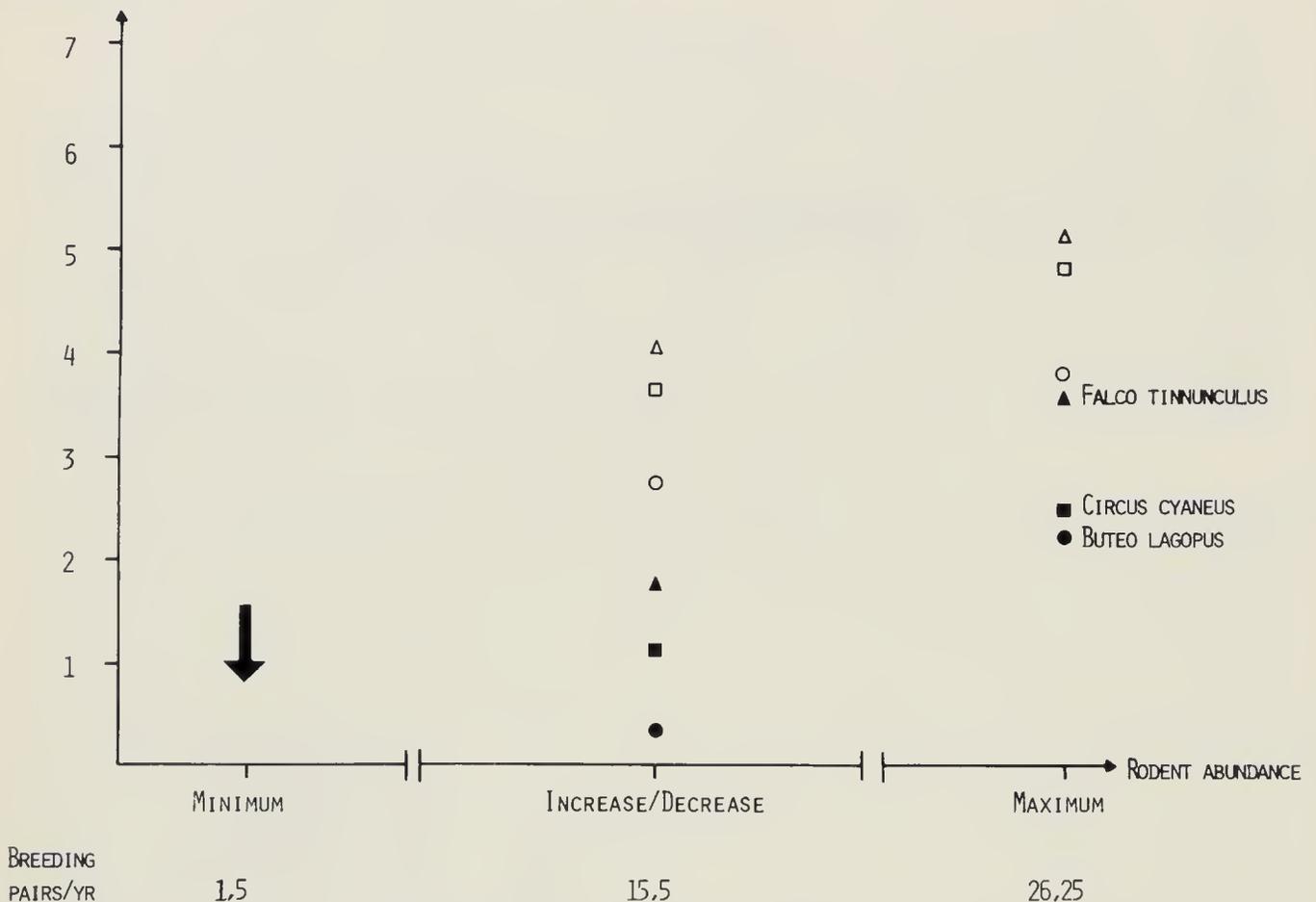


FIGURE 3 - Clutch-size and fledging success for three raptor species, Kestrel *Falco tinnunculus*, Hen Harrier *Circus cyaneus*, and Rough-legged Buzzard *Buteo lagopus* in bad, intermediate, and peak rodent years, respectively. From Hagen (1952).

Raptors (Falconiformes) and Owls (Strigiformes)

There is much evidence suggesting a positive relationship between food levels and reproductive success in these groups. This is because the food of many raptors and owls is easy to estimate, and because many of the members of these groups are food specialists, responding to the occurrence of one kind of prey, only. Such a relationship is revealed in Hagen's (1952) data on clutch-size and fledging success for three rodent specialists in bad, intermediate, and good vole years, respectively (Figure 3). For the Kestrel *Falco tinnunculus*, Cave (1968) found a similar response, and in addition he established that Kestrels lay earlier in rodent peak years. Ingenious experimental work by Meijer et al. (1988) showed that food directly controls date of laying but not clutch-size, which is a consequence of laying date. Another prominent feature of rodent specialists is their high breeding densities in good years, (see also Cave 1968, Wijnandts 1984, Village 1982, Korpimaki 1987a). Generalist predators, with a

diverse diet, are on the other hand capable of breeding successfully in most years, irrespective of the fluctuations in abundance of one prey species. This can be seen in the Common Buzzard *Buteo buteo* in areas with alternative prey (Mebis 1964), or alternative sources of food, e.g. sheep carrion (Newton et al. 1982). In regions where other prey is scarce, reproductive success of the Common Buzzard closely follows rodent abundance (Spidso & Selas 1988).

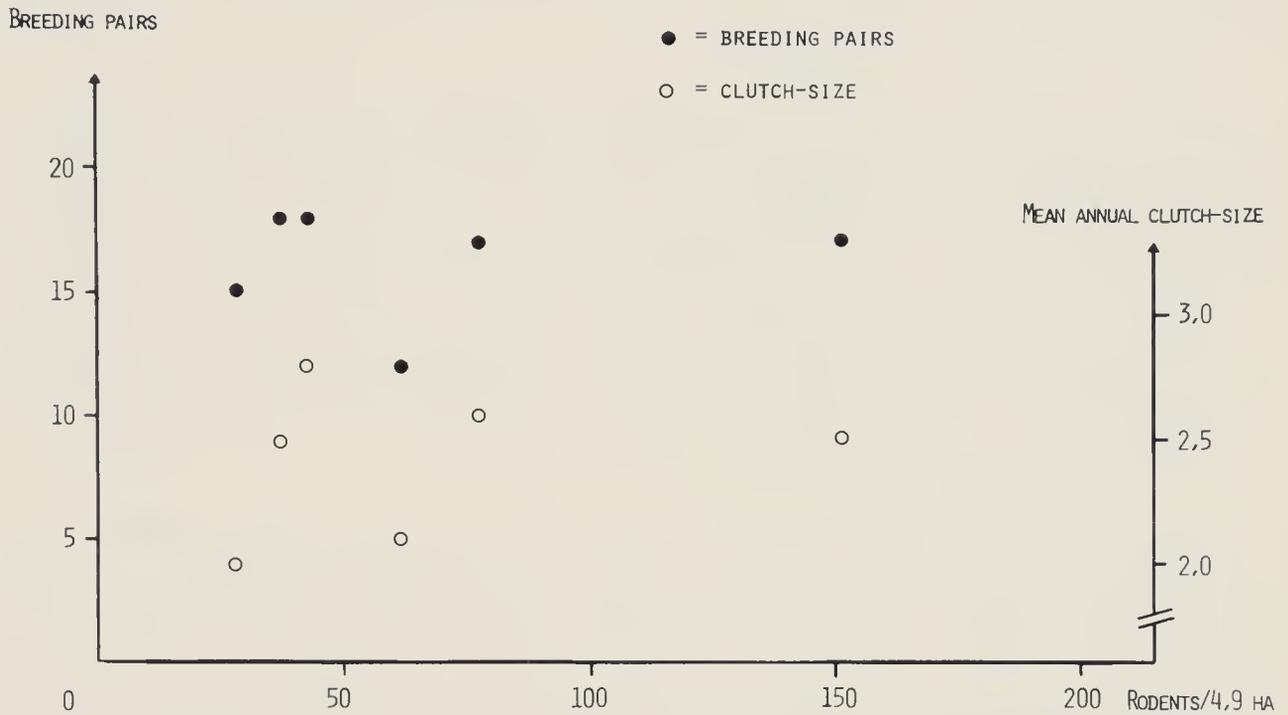


FIGURE 4 a - Proportion of Tawny Owl *Strix aluco* breeding and clutch-size in relation to rodent numbers 1949-54. After Southern (1970).

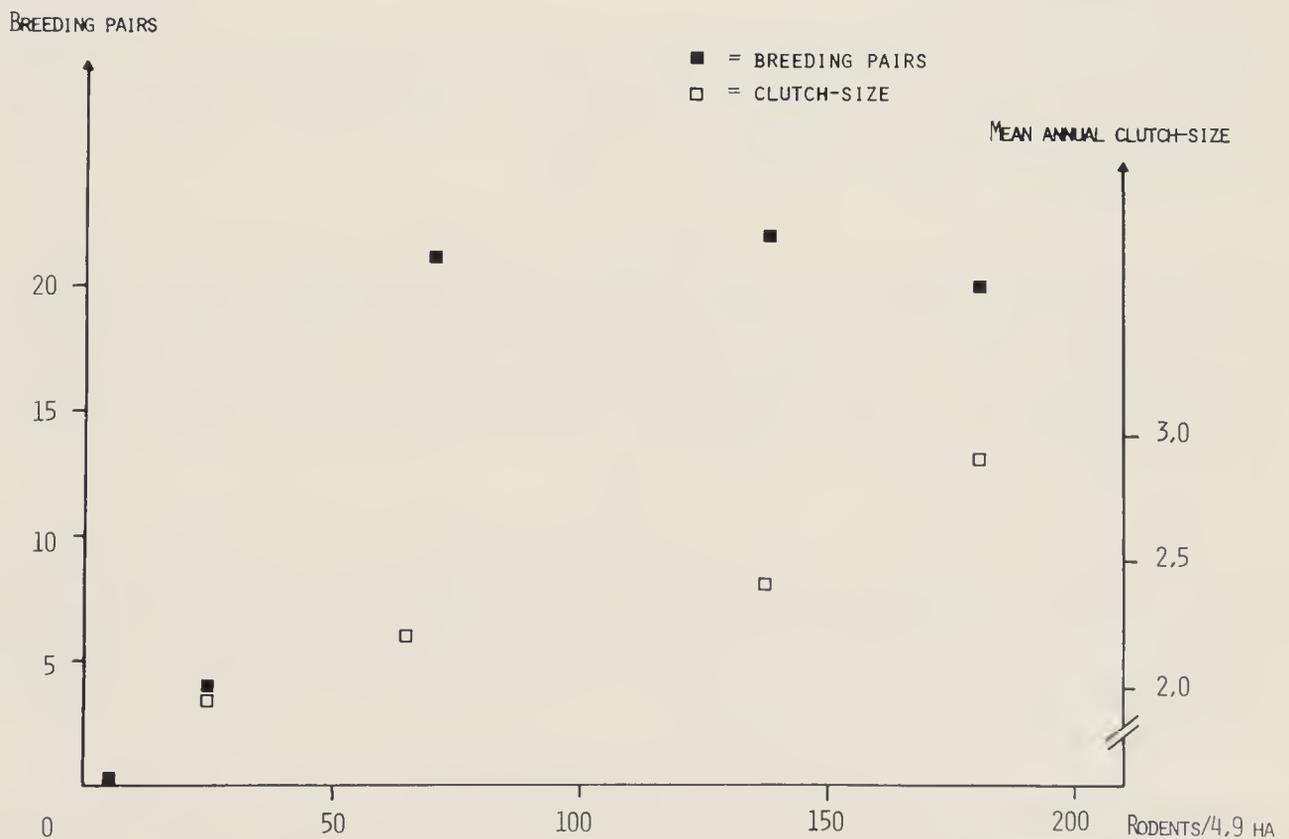


FIGURE 4 b - Proportion of Tawny Owls *Strix aluco* breeding and clutch-size in relation to rodent numbers 1955-59. After Southern (1970).

Similarly, owl rodent specialists breed earlier and at higher densities, lay larger clutches and raise more young in peak vole years. Between-year comparisons have convincingly demonstrated this for Barn Owl *Tyto alba* (Schonfeld & Girbig 1975), Long-eared Owl *Asio otus* (Wendland 1957, Village 1981, Wijnandts 1984), Short-eared Owl *Asio flammeus* (Hagen 1952, Lockie 1955, Village 1987), Tengmalm's Owl *Aegolius funereus* (Korpimäki 1987 b, Hornfeldt 1990), Tawny Owl *Strix aluco* (Linkola & Myllymäki 1969, Southern 1970), and Ural Owl *Strix uralensis* (Lundberg 1981, Pietiäinen 1989).

Owls with a more diverse diet respond less dramatically to changes in rodent abundance. The Tawny Owls studied by Southern (1970) in England exhibit features of both ends of the generalist-specialist dichotomy: Up to 1954 the owls raised their young on a mixed diet of small rodents and young Rabbits *Oryctolagus cuniculus*, but after this year the latter prey almost disappeared due to an outbreak of myxomatosis, forcing the owls to switch to rodents. In the early years of Southern's study there was no relationship between rodent numbers and the proportion of the owls breeding, or their clutch-size (Figure 4a), but from 1955 onwards, breeding was clearly affected by rodent numbers (Figure 4b).

In all the above studies reproductive variables and food levels were compared over years. I know of only one paper reporting on such comparisons for individual pairs. Figure 5 shows Hagen's (1969) data for pairs of owls and Common Buzzard, and again we see the association between rodent density and reproductive success. The high correlation coefficient ($r = 0.71$), despite between-year differences and the many species involved, suggests a similar reproductive response to food levels for all the monophagous rodent specialists.

Gamebirds (Galliformes)

Despite much effort invested in gamebird research few studies have reported on changes in food supplies for these birds. However, Potts (1986) showed that survival of young Partridge *Perdix perdix* chicks is closely correlated ($r = 0.69$) with a high density of preferred insects (data from 17 years).

The obvious difficulties of estimating food availability for herbivorous birds have been overcome in a few studies. Moss et al. (1975), in their long-term project on the Red Grouse *Lagopus lagopus scoticus*, constructed an index of maternal nutrition, based on the annual variation in density and growth period of the food plant, Heather *Calluna vulgaris*. This index accounted for 65 % ($r = 0.81$) of the variation in breeding success over six years at two different moors.

Brittas (1988), disregarding densities of food plants, used in vitro digestibility (%) of crop contents from breeding Willow Grouse *Lagopus lagopus* as a food index. Annual variation in this index explained 71 % ($r = 0.85$) and 84 % ($r = 0.92$) of the variation in breeding success and female condition (fat weight corrected for size), respectively, but the study lasted only for five years.

Shorebirds, skuas, gulls, and auks (Charadriiformes)

Generally, clutch-size variation is small in this group, and instead there seems to be a selective premium on large eggs, producing large chicks. Also, various forms of parental behaviour put a limit to clutch-size, e.g. incubation and brooding (Winkler &

Walter 1983), but there is evidence that food levels affect reproductive output. Hogstedt (1974) found an inverse relation between lumbricid density and the length of the pre-laying period ($r = -0.95$, $p = 0.001$) in Lapwing *Vanellus vanellus* territories, and Baines (1990) found a positive correlation between beetle (important food for Lapwing chicks) abundance and breeding density ($r = 0.70$, $P = 0.002$).

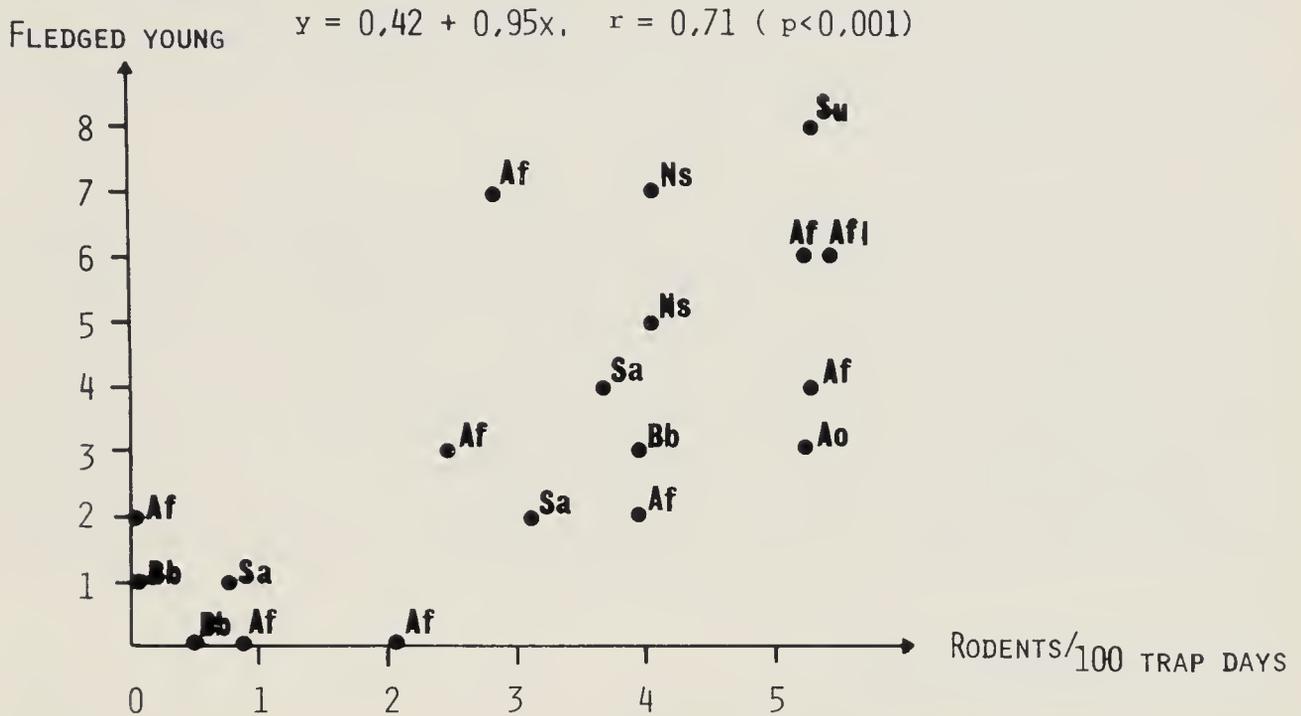


FIGURE 5 - Number of fledged young and rodent density for pairs of rodent specialists. ($r = 0.71$; $P < 0.001$.) After Hagen (1969). Af = Tengmalm's Owl *Aegolius funereus*, AfI = Short-eared Owl *Asio flammeus*, Ao = Long-eared Owl *Asio otus*, Bb = Common Buzzard *Buteo buteo*, Ns = Snowy Owl *Nyctea scandiaca*, Sa = Tawny Owl *Strix aluco*, Su = Hawk Owl *Surnia ulula*.

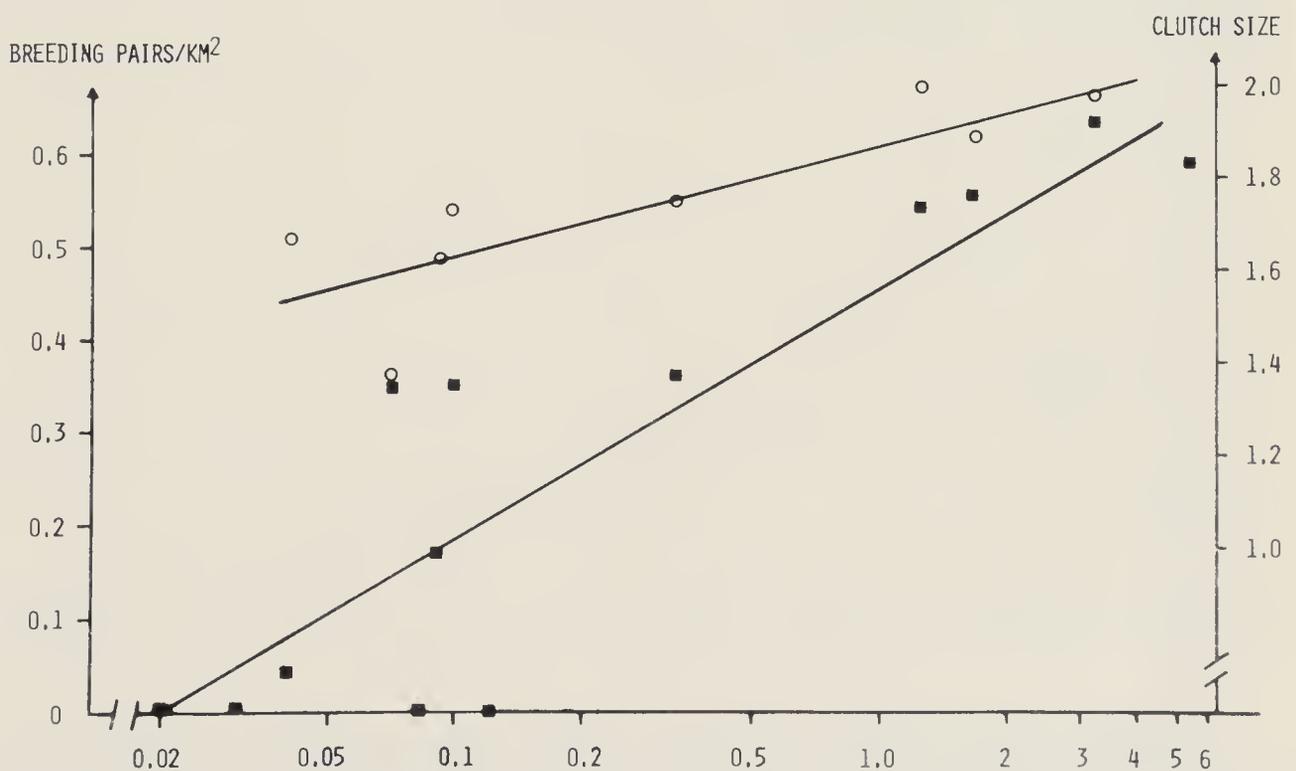


FIGURE 6 - Density of breeding pairs and clutch-size of Long-tailed Skua *Stercorarius longicaudus* in relation to abundance of small rodents. After Andersson (1981). ■ = density of breeding pairs ($r = 0.89$; $P < 0.001$) O = clutch-size ($r = 0.84$; $P < 0.01$).

In the Long-tailed Skua *Stercorarius longicaudus*, Andersson (1981) found smaller clutches in rodent-poor years and, more importantly, that fewer pairs started to breed in such years (Figure 6). The combined response in these two variables has a ten-fold range, despite the low maximum clutch-size (2 eggs) in this species. In Shetland, the piscivorous Arctic Tern *Sterna paradisaea* recently suffered a dramatic decline in breeding success, following a shortage of young sandeels *Ammodytes marinus*, due to overfishing (Monaghan et al. 1989a). Recruitment of young Sandeels accounted for 79 % of the variation in Arctic Tern breeding success, which was largely determined by chick survival (Monaghan et al. 1989b).

Overfishing by humans has been held responsible also for the dwindling breeding success of auks, which has been prominent in Norway for 15 years and recently caused heavy chick mortality in the auk colonies of Shetland (Nettleship & Birkhead 1985, Martin 1989). Although little data on fish abundance are easily available, Martin (1989) mentions 1984-85 as bad and 1986-88 as catastrophic recruitment years for Puffins *Fratercula arctica*, with good chick production before that period. This coincides qualitatively with abundance of sandeels, the main food of Puffin chicks, in Shetland. Historic data on the Norwegian fisheries (Rottingen 1990) also suggest food shortage as the decisive factor in causing excessive chick mortality in seabird colonies of that country.

Passerines (Passeriformes)

Some of the most well-studied birds belong to this huge order in which a plethora of life history strategies is represented. Yet, there are relatively few European studies on passerine reproductive performance as a result of variation in the availability of natural food.

YEARLY MEANS OF 1ST EGG,
1ST APRIL = 1,

$$y = 33,1 - 0,013x, \quad r = 0,56 (17); p < 0,05$$

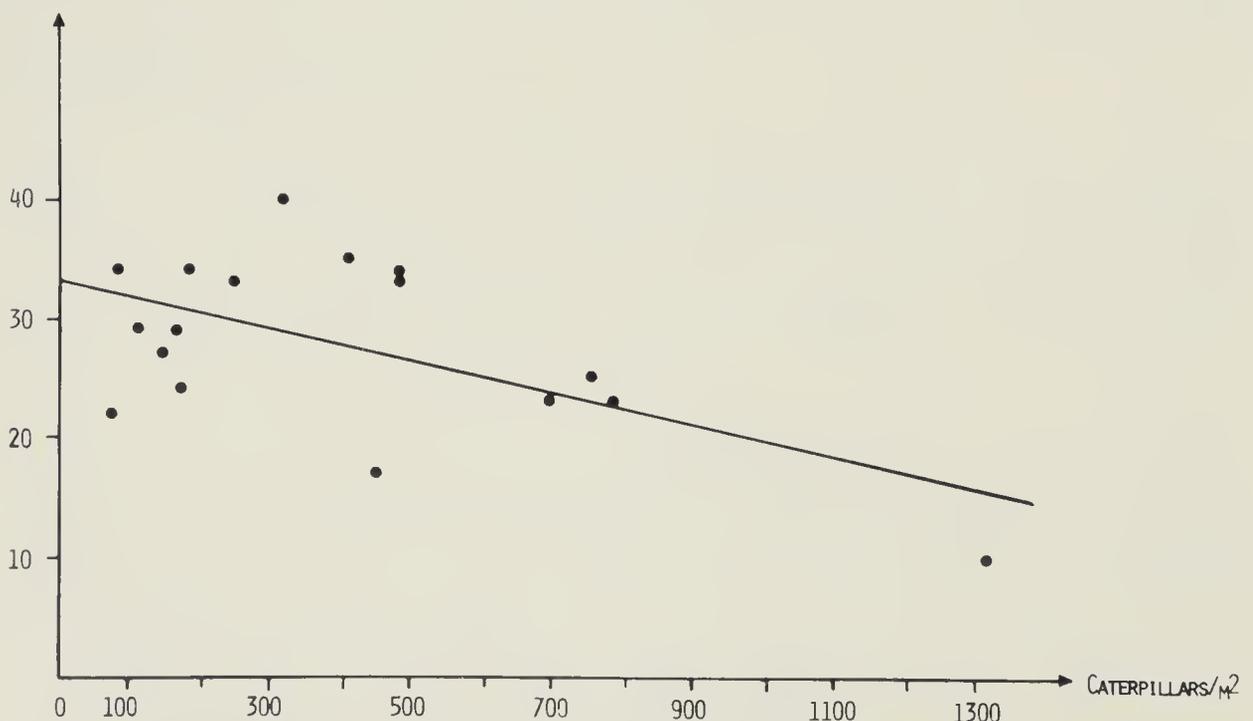


FIGURE 7a - Laying date of Great Tits *Parus major* in —relation to caterpillar abundance in the years 1947-63. ($r = -0.56$; $P < 0.05$.) After Perrins 1979.

In Europe, parids are by far the best studied birds, with long-term research projects in many countries. With respect to food availability and reproduction the British study initiated by Lack (1954, 1966) and continued by Perrins is the most detailed. Generally, food levels and reproductive variables covary, both for Great *Parus major* and Blue Tits *P. caeruleus*, but as pointed out by several workers (e.g. Perrins 1979), it is difficult to separate cause and effect from such correlations. In spring and summer, Great and Blue Tits largely rely on caterpillars as food, and the density of these has been measured for many years (see Perrins 1979). The fact that both date of laying (Figure 7a) and clutch-size (Figure 7b) in the Great Tit are correlated with caterpillar density over 17 years points to a food effect, but these patterns could also have been brought about by another factor. For example, high spring temperature may enhance caterpillar survival and at the same time make the birds lay earlier and larger clutches. However, to me it appears more likely that the tits themselves affect caterpillar numbers, since estimated winter densities of tits (Lack 1966, Table 11) are inversely related to caterpillar densities in the following spring ($r = -0.70$; $P < 0.05$) (von Schantz 1984). Therefore, it is feasible that food levels, directly affecting reproductive variables (von Schantz 1984), are determined by the density of birds in the preceding winter. Earlier, this view was considered unlikely, since it was thought that breeding tits enjoyed superabundant food supplies (e.g. Perrins 1979, p.199), but since Minot's (1981) experimental demonstration that breeding Great and Blue Tits compete for food (caterpillars) the role of food in directly determining reproductive rates has been revived (Perrins & McCleery 1989).

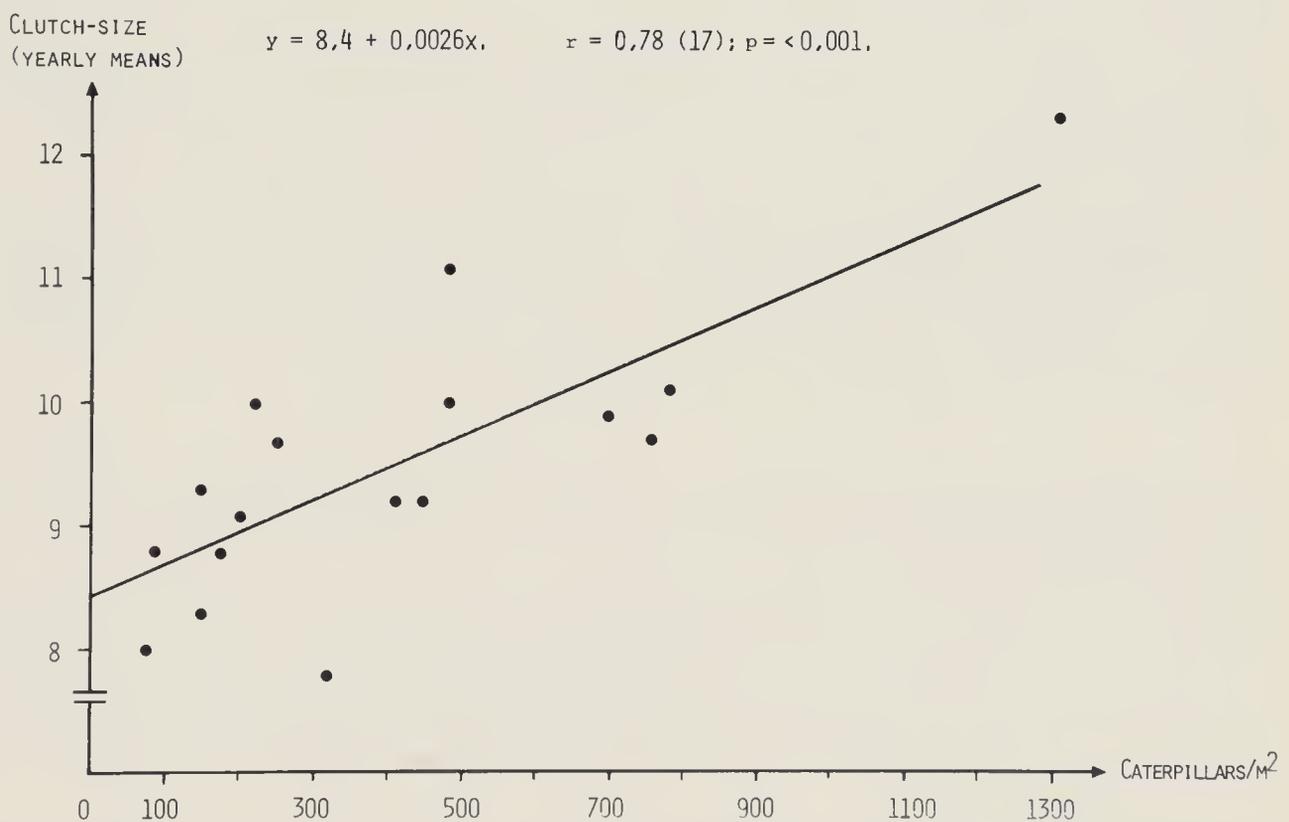


FIGURE 7b - Clutch-size of Great Tits *Parus major* in relation to caterpillar abundance in the years 1947-63. ($r = 0.78$; $P < 0.001$.) After Perrins 1979.

Food abundance has been shown to directly affect breeding also in other passerines. Swanberg (1981) presented data showing that clutch-size in the Nutcracker *Nucifraga caryocatactes* is adjusted to the amount of hazelnuts *Corylus avellana* cached in the preceding autumn by the parents, and Newton et al. (1982) found a significant relation between number of carrion and clutch-size in the Raven *Corvus corax*. Also, Enermar & Nystrom (1981) found that Redpolls *Carduelis flammea* responded to ex-

ceptionally good seed crops of the Mountain Birch *Betula tortuosa* by breeding at much increased (3-4 times) densities and laying larger clutches compared with normal years. Unexpectedly, however, hatching losses were greater in the peak years so that the number of fledglings per pair remained normal. Even if birch seeds dominated the diet of Redpoll chicks (Enemar & Nystrom 1981), insects made up a substantial part of the food and may have been essential for successful development. This could explain why the Redpolls didn't start breeding earlier in the seed peak years (seeds were available all winter) and why the birds responded by laying significantly ($P < 0.001$), but only moderately (10 %) larger clutches in those years. Bryant (1975) found that House Martins *Delichon urbica* laid larger clutches ($P < 0.01$) at higher aphid abundances, and that the young grew better ($P < 0.001$) when aerial insects were more plentiful. On the other hand, Otto (1979) didn't find any relationship between worm density and reproductive variables, except for egg weight in Fieldfare *Turdus pilaris* colonies.

CONCLUDING REMARKS

When reviewing the data for an expected relationship, such as between food supplies and reproductive performance, you eagerly list the positive evidence but, at the same time, wonder whether there are many studies unpublished, because they produced negative or inconclusive results. One cannot help feeling that such work must appear less attractive to publish, both for authors and editors. An unexpected result is likely to receive stronger criticism than confirmatory work, with the result that the scientific literature is biased in favour of positive evidence. In many cases you see this tendency also in published papers, where often the expected results are detailed, but with little or no mention of relationships hard to explain, for which the relevant data, nevertheless, are at hand. Studies reviewed here presented only two pieces of "negative" information (Eriksson's (1986) work on fledging success in the Black-throated Diver, and Enemar & Nystrom's (1981) study on hatching success in the Redpoll). However, other papers than these two contain data suggesting negative correlations, which were not further analysed or reported by the author.

Despite the above proviso, there is convincing evidence that abundant food supplies have a beneficial effect on breeding performance. However, one must bear in mind that this relationship may have been caused by one or several unknown factors (e.g. temperature), independently and simultaneously affecting both food and reproduction positively. In some studies this is less likely than in others, e.g. where food production occurred much earlier than breeding (Swanberg's (1981) work on the Nutcracker and Enemar & Nystrom's (1981) study on the Redpoll), or where there was a pronounced local (spatial) variation in the same period of time (Hagen's (1969) paper on birds of prey (Figure 5)).

Interestingly, there seems to be variation in the degree of reproductive response to food conditions. Tentatively, but logically, food specialists tend to respond more dramatically than food generalists. This is particularly obvious among birds of prey eating cyclic rodents, only, and among granivorous birds. Generalists, on the other hand, can switch to alternative food supplies if one component of the diet is rare. Tawny Owls in Marley Wood (Southern 1970) are interesting in this respect, since they became food specialists after 1954, when an important prey, the Rabbit, was wiped out, and showed a strong response to the abundance of voles and mice.

Variation in reproductive response to changing food conditions may also depend on the factor(s) limiting breeding success. In species less vulnerable to predation (e.g. larger species, hole-nesters) reproductive rates may be finely attuned to food levels, whereas smaller species may be forced to be less prolific, in relation to food resources, in order to minimise the number of nest visits and keep the young satiated and silent, i.e. minimizing predation risks.

In conclusion then, birds adjust reproductive rates to food availability, but the variation between species in responsiveness is poorly understood and deserves further study.

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FOOD LIMITATION IN TERRESTRIAL BREEDING BIRD POPULATIONS: IS THAT ALL THERE IS?

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ABSTRACT. Food commonly limits reproductive output, which can affect fitness of individuals and influence population sizes. However, food may not limit reproductive output in all individuals and may have little effect on population sizes while exerting selection on evolution of reproductive tactics. Food limitation has been given priority attention in studies of demography and, particularly, evolution of life history traits. Yet, effects of food limitation during breeding are rarely experimentally tested at the population level. Moreover, much previous work has focused on nest box studies which enhance the probability of food effects while minimizing nest mortality effects. A review of studies of the effects of nest predation at the population and individual levels through predator removal experiments demonstrate clear and strong limits by predation. Thus, while food limitation may commonly exist, it is not the only important influence on demography and demographic traits.

Keywords: Food limitation, nest predation, reproductive strategies, population dynamics, open-nesting birds.

INTRODUCTION

An ecological process (e.g. food limitation, nest predation) can be considered limiting when amelioration results in an increase in fitness (Martin 1986). Limitation at this "individual" level can influence evolution of reproductive traits and behaviors such as clutch size, developmental rates, and parental care. If the process is limiting for all or most individuals (and genotypes) in the population, then amelioration at the "population" level can influence demography; e.g. an increase in fitness summed across all individuals in the population yields an increase in numbers of surviving individuals and/or numbers of young recruited to the population.

Both individual fitness and population change are determined by fecundity and survival. Fecundity is the result of breeding probability, clutch size, and number of nesting attempts. Survival to reproductive age is determined by survival during nesting, survival of the fledglings on the breeding grounds, and survival over winter until the first breeding season. When summed across all individuals in the population, these components determine population change. Conversely when summed across years for an individual instead of summing across individuals, then these components determine individual fitness. These components can thus be viewed as potential fitness components that reflect standard life history traits as well as population demography.

An increase in one of these components does not necessarily translate into increased population size or fitness because the increase may be offset by a decrease in another component. Offsetting effects do not necessarily reflect "trade-offs", where an increase in one trait exacts a direct cost on expression of another trait, such as the assumed trade-off between fecundity and adult survival. As an example, food

commonly limits fecundity (reviewed in Drent & Daan 1980, Martin 1987) and population sizes (Newton 1980) of breeding birds. However, an increase in fecundity with increased food may not incur a reproductive cost (no trade-off), but the increase in fecundity may be offset by limitation during winter and thereby yield no increase in fitness or population size with increased fecundity. On the other hand, increased fecundity for a few individuals due to more effective reproductive strategies or ability to acquire higher quality territories can yield increased fitness for those individuals without affecting population size. Such traits or strategies will be favored by natural selection if they are heritable. Thus, an ecological process such as food limitation can exert selection on evolution of traits without limiting the population. However, when population size is affected, the process is acting on a greater number of individuals in the population and, therefore, can potentially cause faster and broader evolutionary change.

While food limitation may influence population size and evolution of traits, food is not the only limiting process. Nest predation has been given less attention, but it may exert stronger selection than previously recognized (Slagsvold 1982, 1984, Milonoff 1989, Kulesza 1990, Martin 1991a); predation commonly accounts for 80 to 90% of nest mortality and, on average, causes loss of approximately 43% of nests that are initiated by open-nesting passerines in a variety of habitats and geographic areas (see Kulesza 1990, Martin 1991b). If these predation rates are limiting at the individual and population levels, then a reduction in predation mortality should 1) cause an increase in nesting success without a strong increase in compensatory mortality from other sources, and 2) the increase in nesting success will result in increased population sizes in subsequent breeding seasons. These predictions are most clearly tested by removing predators to examine breeding and population responses.

EFFECTS OF NEST PREDATION

The best experimental work on nest predation on open-nesting birds has been on game species that nest in open nests on the ground, such as Anatinae, Tetraoninae, and Phasianinae. Nest predation for Anatinae averages 51% and represents about 80% of nesting mortality (Table 1) similar to open-nesting passerines (see Martin 1991b). If predation is eliminated as a source of mortality and no compensatory mortality occurs, then nesting success should average 87% (nest success plus nest predation rates in Table 1). Indeed, nesting success of these species on islands or other relatively predator-free environments (e.g. Wildlife Refuges where predators have been removed) averages 81% when predation is reduced to 5% (Table 2). Moreover, predator-removal experiments show that nesting success averages 86% in predator-removal areas and 49% in nearby non-removal areas of similar habitat structure (Table 3). These experiments provide unequivocal evidence that nest predation is the primary source of nesting mortality.

The consequences of nest predation for population sizes was clearly documented by rapid increases in population sizes following predator removal or in predator-free environments. Population densities increased as much as two orders of magnitude on islands as compared to nearby mainland areas (e.g. Girard 1941, Keith 1961, Duebbert 1966, Vermeer 1968, Duebbert et al. 1983) and as much as 500% on predator removal areas as compared to nearby non-removal areas (Kalmbach 1937, Duebbert & Kantrud 1974, Duebbert & Lokemoen 1976, 1980).

TABLE 1 - Nesting success (% of nests that successfully hatch at least one egg) and loss to predators.

	Number of Nests	Percent Success	Percent Predation	Source
Mallard <i>Anas platyrhynchos</i>	36	33.3	33.3	1
Mallard	510	12.7	73.7	2
Mallard	206	51.5	34.0	3
Mallard	124	16.9	66.1	4
Mallard	1942	30.5	64.9	5
Mallard	95	44.2	46.3	6
Mallard	304	38.5	53.0	7
Pintail <i>Anas acuta</i>	34	23.5	38.2	1
Pintail	98	39.8	51.0	3
Pintail	93	40.9	53.8	4
Pintail	126	40.5	55.7	5
Gadwall <i>Anas strepera</i>	95	10.5	75.8	2
Gadwall	31	54.8	32.3	3
Gadwall	66	28.8	57.6	4
Gadwall	25	52.0	37.7	5
Gadwall	83	49.4	33.7	6
Widgeon <i>Anas americana</i>	25	20.0	72.0	4
Widgeon	44	43.2	52.3	5
Shoveler <i>Anas clypeata</i>	49	38.8	49.0	4
Shoveler	43	46.5	40.7	5
Blue-winged Teal <i>Anas discors</i>	223	59.6	17.0	8
Blue-winged Teal	33	36.4	51.5	1
Blue-winged Teal	173	21.4	70.8	9
Blue-winged Teal	106	36.8	47.2	10
Blue-winged Teal	158	42.4	44.3	4
Blue-winged Teal	691	40.5	53.7	5
Blue-winged Teal	173	56.6	30.6	6
Blue-winged Teal	691	9.0	81.0	11
Cinnamon Teal <i>Anas cyanoptera</i>	126	11.9	70.6	2
Cinnamon Teal	147	55.8	26.5	3
Green-winged Teal <i>Anas crecca</i>	21	23.8	57.1	4
Green-winged Teal	43	25.6	61.4	5
Various Anatinae	512	48.8	42.6	12
Various Anatinae	88	43.2	44.3	13
Various Anatinae	570	56.1	43.9	14
Various Anatinae	182	20.9	60.4	15
X		36.3	50.7	
SE		2.43	2.54	

References: (1) Sowls 1948, (2) Anderson 1956, (3) Hunt & Naylor 1955, (4) Keith 1961, (5) Stoudt 1971, (6) Oetting & Cassel 1971, (7) Anderson 1957, (8) Bennett 1938, (9) Glover 1956, (10) Burgess et al. 1965, (11) Livezey 1981, (12) Kalmbach 1937, (13) Schranck 1972, (14) Duebbert & Lokemoen 1976, (15) Higgins 1977

Similar results exist for tetraonids and phasianids. Predation caused loss of approximately 36% of nests and accounted for 80% of nesting mortality based on a summary of 82 studies and including more than 5400 nests of a variety of species of Tetraoninae (Bergerud 1988). Removal of predators caused an increase in nesting

success and population size of three species of tetraonids (Marcstrom et al. 1988). Moreover, 30 of 37 data sets with large sample sizes yielded correlations between nesting success and population size in the following year, indicating that nesting success and predation mortality strongly influence population sizes (Bergerud 1988). Similarly, phasianids, including partridges (*Perdix perdix*, *Alectoris rufa*) and Ring-necked Pheasants *Phasianus colchicus*, increased both nesting success and population sizes following predator removal (Chesness et al. 1968, Potts 1980, Potts & Aebischer 1989).

TABLE 2 - Nesting success on islands or other relatively predator-free environments.

	Number of Nests	Percent Success	Percent Predation	Source
Mallard	1427	83.4	0.8	1
Mallard	185	60.2	3.3	2
Mallard	252	71.2	9.5	3
Mallard	604	81.8	7.6	4
Pintail	260	91.2	5.4	4
Pintail	135	82.1	4.2	2
Gadwall	811	87.9	0.0	1
Gadwall	287	82.0	12.0	5
Gadwall	29	90.0	0.0	6
Gadwall	179	89.9	5.6	7
Gadwall	658	89.1	3.8	4
Gadwall	660	85.1	4.9	2
Widgeon	45	74.9	7.7	3
Shoveler	189	80.4	6.9	2
Shoveler	132	69.7	8.5	3
Shoveler	106	92.5	2.8	4
Blue-winged Teal	107	71.8	7.4	3
Cinnamon Teal	326	84.1	2.6	2
Cinnamon Teal	77	77.9	6.5	4
Various species	85	82.4	8.2	8
Various species	55	76.4	5.6	9
X		81.1	5.4	
SE		1.80	0.69	

(1) Duebbert et al. 1983, (2) Williams & Marshall 1938, (3) Girard 1941, (4) Rienecker & Anderson 1960, (5) Hines & Mitchell 1983, (6) Vermeer 1968, (7) Duebbert 1966, (8) Townsend 1966, (9) Keith 1961.

Effects of predation on passerines and other small birds with altricial young in open nests should be similar to those for the ground-nesting precocial species reviewed above given that predation rates are similar. Unfortunately, predator removal experiments have rarely been used to examine the consequences of predation for birds with altricial young. However, Blankinship (1966) removed avian predators on White-winged Doves *Zenaida asiatica* and obtained increased nesting success and population sizes. Also, Sherry and Holmes (1991) found that nest predation was the major cause of nesting mortality for American Redstarts *Setophaga ruticilla* and that nesting mortality in the preceding season explained 70% of the variation in number of first-year recruits. Thus, nest predation can clearly form an important limit on population sizes and a strong selection pressure on demographic traits.

TABLE 3 - Comparisons of success of natural and artificial nests in areas with and without predator removal.

	Predator Removal	No Removal (Control)	
NATURAL NESTS			
Various Anatinae	63 ^a	23	Balser et al. 1968
Various Anatinae	89	60	Duebber & Kantrud 1974
Mallard	92	58	Duebber & Lokemoen
Gadwall	94	55	1976, 1980
Pintail	94	74	"
Blue-winged Teal	87	65	"
Various Anatinae	81	6	Greenwood et al. 1990
X	85.7	48.7	
(SE)	(4.16)	(9.31)	
ARTIFICIAL NESTS			
	84	66	Lynch 1972
	81	34	Balser et al. 1968
	73	46	Schranck 1972
X	79.3	48.7	
(SE)	(3.28)	(9.33)	

^a Predator control was not complete.

INTERACTION OF NEST PREDATION AND FOOD LIMITATION

An influence of nest predation does not eliminate an interactive influence of food. For example, long-term studies on partridges (Potts 1980, Potts & Aebischer 1989) demonstrate interacting influences of both predation and food on demography. Moreover, a variety of studies have shown an influence of food on life history traits (reviewed in Drent & Daan 1980, Martin 1987). On the other hand, much work on life history traits in birds has focused on birds nesting in boxes because of the ease of study. Yet, predation rates are abnormally low in nest boxes (Nilsson 1986) and densities may be artificially increased over conditions of natural holes. Such effects may increase demonstrable food limitation effects while minimizing the influence of nest mortality.

Effects of nest predation on demography and fitness are not necessarily reflected simply by nest predation rates because birds are able to compensate for nest predation to some extent through renesting effort. Food may interact with nest predation by influencing renesting efforts (Slagsvold 1984). Food may influence renesting by affecting: 1) probability of renesting, 2) clutch size in the renesting attempt, and 3) the date of nest initiation at the beginning of the season. Food supplementation experiments rarely show consistent effects on clutch size and while they often cause increased nesting success, the increase is usually relatively minor (see Martin 1987). Yet, food supplementation experiments consistently advance the initiation date of the breeding season (see Martin 1987) and thereby provides more opportunities for renesting efforts. Increased food abundance can also affect incidence of multiple brood attempts (Martin 1987, Simons & Martin 1990). Such food effects can potentially ameliorate

predation losses and affect population sizes (Rodenhouse 1986). The relative influence of food versus predation will then depend on the extent to which differences in food abundance influence clutch size and number of nesting attempts versus differences in predator and alternative prey populations affect nesting success in space and time. Effects of food on demography need more careful study in natural (not nest boxes) conditions because of potential interacting effects; greater food abundance may yield an increase in population size not only from effects on increased fecundity but also because nest predation is markedly reduced by an increased abundance of alternative prey (e.g. see Marcstrom et al. 1988). Moreover, interaction of food and predation can influence evolution of life history traits in a variety of ways (Slagsvold 1982, Martin 1991a) and this interaction needs more specific study.

In summary, food limitation has been given priority attention in studies of demography and, particularly, evolution of life history traits. Yet, effects of food limitation during breeding are rarely experimentally tested at the population level. Moreover, much previous work has focused on nest box studies which enhance the probability of food effects while minimizing nest mortality effects. Experimental studies of the effects of nest predation at the population and individual levels demonstrate clear and strong limits by predation. Thus, while food limitation may commonly exist, it is not the only important influence on demography and demographic traits.

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SYMPOSIUM 28

BIRD-PLANT INTERACTIONS

Conveners M. N. CLOUT and D. C. PATON

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NEW PERSPECTIVES ON NEOTROPICAL PLANT-HUMMINGBIRD INTERACTIONS

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ABSTRACT. In Neotropical wet forests, some co-occurring plants pollinated by hummingbirds (Trochilidae) differ in flowering season, leading to speculation that competition for pollination shapes these assemblages. At Monteverde, Costa Rica, experiments focused on interactions among three shrubs that simultaneously use *Lampornis calolaema* for pollination. In laboratory trials with captive hummingbirds feeding at sequences of flowers, pollen transfer among flowers of one species was invariably decreased by intervening flowers of a second. In field experiments using free-ranging birds and controlled arrays of flowering plants, effects of neighboring "competitors" on pollination of focal plants varied from strong to very weak. These and other studies suggest that competition for pollination does not operate uniformly among bird-pollinated plant species and is unlikely to act as a consistent selective force.

Keywords: Central America, competition for pollination, Costa Rica, floral neighborhoods, flowering seasons, hummingbirds, *Lampornis calolaema*, phenology, pollination, Purple-throated Mountain-gem, Trochilidae.

INTRODUCTION

Plants with colorful, conspicuous flowers pollinated by tropical hummingbirds (Trochilidae) seem especially likely candidates for strong interspecific competition and its consequences. A typical wet forest in Central or South America hosts dozens of such plant species, with hummingbirds often flying from one species to another. There is ample theoretical justification for expecting animals' indiscriminate foraging among plants to result in character displacement among the plant species involved (Waser 1983), either through eliminating one or another of species that overlap highly in "pollination niches" or through adjusting flowering phenologies and flower morphologies by natural selection in situ. Indeed, tropical hummingbird-pollinated plants as a whole provide nectar throughout the year as a result of different species coming into peak bloom asynchronously. In the 1970s, initial evidence suggested that the phenological displacement among species might exceed that expected by chance alone (Feinsinger 1983, 1987). Subsequent debate over statistical analyses (cf. Rathcke 1984) shed little light on the basic premise: that strong competition (through any one of several mechanisms) occurs among plants sharing pollen-carrying space on hummingbirds and that plants flowering simultaneously with other species suffer as a result.

FLORAL NEIGHBORHOODS

Consider an individual plant pollinated by hummingbirds. This focal plant's flowering neighbors may be many or few, conspecifics or other species sharing the same hummingbirds. The floral neighborhood is likely to affect the behavior and pollen load of a hummingbird arriving at the focal plant, and subsequent dispersal of the focal plant's pollen. As different plant species come into or go out of bloom, the neighborhood's makeup changes, and so does the quality of pollination.

In the understory of the Monteverde cloud forest in north-western Costa Rica, Central America, more than 50 species of plants are pollinated by hummingbirds, forming two pollination guilds. Plants with long flowers are pollinated by hummingbirds with long bills, particularly the Green Hermit, *Phaethornis guy*. Plants with short flowers are pollinated almost exclusively by the Purple-throated Mountain-gem *Lampornis (castaneiventris) calolaema*. Plants' floral neighborhoods vary, but most contain several additional species in flower. Hermits and mountain-gems have broad diets and may carry up to 16 species of pollen at once. Because flowers are insufficiently pollinated (Feinsinger et al. 1986), there is potential for strong competitive interactions.

MECHANISMS OF COMPETITION: LABORATORY EXPERIMENTS

One potent mechanism by which the floral neighborhood might influence a focal plant's pollination is the neighborhood's effect on the numbers of pollen grains delivered to the plant's stigmas (Feinsinger 1987). At Monteverde, floral neighborhoods of the understory shrubs *Besleria triflora* (Gesneriaceae) and *Palicourea lasiorrachis* (Rubiaceae) usually contain mixtures of their respective conspecifics and the widespread treelet *Cephaelis elata* (Rubiaceae). Individual Purple-throated Mountain-gems forage freely within these mixtures. All three plants deposit pollen at similar points on Mountain-gems' bills (Feinsinger & Tiebout in press).

What happens when a Mountain-gem entering the floral neighborhood of a *Palicourea* or *Besleria* forages first at a conspecific neighbor, then at a *Cephaelis* before reaching the focal plant? We used temporarily captive Mountain-gems that were trained to visit sequences of hand-held flowers (Feinsinger & Tiebout in press). In a given trial, the bird first fed at either 2 or 15 pollen donor flowers of the focal species (*Besleria* or *Palicourea*), then at 0, 2, or 10 *Cephaelis* flowers, and finally at 20 recipient flowers of the focal species. Styles of recipient flowers were later examined for pollen tubes. With *Palicourea*, we used long-styled flowers as donors and short-styled flowers as recipients; each pollen tube represents a pollen grain transferred from donor flowers, for one morph can only be fertilized by the other. Each *Besleria* flower is first male and then female; we used males as donors and females as recipients.

Whether 15 or 2 pollen donors were used, intervening *Cephaelis* flowers strongly decreased pollen transfer in both focal species (Feinsinger & Tiebout in press). Amounts transferred in these experiments were similar to amounts encountered on stigmas in the field, quantities often insufficient for full seed set (Feinsinger & Tiebout in press). Thus, these controlled experiments confirmed the existence of a strong competitive mechanism.

EFFECTS OF FLORAL NEIGHBORHOODS: FIELD EXPERIMENTS

We next asked whether the mechanisms demonstrated in the laboratory also operated in a forest setting. We manipulated floral neighborhoods of individual *Besleria* and *Palicourea*, choosing four representative densities of conspecific and *Cephaelis* flowers. In each experiment, each focal plant was the center of a floral neighborhood, 20 m in radius, which contained at different times: 10 conspecific flowers (i.e., either *Besleria*, or long-styled *Palicourea* compatible with short-styled focal plants) plus 10 *Cephaelis* flowers (Treatment A); or 90 conspecifics plus 10 *Cephaelis* (B); or 10:90 (C); or 50:50 (D). We predicted pollination success and seed output to increase with increasing flower density in the neighborhood (Treatment A < D); to increase with a decreasing proportion of *Cephaelis* flowers (C < D < B); to increase with a decreasing absolute number of *Cephaelis* flowers (C < A); or, combining predictions, C < A < D < B. We assigned the sequence of four treatments to each focal plant in a Latin square crossover design using 3 blocks of 4 plants each. Flower numbers and dispersions were controlled daily (Feinsinger et al. in press).

In *Palicourea*, where only pollen delivered from long-styled neighbors could effect fertilizations in short-styled focal plants, pollination varied strongly with shifts in floral neighborhood. Treatment means nearly always followed the predicted sequence C < A < D < B, although in pairwise comparisons the means for treatments B and D seldom differed significantly. Increasing the absolute or relative densities of neighboring *Cephaelis* flowers apparently diluted the loads of *Palicourea* pollen with which birds arrived at focal plants. Highly significant treatment effects on pollination *per se* persisted through fruit and seed maturation. In *Besleria*, treatment means also followed the predicted sequence C < A < D < B, but overall treatment effects were much weaker and often insignificant (Feinsinger et al. in press).

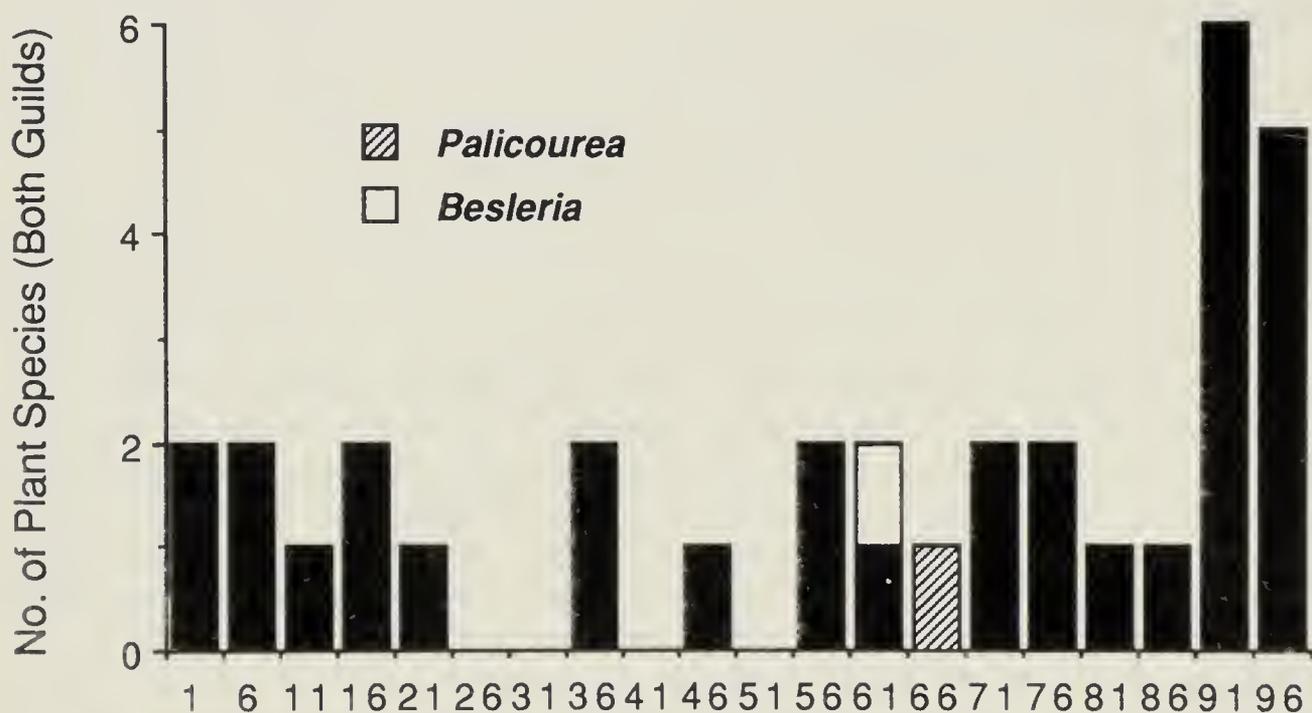
Thus, floral neighborhood influences pollination success, reproductive output, and plant fitness sometimes but not always. Self-incompatible plants such as *Palicourea* may be more sensitive to neighborhood make-up than are self-compatible species such as *Besleria*. Both guilds of hummingbird-pollinated plants at Monteverde and elsewhere in the Neotropics contain a mixture of both self-incompatible and self-compatible species, with the latter predominating (J. H. Beach and W. Zuchowski, unpublished data). Still, even self-compatible species might be expected to face selective pressures to minimize competitive effects no matter how sporadic those effects might be. Do Monteverde's plant species display the patterns of character displacement expected to result?

PHENOTYPIC PATTERNS? NULL-MODEL ANALYSES

We examined each of the two guilds at Monteverde for patterns of character displacement among species (Murray et al. 1987). Theoretically, patterns of character displacement reflecting past competition could involve one of two modes (Waser 1983). Displaced flowering times are cited most often; alternatively, plants that flowered simultaneously could differ in the placement of reproductive parts.

We calculated an observed phenological overlap value for each species, based on how much its flowering season overlapped with that of its summed guildmates. We

compared this value with values obtained after 100 computer-generated randomizations of flowering seasons. The null model assumed that each month was equally suitable for flowering, a reasonable assumption for plants living in a nearly aseasonal environment with stable pollinator populations. We found that only two of 33 species minimized overlap in flowering season with the remainder of their guild (Figure 1). In fact, more plants converged phenologically on their guildmates than diverged from them! Neither *Palicourea* nor *Besleria* minimized overlap with the remainder of its guild. Furthermore, we found no evidence for morphological displacement among simultaneously flowering plants (Murray et al. 1987). Species using the same pollinator at the same season did not partition space on hummingbirds any more than did species separated by season.



Times (per 100) Observed Overlap on Species > Overlap After Randomization

FIGURE 1 – Results of randomization analysis to evaluate phenological displacement in flowering among plants in each of Monteverde's hummingbird-pollinated guilds (details in text and in Murray et al. 1987). Species with low values (< 6) on X axis overlap less with their guildmates than expected by chance alone; species with high values (≥ 96) overlap more than expected by chance alone. Results from both guilds included. Note that very few species overlap less with the remainder of their guild than would be expected by flowering at random.

CONCLUSIONS

Intense competition, demonstrated by manipulating sequences of flowers that hummingbirds visit, did not produce a detectable pattern at the community level. The sequence of flowers that hummingbirds visit before arriving at a focal plant may matter less for some plant species than for others. It may be that selective pressures against sharing flowering seasons or space on pollinators are simply not consistent or strong enough to generate community-level patterns. Each bird-pollinated plant population at Monteverde displays a complex spatial distribution. Different parts of the deme interact with different sets of competitors capable of generating opposing selective pressures. Even at one location, selective pressures undoubtedly vary year to year or

generation to generation: flowering phenologies vary somewhat from one year to the next, so that one year a flowering plant population might encounter one set of guildmates (and the selective pressures these generate) but the next year quite another set. Furthermore, the landscape of volcanic Central American mountain chains, and of many other regions of Central and South America, is highly dynamic in the long term as well (Castillo-Munoz 1983). Plant populations are likely to migrate somewhat independently over this changing landscape, such that the species membership of a bird-pollinated guild at any one site is frequently re-shuffled.

Still, tantalizing questions remain. Why is it that those wet tropical forests examined to date, and even a comparatively species-poor temperate rain forest in Chile (C. C. Smith, unpubl. data), have at least one bird-pollinated plant species in good flower on any given day of the year? If the assembly of pollination guilds were entirely random with regard to flowering peak, there should be some cases where some months are bereft of flowers or nearly so. Perhaps there is a diffuse advantage to flowering when other species do not and when hummingbirds' attention is not diverted elsewhere, even if the disadvantage of flowering simultaneously with others is not sufficiently strong to prohibit coexistence. Why is it that the clearest evidence for displaced flowering peaks comes from congeneric species known to hybridize (Stiles 1975, 1985)? Focal plants whose neighborhoods contain mixtures of species often receive other species' pollen on their stigmas (Feinsinger et al. 1986). These grains might have little effect if coming from unrelated species but much more serious effects on focal plants' fitness if capable of using up stylar nutrients and wasting scarce ovules on non-viable offspring. Perhaps selection against hybrids is a strong structuring force at the community level. This possibility remains to be tested, and we hope that additional assemblages of bird-pollinated plants will be examined carefully. Meanwhile, the initial burst of enthusiasm over accepting competition *sensu stricto* as a structuring force in bird-pollinated plant assemblages appears to have been premature.

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VARIATION IN MELIPHAGID MORPHOLOGY AND ITS INFLUENCE ON POLLEN DISPERSAL IN AUSTRALIAN PLANTS

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ABSTRACT. Morphological features of Australian honeyeaters influenced the frequency and extent to which a particular bird species contacted the reproductive parts of flowers of two plant species. For *Lambertia formosa*, Little Wattlebirds *Anthochaera chrysoptera* made more probes during a visit to an inflorescence, dislodged more pollen from pollen presenters, and deposited more pollen on the stigmas than did several smaller species of honeyeater. For *Correa reflexa*, New Holland Honeyeaters *Phylidonyris novaehollandiae* and Eastern Spinebills *Acanthorhynchus tenuirostris* differed in how they probed flowers, and in the quantities of pollen they dislodged from anthers. Despite having long tubular flowers, neither plant species was guaranteed of receiving pollen on their stigmas when a honeyeater probed a flower, and the quantities of pollen transferred were highly variable.

Keywords: Pollen dispersal, Australian plants, honeyeater morphology, *Correa reflexa*, *Lambertia formosa*, pollination by birds, Meliphagidae.

INTRODUCTION

Honeyeaters (Meliphagidae) are important pollinators of many Australian plants (Paton 1988). These plants are all visited by a variety of honeyeaters that differ in body mass (8-152 g) and bill morphology from almost straight to decurved bills, 11-44 mm long and 3-8 mm thick (depth or width of bill at nares). These features influence the speed with which nectar can be extracted from flowers, the speed and mode of movement between flowers as well as the energetic costs of the birds (Paton & Collins 1989). The relevance of these differences in honeyeater morphology to the plants has not been considered, although several authors have argued that differences in honeyeater behaviour may alter patterns of pollen dispersal (Paton & Ford 1983, Ramsey 1989). These studies, however, have not examined whether honeyeaters that differ morphologically also differ in the amounts of pollen that they dislodge from anthers, and deposit on stigmas, of *Lambertia formosa* and *Correa reflexa*.

METHODS

The flowers of *Lambertia formosa* are tubular, about 30 mm long, and arranged in inflorescences that consist of a central flower surrounded by six others. A single style protrudes from each flower a further 20 mm beyond the tubular perianth. The seven flowers on an inflorescence are synchronous, with anthesis occurring at dawn. At anthesis, the four adnate anthers of each flower deposit their pollen on the tip of the style (pollen presenter) before the tips of the perianth curl back. On the second or third day when most, if not all, of the pollen has been dislodged, a small slit (stigmatic cleft) at the tip of the style opens, and the flower is then ready to receive pollen. On the third or fourth day the flowers wilt.

Field work on *Lambertia formosa* was conducted at Brisbane Waters National Park near Pearl Beach, New South Wales. Pollen removal from flowers of *Lambertia formosa* was measured by selecting inflorescences that were just opening at dawn and watching these until they were visited. When an inflorescence was visited, I recorded the species of honeyeater, counted the number of probes made into flowers on the inflorescence, and then carefully clipped the seven pollen presenters into a small vial. The pollen remaining on these seven presenters was then suspended in 0.5 ml of lactophenol and the number of pollen grains present estimated by counting small aliquots with a haemocytometer. These quantities were then compared against the quantities present at recently-opened inflorescences that were not visited. The amounts of pollen deposited in the stigmatic clefts of *Lambertia formosa* flowers were determined using pollen-free inflorescences. These were obtained by removing all the pollen from the pollen presenters of recently-opened inflorescences on the afternoon of the first day using a soft cloth. Initially, I bagged these inflorescences overnight to prevent animals from visiting the flowers and depositing pollen in the clefts. However, visitation rates to flowers in the late afternoon were low and this was not necessary. On the next morning, when the stigmatic clefts had opened, all flowers were checked for the presence of pollen in their stigmatic clefts using a 30X pocket light microscope. If there was no pollen in the clefts of all seven flowers, the inflorescence was then watched. If a honeyeater visited the inflorescence, the species of honeyeater and the number of probes made were recorded. I then counted the number of pollen grains that had been deposited into each stigmatic cleft.

In addition to these field measurements, I also used museum specimens of the birds to confirm the patterns observed in the field. This consisted of probing specimens of different honeyeaters into *Lambertia* inflorescences and measuring the amounts of pollen dislodged from pollen presenters, or deposited in stigmatic clefts. For pollen removal I probed the specimens into recently-opened pollen-bearing inflorescences once and then measured the amount of pollen remaining as explained above. For pollen receipt, I first loaded the stuffed specimen with pollen by probing 10 recently-opened pollen-bearing inflorescences each seven times. The specimen was then probed once into a single pollen-free inflorescence and the pollen that was deposited in each stigmatic cleft counted.

Studies on *Correa reflexa* occurred near the National Parks and Wildlife Service headquarters at Rocky River in Flinders Chase National Park on the western end of Kangaroo Island, South Australia. This population of *Correa reflexa* had tubular flowers (perianths) that were about 25 mm in length. When the flower first opened the eight stamens and the stigma were both located within the perianth and during the next three days both the style and filaments grew until they reached their final length 5-15 mm beyond the perianth. The style usually protruded several millimetres beyond the anthers. The anthers then dehisced on about the third day, followed by the parting of the stigmatic lobes. The stigmatic surfaces remained parted and receptive for pollination until the flower wilted on about the ninth day. The flowers, therefore, were only weakly protandrous depending on how quickly pollen was dislodged from the anthers by animals.

The quantity of pollen dislodged from anthers and deposited on stigmas of flowers of *Correa reflexa* by various honeyeaters was measured in an aviary (3 m x 2 m x 2 m) by presenting captive birds with flowers that were either fully loaded with pollen (for pollen removal) or emasculated flowers that were free of pollen (for pollen receipt).

TABLE 1 – Morphological variation in Australian honeyeaters and its influence on pollen removal and receipt for *Lambertia formosa* and *Correa reflexa*. Species of honeyeater differed in the quantities of pollen removed and deposited in flowers (ANOVAs, *** $P < 0.001$, ** $P < 0.025$, * $P < 0.05$). Standard errors were usually less than 10% for the mean, except for pollen receipt (up to 20%). Sample sizes ranged from 8 to 368.

	Little Wattlebird	New Holland Honeyeater	Whitecheeked Honeyeater	Eastern Spinebill
Avian Morphology (after Paton & Collins 1989)				
Mass (g)	69.0	20.4	18.3	10.7
Head width (mm)	22	18	18	14
Bill length (mm)	29.0	21.0	23.7	24.1
Bill width/depth (mm)	7	5	5	3.5
Bill curvature	0.06	0.05	0.05	0.12
<i>Lambertia formosa</i> and wild birds				
Probes/inflorescence***	6.8	5.8	5.4	4.3
Pollen removed (%)***	72	50	48	37
# stigmas with pollen***	4.9	3.3	3.5	2.0
# pollen grains rec'd*	23.9	14.4	16.8	7.4
Inflorescences with pollen (%) *	100	93	95	60
<i>Lambertia formosa</i> and museum specimens				
Probes/inflorescence	1	-	1	1
Pollen removed (%)***	33	-	23	14
# stigmas with pollen***	2.8	-	2.1	1.7
# pollen grains rec'd***	40.5	-	31.8	22.1
Inflorescences with pollen (%)	100	-	97	97
<i>Correa reflexa</i> and captive birds				
Pollen removed (%)	-	53.0	-	33.9
# pollen grains rec'd	-	4.4	-	5.5
Flowers receiving pollen (%)	-	40.0	-	36.8

Flowers that had full complements of pollen were obtained from plants in the field by collecting 20-30 cm long branches that had large buds that were about to open. These stems were placed in vases of water and isolated in a room until the anthers had dehisced. These stems were then presented to birds in the aviary. Once a flower was visited, the anthers were collected in a small vial and the quantity of pollen that still remained determined as above. Emasculated pollen-free flowers were obtained in a similar way, except that the anthers were removed from the large buds at the time of collection and the flowers kept until the stigmatic lobes had opened. The stigma of each flower was then examined with a 30x or 100x pocket light microscope to confirm that each was free of pollen before presentation to a bird. The procedure for

measuring pollen deposition involved training birds to first visit an intact flower with a full complement of pollen and then a series of five emasculated pollen-free flowers. Each of these emasculated flowers was then examined and the quantity of pollen deposited at each counted under a microscope.

RESULTS

Pollen removal and receipt at inflorescences of *Lambertia formosa*

Four species of honeyeater were frequent visitors to the flowers of *Lambertia formosa* in Brisbane Waters National Park. These were the Little Wattlebird *Anthochaera chrysoptera*, the New Holland *Phylidonyris novaehollandiae* and White-cheeked *P. nigra* Honeyeaters, and the Eastern Spinebill *Acanthorhynchus tenuirostris*. Table 1 provides a summary of avian morphology and results.

On average, Little Wattlebirds made more probes on a visit to an inflorescence than the intermediate-sized New Holland and White-cheeked Honeyeaters, and small Eastern Spinebill. They also dislodged more pollen from intact inflorescences with full complements of pollen, and deposited more pollen on a visit to a pollen-free emasculated inflorescence than did the smaller honeyeaters. The smaller honeyeaters occasionally failed to transfer pollen to any of the stigmas.

The patterns shown were confirmed with museum specimens. There is a logical reason for this difference. The average distance between the pollen presenters or stigmas of adjacent flowers in an inflorescence was 12.1 ± 0.2 mm (S.E., $n = 100$), which is smaller than the head width of the birds. In probing one flower the birds were likely to contact more than one pollen presenter or stigma. Since Little Wattlebirds have larger heads, they would be expected to contact more pollen presenters or stigmas and hence remove and deposit more pollen.

Pollen removal and receipt at flowers of *Correa reflexa*

Four species of honeyeater were recorded visiting the flowers of *Correa reflexa* at sites near Rocky River: the Eastern Spinebill, New Holland Honeyeater, Crescent Honeyeater *Phylidonyris pyrrhoptera* and Purple-gaped Honeyeater *Lichenostomus cratitia*. These are all small to medium-sized honeyeaters. The larger wattlebirds, although present in the area, did not visit the flowers of *Correa*. Eastern Spinebills and New Holland Honeyeaters, however, were the most frequent visitors to *Correa* flowers in this area over several years, and my aviary assessments of pollen removal and receipt are confined to these two species.

Eastern Spinebills generally accessed *Correa reflexa* flowers from the side, probing between the filaments; contact with the anthers and stigma occurred largely with feathers on the crown (Figure 1). New Holland Honeyeaters usually probed between the anthers and down the centre of the flower such that the anthers were spread apart, making contact with feathers on the chin, face and forehead. The amounts of pollen removed differed significantly. In probing the flowers, the bills of both species often displaced the style to one side, and consequently the stigma often failed to contact the feathers of the birds (see Figure 1).

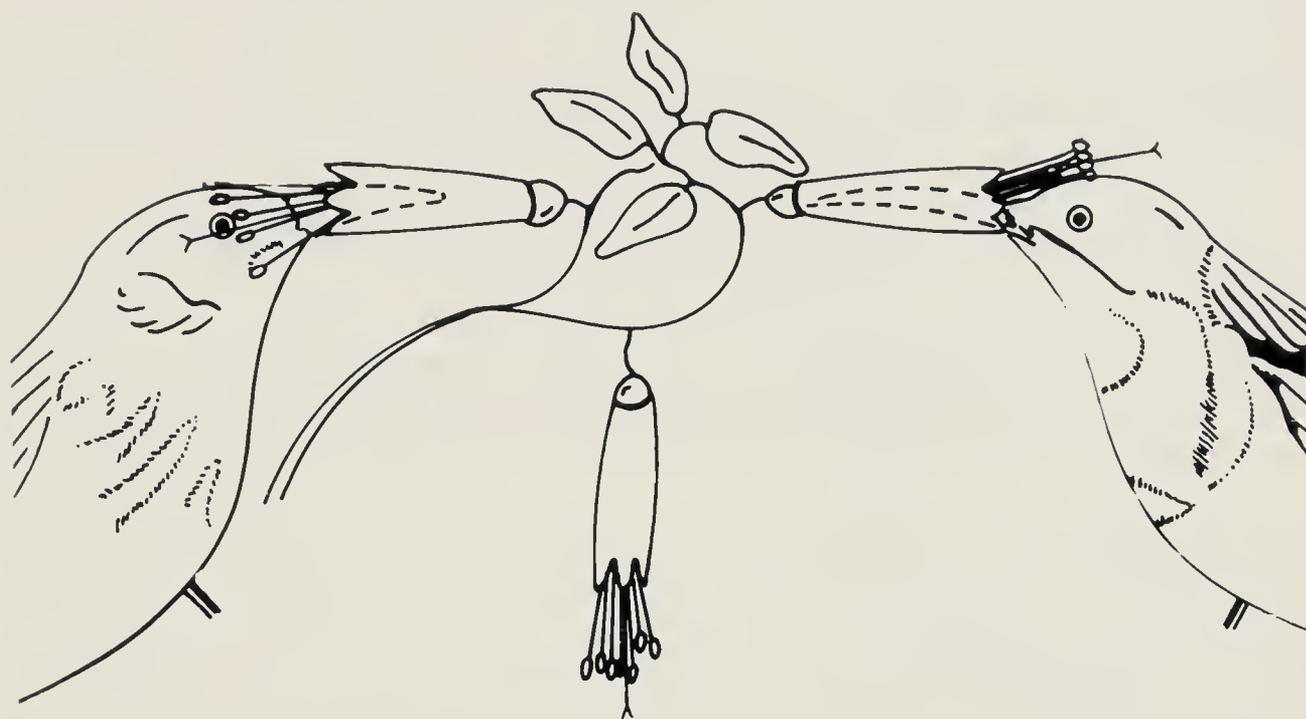


FIGURE 1 – Usual positions in which anthers strike the feathers of Eastern Spinebills (right) and New Holland Honeyeaters (left) when probing *Correa reflexa*.

DISCUSSION

Morphological features of Australian honeyeaters clearly influence the quantities of pollen transferred during visits to flowers. Differences between honeyeaters in the service that they provide for plants is a necessary pre-requisite if specific relationships are to evolve between certain birds and plants. As a general rule, larger honeyeaters should dislodge more pollen from anthers and deposit more pollen on stigmatic surfaces than smaller honeyeaters. One reason is that larger honeyeaters have a greater surface area and hence present a greater target at the reproductive organs of flowers. Also, when large birds probe clusters of flowers they should probe more of the flowers than smaller birds before travelling to another inflorescence. For larger honeyeaters, the costs of travelling to other inflorescences are greater relative to the costs of staying and probing more flowers, so they should stay longer at an inflorescence.

At present, there is insufficient information on other aspects of pollen dispersal in these systems to determine which honeyeaters provide the better service, if any. Although larger honeyeaters removed and deposited more pollen at flowers, larger species may also effect greater levels of self-pollination, and so not be as effective cross-pollinators as smaller species. Both *Correa reflexa* and *Lambertia formosa* are largely self-incompatible and need cross-pollination for maximum seed production. One factor that may now favour larger birds is the introduced honeybee, *Apis mellifera*. Bees can remove as much as 90% of the pollen from some bird-pollinated species, including *Correa reflexa* and *Lambertia formosa*, without effecting much pollination (Paton 1990). Since larger honeyeaters dislodge more pollen from the anthers when they visit a flower, the quantity of pollen that can then be lost to honeybees should be less than when smaller species visit flowers.

Although the potential exists for the evolution of more precise relationships, there are no highly specialized birdflowers in Australia. Each species of plant is visited by a morphologically diverse range of birds, and vice versa (Paton 1988). Many factors contribute to this. Although different honeyeaters may differ in their overall performance, the performance at individual flowers and plants is highly variable, and there is no sharp distinction or consistent difference between various birds as pollinators as far as individual plants are concerned. Most Australian plants pollinated by birds are long-lived and experience varying environmental conditions, and the availability of specific species of birds as pollinators may also vary. What may be more relevant to the evolution of specific relationships is how reliable a particular pollinator is from one year to the next, rather than performances at individual flowers. Equally important for the evolution of a more specific relationship is that the plants are adequately pollinated. Plants that attract the most effective pollinators and deter less effective pollinators should have a selective advantage, but when there is inadequate service, plants that deter less effective pollinators may be selected against. Inadequate pollination has been found to occur in a variety of Australian plants pollinated predominantly by birds (Paton 1988, Zimmerman & Pyke 1988). These plants, at least, should not evolve more specific relationships with certain birds but should take advantage of all birds and possibly other animals that visit their flowers.

Both *Lambertia formosa* and *Correa reflexa* are regarded as being highly specialized towards birds for pollination. Despite this, the flowers of both species are not guaranteed of receiving pollen on their stigmas when a honeyeater probes a flower. The quantity of pollen dislodged from anthers during a visit is also highly variable. Furthermore despite the dislodging of tens of thousands of pollen grains only a few ever reach stigmas. This is due to a number of factors including the morphology of the flowers and birds, which allows considerable imprecision and variability in the ways in which even these 'specialized' flowers are probed.

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AVIAN DISPERSERS AND FLESHY FRUITS IN NEW ZEALAND

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ABSTRACT. Long isolation of New Zealand, climatic and geographic fluctuations throughout the Cenozoic, and impacts of human settlement have resulted in a depauperate and depleted native avifauna, with few obligate frugivores. This is despite the abundance of native plant species which produce fleshy fruits (c. 250, mainly evergreen and woody). Fruits are typically small (<10 mm diameter) and reddish (67%). There are three major frugivores reproductively sensitive to the availability of fruit, eight opportunistic frugivores seasonally dependent on nectar and insects, and several omnivores that occasionally eat fruit. All frugivores are non-migratory generalists and eat a wide range of fleshy fruits, but with recent extinctions of moa and other frugivores some large-fruited plant species now depend on one pigeon species for their dispersal. Past and present interactions between avian frugivores and fleshy plants in New Zealand are discussed.

Keywords: Frugivory, breeding, seed dispersal, extinction, conservation.

INTRODUCTION

New Zealand has been isolated since the Cretaceous. The archipelago has spanned a wide latitudinal range, and the biota has both subtropical and cool temperate affinities. Isolation has limited immigration, producing a high degree of endemism in a relatively depauperate biota, further depleted by geological change and climatic oscillations through the Tertiary and Quaternary. Many species consequently have broad ecological niches. Lacking terrestrial mammals apart from three species of small bat, the main fruit-eating vertebrates are birds or small lizards. We review interactions between birds and fleshy fruits in New Zealand, speculate on past interactions and comment on conservation implications.

AVIAN FRUGIVORES

Extant frugivores

Most of the c. 45 indigenous terrestrial bird species in New Zealand eat fleshy fruits. None are exclusive frugivores; a few, mainly small parrots, are largely seed predators, and for many birds, fruits are a minor component of the diet (Clout & Hay 1989). There are also several introduced passerines, including at least five partial frugivores. New Zealand lacks migrant frugivores; seasonal movements are typically less than 20 km, and some species are permanently resident on territories.

We distinguish three groups of indigenous birds from the relative importance of fleshy fruits in their feeding and breeding ecology.

Three species are reproductively sensitive to the availability of fleshy fruits and feed solely on fruits at certain times. Breeding is irregular and correlated with fruit availability. The species are Kereru (*Hemiphaga novaeseelandiae* – Columbidae), distributed throughout New Zealand; Kakapo (*Strigops habroptilus* - Psittacidae), flightless and now extremely rare; and Kokako (*Callaeas cinerea* - Callaeidae), also rare with a limited distribution in the North Island. All three are relatively large (0.25 - 2.50 kg), long-lived forest-dwelling generalist herbivores. They eat mainly fruits, foliage and flowers, and have extended incubation and fledging.

The second group are opportunistic fruit feeders that consume nectar and insects as seasonally important food items. Foliage is rarely eaten. Species include the three Meliphagids - Tui *Prothemadera novaeseelandiae*, Bellbird *Anthornis melanura* and Stitchbird *Notiomystis cincta*; Saddleback *Philesturnus carunculatus*; Silvereye *Zosterops lateralis* - Zosteropidae; Kea *Nestor notabilis* and Kaka *Nestor meridionalis*. The Stitchbird and Saddleback are extinct on the mainland but the others are widely distributed.

These species usually eat smaller fruits (< 10 mm) but Kaka often crush and digest seeds in larger fruits.

The third group of frugivores comprises most of the remaining terrestrial avifauna. These are primarily omnivores or insectivores, and their frugivory is mostly occasional. They include flightless omnivores (e.g. Kiwi *Apteryx* spp., Weka *Gallirallus australis*); several small insectivores (e.g. Robin *Petroica australis*); and a variety of other species, including parakeets (*Cyanoramphus* spp.).

Extinct species

Approximately half the native frugivorous bird species of New Zealand have become extinct since human settlement, c. 1000 years ago. Those known to have eaten fleshy fruits include the Piopio *Turnagra capensis*, Huia *Heterolocha acutirostris*, and moas. Only the diet of moas is known in any detail.

The extinction of moas (about 300 years ago) represented the loss of the entire mega-avifauna. Eleven species occupied a broad range of habitats from lowland through to subalpine areas (Worthy 1990) and ranged in weight up to 200 kg (Atkinson & Greenwood 1989). From gizzard contents, it is clear that moa were herbivores, eating seeds, leaves, twigs and fleshy fruits. Moas could potentially have eaten a wide size-range of fleshy fruits in New Zealand, although their flightlessness limited them to taking fallen fruit, and those in situ up to 3 m above ground. Because of their size, ingested seed load of moas may have been many times greater than other birds. Some moa species carried up to 5 kg of gizzard stones, indicating that ingested seeds would have been subject to considerable grinding.

PLANTS PRODUCING FLESHY FRUIT

The native flora includes 250 species bearing fleshy fruits, in 50 families. Most are evergreen and (70%) woody. Fleshy-fruited species predominate amongst the conifers (75%) but form only a small proportion of angiosperms (dicotyledons 14%, monocotyledons 6%). *Coprosma* (Rubiaceae), with over 53 taxa, is the largest genus. Most fleshy fruits are reddish (67%), the other significant colours being white

(18%) and black (15%). Most fruits are small, with 90% being <10 mm in diameter. Spherical fruits have a maximum diameter of about 20 mm (e.g. *Vitex lucens*). The few very large fruits are oblong or elliptical (e.g. taraire *Beilschmiedia taraire*) and may reach 40 mm in length.

Availability of fruits varies seasonally, with peak abundance and diversity from late summer through to late winter, although in northern regions fruit may be present all year. Fruit production in many species may extend from summer to winter. Where altitudinal gradients are steep, fruits are available locally over an extended period. At high altitudes fruits often overwinter beneath snow and become available after spring snow melt.

Most plant species fruit annually, but there is high annual variation in productivity amongst many small-fruited conifers and some large-fruited angiosperms. Greatest fruit production and seed viability follows warmer than average summers.

Species with fleshy fruits are most important in lowland tall podocarp-broadleaved forests at their early successional stages where they form approximately 70% of the vascular flora. Beech (*Nothofagus* spp.) forests contain fleshy-fruited species only as a minor structural component, usually as understory shrubs. In most other woody and herbaceous communities fruiting plants are a consistent but generally minor component (c. 20%) of the vascular flora.

INTERACTIONS

Degree of frugivory

Fewer than 12 indigenous bird species are regular frugivores and only three (Kereru, Kokako and Kakapo) seem reproductively dependent on fruits. Most fruits are eaten by several different birds, but the largest fruits (> 12 mm diameter) are dispersed only by Kereru in most forests. The importance of fruit in the diet of many birds varies spatially and temporally in relation to the relative abundance of other food items. Consumption of fruits by honeyeaters appears to be more important in New Zealand than in Australia but may simply reflect the shortage of nectar here through much of the year.

Fruiting and breeding in major frugivores

In the Kereru, Kokako and Kakapo, fruit supply and breeding seem to be closely linked. Irregular breeding in these species is probably nutritionally based. For example, in Kereru, nesting coincides with the onset of fruiting, and may be cued by the relative abundance of green fruit or perhaps by the same environmental factors that initiate heavy plant fruiting.

Bird behaviour in relation to fleshy fruits

New Zealand lacks migrant frugivores. A few flock to trees with short fruiting seasons, but Kereru and Tui will sometimes defend heavily fruiting trees. Most frugivorous species occur in a range of plant communities, and some (e.g. Tui, Bellbird, Kereru) move seasonally between communities. The permanent residence of native birds may have contributed towards the extended fruiting season and the relatively high proportion of plant species with fleshy fruits in New Zealand plant communities, despite a depauperate avifauna.

While most frugivores in New Zealand ingest entire fruits, a few small minor frugivores may only pick fruit flesh. Seed regurgitators are not common, although it is apparently usual for Kokako (but not the larger Kereru) to regurgitate the sharply ridged stones of *Vitex lucens* and to peck the flesh from other large fruits. Some bird species (e.g. Weka, Kiwi spp.) apparently ingest fruit stones in lieu of gizzard stones.

Seed predators

The only native birds that regularly digest seed are Psittacidae, particularly Kaka and parakeets. Beveridge (1964) noted that destruction occurs when the fruits are unripe or on the ground; usually up to 40% of fallen *Podocarpus totara* seed is destroyed by parakeets.

Traits of bird-dispersed fleshy fruits

Not all types of fleshy fruits are regularly eaten. There are records of birds eating approximately 50% of the native species bearing fleshy fruit. Such fruits are typically red, orange, black, purple or blue, and >4 mm in diameter. Very small fruits (<3 mm), typically white, green or yellow, are rarely taken and small lizards are probably their main dispersal agent (Whitaker 1987). *Coprosma* species in different fruit colour groups are ecologically segregated (Lee et al. 1988). Species with reddish fruits predominate at higher altitudes (where birds are the main vertebrate dispersers) and at lower altitudes on large-leaved species where the colour contrast may make the fruits particularly conspicuous to birds. White and blue-flecked fruit are common amongst small-leaved shrubs.

Bird-dispersed fruits in New Zealand have highly variable ratios of flesh to seed load. Within *Coprosma*, ratios range from 0.5 to more than 2.0 (on a dry weight basis). In general, reddish fruits have lowest ratios of flesh to seed, and the ratio is positively correlated with altitude. Among *Coprosma* with very large fleshy fruits the ratio is reduced to 0.5, but it is likely that the flesh is lipid-rich and so of greater energy value to the disperser.

The flesh of most fruits is readily removed, facilitating efficient digestion of the pulp. In two notable exceptions the flesh near the stone is viscous and is unlikely to be removed during passage through a bird. In the hemi-parasitic mistletoe species (*Peraxilla*) this may assist lodging of the seeds on the tree branches, while flesh remaining around the stone of *Vitex lucens* protects the dispersers from the sharp raised ridges.

Enhanced germination, seed dispersal and species regeneration

Generally avian frugivores void intact seed but there is little evidence that gut passage affects germination. Germination rates for miro *Prumnopitys ferruginea* did not differ between intact fruit and seeds voided by Kereru (Clout & Tilley in prep.). Improved germination of tawa *Beilschmiedia tawa* may occur following artificial removal of fruit pulp (West 1986), but comparisons have not been made with voided seed.

Seedling survival in mixed podocarp-broadleaved forests is lowest beneath the crowns of the parent tree and greatest 30-40 m away, distances achievable only by bird dispersal. In this forest type, Kereru deposit 35% of miro seed beneath the parent tree, 40% between 10-30 m away, and a small proportion beyond 40 m (Clout, unpublished data). Without bird dispersal it is unlikely that tall podocarps would remain widely and uniformly distributed in these forests.

Frugivores help in shrub and tree invasion of disturbed sites. Clearings created by fire in podocarp-broadleaved forest in the central North Island are largely reforested within 50 years by bird dispersal from canopy species in adjoining intact forest, as indicated by the clustering of podocarps around perches on old stumps and emergent trees (Beveridge 1964).

Masting

Irregular heavy fruiting by many diverse plant species with a range of dispersal modes is often considered as an adaptative response to satiate seed predators. Ogden (1985) suggested that podocarps that produce fleshy fruits gain advantages in pre-dispersal survival; the risk of disperser satiation being offset against the advantage of the attractiveness of these trees. He argued that local variability in mast production, and the spatial scale of masting, even in mast years, is sufficient to satiate fruit-eating insects, while some asynchrony between locations prevents the frugivores becoming satiated and thus keeps the dispersal system going. However, there is no information on the relative mobility of these insects, the degree of host specificity or the spatial scale of masting. Bawa (1980) suggested that amongst fleshy-fruit-producing plant species masting could arise from the attraction of generalist animal dispersers of the seed. The concentrated food resource may induce some opportunistic frugivores to become completely frugivorous for a short time, thus enhancing opportunities for dispersal; a phenomenon characteristic of New Zealand.

More information is however required on masting and its relation to fruit quality for dispersers, before the role of frugivory in its evolution can be determined.

Moa

Keogh (1989) suggested that moas may have influenced the structure and germination ecology of fruits. Thick endocarp development common in small fruits may have given the seeds additional protection while passing through the grinding, stone-filled gizzards of moas. The related cassowaries in Australia eat mostly fallen fruit, and effectively disperse seed, although they do not have gizzard stones.

The large seed load of moas would have resulted in deposition of clumps of seeds. Howe (1989) predicted that seedlings of clumped-dispersed plant species will be strongly shade tolerant, resistant to insects, herbivores, pathogens, and seedling competition, and capable of regenerating near parent trees. In New Zealand these features occur in several large-fruited species, including some with stony seeds (e.g. hinau *Elaeocarpus dentatus*, miro), and some with thinner endocarps (e.g. tawa, taraire), which may have been less resistant to grinding in moa gizzards. The possible influence of moas on the morphology and ecology of fruiting plants merits further study.

CONSERVATION IMPLICATIONS

The recent loss of major avian frugivores and seed dispersers from New Zealand over the period of human settlement has been partly offset by the introduction of several European frugivores (e.g. *Turdus merula*, *T. philomelos*), but none are capable of dispersing seeds larger than 12 mm (Clout & Hay 1989).

The extinction of moas in the 17th century has not resulted in the obvious regeneration failure of any native plant species, although any impact may not yet be apparent amongst some long-lived podocarps.

Of greater concern is the decline of many extant frugivores (Clout & Hay 1989). The Kakapo and the Kokako, two frugivores dependent on fleshy fruits for breeding, have become endangered since European settlement - primarily through predation and habitat loss, but perhaps also through depletion of fruits by introduced mammals (Leathwick et al. 1983). Current conservation management of the Kakapo involves supplementary feeding in an attempt to improve the birds' nutritional status and induce breeding. In many New Zealand forests, the Kereru (which takes a greater range of fruit than any native or introduced bird species) is now the only common frugivore capable of swallowing fruits > 12 mm diameter. The loss or decline of this species, in particular, could have a serious impact on the distribution and regeneration of several native plant species.

CONCLUSION

New Zealand's long isolation, the high degree of endemism among both plants and birds, and the dominance of birds among vertebrates contrast vividly with the conditions prevailing on the continental land masses where most studies of plant-frugivore interactions have been hitherto conducted. Several factors thought to constrain coevolution between plants and frugivores (Herrera 1985) are absent here - for example, long-distance gene flow between plants and seasonal emigration and immigration of dispersers. Much remains to be learned of the nature of past and present bird-fruit interactions in New Zealand. We hope that this paper draws attention to the unique opportunities for such studies.

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DIGESTIVE PROCESSING OF FRUITS AND ITS CONSEQUENCES FOR FRUIT-FRUGIVORE COEVOLUTION

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ABSTRACT. Fruit processing by birds may influence the chemical composition of fruit pulp. Most fruit are bulky and fruit-eating birds display several mechanisms that allow them to process fruit quickly. Large seeds are often not ingested. If they are, they may either be regurgitated or passed through the gut quickly. Rapid seed processing increases consumption rate, but may reduce digestive efficiency. Some birds have apparently compensated for this by separating pulp and seeds in the gut, defecating seeds extremely rapidly and retaining pulp for more thorough assimilation. Nevertheless, pulp is still defecated relatively quickly and with low digestive efficiency. This compromised ability to assimilate nutrients in fruit pulp may have selected for the easily absorbed monosaccharides and free amino acids that dominate the pulp of fleshy fruits.

Keywords: Digestive efficiency, frugivores, fruit, fruit-processing, passage rates, seeds, fruit pulp.

INTRODUCTION

For more than 150 million years fruiting plants have relied on vertebrates to disperse their seeds. The evolutionary importance of this interaction is clearly reflected in the number and diversity of plant species that depend upon vertebrates to disseminate their seeds. In neotropical forests for example, 50-90% of trees and up to 98% of shrubs produce fruits of the type taken by mammals and birds (e.g. Willson et al. 1989) and 30-40% of bird species in these forests regularly consume fruit (Levey & Stiles in press). However, we are still uncertain of the coevolutionary mechanisms that produced this interaction. The two groups have provided reciprocal selection pressures—they have certainly coevolved at some level. At issue is the level at which coevolution has occurred (Jordano 1987). Stating that the interaction is an example of "diffuse coevolution" does not yield much insight.

Here I examine attributes of fruiting plants and fruit-eating birds and look for patterns in one that can be explained by selective pressures of the other. Presumably, the more general the patterns, the more "diffuse" is the coevolution, although a shortcoming of this approach is that it fails to answer the coevolutionary equivalent of "Which came first: the chicken or the egg?" We must determine the level of interaction and be able to tease apart cause and effect.

Here I examine the evolutionary relationship between two broad patterns in fruits and fruit-eating birds. First, fleshy fruits contain a high proportion of indigestible seeds and easily assimilated nutrients (Herrera 1987). Second, frugivores have unusually short retention times (Karasov & Levey in press). By investigating the techniques and consequences of how birds process seeds and pulp, I develop an answer to the question: Are the short retention times of fruit-eating birds the evolutionary cause or effect of easily absorbed nutrients in fruit pulp?

METHODS

This paper is largely based on a series of experiments on captive fruit-eating birds conducted from 1982-1988. Detailed accounts of methodology and results are given by Levey (1986, 1987), Levey & Karasov (1989), and Levey & Grajal (in press). Here I will outline the general approach of determining how birds process fruits.

Twelve species of small (< 80 g) nearctic and neotropical frugivores were used in the experiments. The group consisted of five tanagers (*Euphonia gouldi*, *Tachyphonus delatrii*, *Ramphocelus passerinii*, *Thraupis palmarum*, *Mitrospingus cassinii*; N = 2 of each), two emberizid finches (*Arremon aurantiirostris*, *Caryothraustes poliogaster*; N = 2 of each), two manakins (*Pipra mentalis*, *Manacus candei*; N = 2 of each), one waxwing (*Bombycilla cedrorum*, N = 7), one thrush (*Turdus migratorius*; N = 10), and one sturnid (*Sturnus vulgaris*; N = 5). All birds were kept in cages (approx. 1 x 1 x 0.5 m) and fed a nutritionally-balanced diet of mashed bananas and soy protein isolate (Denslow et al. 1987). Food was available ad libitum and birds were not starved before the start of trials. Each bird was given at least 10 natural or artificial fruits. The natural fruits were chosen primarily for their fleshy pulp and seed size. (Seed diameter ranged from 0.3 to 9.5 mm, fruit diameter was approximately constant, 6-7 mm.) The artificial fruits were made by dissolving 2 g of agar, 7.5 g fructose and 7.5 g glucose in 100 ml of a boiling solution of Phenol Red (1.7 g per 1 litre water), an inert fluid marker used to measure retention time of "pulp". The solution was injected into a slingshot pellet mold and cooled. The resulting 6 mm "fruits" contained either one large (4.0 mm diameter) or four small (2.5 mm) plastic beads (hereafter "seeds"). Total seed mass in artificial fruits was equal; the only difference between the two fruit types was the size and number of seeds.

Birds fed on fruits for 5 min, after which the remaining fruits were replaced by the maintenance diet. Seeds dropped while the birds handled fruits were counted. Sheets of paper or plastic were removed from the floor at 5 min intervals to estimate seed and pulp retention times.

RESULTS

Seed processing depends primarily on bill morphology and seed size. Species with strong, stout bills (tanagers and finches, "mashers") crush fruits before swallowing, working some seeds to the edge of the bill where they are discarded with a flick of the head. Species with wider gapes and flatter bills (manakins and thrushes, "gulpers") swallow fruits whole, making no attempt to separate and drop seeds beforehand.

Seed size is the most important variable influencing seed processing. Although absolute size of the seed is less important than size relative to the bird, I will use an absolute standard here (> 4 mm = large; < 2 mm = small) because most the experimental bird species were of the same general body size (20-35 g). For mashers, four categories of seed size explain a significant proportion of the variation in the number of seeds dropped (ANOVA; $F_{3,44} = 26$; $P < 0.001$). Nearly all large seeds were dropped, compared with 80% of 2-4 mm seeds, 50% of 1-2 mm seeds, and less than 20% of seeds smaller than 1 mm. For gulpers, all seeds were ingested, regardless of their size. After ingestion, however, seed size dramatically influenced processing.

Large seeds were regurgitated and small seeds defecated, while seeds of intermediate size were voided either way. Median time of regurgitation in the two manakins was significantly less than that for defecation (8.1 and 15.6 min, respectively; $U = 290$, $N = 24$, $P < 0.01$).

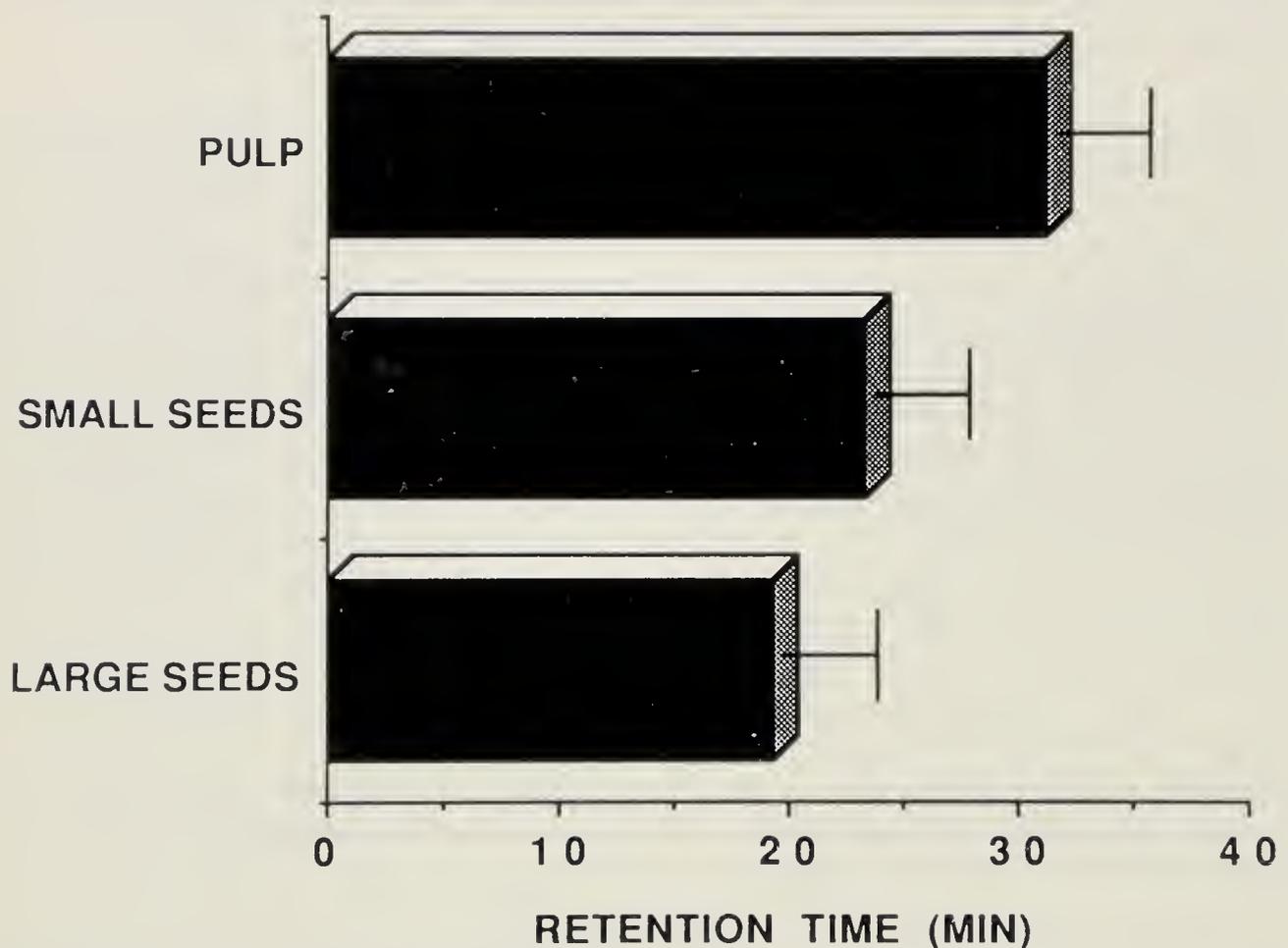


FIGURE 1 – Mean times (and standard deviations) between ingestion of one *Ardisia nigropunctata* fruit and regurgitation of its seed, and between regurgitation of a seed and ingestion of the next fruit. Data are from observations on four freely-feeding birds, two *Manacus candei* and two *Pipra mentalis* (both Pipridae). Sample size for each bar = 9.0 ± 1.3 . Differences between ingestion-to-regurgitation time and regurgitation-to-ingestion time are significant for each individual bird (t -values = 8.1, 4.2, 3.9, 5.7; P -values < 0.005).

Small seeds, which must be passed through the entire digestive tract, were voided with surprising speed. Modal retention times for tanagers, finches, and manakins were generally less than 30 min (average = 29.5 ± 15.4). Even for defecated seeds, size was important in determining how quickly the seed could be voided. In experiments with artificial fruits fed to waxwings, the larger of two seed types had significantly shorter retention times. Furthermore, in all cases seeds were defecated well in advance of fruit pulp (paired $t = 9.96$, d.f. = 13, $P < 0.001$; Pulp was retained approx. 32 min, whereas large seeds and small seeds were retained about 19.2 and 23.3 min, respectively; paired $t = 4.8$, d.f. = 6, $P < 0.002$). Waxwings separated pulp and seeds internally and passed the seeds approximately 10 min before the pulp. These results are not artifacts of using artificial fruits. Comparable passage rates and pulp-seed separation were also found in manakins fed natural fruit (Levey 1986). For example, in four trials with *Manacus candei* fed *Miconia affinis* fruits, the last seeds were defecated 45 min after consumption, whereas pulp continued to be defecated for at least an additional 30 min.

Rapid seed processing may clear the gut and increase ingestion rate. Indeed, waxwings feeding on the artificial fruits with the larger seeds ate significantly more of these than the smaller-seeded fruits, which took longer to process (Levey & Grajal in press). Likewise, freely feeding manakins showed evidence of an ingestion bottleneck when eating *Ardisia* fruits (Figure 1). They took less time between regurgitating seeds and ingesting the next fruit than between ingesting of a fruit and then regurgitating its seed. This not only shows that they took fruits very quickly after regurgitation but also suggests that seeds in the crop limited the ingestion of more fruit.

DISCUSSION

These results demonstrate that fruit-eating birds have several methods for quickly processing seeds. How quickly and how thoroughly seeds are processed has important evolutionary consequences for both fruiting plants and frugivores. Most studies of seed processing have focused on the consequences for the plant (e.g. Murray 1988). The birds' perspective remains little studied (Willson 1989, Worthington 1989), even though the ability to void seeds rapidly may be an essential adaptation to frugivory.

Ingested seeds represent a cost to frugivores because they displace gut volume that could be filled by fruit pulp, and their mass increases the energy demands of locomotion. The high water content of fleshy fruit presumably adds in a similar way to the cost of ingesting fruit, regardless of seed mass. Thus, fruits are generally considered to be a resource high in bulk (Herrera 1987).

A common trait among animals that feed on high bulk diets is "intake" or "process rate" limitation, in which ingestion rate is limited by digestion rate (Sorensen 1984). Frugivores appear to fit this pattern. In both the laboratory and field, their foraging behavior is characterized by long periods of little activity (i.e. "loafing", Fleming 1988, Snow & Snow 1988). This type of behavior is typical of other intake-limited animals and is predicted if meal processing takes longer than meal acquisition (Sibly 1981). Direct evidence of process rate limitation comes from the experiments with waxwings (Levey & Grajal in press). These birds exhibited significantly higher ingestion rates when feeding on fruits whose seeds they could process faster.

Process rate limitation helps explain why quick seed processing appears to be widespread among frugivores. Rapid elimination of seeds may be an important adaptation to a fruit diet because it allows an increased consumption rate, and thus fewer limits on intake. However, this may result in short pulp retention time (at least for defecated seeds). Rapidly voiding seeds may therefore also involve an important cost, low digestive efficiency. In general, there is a tradeoff between how quickly food is processed in the gut and how thoroughly it is assimilated. Animals with short retention times tend to have low digestive efficiencies. Fruit-eating birds are not an exception (Karasov in press). By rapidly passing seeds through their digestive tracts, they apparently must also pass pulp quickly, which results in poor assimilation. Presumably, fruits are sufficiently common so that frugivores can find, feed, and process them quickly enough to maintain a high net rate of energy gain (Sorensen 1984) despite low digestive efficiencies.

Rapid seed processing and low digestive efficiencies have several implications. First, fruit-eating birds will need to consume more fruits per day to meet nutrient requirements than would be predicted solely on the basis of pulp nutrient content. Thus, they will process (and presumably disperse) more seeds than if they assimilated fruit pulp with 100% efficiency. Second, because seeds are processed quickly, they do not require hard seed coats for protection against digestion. Thus, it is not surprising that large, regurgitated seeds (which spend a minimum amount of time in the digestive tract) seem to have especially thin seed coats (McKey 1975). Third, the relationship between rapid seed processing and digestive efficiency of pulp suggests that although easily absorbed nutrients could have allowed the evolution of short retention times, it is more likely that fruit-eating birds with short retention times selected for easily absorbed nutrients in fruit pulp.

Assuming that fruit pulp evolved as a mechanism to enhance seed dispersal and given that all fruits (except some domestic varieties) contain a large proportion of seeds (often 50% by volume), frugivores likely evolved the above methods of rapidly processing their high-bulk diet. Then, because a consequence of rapid gut processing is low digestive efficiency (especially of structurally complex nutrients), frugivores selected for pulp constituents that could be most easily assimilated. Ideal constituents are monosaccharides (glucose and fructose) and free amino acids, both of which require no further chemical breakdown in the gut and are actively transported by independent transporters across the brush border membrane of the intestine (Karasov in press, Karasov & Levey in press). Indeed, the pulp of fleshy fruits consists mostly of these hydrolytic products of complex carbohydrates and starch (Baker & Baker 1986).

Because most frugivores have short retention times when feeding on fruit (Karasov & Levey in press) and most fleshy fruits are rich in simple sugars and free amino acids, the type of mutual selective pressures hypothesized above apparently led to diffuse coevolution at a high taxonomic level. Perhaps the best test of this hypothesis lies in examining fruiting plants and frugivores that do not fit the pattern. Are there fruits with more chemically complex nutrients and if so, are they fed upon by frugivores with relatively long retention times?

Thus far we have only considered fleshy fruits. Arillate fruits are a second major fruit type, typically containing a single large seed surrounded by a lipid-rich aril. Furthermore, they are often taken by large birds (Howe 1986). Because retention time is a positive function of body size (at least in frugivores < 50 g; Levey 1986), these large frugivores may indeed have relatively long retention times, which presumably would allow the assimilation of lipids (which are absorbed slowly). Large body size, however, is not a requirement for feeding on arillate fruit (Wheelwright et al. 1984). In smaller birds, long retention times of the lipid-rich aril may be possible because arillate seeds are typically large and regurgitated. When separate from seed in the stomach, the aril can pass through the intestine at a slower rate than if the seed were defecated along with the aril. In short, by separating aril and seeds in the intestine, and voiding seeds quickly, small birds may be less intake-limited and may therefore be able to process the aril more slowly and thoroughly in the intestine. Whether this occurs awaits testing.

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BIRDS AND FRUITS: HOW DOES THIS MUTUALISM MATTER?

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ABSTRACT. Fruit-eating birds and fleshy-fruited plants engage in a diffuse mutualism that is common in forests and shrublands around the world. A considerable natural history lore has documented the geographic and ecological distributions of fleshy fruits and frugivores for some regions, some ecological correlates of frugivory for birds, seed handling and passage rates for a few kinds of seeds and birds, certain characteristics of fruits and frugivores in some regions, and a few cases of seed fates. We lack a significant body of information on several points that are critical to establishing how much the mutualism matters: e.g. degree and consequences of intraspecific variation in dispersal success and frugivory, effects of dispersal and frugivory on life history and population dynamics, comparative seed shadows for dispersal by different vectors and their ecological consequences, the ecological significance of variation in dispersal phenology, and the ecological/evolutionary pressures influencing most fruit and seed traits.

Keywords: Frugivory, fruit-eaters, seed dispersal, fleshy fruits, mutualism.

INTRODUCTION

Fruit-eating vertebrates and fleshy-fruited plants engage in a diffuse mutualism that dates at least from Permian (and possibly Carboniferous) times and occurs in almost all habitats that support vascular plants, from tropical to arctic (and subantarctic) latitudes. In some communities, a majority of the vascular plants and birds interact in this mutualism. At what time in geological history the birds became involved with the interaction is uncertain, but in view of the many and sometimes ancient lineages containing serious frugivores, it seems likely that fruit-eating has been an important component of avian foraging ecology from the early days of feathered creatures. Unlike certain established or probable mutualisms between plants and arthropods, the interactions between birds and fruits seems to have been accepted as mutualistic since the early days of recorded natural history. The birds obtain nutrition and water; the plants obtain dispersal of offspring.

Despite its apparently long standing in natural history lore, bird-fruit interaction has been subjected to intensive and extensive scientific scrutiny only rather recently. Therefore, the sum of our knowledge of such interactive systems is necessarily patchy - unevenly distributed across taxa, geographic regions, ecological and evolutionary questions. This symposium provides a good opportunity to assess the progress of our understanding of an ancient mutualism that spans the globe. I will try to evaluate the mutualism in terms of assessing the benefits and of the implications for morphology and behavior, life histories, and communities. A review of such dimensions by rights should include a prodigious list of pertinent references, which is obviously precluded by limitations of space, and so many statements will not receive the documentation they deserve.

ASSESSING THE BENEFITS

A principal benefit of the mutualism for the plants presumably lies in the nature of the seed and seedling shadows generated. However, the few extant documentations of bird-generated seed shadows are often based on different sampling methods and small samples, cover quite short distances from the parent plant, and rarely examine seed and seedling survival and growth. We know that the effectiveness of seed removal from the parental site varies among species of consumer, and that the post-foraging behavior varies among bird species, but removal patterns may also vary with fruit species, habitat, and many other factors. The prodigious difficulties of measuring the tail of the seed distribution curve have meant that, at this point, we cannot compare quantitatively the seed shadows generated by birds vs. other seed vectors or by different kinds of birds in different circumstances. We can seldom say which portion of the seed shadow is most likely to have the greatest effect on eventual offspring survival - is it the modal region, which is sometimes subject to intense depredation by predators and pathogens, is it the tail region, which may suffer relatively less density- or distance- responsive mortality and which potentially reaches a greater variety of sites for offspring establishment, or could it even be the *far* tail of the seed shadow, where rare events might acquire disproportionate importance?

For the avian consumers, the principal benefit must lie in nutrition, but we are still learning which birds eat what fruits when. In some tropical forests certain kinds of fruits appear to be critical in maintaining frugivore populations over periods that would otherwise be times of famine, and when such fruit crops fail, widespread starvation and/or emigration may follow (e.g. Gautier-Hion & Michaloud 1989, Howe 1984). But in general we seldom know in any quantitative sense how important fruits are for feeding young, for maintaining adults during the breeding season, for fledgling growth rates, or for laying up energy for migration. How fast can birds gain weight on fruit a vs. fruit b, for instance when a (or b) is some given fraction of the diet? Presumably any meal is of some benefit - but how much? Given the huge differences among fruits in nutrients and presumably in digestibility, how substitutable are they as food resources? Are they less substitutable than insects or seeds, size for size?

IMPLICATIONS FOR MORPHOLOGY AND BEHAVIOR

Fruit displays

Fruits of bird-dispersed plants vary enormously in size (up to several centimeters), color (from dull brown to gaudy scarlet and brilliant purple; presence of color contrasts between edible and inedible parts of the display), display structure and size (from solitary fruits to dense clusters in diverse arrangements), texture (watery to mealy), composition (sugary to oily; defensive compounds), accessibility, ease of detachment, persistence on the plant, degree of fruit concealment, etc. In some areas bird-dispersed fruits are, on average, distinct in many of these characters from fruits dispersed by mammals, but considerable overlap is commonly evident, varying from region to region (reviewed in Willson 1990). One may legitimately argue that certain traits are likely to have evolved in response to selection for particular kinds of vertebrate dispersers (e.g. larger fruit size and/or protective husks for primate rather than

bird-dispersal), but broadly applicable generalities are few and slow to emerge. There are over a dozen extant hypotheses for the evolution of fruit colors, for example, with little more than circumstantial evidence for any of them (Willson & Whelan 1990). And clear seasonal trends in fruit-pulp composition are reported for some regions but not for others. In general, the variation in fruit traits defies attempts to pigeon-hole it in any simple, globally applicable, fashion.

Avian morphology, physiology, and behavior

Morphological and physiological traits associated with frugivory should be expected chiefly in birds that depend heavily on fruits. Indeed, some studies have found that highly frugivorous birds differ in certain alimentary features from less frugivorous species (e.g. Herrera 1984, Jordano 1987, Moermond & Denslow 1985), and other differences may emerge as we learn more about the ability of the gastrointestinal tract to process fruit. Nevertheless, frugivory does not seem to be characterized by a dramatic, distinctive suite of trait associated with that foraging habit. It seems likely that the most salient advances in the study of this mutualism will not lie in the realm of special adaptational morphology.

However, there is a virtual lack of information on the *process* of fruit-foraging: How do birds select fruits? What criteria are used, and in what circumstances? To what extent do birds use fruiting displays or fruits themselves to locate and choose fruits, and to what extent do they use possible ancillary cues such as leaf shape? To what extent are fruiting traits determined evolutionarily by seed dispersal agents, and to what extent by natural enemies, physiological or developmental constraints, or other ecological pressures? Fruit-feeding birds with different morphologies will use that morphology in different ways (Moermond & Denslow 1983). But how much morphological variation exists among conspecific individuals in traits relevant to fruit-feeding efficiency or effectiveness? Increased knowledge of process will help discern patterns.

Seed-handling

Once a fruit is chosen, birds handle the seed in a variety of ways. Some fruit consumers digest the seed along with the pulp and some discard the pulp in favor of the seed. Certain birds may be seed predators for some plant species but decent dispersal agents for others. When a seed is swallowed by a bird that is not a predator, it becomes unwanted ballast in the gastrointestinal tract and is often eliminated quickly by regurgitation, usually within a few minutes of ingestion, or by defecation, which commonly takes longer. The length of time spent by a seed in an avian gut and its treatment there can vary greatly. The duration of gut residency no doubt depends both on gut characteristics (and the ability to sort out and eliminate seeds) and on fruit structure and chemistry (the presence of cathartics, or of slip-zones that quickly separate pulp from seeds). The consequences of gut residency vary enormously, from destruction or dormancy breakage and premature germination to no detectable effect at all; cases of demonstrable benefit from gut passage are few indeed.

Although such variation in seed treatment has been documented (e.g. Izhaki & Safriel 1990), we do not know, for any fruit-eating bird or for any fleshy-fruited plant, the entire range of seed-handling fates. Is bird species #1 usually a predator for fruit species a to c, a dormancy-breaker for fruit species d to g, and a passive carrier for fruit species h to m, and is that pattern different for bird species #2? Are the seeds of some species more susceptible to bird predation or dormancy-breaking than others?

What seed or fruit traits affect seed-handling fates? How does gut residency vary among fruit-consumers - does it vary with avian body size, other diet components, etc? To what extent is gut passage rate of seeds a function of fruit chemistry/morphology or of gut physiology/morphology?

IMPLICATIONS FOR LIFE HISTORY

Phenology

Frugivory in the tropical rain forest can be a year-round process for many vertebrates, with seasonal peaks. Bird dispersal of seeds is largely a late-summer and fall process in most of temperate North America, extending into winter. Indeed, winter-persistent fruits are common in temperate and subtropical North America and much of Europe, sometimes lasting into spring (with local variations). Moreover, in the arctic and boreal regions of North America (and Scandinavia), many fruits are persistent through the winter, frequently under snow-cover, and are consumed avidly by spring passage-migrants and breeders. Early-spring fruit consumption on the breeding ground may be important for several species commonly thought to be insectivorous at that time (Cooper 1984).

Resource bases

Fleshy fruits as food for nestlings and juveniles is best known in the tropics, and several researchers have contemplated the causes and consequences of raising young on fruits (e.g. Foster 1978). Very few temperate-zone birds are known to depend heavily on fruits for nestling foods, the quasi-nomadic *Bombycilla* being the salient exception. Nevertheless, thrushes, mimids, and sylviids often include fruit in the nestling diet, and other birds may do so more than currently believed. Fruit is an important resource for juvenile geese in some areas of Alaska (J. Sedinger, pers. comm.). Most existing comparisons of juvenile frugivory contrast the tropics with mid latitudes in the northern hemisphere, where few fruits are usually available until later in the summer. Comparison with higher latitudes, where many fruits overwinter and become available to spring breeders and their young, may change our present perceptions at least somewhat.

For North America (a region of intense activity in avian ecology), we are still generally ignorant of the foraging behavior of fall migrants - every year in the fall I have added new species of regular frugivore and potential seed disperser to my notebooks for the American Midwest. Frugivory by "shorebirds" (e.g. *Numenius*) and geese on the Arctic tundra (B. Kessel, pers. comm.) and by gulls in Australia has received little notice. It seems likely that fruit is an important resource, at least at times, for many other birds not now included in this mutualism.

Social systems

Extensive frugivory is suggested to contribute to evolutionary shifts in parental roles and mating systems, as well, at least in some tropical birds (e.g. Beehler 1987). Frugivory may be one factor that facilitated the spectacular radiation of several taxonomic families of tropical frugivores (e.g. cotingas, manakins, bird-of-paradise) - often in ways that fit Darwin's scenario for the operation of sexual selection in species diversification (groups of species with morphologically similar females but very distinctive males).

IMPLICATIONS FOR COMMUNITIES

Fleshy-fruited, bird-dispersed plants occupy nearly all stages of succession and most kinds of terrestrial vegetation. We know that the presence of perches in otherwise open habitats can often serve as foci of seed deposition by birds and potentially of recruitment for fleshy-fruited plants (references in Willson 1990). How does this influence the pattern and process of succession? If foci of recruitment establish pattern in the vegetation, how long do such patterns persist? Does the presence of such perches alter the shape of the seed shadow (e.g. by extending the tail)? How often do seed-carrying birds cross habitat boundaries (e.g. forest to meadow) and what proportion of their seed burden can survive and establish in the habitat of seed deposition?

We know that, in some forest regions, many migrating bird species concentrate their activities in treefall gaps (e.g. Levey 1988). What proportion of the forest floras of different regions are dependent on treefall gaps for recruitment, and what fraction of those depend on birds for dispersal (compared to in-shade recruiters)? Is the frequency of dependence by the flora on treefall gaps for recruitment related to the patterns of habitat use by birds of the region? Biogeographic patterns in the occurrence of fleshy-fruited species (and of frugivorous birds) have been partially documented (e.g. Snow 1981), with marked regional differences in the number of fleshy-fruited species (and fruit-eaters) among both tropical and temperate regions. These differences have consequences not only for the frugivore community but also potentially for the responses of plant populations to habitat disturbance, patterns of range expansion, island colonization, vulnerability of offspring to certain natural enemies, and other ecological questions.

Consumption of fleshy fruits is considered to be more common among tropical birds than among temperate birds, and the use of abundant and diversified fruit resources is thought to contribute to a high diversity of tropical birds, especially in some biogeographical regions. Such comparisons are, however, customarily based on *breeding*-bird censuses for the temperate zones, thus focussing on the season of least frugivory in temperate regions and exaggerating the magnitude of the latitudinal differences. Certain habitats in some extratropical regions support very high abundances (albeit low diversities) of fleshy fruits, which may temporarily support many species of migrant birds. Also, as more becomes known about fruit-eating by birds of the arctic tundra, the proportion of the high-latitude avifauna depending upon fleshy fruits may increase substantially.

IN CLOSING

I have tried to summarize not only a sizable portion of the current state of understanding of the ecology and evolution of bird/fruit mutualisms (see also Wheelwright 1988) but also some important vacancies in our knowledge. Two additional basic points are emphasized in closing:

- (1) Surely the bird/fruit mutualism matters to both sides of the interaction. The interaction is ancient, common, and widespread, and has important repercussions for ecology and evolution of all participants. What we need to establish, however, is

a more quantitative assessment of costs and benefits. And we need to move toward more mechanistic, process-oriented studies. Several essential measures of the consequences of the interaction are still lacking.

- (2) At the same time, however, I note that bird/fruit interactions are one area in which simple natural history observations are still essential (and we have at least the skeleton framework by which to organize them). That some boreal and arctic birds may eat large quantities of overwintered fruits could change our view of several established generalizations. In addition, frugivores were once thought not to cache fruits, but we now know that a bowerbird does so, and I have seen ravens and crows do it too, and there may be others. Although it is fashionable to denigrate "natural history" in favor of "real science", good natural history both provides the raw material for more conceptual constructs and yields an endless supply of new questions.

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SYMPOSIUM 29

RECRUITMENT IN LONG-LIVED BIRDS

Conveners G. M. DUNNET and J. M. PORTER

SYMPOSIUM 29

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INTRODUCTORY REMARKS: RECRUITMENT IN LONG-LIVED BIRDS

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INTRODUCTION

For this symposium recruitment is defined as the establishment of new young breeders, and bereaved previous breeders, into the breeding component of bird populations. In short-lived species birds generally breed in their first year so that pre-breeders are not usually distinguishable by behaviour or ecology after their first winter. Their recruitment to the breeding population has not attracted much attention.

In long-lived species, however, first breeding may not take place for up to ten years or so, and substantial numbers, e.g. over 50% of the total Fulmar population (Dunnet 1982), exist as pre-breeders before eventually becoming established in a local breeding population. The ecology of these pre-breeders may differ markedly from that of the breeders: e.g. Carrick (1972) described the flocks of pre-breeding Australian Magpies *Gymnorhinus tibicen* living in open habitats unsuitable for the breeders; similarly, Shelduck *Tadorna tadorna* associate in cohesive flocks, in which they may pair, for some years before securing a territory and beginning to breed (Patterson 1982). Some seabirds form distinct segregated "clubs" of pre-breeders at breeding colonies, e.g. Great Skua *Catharacta skua* (Furness 1987) or establish themselves on the fringes, e.g. Royal Penguin *Eudyptes chrysolophus schlegeli* (Carrick 1972). Other seabirds have no obvious segregation of pre-breeders at colonies, but such birds visit and may move extensively between colonies during the breeding season before settling in one and "prospecting" for a year or two before actually breeding. Even more challenging, the pre-breeding population may be virtually undetected, and evidence for its existence comes mainly from the rapid replacement of established breeders by new recruits in removal experiments, e.g. the European Sparrowhawk *Accipiter nisus* (Newton, this symposium). Bereaved breeders, currently not breeding, may also be present among the pre-breeders and are also, of course, potential recruits.

Few studies have concentrated on these pre-breeding populations, for obvious practical reasons. Yet important processes go on in them which have a major influence, qualitative and quantitative, on the eventual establishment of these birds as breeders. These include survival, dispersal, population control, acquisition of social and other skills, and competition with members of the breeding populations. These aspects, important though they are, will not be pursued here.

This symposium is primarily concerned with recruitment as a process, i.e. the ways in which birds from the pre-breeding population (potential recruits) become

established as breeders, and the role of such recruitment in the regulation of breeding populations. In long-lived species the annual mortality rates of adults are by definition, low - often less than 10% - and variations from year to year make only a minor contribution to changes in population size. By contrast recruitment can vary over a wide range, and greatly influence changes in the numbers of breeding birds between years. In modelling the role of recruitment in determining the size of a population of breeding Fulmars (Ollason & Dunnet 1983) we were forced to recognise that birds recruited in one year may not breed the next, so that intermittent breeding, and possibly even desertion of the colony, may be a feature of inexperienced breeders. To take account of this we had to develop the idea of "negative" recruitment.

Recruitment is clearly a complex process, especially important in the dynamics of long-lived species. It is a challenging subject for study involving many aspects of ecology, social organisation and behaviour, and there are many and marked contrasts between species. Our understanding of the subject has direct practical application to management for conservation.

This symposium is designed to review the subject in a set of five papers: Danchin will review the conceptual framework and behaviour mechanisms; Wooller and Bradley will discuss the relevance of philopatry and deferred breeding; Cooke and Rockwell will review genetic aspects; Klomp and Furness will give an account of clubs of pre-breeders in the Great Skua in Shetland; and Newton will consider the role of recruitment in population regulation in birds of prey, especially the Sparrowhawk in Britain.

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RECRUITMENT IN LONG-LIVED BIRDS: CONCEPTUAL FRAMEWORK AND BEHAVIOURAL MECHANISMS

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ABSTRACT. A survey of literature shows that prospecting (i.e. seeking a breeding site) occurs widely among birds, and so must play a prominent part in population biology. The peculiarities of prospecting and recruitment in long-lived birds are underlined. A detailed study of prospecting in the Kittiwake shows that prospectors are attracted by the social activities and presence of chicks in the nests before acquiring breeding status. The main function of prospecting is to allow the assessment of the quality of the possible places for future breeding: social activities and breeding success are good criteria of population health. A mechanism by which the young are attracted to and recruited into a breeding population is developed. This attraction-recruitment mechanism of population regulation leads to preferential recruitment in the most productive sites. It spreads the birds among the different possible breeding places according to their quality and leads to an optimisation of the total fecundity and hence of the numbers of the metapopulation.

Keywords: Behaviour, immaturity, prospecting, squatter, recruitment, attraction, attraction-recruitment mechanism, population regulation, Kittiwake.

INTRODUCTION

The changing numbers of a breeding population result from the effect of different demographic parameters (Leslie 1945, 1948, Lebreton 1981). Among them, parameters of fecundity quantify the production of new individuals. The ultimate end of reproduction is to produce birds that become reproductively active (i.e. are recruited) in the population. Parameters of fecundity are relatively well studied but less is known on recruitment, particularly in long-lived species. Some authors quantified recruitment either through philopatry to or dispersal from breeding population (Duncan 1978, Greenwood 1980, Harvey et al. 1984, Porter & Coulson 1987, Ratcliffe et al. 1988, Court et al. 1989) but the underlying behavioural mechanisms are almost unknown (Coulson & Neve in press). Many studies show that dispersal, and then recruitment play a prominent part in the regulation of animal numbers (Clark 1949, Lidicker 1962, 1975, Duncan 1978, Greenwood et al. 1978, Coulson 1984, O'Connor 1985, Bauer 1987, Porter & Coulson 1987, Danchin 1988, MacMahon & Tash 1988, Danchin & Monnat in press).

CONCEPTUAL FRAMEWORK

Definitions

Long-lived birds are species in which the youngest recruits are at least two years old. Three periods can be distinguished in their individual life-time and these are shown

in diagram form in Figure 1. This leads to the definition of important concepts for the study of recruitment processes.

Immatures are birds that have never bred previously. This term does not deal with characteristics of the plumage. Immaturity can be physiological and/or behavioural (Figure 1). These two levels of maturity must be achieved to allow reproduction.

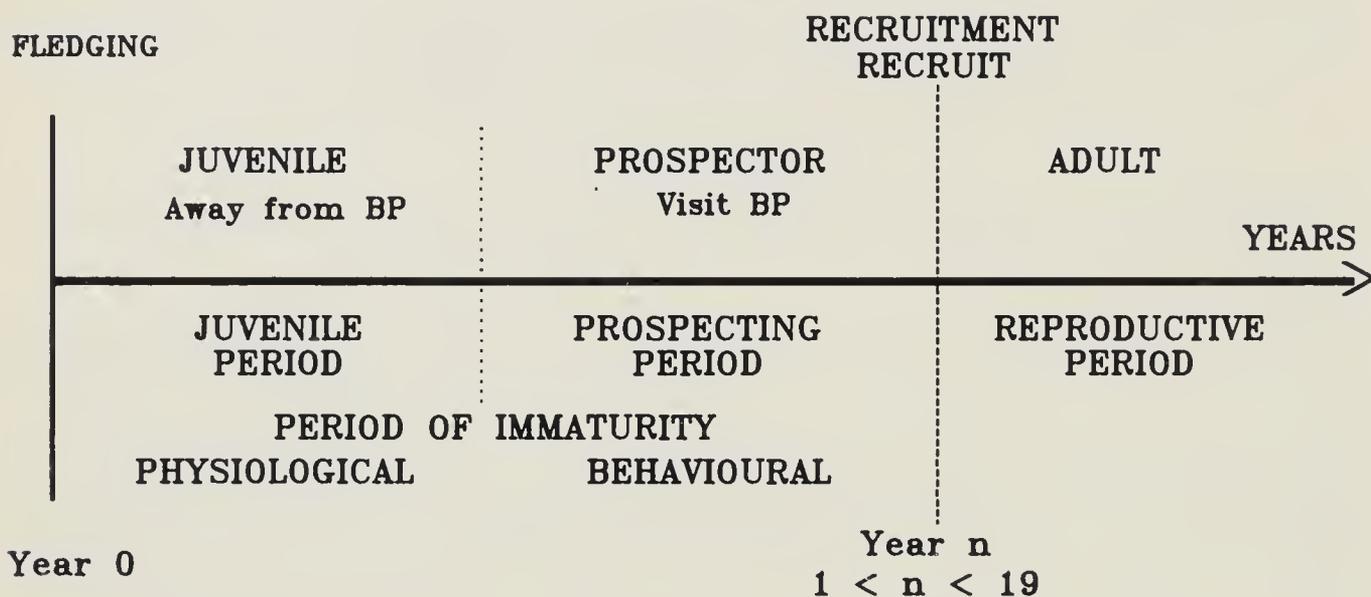


FIGURE 1 – The three periods of an individual life-time in long-lived birds (BP: breeding place).

Prospecting (the action) and *prospectors* (the category of birds) refer to birds which are more or less actively looking for a breeding site. Some are immature. Others have already bred in another place. Prospectors visit different breeding places of their species, sometimes in the same year. Immature prospectors usually arrive at the breeding places relatively late so that most prospecting occurs in the second half of the breeding season.

Recruitment is the addition of new birds to a nesting population.

Recruits are birds breeding for the first time in the population in the current year. Some breed for the first time (i.e. first recruitment). Others have already bred elsewhere and were unfaithful to their previous breeding place.

Philopatry is the fact that birds return to breed at the place where they were born. Other birds are allopatric.

Framework

The study of mechanisms of recruitment leads to questions dealing with both physiological and behavioural maturity.

- 1) Do birds visit different breeding places during their immaturity or before changing breeding places ?
- 2) How do birds choose a breeding place ? Do they recruit according to the quality of the different breeding places ? If yes, how do they assess the quality of a breeding place ? What makes a breeding place more attractive than another ?

- 3) How do they recruit into a population ? What are the different behavioural stages the birds must go through to reach a breeding status ?
- 4) What is the part played by philopatry in recruitment ?
- 5) What is the part of recruitment in population regulation ?
- 6) What are the genetic implications of recruitment in terms of gene flow ?

We already have some answers to part of those questions and in the present symposium we will discuss some of them. As the ultimate effect of population regulation is evolution, all the papers of this symposium lead to questions dealing with evolution. The present paper will deal with prospecting in relation to the mechanisms of population regulation. A behavioural mechanism of recruitment is proposed and the part of recruitment in population regulation is discussed.

Immaturity in long-lived birds.

In long-lived birds, immaturity can last from two to 19 years according to the species and individuals (Table 1, Burger 1980, Croxall 1984, Nelson 1988, see Bradley & Wooller, this symposium). Consequently, long-lived species are particularly good models to study recruitment processes for prospecting can last for several years and the mechanisms of recruitment can be analyzed in detail during all that period.

TABLE 1 – Extreme ages of first recorded breeding, occurrence of immature prospectors (IP) and squatters (SQ) in some long-lived birds.

Species	First Breeding		SN	IP	SQ	Reference
	Earliest*	Latest				
<i>Eudyptes chrysolophus</i>	5	11	G	+		Carrick & Ingham 1970
<i>Aptenodytes forsteri</i>	3	9	G	+		Mougin & Van Beveren 1979; Jouventin 1971
<i>Pygoscelis adeliae</i>	3	7	G	+		Le Resche & Sladen 1970; Ainley 1975
<i>Diomedea epomophora</i>	8	13	G	+		Carrick & Ingham 1970
<i>Diomedea exulans</i>	4	16	G	+		Barrat et al. 1976; Croxall 1982; Pickering 1989
<i>Diomedea irrorata</i>	4	11	G	+		Harris 1973
<i>Diomedea immutabilis</i>	5	16	G	+		Van Rysin & Fisher 1976
<i>Diomedea melanophris</i>	4	≥11	G	+		Tickell & Pinder 1975; Pascal 1979; in Croxall 1982
<i>Diomedea chrysostoma</i>	9	≥13	G	+		Tickell & Pinder 1975; in Croxall 1982
<i>Phoebastria fusca</i>	9	15	C	+		Weimerskirch 1982; Jouventin & Weimerskirch 1984
<i>Fulmarus glacialis</i>	6	19	C	+		Coulson & Horobin 1972; Ollason & Dunnet 1978; Dunnet pers. comm.
<i>Calonectris diomedea</i>	6	15	B	+		Jouanin et al. 1980; Mougin et al. 1984a, 1984b
<i>Puffinus tenuirostris</i>	5	8	B	+		Serventy 1967
<i>Puffinus griseus</i>	5		B	+	?	Richdale 1963
<i>Puffinus puffinus</i>	3	≥9	B	+	+	Harris 1966; Perrins et al. 1973; Brooke 1977

TABLE 1 – Continued

Species	First Breeding		SN	IP	SQ	Reference
	Earliest*	Latest				
<i>Oceanodroma castro</i>			B	+	+	Allan 1962; Harris 1969
<i>Oceanodroma leucorhoa</i>	3		B	+		Wilbur 1969; Podolsky & Kress 1989
<i>Hydrobates pelagicus</i>	3	>4	B	+	?	Davis 1957
				+	+	Scott 1970
				+		Fowler et al. 1986
<i>Sula bassana</i>	4		C	+	-	Nelson 1978, pers. comm.
<i>Phalacrocorax aristotelis</i>	2		C	+		Potts et al. 1980; Aebischer 1985
<i>Fregata minor</i>	6		GT	+	\$	Nelson 1975; de Vries 1984; Reville 1988
<i>Pandion haliaetus</i>			T	+		Thibault, J.C. pers. comm.
<i>Falco peregrinus</i>	2	5	C	+	H	Ratcliffe 1980; Monneret 1987
<i>Dendragapus obscurus</i>	2		G	+		Jamieson & Zwickel 1983
<i>Stercorarius maccormicki</i>	3	≥9	G	+		Jouventin & Guillotin 1979; Ainley et al. 1990
<i>Anous tenuirostris</i>			C	+	+	Cullen & Ashmole 1963
<i>Sterna fuscata</i>	4	10	G	+		Harrington 1974
<i>Sterna paradisea</i>	3		G	+	H	Cullen, J.M. 1957
<i>Rissa tridactyla</i>	3	8	C	+	+	Cullen, E. 1957; Coulson 1959; Hodges 1974; Wooller & Coulson 1977; Coulson & Thomas 1983; Porter 1988; Danchin et al. 1987; Danchin 1987, 1988; Monnat et al. in press.
<i>Larus argentatus</i>	3	7	G	+		Chabrzyk & Coulson 1976; Coulson et al. 1982
					H	Shugart et al. 1987
					?	Henzi et al. 1990
<i>Larus (Creagrus) furcatus</i>			C	+	+	Hailman 1965
<i>Ptychoramphus aleuticus</i>	2		B	+	?	Manuwal 1974; Speich & Manuwal 1974
<i>Alca torda</i>	3	6	BC	+		Lloyd & Perrins 1977; Hudson 1985
<i>Uria aalge</i>	4	6	C	+		Birkhead & Hudson 1977; Hudson 1985
<i>Uria lomvia</i>			C	+		Gaston & Nettleship 1981
<i>Fratercula arctica</i>	3	10	B	+		Petersen 1976; Harris 1983; Hudson 1985; Kress & Nettleship 1988

* When the youngest age of first reproduction varied according to sex or population, the earliest one was selected.

+ This category of bird was recorded for this species.

- Squatters are not possible because nests are attended continuously.

? Presence of squatters suspected from the literature but not certain.

H Presence of helpers.

\$ Occurrence of nest usurpation: birds disrupting breeding pairs (with nest, eggs or chicks) and in some cases breeding on the stolen nest in the same year.

SN : Situation of nest; B: Burrow; C: Cliff; G: Ground; T: Tree.

MECHANISM OF RECRUITMENT

Generality of prospecting

Prospecting by immature birds has been observed in most, if not all, of the species in which chicks were individually marked and controlled in the following years until the recruitment of all the cohort (Table 1). "In marine birds, the subadults normally frequent the colonies at least a year before they breed" (Lack 1966). In fact, recruitment probably always implies a prospecting phase. Likewise, before changing breeding colonies after a breeding failure, unfaithful birds prospect other colonies during the rest of the season (Monnat et al. in press).

In short-lived species (i.e. in which most recruits are one year old), fledglings can disperse just after fledging and then prospect many different breeding places before migrating (Baker 1982, 1984, Bauer 1987, Vansteenwegen 1987, Table 2).

As prospecting seems to be a widely represented activity among birds it probably has an important function in the life cycle. What is that function and what is its relationship with recruitment? A study of prospecting and recruitment in the Kittiwake *Rissa tridactyla* in Cap Sizun (Brittany, France) will give some insight to that question. In that species, first breeding occurs on average when four years old (Coulson & White 1959, Wooller & Coulson 1977, Danchin & Monnat in press).

TABLE 2 – Occurrence of immature prospectors (IP) and territorial behaviour adopted by prospectors (TB) in some short-lived birds (legend as in Table 1).

Species	IP	TB	Reference(s)
<i>Progne subis</i>	+	+	Finlay 1971
<i>Parus</i> spp.	+		Blondel pers. comm.
<i>Sitta europaea</i>	+	+	Matthysen 1987
<i>Hirundo rustica</i>	+		Vansteenwegen 1987; G. Jarry pers. comm.; H. Coquillart pers. comm.
<i>Riparia riparia</i>	+	+	Peterson 1955
<i>Melospiza melodia</i>	+	+	Nice 1937
<i>Sturnus vulgaris</i>	+		Dhont pers. comm.
<i>Bonasa umbellus</i>	+	+	Small & Rusch 1989
<i>Acrocephalus scirpaceus</i>	+		Catchpole 1972
<i>Acrocephalus schoenobaenus</i>	+		Catchpole 1972
<i>Accipiter nisus</i>	+	+	Newton 1986

Particularities of prospecting in the Kittiwake

DEFINITION. According to Porter (1988) in the Kittiwake every recruit attended the colony at least one year prior to breeding. However, 5.7% of the birds reared and recruited in our study plots from 1983 to 1989 were never controlled in Cap Sizun colonies before recruitment (N=283). As our control rates in those study plots are very high ($P > 0.992$, Danchin & Monnat in press) those birds almost certainly did not visit their colony of recruitment in the years before breeding. Thus, more than 94% of the young birds prospecting in the colony to which they recruited.

Three categories of prospectors were distinguished:

- those landing on the breeding cliffs on non-nesting sites only. They will be called 'mere prospectors';

- those landing only on nests without chicks present. As they are not the owners of those nests, they will be called 'squatters on nest' (Danchin 1987a, 1988, Danchin et al. 1987, Monnat et al. in press);
- those which were seen at least once on a nest with chicks. For the same reason, they will be called 'squatters on chicks'.

Squatting can occur when nests are left unattended by breeders (i.e. the 'owners', Danchin 1987a): the attendance of breeders diminishes rapidly when the chicks are about 23 days old (Danchin 1988, Cadiou 1990, Monnat et al. in press, Figure 2A). The fall in attendance of the breeders is fairly synchronous and marks the beginning of the squatter period (Figure 2A). When the breeders return to feed their chicks, squatters not resisting, fly away.

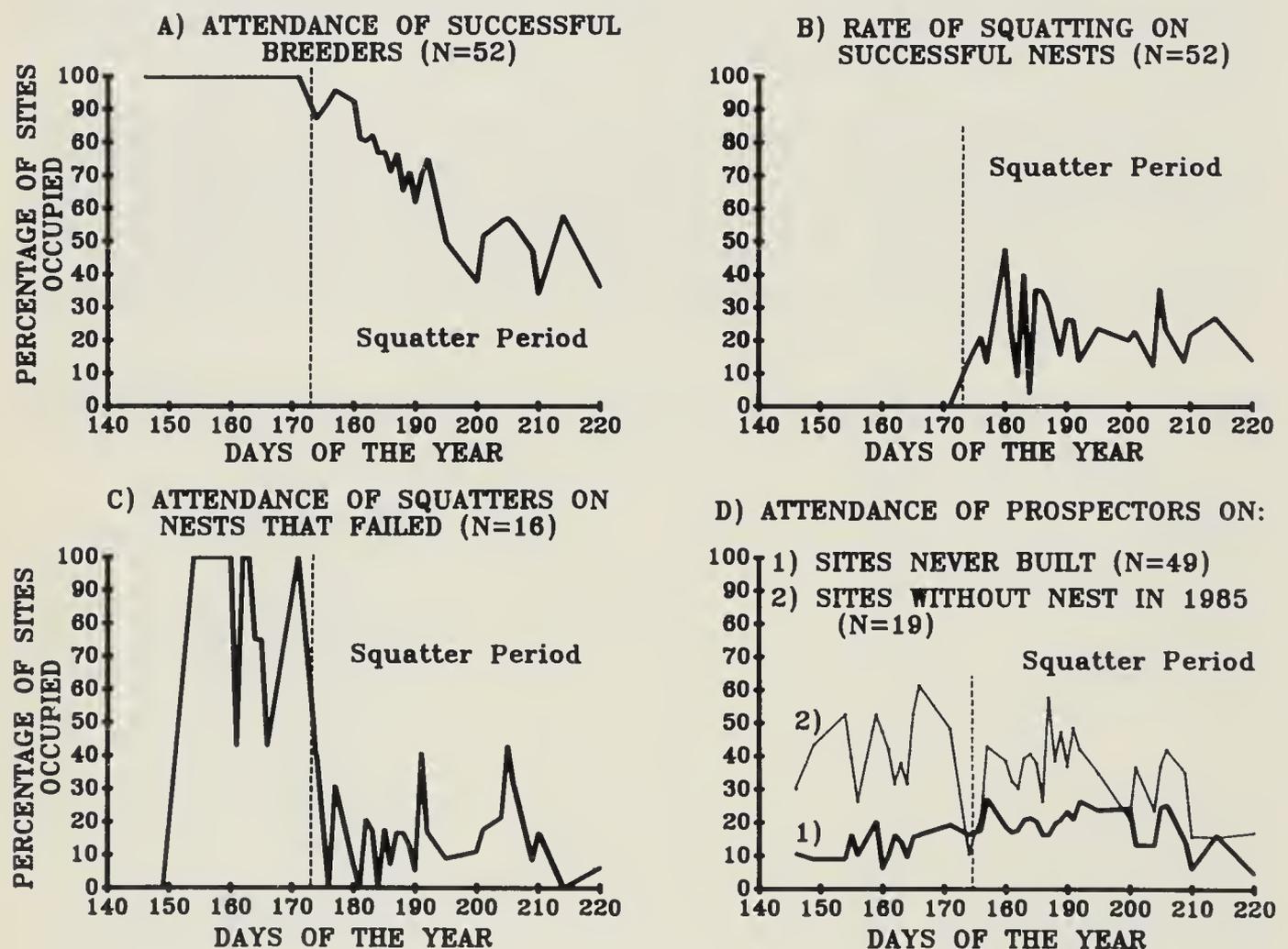


FIGURE 2 – Attendance of successful breeders (A), rate of squatting (B and C) and attendance of prospectors on sites without nest in 1985 (D), during the second half of the breeding season. Vertical dotted line: beginning of the squatter period. Rates of squatting are the percentages of nests vacated that are occupied by prospectors. Figure C shows that nests that failed before the fall in attendance of the successful breeders are highly squatted as soon as vacated.

In the Kittiwake, the status of the birds in relation to the site on which they are observed (owner or non-owner) can be identified if the birds are ringed, or through behaviour (Danchin 1987a,b, 1988, in press, Danchin et al. 1987, Monnat et al. in press).

Data were collected on a portion of cliff with 68 nests in 1985. All the sites on which Kittiwakes were able to land were referenced. Four categories of sites were distinguished: sites which never received a nest before, sites which had previously had a

nest but not in 1985, sites with a nest in which breeding failed at some stage in 1985 and sites in which chicks were fledged in 1985. Sites were checked regularly and the presence, identity (colour rings) and status of the birds present were recorded. In case of doubt about the status of the adults, they were considered to be the breeders of the nest. Rates of squatting are the percentages of nests left unattended by the breeders which are occupied by squatters. Similar methods were used on 82 nests with chicks out of 135 nests in 1990 when nests were checked at least twice daily.

WHERE DO PROSPECTORS LAND ON THE BREEDING CLIFFS ? Before the beginning of the squatter period many prospectors already attend the breeding cliffs (Figure 2C, D). At that time, the few nests in which the pair failed to reproduce are rapidly and assiduously occupied by prospectors when vacated (Figure 2C).

Individual marking showed that, following the fall in attendance of successful breeders, many categories of birds change sites on the breeding cliffs. Immatures settled on a ledge and failed breeders move from their previous sites to neighbouring nests with unattended chicks (Figure 2 B). One third of the nests with chicks are squatted from the day when the owners stop continuous attendance (Cadiou 1990). Consequently, nests with chicks seem to be the most attractive sites. New prospectors already in the neighbourhood of the breeding cliffs rapidly occupy the non-breeding sites thus left unattended, and the total number of prospectors in the breeding cliffs increases. At least 90 % of the nests are visited by squatters (Danchin 1988, Monnat et al. in press), but when vacated, late and unsuccessful nests are less attended by squatters than early nests (Danchin 1988, Cadiou 1990).

BEHAVIOUR OF THE SQUATTERS. From hatching, prospectors are obviously attracted by the activities in the neighbourhood. They join in the greetings and the nest reliefs of the breeders rearing chicks. They often interfere with pairs either by landing on a close site or by trying to land on the nest with the pair. Meanwhile they call loudly. Individual marking indicated that at least some prospectors behaving like this later squat on those nests. In the same way, squatters are active birds. They often attack each other and participate noisily in the activities in the neighbourhood. However, in spite of their obvious attraction to the nests with chicks, squatters never feed the chicks. On the contrary, they often attack chicks, sometimes violently, causing the chicks to react with an appeasement display (Cullen 1957). Chicks occasionally get used to the presence of a particular squatter and stop showing appeasement display.

WHO ARE THE SQUATTERS ? Up to 52% (N = 201) of the birds may squat on nests in a given year (Monnat et al. in press). Before first breeding, 79.6 % of the immatures were seen squatting at least once (Monnat et al. in press).

Squatting concerns all categories of birds but its incidence varies with the age and social status of the bird.

Among breeders of the current year, the highest incidence of squatting is shown by failed breeders (Monnat et al. in press). Successful breeders rarely squat and when they do so it is often because they fly from their old chicks begging for food insistently.

Among immature birds present at the colony, the proportion which is observed squatting at least once increases until the age of three (i.e. one year before average age

of first breeding) and decreases after. Immatures younger than three scarcely squat on chicks while older pre-breeders do so regularly (Table 3). Immature squatters on chicks have more often been settled on a ledge before the squatter period than squatters on nests (Table 3). During the squatter period they are less often controlled outside of their colony of squatting than squatters on nests (Table 3). The sex ratio was biased to the males for the squatters on chicks but not for squatters on nests in 1990 (Cadiou 1990, Table 3).

TABLE 3 - Behavioural differences between the three categories of prospectors in the Kittiwake (see text). In brackets: sample size (when different from the top line).

	Mere prospectors £	Squatters on nests \$	Squatters on chicks *
Number of immature birds @	38	31	17
Age: % of each category among @:			
immatures younger than 3	63.3	33.3	3.3
immatures 3 or older	33.9	37.5	28.6
Sex ratio μ , @:			
Males	21.0	32.2	64.7
Females	21.0	25.8	17.6
unknown	58.0	42.0	17.6
Proportion in pairs:	3.5 (57)	25.5 (32)	
Attachment to the colony:			
% of birds settled before the squatter period @	7.9	19.3	35.3
% seen outside study plot during the squatter period @	52.6	41.9	17.6
Attachment to the breeding sites °:			
% seen squatting in the three periods		7.8 (51)	61.4 (44)
only one period		60.8 (51)	6.8 (44)
Number of nests squatted °:			
Period 1		1.50 (18)	2.56 (34)
Period 2		1.39 (23)	2.68 (38)
Period 3		1.68 (34)	3.03 (40)
Attendance at the end of the season:	diminishes rapidly	remains high longer	

£ Never seen squatting that year.

\$ Seen squatting on nests without chicks only.

* Seen squatting on chicks at least once.

μ Birds sexed by behaviour.

@ Proportions estimated for immature squatters only. Other indices are estimated for the total sample of squatters.

° Period 1: from the fall in attendance of the breeders to first fledging; Period 2: until the first chick left the colony finally; Period 3: until the median of the final departures of the chicks.

Among all birds, those which were settled on a ledge without breeding in the current year spent the highest proportion of time squatting. Squatters were more often in pairs than mere prospectors (Table 3). At the end of the breeding season, squatters maintain their presence longer than the breeders and other prospectors (Figure 2). Squatters on chicks squat on more nests than squatters on nests (Cadiou 1990, Table 3). Most squatters on chicks are seen squatting during the whole squatter period (Table 3).

SUMMARY. Squatters are prospectors. Eighty-nine % of the birds seen squatting in 1990 (N=105) were failed breeders and immatures in the year prior to first breeding. Both are actively looking for a site: breeders that failed often change nest sites in the following year (Davis 1957, Munkejord & Folkedal 1981, Greenwood & Harvey 1982, Rodgers 1987, Jackson et al. 1989, Monnat et al in press).

The three categories of prospectors we distinguished on the basis of the sites where they land clearly differ behaviourally (Table 3). They correspond to successive development stages in the processes leading to recruitment: geographical stabilization, settlement, appropriation and pair formation.

Recruitment and squatting

If regular occupation of a nest leads to appropriation, the former squatter should recruit on that ledge in the following year. This is possible only if the male owner dies during the non-breeding season ($P = 0.15$; Coulson & Thomas 1985, Danchin & Monnat in press, Monnat et al. in press). Among 202 squatters which were subsequently recruited in our study plots, 36 (17.8%) bred on one of the nests they squatted in the year before, and 18 (8.9%) of them on the nest they squatted most (Monnat et al. in press). As the latter rate is between the mortality of the male alone (15 %) and that of both breeders (2.3%), in some instances, squatters of year n must have removed the owners of year n still alive in year $n+1$ to breed there in year $n+1$. Squatting appears to be a behavioural stage allowing appropriation and recruitment in the following year.

The attraction: a mechanism of population regulation

The attraction of a breeding place (i.e. a population in its environment) on the members of a population can be defined as 'the capacity of a breeding place to attract and recruit new breeders'. It is an important component of the behavioural mechanisms of recruitment. Attraction depends on two interdependent components (Figure 3).

- *The social context* contributes to the attraction of a breeding place to prospectors. Consequently, prospectors attend a breeding place where they can settle on a ledge.
- *The presence of chicks* (i.e. good breeding success) in individual nests influences the choice of the future breeding ledge.

The social context can differ greatly between two neighbouring breeding places. In Cap Sizun, in a flourishing colony (see Danchin & Monnat in press) breeding density and synchrony, sound level per pair and the frequency of reproductive activities (courtship, care of the clutch and brood) were higher than in a declining colony (Danchin 1988). Aggressive interactions were more common in the declining colony, where adults spent more time preening than in the flourishing colony. Chicks in the

flourishing colony were more active: they slept less and spent more time preening or wing flapping (Danchin 1988). Attendance of breeders was higher in the flourishing colony than in the declining one before the fall in attendance, and lower after. In the same way, breeding success was twice as high in the flourishing colony than in the declining one (Danchin & Monnat in press).

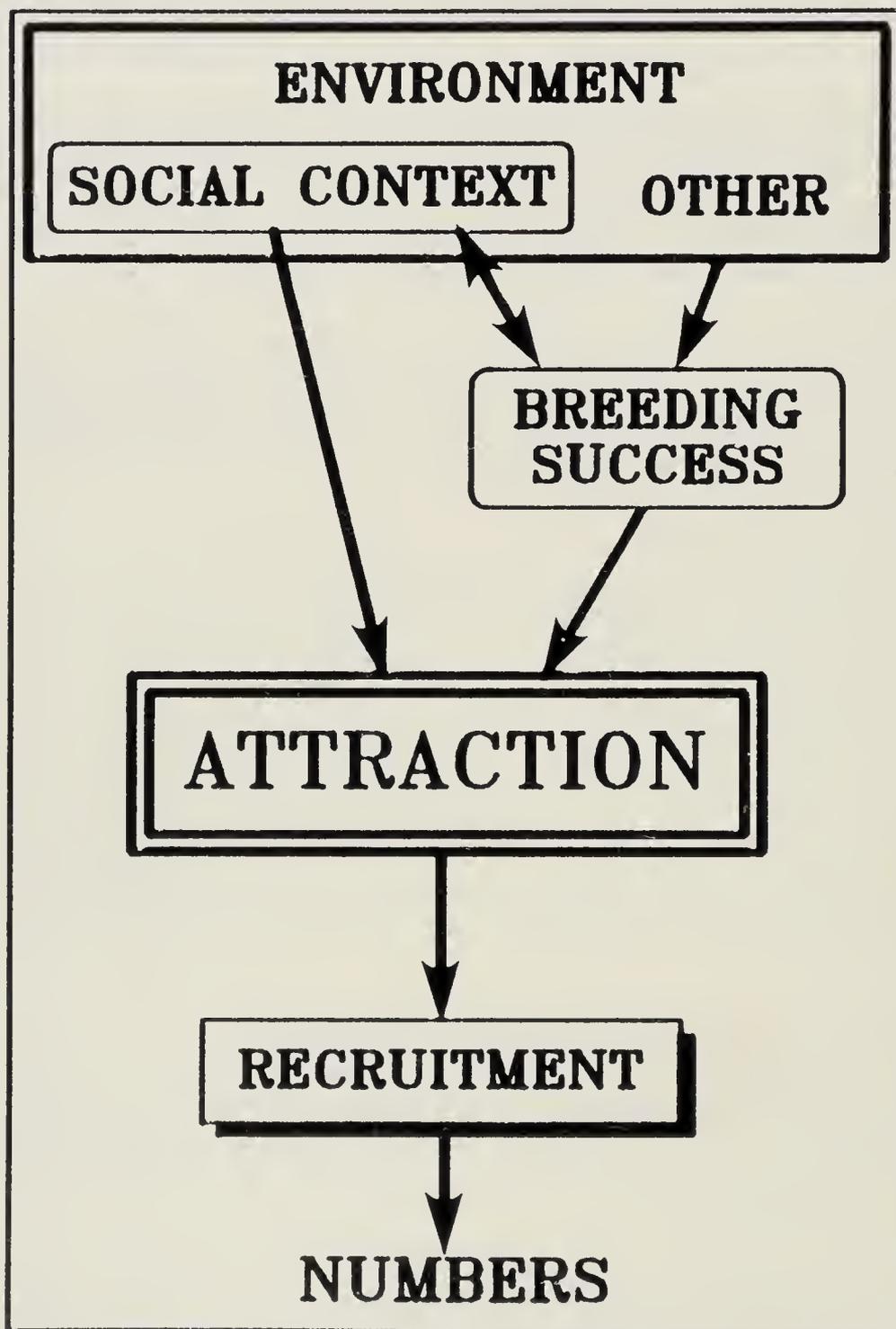


FIGURE 3 – The two components of the attraction made by a breeding place on prospectors.

The above differences in social context may influence greatly attraction and recruitment either directly or through their action on fecundity (Figure 3) and we observed that the rates of squatting, recruitment and adult site fidelity were higher in the flourishing colony (Danchin & Monnat in press).

ATTRACTION AND RECRUITMENT. Immature Kittiwakes visit several breeding places. Through social context and breeding success they are attracted to colonies. The

higher the attraction, the longer they stay in a given breeding place and the better they can learn the environmental characteristics of that particular location. If the attraction is high enough and if the bird is physiologically mature, it may establish on a site, start pair formation and recruit into the population. For failed breeders, the future recruitment depends on the attraction to the different breeding places they prospect after failure. If the attraction in their former breeding place is high enough they may not move elsewhere. We believe that this behavioural mechanism of recruitment (i.e. attraction-recruitment mechanism) can be extended to most species of birds.

Function of prospecting

From its peculiarities, squatting can be interpreted as a way for prospectors to assess the quality of breeding places: the presence of chicks and good social context are among the best criteria to assess the health of a breeding population (Monnat et al. in press). Consequently, prospecting by immatures can be functionally reinterpreted as a "visit to the brood of the elders" allowing the assessment of the quality of the visited populations (Monnat et al. in press). In failed breeders, the same function can be assumed.

In short-lived species, early post-fledging dispersion may include prospecting (Baker 1982, 1984, Vansteenwegen 1987) and allow young to assess the quality of the breeding places visited. In migratory short-lived birds, some observations suggest that during the juvenile dispersion some fixation on the future breeding place might occur (see in Bauer 1987). Part of allopatry may result from those post-fledging visits.

Why landing on the nests themselves?

Since social context and breeding success can be assessed from a distance, a visit to peripheral sites should suffice to prospectors. Indeed, many authors noticed prospecting (Table 1), but prospectors on nests were reported only in species breeding underground (*Hydrobates pelagicus*: Scott 1970, *Oceanodroma castro*: Allan 1962, Harris 1969, *Puffinus puffinus*: Brooke 1977) or on cliffs (*Anous tenuirostris*: Cullen & Ashmole 1963, *Larus (Creagrus) furcatus*: Hailman 1965, *Rissa tridactyla*: Cullen 1957, Coulson 1959, Hodges 1974, Danchin et al. 1987, Monnat et al. in press). In the Black Noddy (the only other species for which the description of squatters is well documented), squatters are also 'wandering adults, house-hunting pairs and failed breeders' (Cullen & Ashmole 1963). In species breeding underground, nest content cannot be assessed by prospectors without visiting the nests themselves. In cliff-nesting species, nesting on narrow ledges on sheer cliffs deeply modified their ethology (Cullen 1957, Cullen & Ashmole 1963, Hailman 1965, Smith 1966, McLannahan 1973, Burt & Chow 1983). Only a good experience of the landing conditions which vary greatly according to the wind and between two close sites, allows appropriation. Furthermore, two close sites can be very different in their capacity for receiving a solid nest. Therefore, landing on the site itself appears to be necessary for prospectors in cliff-nesting species. Hence, squatting may find its origin in burrow and cliff-nesting.

CONCLUSION: RECRUITMENT AND POPULATION REGULATION

For Darling (1938) social interactions play an important part in population regulation through their action on breeding success. According to Darling, breeding success acts *directly* on numbers of breeders. However, changes in fecundity can only act on the

numbers of breeders when the cohort is recruited. This may take up to 10 years after fledging in some species. Such delay would be too long to adapt the numbers of breeders to the changing conditions. Furthermore, in long-lived species, populations are more sensitive to variations in survival rates than to variations in fecundity (Cull & Vogt 1973, Lebreton 1981, Lebreton & Clobert in press): even big variations of fecundity do not have real effect on the populations' growth rate.

Because of these two major defects, in long-lived species, numbers of breeders cannot be regulated only by changes in breeding success. In fact, this is mainly a matter of scale.

At the scale of a local population the above attraction-recruitment mechanism provides immediate and very efficient regulating actions. Intense recruitment can lead to high increase in numbers. No recruitment leads to the decrease of the population numbers by the mortality except if previous breeders move elsewhere, which would lead to more rapid decrease.

On the wider scale of a metapopulation (i.e. an isolated group of more or less isolated populations), the regulation of the numbers is the result of the regulation of each local population. The attraction-recruitment mechanism leads to preferential recruitment in the most productive sites at a given time. It spreads the birds over the different possible breeding places according to their present quality. Consequently, it leads to an optimisation of the total fecundity and then of the numbers of the metapopulation. The movements of birds that result from this mechanism create genetic flow which maintain the homogeneity of the metapopulation.

This attraction-recruitment mechanism is in good agreement with Darling's basic idea: as a component of attraction, social interactions play a prominent part in population regulation (Figure 3). However, systematic recruitment in the birth population is only true at the scale of a metapopulation. At any smaller geographical scale (i.e. the one we study), many birds are allopatric. This important statement is often neglected. Perrins (1966) and Brooke (1990) for instance, equated recapture rates of juvenile Manx Shearwater at the colony of birth to survival rates. This denies the reality of dispersion-recruitment processes.

This attraction-recruitment mechanism takes into account the ontogeny of the birds because it is on the basis of the conditions experienced in the different breeding places visited during immaturity that the birds eventually establish in one population. It leads to a social limitation of the size of local populations: when density increases, the most attractive populations are likely to become the most difficult to recruit. Social context and breeding success can be considered as epideictic traits (Wynne-Edwards 1962, 1986) emerging from a population. However, the present mechanism does not imply any form of group selection.

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PHILOPATRY AND AGE OF FIRST-BREEDING IN LONG-LIVED BIRDS

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ABSTRACT. Most established breeders remain strictly faithful to an area and any movements away from their natal area occur prior to first-breeding, often being more marked in females. Estimates of natal and breeding philopatry based on study of only one location may be misleading. Differences between species in natal recruitment rates may reflect different balances between the advantages of familiarity with the foraging, predation and social environment in their natal area, and disadvantages there (competition for resources, deleterious inbreeding etc.). The age of first-breeding is greater and more variable in species with higher survival rates but differences between the sexes are usually slight. Anatomical or endocrinological incompetence rarely accounts for deferred breeding. Rather, age at first-breeding seems related to the acquisition of sufficient foraging, social or other skills. Individuals starting to breed when older than conspecific first-breeders may be more cautious, or less fit, or both. **Keywords:** Philopatry, first-breeding, recruitment.

PHILOPATRY

Many studies of birds have documented the relationship between an individual's birthplace and the location of its first breeding attempt. In species with an annual adult survival rate more than about 70-80% there is normally an interval of more than a year between these events. Some long-lived species (e.g. many diurnal raptors and owls) are resident on, or near, breeding territories all year, and the young disperse outwards from their parental territory early in life, most breeding near their natal area thereafter (e.g. Newton 1989). However, other species (e.g. waterfowl and seabirds) leave their breeding areas each year. Philopatry is the phenomenon whereby individuals then return to areas with which they have had prior associations. Once an individual starts breeding in an area, it tends to return there for most, if not all, subsequent breeding attempts. This is termed breeding philopatry and appears nearly absolute in most long-lived species (Greenwood 1980), although exceptions occur (Harris 1972). Natal philopatry is the tendency for young, marked in their natal area, to return to that area to breed, or prior to moving or breeding elsewhere.

Most studies involve intensive work at only one location with limited recoveries or observations from elsewhere, so that natal philopatry results in only minimal estimates of total recruitment or pre-breeding survival. Only rarely are two locations monitored, as for instance by Savard & Eadie (1989) who found that the return rates of Goldeneyes *Bucephala* spp. were similar at two sites 100 km apart. Intensive searches at varying distances away from a single location often show birds from the study area breeding elsewhere but only rarely after breeding at the study area first (Coulson & Neve in press).

Some individuals return to their natal area, albeit only briefly or intermittently, before moving elsewhere, often to breed. Their detection will depend upon the frequency and intensity of monitoring at the natal area and the size of the area monitored. Randall

et al. (1987) found that although adult Jackass Penguins *Spheniscus demersus* were strictly faithful to their breeding islands and only 2-10% of birds started breeding anywhere other than their natal island, many visited one or more islands before returning to their natal islands to breed. Similar situations have been recorded in Kittiwakes *Rissa tridactyla* (Coulson & Wooller 1976, Coulson & Neve in press) and Short-tailed Shearwaters *Puffinus tenuirostris* (Bradley et al. 1990).

In monogamous birds, gains from breeding in a familiar natal area may be offset by new mating opportunities following dispersal (Greenwood 1980). Stronger philopatry in males should result from their greater need to establish a territory in known surroundings (Greenwood 1987, Greenwood & Harvey 1982). If dispersal is driven, instead, by parent-offspring conflict, daughters should be driven away by mothers, again resulting in male-biased philopatry (Liberg & von Schantz 1985). Shields (1983) has argued that philopatry may result in a beneficial amount of inbreeding in long-lived, low fecundity organisms.

No sexual bias in natal philopatry is evident in monogamous sandpipers *Calidris* spp. (Gratto 1988) and plovers (Haig & Oring 1988) but more females move away from their natal area in the Manx Shearwater *Puffinus puffinus* (Brooke 1978, 1990), Herring Gull *Larus argentatus* (Chabrzyk & Coulson 1976), Red-billed Gull *Larus novaehollandiae scopulinus* (Mills 1973) and the Kittiwake (Porter & Coulson 1987). Females also disperse further outwards from their natal territory in the Sparrowhawk *Accipiter nisus* (Newton & Marquiss 1983) and the Magpie *Pica pica* (Eden 1987). Of 287 Short-tailed Shearwaters recruited to one island breeding population since 1960, 50% have been natal returnees. Of these natal birds, 58% were males compared with 47% males among non-natal recruits, a marginally significant difference ($\chi^2 = 3.38$, $0.1 > P > 0.05$). Among natal recruits which bred near the burrow of their birth, 58% were males, whereas those moving away contained only 50% males. Although this difference was not significant, these trends may indicate a slightly stronger philopatry in males.

Considering breeding philopatry in waterfowl, site fidelity is thought to be more common in females (Greenwood 1980) because female anatids provide most or all parental care of the young (Lessels 1985) and may, therefore, derive advantage from information on the breeding areas. Nonetheless, although both adult and young female Snow Geese *Anser caerulescens caerulescens* show a high fidelity to a specific colony, some movement of females does occur. Indeed, in this species, non-natal (immigrant) females may differ from the rest of the colony in their clutch size and laying date (Geramita & Cooke 1982). In Kittiwakes (Wooller & Coulson 1977) and Short-tailed Shearwaters (Bradley et al. 1989), immigrants and natal recruits show no differences in their sizes, survival rates, or breeding performance.

Differences between species, and between the sexes within a species, in the degree of natal philopatry may depend upon a balance between the advantages of familiarity with the natal area (e.g. more efficient foraging or predator avoidance; familiarity with social conventions) and the disadvantages of competition for resources in the natal area (including parent-offspring competition) and deleterious inbreeding. This last is unlikely to be very important in colonial species. In the Pied Flycatcher *Ficedula hypoleuca*, Part & Gustafsson (1989) have suggested that breeding dispersal distances relate to an individual's familiarity with a local area and that they choose to disperse on the basis of their experience. Natal philopatry in non-sedentary species

implies that young imprint on their hatching location prior to dispersal. Table 1 shows the results of transference of nestling Short-tailed Shearwaters, which later returned to their foster colony rather than the island of their birth. In this species, the spatial and temporal limits to locality imprinting appear very precise.

TABLE 1 – The numbers of Short-tailed Shearwaters which returned to their natal island compared with the return rates of birds transferred to this island from elsewhere.

Years born	Distance transferred (km)	Number born	Percentage which	
			Returned	Bred
1960-1962	0	89	53	21
	1	29	14	0
1964-1971	0	238	46	13
	3	157	3	2

Measures of breeding philopatry may depend upon how site fidelity is defined, since small movements of breeding site are common in many species. Similarly, the degree of natal philopatry, or dispersal prior to recruitment, may depend crucially upon the size of a study area relative to the scale of the movements. In Caspian Terns *Hydroprogne caspia* in the Great Lakes, L'Arrivee & Blokpoel (1988) showed that while 80% of adults returned to their natal lake, about 60-70% bred at a colony other than their natal colony. If many birds follow a geometric model of dispersal outwards from their natal area (Buechner 1987), the boundaries of study areas, often defined for logistical reasons, rather than in terms of population dynamics, may greatly affect measures of immigration or emigration.

In no species of long-lived bird studied are natal recruits known to sustain a population but the origins of most immigrants to study populations remain unknown, as does the extent of emigration. Work at several locations simultaneously would be required to determine the probable spatial, and indeed temporal, patterns of recruitment within a species. Estimates of natal philopatry derived from single locations show differences between species, between sexes, between colonies of the same species (Danchin & Monnat 1990) and, possibly, over time at the same colony or area. Given the uncertainty about such estimates, caution seems advisable at present in interpreting apparent differences in philopatry.

AGE OF FIRST BREEDING

In bird species whose breeding adults have an annual mortality rate less than about 20-30%, most individuals commonly do not breed in the year following their birth. The mean duration of the delay between birth and first-breeding (i.e. first association with an egg) has long been known to be greater in birds with higher survival rates (Lack 1968, Croxall 1981). Indeed, there appears to be a significant relationship in long-lived birds between the mean age of first-breeding and the expectation of life of breeding birds (Figure 1). The range of ages over which breeding starts also appears to be greater in long-lived species (Figure 2).

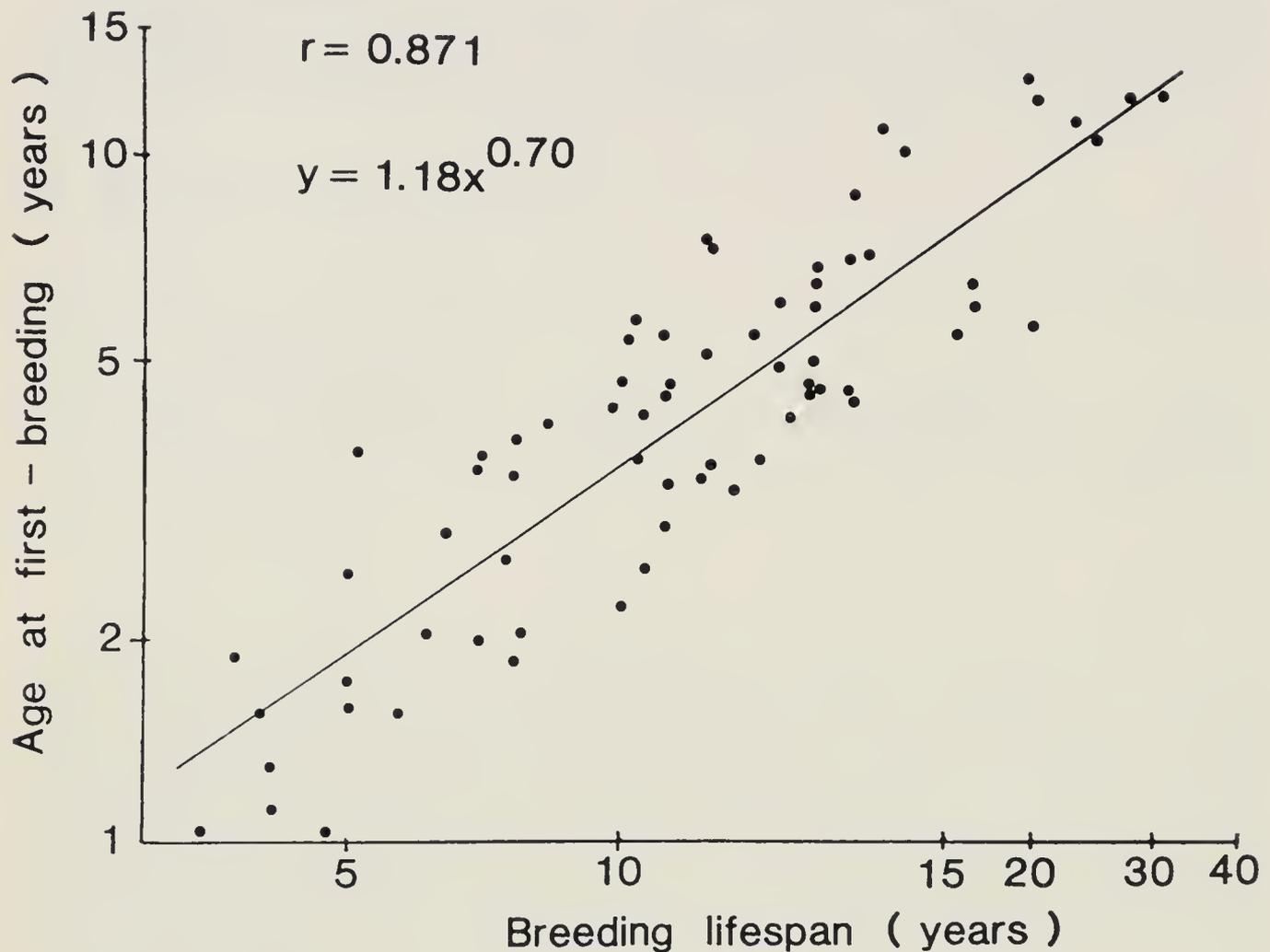


FIGURE 1 – The mean ages of first-breeding of some long-lived bird species in relation to their mean breeding lifespans. Data from Croxall (1981), Clutton-Brock (1988) and Newton (1989).

In some species, one sex appears to start breeding at an earlier age, on average, than the other and this has been related to differences between the sexes in their survival and reproductive effort (e.g. Mills 1973, Wooller & Coulson 1977). However, the sample sizes of known-age first-breeders in most studies are often small and the overlap in the ages at which males and females start to breed is often great. As a result, differences between the sexes in their mean ages of first-breeding rarely exceed one year and the reality of such differences and interpretations remains to be resolved.

There is little evidence that males which have returned to their natal, or other, breeding area after several years absence, but have not yet started to breed, lack functional testes (e.g. Ainley 1975, Brooke 1990, Hector et al. 1990). Although most long-lived birds may be completely unable to breed for the first year or two of life, by the time they return to their breeding grounds, reproductive immaturity seems attributable to some, or all, of the following:

- (a) the time taken to learn and perfect generalised skills (e.g. foraging), and to acquire knowledge (e.g. of foraging areas);
- (b) the time taken to develop sociosexual skills (e.g. courtship displays), to find a nest-site and/or partner and establish residency and/or a stable pair-bond;
- (c) the time taken for maturation of the physiological/endocrinological mechanisms underlying successful breeding.

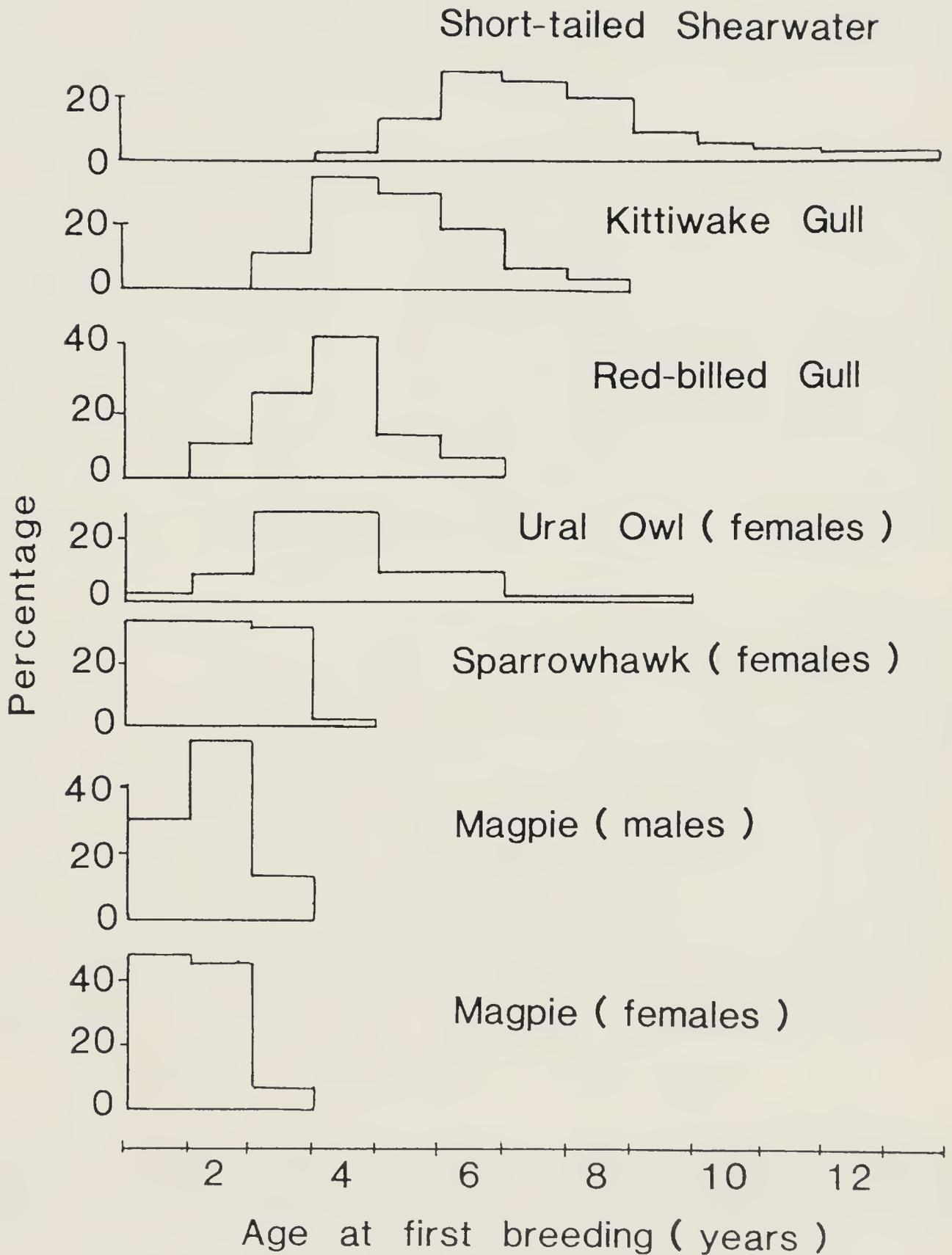


FIGURE 2 – Percentage frequency distributions of the ages of first-breeding of some long-lived birds, ranked according to their mean age at first-breeding. Data as for Figure 1.

An increase in foraging efficiency with age occurs in the subadults of several species of gulls and terns (Greig et al. 1983, Carroll & Cramer 1985, MacLean 1986). For example, Herring Gulls *Larus argentatus* showed a year by year improvement in feeding efficiency up to four years old before starting to breed at about five (Greig et al. 1983).

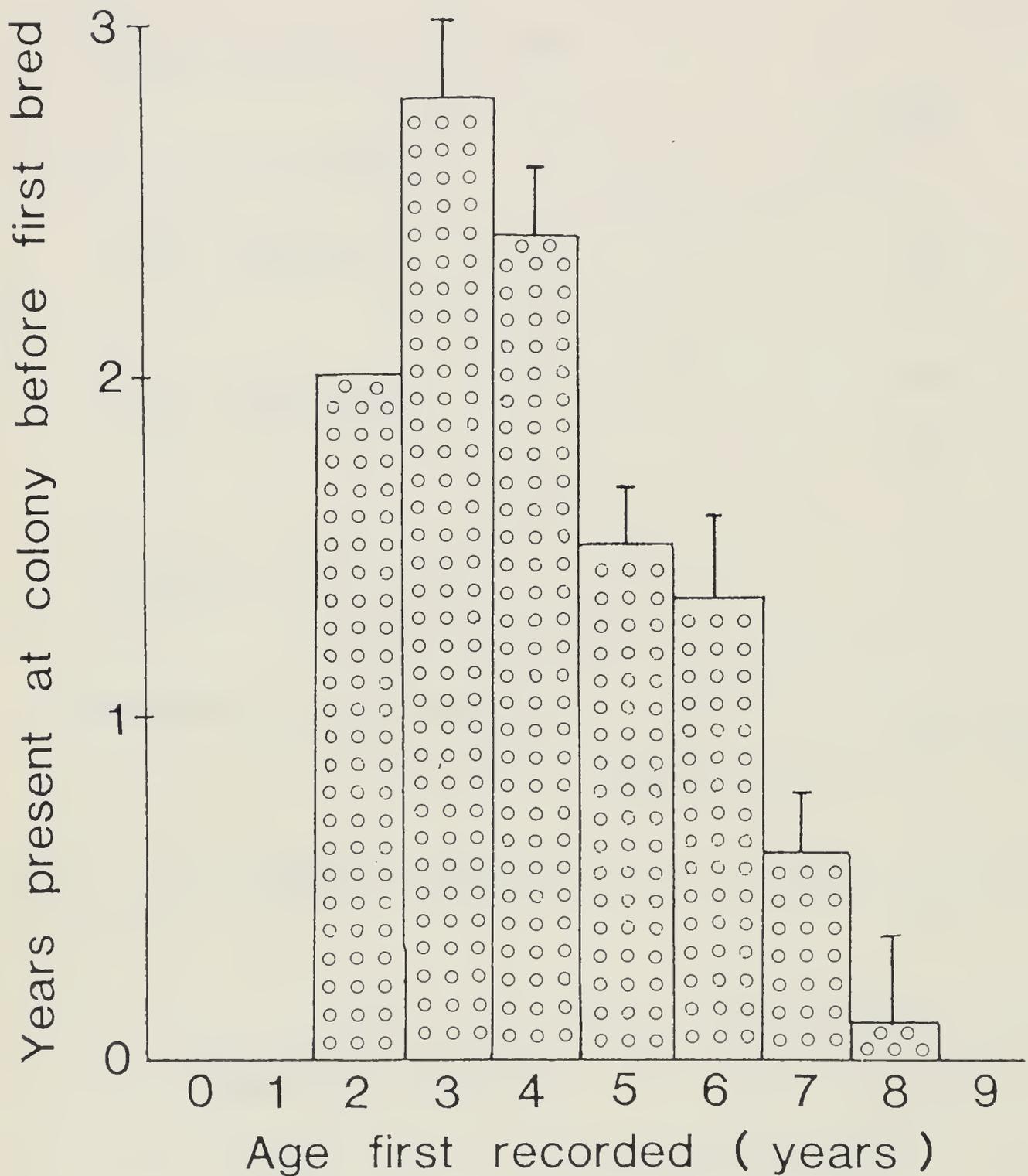


FIGURE 3 – The ages at which Short-tailed Shearwaters were first recorded returning to their natal island in relation to the numbers of years which then elapsed until they first bred.

In colonial breeders, a gradual involvement of young birds with the activities of the breeding colony is common (e.g. Nelson 1978, Ainley et al. 1983, Porter 1988, Ollason & Dunnet 1988). Most do not attempt to breed on their first visit to the colony. The youngest immatures commonly appear latest in the season, sometimes after breeding has ceased, and return progressively earlier in each year as they age (e.g. Porter 1988, Serventy 1967, Carrick & Ingham 1970). In the season(s) before they first breed they may defend nest-sites and/or interact with conspecifics (e.g. Harris 1973, Wooller & Coulson 1977, Ainley et al. 1983). The sexual display rates of pre-breeding Wandering Albatrosses *Diomedea exulans* increased as mate selection and pair formation took place, then fell as stable pairs were formed (Pickering 1989,

Hector et al. 1990). Interestingly, in Wandering Albatrosses, the time between first arrival at the colony and starting to breed was substantially longer in those birds first arriving at younger ages, suggesting that some physiological maturity may be a prerequisite for the formation of a stable pair bond (Hector et al. 1990).

In penguins, storks, pheasants, gulls and ducks, the gonads of young pre-breeders are not usually fully functional until most adults are already breeding and, often, not until breeding is no longer possible (Hall et al. 1987). Hector et al. (1990) have suggested two underlying concurrent mechanisms to account for such observations. Firstly, photoperiodic control of the annual reproductive cycle would restrict gonadal maturity to a short period each year. Secondly, as birds got older, the duration and amplitude of this cycle would increase until, by the observed age of first-breeding, a full cycle occurred. In males, this would involve an increasing amplitude of the testicular cycle, for instance as in California Gulls *Larus californicus* (Johnston 1956). In females, this might involve a changing gonadal sensitivity to gonadotrophin secretion and age-dependent inhibition of the photoperiodic response, and hence of the hypothalamus-pituitary-gonadal axis. The ovaries of Wandering Albatrosses respond to gonadotrophin stimulation either by oestradiol secretion, in breeding birds, or by progesterone secretion, when they are unable to breed (Hector et al. 1990).

Thus, while endocrine status and gonadal sensitivity may determine the ages at which breeding becomes possible, in birds close to maturity it is probably social and other environmental factors which influence the actual ages at which individuals start breeding. Some raptors and gulls may start breeding while still in immature plumage, if food is abundant, although breeding tends only to be advanced by one year (Lack 1968). Captive seabirds (Harris 1984), but not captive storks (Hall et al. 1987) breed at younger ages than wild counterparts, presumably as a result of favourable environmental conditions. Birds at less dense colonies may start to breed when younger than conspecifics at more dense colonies (Chabryk & Coulson 1976, Kress & Nettleship 1988). Similarly, a reduction in density at a colony, either due to natural events or human intervention, also results in more birds first breeding at younger ages, presumably as a result of reduced competition for resources such as nest-sites or food (Potts et al. 1980, Duncan 1978, Coulson et al. 1982, Porter & Coulson 1987). Physiological maturation, therefore, imposes only very broad constraints upon the ages of first-breeding and variation in these ages must be sought elsewhere.

Although it is often suggested that there is a cost to reproduction, and that current fecundity can only be increased at the cost of future fecundity and/or survival, evidence for this among wild birds has been equivocal (Partridge 1989). For instance, in Sparrowhawks, Newton (1989) showed that there was no apparent advantage in delaying the age of first-breeding but, rather, that delays were greater in females unable to obtain food, territories or mates in competition with conspecifics. In contrast, Kittiwakes starting to breed at younger ages had a higher subsequent mortality rate than those starting later (Wooller & Coulson 1977).

In addition to a trade-off between first and future reproduction influencing the age of first-breeding, there is also evidence, in some species, of selection at the time of first-breeding on the basis of individual quality (Curio 1983). Some individuals which breed first at a young age relative to conspecifics have a relatively high breeding success, both initially and subsequently, coupled with a high survival rate, and appear to suffer no penalty for starting early (Porter 1988, Thomas & Coulson 1988, Bradley et al. 1990).

It would be interesting to know whether birds of high "quality", starting to breed at the younger ages, also shortened the period spent at the breeding area between their first arrival and the time they first bred. In Wandering Albatross, those arriving first aged three took six more years, on average, before they started breeding, whereas those not arriving until eight years of age took only about two more years before they bred (Hector et al. 1990). In Short-tailed Shearwaters, a similar negative relationship between age at first arrival and the number of years then elapsed before breeding was also apparent (Figure 3). Interestingly, non-natal recruits spent only 1.1 years, on average, at the study colony before they first bred, significantly less than the 2.1 years of natal recruits ($z = 7.33$, $P < 0.001$). As mentioned earlier, these non-natal recruits may well have visited their natal, or other, islands before being recruited to the study population, so that their total period of pre-breeding colony attendance may have been equivalent to that of natal recruits. It is clear that much still remains to be learned about the interactions between spatial and temporal aspects of recruitment in such long-lived birds.

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RECRUITMENT IN LONG-LIVED BIRDS: GENETIC CONSIDERATIONS.

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ABSTRACT. Recruitment influences the genetic structure of a bird population through possible changes in gene frequencies. Genetic drift, gene flow and selection are three major factors moulding a population's genetic composition. In long-lived birds, a small proportion of the population provides recruits for the next generation, thus stochastic events (genetic drift) may play a role in determining the gene frequencies of future generations. Recruits can be either newly-breeding offspring from the population itself or immigrants from elsewhere. Native recruits reflect the genetic structure of the breeding segment of the population and any selective forces acting between birth and recruitment. Immigrants reflect the genetic composition of their place of origin and selective forces operating prior to entry into the population under study. Using a fitness components model with a marked population of birds, one can compare the genetic composition of resident breeders, native and foreign recruits, and birds that fail to enter the breeding population. In this way, one can examine both the genetic effects of recruitment and the factors influencing phenotypic characters associated with recruitment.

Keywords: Gene-flow, selection, immigration, recruitment, Snow Goose, genetic drift, body size, egg size, *Anser caerulescens*.

INTRODUCTION

Most studies of long-lived birds emphasize the importance of ecological factors associated with recruitment. There are also, however, microevolutionary factors that operate through recruitment to alter the genetic structure, phenotypic attributes, and dynamics of populations. In this presentation, we consider three of them, namely, genetic drift, gene flow and selection. While evolutionary biologists have focused more on selection than the other factors, we will argue that both genetic drift and gene flow can be critical, particularly in considering evolutionary dynamics of long-lived species. In pursuing these points, we will draw primarily on examples from our long-term study of the Lesser Snow Goose *Anser caerulescens caerulescens* L.

GENETIC DRIFT

Many gene frequency changes occur as a result of stochastic events. In most species of birds studied to date, a large proportion of the individuals produce no young during their lives and a quite small proportion produce recruits (Newton, 1989). Even among successful breeders, there is considerable variability in lifetime production of offspring. Among long-lived birds with a stable population size, few individuals per generation can recruit into the breeding stock. Whether a bird survives to breeding age may depend on such unpredictable events as year of birth, predator cycles, weather, and food availability. Young of species with delayed maturity will face several seasons of in part stochastic mortality prior to breeding. Among breeders, longevity is a major component of variance in lifetime reproductive success (Clutton-Brock 1988, Oring et

al. in press), and the number of years lived has a reasonably high stochastic component, particularly in long-lived species (Newton 1989).

The alleles carried by successful breeders can change the gene frequencies of a population, even if the characters they contribute to are not directly related to fitness. The combination of small sample size and stochastic events leads to unpredictability in gene frequency changes. The genetic consequences of high variability in lifetime reproductive success are that the effective size of the population is decreased and the within population genetic variance is reduced due to fixation of alleles at polymorphic loci. Since such fixation is random, different alleles are fixed in different populations leading to an increase in between population genetic variance (see Falconer 1989).

In long-lived species, new recruits (usually the youngest members of the age structure) make a relatively small contribution to the population's gene pool. The larger contribution of the older, established members of the population act as genetic inertia slowing the rate of change in genetic variance both within and between populations (Charlesworth 1980). Thus, while genetic drift may play a relatively more important role in determining the genetic structure of long-lived than short-lived species, the rate and detection of changes attributable to drift will be slower.

GENE FLOW

Gene flow and selection are evolutionary forces that can alter gene frequencies in a directional fashion, in contrast to the random effects of drift. We consider first the effect of gene flow on the genetic structure of a population using a well documented case of a single gene marker in a long-lived bird, the Lesser Snow Goose. By gene flow, we mean the movement and incorporation of alleles between populations (Rockwell & Barrowclough 1987). Lesser Snow Geese come in two colour phases, blue and white, with the phenotypic difference being determined by a single autosomal allelic difference in which blue is dominant to white. The genetic effects can be investigated because of the pattern of philopatry found in this and other species of waterfowl. Females are highly philopatric, thus females that are recruited into the breeding population are primarily locally hatched birds. Males on the other hand follow their mates to the female's colony of origin. Mate choice occurs away from the breeding grounds where birds from several breeding colonies are intermingled. Depending on the relative size of the colony and whether mate choice is random with respect to the male's colony of origin, male dispersal can be very high (Rockwell & Barrowclough 1987).

At the La Pérouse Bay breeding colony, almost all male recruits are immigrants from elsewhere. Birds from La Pérouse Bay mix during migration and winter with birds from much larger breeding colonies on west Hudson Bay, Queen Maud Gulf, Cape Henrietta Maria and Baffin Island. These latter two colonies have a high proportion of blue phase birds. Table 1 shows the colour-phase ratios among known native recruits (98% females) versus males of unknown origin. There is likely a very small number of unmarked (and therefore undetectable) native recruits among our male sample. Nevertheless, in general, the data in Table 1 represents a comparison between resident and immigrant birds. The data show a significantly higher frequency of the blue allele among the immigrants than among the native recruits. This is expected since the blue allele is more frequent among birds from the areas where La Pérouse Bay females choose their mates.

TABLE 1 - Phase ratios of Snow Goose breeding at La Pérouse Bay known to have been native to the colony versus those of males of unknown natal colony 1969-1987. Nearly all of the males are immigrants.

Natal Colony	% Blue	N
La Pérouse Bay (males + females)	28.3	1594
Unknown (males)	31.7	16232

G = 7.67

P = 0.006

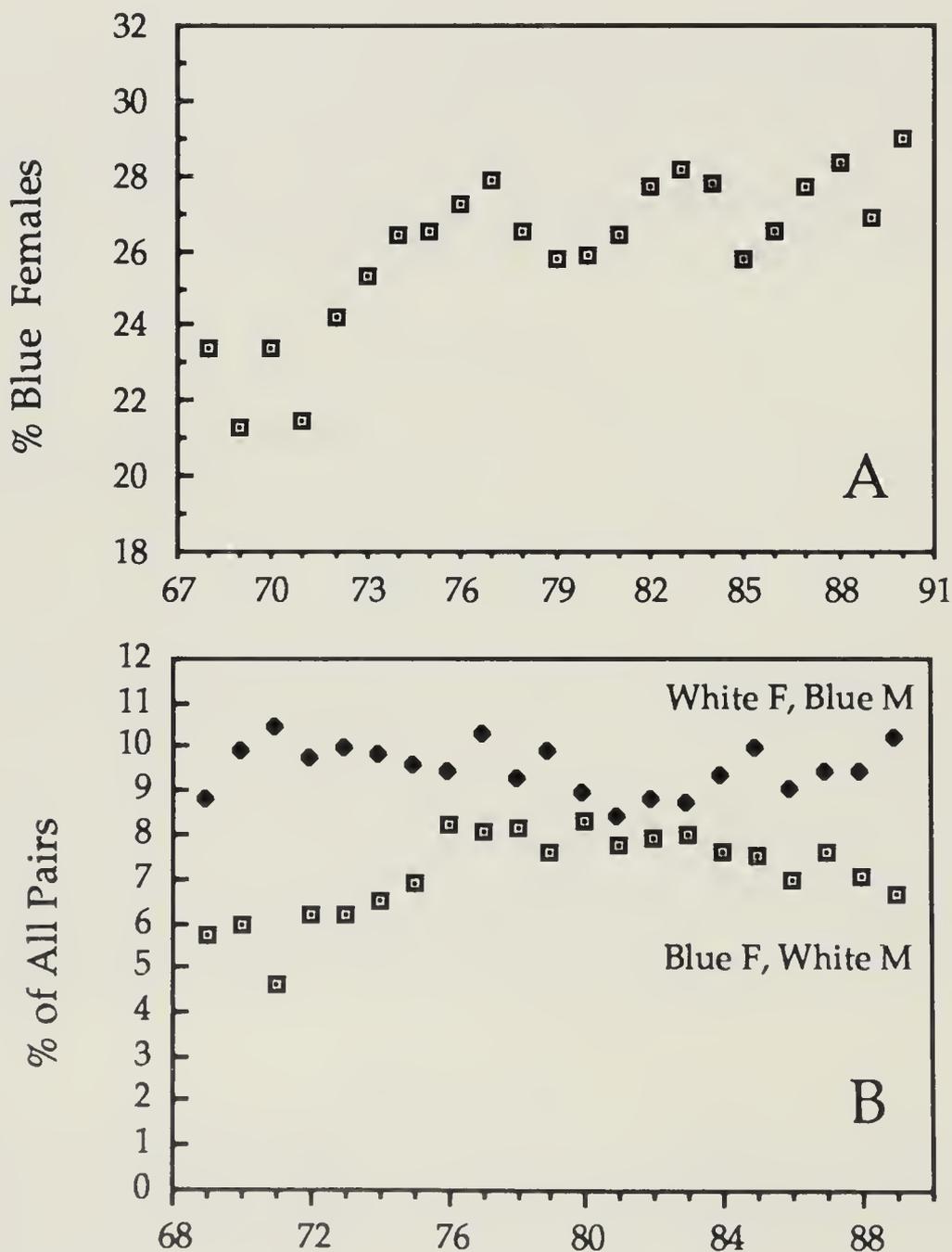


FIGURE 1 – A. The proportion of blue female Snow Geese in the annual nesting samples at La Pérouse Bay. B. The proportion of mixed-phase pairs of Snow Geese in the annual nesting samples at La Pérouse Bay. Dark diamonds = white females with blue males; squares = blue females with white males.

There are two genetic consequences of this gene flow to the La Pérouse Bay population. First, there is a slow increase in the frequency of the blue allele in the population. Second, there is always an excess of mixed pairs in which the male (immigrant) is blue. These findings are illustrated in Figure 1. It is also clear from Figure 1 that even with high gene flow into the population, gene frequency change is very slow in this long-lived species. This is because of slow population turnover, such that the relatively few recruits, even if they have a substantially different allele frequency, have little immediate impact on the population allele frequency.

This example illustrates another important feature. Simple mathematical models for calculating the effect of gene flow on allele frequencies assume that alleles enter the recipient population from the donor population in proportion to their relative frequency in the donor population. In reality, however, some alleles may have a greater tendency to move or be incorporated than others. For example, if there were genetic variability in terms of dispersal, those alleles associated with dispersal could flow more than alleles associated with philopatry. In our colour phase example, there is positive assortative mating in terms of plumage colour, thus a female from the La Pérouse Bay population (the recipient population) is more likely to choose a male from the donor population that is carrying the same alleles, in terms of plumage colour, as herself. The actual immigrant allele frequencies are influenced by the phase ratios of both recipient and donor populations and are expected to be intermediate between the two. Although we know that the donor population has a higher frequency of blue phase birds than the recipient, we do not know the exact frequency. Thus, we cannot test whether the allele frequency of the immigrants differs from that of the donor population in the way the assortative mating behaviour of the geese would suggest.

The only other bird population study of which we are aware which has considered the consequences of gene flow is that of O'Donald (1983) who attributed a lack of change in gene frequencies in a dimorphic Arctic Skua *Stercorarius parasiticus* to immigration of birds from a colony with different phase ratio to the colony under study. O'Donald calculated that the directional selection acting on the population of skuas on the Fair Isle population was sufficiently strong that the pale morph should eventually be extinguished. Yet he saw no detectable change in phase ratio during his study. To explain the discrepancy he pointed out that plumage colour had a clinal distribution with pale birds representing about 20% of the population in the south of the cline and 100% in the north. He argued that the cline is a diffusion cline and that migration must carry genes along the cline from areas where they are advantageous to areas where they are disadvantageous. Since dark phase birds are more frequent in other parts of the Shetland Islands they could easily migrate into the Fair Isle population and counteract the differential selection in favor of dark phase birds at the Fair Isle colony itself. He has no direct evidence that this explanation is the correct one, however.

Gene flow serves as a retarding force to differentiation among populations and can work against local adaptation. In long-lived species, however, the rate at which these effects accrue will be slower and their impact smaller. Again, this is due to inertia in the gene pool related to the smaller relative genetic contribution of young, new recruits to the multiple age class structure of long-lived species.

SELECTION

More attention has been given to the effect of natural selection on the genetic structure of bird populations than to the effects of other microevolutionary forces. We will examine selection first using the same simplified, single gene case that we used to examine gene flow and then examine some more general but less tractable polygenic traits. If recruits represent a selected subset of the population, and if the variability of the character under selection has some genetic basis, then a directional genetic change in the population is expected.

Following the methodology outlined by Endler (1986) for longitudinal studies, a valuable way to examine the effect of recruitment on the genetic structure of the population is: a) to note the frequency of the character among the recruits relative to the parental population that produced them; b) to investigate the heritable component of the character; c) to calculate the change in gene frequency that should result; and d) to consider the phenotypic consequences to the population of these changes. Any character, whether controlled by a single locus or multiple loci can be examined this way. The method allows the investigator to understand the selection pressures operating on the population and to predict the long-term consequences of such selection.

TABLE 2 - Phase ratios of breeders, hatching goslings, and recruiting Snow Geese breeding at La Pérouse Bay, 1973-1985. The significance of color-phase terms of MDCA models including year terms are given at the bottom.

Year	% Blue			N		
	Parents	Goslings	Recruits	Parents	Goslings	Recruits
73	26.7	29.0	27.2	2010	3771	103
74	28.1	30.2	32.3	2216	4367	62
75	27.8	28.6	25.6	2358	4453	125
76	27.7	28.0	25.5	2358	4864	165
77	28.0	29.1	28.1	2668	4796	199
78	27.6	29.0	29.0	2358	4250	100
79	26.9	27.7	22.6	2438	4960	106
80	26.3	26.9	24.1	2950	5450	170
81	26.0	27.2	24.0	2946	5409	100
82	27.9	28.2	22.4	3110	5543	107
83	28.7	30.4	28.6	3452	5766	56
84	29.0	29.8	29.9	4108	7160	97
85	27.4	28.0	21.1	4224	7836	71
Annual mean + SD	27.6+0.9	28.6+1.0	26.2+1.8			
G and P of color-phase term in MDCA model:	G = 12.2 P < 0.001	G = 3.67 P = 0.05				
	G = 1.21 P = 0.27					

Using Endler's approach on the plumage dimorphism in Snow Geese, we can investigate whether either colour morph has a selective advantage and predict the consequences for the population. We compared the phase ratios of parents sighted at nests, their day-old goslings, and recruits seen subsequently at the colony for each year of our study (Table 2). Day-old goslings are significantly more often blue than their parents (MDCA analysis, controlling for yearly differences in phase ratios, see Rockwell et al. 1985 for analysis methodology). This increase is due to gene-flow; it reflects the immigration of homozygous blue males whose offspring will be entirely blue, making goslings more blue than their parents. The sample of recruits is marginally more white than that of the goslings, and not significantly different from the phase ratio of the parents. We have previously shown no differences between the colour morphs when directly comparing fitness components (Cooke et al. 1985, Rockwell et al. 1985). Since selection clearly does not favor blue goslings, we would not expect any long-term increase in phase ratio in this population due to selection. But, in Figure 1, we showed that there had been an increase in blue frequency in this population during the study. As we explained, gene flow and the global distribution of colour morphs in the wintering population are sufficient to account for the observed change in colour ratio at our study colony (see Geramita et al. 1982). Thus, a change in a population's mean phenotypic distribution over time need not necessarily imply the action of directional selection.

In the only other study of selection of a simple genetic character in a long-lived bird, O'Donald (1983) estimated that selection favoured dark phase Arctic Skuas overall. Sexual selection by female choice favoured the dark morph and more than counteracted the tendency of pale morphs to begin nesting at a younger age. As mentioned earlier he explained the lack of long-term change in phase ratio in his population as a result of counterbalancing gene flow favouring light phase birds.

While analyses of conspicuous polymorphisms are relatively straightforward, they may give a misleading picture of the effects and importance of directional selection on characters that are polygenically inherited and for which phenotypic expression is affected by both genes and environment. There are many examples of characters under directional selection, where some phenotypes are more heavily represented among the recruits than among the population from which the recruits are drawn.

Price & Grant (1984) found that Darwin's Medium Ground Finches *Geospiza fortis* that survived to 7-10 months of age were substantially smaller on average than the adult breeding population from which they were descended. This suggested weak directional selection for small body size at this stage of the life cycle. Since body size is highly heritable in this species, this further suggested that genetic changes in the population may result from the recruits being a selected sample of the gene pool.

In Lesser Snow Geese, some polygenic characters, such as clutch size and laying date, show evidence of directional selection whereas others such as egg size do not. In general characters showing directional selection have lower heritability values while those with no detectable directional selection have higher heritability (Mousseau & Roff 1987). Rockwell et al. (1987) showed that the offspring of females laying large clutches were more likely to become recruits than offspring from small clutches. Since there is a significant heritable component to the variability in clutch size ($h^2 = 0.24$; Findlay & Cooke 1987), one might imagine that alleles associated with large clutch size would increase in the population. Similarly with laying date, offspring from birds

laying early in the season are more likely to recruit into the breeding population. Laying date also has a low but significant heritability ($h^2 = 0.22$) (Hamann unpublished, fide Boag & van Noordwijk 1987) and again this might lead to the conclusion that alleles associated with early laying might increase in the population.

A similar analysis of body size is summarized in Table 3. Body mass, tarsus and culmen length were measured during the annual moulting period on a large number of almost fledged goslings of known hatch date. Measurements were standardized for differences in age (see Cooch et al. in press, for methodology). From these variables, we generated a PCI value which reflects the overall size of the bird (see Davies et al. 1988). In Table 3, we compare the means and variances of those goslings measured from the years 1979 - 1984 which subsequently recruited into the population with those which were not known to recruit. This latter sample consists of both birds which did not survive to recruit and those which were not detected. Nevertheless the majority of the non-recruited sample can be assumed to have died before recruitment since approximately 70% of all fledglings die in the first two years of life (Cooke & Rockwell 1988). Recruits are larger than non-recruits in five of the six years, and in two years the differences are significant. In three of the years the recruits are significantly less variable suggesting some normalizing selection although directional selection per se can lead to apparent normalizing selection. These data show that there is directional selection between fledging and recruitment which favours larger birds. At other stages of the life cycle there is little evidence of fitness difference among birds of different size, and the heritability value of this character is reasonably high ($h^2 = 0.44$, Davies et al. 1988).

We believe that the directional selection documented in Table 3 mainly acts on the environmental component of the variation. Most of the recruits come from the early nesting females (Cooke et al. 1984). The body size of the goslings is highly influenced by their growth rate, which depends heavily on the availability of nutrient from the salt marsh vegetation. Goslings hatching later in the season grow more slowly than earlier hatching birds, due to decreased availability of nutrient as the season progresses and competition on the salt marshes increases. In the very late year of 1983 few goslings survived overall, average growth rate was much less than average and the selection differential favouring large birds was highly significant. All these facts and others enumerated by Cooch et al. (in press) suggest that selection is acting on the environmental component of variation as has been shown by van Noordwijk (1988) for body size in Great Tits and Alatalo et al. (1990) in Collared Flycatchers *Ficedula albicollis*. Price & Liou (1989) have provided realistic models to show that such directional selection would not necessarily reduce the genetic variability of the population.

The fourth polygenic character we have investigated in Snow Geese is egg size. It has high heritability ($h^2 = 0.78$; Newell, 1988), and there is no evidence of either directional or variance selection in the population. Figure 2 and Table 4 summarize data on egg masses from 6003 eggs laid by adult geese (>4 years old), adjusted for annual variation. Figure 2 shows the frequency distribution of the individual eggs laid, those which hatched, those whose goslings survived and were captured at fledging, and those whose goslings eventually recruited into the breeding population. Table 4 presents tests for differences in the distributions of individuals transiting or not transiting between stages. All the distributions show similar means and variances, showing that differences in egg mass have no detectable effect on survival.

TABLE 3 - Tests for evidence of selection on egg size distributions. The mean and standard deviations of eggs laid, and of eggs producing geese surviving to hatch, fledgling and recruitment, are given. Egg size was adjusted for annual variation (see text), but there were no significant annual interaction terms. Distributional difference between populations transiting or not transiting to the next stage were tested with t-tests, for directional selection on means, and f-tests, for normalizing or diversifying selection on variance. Recr = recruits; NotR = not detected recruits.

Year	PCI							
	Means			Variances			N Measured	
	Recr	NotR	Pt	Recr	NotR	pf*	Recr	NotR
79	0.12	-0.02	ns	0.66	1.07	ns	30	142
80	-0.15	0.05	ns	0.64	1.07	.007N	82	354
81	0.14	-0.02	ns	0.60	1.06	.03 N	41	300
82	0.20	-0.03	ns	0.67	1.18	ns	42	240
83	0.74	-0.05	.001	0.95	0.98	ns	12	168
84	0.57	-0.10	.02	0.56	1.00	ns	11	89

*N = normalizing selection suggested.

TABLE 4 - Tests for evidence of selection on gosling body size, measured as PCI calculated on fledgling tarsus, culmen, and mass. We compare the annual distributions of goslings measured at fledgling which did or did not return as recruits. t-tests test for evidence of directional selection on means; f-tests test for evidence of normalizing or diversifying selection on variance.

Life Stage	Natal Egg Size			Statistics for transitions	
	Mean	S.D.	N		
Eggs laid	124.9	9.0	6003	t = -0.07, 6001 d.f. f _{916,5085} = 1.04	ns ns
Hatching	124.9	8.9	5806	*t = -1.31, 3677 d.f. f _{3128,549} = 0.59	ns ns
Fledged	125.1	8.7	550	t = 0.88, 548 d.f. f _{447,101} = 0.94	ns ns
Recruited	124.5	8.8	102		

*The data set for this transition includes only hatchlings which were tagged and thus individually identifiable as fledglings.

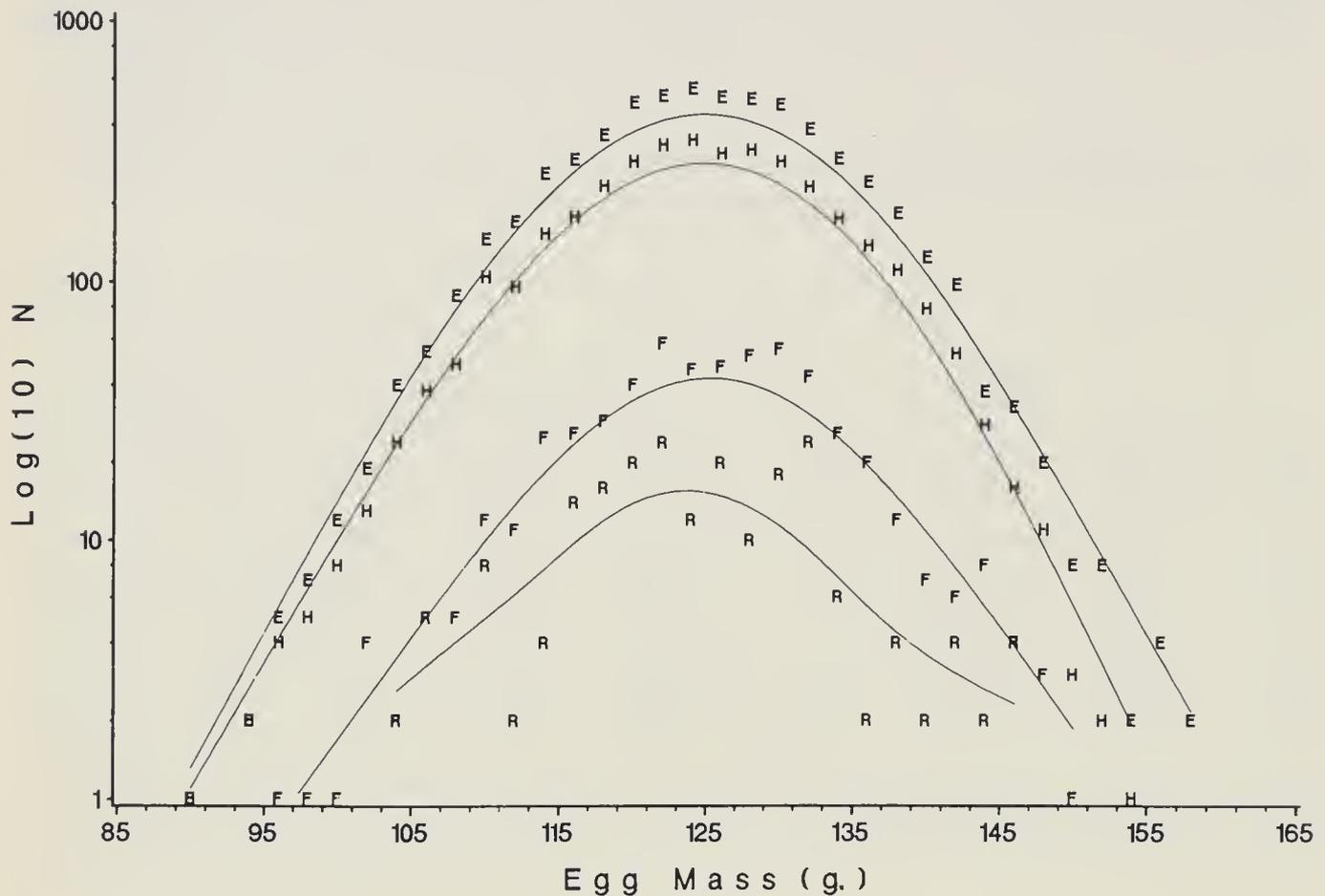


FIGURE 2 - Frequencies of eggs laid (E) and hatched (H), fledglings (F) and recruits (R) plotted as a function of original fresh egg mass. The curves shown are cubic splines for each stage, with the same smoothing function applied to each stage. Choice of smoothing function was by eye.

PREDICTING EVOLUTIONARY TRAJECTORIES

From the above examples, we see that in cases where heritability is high (e.g. egg size), there is no evidence of directional selection and therefore no necessary tendency for gene frequency change across generations. In cases where there is a directional selection gradient (e.g. clutch size and laying date), much of the character variation is due to non-genetic factors and future gene frequency changes may be limited. It must be remembered, that while directional selection operates on existing (additive) genetic variance, it will not necessarily erode all of that variance. Using somewhat different models, Lande and Turelli each showed that for polygenic characters, mutation pressure is sufficient to balance the levels of directional selection normally found in nature. Thus, even under directional selection, genetic variance and heritability will not necessarily become zero (see Barton & Turelli (1989) for a lucid review of this topic.)

Several recent theoretical papers (Price et al. 1989, Price & Liou 1990, Cooke et al. 1990) have shown that even if one can demonstrate a directional selection gradient and a heritable component to the character under study, it is not necessarily true that

there will be a phenotypic (or even a genotypic) change in the population as a result. The usual univariate formula for predicting the consequence of directional selection on gene frequency change is $R = h^2S$ where R is the phenotypic response of the population to selection, h^2 is the heritability and S is the selection differential for the character between the parental and offspring generations. For example, consider a population with a mean bill length of 10 mm. We choose a sample with a mean bill length of 12 mm to produce the next generation. This represents a selection differential of 2 mm. If the heritability of the character in that population is 0.5 then according to the classical equation we expect the response to selection R to be 1 mm, and the mean bill length of the progeny to be 11 mm.

This classical expectation is subject to many qualifications that make its utility for prediction in field situations suspect. First, it assumes that the environment stays constant from generation to generation and the genotype-environment correlations and interactions do not change. If the mean genotypic value of the offspring generation changes across generations, then this alone may lead to changes in the environment (Cooke et al. 1990). Alternatively, there may be known environmental changes that occur with time. For example, food supply may change as a population expands. Cooch et al. (1989) have shown a long-term decline in mean clutch size among the geese at La Pérouse Bay that resulted from environmental rather than genetic change. This occurred despite the strong directional selection favouring females laying larger clutches mentioned earlier.

Second, the classical equation assumes that when there is directional selection operating on characters with a heritable component, there will be some change in the allelic frequencies of the next generation. But as Price et al. (1989) point out for laying date in birds, and Price and Liou (1990) for clutch size, that selection may be operating only on the environmental component of the variation. If this happens, then no allelic frequency changes are expected and there will be no genetic consequences for the population. Merely showing a directional selection gradient is no proof that the characters being favoured will necessarily increase in the population. For example, just because early nesting birds are more likely to be recruited into a breeding population does not mean that mean laying date will become progressively earlier with time nor that the proportion of early nesting birds will increase in the population.

Overall, the effects of selection in polygenic situations are extremely complex, and the situation is further complicated if selection occurs on correlated characters (Lande & Arnold 1983). Where there is high heritability for the character in question, selective differences may often be small and the effect on the population negligible. There is however the potential for rapid evolutionary change in such populations. Where there is low heritability, although directional selection may be strong, the consequences of such selection in terms of phenotypic or genotypic changes to the population may also be slight.

GENERAL CONCLUSIONS

In conclusion, there are four important messages from our studies. Firstly, ornithologists who embark on field studies should consider their study organism not only from an ecological or behavioural standpoint but also consider the genetic structure and

dynamics of the species. Secondly, although it is extremely important to study selective processes in natural populations in order to understand the factors important to the survival and reproduction of the population, many other factors need to be taken into account. It is clear that genetic drift and migration may have an important impact on the changing genetic structure of a population in addition to selection and yet most evolutionary biologists continue to emphasize the importance of natural selection. For example, it is important to try to assess the role that immigrants into their study population can play in changing the genotypic and phenotypic structure of the population during the course of their studies. Thirdly, in long-lived species, there is genetic inertia resisting change from the three microevolutionary factors of drift, gene flow and selection, since recruits represent a small proportion of the breeding population. Fourthly, the methodology described by Endler (1986) where individual traits are examined in terms of the variability, selection differentials and heritable components is a useful beginning. It provides a basis for examining the ways natural selection is acting on the population under study. The approach may be less effective for predicting future changes in the phenotypic structure of the population. Nevertheless, predictions are crucial for evolutionary studies and it is important to test the population genetic models against the real world of the field ornithologist.

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RECRUITMENT IN LONG-LIVED BIRDS: STUDIES OF NONBREEDING GREAT SKUAS

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ABSTRACT. Studies of colour-ringed, nonbreeding Great Skuas on Foula, Shetland, were conducted during 1974, 1975, 1988, 1989 and 1990. Nonbreeders consistently gathered in groups, or 'clubs', and were mostly 3-7 years old. The age-structure of club gatherings varied during the season due to older birds arriving earlier than younger birds. Individual birds spent an average of 19 and 25 days at clubs in 1989 and 1990, respectively. The total number of nonbreeders attending clubs on Foula was estimated at 3400 birds. A comparison of population parameters of different colonies in Shetland revealed correlations between numbers of breeders, nonbreeders and clubs, and between growth rates of colonies and the ratio of breeders to nonbreeders present. Recruitment of 13.0% of all nonbreeding birds frequenting Foula was recorded in each year of the study. The median age of first breeding was 7 years. First-time breeders generally chose territories in the vicinity of the club most frequented in previous years, chose partners of similar ages, and bred less successfully than established breeders. A model of recruitment with four possible strategies of mate- and site-selection is suggested.

Keywords: Great Skua, *Catharacta skua*, recruitment, clubs, nonbreeders, age-structure, mate-selection, site selection.

INTRODUCTION

Recruitment is a major determinant of changes in breeding populations from year to year, yet remains poorly understood (Porter & Coulson 1987). A knowledge of the behaviour and movements of potential recruits in a seabird colony is basic to a greater understanding of the recruitment process in seabirds (Ollason & Dunnet 1983). Although there are several important studies of recruited birds, including removal experiments that altered recruitment rates and age at first breeding in seabird colonies (e.g. Coulson et al. 1982), the difficulty in studying pre-recruits has resulted in few investigations being attempted.

Nonbreeders gather in "clubs" in the colonies of some seabird species. Nonbreeding Herring Gulls *Larus argentatus* and Gannets *Sula bassana* form such clubs, but the sites are usually transitory and not all nonbreeders present at the colonies join these gatherings (Tinbergen 1953, Nelson 1978). Great Skuas *Catharacta skua* are particularly suitable for studies of prerecruits and recruitment because, during the breeding season, nonbreeders gather in traditional clubs in and around the colonies (Klomp & Furness 1990).

Foula, Shetland, is by far the largest colony of Great Skuas in the northern hemisphere, with 2340 breeding pairs in 1990. Extensive research and a consistent chick-ringing effort on the island during the last 20 years has produced an opportunity to study recruitment of Great Skuas in a colony with known previous population changes, breeding success, and mortality. The previous fieldwork on Foula has made it possible to examine the ages of nonbreeding birds, the behaviour of individuals as nonbreeders and the ways in which they attempt to become established in territories

as breeders. Great Skuas are long-lived, highly site-faithful as breeding adults and their populations tend to be stable. Adults are able to exploit a wide variety of foods and their foraging success is rather little affected by variations in weather (Furness 1987). Increased recruitment following removal experiments have suggested that skua colony sizes (numbers of breeding pairs) are limited by territorial behaviour (Young 1972, Furness 1987). These features suggest that Great Skuas may be less responsive to short-term or local environmental variations than other species, such as the Arctic Tern *Sterna paradisaea*, that tend to respond to changes in food supply from season to season.

This paper describes the size and structure of the nonbreeding population of Great Skuas on Foula, the movements and activities of nonbreeders, and the role of clubs in recruitment. A model of recruitment is suggested, incorporating the results of this study, including such factors as natal philopatry, club choice, duration of prebreeding colony attendance, age at first breeding, mate selection and site selection.

METHODS

Foula (60°08'N, 2°05'W) is an island 5 km long and 4 km wide, 25 km west of Shetland mainland. It holds the largest British colony of Great Skuas, with 2340 pairs holding territories on the island in 1990. These birds nest on grassy ground over most of the inland areas of Foula.

Between 300 and 2900 Great Skua chicks were ringed with individually numbered monel rings on Foula every year since 1963. In addition, from 1968 to 1974, 400 to 1400 chicks were ringed each year with plastic colour-rings in combinations unique to the year. During the 1973 and 1974 breeding seasons (May to August), the proportions of birds in a club with different colour-ring combinations were monitored regularly. In 1988, 1989 and 1990, 494 birds were trapped on five different clubs using cannon-nets, and these birds were ringed using individual colour-ring combinations.

Regular, thorough searches of the clubs and breeding territories allowed individually marked birds to be monitored throughout the breeding seasons. The location and size of breeding territories established by known individuals and the success of their breeding attempts were recorded. In addition, all breeding attempts at clubs were recorded. The time spent by individual birds at bathing sites (i.e. bathing and preening) was recorded on several dates in the 1988 breeding season.

RESULTS

Clubs

Great Skua gathering sites can be divided into three groups: "club-sites", "bathing sites" and "temporary clubs". Figure 1 shows the location of 11 club-sites on Foula, although since 1988 only nine of these sites were used by the birds. Nonbreeding Great Skuas gathered on these club-sites during the breeding seasons. Four bathing sites (see Figure 1), located next to small, peaty pools on the island, were used by both breeding and nonbreeding birds. Each bathing site had a nonbreeding component (club) associated with it.

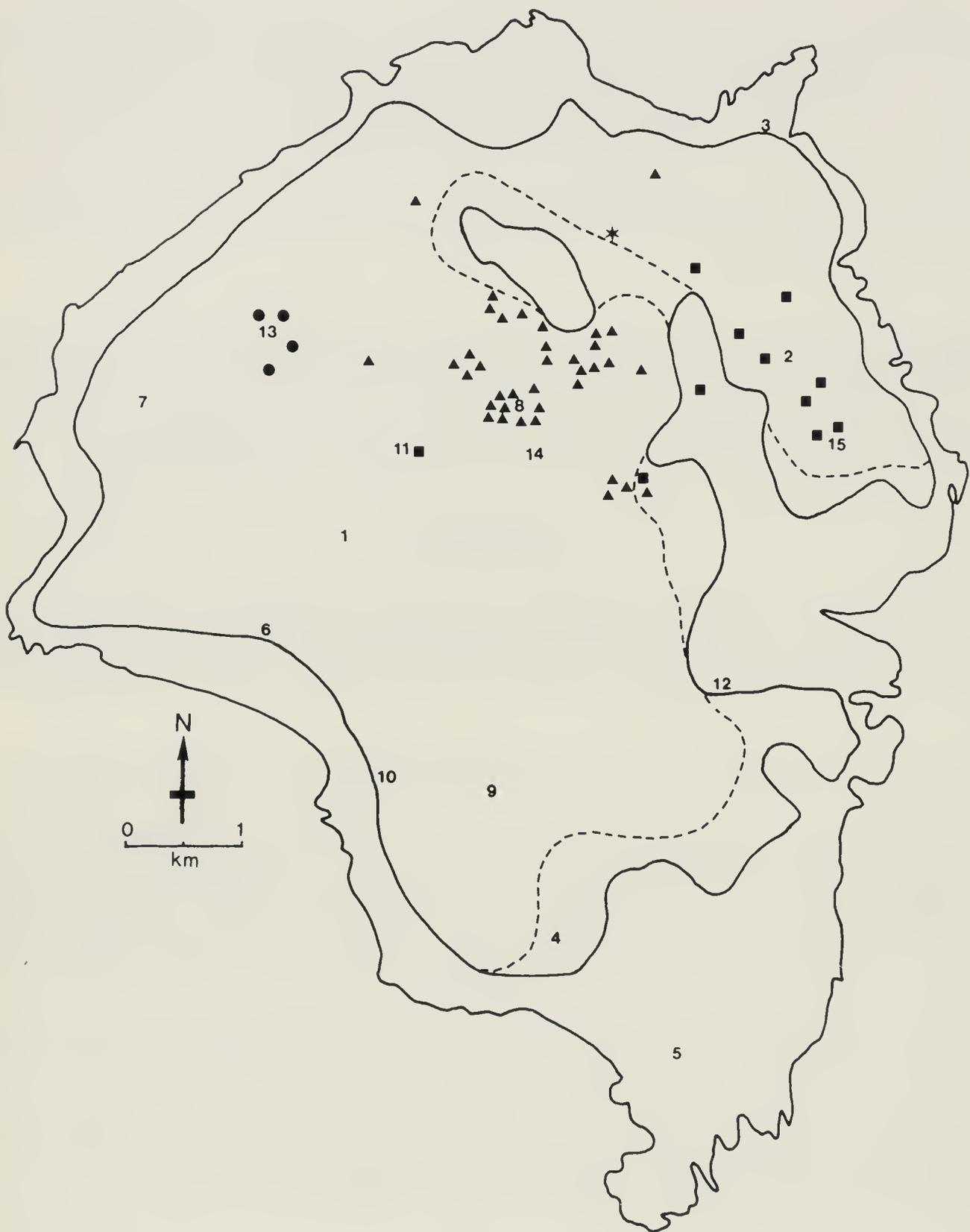


FIGURE 1 – Map of Foula, Shetland Islands, showing the location of club-sites (1-11) and bathing sites (12-15). The edge of the Great Skua breeding colony is indicated for 1988 (dotted line) and 1990 (solid line). The locations of nests of colour-ringed first-time breeders in 1989 and 1990 are shown with symbols, indicating the club mainly or solely attended in previous years: clubs 2 (squares), 3 (stars), 8 (triangles) and 13 (circles).

Bayes et al. (1964) found that all nonbreeding Great Skuas attending a colony settled at the clubs at night. This was confirmed by Klomp & Furness (1990). Although there are no obvious plumage differences between breeders and nonbreeders, colour-ringing and time-budget studies (Furness 1987, Furness & Hislop 1981, Hamer et al.

1991, this study) have confirmed that breeding Great Skuas rarely, if ever, attend clubs. Established breeders that did not breed in a particular year generally continued to defend their breeding territories.

Great Skuas only spent comparatively short periods at bathing sites, except for those birds associated with the club. The mean period of time spent at a bathing site, of 100 observations of individual birds, was 7.1 min (SD = 5.4 min, median = 6 min).

Klomp & Furness (1990) described the diurnal and seasonal variations in numbers of nonbreeding Great Skuas on Foula. Numbers of birds at clubs were maximum and stable at night. The proportion of this night-time total present during the afternoon appeared to be relatively constant within years, but may have been related to differences in prey availability and, hence, foraging effort among years. Total numbers of nonbreeders in a colony also varied seasonally, with the peak and subsequent decline apparently coinciding with changes in food availability, and numbers of nonbreeders correlating with the numbers of breeders at the colony over the 1970s and 1980s (Klomp & Furness 1990).

TABLE 1 – Population parameters of the eight largest Great Skua colonies in Shetland. The number of AOTs (apparently occupied territories, after Furness 1982) in 1974/5 and 1985/6, the number of clubs in 1985/6 and the number of nonbreeders present on the clubs in daytime in 1985/6 have all been determined using similar counting methods at similar times of year. Data after Furness (1986) and Ewins et al. (1987).

Colony	AOTs		Clubs	No. non-breeders	% change ¹ in AOTs per year	Ratio ²
	1974/5	1985/6				
Foula	2131	2495	13	858	+ 1.32	0.172
Hermaness (Unst)	786	819	6	145	+ 0.38	0.089
Noss	255	378	2	161	+ 3.64	0.213
Saxavord (Unst)	250	355	2	58	+ 3.24	0.082
Lamb Hoga (Fetlar)	129	139	1	40	+ 0.62	0.144
Bressay	160	115	1	35	- 2.96	0.152
Fitful Head (Mainland)	30	95	1	35	+ 10.08	0.184
Fair Isle	17	84	2	54	+ 14.24	0.321

¹ The percentage change in the number of AOTs per year was calculated using the following formula, despite some colonies increasing and then declining within this period:

$$\% \text{ change per year} = \left(\text{antilog} \frac{\log_e Y_1 - \log_e Y_0}{\text{no. of years}} - 1 \right) \times 100$$

² The ratio of the number of nonbreeders to breeders (twice the number of AOTs) is based on 1985/6 data.

Based on observations of known individuals, the mean time nonbreeding Great Skuas spent at Foula in 1989 and 1990 was estimated to be 19 and 25 days, respectively. There was no evidence of older or younger birds, nor earlier or later arriving birds showing any difference in their duration of stay at the colony. The total number of Great Skuas frequenting the clubs throughout the 1989 and 1990 breeding seasons was estimated from retrap data to be 3400 individuals.

Table 1 shows the numbers of nonbreeders and clubs associated with the eight largest Great Skua colonies in Shetland. There is a significant, positive correlation between the number of breeding birds and the number of nonbreeders ($r_s = 0.83$, $n = 8$, $P < 0.05$) and clubs ($r_s = 0.74$, $n = 8$, $P < 0.05$) in a colony. Also, the percentage growth of the colonies from 1974/5 to 1985/6 was positively correlated to the ratio of numbers of nonbreeders to breeders in the colony in 1985/6 ($r_s = 0.67$, $n = 8$, $P < 0.05$).

Age-structure of the nonbreeding population

Figure 2 shows the age-structure of Great Skuas ringed as chicks with individually numbered Monel rings and trapped at clubs during 1988-1990. The majority of birds present on the clubs were 3-7 years of age. The presence of birds older than nine years was rare.

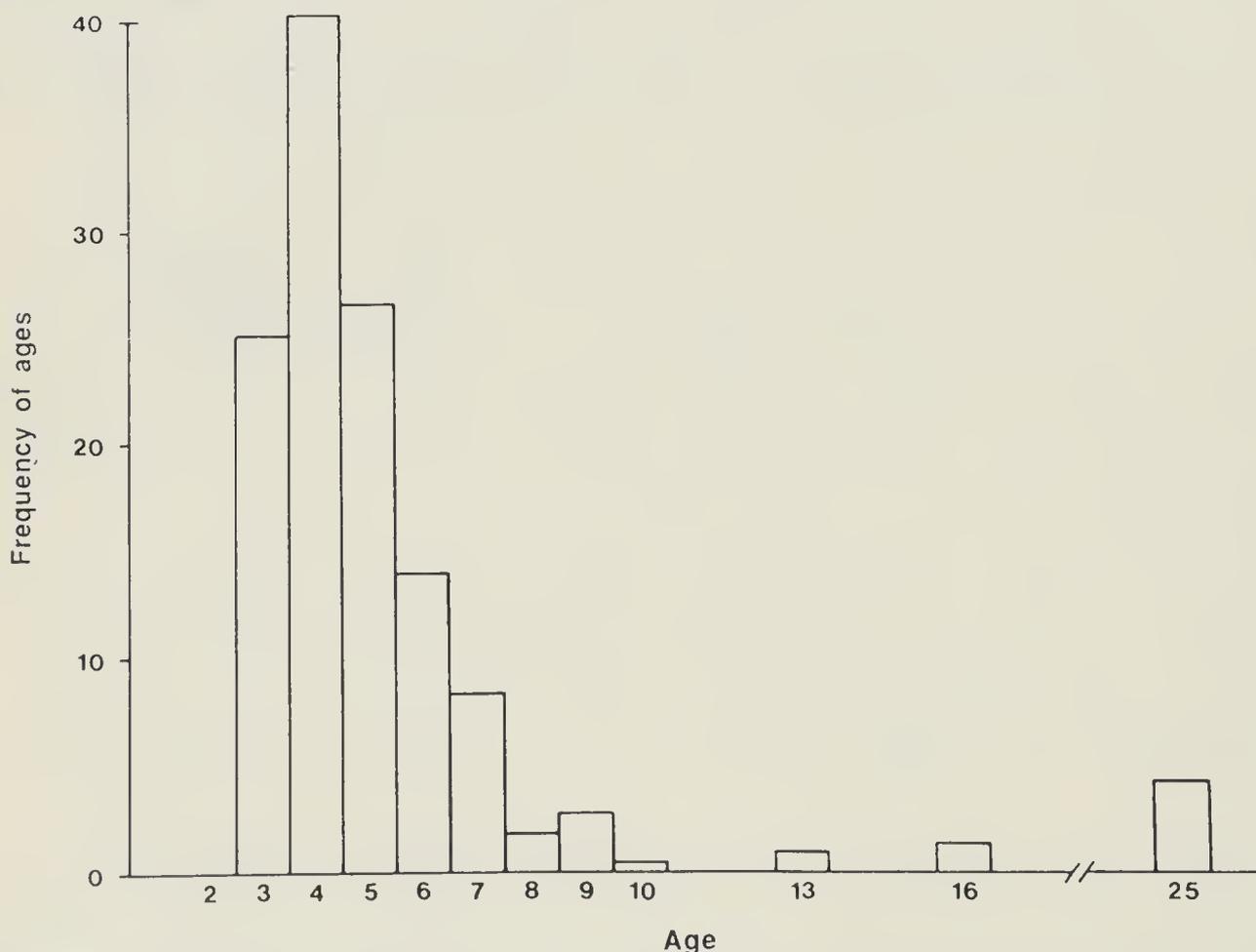


FIGURE 2 – Frequency histogram of known ages of Great Skuas caught at clubs during 1988-1990, corrected for the different ringing efforts in the different years the birds were ringed as chicks (as if 1000 chicks were ringed on Foula each year).

Although no seasonal variation in the age-structure of nonbreeders was observed in 1988-1990, possibly due to relatively small sample sizes, observations of larger samples of known-age birds in a club in 1973 and 1974 revealed a distinct seasonal pattern. Figure 3 shows the number of birds of different ages present at a Foula club at

different times of the season. It can be seen that younger birds (2-4 years old) were present at the club in greater numbers later in the season, and older birds tended to be at the club earlier in the year. This seasonal variation in age-structure of club-birds could arise if nonbreeders generally return to the colony earlier each year until they recruit into the breeding population. Indeed, it can be seen from Figure 4 that in 1989 and 1990, known individuals were first sighted on the clubs significantly earlier than in the previous year (Dependent $t = 9.8$, $n = 104$, $P < 0.001$).

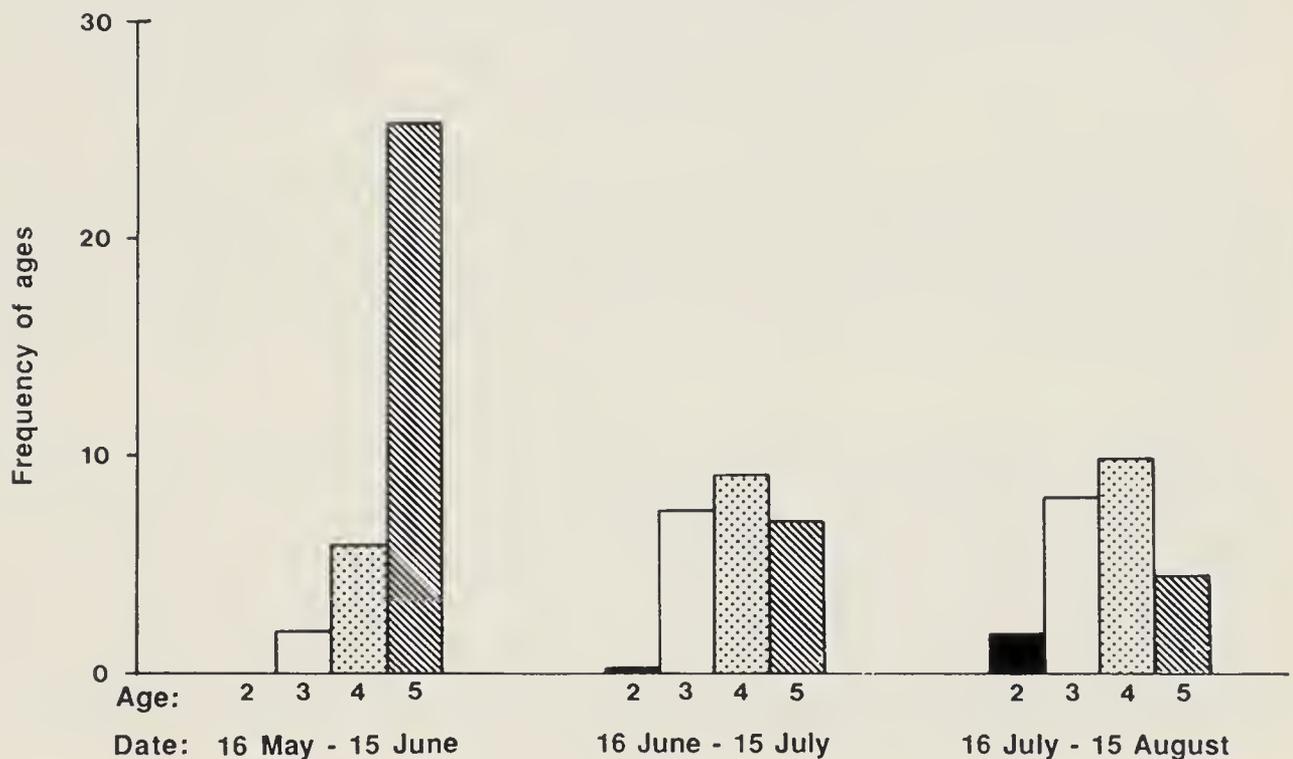


FIGURE 3 – The frequency of birds aged 2 to 5 years at a club on Foula in 1973/1974, corrected for ringing effort (as if 1000 chicks were ringed on Foula each year) and observational effort (as if 100 birds were observed in each time period).

There were only 13 sightings of 2-year-old birds at a club in 1973 and 1974, despite approximately 1600 chicks having been colour-ringed on Foula two years prior to the observations. No 2-year olds were recorded on clubs in 1988-1990. It is clear from Figures 2 and 3 that most birds first arrived at the colony at 3-5 years of age.

Philopatry

Although philopatry is difficult to measure directly, the levels of immigration and emigration can be determined indirectly. The average proportion of chicks that survived to fledge and carried rings was calculated to be 50% for years 1963-1984 (29,875 chicks ringed of 59,860 chicks that fledged). Due to a much lower chick-ringing effort in all other colonies, immigration would result in a reduction of this proportion among adults at Foula. However, in 1988, 60 of 120 nest-trapped breeders (50%) aged 4-25 years had been ringed as chicks on Foula. Hence, it can be assumed that the level of immigration into Foula is very low. Some individuals that fledged from Foula emigrated to breed in other colonies, although the numbers known to have done so are small. Further, once individuals visit Foula, they rarely visit another colony. Indeed, of 494 Great Skuas colour-ringed on Foula as nonbreeders, only one bird was seen at another colony, despite regular, thorough searches at the other major colonies in Shetland.

Of 121 individually colour-ringed nonbreeding Great Skuas present on Foula in 1988-1990 that hatched in known natal areas on the island in previous years, 101 frequented a club within their natal area, a greater proportion than expected by chance ($\chi^2_1 = 30.5$, $P < 0.0001$). Figure 1 shows the location of breeding sites of new recruits in 1989 and 1990. It can be seen that these birds generally bred within the vicinity of the club they frequented in previous years. This resulted in most birds breeding within their natal area. Of 64 breeding birds from known natal areas on Foula, 49 bred within their natal area, a greater proportion than expected by chance ($\chi^2_1 = 9.72$, $P < 0.001$).

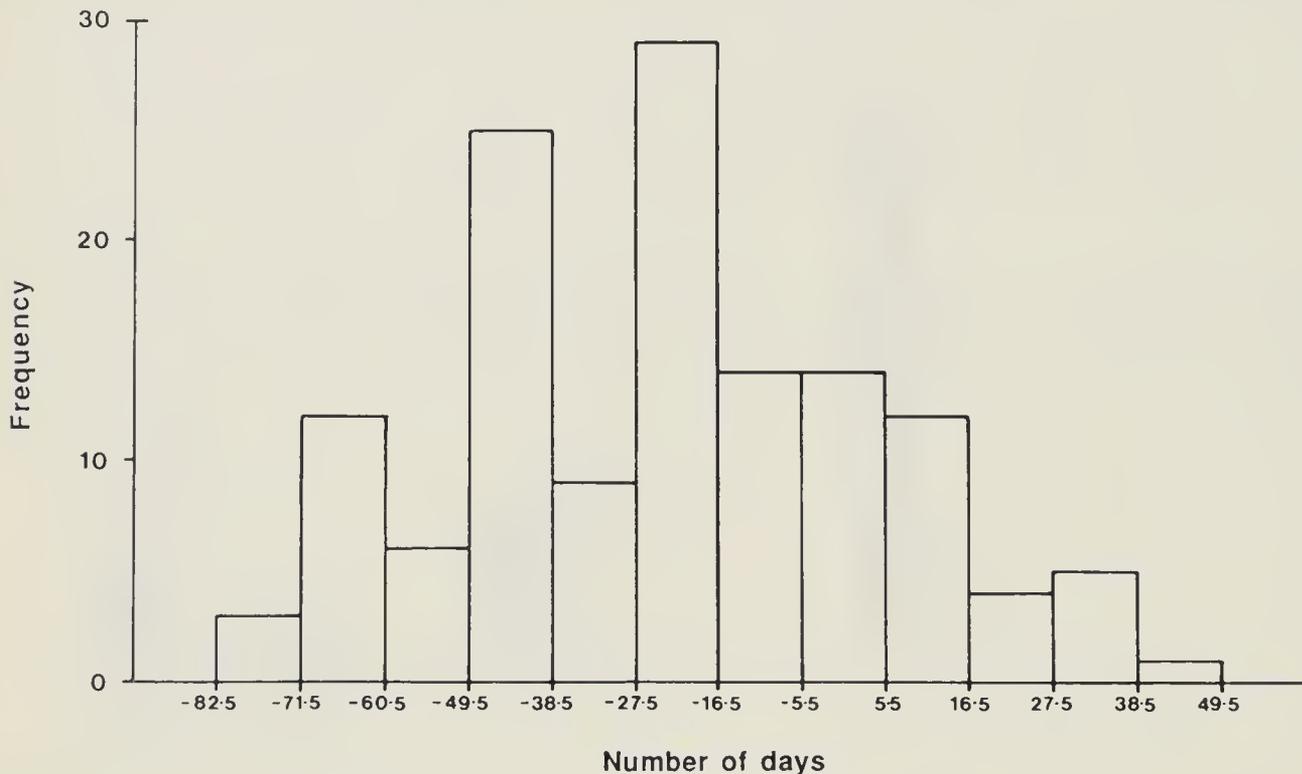


FIGURE 4 – Frequency histogram of the time differences between first sightings of individual birds in clubs in 1989/1990 and first sightings of the same individuals in clubs in the preceding year.

Recruitment

In 1989, 13 Great Skuas colour-ringed in 1988 recruited into the breeding colony on Foula. This represented 13% of the available number of colour-ringed birds at clubs (allowing for 10% mortality of birds from 1988 to 1989). In 1990, 12.6% of the available 1989 colour-ringed birds recruited, and 20.3% of the remaining available 1988-ringed birds. As the 1988-ringed birds were likely to be, on average, one year older than the 1989-ringed birds in 1990, this higher rate of recruitment (20.3%) does not represent the average rate of recruitment from the pool of nonbreeders in one year, although 13.0% and 12.6% are considered to be close to the actual rates of recruitment in 1989 and 1990, respectively. The results suggest that 350-430 birds recruited from the pool of 3400 nonbreeders that frequented the island in those years. This estimate is consistent with known population changes and the adult mortality rates on Foula (see Hamer et al. 1991).

The mean age of known new recruits was 7.9 years (SD = 3.0, $n = 18$), with a median and mode of 7 years, although a few cases of 4-year-old recruits have been recorded. This implies that most birds spend three or four years in the colony prior to breeding. Indeed, many birds have been recorded at clubs for the three consecutive years 1988-1990. Birds have only been observed holding breeding territories, with-

out breeding, for one season. In all cases ($n = 10$) they either bred the following year or did not return to the site.

Studies of seabird species where large numbers of breeding known-age birds are available show that members of pairs are usually of closely similar ages (Coulson 1966), although in some species the average age of recruitment appears to differ slightly between males and females (Mills 1973, Ollason & Dunnet 1983, Wooller & Coulson 1977). Since 1975, only eight breeding pairs of Great Skuas were known to comprise birds where both partners were of known age. Of six pairs all under nine years old, three pairs were of the same age and three pairs differed by only one year. The remaining two pairs were 14/17 and 21/24 years old.

In 1989 and 1990, 77.4% of pairs comprising at least one known new recruit failed to raise a chick to fledging in their first year of breeding together, whereas 67.9% of pairs failed in the colony overall. Pairs comprising at least one known new recruit had a significantly higher proportion of one-egg clutches than the rest of the breeding population ($\chi^2_1 = 38.7$, $n = 389$, $P < 0.001$).

Great Skua breeding sites can be divided into three groups: "colony", "periphery" and "club". Those birds first breeding at the "periphery" (see Figure 1) or breeding within 40 m of the centre of a club produced significantly less chicks that survived for at least 14 days than those birds first breeding within the "colony" ($\chi^2_1 = 8.39$, $n = 53$, $P < 0.05$). Known new recruits that bred on or near clubs had significantly smaller territories (nearest nest distance) than other first-time breeders (Student's $t = 2.13$, $df = 51$, $P < 0.05$). All breeding attempts within 40 m of the centre of the site of a club failed. Known birds that bred in consecutive years in these areas always moved further away from the club and usually occupied bigger territories in the following year.

DISCUSSION

In many seabird species, prebreeders are known to frequent a colony for one or more years before attempting to breed. Prebreeding Kittiwakes *Rissa tridactyla* and Guillemots *Uria aalge*, for example, mix with established breeders on ledges or gather on rocks below colonies (Cramp & Simmons 1977, Birkhead & Hudson 1977). This period in the colony, prior to breeding, affords experience of local conditions and foraging. It also enables a breeding partner and site to be chosen and, hence, enables recruitment into the colony. Since attendance at a club will allow a prebreeder to obtain information about local food supplies, breeding success of established pairs, availability of potential mates and levels of competition for territories one might expect prebreeders to visit several clubs or colonies to select where to breed. However, this study found a high level of philopatry.

The results of comparing population parameters among Great Skua colonies in Shetland suggest that larger colonies have more nonbreeders and clubs associated with them. This is likely to be due to prebreeders generally returning to their natal colonies. However, it also appears that faster growing colonies have proportionally more nonbreeders than slower growing colonies, which may indicate that colonies vary in attractiveness to prebreeders and that differential rates of emigration exist between colonies.

Most birds in clubs were aged 3-7 years (Figure 2). The reducing frequency of birds older than four years is partly explained by a yearly mortality of approximately 10% in these age-groups (see Furness 1987, Hamer et al. 1991), but can mostly be attributed to birds leaving the clubs and recruiting into the breeding population. The age-structure of birds in clubs suggests that most birds leave the clubs between five and nine years of age. This agrees with the known ages of first-time breeders. Of 129 known age birds in clubs, only five were older than 10 years. The mean age of known new recruits in this study was 7.9 years (SD = 3.0, n = 18). The youngest new recruits were four years old. This result is similar to the mean age of first-breeding on Foula in the mid-1970s of 7-8 years (Furness 1987).

If nonbreeding Great Skuas spend, on average, four years at the colony before breeding, a recruitment rate of 25% of the nonbreeding population per year would be expected if all nonbreeders recruited into the colony. This study recorded approximately half this rate in 1989 and 1990. Hence, the recorded recruitment rate may be atypical, or it is possible that some Great Skuas simply do not recruit. It is unlikely that emigration is responsible for this anomaly.

Where both partners of a pair were of known age, the ages of partners were found to be similar. Such age similarities may be a result of opportunity rather than intent. Recruiting birds are most likely to select a partner from the club that they attend. As nonbreeders return to their clubs earlier in successive years (see Figures 3 and 4), selection of a similar-aged partner is made more likely. Colour-ringed birds were often seen at clubs with the same individuals in successive years, and two such pairs recruited. Thus, at least some pair-formation occurs at clubs before a territory is established.

A model of recruitment in Great Skuas

Great Skuas generally return to their natal colony at three or four years of age. Of those prebreeders that are not faithful to their natal colony, rapidly expanding colonies may be more attractive than slower growing or declining colonies. The birds generally spend two-four breeding seasons in the colony, at clubs, without breeding. They are generally faithful to one club. During these years they develop skills necessary for breeding (eg. foraging and social skills). Each year individual birds arrive at the colony earlier than in the previous year and stay for an average of three weeks. After a few years the birds choose a territory and a mate and commence breeding, although some pairs may only defend a territory in their first year together and commence breeding in the following year.

Based on the results of this study, it would appear that a recruiting bird has four possible choices in selecting a mate and site.

1. A bird can attempt to breed for the first time on the edge of the site of a club, probably with another club bird, but only defend a small territory. This breeding attempt will fail. In the following years the bird will defend an enlarged territory, further away from the club.
2. A pair can establish a territory on the edge of the breeding colony, thus allowing a larger territory to be held. Such breeding attempts are also generally unsuccessful. It is possible that lower quality recruits - unable to establish a territory

elsewhere - breed in these locations, as seen in other seabird species (e.g. Kittiwakes; Coulson & Thomas 1985).

3. A pair of new recruits can defend a territory within the breeding colony, and attempt to breed, perhaps after a delay of one year. Most recruits adopt this strategy and many of these birds breed successfully in their first year.
4. A bird that breeds for the first time in the established breeding area may do so with an established breeder that has lost or abandoned its previous partner. This is likely to be the most successful mode of recruitment because a territory is already established. It is possible that many first-time breeders recruit into the colony in this way, particularly in a colony of limited physical size and stable population, due to mortality of established breeders. However, based on known pairs and the ages of partners, it appears that many recruits select partners from the club they frequented in previous years. It is unlikely that any first-time breeders that breed on the edges of sites of clubs or the periphery of the colony are paired with established breeders because of the site faithfulness of established breeders and the changing periphery of the colony (see Figure 1), and the movement of the territories of club-breeders away from clubs in successive years.

It is, perhaps, surprising that Great Skuas show such a high degree of natal philopatry and club-site fidelity. There is rather little evidence of birds sampling a range of colonies. Similar studies of a variety of seabirds may show that different species exhibit behaviours in different places on a continuum from the high site-fidelity of prebreeding Great Skuas to the regular intercolony movements of prebreeding Atlantic Puffins *Fratercula arctica* (Harris 1984) and the extreme "wandering" colony-visiting behaviour of prebreeding British storm-petrels *Hydrobates pelagicus* (Mainwood 1976).

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THE ROLE OF RECRUITMENT IN POPULATION REGULATION

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ABSTRACT. Recruitment was studied in three Sparrowhawk *Accipiter nisus* populations, one stable, another decreasing, and the third increasing. Annual recruitment of new breeders was highest in the increasing population and lowest in the decreasing one. Age of first breeding was lowest in the increasing population and highest in the decreasing one. Comparison with other raptors revealed two scenarios with respect to recruitment. (1) In stable nesting populations, close to the limit imposed by habitat resources, recruitment was more or less restricted to the replacement of previous breeders which died (or emigrated). Such populations typically contained many pre-breeders, at least some of which were capable of breeding whenever a vacancy arose. (2) In depleted populations, below the level that habitat resources would support, the size and rate of increase of the nesting population was restricted by the availability of potential recruits. Not all pre-breeders were capable of breeding in a given year if they could gain a territory, possibly because some lacked sufficient foraging skill.

Keywords: Sparrowhawk, *Accipiter nisus*, raptor, recruitment, population regulation.

INTRODUCTION

Recruitment is here defined as the addition of new breeders to a nesting population. It is one of two opposing processes, of gains and losses, the net effect of which determines change in breeding numbers, year-to-year and longer term. The study of recruitment also involves consideration of the ages at which birds first breed, and of the non-breeding component of a population.

This paper is based mainly on population studies of the European Sparrowhawk *Accipiter nisus*, conducted in three areas of Britain over periods of 10-19 years (Newton 1986, 1988, Newton & Marquiss 1986, Wyllie & Newton 1991). It also refers to findings from other raptors, and to a lesser extent to those from other birds.

The breeding densities of raptors are generally determined by the resources of their habitats - by the availability of food or nest-sites (Newton 1979). However, populations may often be reduced by human persecution or pesticide use below the level that the habitat would otherwise support, increasing again when the controlling factor is relaxed. Recruitment can thus be compared between populations limited by different means.

SPARROWHAWK STUDY POPULATIONS

Sparrowhawks breed in forest and woodland throughout the Palearctic region and eat other birds, especially song-birds. As in some other raptors, pairs tend to nest in the same places year after year over long periods. In each study area (Figure 1), attempts were made to find all the nests, record the breeding performance, ring the young, and catch for ringing and identification as many of the breeders at possible. Females were easier to catch than males, so certain analyses were possible only for females.

In one study area, centred on Eskdale, south Scotland (lat. $55^{\circ} 10'N$, long. $3^{\circ} 0'W$), the breeding population remained fairly stable during the 19 years of study (1972-90). Nest numbers fluctuated from year to year, but remained throughout within 15% of the mean level of 34, and showed no long-term trend (Figure 2).



FIGURE 1 – Map of Britain, showing locations of three study areas.

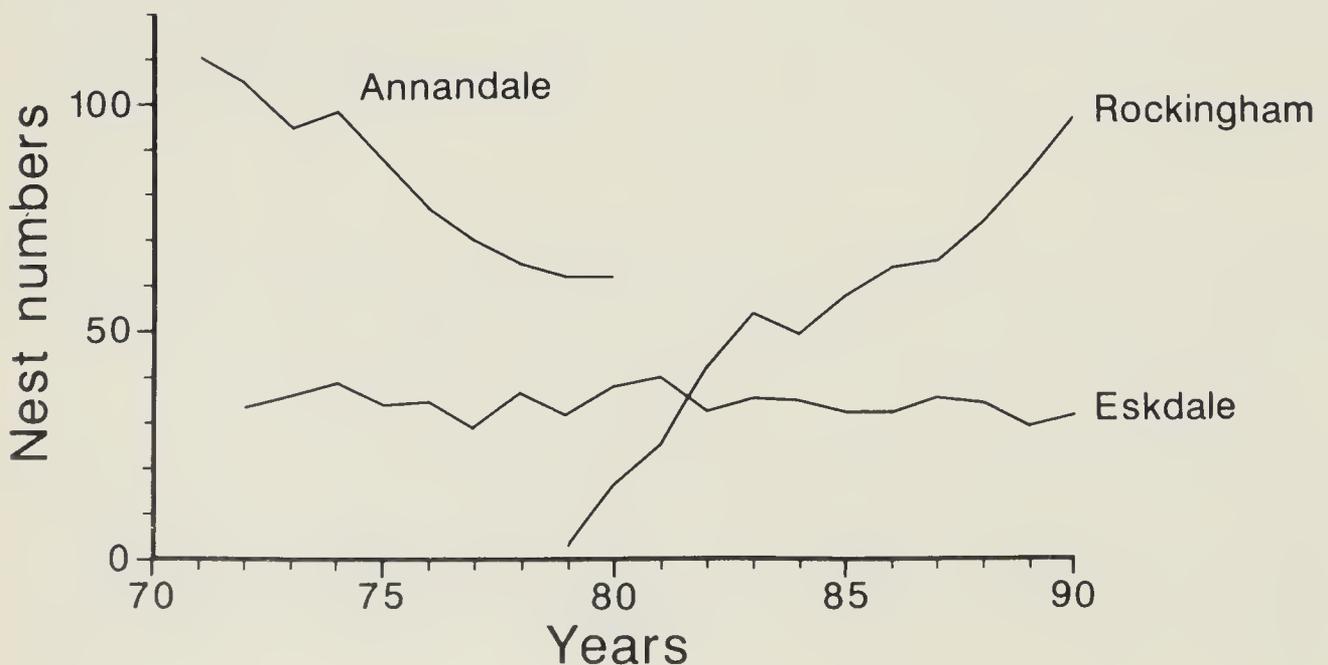


FIGURE 2 – Trends in the nesting population of Sparrowhawks in three areas: (a) Eskdale, 1972-90; (b) Annandale, 1971-80; (c) Rockingham, 1979-90.

In the second area, Annandale, also in south Scotland (lat. $55^{\circ} 15'N$, long. $3^{\circ} 25'W$), the breeding population decreased steadily during the ten years of study, from 110 nests in 1971 to 61 in 1980, a mean decline of about 8% per year (Figure 2). This decline was associated with the felling of woodland, and a consequent reduction in the area of suitable nesting and foraging habitat (Newton & Marquiss 1986).

In the third area, Rockingham Forest, in east-central England (lat. 52° 30'N, long. 0° 30'E), the breeding population increased during the twelve years of study, from three nests in 1979 to 96 in 1990, a mean rise of about 21% per year (Figure 2). Sparrowhawks had been eliminated from this area by about 1960, after years of organochlorine use. Then, following restrictions in the use of these pesticides, birds began to recolonise the area from 1979, increasing rapidly to occupy the vacant habitat (Wyllie & Newton 1991).

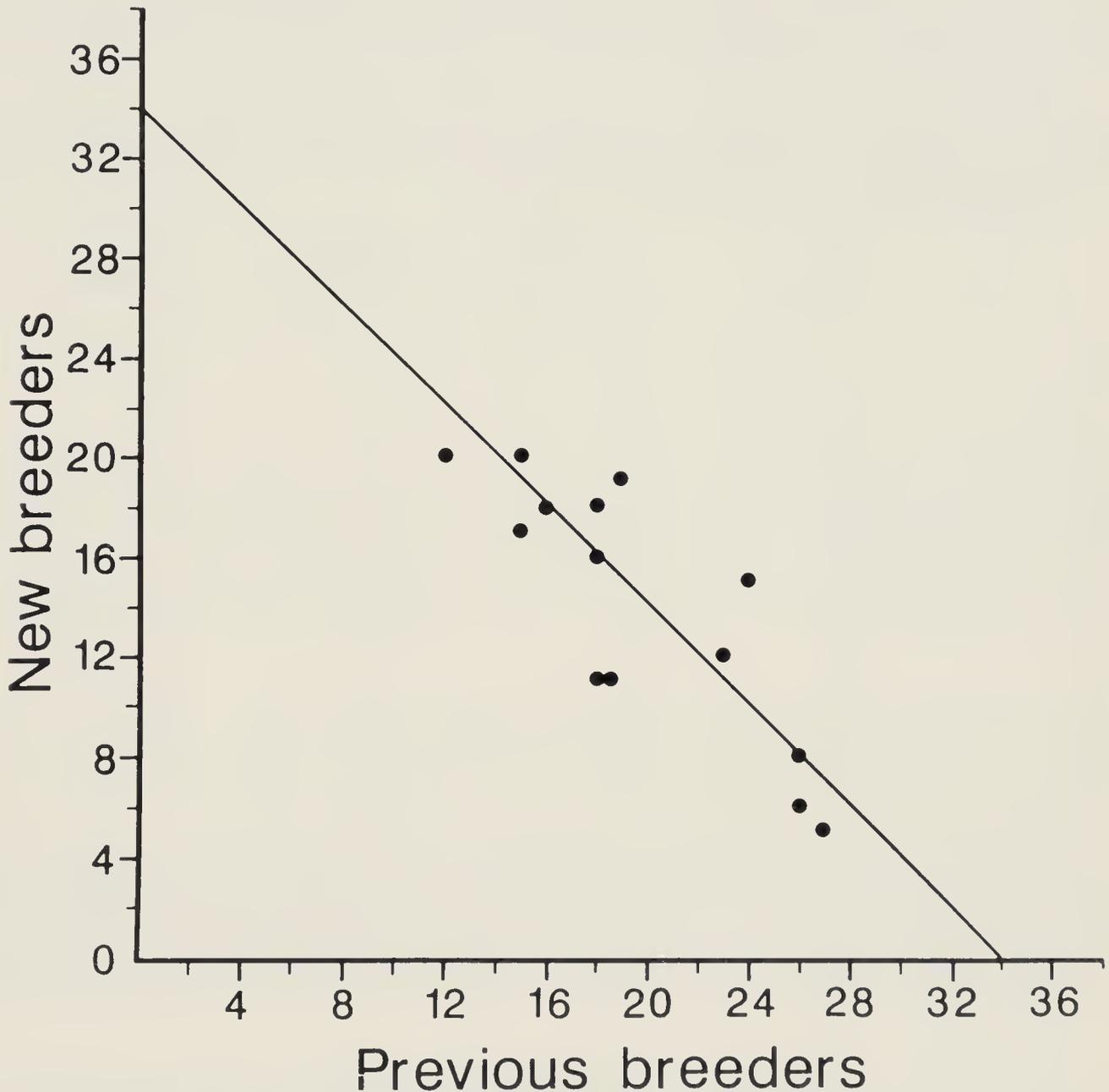


FIGURE 3 – Relationship between the numbers of previous breeders and new breeders (females only) in the Sparrowhawk population of Eskdale, 1975-89. Because the population remained fairly stable during this period, the numbers of new breeders recruited each year (y) were inversely related to the number of previous breeders remaining from the preceding year (x). [$y = 31.7 - 0.90x$, $r = 0.69$, $P < 0.003$.] Data from Table 1. Over the study period, the mean level of the nesting population was 34 pairs, indicated by the line on the graph (which is not a regression line). Points to the left of the line indicate years when recruitment of new breeders did not completely offset the deficiency in previous breeders and the population was below average, whereas points to the right of the line indicate years when recruitment exceeded deficiencies and the population was higher than average. In a completely stable population recruitment would have exactly matched the losses every year, and all the points would have laid on the line.

RECRUITMENT IN STABLE POPULATIONS AT CAPACITY LEVEL

The Eskdale Sparrowhawk population

The annual nesting population could be divided into established breeders, present in the population since the previous year (or longer), and new breeders nesting in the area for the first time (Table 1). The numbers of both groups fluctuated from year to year, but over the period as a whole were inversely correlated: low numbers of previous breeders were associated with high numbers of new breeders, and vice versa (Figure 3). This was expected considering the relative stability in the total breeding population over the study period.

TABLE 1 – Numbers of previous breeders and new breeders (females only) in the Sparrowhawk population of Eskdale, 1977-89.

	Total females	% annual survival	Previous breeders	New breeders
1975	33	79	–	–
1976	34	53	26	8
1977	29	62	18	11
1978	36	74	18	18
1979	32	60	27	5
1980	38	62	19	19
1981	39	66	24	15
1982	32	46	26	6
1983	35	52	15	20
1984	34	45	18	16
1985	32	38	15	17
1986	32	73	12	20
1987	35	46	23	12
1988	34	54	16	18
1989	29	–	18	11

Because not all females were caught each year, the number of new females was estimated indirectly, making use of annual survival estimates (Newton et al. 1991). Thus with 33 nests in 1975, and a female survivorship to the next year of 79%, there should have been about $(33 \times 79\% =)$ 26 previous breeders in the nesting population of 1976 (assuming that all previous breeders alive in 1976 nested that year). Then with 34 nests in total during 1976, the number of new female breeders that year could be estimated at $(34 - 26) = 8$.

Population stability was itself a consequence of a fairly stable territorial system, in which the landscape was apparently occupied close to maximum level each year (Newton 1986). The number of new breeders recruited in any one year was thus largely dependent on the number of vacancies created by the loss (death or emigration) of previous breeders. In other words, in such a stable system, the annual recruitment more or less matched the annual loss.

Of 120 first-time female breeders identified in Eskdale over the years, 48 were in their first year of life, 37 in their second and 35 in their third. By the fourth year all females had bred on at least one previous occasion. Because some individuals delayed first breeding for one or more years beyond the age of physiological maturity (at one year), there must have existed in the population a pre-breeding contingent, unseen and uncountable. Their numbers could be estimated indirectly, however, from knowledge

of the survival rate at different ages (Newton et al. 1981). Thus, the 35 females first breeding in their third year must have been derived from about 58 second-year pre-breeders, and these in turn would have been derived from about 97 first-year pre-breeders (Table 2). It could be further calculated that about 43% of all females associated with the population in the breeding season were pre-breeders. The percentage formed by all non-breeders would have been slightly greater, however, because occasional breeding females skipped a year (Newton 1985). Although these figures were for females, the figures for males were probably similar in this monogamous species.

TABLE 2 – Numbers of females which first bred at different ages, and estimates of the numbers of pre-breeders at different ages. B = breeders, PB = pre-breeders.

Fledglings (%)	Number of females of following ages (years)		
	1	2	3
75 (19)	<u>48</u> B		
126 (31)	62 PB	<u>37</u> B	
198 (50)	97 PB	58 PB	<u>35</u> B

Note: The figures underlined refer to the numbers of females first found breeding at different ages, and all other figures are estimates of the numbers present at earlier ages, but not breeding, based on survival rates of 49% from fledging to year 1, and 60% for each succeeding year (Newton et al. 1981). The above figures are for Eskdale only and thus differ from previous figures (Newton 1985), which refer to Eskdale and Annandale combined. They give a similar estimate of 43% pre-breeders in the total female population at the start of breeding.

The existence of non-breeders, capable of breeding if a suitable nesting territory became available, was confirmed by experiments in which seven males and seven females were removed from 14 territories near the start of breeding (Newton & Marquiss 1991). Within a month, at least three males and three females had been replaced by newcomers which proceeded with a nesting attempt. There was no indication that these replacement birds had moved from nearby territories, and without the removals they would almost certainly not have bred that year. Of five such birds that were trapped, three were in their first-year and one was in its second, while the fifth (a female) was older.

With so many pre-breeders estimated to be present in the area, it was perhaps surprising that so few removed breeders were replaced. However, not all pre-breeders may have been capable of breeding when a territory was made available, and not all experimental territories may have had pre-breeders in close proximity. Radio-tracking work showed that pre-breeders lived mainly away from the larger woods used for nesting, in more open country with smaller woods.

To conclude, the picture that emerged for Eskdale was of: (1) a fairly stable breeding population probably close to the maximum that the landscape could support; (2) an annual recruitment of new breeders which was inversely density-dependent, more or less matching the annual loss of previous breeders; and (3) a contingent of pre-breeders which were prevented from breeding in any given year, in at least some cases because all suitable nesting territories were taken. On this basis, entry to the breeding population was likely to be competitive, with the older individuals from

among the pre-breeders generally taking precedence, and leading to deferment of first breeding in some individuals beyond the age of physiological maturity.

Comparison with other stable raptor populations

Such a pattern is probably typical of many bird-of-prey populations, in some of which nesting pairs show great stability in numbers and distribution over many years. In a recent review, Newton (1990) listed eleven studies of seven species in which pair numbers stayed within 15% of the mean level over periods of 10-26 years. The greater the constancy in breeding numbers, the more exactly must annual recruitment have matched the annual losses.

Again stability in the breeding sector is helped by the continued presence of additional adults, capable of rapidly filling vacancies which arise at nesting territories. The chief evidence for the existence of such birds again comes from the rapid replacement of breeders removed from nesting territories, by newcomers which breed the same year. Incidental observations in the literature refer to replacements in at least 26 species, from small falcons to large vultures (Newton 1979), while controlled removal experiments, of the kind done on Sparrowhawks, have been reported for European Kestrels *Falco tinnunculus* (Village 1983) and American Kestrels *F. sparverius* (Bowman & Bird 1986). In both these species, replacements of both sexes occurred, sometimes within days, by newcomers that were known not to have moved from nearby nesting territories. As an alternative to removals, Village (1983) created additional breeding habitat by placing nest sites late in the season (after most pairs had laid) in areas previously lacking them. As these were promptly occupied by Kestrels which then bred, they provided further indication of the presence of surplus birds capable of breeding when given the chance.

It may be surmised, therefore, that the breeding populations of raptors are often held close to the level that the habitat will support by the continuing presence of potential recruits, able to fill rapidly any openings that arise, but otherwise prevented from breeding by the territorial behaviour of established pairs. In stable habitats, annual recruitment is thus limited to a large extent by the number of losses among established breeders. A similar situation has been described in some non-raptorial birds, for example Carrion Crow *Corvus corone* (Patterson 1980), Oystercatcher *Haematopus ostralegus* (Harris 1970) and Cassin's Auklet *Ptychorhamphus aleuticus* (Manuwal 1974).

Other raptor populations, although perhaps stable in the long-term, fluctuate from year to year, in step with a fluctuating food supply. Such populations typically depend on a small number of cyclic prey species, such as voles or grouse. In the years of increase, not only is recruitment higher, but it also involves a greater proportion of young birds than in years of decline. Thus five out of 13 nesting female Goshawks *Accipiter gentilis* were yearlings in a year of good food supplies, compared with none out of 34 in three years of poorer food supplies (McGowan 1975). Comparable figures for European Kestrel females were 55% of 38 in a good vole year and 18% of 22 in a poor one, and for males 35% of 37 and 4% of 25 respectively (Village 1980). Even in the good springs, however, there were still non-breeding Kestrels of both sexes present, some of which subsequently nested as a result of removal experiments (Village 1983). In such species, annual recruitment exceeds the annual loss in good food years, and falls short in poor ones (although over a period of years, the two may match as long-term averages).

Other, non-raptorial birds in which young individuals are more likely to breed in good food years than poor ones include Lesser Snow Geese *Anser caerulescens* nesting in the arctic (Cooke & Rothwell 1988).

RECRUITMENT IN DEPLETED POPULATIONS, BELOW CAPACITY LEVEL

Other Sparrowhawk populations

The three Sparrowhawk populations, which showed different trends, also showed different levels of recruitment. Over the study period as a whole, the mean level of recruitment was highest in the increasing Rockingham population, intermediate in the stable Eskdale population, and lowest in the decreasing Annandale population (Table 3). Indeed, these differences in mean recruitment between areas largely accounted for the differences in population trend. There were also differences in the annual loss of breeders between populations, but these had only a minor effect on trend (Wyllie & Newton 1991).

TABLE 3 – Recruitment in different Sparrowhawk populations.

Area	Population trend (% change per year)	Mean number of new breeders per established breeder*
Rockingham, 1981-88	Increasing (+21)	0.646 ± 0.087
Eskdale, 1975-82	Stable (0)	0.566 ± 0.172
Annandale, 1972-79	Decreasing (-8)	0.374 ± 0.051

* Calculated as in Table 1 from survival estimates. The difference between Annandale and Rockingham was significant ($t_{14} = 2.70$, $P < 0.05$).

TABLE 4 – Proportions of first-year birds among breeders in different Sparrowhawk populations.

	First-time breeders ^{1,2}				All breeders ³			
	Total males	% year- lings	Total females	% year- lings	Total males	% year- lings	Total female	% year- lings
Rockingham, increasing 1980-89	80	60	190	50	237	35	492	25
Eskdale, stable, 1972-89	–	–	120	40	107	21	438	18
Annandale, decreasing, 1971-80	–	–	83	28	221	18	584	16

¹ A bird was classed as a first-time breeder only if it was identified by capture, and (a) it was known to be new to a particular territory, (b) it (or its mate) laid one or more eggs, and (c) it was not known to have bred elsewhere.

² The variation in age composition between areas was statistically highly significant both among first-time breeders (females, $\chi^2_2 = 12.8$, $P < 0.01$), and among all breeders (males, $\chi^2_2 = 18.1$, $P < 0.001$; females, $\chi^2_2 = 17.5$, $P < 0.001$). As may be seen, the difference was mainly between Rockingham in the Scottish areas, rather than between the two Scottish areas.

³ The totals include all identifications from all years, based on captures, sight records or moulted feathers, so the same individuals may figure more than once in successive years.

Linked with the differences in recruitment levels, the proportion of first-year birds, both among new breeders and among the whole nesting population, was highest in Rockingham, intermediate in Eskdale, and lowest in Annandale (Table 4). In the first two areas, all individuals bred for the first time in their first, second or third year, but in Annandale some birds did not breed until their fourth year. In this last area, with shrinking nesting habitat (through tree felling), competition for available nesting territories in the remaining woodland was probably exceptionally strong.

The Rockingham Sparrowhawks which did not breed until their second or third year could not have been prevented from breeding at an earlier age by lack of a nesting territory, because in this area surplus (= unoccupied) habitat was available throughout. These birds must therefore have experienced some other constraint on breeding. One possible constraint was poor nutrition (or poor body-condition), imposed by inadequately developed foraging skill or low social status. Such a nutritional constraint could have been especially important for males which, in addition to feeding themselves, had to hold a territory and feed a female (Newton 1986).

Whatever the cause, it seems that not all the pre-breeders in the Rockingham area were potential recruits in a given year, and that if more such birds had been available, the breeding population may have increased faster than the observed 21% per year. Birds not available for recruitment in one year may have become so in a later year if their nutritional or social status improved. This type of constraint may have held in the other areas too, but with another limiting factor there (shortage of good vacant nesting habitat), it was not obvious.

Comparison with other depleted raptor populations

The rate of increase in other raptor populations may also be limited by the availability of recruits. This is evident in those populations which, like the Rockingham Sparrowhawks, were reduced by organochlorine pesticides and then recovered following reductions in organochlorine use. One major chemical widely involved was DDE (derived from DDT) which reduced the breeding rate (Newton 1979).

Among Ospreys *Pandion haliaetus* nesting on the American coast between New York and Boston, year-to-year changes in breeding numbers were related to the previous reproductive rate, which influenced the number of recruits subsequently available (Spitzer et al. 1985). A threshold production of at least 0.8 fledglings per pair appeared to be necessary to prevent population decline, and productions greater than this were followed by increases in breeding numbers. Again, however, not all Ospreys nested at the earliest age recorded: of 20 known first-time breeders, ten were in their third year, six in their fourth and four in their fifth. Similar figures on threshold productivity and ages at first breeding were also obtained from another increasing Osprey population in Michigan (Postupalsky 1989). Yet in a stable population around Chesapeake Bay, most birds did not breed until five-seven years old (Poole 1989).

In all three areas, Ospreys usually retained the same mate in successive years, but there were differences in the age composition of mated pairs. As the New York-Boston population expanded, young birds tended to pair together, so that for some years most breeders had partners of similar age to themselves. In the Chesapeake Bay area, by contrast, entry to the breeding sector was dependent on the death of a previous breeder, so that many first-time breeders had partners much older than themselves (Poole 1989).

Similar studies have been made of Peregrine populations that were reduced by organochlorine use. In this species, a threshold production of around 0.5-0.6 fledglings per pair was necessary before any recovery in breeding numbers occurred (Ratcliffe 1980, Newton et al. 1989). Prior to population decline, Peregrines in first-year plumage were seldom seen at nesting cliffs, but in depleted and increasing populations such birds became more numerous (Mearns & Newton 1982; various papers in Cade et al. 1988). In the French Jura, yearlings formed up to 19% of territorial females seen during the main years of increase, falling to less than 6% in later years, as numbers reached a plateau (Monneret 1988).

In these studies of Osprey and Peregrine populations, the correlations between increased reproduction and increased breeding numbers have been widely assumed to result from cause-and-effect. It remains possible, however, that some other parameter, such as adult survival, changed at the same time, and helped to promote the increase in breeding numbers. Nonetheless such studies do indicate the limitation in the rate of population increase which is imposed by the availability of recruits, and the earlier age of recruitment in populations below capacity level.

Other raptor populations, subject to intense human persecution, also appear to be limited by shortage of recruits. Through killing, the mortality of established breeders is raised well above the natural level, so that recruitment much greater than normal is needed to offset the losses. In such circumstances, younger birds than usual can obtain nesting territories, but they may still not suffice to fill all vacancies and prevent a decline. In a region of Scotland, where Golden Eagles *Aquila chrysaetos* were often shot or trapped, some territories were vacant in certain years, others were occupied by single unmated adults, while yet others were occupied by pairs in which one partner was in sub-adult plumage. But in another region, where eagles were not molested, all territories were occupied every year by pairs in adult plumage (Sandeman 1957). Likewise, in southern Spain ten pairs of Imperial Eagles *A. heliaca* in adult plumage bred each year from 1954 to 1959; but when human persecution had reduced the population to 2-4 pairs at the end of the 19th Century several birds in immature plumage mated with adults and produced eggs (Valverde 1960). These and other observations (Newton 1979) confirm that some raptors have held nesting territories, mated and sometimes bred successfully before they would normally do so, when vacant nesting territories were freely available.

A reduced age of recruitment has also been noted in depleted or increasing populations of some non-raptorial birds, for example Herring Gull *Larus argentatus* (Coulson et al. 1982) and Kittiwake *Rissa tridactyla* (Porter & Coulson 1987).

CONCLUSIONS

Studies on raptors reveal two distinct situations, with respect to recruitment. The first is found in populations in which the number of territorial breeding pairs is at capacity level, close to the presumed limit that the local habitat will support. Here recruitment is largely determined by the vacancies that arise on existing territories through the loss (death or emigration) of established breeders. Recruitment is therefore limited, and leads to the presence of a non-breeding contingent, containing at least some individuals of both sexes that are capable of breeding as soon as an opportunity arises. Such birds are usually recruited as singletons, to pair with a widowed bird on

territory. Entry to the breeding sector is thus competitive, generally favouring the older individuals from among the non-breeders.

In populations which experience cyclic fluctuations in food-supplies, the pattern is similar, but in good food-years the breeding population is usually higher, recruitment is greater, and more young birds breed, than in poor food-years.

The second situation is found in populations which have been reduced by human action below the level that the habitat could otherwise support. Here the numbers of breeding pairs, and their rate of increase, are limited by the availability of potential recruits. Many birds are recruited at an earlier age than in capacity populations, but not all at the earliest age recorded, so a non-breeding component still exists. The development of a certain level of foraging skill, or body condition, may be necessary before a bird can defend a nesting territory and breed. And not all birds may develop this level of skill or condition at the same age. It may be added, incidentally, that the acquisition of the definitive adult dress is demonstrably not necessary for a raptor to breed, provided that other conditions are favourable.

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SYMPOSIUM 30

AVIAN BROOD REDUCTION

Conveners D. W. MOCK and T. SLAGSVOLD

SYMPOSIUM 30

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INTRODUCTORY REMARKS: AVIAN BROOD REDUCTION

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Natural selection has apparently favoured the tendency for parent birds of many species to produce one or more offspring than can normally be supported throughout the expensive — and sometimes protracted — period of chick dependency. Such over-production exacts costs, of course, in terms of the extra egg's physical materials plus whatever additional energy must be spent to incubate it along with the others, but the investment can pay off in at least two important ways. (1) *Good Years* — For most species there is the nontrivial chance that ecological conditions may be exceptionally favorable, in which case the parents may be able to raise the full-sized brood at bargain levels of parental effort. (2) *Insurance* — Even in situations where the full brood cannot be raised, there is no guarantee that the zygotes produced first will be free of congenital defects and/or will escape all possible mishaps. If such young are weak, fail to hatch, or die soon after hatching (e.g. are snatched by a grab-and-run predator), the existence of back-up offspring can deliver parents from suffering the loss of a major reproductive opportunity.

In most years, however, over-production of young automatically sets in motion a strong competitive dynamic that must play itself out after the brood has hatched. This squeeze is typically relieved only by the demise of at least one nestling. This overall pattern of pruning brood size back to the parental "carrying capacity" is known as brood reduction (Ricklefs 1965). It has received a considerable amount of field study in many avian taxa and it impinges on a host of important topics, including clutch size, parental care, parent-offspring conflict, hatching asynchrony, cost-of-reproduction, sexual conflict, and the evolution of selfishness.

The pruning process was first pointed out by Schülz (1943) and developed substantially by Lack (1947, 1954) as a crucial component of his explanation for the evolution of hatching asynchrony. According to Lack's hypothesis, the competition for limited parental food in average or poor years is resolved by the size and motoric disparities among nestmates (set up by the asynchronous hatch), such that the youngest chick is normally the first to starve. Because asynchronous hatching appears to be controlled largely by the parents (viz., their decision to incubate prior to the completion of laying), this pattern and its consequences were interpreted as adaptive to them.

In practice, most field biologists rely on two criteria for detecting what we might call classic brood reduction: (1) an inadequate food supply is inferred from evidence of starvation [the unequal growth rates of nestlings, such that the victim typically becomes emaciated]; and (2) the youngest chick usually dies first. Documentation of this pattern is straightforward, requiring only brief periodic visits to a sample of nests. Individual chicks are marked according to their hatching order and, on subsequent

visits, the apparent starvation condition of any single mortalities is established. Because starvation is often a drawn-out process, a convincing series of snapshots can emerge from repeated visits. By contrast, if the whole brood/nest vanishes between two visits, one assumes parental desertion and/or the work of predators. Through the combined results of many such field studies, the basic pattern of brood reduction has now been found in roughly 200 bird species, the taxonomic and ecological diversity of which suggests that only the tip of the proverbial iceberg is visible at this point.

While there is some inconsistency among workers about whether single deaths of brood members other than the youngest should also count as brood reduction (on the one hand, senior sibs are less likely to have been outcompeted; on the other, any death can alleviate a food crunch), this is really a minor problem at the moment. For now, we advocate using the term brood reduction in its broadest and most literal sense, to reflect simply the sequential loss of nestlings, by whatever means and for whatever goal.

There are, after all, several parties whose fitness interests are affected by mortality of other family members (O'Connor 1978). If food is scant, a surviving sibling may gain from sharing with fewer mouths. It may even be willing and able to contribute actively, perhaps aggressively, to the victim's demise. Similarly, while a parent is expected (on theoretical grounds: O'Connor 1978) to be somewhat less enthusiastic about early brood reduction, there are many circumstances under which it, too, probably favours that measure. By virtue of being the only full-grown players in the game, parents have obvious physical advantages over the offspring (Trivers 1974) and may perpetrate more direct executions of their own progeny (e.g. Horsfall 1984) than has been suspected heretofore. Obviously it is an exceedingly complicated task to determine exactly which party is responsible for what deaths in a reasonable sample of nests. For this reason, most of the details currently available come from colonially-nesting species.

Finally, it is at least a hypothetical possibility that an individual nestling with dim personal prospects for survival and successful reproduction might enhance its own inclusive fitness via suicide (Alexander 1974, O'Connor 1978), though no such cases have been documented. Considering the myriad possible permutations of how limiting resources should be shared (see Parker et al. 1989), the variety seen in avian brood reduction is hardly surprising. This symposium brings together a sampling of topics pertinent to brood reduction, while making no claim to full coverage of the subject.

Parents get to make the first move in the game, of course, and eggs do hatch with varying degrees of asynchrony in most brood-reducing taxa. Lack's original hypothesis, that hatching asynchrony and brood reduction are causally related, has been enormously influential. Nonetheless, several recent authors (e.g. Hussell 1972, 1985, Clark & Wilson 1981) have attempted to disengage them, essentially to relax implicit assumptions about which is cause and which is effect. The role of asynchronous hatching has dominated most discussions of brood reduction, yet — as these symposium papers show — the issues are many and complex. For the moment, suffice it to say that hatching asynchrony can evolve for reasons other than the facilitation of brood reduction, but wherever it occurs, asynchrony has unmistakable effects on early sibling competitions.

In our symposium's first paper, Trond Amundsen and Tore Slagsvold seek to clarify the interactions between asynchrony and brood reduction by the simple expedient of pointing out that brood reduction per se need not always be adaptive. Viewed this way, one can see that asynchrony's tendency to promote such mortality may be a cost that parents, for various reasons, cannot escape. For example, if hatching asynchrony is highly advantageous in processes unrelated to sibling rivalry, it may be a cost worth paying. Alternatively, the asynchrony may simply be a by-product of other unavoidable factors and the whole asynchrony-reduction package could be a net minus to parental fitness. On the other hand, while some data show that asynchrony may produce fewer offspring there is reason to believe that average body size is greater for those that fledge. Depending on the subsequent interaction between size and recruitment into the breeding population, production of a few large young could pay greater fitness dividends to the parents.

Next, Scott Forbes steps back and looks at the broad question of when and under what circumstances selfish elder nestmates should favour the loss of a designated 'victim' sib. From dynamic programming models, he shows that the senior sib's optimal decision on whether to campaign actively for brood reduction (specifically, whether to become fatally aggressive) may hinge largely on the variability in resource availability. Thus, if parental food deliveries are highly unpredictable relative to a senior's average future needs, a policy of early siblicide (a "pre-emptive strike") may be favoured. Somewhat counter-intuitively, this can result even when the average amount of food is sufficient for avoiding brood reduction altogether: the bully may do best by taking no chances.

In the third paper, Steve Beissinger and Scott Stoleson present new data on Green-rumped Parrotlets of Venezuela, which show the peculiar combination of large clutches and extremely asynchronous hatching. This may prove to be an especially illuminating system and one amenable to various kinds of experimental manipulations. Here, preliminary results are given comparing artificially synchronized hatching with normally asynchronous hatching, across a range of manipulated brood sizes. Dramatic effects occurred in the largest broods, where asynchrony apparently contributed to substantial brood reduction. Because other parrots show the ability for fine-grained parental control over how food is allocated among unmatched nestlings, albeit in captivity, these field data are suggestive of a parental inability (or unwillingness) to exert such control under more natural conditions.

Fourth, Roger Evans and Sandra Lee consider how parents ought to regard the fitness value of the last-laid egg in a brood-reducing species, given that such individuals are often doomed. It is widely accepted that the last egg's temporal (developmental) disadvantage stems from the headstart its siblings are given (early incubation) before the last egg is even laid. The author's recent work with pelicans and gulls has shown that the terminal egg suffers at the hatching end of incubation as well, as parents change their behaviour to accommodate the diverging needs of the already-hatched senior siblings. Specifically, such parents incubate less consistently, a "neglect" that can lead to cooling and further hatching delay for the last egg. Unhatched chicks in that situation may vocalize loudly, apparently to recall parents to the task of incubation, and/or may be thermally resistant to hatch retardation from cooling.

Finally, a particularly dramatic component of the brood reduction process of many predatory bird species is the use of overt physical aggression by stronger chicks. When such behaviour is used ('siblicide'), it can quickly eliminate the victim. Alternatively fighting can provide an effective but sublethal means of resource control for the senior sibs. However, such active forms of oppression are by no means universal, in fact they are eschewed by the majority of brood-reducing species. Tim Lamey and Douglas Mock review the conditions under which such aggression is apparently *not* used, even in species that have suitable weaponry for its effective deployment.

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HATCHING ASYNCHRONY: FACILITATING ADAPTIVE OR MALADAPTIVE BROOD REDUCTION?

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ABSTRACT. According to Lack's brood reduction hypothesis, asynchronous hatching in birds is a means to facilitate adaptive brood reduction. However, it is not evident that asynchrony-mediated elimination of the smallest nestmates always maximizes fledgling production. A review of 30 experimental studies revealed that asynchrony is most often maladaptive in terms of fledgling success, although in some species asynchrony proved beneficial when conditions were poor. On the other hand, in most species, the fledglings from asynchronous broods were on average heavier than those from synchronous ones. For such species, the advantage gained by hatching asynchrony would depend upon the relationship between fledgling body mass and the subsequent juvenile survival rate. For those species for which asynchrony seems to confer no benefit in terms of fledgling quantity or quality, alternative hypotheses must be considered.

Keywords: Asynchronous hatching, brood reduction, parental investment.

INTRODUCTION

Most altricial birds species do not hatch their entire brood simultaneously, but over a period of one or more days (O'Connor 1978, Clark & Wilson 1981, Mock 1984). Almost half a century ago, David Lack (1947, 1954) suggested that such hatching asynchrony was an adaptation necessary for the partial reduction of brood size under unpredictably poor conditions. It has been convincingly demonstrated, for several species, that growth rates of the last-hatched nestlings were lower (e.g. O'Connor 1978, Zach 1982, Furness 1983) and the mortality rates higher (e.g. Nisbet 1973, Parsons 1975, O'Connor 1979, Shaw 1985, Lessells & Avery 1989, Stouffer & Power 1990) than those of their older nestmates. This has resulted in a general acceptance of Lack's brood reduction hypothesis, although the hypothesis was not critically tested in any experiment until 1976 (Howe 1976). During the last 10-15 years, the results of a number of experimental studies have demonstrated that even synchronous broods may suffer partial reduction when conditions are poor. This has caused a modification of Lack's original statement, that asynchrony is necessary for effective brood reduction, to stating that asynchrony facilitates brood reduction (Mock 1984, Mock & Parker 1986, Skagen 1988, Drummond & Garcia 1989). Other authors have however argued that the present evidence cannot be considered as supporting the brood reduction hypothesis (e.g. Clark & Wilson 1981, Amundsen & Stokland 1988), and several alternative explanations for asynchronous hatching have been proposed (e.g. Clark & Wilson 1981, Hahn 1981, Mead & Morton 1985, Arnold et al. 1987, Mock & Ploger 1987, Slagsvold & Lifjeld 1989, Slagsvold 1990, Magrath 1990).

Apart from demonstrating that asynchronous broods are not necessarily more productive than synchronous ones (see Amundsen & Stokland 1988), some recent studies have indicated that late-hatching nestlings of asynchronous broods may suffer from

their disadvantage in size even when conditions are favourable (Bryant 1978, Slagsvold 1982, 1986, Skagen 1988, see also Clark & Wilson 1981, Price 1985). Hence, even though asynchrony may facilitate brood reduction, it is not evident that such a reduction is always adaptive.

The aim of the present study was to investigate the consequences of synchronous and asynchronous hatching patterns with respect to the quantity and quality of fledged young, in different bird species.

ASYNCHRONY MANIPULATIONS: A REVIEW

In order to reveal the main trends emerging from recent research on hatching asynchrony, we have compiled data for all the experimental studies known to us. These include 30 studies of 25 different bird species (10 non-passerines, 15 passerines). Twenty-two of the studies have been published in international journals (17 during 1985-1991), three are unpublished theses, one is in the form of an unpublished MS, and four are unpublished studies made by ourselves.

All studies involved manipulation of the hatching pattern. The 'synchronous' group of most studies comprises broods hatched within the course of a single day (Table 1). The 'asynchronous' broods were either unmanipulated broods with a natural hatching spread, or manipulated broods with a hatching spread of around or in some cases slightly above the natural mean. Twenty were single-year experiments, the rest included two breeding seasons. In eleven of the studies manipulated synchronous broods were compared with nonmanipulated, asynchronous broods, while in 13 studies both groups were manipulated. In six studies, some, but not all, of the asynchronous broods had been created by manipulation (Table 1). Most studies were based on daily nest visits during the hatching period, and report hatching spread as the number of days elapsing between hatching of the first and of the last eggs. Hatching spread data not reported according to this scheme have been standardized for comparison (Table 1). This method tends to underestimate hatching spread slightly when two or more eggs hatch on the same day, as is most often the case for 'synchronous' broods.

In some of the studies, natural asynchronous broods were compared both with 'synchronous' and with extended asynchronous broods. In the present paper, we focus attention on the productivity of broods with the natural degree of asynchrony compared to synchronously hatched broods; hence data for 'extended asynchronous' treatments have not been included in our review tables.

TABLE 1 - Nestling survival (percent fledged of those hatched) in experimental synchronous and asynchronous broods. Nests taken by predators are excluded. N denotes number of broods. E: experimental treatment; M = manipulated broods, U = unmanipulated broods, B = both manipulated and unmanipulated broods. DS is the percentage gain in nestling survival in asynchronous broods relative to synchronous ones. See text for further details of design and calculation. (See next page.)

Species	Synchronous				Asynchronous				Source*
	Brood size	No. of years	Fledged (%)	Hatch spread (d)	N	E	Hatch spread (d)	DS (%)	
<i>Spheniscus demersus</i>	2	1	71.8	0.3	39	M	2.3	-20.5	1
<i>Phalacrocorax aristotelis</i>	3	1	90.3	0.3	14	M	2.8	- 2.2	2
<i>Phalacrocorax atriceps</i>	3	2	74.2	0-1	32	M	4.0	- 6.6	3
<i>Bubulcus ibis</i>	1-6	1	81.6	0-1	12	M	5.3	-26.1	4
	3	1	65.9	<1	24	M	3.0	+20.9	5
<i>Larus atricilla</i>	3 ^A	1	54.0	<1	13	M	2.3	+31.5	6
<i>Larus argentatus</i>	3	1	13.0	0.4	28	M	2.3	-14.6	7
<i>Rissa tridactyla</i>	2	1	50.0	0.8	6	M	3.1	-28.6	8
<i>Sterna hirundo</i>	3	2	72.9	0.5	35	M	1.9	-23.3	9
<i>Collacalia esculenta</i>	2	1	59.5	0.5	48	M	2.4	-13.4	10
<i>Hirundo rustica</i>	4-6	1	94.2	0-1	11	M	1-4	-22.6	11
<i>Pica pica</i>	2-8	1	72.1	<2	10	M	>2	-18.7	12
<i>Corvus corone</i>	3-6	2	67.3	1.3	17	M	2.5	- 4.8	13
<i>Corvus monedula</i>	4-7	1	56.4	<1	15	M	2.7	-10.5	14
<i>Corvus cryptoleucus</i>	5-6	2	86.7	<1	12	M	2-3	-18.6	15
<i>Parus ater</i>	5-11	1	98.9	0.4	9	M	1.8	- 1.9	16
<i>Parus caeruleus</i>	6-12	1	84.7	0.6	13	M	2.8	- 0.6	17
<i>Parus major</i>	4-12	1	84.5	0.5	17	M	2.6	- 7.1	18
<i>Ficedula hypoleuca</i>	4-8	2	94.5	0-1	103	M	2	- 5.4	19
	4-8	2	87.4	<1	59	M	2	- 8.4	20
	4-8	2	100.0	0.4	15	M	1.2	- 5.0	21
	5	1	66.0	0.5	10	M	2.2	+ 6.1	22
<i>Turdus pilaris</i>	7	2	86.6	0-2	52	M	3-5	- 8.3	23
<i>Turdus merula</i>	4	2	68.3	0.5	29	M	1.3	+ 1.3	24
<i>Sturnus vulgaris</i>	5-7	2	84.0	<1	49	M	1-2	- 1.4	25
<i>Quiscalus quiscula</i>	5 ^A	1	78.0	0.7	23	M	1.2	+10.3	26
<i>Carduelis tristis</i>	3-7	1	93.9	0.5	30	M	2.3	- 9.1	27
<i>Poephila guttata</i>	2-6	1	81.5	0-1	16	B	2	+11.8	28

^A Clutch size. * Source Key: (1) Seddon & van Heezik, in press, Table 2; (2) Amundsen & Stokland 1988, Table 3; (3) Shaw 1985, Table 13; (4) Fujioka 1985, Table 1 (minimum survival estimates, hatch spread of asynchronous from Fujioka 1984; (5) Mock & Ploger 1987, Table 1 (known fates sample, excluding "death from other causes"); (6) Hebert & Barclay 1986, p.2361 (including mortality due to inclement weather); (7) Hahn 1981, Table 1; (8) Amundsen & Stokland, unpublished data; (9) Bollinger et al. 1990, Table 1; (10) Bryant & Tatner 1990, Table 4; (11) Albu 1984, p.15; (12) Lorentsen 1983, Table 5; (13) Sandvik 1987, Table 9; (14) Gibbons 1987, Table 1; (15) Haydock & Ligon 1986, Figure 3; (16) Amundsen, unpublished data; (17) Slagsvold & Amundsen, unpublished data; (18) Slagsvold & Amundsen, unpublished data; (19) Slagsvold 1986, Table 3; (20) Slagsvold & Lifjeld 1989, Table 2 (excluding hatch spread 4 d (1983 only)); (21) Hillström & Olsson, MS, Table 1a; (22) Amundsen & Slagsvold 1991, Table 1; (23) Slagsvold 1982, Table 5; (24) Magrath 1989, Figure 1; (25) Stouffer & Power, in press, Table 1; (26) Howe 1976, p.1202 (percent of original clutch size of five); (27) Skagen 1987, p.1749/1752 (percent of broods without reduction due to starvation); (28) Skagen 1988, Fig.6 (N from Tables 2 and 4).

All the studies included records of nestling body mass and/or survival at a specified age close to fledging time, the proximity being determined by practical considerations. We have extracted data for body mass and survival either directly or, where necessary, by recalculation from relevant tables or figures. In the latter cases, we have extracted the values from enlarged copies, so as to obtain as precise values as possible. For studies covering more than one year, we have used means of yearly means when calculating the results for various treatment groups, thereby eliminating a potential bias due to different sample sizes in different years. Fledging success is expressed as the percentage survival of those nestlings hatched. Nestling body mass, except when otherwise stated, has been calculated as the mean mass for all nestlings (i.e. not mean of brood means). This represents the expected, average, nestling quality, and we found it to be the most relevant measure, in an evolutionary sense, for a comparison of nestling quality between the experimental groups. We have also calculated the relative success of asynchronous broods as the percentage deviation of their nestling survival value (DS) from that of the synchronous group. The relative success of asynchronous broods in terms of nestling body mass (DM) was calculated in the same manner. Positive values of DS/DM thus indicate that asynchronous broods were superior to, and negative values that they were inferior to synchronous broods. Some studies reported markedly different conditions in different years, as indicated by either external environment or by nestling productivity; in such cases we have considered the better of the two years/conditions to represent 'good' conditions, and the worst 'poor' conditions.

Our review demonstrates two consistent trends: synchronous broods produced more fledglings than asynchronous ones (Table 1), but the latter tended to do better in terms of nestling quality (Table 2). This was obvious despite the fact that most of the individual studies were unable to report statistically significant differences between synchronous and asynchronous broods. Among the 28 studies reporting nestling survival data (Table 1), synchronous broods had a higher survival rate in 22 cases while asynchronous broods were superior in six cases (Signed-ranks test, $N=28$, $P=0.01$). The trend for a higher number of fledglings in synchronous broods was statistically significant also at the levels of species ($N=24$, $P=0.004$), genera ($N=17$, $P=0.02$), and families ($N=12$, $P=0.02$). The difference in single-brood productivity of synchronous and of asynchronous broods varied greatly between species, and was less than 5 % in six of the studies.

The tendency for the nestlings of the asynchronous broods to be heavier at fledging time than those of the synchronous broods was slightly less consistent (Table 2), but was also statistically significant (Signed-ranks test, $N=25$, $P=0.02$). This relationship also held true at the levels of species ($N=21$, $P=0.03$), genera ($N=15$, $P=0.02$), and was almost significant for families ($N=12$, $P=0.06$).

When separate analyses were performed for passerine and non-passerine studies, we found that among passerines, the trend for synchronous broods to produce more fledglings than asynchronous ones was significant ($N=18$, $P=0.04$). Also the trend for higher fledging body masses in asynchronous broods was significant in passerines

TABLE 2 - Mean body mass of nestlings close to fledging time, in experimental synchronous and asynchronous broods. Nests taken by predators are excluded. DM is the percentage gain in fledgling body mass in asynchronous broods relative to synchronous ones. See text for further details of design and calculation. (Next page)

Species	Age (d)	Synchronous			Asynchronous			DM (%)	Source*
		Body mass (g)	No. of young	No. of broods	Body mass (g)	No. of young	No. of broods		
<i>Spheniscus demersus</i>	80	2201	56	39	2252	32	28	+ 2.3	1
<i>Phalacrocorax aristotelis</i>	37	1704	34	13	1666	67	30	- 2.2	2
<i>Phalacrocorax atriceps</i>	65	2420	29	15	2468	158	85	+ 2.0	3
<i>Florida caerulea</i>	21	277.2	?	10	280.7	79	?	+ 1.3	4
<i>Rissa tridactyla</i>	30	401.2	6	6	388.2	5	4	- 3.2	5
<i>Collacalia esculenta</i>	21	9.46	50	30	9.70	27	22	+ 2.5	6
<i>Hirundo rustica</i>	15	21.98	49	11	22.08	35	8	+ 0.5	7
<i>Pica pica</i>	24	183.0	34	10	195.1	37	13	+ 6.6	8
<i>Corvus corone</i>	24	396.9	54	17	386.2	151	69	- 2.7	9
<i>Corvus monedula</i>	26	221.5	41	?	221.4	44	?	0.0	10
<i>Corvus cryptoleucus</i>	A ^B	418.9	38	?	476.5	33	?	+13.8	11
<i>Parus ater</i>	15	9.64	67	9	9.73	63	8	+ 0.9	12
<i>Parus caeruleus</i>	14	9.983	129	13	10.76	126	15	+ 8.4	13
<i>Parus major</i>	16	15.3 ^A	?	17	17.0 ^A	?	24	+11.1	14
	12	17.7	?	6	17.7	?	6	0.0	15
<i>Ficedula hypoleuca</i>	11	14.46 ^A	622	103	14.74 ^A	398	68	+ 1.9	16
	12	13.62 ^A	300	54	13.56 ^A	230	48	- 0.4	17
	13	14.14	?	16	13.94	?	19	- 1.4	18
	13	12.6	33	10	13.1	35	10	+ 4.0	19
<i>Turdus pilaris</i>	9	70.7	195	33	72.2	102	20	+ 2.1	20
<i>Turdus merula</i>	8	54.43 ^A	?	32	56.65 ^A	?	47	+ 4.1	21
<i>Sturnus vulgaris</i>	19	68.70	210	?	70.00	196	?	+ 1.9	22
<i>Quiscalus quiscula</i>	12	66.24	82	18	65.57	61	15	- 1.0	23
<i>Carduelis tristis</i>	8-9	11.14	?	26	11.14	?	35	0.0	24
<i>Poephila guttata</i>	12	7.41	45	15	7.42	69	18	+ 0.1	25

^A Mean of brood means; ^B Asymptotic mass.

* Source Key: (1) Seddon & van Heezik, in press, Table 3; (2) Amundsen & Stokland 1988, Table 5; (3) Shaw 1985, Table 15; (4) Werschkul 1979, Figure 4 (N from Figure 3); (5) Amundsen & Stokland, unpublished data; (6) Bryant & Tatner 1990, Table 5; (7) Albu 1984, Table 10; (8) Husby 1983, Table 18; (9) Sandvik 1987, Fig. 5 (N from Table 9); (10) Gibbons 1987, Table 3; (11) Haydock & Ligon 1986, Table 3 (excluding brood size 5 (1981 only)); (12) Amundsen, unpublished data; (13) Slagsvold & Amundsen, unpublished data; (14) Slagsvold & Amundsen, unpublished data; (15) Bengtsson & Ryden 1983, Fig. 4 (N from Table 1); (16) Slagsvold 1986, Table 6 (N from Table 3); (17) Slagsvold & Liffield 1989, Table 2 (excluding hatch spread 4 d (1983 only)); (18) Hillstrom & Olsson, MS, Fig. 2; (19) Amundsen & Slagsvold 1991, Table 1; (20) Slagsvold 1982, Table 5; (21) Magrath 1989, P.538; (22) Stouffer & Power, in press, Table 2; (23) Howe 1976, Fig. 3; (19) Skagen 1987, Table 5; (20) Skagen 1988, Fig. 6 (N from Tables 2 and 4).

TABLE 3 - Effect of 'good' and 'poor' environmental conditions on nestling survival in experimentally synchronous and asynchronous broods. N denotes number of broods. DS is the percentage gain in nestling survival in asynchronous broods relative to synchronous ones. See text for further details of design and calculation.

Species	Good conditions				Poor conditions				DS (%)	Source*
	Synchronous		Asynchronous		Synchronous		Asynchronous			
	Fled- ged (%)	N	Fled- ged (%)	N	Fled- ged (%)	N	Fled- ged (%)	N		
<i>Phalacrocorax atriceps</i>	84.3	17	78.9	125	64.0	15	59.7	82	- 6.7	1
<i>Corvus corone</i>	76.8	13	66.0	33	57.9	4	62.2	36	+ 7.4	2
<i>Corvus cryptoleucus</i>	100.0	5	77.8	6	73.3	7	63.3	3	-13.6	3
<i>Ficedula hypoleuca</i>	98.9	58	96.9	31	88.2	45	84.7	37	- 4.0	4
<i>Turdus pilaris</i>	98.0	13	85.5	12	87.5	9	66.4	13	-24.1	5
<i>Turdus merula</i>	89.0	13	82.1	16	84.4	33	76.4	20	- 9.5	6
<i>Sturnus vulgaris</i>	87.0	8	74.8	13	49.5	21	63.6	25	+28.5	7
<i>Poephila guttata</i>	90.8	13	88.3	12	80.4	8	77.8	9	- 3.2	8
	80.0	6	85.7	12	82.9	10	96.4	8	+16.3	9

* Source Key: (1) Shaw 1985, Table 7; (2) Sandvik 1987, Table 5; (3) Haydock & Ligon 1986, Figure 3; (4) Slagsvold 1986; Table 6 (good I+II, poor III+IV, synchronous: hatch spread 0-1 d, asynchronous: 2 d, N from Figure 4/Table 5); (5) Slagsvold & Liffield 1989; Table 2 (good: reduced broods, four nestlings, poor enlarged broods, eight nestlings, synchronous: hatch spread <1 d, asynchronous: hatch spread 2 d); (6) Slagsvold 1982, Table 7 (good: 1979, poor: 1980, all broods enlarged, brood size 7); (7) Magrath 1989, Figure 1; (8) Stouffer & Power 1990, Table 1 ('good': broods size 5, 1988; 'poor': brood size 7 (enlarged), 1988); (9) Skagen 1988, Table 2.

TABLE 4 - Effect of 'good' and 'poor' environmental conditions on mean body mass of nestlings close to fledging in experimentally synchronous and asynchronous broods. DM is the percentage gain in fledging body mass in asynchronous broods compared to synchronous ones. N(Y) is number of nestlings; N(B) is number of broods. See text for further details of design and calculation.

	Good conditions						Poor conditions						Source *	
	Synchronous			Asynchronous			Synchronous			Asynchronous				
	Body mass (g)	N(Y)	N(B)	Body mass (g)	N(Y)	N(B)	Body mass (g)	N(Y)	N(B)	Body mass (g)	N(Y)	N(B)		DM (%)
<i>Corvus corone</i>	405.8	43	13	399.6	62	33	387.9	11	4	372.5	89	36	- 4.0	1
<i>Corvus cryptoleucus</i>	427.3	28	?	467.8	24	?	410.5	10	?	485.2	9	?	+18.2	2
<i>Ficedula hypoleuca</i>	14.83	?	58	15.15	?	31	13.87	?	45	14.38	?	37	+ 3.7	3
	14.57	?	13	13.78	?	12	13.47	?	8	12.95	?	13	- 5.7	4
<i>Sturnus vulgaris</i>	72.54	57	13	73.31	53	12	66.02	37	8	68.13	44	9	+ 3.2	5
<i>Poephila guttata</i>	8.01	?	6	7.94	?	10	6.80	?	9	6.90	?	8	+ 1.5	6

* Source Key: (1) Sandvik 1987, Figure 5 (N from Table 9); (2) Haydock & Ligon 1986, Table 3 ('good' 1981, poor: 1982 excl. clutch size 5); (3) Slagsvold 1986, Table 6 (good: I-II, 'poor': III-IV, synchronous: hatch spread 0-1 d, asynchronous 2 d); (4) Slagsvold & Lifjeld 1989, Table 6 (1982 only, good reduced broods, size 4, poor: enlarged broods, size 8, synchronous: hatch spread <1 d, asynchronous 2d); (5) Stouffer & Power 1990, Table 2 ('good': broods size 5, 1988; 'poor': brood size 7 (enlarged), 1988); (6) Skagen 1988, Figure (N from Table 4).

($N=19$, $P=0.02$). When only nonpasserine studies were considered, none of the two trends were significant (DS: $N=10$, $P=0.28$; DM: $N=6$, $P=0.84$).

Contrary to the expectation from Lack's original hypothesis, asynchrony was not, in general, more favorable than synchrony under poor environmental conditions, i.e. in cases of high nestling mortality (Figure 1). Of the nine studies that included both poor and good conditions, six reported greater nestling survival of the synchronous than of the asynchronous broods under both conditions (Table 3). In two studies (Sandvik 1987, Magrath 1989), more fledglings were produced in synchronous broods when conditions were good, but fewer when conditions were poor; in one study (Skagen's (1988) aviary study of Zebra Finches *Poephila guttata*) asynchrony was superior under both conditions. In the few studies that reported fledging body mass data for both good and poor conditions (Table 4), no consistent trend was revealed.

There was no correlation between the DS and DM values of the different studies ($r_s=-0.04$, $N=23$, NS). Neither did we find such a relationship at the levels of species ($r_s=-0.07$, $N=20$), genera ($r_s=-0.09$, $N=14$), or families ($r_s=-0.25$, $N=12$).

DISCUSSION

One clearcut result from our review was that, in general, synchronous broods produced more fledglings than asynchronous ones (Table 1). For many of the species studied this seems to have been the case both when environmental conditions were favourable and when not so (Table 3). Good offspring quality, as expressed by fledgling body mass, on the other hand, was favoured by asynchronous hatching for the majority of the species studied (Table 2).

Hence, it would seem that Lack's (1947, 1954) idea of asynchrony as a means of maximizing nestling production is not true in the strict sense. Although a few studies (Sandvik 1987, Magrath 1988, the Pied Flycatcher *Ficedula hypoleuca* studies) have indicated that asynchrony may be more productive under poor environmental conditions, the cumulative comparison for all species (Figure 1) indicated that synchronous hatching most often maximizes single-year nestling production, whether conditions are good or poor. Magrath (1989) found that in the Blackbird *Turdus merula*, asynchrony was advantageous under poor conditions. The results of our review suggest that other species may respond differently from the Blackbird when conditions are poor. It may be argued that only in Magrath's (1989) study were the environmental conditions poor enough for adaptive brood reduction. The lack of a similar effect in another study with a low nestling survival rate (Shaw's (1985) study of the Blue-eyed Shag *Phalacrocorax aristotelis*) supports, however, the idea that different species may respond differently. The lower survival rate of asynchronous broods found in most studies may be due to a competitive inferiority of the late-hatched nestlings, which may lead to their eventual elimination irrespective of the prevailing breeding conditions (Price 1985, Amundsen & Stokland 1988, Amundsen & Slagsvold 1991). In contrast to the lesson learned from recent experiments, Lack (1947, 1954) assumed that late hatching had no effect per se, and hence that hatching spread would not affect nestling production when food was in excess. A parent-offspring conflict (Trivers 1974) may exist over the elimination of junior nestlings; under certain conditions such elimination may be of advantage to the elder siblings, although not to the parent birds (O'Connor 1978, Mock 1987).

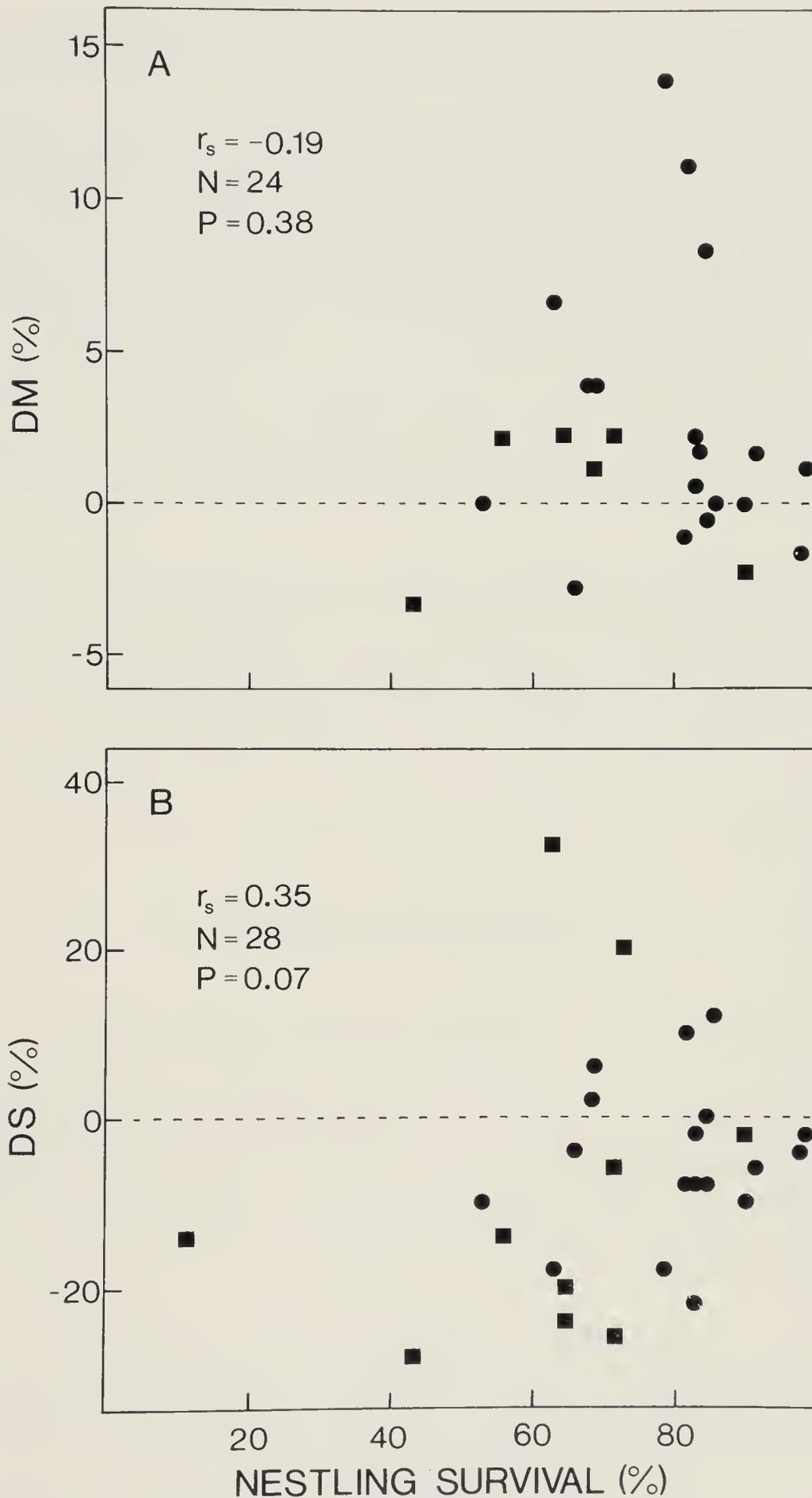


FIGURE 1 - Relationships between average nestling survival of synchronous and asynchronous treatments of each study (indicative of environmental conditions), and, (A) the percentage gain in fledgling body mass in asynchronous broods compared to synchronous ones, DM, and, (B) the percentage gain in nestling survival of asynchronous broods compared to synchronous ones, DS. Filled squares: non-passerines; filled circles: passerines. See text for details of design and calculation.

It does not follow from the above findings that asynchronous is selectively inferior to synchronous hatching. Although fewer fledglings were produced in asynchronous broods of many studies, these were of a higher quality on average than those of the synchronous broods. For most species, the mortality rate between fledging and first breeding is higher than that occurring in the nest, and the survival of a bird as a juvenile may be severely affected by its condition at fledging time (Lack et al. 1957, Perrins 1965, Lack 1966, Garnett 1981, Nur 1984, Alatalo & Lundberg 1989, Linden 1990). A knowledge of the quantitative relationships between fledging body mass and juvenile survival is essential for a proper understanding of the evolutionary implications of the main findings of this study, that, in a single year, asynchronous broods do worse in terms of quantity but better in terms of quality. Unfortunately, we possess no data on this relationship for almost all species covered by this review (but see Perrins 1965, Garnett 1981, Linden 1990). Hence, at this stage the problem can only be tackled by investigating the consequences of hypothetical juvenile survival functions of fledging body mass, as done by Slagsvold (1986) for the Pied Flycatcher.

There are several potential explanations why surviving young of asynchronous broods were heavier than those of synchronous ones. This may be due to (1) monopolization of food by senior (surviving) nestmates of asynchronous broods (but see Amundsen & Slagsvold 1991), (2) an increase in the number of feeds received per nestling, due to the lower number of live siblings on average, (3) an earlier mortality in asynchronous than in synchronous broods (Lack 1966, 1968, Slagsvold 1982, 1986, Gibbons 1987), (4) a reduction in sibling rivalry (Hahn 1981, Mock & Ploger 1987), or (5) an improvement in the division of labour between the parents in rearing the nestlings (Slagsvold & Lifjeld 1989). The above hypotheses are not mutually exclusive.

CONCLUDING REMARKS

The review is based on studies of nestling production during one or a few breeding seasons, and do not consider potential cost-of-reproduction aspects of asynchrony (Williams 1966). In the Cattle Egret *Bubulcus ibis*, Mock & Ploger (1987) found that parents of synchronous broods fed their young significantly more often, but at a lower efficiency, than parents of asynchronous broods. This indicates a parental cost of synchronous hatching. Results of some other studies have provided evidence in the same direction (Fujioka 1985, Gibbons 1987, but see Bryant & Tatner 1990). So far, however, no data exist on the potential consequences of this cost on parental survival and future reproduction.

From our review, it seems clear that hatching asynchrony generally results in fewer but better offspring produced in a single season. This was found in 22 out of the 28 studies, involving 24 species of birds. Hence, in terms of single-year fledgling quantity asynchrony-mediated brood reduction is often maladaptive. The results of some studies (Sandvik 1987, Skagen 1988, Magrath 1989, the Pied Flycatcher studies) have indicated that the reduction in brood size facilitated by asynchronous hatching increased fledging success under poor environmental conditions, but studies of other species have produced the opposite result (Slagsvold 1982, 1986, Shaw 1985, Haydock & Ligon 1986, Slagsvold & Lifjeld 1989, Stouffer & Power, in press), or have suggested that conditions have to be very poor before asynchronous broods do better (Slagsvold 1986). On the other hand, it is evident that many species benefit from asynchronous hatching in terms of fledgling quality. For such species, asynchrony-

mediated brood reduction may be adaptive; although not in the sense predicted by Lack (1947, 1954).

One interesting result to emerge from this review is that although the differences found between synchronous and asynchronous broods were too small for statistical significance in most individual studies, the trend was consistent across species. This was particularly clear as regards nestling survival. Biologically significant patterns may be difficult to detect from the results of single experiments with reasonable, but necessarily restricted, sample sizes, or, if detected, they may be found statistically insignificant and hence unjustified as a basis for biological reasoning.

The adaptiveness of a trait is ultimately determined by the number of offspring that survive to reproduce. Until the quantitative relationship that exists between fledgling quality and juvenile survival has been elucidated for different species, the question of whether asynchrony leads to adaptive or to maladaptive brood reduction remains unanswerable.

Negative values of both DS and DM were recorded for some of the species included in our review, i.e. asynchronous broods produced fewer and lighter nestlings than synchronous ones. For such species, alternatives to the brood reduction hypothesis may be needed to explain the hatching pattern. In particular, potential parental costs of synchrony should be considered.

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BURGERS OR BROTHERS: FOOD SHORTAGE AND THE THRESHOLD FOR BROOD REDUCTION

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ABSTRACT. In siblicidal birds, most chicks perish at an early age when food demands are low and parents should seemingly be able to provision the brood easily. I use dynamic programming to investigate the optimal policies of resource allocation (from the senior sib's perspective) among siblings and the consequences for brood reduction as a function of: (1) chick age, (2) the rate of provisioning, and (3) variability in provisioning. Lower mean rates and higher variability in provisioning favour increasing selfishness of senior sibs, and an earlier threshold age for siblicide. As chicks grow older, the threshold mass of chicks at which siblicide occurs increases. In general we should expect siblicide to be favoured before food becomes proximately limiting. Increasing variability in provisioning favours senior siblings to become risk averse, such that brood reduction may even occur when average rates of provisioning are, from the senior sib's perspective, sufficient to rear the entire brood.

INTRODUCTION

Food has long been considered an ultimate determinant of avian brood reduction, yet in many siblicidal species, brood reduction seems to occur before any proximate food limitation is realized. In the most extreme cases, where siblicide is obligatory, the victim's death occurs soon after hatch, even when food is apparently abundant (Gargett 1978, Cash & Evans 1986). Similarly in facultatively siblicidal species, most chicks perish at an early age (e.g. Owen 1955, Young 1963, Blaker 1969, Drummond 1986, Hagan 1986, Mock & Parker 1986) when food demands are low and parents seemingly should be able to provision the entire brood easily.

But does food have to be presently limiting for brood reduction to be favoured? Stinson (1979), in articulating the 'pending competition hypothesis', suggested that it does not. If food is likely to become limiting at some later point in the nestling period, pre-emptive siblicide may be favoured: dominant siblings avoid the risk of future food shortfall. Using a simple inclusive fitness model, Forbes and Ydenberg (in review) further suggested that obligate siblicide may be favoured in a variable environment even when sufficient food exists to rear both chicks in most years.

In this paper I use a dynamic optimization model to investigate the optimal policies of resource allocation among siblings from the perspective of the senior sibling, and the consequences for brood reduction, as a function of: (1) chick age and mass, (2) the mean rate of provisioning, and (3) variability in provisioning.

THE MODEL

Here I use a simple Markov state variable model to develop a framework in which the allocation of food among contemporary nestlings can be analysed. There are four main components to such models: the state variable(s) and constraints (i.e., the animal's condition at a given time plus the possible range of values this can assume), a strategy set (a finite set of behaviours influencing state variables), the state dynamics (the rules for change for state variables), and an optimization criterion (the fitness associated with different values of the state variable). Mangel and Clark (1988) provide a detailed review of the use of such dynamic optimization models in behavioural ecology.

State variables and constraints:

Consider two full sibs, α and β together in a nest. α is larger and is dominant to β , such that it can take any share of parental food it desires. The state variables in the model are the masses of α and β at time t : $\alpha(t)$ and $\beta(t)$. A chick's mass changes according to how much it eats, and fitness is assumed to be a function of mass at fledgling. Chicks feed and grow over a finite nestling period, which I have arbitrarily divided into seven ($t, T=7$) discrete time periods (e.g. weeks). All feeding and growth occurs in weeks 1 to 6 ($t= 1$ to 6), and in the final period, T (=week 7), the chicks fledge. Chicks perish if they do not attain the minimum fledgling mass, F_{\min} , by time T . Parents deliver a constant amount of food, Z , to the nest during each period, t . Herein lies an important assumption: the amount of food parents deliver today provides the senior sib with information about the level of future provisioning. Here I have assumed for simplicity that such information is perfect, which of course will never be true.

Strategy set

During each period the senior sib must decide what share, m_α , of parental food to take, with the remainder, m_β being left for the junior sib ($Z=m_\alpha + m_\beta$). Thus $0 \leq m_\alpha \leq Z$ and $0 \leq m_\beta \leq (Z-m_\alpha)$. For simplicity, I define three food allocation strategies for the senior sib based on how much food it allows the junior sib to eat: Generosity, where the junior sib receives $\geq 1/2$ of parental food ($m_\beta \geq 1/2Z$); Selfishness, where the senior sib takes $> 1/2$ of parental food but allows the junior sib to satisfy its maintenance requirements ($C_\beta < m_\beta < 1/2Z$), where C_β is the maintenance cost for β ; and Execution where the senior sib reaps all food ($m_\alpha = Z$) and the junior sib dies.

State dynamics:

The masses of α and β change according to:

$$\alpha(t + 1) = \alpha(t) + m_\alpha - C_\alpha \quad (1)$$

$$\beta(t + 1) = \beta(t) + m_\beta - C_\beta \quad (2)$$

where $\alpha(t + 1)$ and $\beta(t + 1)$ are the masses of α and β , respectively, at time $t+1$, and C_α and C_β are the energetic costs of maintenance (e.g., resting metabolism, costs of activity, and thermoregulation) for α and β . In the model, maintenance costs are an increasing function of chick mass (Figure 1). In words, chicks increase their mass from one period to the next when the amount they eat exceeds their maintenance costs; as chicks grow larger, these maintenance costs increase. If during any period a chick

does not eat sufficient food to meet its maintenance costs, it dies. Thus if the senior sib withholds all food from the junior sib long enough, the latter perishes.

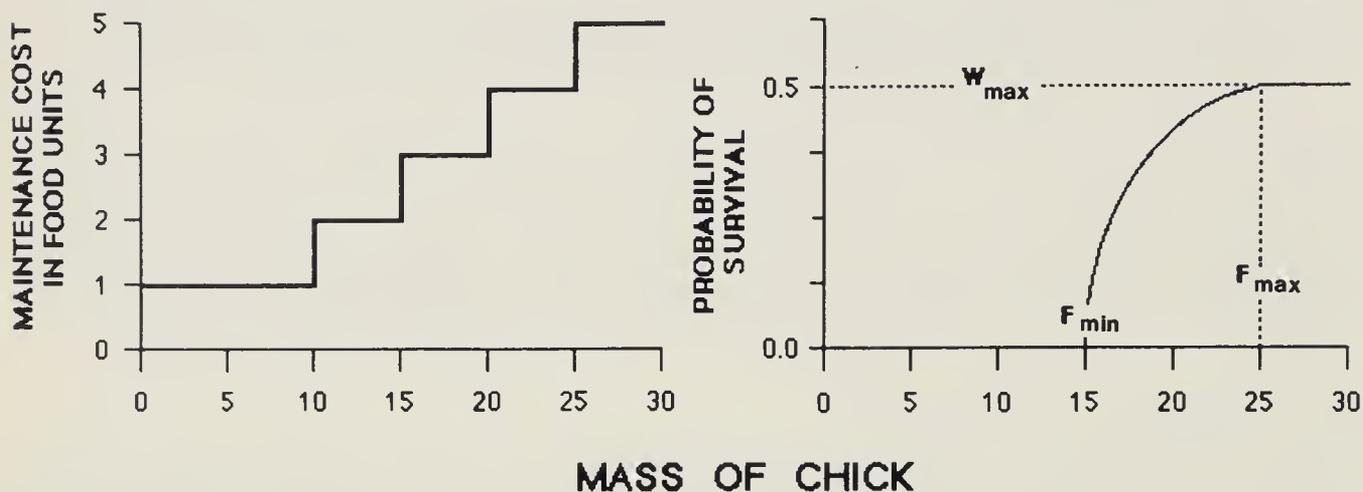


FIGURE 1 – Left panel: Relationship between chick mass and maintenance costs. Right panel: Relationship between chick mass at fledging and the probability of survival to breeding age. F_{min} is the minimum fledging mass, below which offspring do not survive. F_{max} is the mass at which post-fledging survival reaches a maximum. W_{max} is the maximum probability of a chick surviving to breeding age.

Optimization criterion

I define a chick’s fitness at fledging, W , as its probability of survival from fledging to breeding age. W is assumed to be a function of chick mass at fledging (e.g., Perrins 1963, Jarvis 1974, Krementz et al. 1989), such that $W_{\alpha} = f(\alpha[T])$ and $W_{\beta} = f(\beta[T])$ (Figure 1). If a chick’s mass at fledging does not exceed some minimum threshold for survival, F_{min} , it dies and its fitness is zero. At masses above F_{min} , a chick’s fitness increases monotonically at a decelerating rate to a maximum, W_{max} , at masses $\geq F_{max}$ (Figure 1). A simple explicit function satisfying these requirements is:

$$W_{\alpha} = \begin{cases} 0 & \alpha[T] < F_{min} \\ q\{(\alpha[T] - F_{min}) / \alpha[T]\} & F_{min} \leq \alpha[T] \leq F_{max} \\ W_{max} & \alpha[T] \geq F_{max} \end{cases} \quad (3)$$

where q is a constant, and:

$$W_{\beta} = \begin{cases} 0 & \beta[T] < F_{min} \\ q\{(\beta[T] - F_{min}) / \beta[T]\} & F_{min} \leq \beta[T] \leq F_{max} \\ W_{max} & \beta[T] \geq F_{max} \end{cases} \quad (4)$$

(Figure 1). How the senior sib allocates food between itself and its junior sib during weeks 1 to 6 will affect the fledging mass, and hence fitness, of each. Following the general arguments of Parker et al. (1989) and Forbes and Ydenberg (in review), the optimal policy of allocation is that which maximizes the joint probability of survivorship of the senior and junior sib (the latter being discounted by the coefficient of relationship) beyond fledging:

$$w(\alpha, \beta, m_{\alpha}, Z, t, T) = \max (W_{\alpha} + 1/2 W_{\beta}) \quad (5)$$

The ‘goal’ of the senior sib during the nestling period is to allocate food between itself and the junior sib so as to maximize $\{W_{\alpha} + 1/2 W_{\beta}\}$. Thus for any given period t ,

the optimal behaviour for the senior sib will be that which maximizes fitness at time $t + 1$, $\Omega(t + 1)$, or:

$$\Omega(t + 1) = \max_{m_\alpha} \{ f[\alpha(t) + m_\alpha - C_\alpha] \} + 1/2 \{ f[\beta(t) + (Z - m_\alpha) - C_\beta] \} \quad (6)$$

Quite simply, the senior sib should invest parental food in the junior sib whenever the rate of increase in survivorship of the junior sib is $\geq 2x$ its own rate of increase in survivorship were it to eat the same quantity of food. The solution to the above dynamic programming equation is solved by backwards iteration (Mangel & Clark 1988). That is, the fitness associated with senior and junior sibs of different mass at time T , is determined according to eq. (3-5) and the optimal behaviour in the penultimate period ($t=6$) is found according to eq. (6). This defines the fitness associated with different combinations of $\alpha(t)$ and $\beta(t)$ in week 6, and then the optimal behaviour in week 5 can be found by the same methods. This process of backward iteration is repeated for all periods, at the end of which the optimal behaviour (Generosity, Selfishness, or Execution) for all possible combinations of $\alpha(t)$ and $\beta(t)$ from weeks 1 to 6 has been specified. Although the mathematical notation may seem daunting to some, simple dynamic programming models such as the one described here are only slightly more sophisticated than many computer spreadsheet models.

I analysed two versions of this dynamic optimization model. They differed only in the manner in which parental provisioning was simulated. In the deterministic version, the quantity of food, Z , delivered to the brood in each period was fixed. Two levels of provisioning were simulated in the deterministic model: low food (= 8 food units/period), and high food (= 10 food units/period). Other parameter values used in the simulations were: $q = 1.25$, $F_{\min} = 15$, $F_{\max} = 25$, $W_{\max} = 0.5$.

The second version of the model simulated stochastic variation in parental provisioning. Here the mean rate of food delivery was identical to that in the high food simulation of the deterministic model described above, (= 10 food units) but varied about this mean according to a uniform distribution: either 8, 10 or 12 food units might be delivered, each with a 1/3 probability. As in the deterministic model, the senior sib must decide what share of parental food it will take ($0 \leq m_\alpha \leq Z$), the remainder being left for the junior sib. I assume that the senior sib makes this decision before food is delivered, such that it cannot update its decision according to how much food is actually delivered. Expressed in another way, how much should you eat at lunch if you are unsure about the size of supper? The dynamic programming equation is similar to that in eq. 6 except that it must be solved across all possible levels of Z (8, 10, or 12 units) such that:

$$\Omega(t + 1) = \max_{m_\alpha} \sum_{z=8,10,12} \{ f[\alpha(t) + m_\alpha - C_\alpha] \} + 1/2 \{ f[\beta(t) + (Z - m_\alpha) - C_\beta] \} \quad (7)$$

The significance of stochastic variation in provisioning is that more or less food may be delivered than the senior sib expected, which will affect what the junior sib is to receive - e.g. if the senior sib decides to take 8 of the 10 food units it expects the parents to deliver (leaving 2 units for the junior sib), but the parents deliver only 8 units, then the junior sib receives nothing. Conversely, if the parents deliver 12 food units instead of 10, then the junior sib receives 4 food units instead of 2. The fitness increments for a junior sib receiving 0, 2 or 4 food units may be quite different (e.g.

a chick receiving no food will die, whereas a chick receiving 4 food units may enjoy an enhanced probability of survival). The senior sib must weigh these different fitness outcomes in its food allocation decisions.

MODEL RESULTS AND DISCUSSION

Deterministic provisioning: proximate food limitation and siblicide

The solution of the dynamic programming equation answers a very simple question: how much food should the senior sib (α) take for itself, and how much should it leave (if any) for its junior sib (β), at different combinations of chick age and mass. The results are presented in Figures 2 & 3. There, the optimal behaviour for all possible combinations of mass of the senior and junior sibs for weeks 1 to 6 are presented. I assume that the mass of the junior sib never exceeds the mass of the senior sib, and that a chick's mass cannot exceed 10 units on day 1 or 20 units on day 2 (very large chicks early in the nestling period are biologically unreasonable).

DETERMINISTIC FOOD

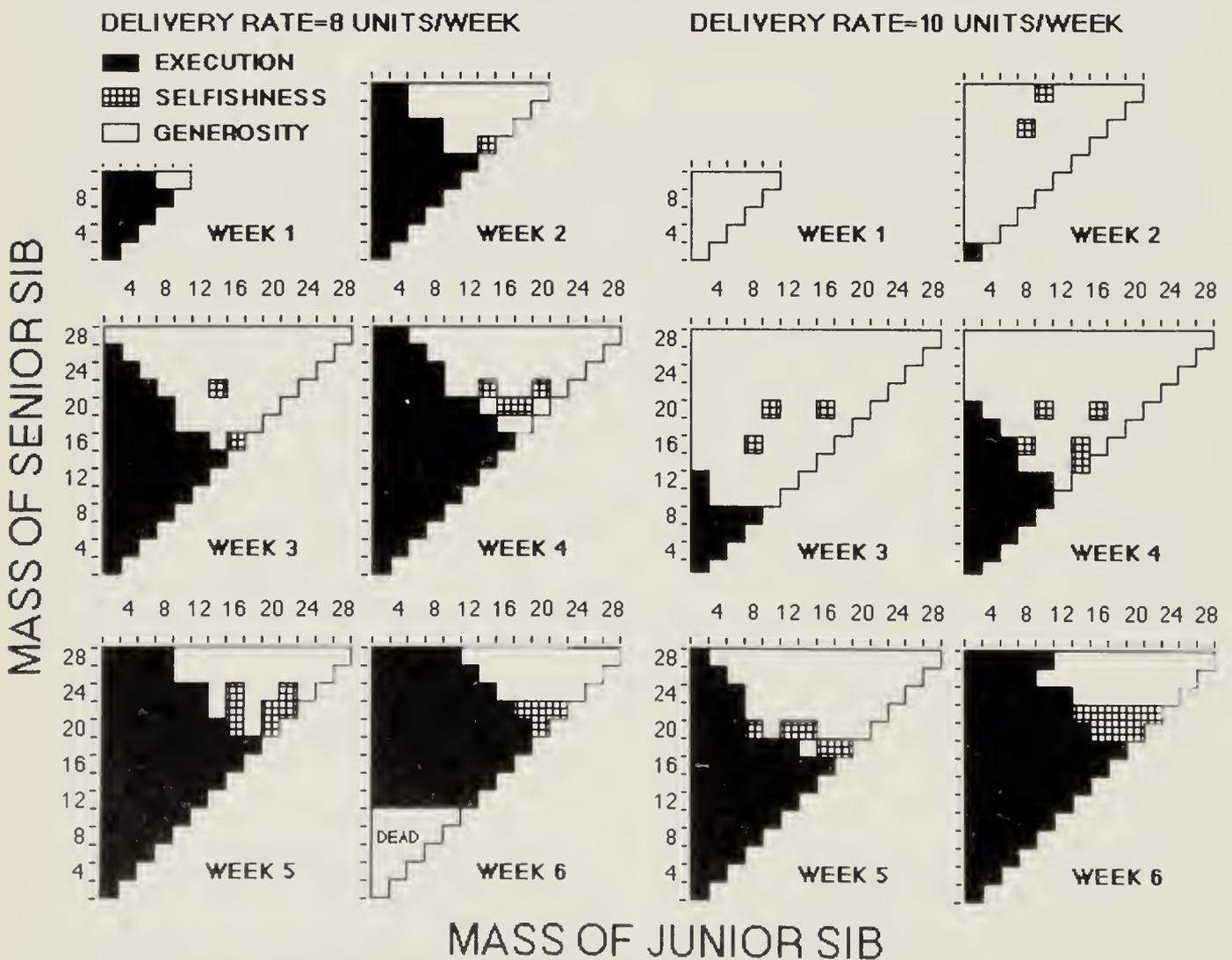


FIGURE 2 – Results of deterministic simulations at low ($Z=8$ units/ period) and high delivery rates ($Z=10$ units/period). The optimal policies of resource allocation of the senior sibling are illustrated for different levels of mass of the senior and junior sibling at weeks 1 to 6 ($t = 1$ to 6) of the nestling period.

From Figure 2 it is evident that chick masses are important determinants of the optimal policy of food allocation. Generosity is only favoured when the mass of the senior sib is high, and the mass of the junior sib is sufficiently high that investment of ad-

ditional food will yield inclusive fitness returns for α (but not so high that there are only small or nonexistent gains to be made). If the mass of the senior sib is lower, Selfishness or Execution is more likely to be favoured, once again depending upon the mass of the junior sib. If $\beta(t)$ is very low, further investment of food in the junior sib is unlikely to yield fitness benefits for the senior sib, and Execution is favoured (Figure 2).

The model results illustrate how brood reduction might be favoured prior to the onset of food shortage (e.g. starvation). Both high and low provisioning in the deterministic simulations easily satisfied the maintenance and growth requirements of both chicks early in the nestling period. Food, therefore, could not be considered presently limiting, yet in the low food simulation, Execution was favoured early. A simple trade-off underlies the behaviour analysed here. At each period the senior sib must decide whether it wants to retain its junior sib: either it must share some food, or it will kill β and reap all food thereafter. By Executing β , α gains access to greater food for the duration of the nestling period. The increment in personal fitness from consumption of this 'future' food (= 'burgers') that the senior sib expects to derive, relative to the increment in inclusive fitness (= 'brothers') it would gain if it shared food with the junior sib, and not proximate food limitation per se, determines whether brood reduction (usually in the form of siblicide) is favoured. This is the burgers or brothers principle. Thus if early provisioning portends inadequate food later on (from the perspective of α), the senior sib should avoid the risk of future food shortfall and eliminate the junior sib.

As the chicks grow older, the threshold mass at which Execution occurs increases (Figure 2). The reason is straightforward. Later in the nestling period, a chick's potential for further growth diminishes because fewer periods remain: the chicks are running out of time - e.g. a senior sib with a mass of 6 units may behave Generously at week 2 but favour Execution at week 5 (Figure 2).

STOCHASTIC FOOD

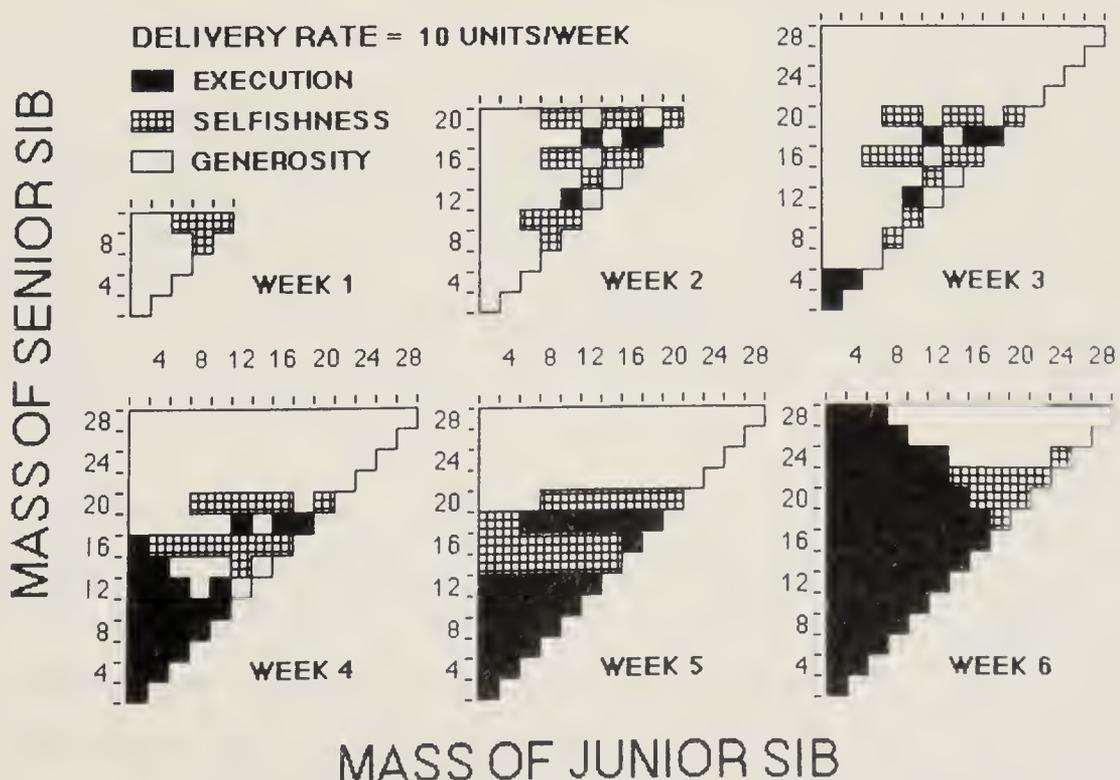


FIGURE 3 – Results of the stochastic simulation at high food levels (mean level of $Z=10$ units per period). Symbols the same as described in Figure 2.

I have assumed throughout that chick fitness is a function of mass at fledging and that the nestling period is of fixed duration. More likely, underweight chicks would delay fledging. Essentially the same results would be obtained, however, because late fledging presumably bears fitness costs of its own (e.g. Perrins 1963, Roskaft & Slagsvold 1985).

Stochastic provisioning

Under stochastic provisioning, senior sibs were more disposed to behave conservatively early in the nestling period (Selfishness or Execution vs Generosity) than when provisioning was deterministic. At low chick masses early in the nestling period, the costs to the senior sib of food shortfalls ($Z=8$ instead of 10) exceeded the benefits of food windfalls ($Z=12$ instead of 10) principally because costs are measured in lost individual (=direct; $r=1$) fitness, but the benefits are measured in the fitness of kin ($r=0.5$) (see also Forbes & Ydenberg, in review). Thus, when food is variable, the senior sib should behave in a risk averse manner (e.g. to favour obligate siblicide). However, later in the nestling period, and particularly when the senior sib has achieved a high mass, stochastic provisioning may favour increased Generosity, particularly if the mass of the junior sib is low (Figure 3). Here the senior sib's prospects for post-fledging survival are secure. Gambling on high food ($Z=12$) may be worthwhile because the potential benefits (increased survivorship of β) are high, while the direct fitness costs to the senior sib are low.

ACKNOWLEDGEMENTS

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NESTLING MORTALITY PATTERNS IN RELATION TO BROOD SIZE AND HATCHING ASYNCHRONY IN GREEN-RUMPED PARROTLETS

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ABSTRACT. In Venezuela, Green-rumped Parrotlets *Forpus passerinus* lay large clutches, averaging 7 eggs, that hatch and fledge very asynchronously over 1 - 2 weeks. In unmanipulated nests that were successful, fledging success was uniformly high for small broods, declined slightly for the last two chicks of medium broods, and declined sharply for the last two nestlings in large broods. We manipulated brood size and hatch asynchrony in a completely randomized design. Only in asynchronously hatched young from large broods did fledging success decline significantly for the last two chicks. Death from apparent starvation occurred independent of hatch order in large synchronous broods, suggesting that the distribution rather than quantity of food limited fledging success. The patterns of offspring mortality in Green-rumped Parrotlets are discussed in relation to predicted patterns of mortality on the basis of size-dependent allofeeding strategies reported for captive Budgerigars. Indirect evidence suggests that parrotlet parents are unable to feed smaller chicks in large broods.

Keywords: Nestling mortality, asynchronous hatching, parrot, clutch size, parent-offspring conflict.

INTRODUCTION

When a bird initiates incubation of a clutch determines how synchronously the eggs will hatch. Asynchronous hatching results in young of different sizes, which in some species can lead to brood reduction (O'Connor 1978, Mock et al. 1990). While parents attempt to fledge as many young as possible from their broods, the young may have selfish interests of their own that drive them to compete among themselves for greater shares of parental investment. Parent-offspring conflict should be expected to occur in these situations (Trivers 1974).

In species without weaponry (i.e. strong bills), parent-offspring conflict might occur most often over the allocation of food among nestlings. Parents could be expected to develop strategies to allocate food between young in a manner that allows them to minimize this conflict and to maximize the survival of their young. While nestlings may compete for parental investment by begging, parents could actively allocate food in a size-dependent fashion. Feeding the smallest and youngest chicks preferentially, despite the more vigorous begging of older and larger sibs, might help to ensure survival of last-hatched young.

Perhaps the most intriguing evidence for parents controlling the allocation of food among young comes from studies of Budgerigars *Melopsittacus undulatus* in captivity (Stamps et al. 1985). Although Budgerigar clutches were hatched very asynchronously, all nestlings grew at similar rates and fledged at similar sizes. The lack of hatch-order effects on fledging success may have been due primarily to the manner in which females fed their offspring. Females fed offspring mainly on the basis of size,

and begging rate was only of secondary importance (Stamps et al. 1985). However, males fed the most vigorous beggars more often, regardless of size.

Because this study was done with captive flocks of Budgerigars, it is not clear whether the results are an artifact of the captive environment (i.e. unlimited food). Stamps et al. (1987) suggested that size-dependent feeding of offspring by parents may also be occurring in a variety of natural situations. Weak evidence of parents retaining control of the timing and conditions of offspring loss through the allocation of food comes from studies of Pied Flycatchers *Ficedula hypoleuca* (Gottlander 1987) and Great Tits *Parus major* (Bengtsson & Ryden 1983).

Parental strategies to allocate food in a size-dependent manner might be expected to occur most often in species that hatch their eggs very asynchronously, because this would result in large differences in ages and sizes among broodmates. Most altricial passerines hatch their eggs only somewhat asynchronously, usually beginning on the penultimately-laid egg (Clark & Wilson 1981). The largest hatching spreads occur in nonpasserines: incubation can begin on the first egg and clutches can hatch over an interval of up to 10 days to two weeks in some owls and psitticines (Stamps et al. 1985, Wilson et al. 1986).

We have been conducting studies to examine the factors favoring a large clutch size and extreme hatching asynchrony in Green-rumped Parrotlets *Forpus passerinus*. This small (25 - 35 g) Neotropical parrot lays large clutches that hatch very asynchronously. Clutch size averages seven eggs and can range up to 10 eggs. Females begin incubation on the first egg, and up to 14 days may elapse between the hatching of the first and last young in a brood. This is one of the largest hatching spreads reported for any bird (Clark & Wilson 1981, Lessells & Avery 1989, Mock & Schwagmeyer 1990).

In this paper we examine offspring mortality patterns in unmanipulated broods of Green-rumped Parrotlets, and in broods where brood size and hatching asynchrony were experimentally manipulated. If parents feed smaller young preferentially and if starvation is the main cause of nestling death, then (1) offspring mortality patterns should occur independent of hatching order, (2) larger broods, which require more food, should not have a greater proportion of later hatched young dying than smaller broods, and (3) the relationship between offspring death from starvation and hatching order at synchronously hatched broods (nestlings of similar size) should not be different from asynchronously hatched broods (nestlings of different sizes).

METHODS

We studied a box-nesting population of parrotlets at Fundo Pecuario Masaguaral (8°34'N, 67°35'W) in the llanos of Venezuela from June through December in 1988 and 1989. The habitat is comprised of seasonally flooded savanna with scattered patches of denser forest. See Troth (1979) and O'Connell (1989) for a description of the study area. Beissinger & Bucher (in press) describe the construction of nest boxes and their use by parrotlets.

Nest boxes were checked daily or every other day to determine precise dates of egg-laying and hatching. Eggs were uniquely marked with indelible ink. Wetness and color

were used to determine hatching sequence if two unmarked chicks hatched on the same day. Nestlings were color-marked on their toenails with nail polish. In 1988, 48 nests were observed from egg-laying through fledging (unpubl. data).

In 1989, brood size and hatching asynchrony were manipulated at 51 nests just prior to or during hatching. Two treatments were randomly assigned to each nest: (1) small, medium and large broods were created consisting of four, six, and eight young, respectively; and (2) chicks in synchronous broods hatched within 2 - 3 days, while chicks in asynchronous broods hatched with a spread typical of *Forpus passerinus* broods of four young (6 - 7 days), six young (9 - 10 days), and eight young (12 - 14 days). Experimental broods were created by moving eggs of known age between nests. Eggs that did not hatch were replaced with nestlings of similar age. Because synchronous nests frequently had more than one egg hatch in a day, eggs were injected with 0.01 ml of nontoxic food dye when pipped to identify individuals during hatching.

After all eggs in a nest had hatched, nests were visited every three to four days. When a chick died, the parents did not remove it, presumably because parrotlets must use their beaks for climbing out of the meter-deep boxes, and the carcasses were usually found at the bottom of the nest box. Carcasses from young that had died within 36 hours were fresh enough to be examined for crop contents and categorized as empty or partly full (containing some food).

Data were analyzed using SYSTAT and SAS microcomputer programs. Hatching order was examined for position effects, and then grouped as first, middle (from second to third-to-last), penultimate, or last hatched young. Nests that failed to fledge any young were excluded from analyses of fledging success and nestling mortality patterns. Multiple contingency models with maximum likelihood estimates (Sokal and Rohlf 1981) were used to analyze the effects of hatching sequence and brood size on fledging success when sample sizes permitted. Otherwise, single classification χ^2 analyses were used.

RESULTS

Fledging success at unmanipulated nests showed strong effects of both brood size and hatching order (Figure 1). Fledging success was uniformly high for nestlings in small broods, declined slightly for the last two chicks in medium broods, and declined sharply for the last two nestlings in large broods. Maximum likelihood analysis yielded significant effects for both brood size ($\chi^2 = 8.4$, $df = 2$, $P < 0.02$) and hatching order ($\chi^2 = 12.4$, $df = 3$, $P = 0.006$).

Hatching order affected fledging success at experimental nests in 1989 only in asynchronously-hatched young from large broods. The two youngest nestlings in large broods had a significantly smaller probability of fledging than did their nestmates ($\chi^2 = 10.7$, $df = 3$, $P = 0.01$). Among synchronous broods and among broods of smaller sizes, no significant differences ($P > 0.10$) existed in the probability of fledging in relation to hatching order.

The causes and implications of nestling mortality in successful nests are unclear. A three-way ANOVA found that neither brood size ($F_2 = 1.3$, $P = 0.28$) nor hatching

order ($F_3 = 0.5$, $P = 0.70$) had a significant effect on the age of death of nestlings. However, the effect of hatching asynchrony on the timing of death was nearly significant ($F_1 = 3.7$, $P = 0.06$): young from asynchronous broods died earlier than young from synchronous broods.

Determining the exact causes of nestling death at successful nests was difficult. At unmanipulated nests in 1988, we found all last- and penultimately-hatched young dead with empty crops, while 40% of their nestmates died with at least some food in their crops (Table 1). This pattern suggested that the two youngest nestlings died significantly more often from apparent starvation than their nestmates (Fisher's Exact Test, $P = 0.03$). Similar results were found for the experimentally asynchronous nests in 1989 (Table 1), though the difference was more equivocal (Fisher's Exact Test one-tailed $P = 0.09$). In nests with synchronously hatching young, the occurrence of starvation (empty crops; Table 1) was independent of hatching order (Fisher's Exact Test $P = 0.5$). However, so few young died in the experimentally synchronous broods that such an effect would be more difficult to detect.

TABLE 1 – Crop contents of nestling Green-rumped Parrotlets found dead in nests that were not victims of predation or infanticide by invading pairs.

Experimental Treatment	Hatch Order	Crop Contents When Found Dead	
		Partly Full	Empty Crop
Unmanipulated	Early chicks	4	6
	Last two	0	13
Synchronous	Early chicks	3	0
	Last two	2	3
Asynchronous	Early chicks	12	4
	Last two	3	4

DISCUSSION

The patterns of offspring mortality caused by apparent starvation in Green-rumped Parrotlets were only partly predicted from size-dependent allofeeding strategies reported for captive female Budgerigars (Stamps et al. 1985). In unmanipulated broods of Green-rumped Parrotlets, the occurrence of offspring mortality due to starvation was strongly influenced by brood size and hatching order. Although hatching order did not affect survivorship in small and medium broods, the two youngest chicks in large broods died more frequently of apparent starvation than earlier hatched chicks (Figure 1).

That offspring mortality was independent of brood size for small and medium broods is consistent with a size-dependent feeding strategy. But because food demand and parental feeding rates increase with brood size in these parrotlets (unpubl. data), significant conflicts between parents and offspring might be expected to occur more often in large broods where food could be limiting. Food may be so abundant that little conflict between parent and offspring occurs in smaller broods. However, it is not clear whether food quantity or the unequal distribution of food among nestlings limited fledging success in unmanipulated nests.

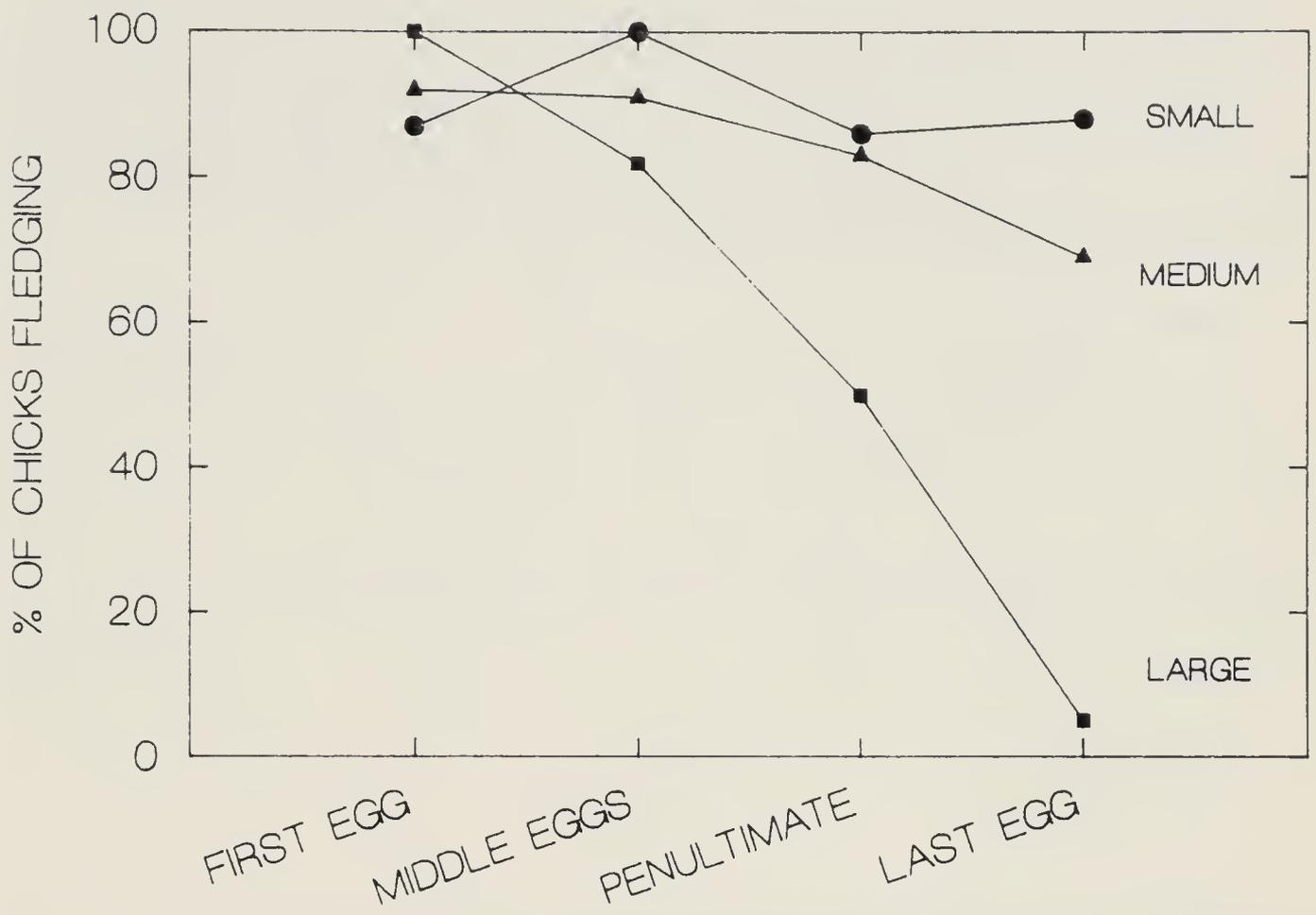


FIGURE 1 – The relationship between hatching order and fledging success for small ($N = 8$), medium ($N = 13$), and large ($N = 4$) broods at unmanipulated nests in 1988.

Evidence against a food limitation (and for an unequal distribution of food among nestlings) comes from the results of experimental manipulations of both brood size and hatching asynchrony (Figure 2, Table 1). Large broods often were able to raise all young if they were hatched synchronously, whereas brood reduction occurred in most large broods with asynchronously hatched young (unpubl. data). Death from apparent starvation was independent of hatching order in large synchronously hatched broods but not in large asynchronously hatched broods (Figure 2). If anything, asynchronous broods should have reduced maximum daily food requirements, compared to synchronously hatched broods, because the peak period of food demand by the brood is spread out due to differences in the energy requirements of young of different ages (Hussell 1972, Mock & Schwagmeyer 1990). Preliminary analysis of food delivery rates by parents to nestlings did not differ between synchronous and asynchronous broods (unpubl. data). Apparently parrotlet parents were able to bring enough food to the nest regularly to fledge eight nestlings, but seemed to be unable to distribute the food to smaller young in asynchronously hatched broods.

It is possible that young in large broods died of causes other than starvation. Finding young dead with empty crops could have been an effect of other causes of death (e.g. hypothermia or being crushed), rather than the actual cause of death. Some chicks died with full crops, which suggests that causes other than starvation may also be important mortality factors.

Although we have no direct observations of parents feeding young in nest boxes, experiments in progress are gathering data to address this point more directly. Morning nest checks indicated that the smallest chicks in large broods were rarely fed before their nestmates, and sometimes skipped whole days between feedings during their first week of life. Usually the two youngest chicks were found at the bottom of the nest box under a mass of older nestmate's bodies. It appears that seeking out the smallest chicks would require strong measures by parents and the development of strategies to avoid efforts by older chicks to be fed.

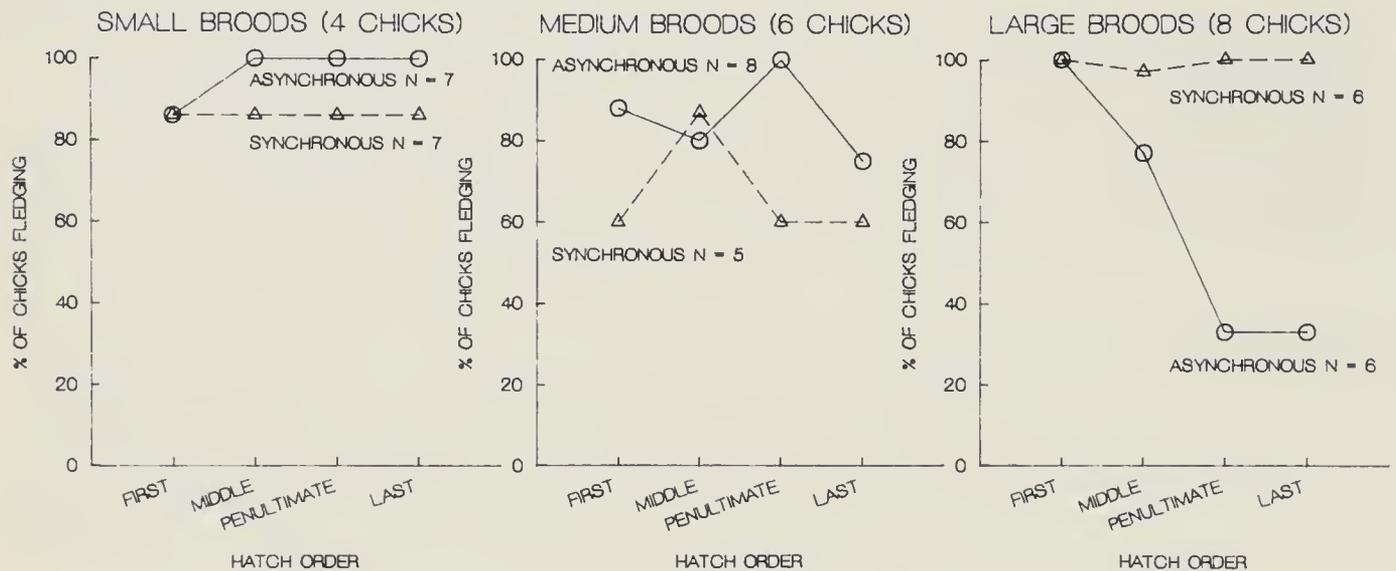


FIGURE 2 – The relationship between hatching synchrony, hatching order, and fledging success for experimental broods of different sizes in 1989.

In conclusion, offspring mortality patterns in our studies of a very asynchronously hatching parrot can not confirm that parents are controlling the distribution of food to offspring when food is in demand (e.g., broods are large). However, our data are indirect and require corroboration from more direct sources in progress.

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TERMINAL-EGG NEGLECT: BROOD REDUCTION STRATEGY OR COST OF ASYNCHRONOUS HATCHING?

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ABSTRACT. Terminal egg neglect arises when parents begin to tend their first-hatched young and consequently spend less time incubating the remaining eggs. It has been documented mainly in species exhibiting asynchronous hatching and brood reduction, especially where nests are open and at ground or water level. Negative effects of neglect on embryos include failure to hatch and retarded development. Embryonic adaptations to neglect include increased resistance to chilling, faster hatching, and vocal appeals to cooperative parents. In some species, the occurrence of successful embryonic adaptations to neglect suggests that it is not being employed by parents as a brood reduction strategy. Under these circumstances residual neglect may be a largely unavoidable consequence of asynchronous hatching. More severe neglect may result from tradeoffs between incubating terminal eggs and anti-predator or food-related benefits of moving older young away from the nest. In these situations terminal egg neglect may be part of an adaptive parental brood reduction strategy.

Keywords: Terminal egg neglect, brood reduction, hatching asynchrony, embryonic adaptations.

INTRODUCTION

Terminal egg neglect arises when parents caring for asynchronously hatching young begin to tend newly-hatched nestlings at the expense of continued full incubation of the remaining eggs (Greenlaw & Miller 1983). In severe instances, neglect can lead to egg abandonment and mortality (Gullion 1954, Nuechterlein & Johnson 1981). Less severe instances of neglect arise when parents fail to maintain incubation temperatures (Greenlaw & Miller 1983, Lee 1988, Evans 1989, 1990a). It has been suggested (Graves et al. 1984) that the loss of a terminal egg through neglect would be a simple way for parents to achieve brood reduction. Sub-lethal cooling may also facilitate brood reduction if hatching time is extended and within-brood hatching asynchrony increased (Forbes & Ankney 1988, Evans 1990b,c).

There seems little doubt that terminal egg neglect, if sufficiently severe, can lead to or facilitate brood reduction. Whether this association between terminal egg neglect and brood reduction represents an adaptive parental brood reduction strategy, or is a potentially costly and largely unavoidable consequence of hatching asynchrony remains unresolved, and will provide the focus for this review.

NATURE AND SCOPE OF TERMINAL EGG NEGLECT

Disruptions to incubation commonly begin with the onset of pipping of the first egg (Beer 1962, Lee 1988, Evans 1989). In gulls (Laridae), which have been intensively studied, pipped eggs are no longer held in close contact with the brood patches and a significant increase in rising and resettling occurs (Beer 1966, Drent 1970). In Herring Gulls *Larus argentatus* Lee (1988) found a progressive decrease in both incuba-

tion attentiveness and egg temperatures, combined with greater variability in these measures, as hatching proceeded in asynchronously hatching three-egg clutches. After the second, or "b"-egg hatched, the pipped terminal *c*-egg cooled to a mean of about 33°C, down about 4°C from pipped *a*-eggs and 3°C from pipped *b*-eggs. Neglect of the *c*-egg in Herring Gulls was especially evident when parents led the newly hatched *a*- and *b*-chicks off the nest for feedings, or began to stand away from the nest, leaving the *c*-egg exposed. It is likely that egg neglect in gulls can sometimes be severe enough to lead to mortality of terminal eggs (Beer 1962, Drent 1970, Haycock & Threlfall 1975).

Changes in incubation behavior just before hatching have also been noted in some Pelecaniformes, including Gannets and Boobies (Sulidae) (Nelson 1978) and American White Pelicans *Pelecanus erythrorhynchos* (Evans 1988a). With the onset of pipping, parents in these species move their eggs from under their foot webs to a position between their legs. In pelicans, rising over the eggs increased, eggs were sometimes left exposed beside the parent, egg temperatures became more variable and ranged to lower levels (Evans 1989), and upper surface temperatures of unpipped *b*-eggs were significantly reduced (Evans 1990a). Unlike the Herring Gull, neglect in pelicans ended after the terminal egg pipped (Evans in press a).

Reduced incubation attentiveness during hatching has been found in the Pied-billed Grebe *Podilymbus podiceps* (Forbes & Ankney 1988). Grebes (Podicipedidae) have young that are both precocial and hatch asynchronously, so it is perhaps not surprising that grebe parents are especially prone to desert late-hatching eggs as they move their first-hatched young away from the nest (Simmons 1955). The most striking example of terminal egg neglect that we have found occurs in the Hooded Grebe *Podiceps gallardoi*, where abandonment of the terminal egg appears to be obligate (Nuechterlein & Johnson 1981). Terminal egg neglect has also been reported in the Raillidae, which also have precocial young that hatch asynchronously. In Soras *Porzana carolina*, terminal and penultimate egg hatching delays of up to one day have been attributed to neglect during the hatching period (Greenlaw & Miller 1983). Instances of terminal egg abandonment have been reported in the American Coot *Fulica americana* (Gullion 1954) and European Coot *F. atra* (Horsfall 1984). Species in which precocial young hatch relatively more synchronously (Anseriformes, Galliformes, many Charadriiformes) are less prone to severe incubation neglect, but moderate disruptions of incubation at the time of hatching do occur (Orcutt & Orcutt 1976), and can result in altered thermal conditions at the nest (Norton 1972). Even in these species, late-hatching terminal eggs are sometimes abandoned (eg. Bergstrom 1988).

Terminal egg neglect is evidently neither severe nor common in altricial Passeriformes, especially in those species with biparental care. However, the attentiveness of incubating parents may be disrupted at the time of hatching (Kendeigh 1952), and some corresponding changes in egg temperature, both increases (Weathers & Sullivan 1989) and decreases (Magrath 1988), have been reported.

We have not attempted an exhaustive review of the avian incubation literature, but from the evidence we have seen, terminal egg neglect seems most likely to occur in species that use relatively open nests placed at ground or water level, especially when the young are precocial or semi-precocial and hatch asynchronously. Some neglect is also present in open nesting altricial species like pelicans. Many studies of nest or

egg temperatures have not reported specifically on events during the hatching period (Webb 1987), so it may be that terminal egg neglect is more widespread than we have indicated here. Further detailed studies are required.

EFFECTS OF CLUTCH SIZE AND HATCHING ASYNCHRONY

In the Herring Gull, reduced clutches produced by experimental removal of the *b*-egg significantly reduced neglect of the *c*-egg (Lee 1988). In the Glaucous-winged Gull *L. glaucescens*, artificially enlarged clutches hatched less successfully, probably because the terminal eggs were neglected more (Reid 1987). Clutch size was also implicated as a factor in naturally occurring terminal egg abandonment in coots (Gullion 1954, Horsfall 1984), with terminal eggs in large clutches being more subject to abandonment.

Within-clutch hatching asynchrony is a necessary correlate of terminal egg neglect, since there would be no "terminal" egg in perfectly synchronized clutches. In precocial species, the much greater incidence of neglect reported for species in which the hatch is strongly asynchronous (coots, grebes) than for the many species where the young hatch relatively synchronously suggests asynchrony facilitates neglect. Reid (1987) found a greater incidence of terminal egg neglect when hatching asynchrony was experimentally increased in Glaucous-winged Gulls. The same effect of experimentally increased hatching asynchrony has been found in some open nesting thrushes *Turdus* and finches *Fringilla* (Slagsvold 1985).

EFFECTS OF EGG CHILLING

There is much evidence that chilling eggs during incubation can retard hatching (Lundy 1969, Webb 1987), but less is known about the effects of chilling during the final hours of incubation when neglect of terminal eggs occurs. Evans (1990b,c) studied effects of chilling eggs during the final stages of incubation in the laboratory. In Domestic Chickens *Gallus gallus* significant retardation of hatching occurred with either constant or intermittent chilling of pipped eggs to 30°C or lower. Clutches of Ring-billed Gull *Larus delawarensis* eggs chilled to 33°C from pipping of the *a*-egg onwards also exhibited a delay in hatching and an increase in within-clutch hatch asynchrony. In American White Pelicans, *b*-eggs chilled from pipping of the *a*-egg onwards were not affected at 36°C (normal internal temperature of pipped eggs has a mean \pm SE of $37.8 \pm 0.3^\circ\text{C}$, Evans in press a), but were markedly retarded at 33°C (Evans 1990c).

The effect of terminal egg neglect on hatching time has been examined experimentally under natural conditions in Herring Gulls. Lee (1988) compared normally incubated control clutches with clutches in which pipped *c*-eggs were incubated without neglect by foster parents that were at a slightly earlier stage of their incubation cycle. In contrast to the results from laboratory studies cited above, pip-to-hatch intervals were slightly but not significantly shorter for neglected *c*-eggs, and *a*- to *c*-egg hatch intervals at nests with neglected *c*-eggs were significantly shorter. The latter result was not due to differences in laying intervals between experimentals and controls. Effects of chilling Herring Gull eggs were subsequently examined in a laboratory

incubator, following procedures used previously for Ring-billed Gulls and pelicans. As in the other laboratory studies, there was a tendency for chilling to increase pip-to-hatch intervals, but in Herring Gulls this effect was not statistically significant at 33°C. Significantly lower hatchability and hatch retardation did occur when chilling extended down to and below 30°C (R. Evans and S. Bugden, unpublished data). These results suggest that Herring Gull pipped eggs are resistant to the retarding effects of chilling down at least to 33°C, making possible a net hatch acceleration by other stimuli when c-eggs are only moderately neglected. In arctic-nesting Calidridine sandpipers, Norton (1972) found an increase in hatching synchrony during periods when parents were less attentive to their terminal eggs. This result also suggests that moderate amounts of neglect sometimes may accelerate hatching of terminal eggs. There is a large body of evidence that hatching synchrony can be accelerated under laboratory conditions by non-vocal embryonic clicks emanating from siblings in some precocial species (Vince 1969), but the relevance of this synchronizing mechanism for normally asynchronous clutches incubated under natural conditions has yet to be demonstrated (Schwagmeyer et al. in press).

Last-hatched embryos can also adapt to incubation neglect by direct vocal appeal to their parents (Evans 1988b). Simmons (1955) was evidently the first to suggest that embryonic vocalizations (in grebes) reduce the likelihood that parents will neglect terminal eggs, but we have found no documentary evidence for this effect of embryonic vocalizations in grebes. Experimental evidence for a positive effect of embryonic vocalizations on parental incubation behavior has been reported for the Guillemot *Uria aalge* (Tschanz 1968) and for geese *Anser indicus* (Wurdinger 1970, cited in Drent 1973).

The ability of embryos at the pipped egg stage to influence parental behavior and hence incubation temperature has been examined in more detail in the American White Pelican. Temperature measurements taken from the upper egg surface during natural incubation indicated that pipped *a*-eggs were kept significantly warmer than unpipped terminal *b*-eggs, and *b*-eggs in nests containing hatched *a*-offspring were kept warmer after pipping than before (Evans in press a). Laboratory studies showed that pelican embryos within pipped eggs call vigorously when chilled or heated, and can thermoregulate for periods of up to at least 5 h when these vocalizations control the temperature of a surrogate heat source (Evans 1988b, in press b).

COSTS AND BENEFITS TO PARENTS

To the extent that eggs normally require incubation by a parent, terminal egg neglect would be expected to decrease the individual fitness of the affected offspring. Examples of hatch retardation and mortality cited above agree with this supposition. The possibility that moderate amounts of neglect in Herring Gulls and arctic-nesting Calidridine sandpipers may reduce within-clutch hatching asynchrony, thereby potentially benefiting the terminal offspring, provides an apparent exception. Even if one assumed that the usual effect of neglect can be best represented as a cost to the offspring, it does not follow that it will always be a net cost to the parents. In particular, for species exhibiting brood reduction the reproductive value of terminal offspring is typically depressed relative to their older siblings (Mock 1987). In these species, parents may be able to benefit by providing relatively less care to terminal offspring, before as well as after hatching (Quinn & Morris 1986).

The adaptive consequences of investing differentially in terminal and nonterminal young will also depend on the costs of such investment (Evans 1990d). Incubation consists largely of unshared care, i.e. care can be received simultaneously by more than one offspring (Lazarus & Inglis 1986), although some additional cost in the form of greater energy expenditure or longer incubation periods may be required (Haftorn & Reinertsen 1985, Moreno & Carlson 1989). In species like pelicans having altricial young and biparental care, first-hatched young normally remain at the nest and require close brooding until all eggs have hatched (Evans 1989), so a terminal egg can continue to be incubated at little extra cost. Given this low cost, the substantial insurance value (up to 20%) of pelican terminal eggs (Cash & Evans 1986) appears to be more than adequate to provide a net parental benefit for caring for them, hence the low levels of neglect found in this species.

In species where precocial or semiprecocial young can leave the nest soon after hatching, costs of continuing to incubate terminal eggs may be greater. In Herring Gulls, the tendency to feed the first-hatched young away from the nest is not compatible with continued close attentiveness to the unhatched terminal egg. The adaptive significance of early brood movements away from the nest has not been studied in detail in gulls, but early nest leaving may be an anti-predator adaptation facilitating a spacing out of the offspring, as suggested for territorial spacing in this species (Tinbergen 1952). In coots, abandonment of terminal eggs allows both parents to feed the older chicks (Gullion 1954, Horsfall 1984). Where anti-predator or food-related benefits of moving older offspring out of the nest outweigh costs of reduced care to the remaining egg(s), terminal egg neglect can be an adaptive parental strategy.

CONCLUSIONS

Terminal egg neglect does not appear to be a necessary correlate of brood reduction, as illustrated by the low levels of neglect in the American White Pelican, a species in which brood reduction is virtually obligate (Cash & Evans 1986). In this species, the sudden cessation of *b*-egg neglect as soon as it pips and can communicate vocally with its parents is instructive, since such apparently cooperative parental behavior would seem unlikely if parents benefited from terminal egg neglect as part of a brood reduction strategy. As suggested elsewhere (Evans in press a), neglect of the *b*-egg may arise in pelicans not because it benefits the parent, but because at the time it occurs the *b*-embryo is still pre-vocal and unable to communicate adequate information about its current temperature.

The situation in gulls is complicated by the occurrence of different levels of neglect, ranging from moderate neglect that appears to be characteristic of Herring Gulls (Drent 1970, Lee 1988), to the relatively rare but more severe neglect culminating in abandonment and mortality of terminal eggs as reviewed above. The finding that hatching in Herring Gulls is not retarded by moderate chilling and may even be accelerated by neglect under natural incubation conditions suggests that a moderate level of terminal egg neglect, although common, is not normally employed as an adaptive brood reduction strategy in this species. As is the case for pelicans, moderate levels of terminal egg neglect in gulls seem more likely to represent a largely unavoidable consequence of asynchronous hatching.

Where there is a significant tradeoff between caring for first-hatched offspring away from the nest and remaining at the nest to incubate terminal eggs, it evidently can benefit parents to care for the older offspring at the expense of terminal eggs. Whether the benefit to parents arises from brood reduction itself or from other sources such as avoidance of predation risks at the nest or an enhanced ability to feed precocial young away from the nest remains uncertain. Evidence that neglect may be part of an adaptive brood reduction strategy comes from studies showing a positive relationship between terminal egg neglect and clutch size. At unmanipulated nests (eg. coots), results may be confounded by a tendency for hatch asynchrony to increase with clutch size. In gulls, where hatch asynchrony was controlled experimentally, removals of *b*-eggs from natural three-egg clutches reduced neglect (Lee 1988) while additions increased terminal egg desertion (Reid 1987). Although not conclusive, these results suggest that at present there is no compelling reason to reject the hypothesis that terminal egg neglect can sometimes be part of an adaptive parental brood reduction strategy. More experimental studies of terminal egg neglect, its causes and consequences, are required.

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NONAGGRESSIVE BROOD REDUCTION IN BIRDS

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ABSTRACT. Brood reduction is only sometimes associated with overt fighting among nestmates. Despite detailed studies of the dynamics of aggressive (siblicidal) brood reduction, few researchers to date have considered how sibling rivalry is resolved in brood-reducing species that exhibit little or no aggression. In such taxa, competition is based on gaining favorable positions during meals and/or consuming food rapidly. The resulting mortality generally takes the form of starvation of the younger/smaller nestlings. While nonaggressive forms of rivalry avoid the usual costs of fighting, they clearly impose costs of their own, such as greater begging effort and increased risk of accidental ejection from the nest during jockeying. We propose that the general tendency for overt aggression to be common in predatory species stems from the economics of intimidation: in species that lack weaponry, nestlings may simply be more effective competitors by relying on 'scramble competition'.

Keywords: Brood reduction, nonaggressive reduction, siblicide, sibling aggression, sibling competition.

INTRODUCTION

Although sibling aggression can be an important element in the brood reduction process (e.g. Mock 1984a, Simmons 1988), most partial-brood mortality occurs in taxa whose nestlings seldom or never engage in overt combat with each other. As interest in various facets of brood reduction appears to be increasing, this seems an opportune moment to call attention to some of the ways brood reduction is settled in the absence of aggressive interactions between nestlings.

Early interest in aggressive brood reduction ("siblicide") stemmed from the natural history descriptions of the habit in raptors (e.g. Salter 1904, Bent 1937-8, Witherby et al. 1938, Rowe 1947, Ingram 1959). The recent surge in research on aggressive brood reduction systems seems due largely to three factors: (1) an appropriate evolutionary framework for the problem; (2) the realization that several easily observed (i.e., colonial) species are siblicidal (e.g. kittiwakes: Braun & Hunt 1983; boobies: Drummond et al. 1986, Anderson 1990; pelicans: Cash & Evans 1986; ardeids: Mock 1984b, 1985, Fujioka 1985); and (3) concern for endangered species that seem to squander potential reproductive success by being siblicidal (e.g. Whooping Cranes *Grus americana*: Novakowski 1966; various eagles: Gargett 1967, Meyburg 1978).

The theoretical underpinnings were first sketched out by Lack (1947), who explained how brood reduction can be beneficial to parents, then developed more fully by O'Connor (1978), drawing heavily from Hamilton's (1964) theory of inclusive fitness. Lethal combat among sibs now tends to be regarded as an extreme manifestation of selfishness, which can be adaptive when conditions are so severe as to necessitate a choice between the sacrifice of the attacker's closest genetic relatives and its own survival. Predictions derived from this perspective have been field-tested increasingly with colonial species, where the sheer logistical luxury of monitoring numerous broods

— and even observing behavioral details directly — has accelerated empirical progress on several issues. Studies of species with aggressive chick interactions have provided detailed information on how variability in environmental conditions (notably food availability) influences the frequency of sibling interactions and how such interactions affect the frequency and timing of brood reduction.

Compared with the considerable quantity of information amassed on siblicide, the components of nonaggressive brood reduction (Lack 1947, 1954, Ricklefs 1965, Magrath 1989) have received little attention. This is somewhat ironic, since such brood reduction is probably more widespread than siblicide (nonaggressive brood reduction has been reported for at least 108 species of birds, while siblicide occurs in 83 species: Mock & Parker unpubl.). Thus we know quite a bit about which taxa have reduction without aggression and have an array of models (plus some nice field data: e.g. Crossner 1977, Skagen 1987, Magrath 1989) to explain why they do it, but few details to date, on exactly how nonaggressive brood reduction is resolved. Assuming that the interests of the participants (parents, older, and younger nestlings) in this form of brood reduction are basically similar to those in siblicidal species, we here examine why aggression per se is not used. Basically, we shall argue that ineffective weaponry, indefensible parental resources, and/or large initial size asymmetries between chicks can reduce the need for, or even preclude, effective sibling aggression.

It seems worth emphasizing that nonaggressive reduction is neither a passive process nor intrinsically “better” than siblicide, just different. Superficially, pacifist nestlings might be expected to come out far ahead of aggressive ones, simply because they are spared the costs of combat. Such costs must include the time, energy, and opportunities lost while blows are actually being exchanged, plus any risks of being injured. On the other hand, fighting presumably evolves in siblicidal species because there are some circumstances in which paying those combat costs is worthwhile, specifically when fighting alleviates competition for limited parental resources more efficiently than other solutions. If a life-threatening shortage is likely to arise during the period of chick dependency, as we infer from the frequency of partial-brood mortality, avoiding the use of aggression seems likely to impose its own special costs. These costs may include escalated begging effort and perhaps enhanced vulnerability associated with intensified solicitation activities.

To illustrate a bit of what is known about nonaggressive brood reduction, we start by sketching a few systems for which descriptive information exists. We follow that with a general framework we think may prove useful in future studies of sibling rivalry.

SELECTED EXAMPLES

Passerines

Large brood size and lack of sufficient weaponry make aggressive monopolization of food unprofitable. In many passerines, there are simply too many nestmates for efficient intimidation. Instead, chicks compete for position within the nest. When parents return, they tend to feed the closest and most conspicuous young (Ryden & Bengtsson 1980, Bengtsson & Ryden 1981, Gottlander 1987). Hungry young move in the direction of positions with the highest probability of receiving food while passive,

recently fed young are pushed to the bottom or back of the nest (Greig-Smith 1985, Haftorn 1986). On those occasions when several young are equidistant from the parent, increased begging intensity by one chick enhances its probability of being fed (Ryden & Bengtsson 1981, Haftorn 1986, Gottlander 1987).

When food is plentiful, the frequent shifting of positions within the nest results in food being distributed randomly among all nestlings (Reed 1981, Haftorn 1986). However, such a system may allow aggressive chicks to dominate food distribution patterns during periods of critical food shortage (Reed 1981) either through preventing smaller young from gaining favored locations in the nest or because older nestlings are better at attaining food from a "bad" position (Ryden & Bengtsson 1981, Haftorn 1986).

The costs of nonaggressive competition in passerine broods not only include energy expended on begging and jostling for position within the nest, but may include an enhanced risk of accidentally falling from the nest (B. Chapman, pers. comm.). In addition, the entire brood sustains an added cost if high levels of begging increase vulnerability to predators (Perrins 1977).



FIGURE 1 – Relative chick positions during crested penguins feeds. Successful chicks typically stand in front, pinning their sibling against the parent's breast.

Crested Penguins

Penguins in the genus *Eudyptes* lay two eggs, yet almost never raise more than one chick (Warham 1975, Williams 1980, Lamey 1990). Whereas most obligate brood reduction (e.g. eagles: Gargett 1978; boobies: Drummond 1987, Anderson 1990; pelicans: Cash & Evans 1986) is siblicidal, that is, the result of unsparing aggression by the older chick against the younger, *Eudyptes* chick loss stems from nonaggressive

competition between two badly mismatched opponents. Crested penguins may be the only example of brood reduction that is both obligate and nonaggressive (the other candidates are ground hornbills, *Bucorvus* spp.).

Competition for food in crested penguin broods is greatly influenced by the nestlings' size disparities, which result from physical and temporal advantages given to one chick. In addition to hatching their two eggs as much as seven days apart (Williams 1980), crested penguins lay clutches with the greatest egg size disparities of any avian group (Slagsvold et al. 1984). Even more peculiarly, the second-laid egg is the larger, averaging 20-70% greater than the first (Warham 1975, Williams 1980, Lamey 1990). Since the first chick to hatch in each nest usually comes from the second-laid egg, it enjoys a temporal advantage in addition to the size advantage. As a consequence of the size mismatch, the smaller chick usually is never fed and dies of starvation less than 10 days after hatching (Warham 1974, Lamey unpubl.).

Even when the sibling asymmetry is relatively small (in which case rivalry for resources intensifies), competition between chicks consists primarily of a scramble for the 'best' position during meals. The location of the chicks during meals, both relative to each other and to the mother, is important in deciding which chick succeeds in obtaining the food bolus. In nests with (typically) large size asymmetries, the successful chick usually stands in front of its nestmate such that the loser is pinned against the parent's breast (Figure 1).

Crested penguins feed their chicks with monopolizable, "direct" (bill-to-bill) passes of boluses (sensu Mock 1985), yet the older chick does not use aggression or intimidate its younger sibling so as to increase its own share of food. It does not have to: enormous size asymmetries suffice, eliminating any need for aggressive interactions. Basically, the larger chick just takes whatever it wants. Moreover, a young crested penguin may lack adequate weaponry to intimidate its nestmate.

Great Blue Herons

In Texas, Great Blue Heron *Ardea herodias* brood reduction occurs as frequently (ca. 2/3 of all nests) as in the adjacent nests of siblicidal Great Egrets *Casmerodius albus*, yet involves 94% fewer fights (Mock 1985). Many youngest members of heron broods simply fail to grow and eventually starve as their slightly older and stronger nestmates consume virtually all the food. This establishes a positive feedback loop by which the senior siblings further enhance their size and strength advantages. That is, in these birds the fatal competition for food is based mainly on ingestion speed, literally the chiseling of semi-digested mouthfuls from large fish carcasses that have been regurgitated by parents. This 'scramble competition' for food results from prey items that are too big for chicks to swallow whole. The large, partially digested fish simply lies on the nest floor where it is not "economically defendable" (sensu Brown 1964) via intimidation.

Actually, Great Blue Heron sibling aggression is quite facultative, occurring only when food items are monopolizably small. Normally "pacifistic" Texas herons become active (siblicidal) fighters when raised on a diet of tiny fish by Great Egret foster-parents (Figure 2; Mock 1984b). Furthermore, nestling Great Blue Herons in Quebec, where they are fed mainly small sticklebacks (by their natural parents), also show highly elevated levels of sibling aggression (Mock et al. 1987a).

In siblicidal species generally, chicks tend to receive food as monopolizably small pieces and such items are transferred to them from the parent by some form of direct pass (Mock 1985). Conversely, when food is delivered in large pieces and spends considerable time on the nest floor, aggression may not be cost effective.



FIGURE 2 – Great Egret and Great Blue Heron cross fostering nests. Normally pacifist Great Blue Heron chicks increase their fighting levels dramatically when raised on the small fish presented by adult Great Egrets.

A GENERAL FRAMEWORK FOR THE STUDY OF NONAGGRESSIVE REDUCTION

Fatal sibling competitions involve a set of players possessing a similar array of behavioral options and each player attempts, albeit subconsciously, to maximize its inclusive fitness (i.e. its own future reproductive success plus the sum of its kin's future success, devalued by the appropriate degrees of relatedness). Because virtually all brood-reducing birds show asynchronous hatching, the nestmates start the game substantially mismatched and the best behavioral choice for each is rank-specific, depending on hatch-order. For example, in 3-chick broods, the behavior best for a

would be disastrous for *c* and vice versa. There is every reason to view these roles as flexible; moving a *c*-chick from its home nest, where it would be subordinate and increasingly timid, to a younger brood quickly produces an arrogant bully.

For simplicity, we assume that parents show perfect impartiality once hatching is complete. This accords with most (Drummond et al. 1986, Mock 1987), but not all (Stamps et al. 1985, Gottlander 1987), published accounts.

Each behavioral option confers a mixture of costs and benefits that accrue to the focal individual whose actions are under consideration. In truly monogamous species (where mean sibling relatedness is 0.5), *a*'s option of destroying a sibling as quickly as possible might consist of some short-term energetic costs of execution and a sizable long-term cost of lost indirect fitness (half of *b*'s reproductive value). On the positive side, such an act is likely to enhance *a*'s direct fitness once *b* has been eliminated as a competitor for parental resources (food). If these benefits invariably outweigh the costs, then obligate brood reduction should be favored by natural selection. The game ends with one chick's demise (usually *b*, but if *a* is defective and predeceases *b*, the game ends at that moment). In facultative brood-reducing species, of course, the key question is whether anyone must die.

Costs and Benefits

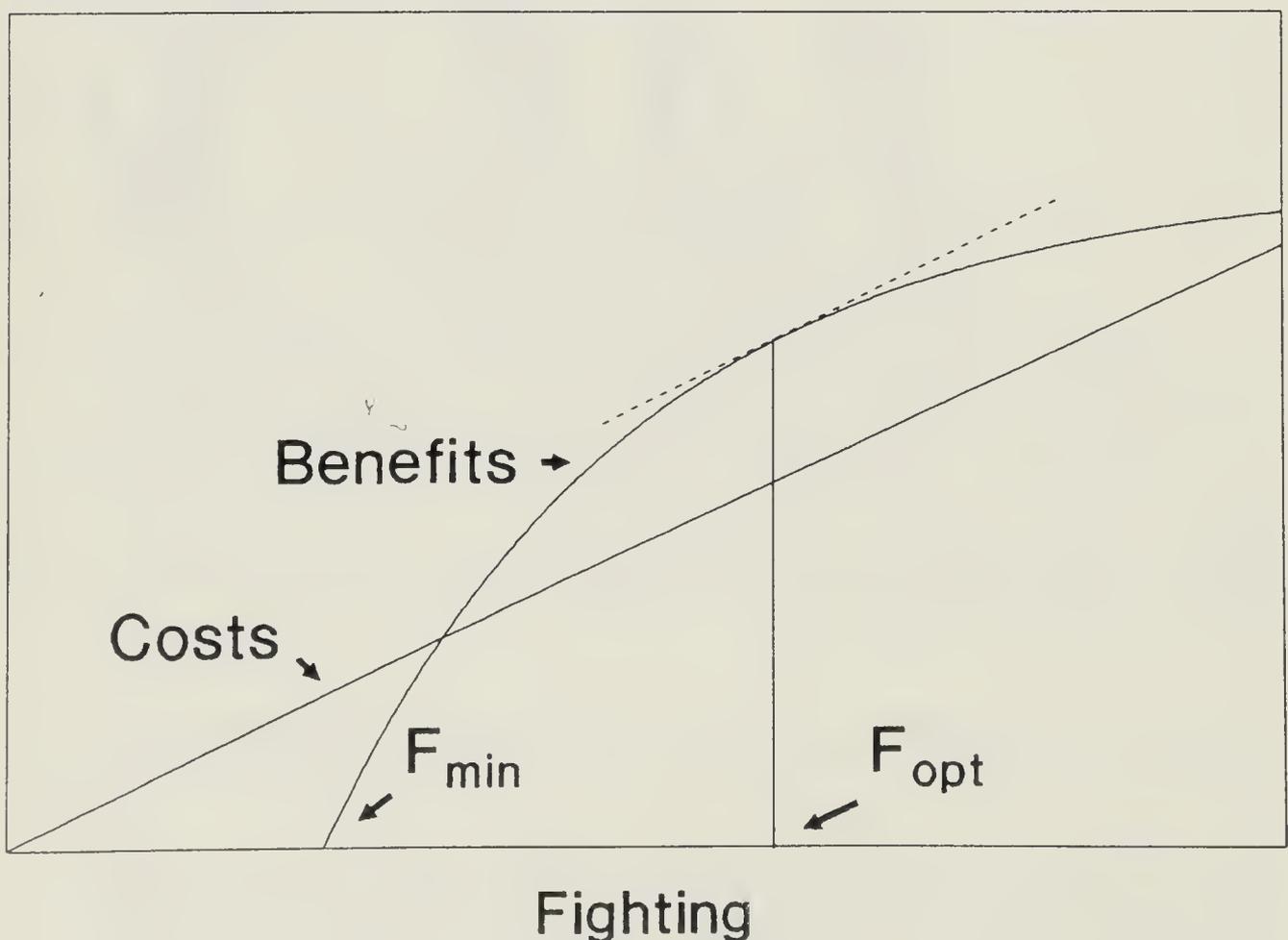


FIGURE 3 – Graphical representation of the costs and benefits of fighting. The optimal fighting rate (F_{opt}) occurs when the slope of the benefit curve equals the slope of the cost line.

In all brood-reducing systems, the behavioral problem remains of what is the best method of effecting a chick loss once it is truly necessary. The decision to fight or not hinges on the relationship between the overall costs and benefits for that species's style of competition.

The direct-fitness costs of fighting take at least three forms: energy, risk, and lost opportunity. Little is known about any of these. The energy spent in combat appears, at least superficially, to be nontrivial. Great Egret chicks may exchange over 100 pecks in rapid order (Mock 1985) and one Black Eagle *a*-chick was recorded as having pecked its nestmate 1,569 times during their 3-day coexistence (Gargett 1978). Even less is known about the risk of injury, though this clearly depends on who attacks whom: lower ranking sibs do occasionally start fights and vigorous retaliation typically follows. Finally, in broods containing more than two chicks aggression during meals often takes both combatants out of contention for food items that are available only briefly. Fighting often intensifies during meals, perhaps because a bullying sib often obtains more food (between attacks) than its victim, thereby improving its relative status. In general, we suspect that total fighting costs are either linear with fighting rate or only mildly accelerating (e.g. if retaliation injury is more likely when the aggressor is fatigued).

Costs and Benefits

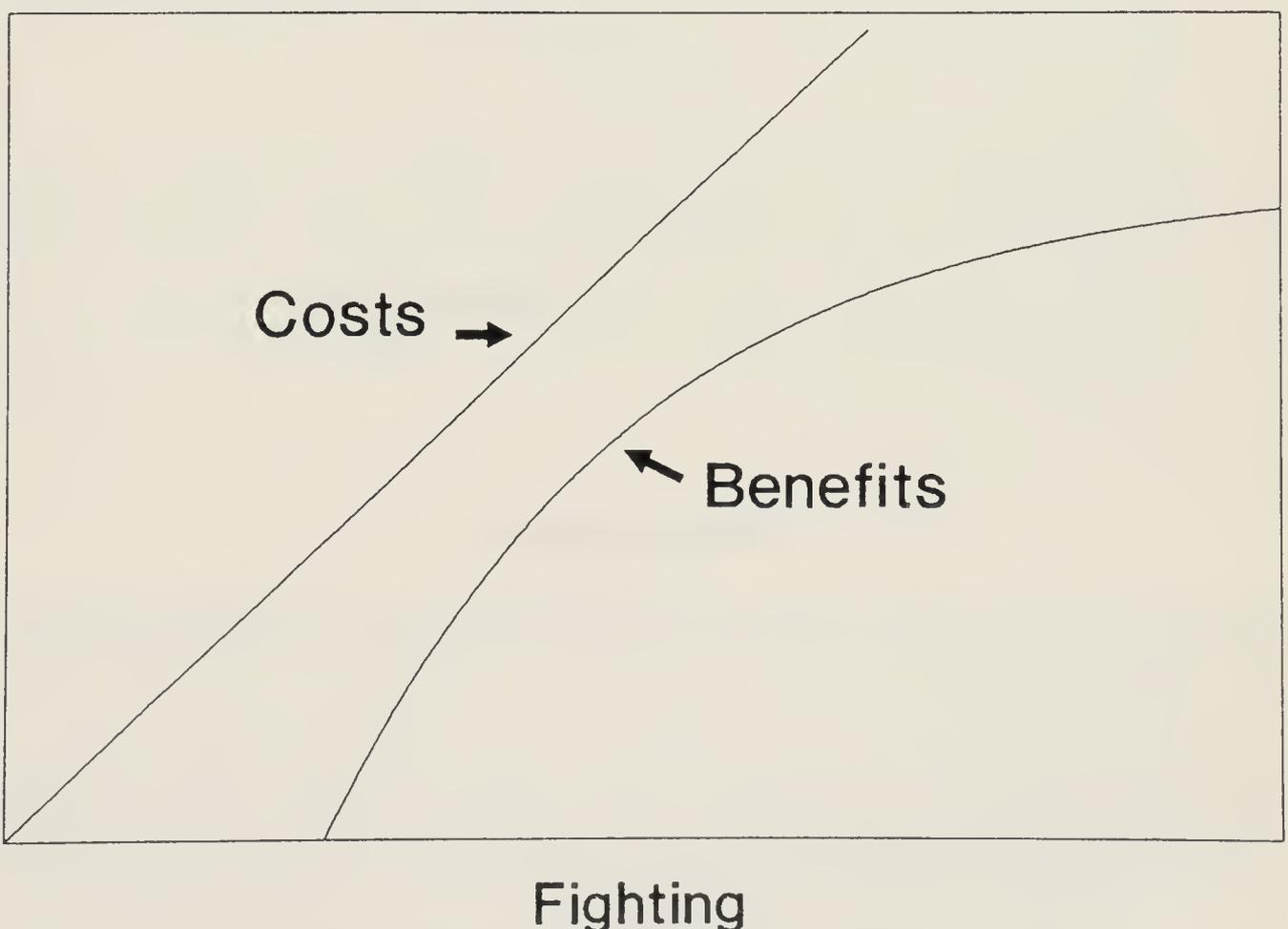


FIGURE 4 – Costs and benefits of fighting in a hypothetical species with no weaponry. Even a high benefit curve still fails to exceed the costs of fighting.

The cumulative benefits for fighting are likely to follow a decelerating function that commences only after an initial investment. That is, effective intimidation is not instantaneous. Therefore, while the cost function passes through the origin (the very first

fight costs more than no fighting), the benefit curve stays at 0 until some point, F_{\min} . We propose a cumulative gain curve rising rather steeply, if sigmoidally, from F_{\min} but reaching an asymptote when all rivals are intimidated.

The economics of intimidation should depend on factors that influence the shapes of these cost and benefit functions. The optimal amount of fighting (F_{opt}) lies where the benefit minus cost difference is maximized, which occurs when the slopes are equal (Figure 3). If the curves do not touch, then aggression is never "cost-effective" (Figures 4 and 5). Note that brood reduction may still be beneficial, in which case other methods of effecting chick loss may have to be used.

Costs and Benefits

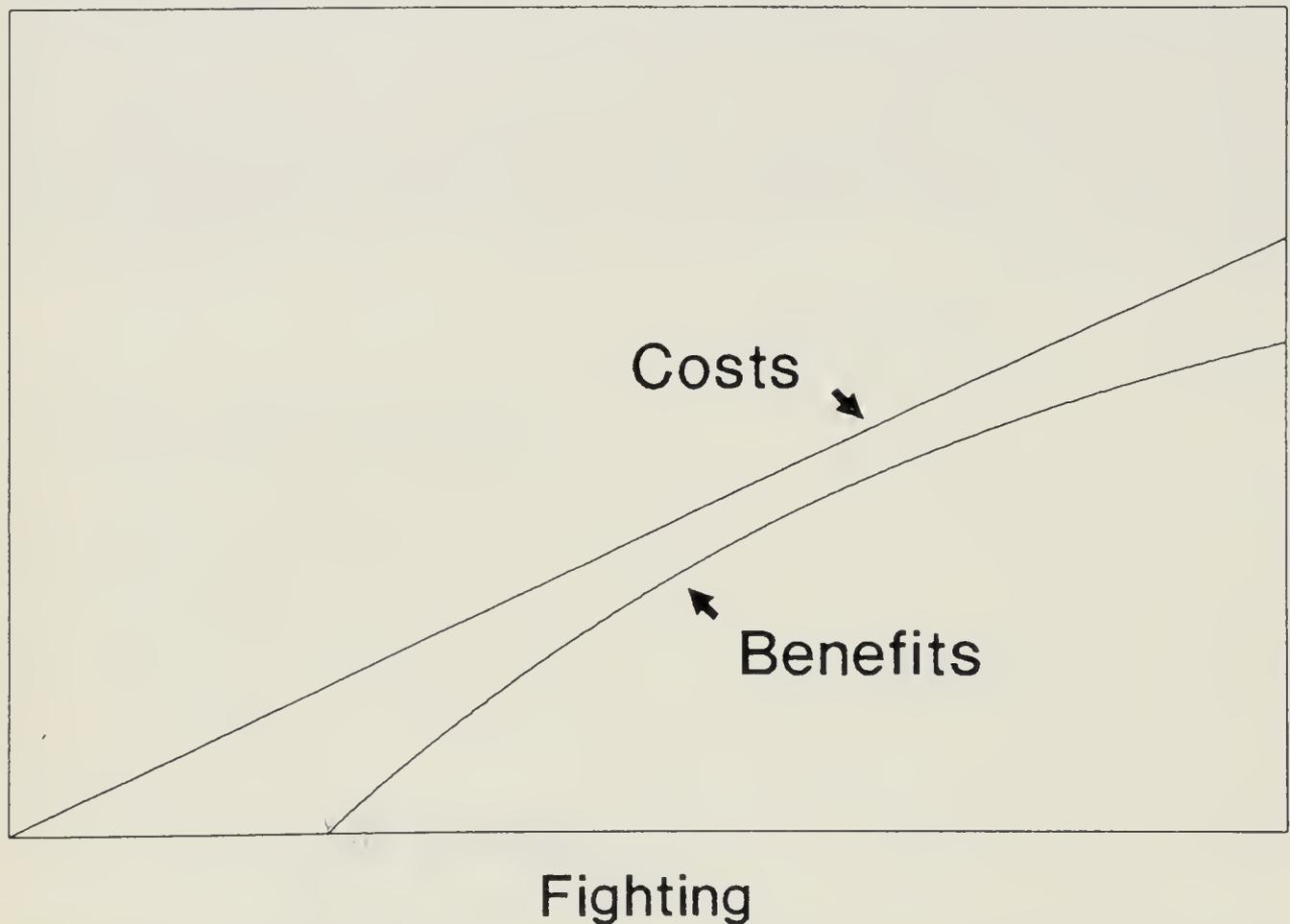


FIGURE 5 – In other hypothetical species the benefits of fighting may be so low (due to large prey, large brood, or great hatching asynchrony) that even a low cost slope (weapon-laden) fails to intersect it.

Probably the factor that most clearly affects the cost slope is the presence or absence of "weaponry" (especially a bill capable of inflicting serious injury). In general, weak-billed taxa (e.g. most passerines) probably have steeper cost slopes than predatory species (e.g. raptors). By analogy, consider that a human prizefighter allowed to carry a handgun into the ring would not need to be in particularly good physical condition. A very few animals even acquire temporary weapons during the time of acute sibling competition (e.g. deciduous eyeteeth of piglets: Fraser & Thompson in review; special 'cannibal-morph' dentition of spadefoot toads: Bragg 1956; necrotic tail tip of pronghorn embryos: O'Gara 1969). In birds, a parallel case has recently been reported. Siblicidal nestlings of the Blue-throated Bee-eater *Merops viridis* apparently use an ephemeral bill-hook to kill nestmates (Bryant & Tatner 1990). In other birds,

the nestling "weapon morphology" probably exists mainly because of various adult functions.

The benefit curve for a particular species/population is likely to be determined by: (1) the balance between food supply and demand (i.e. the severity and duration of resource shortages), either current or pending, and (2) factors that influence the economic defendability of limited resources. In the first category, decreased parental food deliveries may stiffen competition and stimulate aggression, as in the case of Blue-footed Boobies *Sula nebouxii* (Drummond et al. 1986, Drummond & Garcia Chavelas 1989). Alternatively, egrets are quite insensitive to food amount (Mock et al. 1987b), but curtail fighting sharply when demand is reduced (e.g. after brood reduction: Mock & Lamey in press).

Economical defendability of food can be influenced by prey size (i.e. monopolizability, as discussed above), nest type (e.g. narrow subterranean tunnel vs. open cup), and within-brood size asymmetries. Each of these factors has been related to the intensity of fighting during brood reduction. For example, Cattle Egrets *Bubulcus ibis* fight much more when normal size differences among brood members are eliminated experimentally (Fujioka 1985, Mock & Ploger 1987) and somewhat less when those differences are exaggerated.

DISCUSSION

From this framework, it follows that nonaggressive brood reduction should be found whenever resources (especially food) are insufficient to support all nestlings and when various combinations of the following occur: (1) very steep costs (typically associated with poor weaponry), (2) non-monopolizable food items (and "indirect" delivery of large prey from parents to offspring), (3) large brood size (high opportunity costs for fighting), and (4) extraordinarily great initial size disparities among nestmates (e.g. *Eudypetes*).

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SYMPOSIUM 31

ADAPTATIONS TO EXTREME ENVIRONMENTS

Conveners R. PRINZINGER and R. E. REINERTSEN

SYMPOSIUM 31

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INTRODUCTORY REMARKS: ADAPTATIONS TO EXTREME ENVIRONMENTS

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Birds and mammals are the only real homoiothermic (endothermic) animals. This physiological ability allows them to keep temperature-dependent physiochemical processes of the organism working even in a broad range of ambient temperatures. By this, both vertebrate classes could have colonized subsequently nearly all habitats of the world by adaptive radiation. Birds therefore live and breed not only in temperate but also in extreme environments even in regions where we do not find mammals. The following symposium deals with this phenomenon.

The main environmental challenges are caused by the following abiotic factors (see e.g. Davenport 1985):

- ambient temperature
- solar radiation
- salinity and water supply
- food supply
- oxygen tension
- desiccation, and last, but not least,
- pollutants

The last factor is a modern anthropogen problem which will not be treated in our symposium.

Even small birds of 10-12g, e.g. the Willow Tit *Parus montanus* or the Redpoll *Acanthis flammea*, face in the northern USSR (basin of Worcuta) for example minimum ambient temperatures of -60°C. Mean value in January is -25 to -30°C. Snow is covering the ground on 240 days a year and 15-20 snow-storms (so called "Purgas") with wind speeds up to 40m/s rush over the land and often last several days each winter. Additionally the light-time is very short (below 8 h) (Schaefer 1957).

Conversely, in deserts, air temperature may soar above +60°C during the day. Ground temperatures may be even higher in the tropics because the low specific heat of the atmosphere allows the ready passage of the sun's radiant heat. Substratum temperatures above +80°C are not uncommon - it is feasible to fry an egg on desert rocks. Nevertheless, this is of course not the aim even of a breeding bird. For the birds water supply is often very limited and desiccation by evaporative water loss is a great problem. Nevertheless, we can find a lot of birds in this extreme environment. In the Negev desert mean daytime temperature during summer is +36 to +42°C. Solar radiation amounts to 300-365 J/cm². This is the 3- to 4-fold value of heat production per surface of the Brown-necked Raven *Corvus corax ruficollis* for example, a 900g bird. Its

black feathers can reach surface temperatures up to 100°C and more (Marder 1973 a,b, Prinzing 1990). Free water for temperature regulation is additionally very rare. Striking adaptations can be observed in other environments. On the oceans some petrels (e.g. the Giant Petrel *Macronectes giganteus*) can live outside their breeding season exclusively flying over the open sea rounding the whole world and drinking only salt water.

There are geese species (e.g. the Bar-headed Goose *Anser indicus* and the Andean Goose *Chloephaga melanoptera*) and vultures (the Ruppel's Griffon, *Gyps rueppellii*) which may soar up within a few minutes from sea level to more than 11000 m height where oxygen tension is only 22% of sea level (Hiebl & Braunitzer 1988, Bezzel & Prinzing 1990).

On the other hand, penguins (e.g. the Emperor Penguin *Aptenodytes forsteri*) can dive more than 260m deep (partial pressure of oxygen is here 26-fold as high as under sea level conditions) and remain under water for up to nearly 20 minutes (Flindt 1985).

The survival of all adventurous bird-species depends on the evolution of special adaptations (behavioural, physiological and morphological) to these and less extreme environmental challenges. The following papers will present mechanisms involved in appropriate strategies.

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TEMPERATURE REGULATION AND BIOENERGETICS OF DESERT SANDGROUSE (PTEROCLIDIDAE)

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ABSTRACT. Afro-Asian Sandgrouse live successfully in habitats characterised by temperature extremes (e.g. $T_{\text{air}} > 50^{\circ}\text{C}$ for 7-9 h.d⁻¹) water shortage and low primary productivity, despite unfavourable surface:volume ratios, ground-living habits, and a seed diet low in water. Laboratory studies show that Pin-tailed and Double-banded Sandgrouse (PTS, DBS) have low BMRs (64 & 54%) and low thermal conductances ($C_w = 83$ & 71% respectively) compared to allometric predictions. Black-bellied Sandgrouse (BBS) have normal BMR but a high C_w (97-112 & 145% of allometric predictions respectively). Higher bioenergetic needs of BBS show in time budgets from field studies: BBS spent more daylight time foraging than PTS (57 vs 42%: Spain, spring), or Spotted Sandgrouse (63% vs 50%: Negev Desert). PTS and DBS have more effective evaporative heat dispersal (ca. 100% of metabolic heat at $T_{\text{air}} = T_{\text{b(ody)}}$) than BBS (62%). Sandgrouse are more thermolabile than other birds, and show significant interspecific slope differences for T_b vs T_{air} regressions (BBS, 0.136; DB, 0.095; Namaqua Sandgrouse, 0.056).

Keywords: Sandgrouse, *Pterocles*, deserts, arid zones, temperature extremes, microclimates, body temperatures, thermoregulation, metabolic rates, evaporative heat loss, thermal conductance.

INTRODUCTION

The sixteen species of sandgrouse flourish in arid and semi-arid regions of Afro-Asia (Maclean 1976). The problems they face are those general to animals in such environments (temperature extremes, water shortage and the consequences of low biological productivity), and these place a premium on behavioural and physiological mechanisms which conserve resources. These problems are compounded by several features of sandgrouse biology. As small (150-450 g bm) ground-living diurnal seed-eaters, they are operating in the zone of maximal temperature variation with relatively unfavourable surface:volume ratios, where evaporative water losses are potentially great but dietary water input is low. Consequently, sandgrouse are obligate drinkers, and commute (not necessarily daily) between feeding areas and drinking points over considerable (but often exaggerated) distances. The solutions to these problems may often be conflicting and require trading benefits against risks, as in the dilemma between conserving water in defense of physiological fluid composition and using it in defense of body temperature.

The adaptations of several sandgrouse species (mainly from N. and S. Africa and the Near East) have been studied and reviewed (Maclean 1976, Thomas 1984). Thomas (1984) drew attention to the bioenergetic implications of many of these adaptations, and pointed out the additional benefits of an economical use of scarce energy resources. Therefore, our recent work has been directed towards these bioenergetic questions (Hinsley 1990), in the course of which we have studied several aspects of sandgrouse biology (thermoregulation, energy and water metabolism, time budgets and the benefits of choosing microclimates). This paper reports the major conclusions

of these studies, whose details will be published fully elsewhere (Hinsley & Thomas in prep.).

Sites in Spain (39°N,3°W) and the Negev Desert (31°N,35°E) were used in spring and summer to record time budgets and study the microclimates used by wild sandgrouse. We studied Black-bellied and Pin-tailed Sandgrouse (*Pterocles orientalis* and *P. alchata*: BBS & PTS) in Spain, and BBS and Spotted Sandgrouse *Pterocles senegallus* (SpS) in the Negev. Metabolism and evaporative water loss were measured by open-flow respirometry at the Institute of Desert Research (Sede Boqer, Israel: BBS) and in Cardiff (PTS and Double-banded Sandgrouse *Pterocles bicinctus* DBS). Nomenclature follows Cramp (1985) and Urban et al.(1986).

On a geographical scale, different sandgrouse species occupy areas with markedly different climates and aridity. Choice of study location and species were constrained by availability, and we were able to do most work on species from the less arid end of the spectrum of habitats used by the family as a whole. The following rankings of exposure to key climatic variables has been compiled by quantitative comparison of geographical ranges of our study species (south of 40°N and west of 52°E) with seasonal temperature and aridity classes defined by UNESCO (1977). (NS = Namaqua Sandgrouse *Pterocles namaqua*)

Exposure to minimum temperatures: BBS > PTS > NS > SpS > DBS

Exposure to maximum temperatures: NS ≤ DBS < BBS < PTS < SpS

Exposure to aridity: DBS ≤ BBS < NS < PTS < SpS

THE THERMAL ENVIRONMENT AND BEHAVIOURAL THERMOREGULATION

There is abundant indirect evidence that sandgrouse exploit favourable local microclimatic diversity to reduce the need for physiological regulation (Thomas & Robin 1977, Thomas & Maclean 1981, Thomas 1984). Hinsley (1990) quantified the effects of this behaviour, and showed that even partial shade (from dead or leafless plants) used in summer (Spain, Negev) was significantly beneficial. She used copper taxidermic mounts covered with bird-skin (Bakken 1980) to measure the operative temperature (T_e = thermal potential) of each location. Although differences in T_e between sun and partial shade were only 4-6°C in the heat of the day, this represented a proportionally large reduction ($\geq 50\%$) in the thermal potential difference ($T_{e(\text{sun})} - T_{b(\text{body})}$) commonly +6 to +12°C) driving heat into the bird when ambient T_e 's were more than body temperatures (T_b). It also reduces evaporative water loss markedly, because this increases very rapidly with rising T_{ambient} .

Behavioural thermoregulation

Captive Namaqua Sandgrouse (NS) and DBS showed reduced physical activity (especially when dehydrated) when metabolic activity would presumably have represented an undesirable heat load (Thomas & Maclean 1981, Thomas et al. 1982). This is a behavioural mechanism regulating overall heat balance and contributing to thermoregulation, which now also has been shown to take place in wild sandgrouse. In Spain, PTS adjusted the scheduling of different activities so that metabolically cheaper ones (sitting and standing still) were shifted towards the heat of the day in summer (when $T_e > T_b$), and the more demanding activities (walking, foraging, etc.) became more prominent in the morning and evening, compared to spring (when

$T_e < T_b$: Figure 1). The changes mainly rescheduled the various activities, as there was little change in the the absolute time (or % of daylight) spent on each. However, ecological factors may affect interspecific differences in daily scheduling of activities: in spring in the Negev Desert (where $T_e \leq T_b$ for both species) BBS foraged actively (63% of daytime) at similar frequencies throughout the day but had partial shade (*Zygophyllum* bushes, etc.) in which to do so, whereas SpS lacked equivalent shade in their preferred habitat nearby and concentrated foraging (50% of daytime) into morning and evening periods and were markedly inactive in the heat of the day (Hinsley 1990).

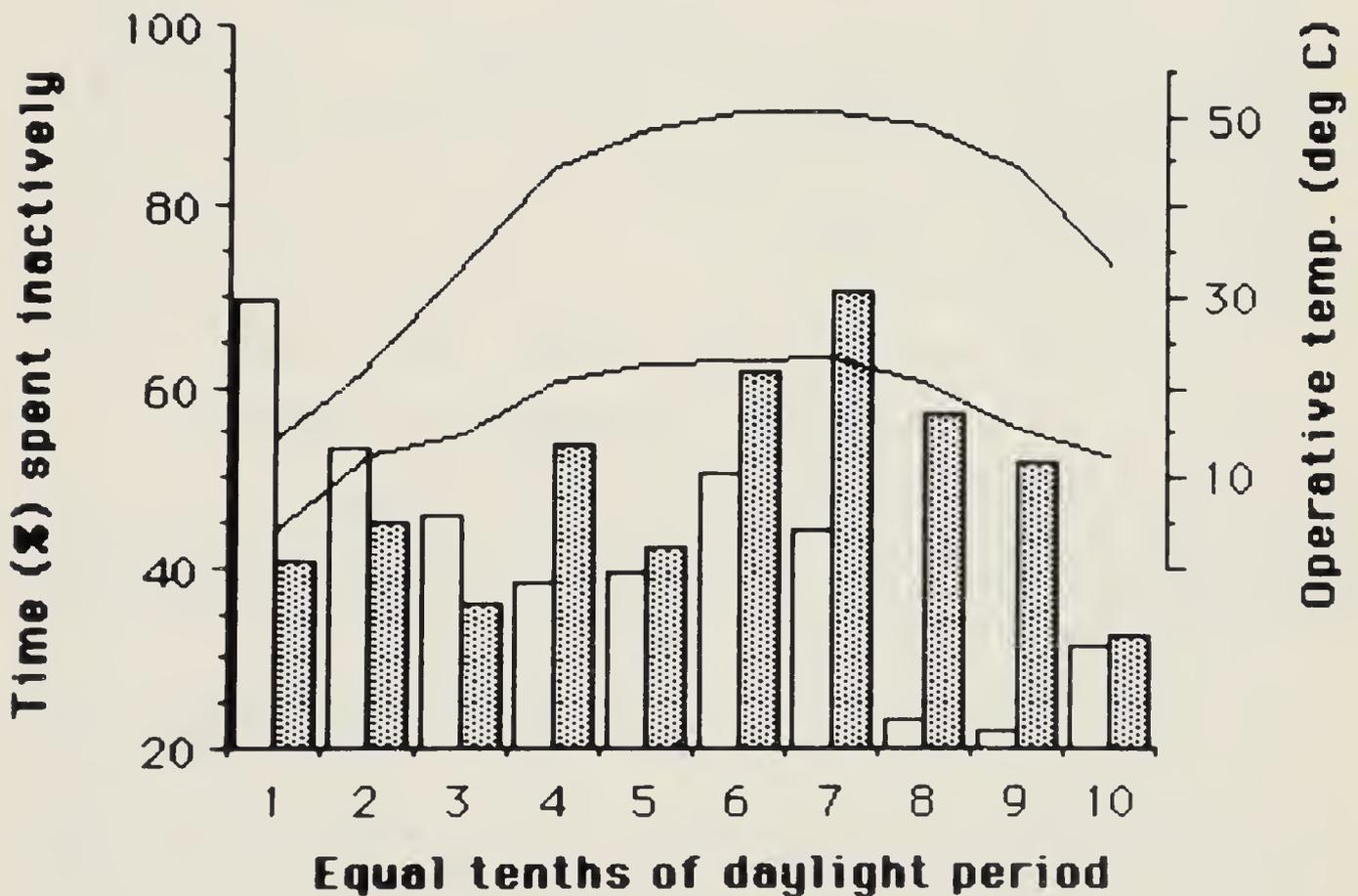


FIGURE 1 – Percentage of daytime spent inactively by adult Pin-tailed Sandgrouse at our Spanish study site in spring (open bars) and summer (shaded bars), compared to contemporaneous measures of operative temperature. Note the shift of inactivity to hotter times of day in summer

PHYSIOLOGICAL THERMOREGULATION

Body temperatures

Sandgrouse tolerate considerable hypo- and moderate hyperthermia by both avian and mammalian standards, and thermolability varies significantly between species (Figure 2). Reduction of $|T_{\text{ambient}} - T_b|$ will always tend to reduce adverse heat exchange and so conserve water or energy reserves even though the effect may be fairly small: <10% of daily water turnover for DBS or NS (Thomas & Maclean 1981). Note that BBS, the most thermolabile species in Figure 2, is also the one with relatively high thermal conductance and metabolic rate (see later), and so would benefit most from minimising $|T_{\text{ambient}} - T_b|$

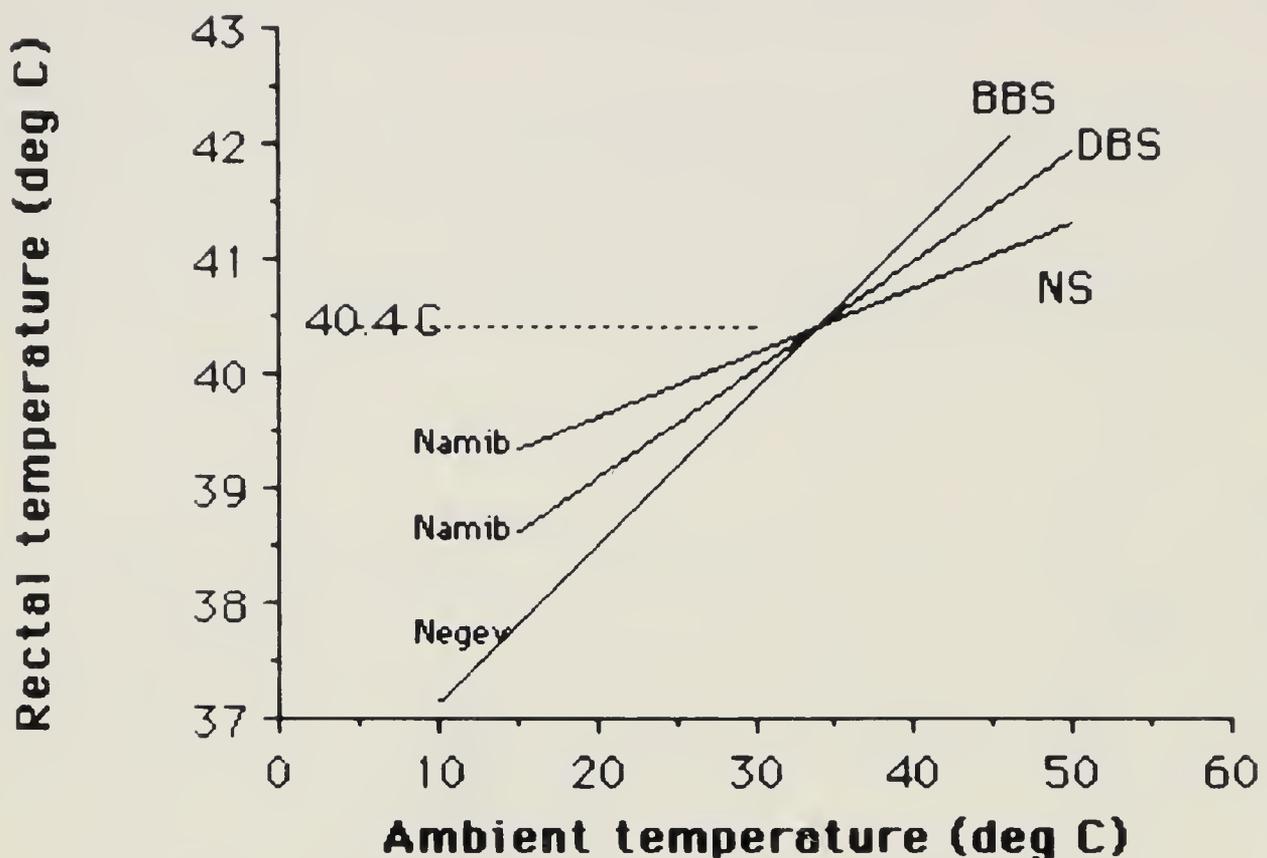


FIGURE 2 – Regression lines of rectal temperature on air temperature for Black-bellied Sandgrouse in the Negev (Hinsley 1990) and Double-banded and Namaqua Sandgrouse in the Namib Desert (Thomas & Maclean 1981). All regressions are significant ($P < 0.001$) and intersect within 0.1°C of 40.4°C .

There is a striking coincidence (so close as to suggest cause rather than chance) between all three intersection points in Figure 2 (within 0.1°C of $T_b = 40.4^{\circ}\text{C}$) despite the wide geographic and climatic divergence of BBS from DBS and NS. Such coincidence invites speculation even though we have no corroborative information: it certainly looks as though their respective thermoregulatory systems evolved differences in “gain control” coupling T_{ambient} and T_b without changing some common “reference level” of T_b .

Metabolic rates

Open-flow respirometry of PTS and DBS showed the type of reduction in “basal” metabolic rate (BMR) within the thermo-neutral zone (TNZ) now well known among many desert homeotherms (Figure 3). Once again, the results show appealingly precise coincidences (too nice to overlook) between Kendeigh et al.’s (1977) allometrically predicted lower critical temperatures (T_{lc}) for non-passerines and the points where similarly predicted BMRs (Kendeigh et al. 1977) intersect observed lines of MR v. T_{ambient} . It is almost as though the low actual BMRs of PTS and DBS has evolved by increased insulatory capacity (reduced conductance C_w) within the TNZ, effectively resulting in a downward extrapolation of the “previous normal” sub- T_{lc} portion of the MR v. T_{ambient} relationship. This is consistent with relatively low C_w observed in these species (see below).

In contrast, BBS showed a BMR level close to that predicted by allometry, but a much reduced TNZ with the observed T_{lc} some 16°C above allometric expectation (Figure 3).

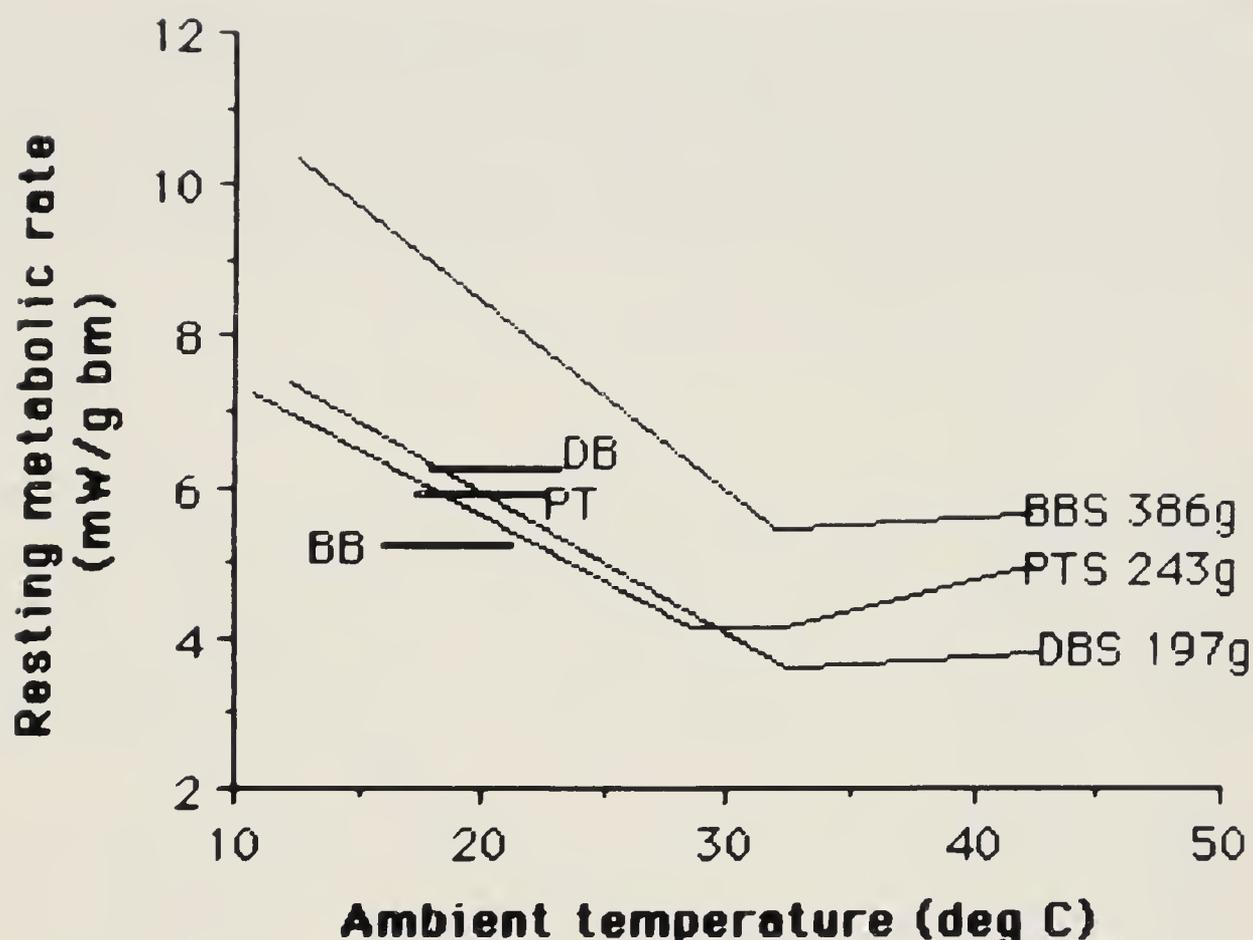


FIGURE 3 – Regression lines of resting metabolic rates on ambient air temperature (in respirometer) for Black-bellied, Pin-tailed and Double-banded Sandgrouse (Hinsley 1990), compared to predictions of BMR (Kendeigh et al. 1977) and lower critical temperature (T_{ic} : Aschoff 1981) shown by level and left hand end of heavy lines. All regression lines below actual T_{ic} are significant ($P < 0.001$).

Thermal conductance

Good insulation has always seemed a likely adaptation for sandgrouse, not only for its obvious benefits in energy-economy at low temperatures, but also to retard passive heat gain when $T_e > T_b$ with resultant savings in water economy (Thomas 1984). This seemed confirmed by observations on feather posture: erection of contour feathers at high ($T_{air} \geq T_b$) as well as low temperatures has been seen in wild PTS (Thomas & Robin 1977) and in captive DBS and NS in the Namib Desert (Thomas & Maclean 1981). Feather erection was interpreted as leading to increased insulation in these contexts, and hence it was not surprising to find wet thermal conductances (C_w) for PTS and DBS (0.28 and 0.29 $mW.g\ bm^{-1}.\ ^\circ C^{-1}$: Hinsley 1990) which were less than allometrically predicted values (84 and 75% of Aschoff's (1981) prediction). Unexpectedly, however, BBS had C_w (0.43 $mW.g\ bm^{-1}.\ ^\circ C^{-1}$) 45% higher than prediction. Occasionally, however, dorsal feathers may be raised to such an extent as to apparently ventilate the plumage: this may facilitate cutaneous evaporative water loss (see below).

Evaporative heat loss

The ability of animals to disperse heat loads at high ambient temperatures is important in hot dry environments. Sandgrouse use gular fluttering to force evaporation, but field observations of some species (PTS, DBS and NS) suggested that this may not be invoked until unusually high threshold ambient temperatures ($T_{air} \geq 45^\circ C$), which can be interpreted as a water-economy (Thomas 1984). However, BBS, SpS and

Crowned Sandgrouse *P. coronatus* in the Negev sometimes started gular fluttering at $T_{\text{air}} > 25^{\circ}\text{C}$; we can not explain these differences, but it is possible that threshold temperatures are affected by the birds' state of hydration. Moreover, there is another important route for regulated evaporation: Marder et al. (1986) showed that cutaneous evaporation is enhanced in PTS at $T_{\text{air}} \geq 42^{\circ}\text{C}$ (associated with $>80\%$ fall in skin resistance to vapour diffusion); these birds also exhibited high frequency panting and gular fluttering at $T_{\text{air}} = 40\text{-}60^{\circ}\text{C}$.

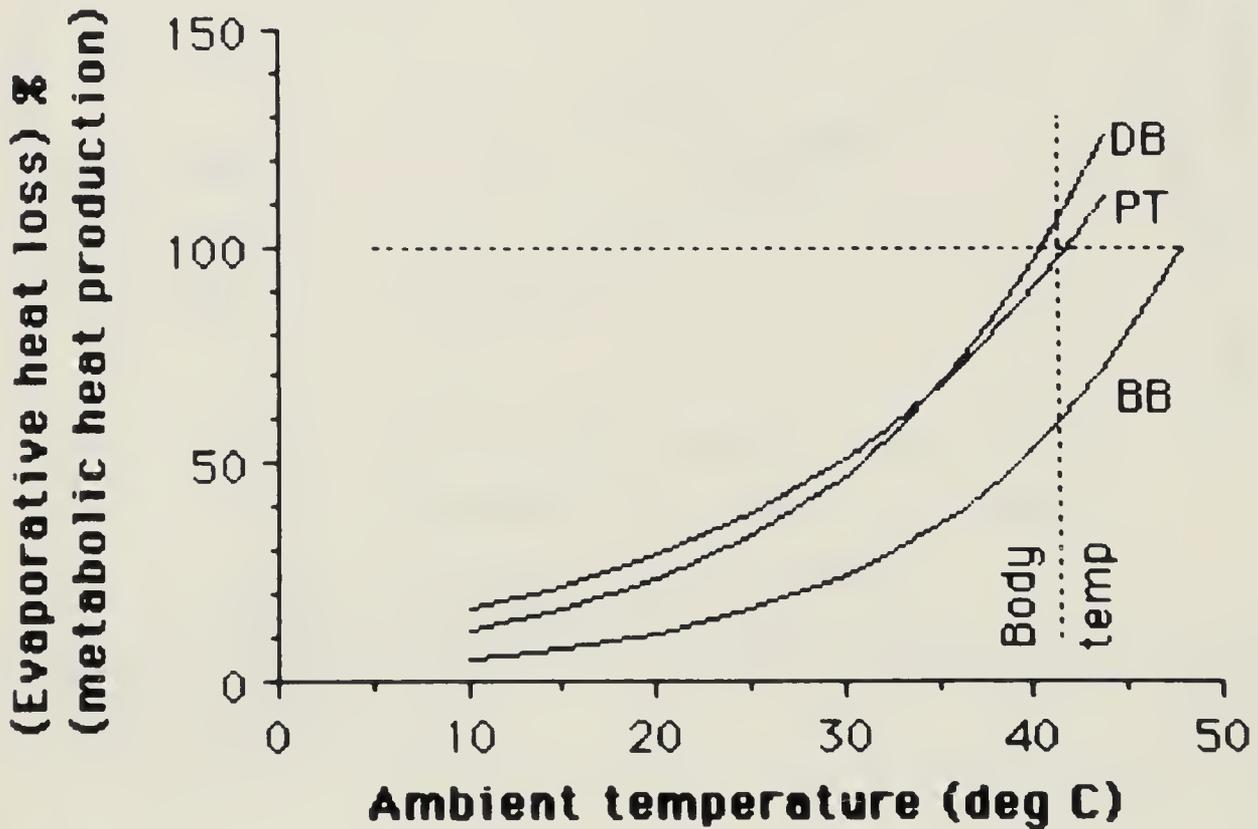


FIGURE 4 – Regression lines of evaporative heat loss as a percentage of metabolic heat production on ambient air temperature (in respirometer) for Black-bellied, Pin-tailed and Double-banded Sandgrouse (Hinsley 1990). Dotted lines indicate body temperature (see Figure 2) and equivalence of evaporative heat loss and metabolic heat production. All regression lines are significant ($P < 0.001$).

In our present studies with fully hydrated birds in respirometers, BBS showed a marked quantitative difference from DBS and PTS in its lower capacity to disperse metabolic heat by evaporation (Figure 4). When $T_{\text{air}} = T_{\text{b}} = 42^{\circ}\text{C}$ and passive heat loss was not possible, BBS could only eliminate 62% of metabolic heat production by evaporation, whereas PTS and DBS could eliminate it all. Obviously such a capacity for effective heat dispersal is valuable whenever body water reserves are adequate. Unfortunately we have no comparable data for dehydrated birds.

CONCLUSIONS

We were surprised to find such marked interspecific differences in energy metabolism and thermoregulatory physiology, despite the apparently monophyletic origins of the Pteroclididae, and the general similarities of size, shape and ecology between the various species. Our results for PTS and DBS tend to confirm earlier conclusions (Thomas 1984). Energy-economy has clearly been a potent selective force: the low-

ered BMR and reduced thermal conductances of these species would tend to conserve energy under cool conditions, both directly (better heat retention to sustain T_b well above T_{ambient}) and indirectly (reduced energy needs yielding proportional further savings in absolute foraging costs). The effect of these economies is demonstrated directly in comparisons of time spent foraging by PTS and BBS (which is relatively poorly insulated and lacks the reduced metabolic rate of PTS and other species). In spring these two species foraged in similar areas at our Spanish field site, yet PTS spent much less time foraging (42% of daylight) than BBS (57%). There was a similar (though less marked) disparity in the Negev in spring, where SpS foraged for 50% of daylight against 63% by BBS.

Such adaptations are also appropriate to life at high ambient temperatures ($T_{\text{ambient}} > T_b$): reduced (B)MR minimises metabolic heat production when this can be dispersed only by evaporation, while good insulation is useful to retard undesirable passive heat exchange (either gains or losses) with the surroundings. Furthermore, PTS and DBS's relatively high capacity to disperse heat by evaporation (Figure 4) has to be useful (when full hydration makes it feasible) in the face of the exceptionally high radiative and advective heat loads in arid environments (Thomas 1984).

It is therefore all the more puzzling to understand the difference between PTS and DBS (on the one hand) and BBS on the other. The fact that our respirometry used summer-adapted BBS but winter-adapted PTS and DBS does not explain BBS's high thermal conductivity and "unreduced" BMR. The substantially greater time-investment in foraging by BBS compared concurrently to PTS (Spain) or SpS (Negev) strongly suggests that there are real interspecific differences in levels of metabolism, and anyway the explanation overlooks the advantages of low BMR and C_w when $T_e > T_b$. Nor can there be any credible supposition that BBS is in any sense maladapted: as a species it is geographically widespread (Iberia and NW Africa to Kazakhstan and the NW Indian subcontinent) and common in suitable habitats (including our study sites). Clearly BBS succeed by another combination or balance of adaptations. Higher energy turnover rates in BBS need be no great disadvantage provided food sources are sufficient, while BBS's greater thermal lability (Figure 2) would be some (limited) compensation.

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BEHAVIORAL AND PHYSIOLOGICAL ADAPTATIONS OF BIRDS TO HOT DESERT CLIMATES

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ABSTRACT. Numerous studies have demonstrated that avian physiological responses to acute heat exposure include effective panting and gular flutter, transcutaneous evaporative cooling, and the tolerance of hyperthermia. Cutaneous evaporative cooling, once considered minimal, constitutes a major heat defense mechanism in columbiform birds and may be important for other groups. Behavioral heat defenses involve postural and plumage adjustments of thermal insulation, bathing, flight at altitude, reduced activity in the heat, and the selection of favorable microhabitats. Renal and lower intestinal reabsorption mechanisms enable birds to exhibit water and electrolyte regulation equal to that of mammals. Acclimation and hydration state significantly influence water use and heat stress responses. Free-living desert birds have lower field metabolic rates and water fluxes than similar sized birds from less extreme climates, and consequently may require less water per unit energy consumed than their nondesert relatives.

Keywords: Thermoregulation, water balance, energetics, Columbiformes, evaporative water loss, osmoregulation.

INTRODUCTION

High levels of endothermic metabolism and metabolic scope confer on birds a locomotor capacity unmatched by most other animals. This feature of their physiology has allowed birds to colonize wide distributional ranges and to occur in widely varied habitats. Birds that occur in harsh climates commonly experience daily and seasonal extremes of meteorological conditions in their physical environment. Because they are unable to store water or energy sufficient for long periods, diurnal in habit, and generally unable to find refuge underground, birds of hot desert regions must use a variety of physiological and behavioral responses to heat and aridity in order to survive and reproduce. The physiological ecology of desert-dwelling birds has been thoroughly reviewed by others (Dawson & Bartholomew 1968, Serventy 1971, Dawson 1976, 1984), but recent advances in the study of avian adaptations to arid, hot climates have prompted the following outline of our present knowledge of the subject.

For brevity, I focus in this essay on research results from the last decade. Many essential and imaginative studies, not acknowledged herein, led to W.R. Dawson's (1976, 1982, 1984) more historically complete syntheses of this subject.

DISCUSSION

Thermal considerations

ENVIRONMENT. The low latitude deserts of Africa, Australia, the Americas and the Middle East are characterized by erratic or low rainfall (< 50 cm annually), low air humidity, daytime temperatures that may exceed 50°C, and intense daytime solar radiation

(Serventy 1971). The desiccating effects of these conditions challenge the physiological capacities of desert-dwelling animals.

Furthermore, clear desert skies and the lack of dense vegetative cover allow the air and ground to cool radiatively at night so that summer nights are chilly and desert winters cold. Avian inhabitants of arid lands therefore encounter both extremes of temperature.

High body temperature (T_b) and a tolerance for hyperthermia in some species (Calder & King 1974) enable birds to tolerate extreme heat, but if heat stress is prolonged they must rely on evaporative cooling to protect against lethal overheating, at the expense of body water. Under cool conditions, birds lose metabolically produced heat to their surroundings principally by convection, radiation, and conduction (Calder & King 1974). When air temperatures are high the gradient for heat loss by these routes is reduced or even reversed and birds must evaporate water to maintain stable T_b . Recent theoretical developments in biophysical modeling enable microclimate analyses to provide estimates of the driving force for heat exchange, expressed as standard operative environmental temperature (T_{es} ; Walsberg 1985 and citations therein). This approach has stimulated the application of physiological methods to ecological problems of desert birds.

PHYSIOLOGICAL THERMOREGULATION. Birds accustomed to hot, dry environments may exhibit lower resting metabolic rates (RMR) than other birds and consequently may require substantially less water to dissipate internal heat production (Dawson & Bennett 1973, Calder & King 1974, Weathers 1979, Dawson 1981, 1984, Arad & Marder 1982). Populational and interspecific instances of depressed metabolism have been observed in which xerophilic birds have lower RMRs than birds from mesic areas (Dawson 1984). Furthermore, desert-dwelling species or summer-acclimatized birds may display lower rates of metabolic rate increase above the upper critical temperature (Weathers 1981). Metabolic adaptations such as these are difficult to establish as climate-related, in part because some desert birds have comparatively low RMRs by virtue of their phyletic affiliation (Dawson & Bennett 1973).

Physiological responses to heat stress in birds include a general cutaneous vasodilation (Calder & King 1974, Wolfensen et al. 1981), increased blood flow to unfeathered skin surfaces, and a controlled hyperthermia in which T_b is allowed to rise 2-4°C above normal (Dawson & Bartholomew 1968, Calder & King 1974, Dawson 1976, 1981, 1982, 1984). These adjustments enhance heat loss by non-evaporative routes if $T_{es} < T_b$, or reduce the gradient for convective heat gain if $T_{es} > T_b$. If heat stress is prolonged, evaporative cooling mechanisms are mobilized to prevent T_b from continuing to rise.

BEHAVIORAL RESPONSES. Heat defense by birds combines behavioral adjustments with physiological mechanisms. Protected environments may be sought, such as rock crevices (e.g. Rock Wrens *Salpinctes obsoletus*), the shady interior of vegetation, or along water courses. Significant water or energy savings may be realized by the selection of sheltered micro-habitats (Walsberg 1983). Some species of North American desert birds such as Verdins *Auriparus flaviceps* and Cactus Wrens *Campylorhynchus brunneicapillus* utilize enclosed nests as shelters from heat, cold, and wind. In severe droughts or periods of extreme heat, desert birds may travel great distances for water or food (Dawson 1981, Davies 1982, 1984). Nomadism and migration patterns

of desert-dwelling species may reflect adaptive evolutionary change favoring the survival of birds that escape, rather than tolerate, extreme conditions of hot climates (Dawson & Bartholomew 1968). Birds respond to heat stress by sleeking the plumage or by alternately fluffing and depressing the feathers (Calder & King 1974), drooping their wings and thereby exposing maximum surface area for heat loss (Dawson 1982, 1984). Dorsal ptiloerection in Charadriiform birds and other dark-backed species may serve to augment convective cooling and simultaneously reduce the heat loading effects of solar radiation (Dawson 1982, Grant 1982, Walsberg 1983). When T_{es} exceeds T_b , sandgrouse (Pteroclididae) erect their plumage and may huddle together, perhaps to increase thermal insulation and defend against heat gain by convection (Thomas 1984). In the heat, birds reduce activity levels to minimize exercise-induced metabolic heat loads. Flight at higher, cooler altitudes by soaring birds may represent a behavioral response to heat (Dawson & Bartholomew 1968, Calder & King 1974). Bathing in water, both to cool the body and to cool young or eggs, has been noted in some species (Dawson & Bartholomew 1968, Grant 1982).

ACCLIMATION. Physiological adjustment to prolonged warm temperatures enables acclimated birds to tolerate higher temperatures than non-acclimated (Chaffee & Roberts 1971, Calder & King 1974, Weathers 1981, Arad & Marder 1982). Under natural conditions the gradual changes in temperature that accompany the onset of summer probably enhance physiological heat tolerance and heat stress responses in birds, but few studies have focused on the role of heat acclimation in avian physiological responses.

Evaporative water loss

RESPIRATORY EVAPORATION. When continued heat stress threatens T_b regulation, most birds resort to panting or gular flutter to augment respiratory air flow and increase evaporative water loss from the respiratory surfaces (Dawson & Bartholomew 1968, Calder & King 1974, Dawson 1981, 1982, 1984). Panting onset occurs at $T_b = 41$ to 44°C (Calder & King 1974). Dehydration increases the T_b threshold for panting of domestic fowl (Arad 1983), but not Chukar *Alectoris chukar* or Sand Partridges *Ammoperdix heyi* (Kleinhaus et al. 1985).

Patterns of respiratory adjustments accompanying heat stress are detailed by Dawson (1982). In pigeons and some other species, two phases of increased respiratory ventilation occur: rapid Phase I panting, in which non-exchange respiratory surfaces are ventilated to increase evaporative heat loss and intermittent "flush-out" breaths deliver air to exchange surfaces; and emergency Phase II panting, in which parabronchial ventilation is raised by increased tidal volume (Bernstein & Samaniego 1981, Dawson 1982). The latter response, which may be accompanied by respiratory alkalosis, is generally reserved for episodes of severe heat stress (Dawson 1982).

CUTANEOUS EVAPORATION. Formerly believed to be a minor avenue for water loss in birds (Bartholomew & Cade 1963, Dawson & Bartholomew 1968, Withers 1983), evaporation from the skin is now known to comprise 40-75% of total evaporative water loss in the several avian species measured (Calder & King 1974, Dawson 1982, Marder & Ben-Asher 1983, Webster et al. 1985). Heat-acclimated pigeons and doves defend against heat stress at rest by augmenting cutaneous evaporative cooling to 5-10 times thermoneutral values (Marder & Ben-Asher 1983, Webster & Bernstein 1987). Control mechanisms for skin water loss may involve B-adrenergic pathways (Marder & Raber 1989) that regulate the flow of blood to evaporating surfaces; alternatively the

TABLE 1 – Whole-body water vapor diffusion resistance (r_v) in resting birds under thermally neutral conditions. Sources are cited in Webster et al. (1985) except as noted.

Species	Body mass (g)	Air temp. (°C)	Est. mean skin temp. (°C)	Cutaneous evaporation rate (mg m ⁻² s ⁻¹)	r_v (s/cm)
<i>Struthio camelus</i> ^a	95400	20-33	36.4	2.78	129
<i>Struthio camelus</i> ^b	—	27	36.4	4.33	83
<i>Dromaius novaehollandiae</i> ^b		27	37.9	4.70	84
<i>Anas platyrhynchos</i>	2500	30	39.0	6.43	61
<i>Gallus domesticus</i>	2040	30	38.0	5.07	101
<i>Cathartes aura</i> ^{bc}	1470	30	39.5	3.46	125
<i>Phalacrocorax auritus</i> ^b	1460	30	39.7	4.45	98
<i>Columba livia</i> ^b	638	25	39.3	4.02	106
<i>Columba livia</i>	473	30	40.6	3.90	97
<i>Corvus cryptoleucus</i> ^{bc}	534	32	41.7	4.43	111
<i>Geococcyx californicus</i>	274	30	39.0	2.96	139
<i>Streptopelia risoria</i>	146	29	36.7	1.12	250
<i>Zenaida macroura</i> ^b	109	25	40.0	3.24	138
<i>Phalaenoptilus nuttallii</i>	43	35	39.0	3.27	125
<i>Ploceus cucullatus</i>	43	30	39.0	3.66	123
<i>Excalfactoria chinensis</i>	42	30	39.0	2.26	199
<i>Melopsittacus undulatus</i>	32	30	39.0	5.16	87
<i>Zonotrichia leucophrys</i>	27	20	38.0	5.59	76
<i>Poephila castanotis</i>	13	30	39.0	4.01	112

^a Computed from Wither's (1983) data, assuming that the gradient for water vapor diffusion from skin to air was 36 g/m³.

^b Webster, M.D. and M.H. Bernstein, unpublished data. Ventilated capsules were placed against the axilla, dorsum, and breast skin of hooded, unanesthetized animals. Measurements were completed within 5 min of restraint. The birds were captives held outside under natural (summer) conditions at Las Cruces, New Mexico or at the El Paso Zoological Park, El Paso, Texas. Methods and calculations followed exactly the procedures of Webster and Bernstein (1987).

^c Body mass values from Dunning (1984).

increased water evaporation that accompanies higher skin temperature in pigeons (Webster et al. 1985) may result from physical changes in skin lipids (Hadley 1989).

Liquid water evaporating from the body surface passes through three resistance layers: the skin, plumage, and a boundary layer of still air (Marder & Ben-Asher 1983, Webster et al. 1985). The sum of these, the whole-body water vapor diffusion

resistance (r_v ; expressed in units of inverse velocity, seconds/cm) ranges from 60 to 250 s/cm in various avian species (Table 1) at rest under thermally neutral conditions. No habitat-related, allometric, or phyletic patterns have yet been identified.

In pigeons at thermoneutrality, the feather coat resistance and the boundary layer resistance together are 6% to 26% of the total resistance to water loss from the skin (Webster et al. 1985), and the skin is the primary barrier to cutaneous evaporation. Temperature-dependent decreases in r_v (Webster et al. 1985), however, apparently decrease the skin's water-vapor barrier function to such an extent that the plumage may limit water loss rates (Marder & Gavrieli-Levin 1987) in heat-stressed birds that utilize cutaneous evaporative cooling. Higher cutaneous water permeability (decreased r_v) in the heat allows domestic fowl, Pekin ducks *Anas platyrhynchos*, Painted Quail *Excalfactoria chinensis*, Chukar *Alectoris chukar* and various columbids to dissipate large percentages of metabolic heat production and even to offset external heat loads (Marder & Ben-Asher 1983, Webster & King 1987). Between 35 and 40°C, pigeons accustomed to 20°C housing conditions evaporate 2.7 to 4.1 mg H₂O g⁻¹ hr⁻¹ via the skin (50% of total evaporation) and thereby dissipate 18 to 27 W/m² latent heat loss or 30% to 45% of metabolic heat production (Webster & King 1987). At 60°C, heat-acclimated pigeons can maintain $T_b < 42^\circ\text{C}$ via latent heat loss rates exceeding 98 W/m² (>300% of resting metabolic heat production) even without panting (Marder & Arieli 1988). At 55-60°C, acclimated pigeons dissipate heat largely (75% of total evaporation) by the cutaneous route (Marder & Gavrieli-Levin 1987, Marder & Arieli 1988).

Considerable variation in barrier function of skin from different body regions is present in the several species of birds for which spot measurements of cutaneous water loss have been made (Marder & Gavrieli-Levin 1987, Webster & Bernstein 1987, M.D. Webster & M.H. Bernstein, unpublished data). In pigeons and Mourning Doves *Zenaida macroura*, higher rates of water loss occur from the back and rump when compared to measurements on feathered skin of the breast or axilla. Regional variation in skin resistance to water loss may reflect differences in epidermal lipid content (Hadley 1989), stratum corneum thickness, or skin vascularization. Cutaneous water loss increases with growth of nestling Zebra Finches *Poephila guttata*, perhaps reflecting developmental changes in a lipid barrier to evaporation from the skin (Menon et al. 1988).

Excretory water loss

URINARY CONTRIBUTION. Significant proportions of the water losses of birds occur via the excretory pathway (Skadhauge 1981). In birds, as in reptiles and amphibians, urine produced by the kidneys is modified in the lower intestine and cloaca (Skadhauge 1981, Thomas 1982, Anderson & Braun 1985). Urine produced by avian kidneys is less concentrated than mammalian urine, but this is a consequence of the organization of the avian excretory system rather than an adaptive failing (Braun 1982). In birds, integrated function of kidneys and lower intestinal epithelia produces efficient osmotic and ionic regulation equal to that of mammals (Skadhauge 1981, Thomas 1982, Dawson 1984).

Efforts to document water-conserving attributes of xerophilic bird kidneys have been so far unsuccessful. In six species studied by Goldstein and Braun (1989), including the arid zone Zebra Finch, urine osmolality ranged from 214 to 500 mosmol/kg and

increased to a maximum of 865 mosmol/kg with dehydration. Of several kidney morphometric characters examined, renal concentrating ability correlated only with decreased medullary cone length. This result, opposite to expectations based on the mammalian renal system, suggests that renal concentrating ability depends on relative medulla thickness rather than absolute length of the cones. Comparison of results from 18 species show that urine concentration during dehydration decreases with increased body mass (Goldstein & Braun 1989).

Avian kidneys contain both reptilian (RT) and mammalian (MT) nephrons (Skadhauge 1981, Braun 1982); antidiuresis in birds results from decreased flow through RT nephrons (Goldstein & Braun 1986). Renal adjustments to dehydration or salt-loading involve changes in glomerular filtration rate (GFR) that are stimulated by arginine vasotocin (AVT; Braun & Dantzler 1984). AVT reduces the number of operational RT nephrons and, in concert with actions on collecting duct water reabsorption, causes the formation of a more concentrated urine.

LOWER INTESTINE AND CAECA. Ureteral urine flows retrograde into the rectum, coprodeum, and caeca (if present) where epithelia reabsorb NaCl and water and secrete K^+ by passive and active processes (Thomas & Skadhauge 1989). Urates and uric acid are degraded microbially in the lower intestine and caecum, freeing bound cations for re-uptake (Long & Skadhauge 1983, Anderson & Braun 1985, Thomas & Skadhauge 1989) and possibly contributing to nitrogen recycling. In vivo perfusion studies of dehydrated domestic fowl showed that cloacal and intestinal reabsorption removed 15% of urinary water and 50% of urinary Na^+ (Skadhauge 1981). In desert-dwelling Gambel's Quail *Callipepla gambelli*, 50% of water and K^+ and 60% of Na^+ in ureteral urine are reabsorbed postrenally (Anderson & Braun 1985). Low dietary Na^+ and aldosterone stimulate intestinal reabsorption by the rectum and coprodeum (Skadhauge 1981) and the caeca (Thomas & Skadhauge 1989, Goldstein 1990).

SALT GLANDS. Some desert species utilize nasal glands to secrete concentrated salt solutions and thereby spare body water. Passerines and phasianids (Thomas et al. 1982) lack this capacity, but the Roadrunner *Geococcyx californicus*, Ostrich *Struthio camelus*, and some hawks and Charadriiform birds utilize this osmoregulatory mechanism (Dawson 1984). Salt glands are particularly useful in desert environments for nestling birds that cannot travel to water (Dawson 1984).

Water balance

SOURCES OF WATER. Birds obtain water by drinking, from water contained in food, and by oxidative metabolism of foodstuffs. Metabolic water contributes importantly to the water economies of small granivorous birds (Skadhauge 1981, MacMillen 1990) and birds in flight (Dawson 1984). Ad libitum drinking rates of captive birds are quite high in comparison to minimal requirements and drinking behavior of birds in the field (Dawson 1976). Many species, especially those that are insectivorous or carnivorous, obtain abundant preformed water in their food and rarely drink in nature. Numerous granivorous species can survive independent of water or succulent food in the laboratory (Bartholomew 1974), but studies of attendance at water sources reveal that granivorous birds are the most frequent users of water in the heat (Dawson 1976). This observation supports the contention that water-conserving adaptations of birds represent a reserve capacity for periods of thermal or hydric stress.

TABLE 2 – Estimated water budgets of captive and free-living birds. Evaporation rates were estimated from weather data and laboratory measurements or predictive equations (Calder & King 1974). Excretion rate was estimated by difference (total measured efflux minus evaporation), and water intakes were computed from metabolic rate, food intake and food water content data. Sources: 1, Withers 1983; 2,3 Kam et al. 1987; 4,6,7, cited in Skadhauge 1981; 5, Goldstein & Nagy 1985; 8, M.D. Webster & W.W. Weathers, unpublished data. Species 1,4,6,7 were captives housed under semi-natural conditions at moderate temperatures; the rest were free-living birds measured during the summer.

Species	Body mass g	Method notes	Losses			Gains			Metabolic ml/day
			Evaporation ml/day	Excretion ml/day	In food ml/day	Drinking ml/day			
1. <i>Struthio camelus</i>	95400	hydrated held outdoors 20-33°C	3070	5410	160	7860		420	
	80700	dehydrated held outdoors 20-33°C	1420	790	30	—		490	
2. <i>Alectoris chukar</i>	359	assumed mean $T_{es} = 30^{\circ}\text{C}$	14.5	28.9	10.6	25.6		7.3	
3. <i>Ammoperdix heyi</i>	156	assumed mean $T_{es} = 30^{\circ}\text{C}$	12.6	5.2	5.5	8.8		3.6	
4. <i>Callipepla gambelli</i>	140	dehydrated, caged 25°C	4.8	6.1	7.0	—		2.5	
5. <i>Callipepla gambelli</i>	141	assumed mean $T_{es} = 30^{\circ}\text{C}$ diet = 95% seeds	6.9	8.8	0.5	12.5		2.7	
6. <i>Melopsittacus undulatus</i>	30	dehydrated caged 25°C	1.86	0.91	2.3	—		4.9	
7. <i>Poephila guttatus</i>	12.5	dehydrated caged 25°C	1.2	0.8	0.46	—		1.57	
8. <i>Auriparus flaviceps</i>	6.2	mean $T_{es} = 30^{\circ}\text{C}$ diet = 95% insects	2.34	1.66	3.11	—		0.70	

WATER BUDGETS. Sufficient information is available to compile estimated water budgets for several species under semi-natural or free-living conditions (Table 2). Verdins in the Colorado Desert of southern California have not been observed to drink in nature, yet water turnover in this species exceeds 63% of body mass per day (M.D. Webster and W.W. Weathers, unpublished data). Feeding on insects (ca. 70% water) and some nectar, Verdins obtain sufficient water to balance evaporative and excretory losses. Zebra Finches can apparently attain water balance in captivity by utilizing metabolic oxidation of food as the principal source of water (Skadhauge 1981). Ostriches (Withers 1983), Chukar, and Sand Partridges (Degen et al. 1983) depend heavily on water availability to maintain water balance.

WATER TURNOVER IN NATURE. Tritiated or deuterated water has been used extensively to evaluate the water economies of animals in their natural habitats (Nagy & Peterson 1988). Field water flux of birds scales as $m^{0.69}$, and does not differ from the allometric relationship for mammals (Nagy & Peterson 1988). Water flux of free-living birds averages 50% higher than captive birds of similar body mass, probably because of activity (Nagy & Peterson 1988). Desert birds exhibit lower water fluxes (about half, on average) than non-desert birds (Figure 1; Nagy & Peterson 1988)

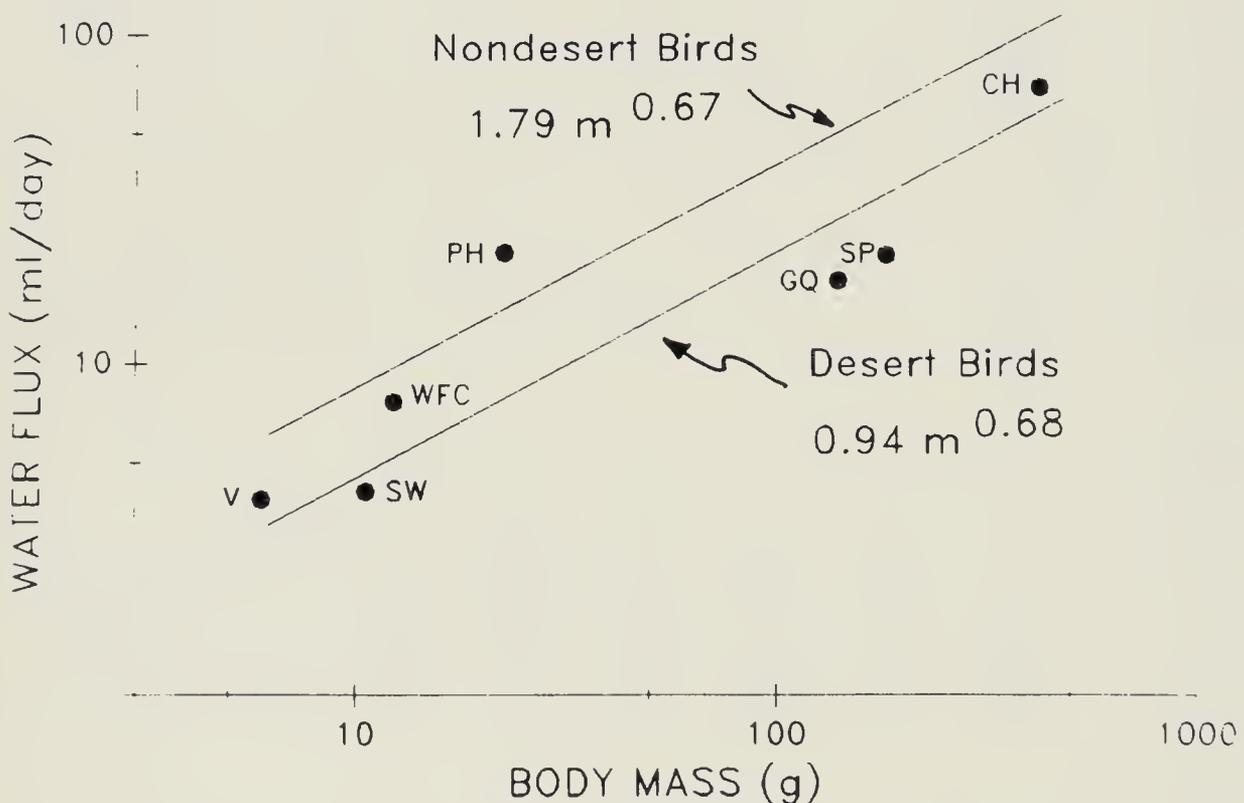


FIGURE 1 – Body mass scaling of water flux rate in free-living birds. Both axes are logarithmic. Data were compiled and the regression equations were derived by analysis of covariance by Nagy and Peterson (1988). Symbols indicate desert species: V = Verdin *Auriparus flaviceps*; PH = *Phainopepla nitens*; GQ = Gambel's Quail *Callipepla gambelli*; SP = Sand Partridge *Ammoperdix heyi*; CH = Chukar *Alectoris chukar*; WFC = White-fronted Chat *Epthianura albifrons*.

DEHYDRATION. The tolerance of birds to water deprivation and consequent dehydration has been summarized by Skadhauge (1981) and Dawson (1976). When deprived of water, birds decrease evaporative and excretory water losses to minimal levels. Dehydrated Emus *Dromaius novaehollandiae* undergo a redistribution of body water, but

are capable of reducing water efflux to one-third normal (hydrated) levels (Dawson et al. 1983). Dehydrated fowl retain thermoregulatory ability even when up to 15% body mass is lost (Arad 1983), but display hyperthermia and increased plasma osmolarity when compared to hydrated birds (Arad & Marder 1983). Blood AVT and prolactin concentrations increase in response to dehydration in fowl (Arad et al. 1985). Cutaneous evaporation decreases significantly in dehydrated pigeons (Arad et al. 1987) and Zebra Finches (Dawson 1976).

Ecological energetics

The energy metabolism of birds in natural environments includes basal plus thermo-static expenditures (maintenance metabolism), costs related to activity, and productive costs associated with growth or reproduction (Walsberg 1983). Until recently, attempts to ascribe patterns to avian energy requirements were generally thwarted by the complexities and technical difficulties of modeling the natural environment. It was predicted, however (Dawson & Bennett 1973, Dawson 1984) that desert birds might have lower costs of existence than birds from more productive habitats.

FIELD METABOLIC RATE (FMR). The metabolic rates of birds living freely in a natural environment can be measured using doubly labeled isotopic water (Nagy 1987). Measurements of birds are relatively few except for seabirds and breeding passerines, but several desert species have been studied. Allometric analysis reveals that desert species exhibit significantly lower FMR's than other birds (Figure 2), perhaps reflecting dietary differences, adaptively reduced standard metabolism, or heat acclimation effects on metabolic rate (Nagy 1987).

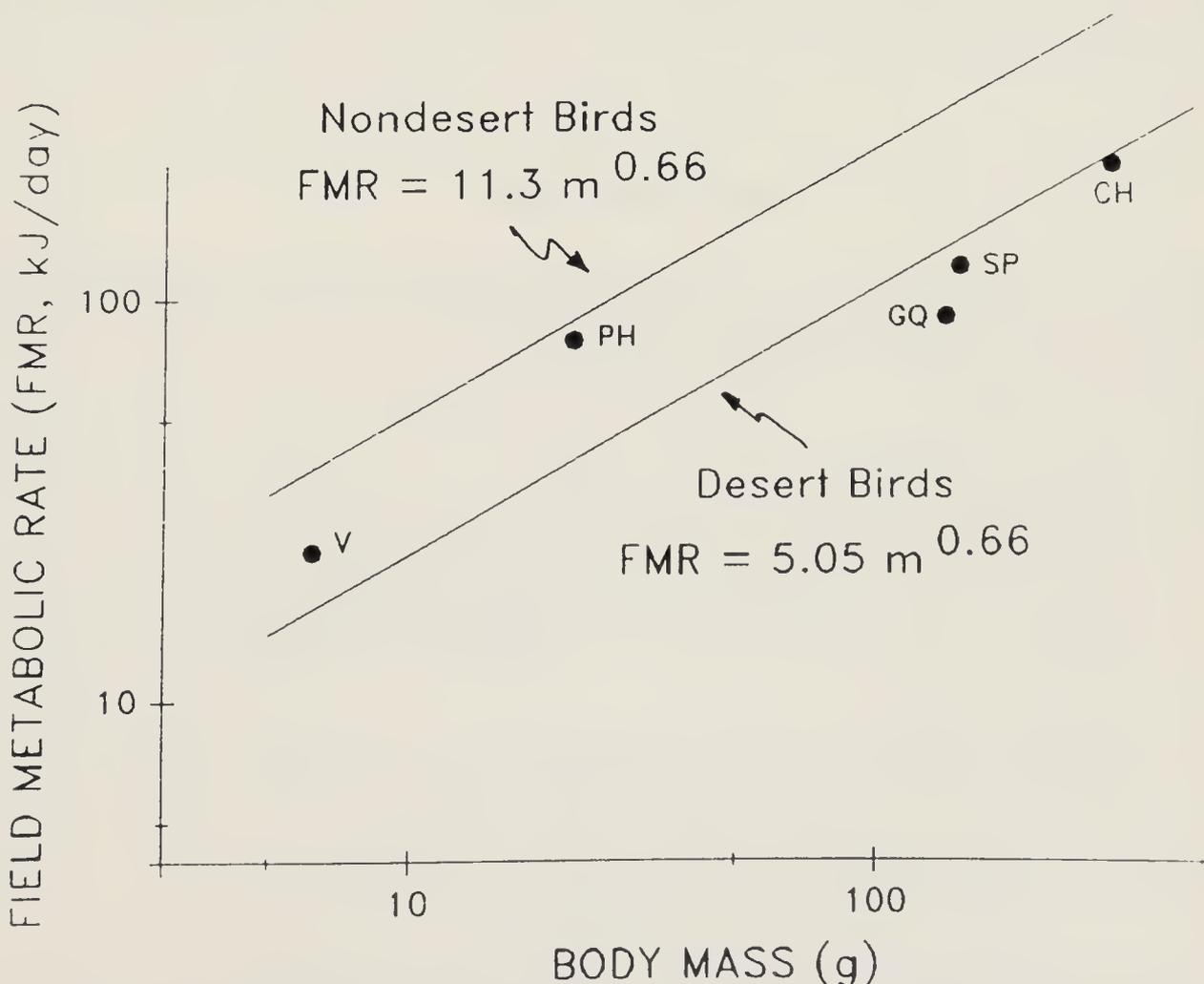


FIGURE 2 – Body mass scaling of field metabolic rate in free-living birds. Data were compiled and the regression equations were derived by Nagy (1987). Symbols as in Figure 1.

WATER ECONOMY INDEX (WEI). The amount of water used by an animal per unit metabolized energy (ml/kJ) has been suggested as an index of water use efficiency (Nagy & Peterson 1988). WEI values for birds range from 0.139 ml/kJ in nestling House Finches *Carpodacus mexicanus* to 0.37 ml/kJ in Red-winged Blackbirds *Agelaius phoeniceus*. Avian WEI values do not differ significantly between desert and non-desert species, but the values for desert birds are generally lower (Nagy & Peterson 1988). This observation supports the hypothesis that desert birds are more efficient water users than other birds, and suggests that xerophilic birds do utilize some of the adaptations described above to conserve water (Nagy & Peterson 1988).

SUMMARY

Recent advances in the study of avian responses to heat and aridity include: 1) improvements in the understanding of the roles of lower intestinal and caecal epithelia in osmotic and ionic regulation (Skadhauge 1981, Thomas 1982, Thomas & Skadhauge 1989); 2) more precise estimates of kidney function and comparative structure (Goldstein & Braun 1988, 1989); 3) re-evaluation of cutaneous evaporation's role in heat defense (Marder & Ben-Asher 1983, Webster et al. 1985, Marder & Gavrieli-Levin 1987, Webster & King 1987); and 4) syntheses of water flux and FMR data for a wide variety of birds (Nagy 1987, Nagy & Peterson 1988). Many avenues for inquiry remain. Studies of the nutritional ecology of desert birds should provide information valuable for our understanding of animal function in resource-poor environments. Continued study of physiological responses to controlled and natural environments will improve our understanding of thermal and osmotic regulation, and assist in efforts to evaluate weather effects on avian energy and water use in natural habitats.

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HYPOMETABOLISM AS AN ADAPTATION TO LIVE AND BREED IN THE COLD

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ABSTRACT. Small birds of at least eight orders save energy through torpor. To minimize energy expenditure, larger birds only have a slight decrease in body temperature. However, it should not then be concluded that hypometabolism is restricted to small birds. There are major similarities in the energy saving adjustments that allow both small and large birds to live and breed in the cold. A key process is that energy saving mechanisms are adjusted in relation to an evaluation of body energy reserves at the time when the bird starts to rely on these reserves.

Keywords: Torpor, hibernation, fasting, energy metabolism.

INTRODUCTION

Power of cold defence by increasing heat production is an essential prerequisite to enable birds to live and breed in the cold. This aptitude is not exclusive to large polar birds, e.g. ptarmigans or penguins. Various small birds are also able to face severe conditions by a surprisingly robust increase in metabolic rate (For review, see Dawson 1989, Marsh & Dawson 1989). However, the energy demand then becomes considerable, which may induce a critical situation because of a possible limitation in food availability. Such a limitation can be the consequence of impairment in climatic conditions. Another possibility, during breeding, is conflicting requirements between an increase in food foraging and attendance of nest for thermal protection of the brood as well as preservation against predation risk (see Reinertsen 1989). This accordingly explains why, to live and breed in the cold, the response of small as well as large species of birds is often to rely on body fuel reserves. Hypometabolic adjustments then play a major role, to minimize the food demand and preserve the body fuel reserves, that obviously are also limited. Energy-saving mechanisms may even be more important than mere consequences of body size to explain the northern distribution of small wintering birds (Moreno et al. 1988).

HYPOMETABOLISM THROUGH HYPOTHERMIA

The most extreme situation of hypometabolism in birds is the hibernating state observed in the Poor-will, as its body temperature may be maintained below 10°C for extended periods of time (Jaeger 1948). This is then similar to the prolonged hibernation bouts seen in small mammals (see Wang 1989).

With at least the exception of the Poor-will, bird hypometabolic state through a drop in body temperature is restricted to night. That body temperature increases again to its previous day level at the end of the night has already been shown more than 100

years ago in the pigeon, when it is experimentally fasted (Chossat 1843). However, the same author and later investigators (Walker et al. 1983, Heller et al. as reviewed in Heller 1989) found that the body temperature of pigeons and doves eventually also drops during day when the fast is prolonged. External heating may become necessary for arousal from torpor (Chossat 1843, Macmillen & Trost 1967).

The level reached in body temperature during nocturnal torpor is variable according to bird species, since it is 38.5°C in Red-tailed Hawks *Buteo jamaicensis* and about 37.5°C in the Kestrel *Falco tinnunculus* (Daan et al. 1989), whereas it is less than 10°C in various small bird species (Reinertsen 1983). Moreover, for a given bird species, the importance of the drop in body temperature varies according to nutritional state and/or ambient temperature (Reinertsen & Haftorn 1986, Daan et al. 1989).

In situations of energy saving, there is only a limited drop in body temperature in large birds. For example, during prolonged fasting, the decrease in body temperature of a domestic goose is limited to 1°C (Le Maho et al. 1981). Accordingly, large birds are often opposed to small birds in such a way that various smaller species are capable of hypothermia, whereas larger species are not able to do so.

LARGER VS SMALLER BIRDS: ABILITY FOR HYPOTHERMIA

In fact, the investigation of Chaplin et al. (1984) in the Red-tailed Hawk and the Great Horned Owl *Bubo virginianus* remarkably illustrates how the importance of the drop in temperature in a bird should be considered in relation to the mean body temperature and its range of variation. The nocturnal drop in body temperature that is induced by food deprivation and cold weather is much larger in the hawk than in the owl. The daytime body temperature in the hawk is nevertheless much higher than in the owl. Then, under normal feeding conditions, the mean body temperature of the owl is lower than that of the hawk. This means that a bird with a usually high body temperature will appear more capable of hypothermia than a bird with a usually lower body temperature. On the other hand, hypometabolism could be characterized as permanent in the owl, whereas it is facultative in the hawk.

The situation may even be found of birds where a facultative hypothermia may be superimposed on a permanent hypothermia. For example, petrels are well known to generally maintain low body temperatures when compared to the other birds. Chicks of Fork-tailed Storm Petrels *Oceanodroma furcata* usually have the relatively low body temperature of about 37°C. However, if the adults leave the chicks unattended in the burrows for long periods of time, their body temperature may decrease to as low as about 11°C (Boersma 1986).

To sum up about the extent of hypothermia in birds, clearly none of the larger birds species is capable of dropping its body temperature to torpid values below about 35°C. Various species of small birds can do so, usually on a nocturnal basis.

IS TORPOR RESTRICTED TO SITUATIONS OF ENERGY EMERGENCY?

Nocturnal torpor has now been described in bird species related to at least eight orders (Wang 1989). The largest bird for which a nocturnal drop in body temperature

has been found is the 2 kg Turkey Vulture. Most of those birds that are known to enter nocturnal torpor are however very small species, with a body mass below 10 g (for review, see Reinertsen 1983). This is not surprising. Based on metabolic measurements in free-flying conditions, as much as about 15-25 % of the daily energy expenditure of Black-rumped Waxbills *Estrilda troglodytes* are used to maintain body temperature at night (Weathers & Nagy 1984). The body fuel reserves of a small bird may be just sufficient to cover overnight energy requirements, particularly if the ambient temperature is low (see Ketterson & King 1977, Reinertsen 1983).

Under normal conditions, even in the smallest birds, nocturnal hypothermia does not seem to be obligatory, as shown for example by the measurements of field metabolic rate in free-living Anna's Hummingbirds *Calypte anna* by Powers and Nagy (1988). Another example is the observations of Reinertsen et al. (1988) suggesting that during the winter the small Goldcrest *Regulus regulus* may be able to balance its nocturnal energy budget at normothermic body temperature. In fact, nocturnal hypothermia is triggered in hummingbirds by an insufficient accumulation of energy reserves during the day (Hainsworth et al. 1977, Tooze & Gass 1985). Again in accordance with a link between hypothermia and an emergency fuel situation, Reinertsen and Haftorn (1986) have shown that nocturnal hypothermia may be induced in small species of arctic birds by an insufficient daily food intake and/or low ambient temperatures. The facultative occurrence of nocturnal hypothermia in small birds, due to either food shortage or low ambient temperatures has been shown in many small bird species inhabiting all latitudes. They range from insectivores of temperate regions, such as the Chimney Swift *Chaetura pelagica* (Ramsey 1970) to frugivorous tropical manakins (Bucher & Worthington 1982).

In breeding birds, for obvious technical reasons, there still is little data on hypometabolism through hypothermia. It has however been shown that incubating Broad-tailed Hummingbirds *Selasphorus platycercus* may become hypothermic when inclement climatic conditions reduce the opportunity for energy intake (Calder & Booser 1973). More recently, Prinzinger and Siedle (1988) demonstrated the regular use of torpor in a breeding population of House Martins *Delichon urbica*.

Then, it could be inferred that small birds get torpid because of an energy emergency, whereas the absence of torpor in larger birds is partly due to the absence of such an emergency situation.

In mammals, for comparison, that an animal with a large body size does not necessitate a profound hypothermia to minimize energy expenditure has already been discussed for the bear versus the ground-squirrel (Hochachka & Guppy 1987). As for small birds, the energy problem of small mammals is the very high metabolic rate in relation to the available energy reserves. The time scale for surviving on energy reserves is completely different. If a hummingbird with reduced energy reserves does not enter nocturnal hypothermia it will die. A male Emperor Penguin with insufficient energy reserves will fail in breeding but may still fast for two months. This explains that the energy saving in small animals is not only achieved through a drop in body temperature (Q_{10} effect) but also by an additional metabolic suppression (Geiser 1988).

However, it should not be concluded that torpor is restricted to situations of energy emergency in birds. When the cost of feeding is high for a pigeon, although the

depletion of its energy reserves is not so large as that there could be an emergency situation, it will not feed and there will be a nocturnal drop in its body temperature (see Rashotte & Henderson 1989).

In addition, a rare but key field observation indicates that migrant hummingbirds may use torpor when they are fat and not presently energetically stressed (Carpenter & Hixon 1988). Captive hummingbirds have also been found to use torpor during the premigratory phase of build up in energy reserves as well as during the period when they later would have migrated (Kenagy 1989).

Thus, in small birds, torpor may be triggered when body fuels reserves are limited due to food restriction and/or low ambient temperature. However, torpor can also be induced by the choice of the bird not to feed or for reducing energy expenditure at the time reserves are being accumulated.

EFFICIENCY OF ENERGY SAVING WITH OR WITHOUT TORPOR

The efficiency of energy saving during prolonged bouts of hibernation in mammals can be considerable, almost of 90% (see Wang 1989). It might then be that the prolonged hypothermia in the Poor-will gives a figure close to that. Because torpor usually occurs on a daily basis in birds, the cost of rewarming is quite high in proportion to the energy saving. For example, it is remarkable that the metabolic rate of a hummingbird is reduced by 60-90% when it is in the torpid state (Kruger et al. 1982). Taking however into account that the daily duration of torpor is eight hours, the saving is of about 30% of the daily energy expenditure (Wang 1989). This figure is close to those calculated by Reinertsen (1983) for small arctic birds.

The question is therefore whether larger birds that do not get torpid are so inefficient in energy sparing, when compared with smaller birds that are capable of getting torpid. To come back to the above example corresponding to the study by Chaplin et al. (1984) on Red-tailed Hawks and Great Horned Owls, it might then be that the permanent quite low body temperature of the owl may lead to an overall efficiency in energy saving that is comparable to the facultative hypothermia observed in the hawk.

There are however some available data that enable us to compare the reduction in energy expenditure in large birds that only have a very slight decrease in body temperature with data for small torpid birds. For example, the metabolic rate of a long-term fasting penguin or goose decreases to only about 50% of the initial value in fed-state. About 20% of the reduction in metabolic rate is during the first few days of fasting, the further drop in metabolic rate is associated with the decreasing body mass (Le Maho et al. 1981, Cherel et al. 1988). Thus, in terms of the proportion of the energy that can be saved, large birds can be as efficient in hypometabolism as smaller birds. The difference may therefore be that large birds do not require a large drop in body temperature to get this efficiency in energy saving, with the further advantage of almost no cost for rewarming. Moreover, with the exception of the degree in the reduction of body temperature, there are important similitudes in hypometabolic adjustments in small and larger birds.

SIMILARITIES IN HYPOMETABOLISM WITH OR WITHOUT TORPOR

Changes in fuel utilization

As for large birds during long-term fasting, hibernating mammals primarily rely on lipids, minimizing the utilization of their body proteins (Le Maho 1989). It is very likely that small birds also do so during torpor.

Energy saving through extension of sleep

Torpor in birds appears as an extension of sleep (Walker et al. 1983, Heller 1989). It is therefore of a particular interest that in large birds, although they do not get torpid, the time spent asleep may be as much as doubled during fasting (Dewasmes et al. 1984).

Evaluation of the availability in body fuel reserves

Some metabolic processes evaluate the availability of body fuel reserves from the time the bird starts to rely on its energy reserves and, in relation to requirements for refueling, at the end of the hypometabolic period.

Considering small birds, the evaluation of energy reserves for initiating hypothermia is indicated by the observation that nocturnal torpor in various species is only used at a minimum threshold of energy reserves (Hainsworth et al. 1977, Reinertsen & Haftorn 1986). Furthermore, when it occurs, nocturnal hypothermia is adjusted in relation to the importance of body reserves at the onset of the night, i.e. the depth of hypothermia is inversely correlated to body weight (Reinertsen & Haftorn 1986).

Ambient temperature is also integrated in the processes that trigger torpor in relation to the evaluation of body reserves at dusk. This is illustrated by the observation that the depth of torpor increases with lower ambient temperature at dusk (Reinertsen & Haftorn 1986). In the fasting pigeon, the deeper and deeper body temperature as well as lower and lower metabolic rate during successive nights are also correlated with energy reserves (Phillips & Berger 1989). In the Rufous Hummingbird *Selasphorus rufus*, the information on energy reserves has been shown to be integrated with elapsed time of night to minimize the duration of torpor. The triggering of torpor and when it occurs may be conceptualized as a response to a sliding threshold in available energy reserves. This threshold decreases as the amount of reserves and the time until morning decline over the night (Hiebert 1988).

A new evaluation of the availability of body fuels is made at the end of the night, which induces an increased food intake during day, that insures a final replenishment of the energy deficit from the end of the previous day (Tooze & Gass 1985). As shown by these authors, it is remarkable that body fuel reserves are however primarily re-established through the nocturnal hypothermia. There is no increase in food intake for the remainder of daytime after a deficit has been induced in body fuels. The increase in food intake the following day is relatively unimportant in regard to the effectiveness of nocturnal hypothermia for regaining normal body reserves. Thus, the evaluation of the energy reserves of a small bird at the beginning of the nocturnal fast plays a role that is essential in regard to an energy strategy primarily oriented towards saving.

There is also a first evaluation of the energy reserves of a large bird at the onset of a fast. Indeed, the further effectiveness in the mobilization of lipid reserves, and accordingly in the sparing of body proteins, is set by the initial amount of lipid reserves. Following this initial adjustment there is thereafter a steady-state in the utilization of body fuels (Le Maho et al. 1988, Robin et al. 1988). A further evaluation of energy reserves when a spontaneous fast is prolonged induces refeeding before a critical stage in the depletion of energy reserves has been reached (Robin et al. 1988, 1989).

CONCLUSIONS AND PERSPECTIVES

How then could this evaluation, that the body fuel reserves of a small hummingbird are sufficient enough for covering night requirements without torpor, fit with the torpor induced despite the large reserves of a fattening or already fattened individual? The answer likely is with the seasonal change in a set point for regulation in the amount of energy reserves (see Tooze & Gass 1985). The concept of this changing set point is essential to allow wild animals to live and breed in the cold. While spontaneously decreasing their food intake in periods of food shortage, many animals regulate their declining body reserves by adjusting food intake in accordance to a sliding set point in body mass (Mrosovsky & Sherry 1981). Birds that face a total fast can only regulate by adjusting their hypometabolic response. How this adjustment is achieved through the evaluation of body reserves and how a critical depletion of these reserves is anticipated by a signal triggering refeeding are some of the major goals of coming years. In this context, an important observation is the link shown in hibernating ground-squirrels between the depth of hypothermia and stored fatty acids (Geiser & Kenagy 1987). More detailed information is necessary about the mechanisms used by birds for entering or arousing from torpor (Geiser 1988, Prinzinger et al. 1981). Promising investigations are manipulations of nocturnal hypothermia in pigeons through the infusion of energy substrates or tube-feeding (Phillips & Berger 1989, Reinertsen 1989) and the study of how the bird solves the conflict between the cost of feeding and energy saving (Rashotte & Henderson 1989).

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BLOOD PRESSURE ADJUSTMENT TO CHRONIC SALT INTAKE IN PEKIN DUCKS

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ABSTRACT. Pekin ducks are able to cope with chronic salt stress by eliminating excess salt via their hypertrophied salt glands. Surprisingly the progress of salt adaptation which includes chronic elevation of Na^+ -content, of osmolality, and of plasma levels of the osmoregulatory peptides ANGII and AVT is accompanied by a significant decrease of mean arterial pressure. Cardiac output and heart rate are significantly reduced while total peripheral resistance, stroke volume and intravascular volume remained stable, despite a significant decrease of extracellular fluid volume. A greater influence of vagal inhibition, as revealed by the effect of muscarinic blockade and a reduced concentration of circulating norepinephrine indicate a central activation of the parasympathetic and an inhibition of the sympathetic system in salt adapted ducks.

Keywords: Osmoregulation, arterial hypotension, osmoregulatory peptides, catecholamines, vagal block.

INTRODUCTION

Pekin ducks, as descendants of sea and shore birds, can adapt to high chronic salt intake without impairment of their vital functions. Their kidneys, like those of most birds, cannot produce urine more than twice as concentrated as the body fluids, so when hypertonic saline is ingested, the main organs for excreting excess salt are specialized supraorbital nasal glands which can concentrate salt to over three times body fluid osmolality. Due to this exceptional concentrating capacity our Pekin ducks, maintained on 2% saline as their only water supply, generate almost 0.5 ml of free water from each ml of ingested saline. One can calculate that to provide the free water necessary for excretion of nitrogenous wastes and to replace evaporative water losses, these ducks must have an average daily salt intake of about 6 g per kg body weight.

Previous studies have shown that osmoregulatory homeostasis of these so-called "salt ducks" is established at plasma tonicities which are significantly elevated in comparison to ducks maintained on freshwater (water ducks). Plasma osmolality and sodium chloride content are significantly higher in the salt ducks and there is no difference in hematocrit, suggesting that blood volumes do not differ (Brummerman et al. 1987).

The plasma concentration of arginine vasotocine (AVT) and of angiotensin II (ANGII) measured by Gray and Simon (1987) in the salt ducks were permanently elevated three to eight-fold and the AVT concentration in the cerebrospinal fluid of the salt ducks was also significantly elevated.

Sustained high salt intake, with elevated plasma sodium and increased circulating concentrations of osmoregulatory peptides, is a condition favouring arterial hypertension in mammals. In several animal models, like the Dahl strain of rats or the desoxycorticosterone-treated rat, high salt intake triggers the onset of arterial hypertension.

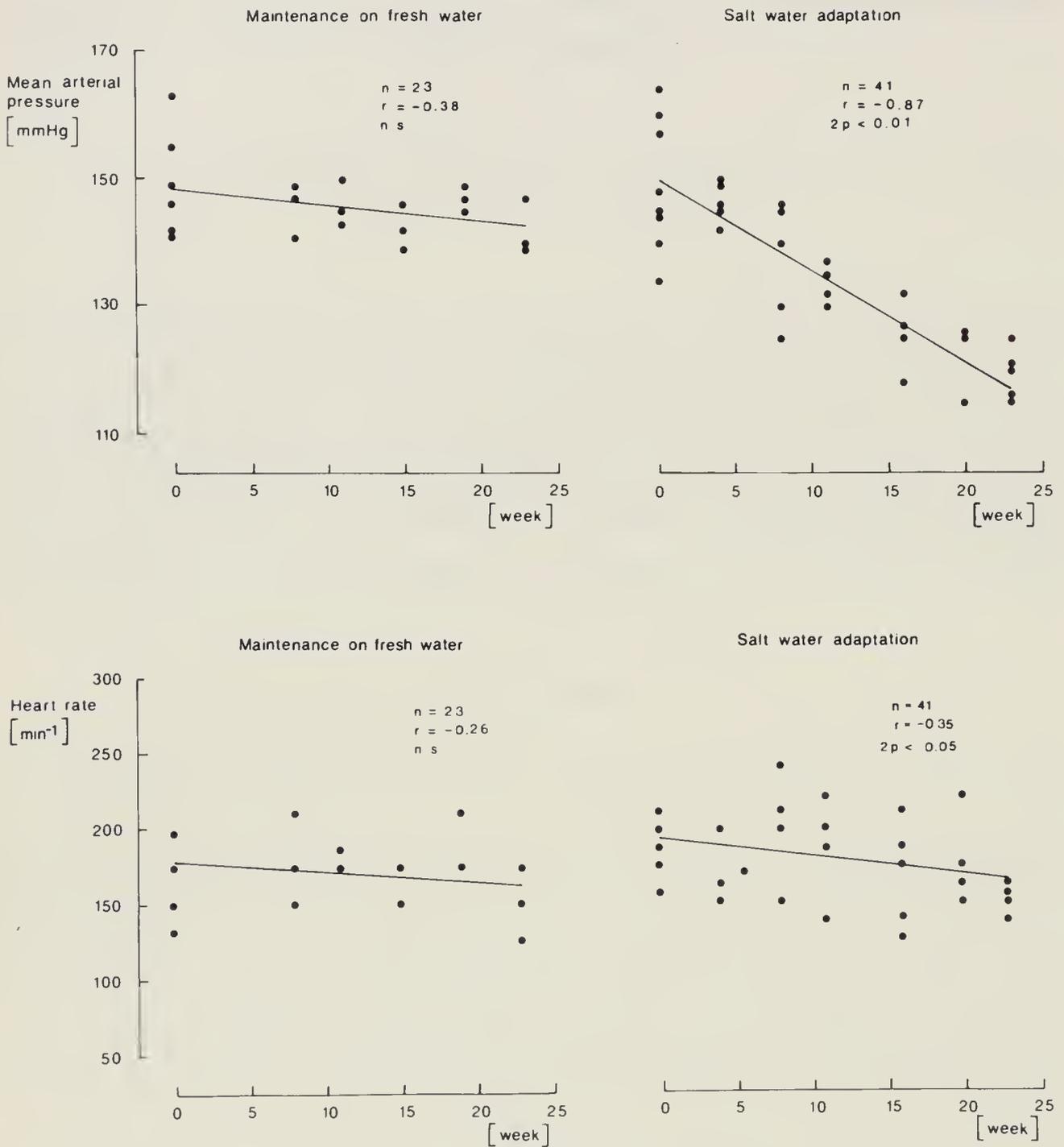


FIGURE 1 - Mean arterial pressure (A,B) and heart rate (C,D) in the course of adaptation of salt water ducks (B,D) to water of increasing salinity (0=start of adaptation in the 8th week), compared to siblings maintained on fresh water (A,C) during the same period. For water ducks correlation coefficients for mean arterial pressure and heart rate were significant for the period of observation.

Previous observations by Szczepanska-Sadowska et al. (1985) had suggested, however, that chronically salt-loaded ducks reduce rather than elevate blood pressure.

So for the study reported here we investigated the development of differences in blood pressure between salt and water ducks under conditions, when differences due to the age or to the strain of the animals were carefully excluded.

METHOD

Thirty siblings were randomly separated into two groups and raised under identical conditions, except that one group was maintained on freshwater and the other group was gradually acclimated to chronic salt stress. During the 10-week period of acclimation, as the salt concentration of their water supply was increased from 200 to 600 mosm/kg, measurements were repeated on salt and water ducks to follow the development of differences which might be of circulatory significance (for detail see Brummermann & Simon 1990).

RESULTS AND DISCUSSION

During the period of salt acclimation, arterial pressure of the salt ducks declined significantly with time, and this was accompanied by a slight but significant reduction of heart rate. The circulatory parameters of the water ducks did not change during this time (Figure 1).

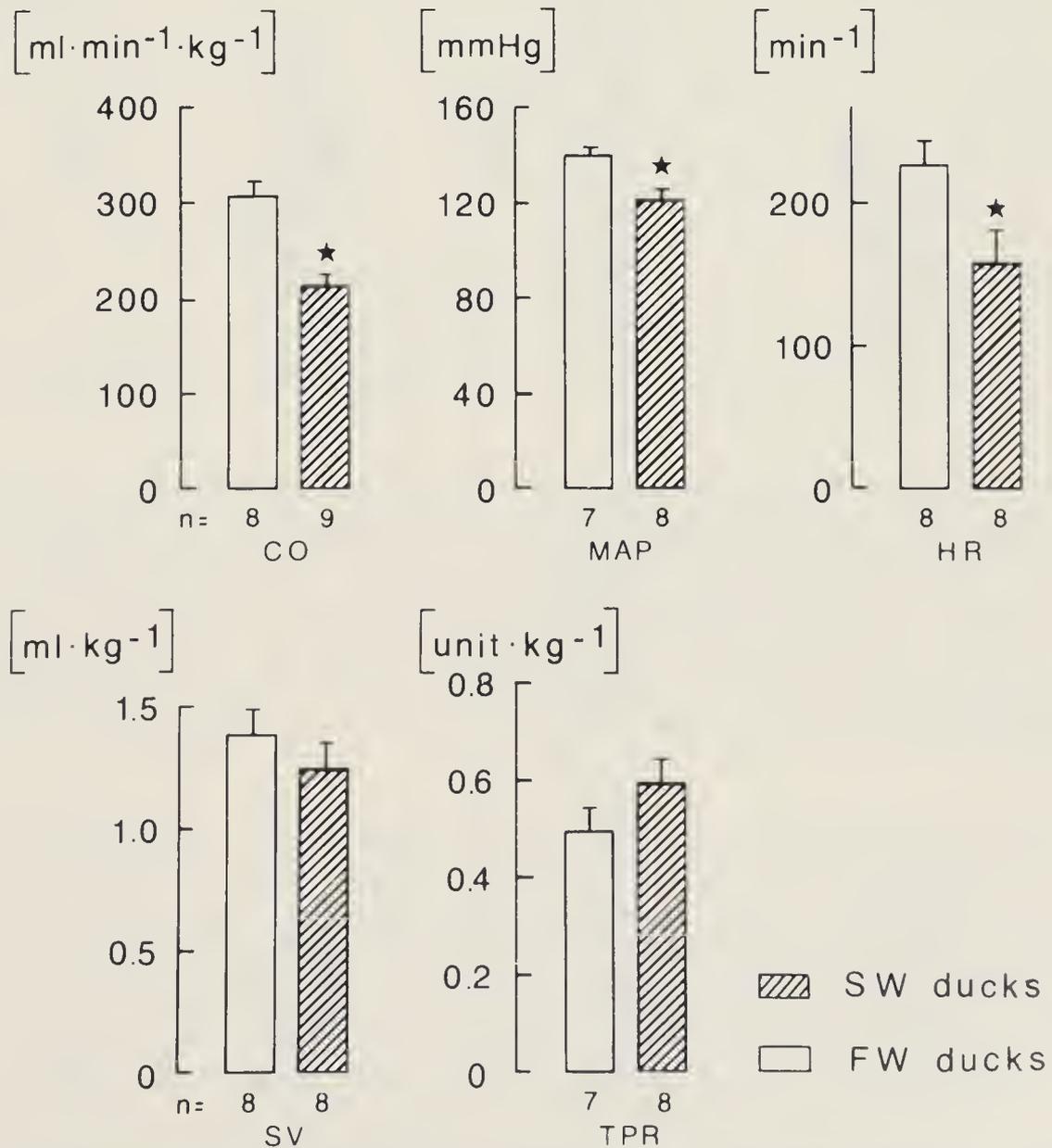


FIGURE 2 - Comparison of circulatory parameters (mean ± standard error) determined in fully adapted salt ducks (hatched columns) and water ducks (white columns) raised under otherwise identical conditions. CO, cardiac output per unit body mass; MAP, mean arterial pressure; HR, heart rate; SV stroke volume per unit body mass; TPR total peripheral resistance; * = significant difference between salt and water ducks (P<0.05).

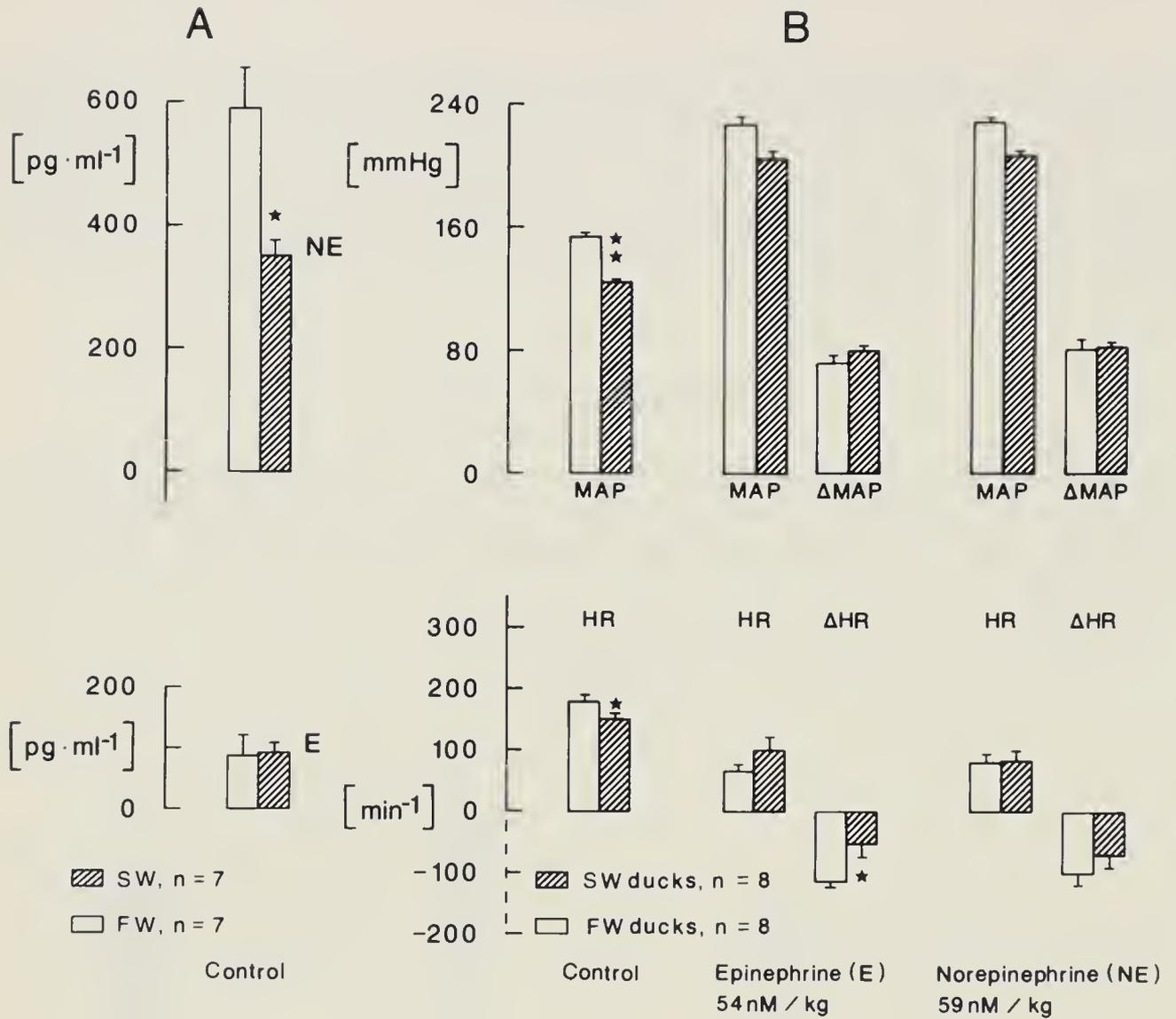


FIGURE 3 - A: concentration of epinephrine (left columns) and norepinephrine (right columns) determined in arterial plasma samples from water ducks (white) and salt water ducks (hatched). B: Mean arterial pressure (upper columns) and heart rate (lower columns) of fully adapted salt ducks (hatched) and water ducks (white). Left hand columns present control values. Absolute levels and changes induced by IV bolus injections of catecholamines are shown for epinephrine by the middle two pairs of columns and for norepinephrine by the two right pairs of columns. Mean values with standard errors from seven animals.

The cardiac performance was studied in eight water ducks and eight salt ducks which were acclimated to the highest salt load of 600 mosm for more than four weeks. While monitoring arterial pressure and heart rate, cardiac output was measured by thermodilution. In accordance with their significantly lower heart rate, cardiac output per unit body weight was significantly lower in the salt ducks. Stroke volume did not differ between salt and water ducks. Total peripheral resistances - estimated as the quotient of mean arterial pressure over cardiac output - were in the range previously reported for ducks by Sturkie (1970) and did not differ between salt and water ducks. These data strongly suggest that decreased cardiac output is responsible for the hypotensive circulatory adjustment observed in saltwater-acclimated ducks (Figure 2).

Since nervous control of cardiac performance is achieved by the interplay of parasympathetic and sympathetic innervation - and cardiac function is also affected

by circulating catecholamines – we investigated if the depressed cardiac function of salt ducks was due to changes in sensitivity to adrenergic transmitters or to changes of the plasma concentration of the transmitters during the course of chronic salt acclimation.

Seven water and seven salt ducks received bolus injections of epinephrine and norepinephrine, the doses chosen to produce about 75% of the maximum pressor response, according to previously determined dose-response curves. While there were no significant differences in the pressor responses between the two groups, the reflex bradycardia was significantly more pronounced in water ducks, perhaps due to their higher resting arterial pressure (Figure 3 B). Thus, the sensitivity to adrenergic transmitters seemed not to be changed during salt acclimation.

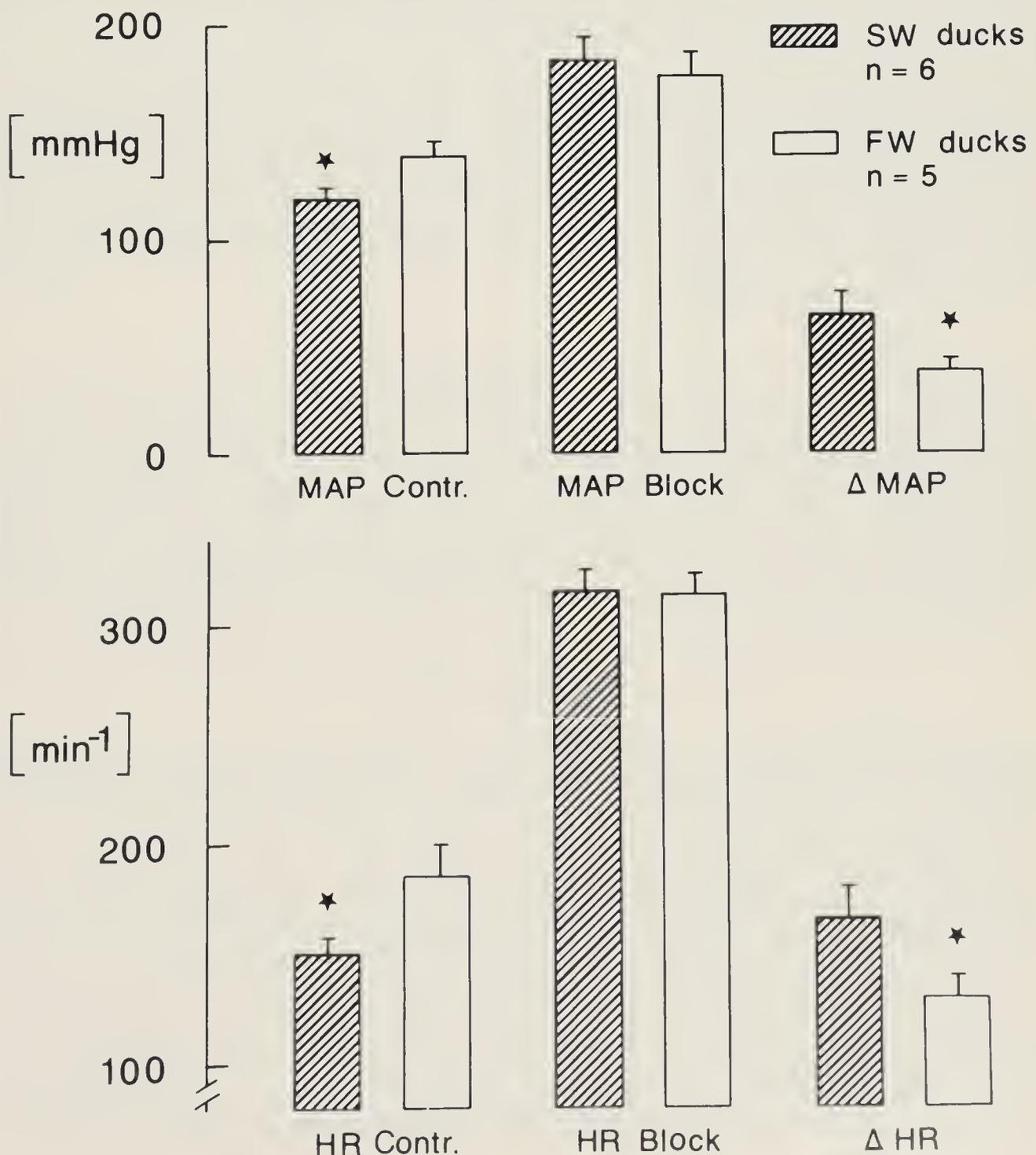


FIGURE 4 - Mean arterial pressure (upper columns) and heart rate (lower columns) of fully adapted salt ducks (hatched) and water ducks (white). Left hand columns present control values and middle columns values during muscarinic blockade; right hand columns show the changes in pressure and heart rate caused by muscarinic blockade.

The endogenous plasma levels of epinephrine and norepinephrine were measured in arterial blood samples by high pressure liquid chromatography using an electrochemical detector. Levels of epinephrine were similar in salt and water ducks, but the circulating norepinephrine concentration was significantly lower in salt ducks (Figure 3 A). This suggests that a reduced activity of the sympathetic system may contribute to the reduced cardiac output we found in salt ducks.

To explore the influence of parasympathetic activity we used the atropinase-resistant muscarinic blocker tridihexethylchloride. Heart rate and mean arterial pressure increased during the first minute of application. After 10 to 15 min the pressure decreased slowly, but tachycardia persisted. The increases of pressure, as well as of heart rate, were more pronounced in salt ducks, abolishing the pre-existing difference between salt and water ducks (Figure 4). This result indicates a stronger vagal inhibition of cardiac performance in salt ducks than in water ducks.

Since, as already mentioned, the plasma levels of ANGII and AVT were greatly elevated in salt ducks, we compared the effects of these peptides on arterial pressure between salt and water ducks. The dose response curves show that AVT in high doses tends to decrease arterial pressure. Conversely, high doses of ANGII increase arterial pressure, as previously reported by Wilson and West (1986). Salt and water ducks, though, did not respond differently to these peptides, indicating no change in sensitivity during salt adaptation.

In any case, the lack of any physiological significance for the hypotensive effect of AVT became obvious when we found no change in blood pressure while continuously infusing AVT to maintain plasma levels at least 10 times the resting concentration. It is possible, though, that the increased concentration of AVT in the cerebrospinal fluid of salt ducks may play an important role in the hypotensive adjustment to chronic salt stress. Since in dogs and rats AVT acts centrally to inhibit the activity of the sympathetic and to stimulate the activity of the parasympathetic nervous system (Courtice et al. 1984) it could have the same modulator activity in the CNS of salt ducks.

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SURVIVAL STRATEGIES IN GOLDCREST AND FIRECREST (*REGULUS REGULUS*, *R. IGNICAPILLUS*) DURING WINTER

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ABSTRACT. The genus *Regulus* includes the smallest passerine birds (5-8g). All feed exclusively on arthropods, and most are able to survive winter conditions in northern regions. Although day length is short and time available for foraging is limited, kinglets survive long cold nights roosting in the open. In order to cope with this situation they employ various strategies involving different functional systems. a) Since the kinglets are unable to save energy by torpor, they reduce nocturnal heat losses by huddling. During the daytime they have to feed at a very high rate, > 99%; see also Gibb (1960). b) Kinglets feed mainly on springtails (Collembola). c) They avoid intraspecific competition. Aggressive behaviour decreases at lower temperatures. d) The birds avoid unnecessary movements (wing flicking, rapid flights). They take less notice of predators, to which they also seem to be less attractive at this time (e.g. Pygmy Owl *Glaucidium passerinum*). Some preliminary data on wintering New World kinglets suggest similar adaptations.

Keywords: Regulidae, *Regulus regulus*, wintering, feeding strategies, social interactions, huddling behaviour.

INTRODUCTION

The family Regulidae, the kinglets, includes five species: *Regulus regulus*, *R. ignicapillus*, *R. calendula*, *R. satrapa*, *R. goodfellowi*. Extremely small (5-8g), they are among the tiniest representatives of the passerine birds. Most of them live in the northern parts of Europe, Eurasia and North-America. *R. regulus*, *R. ignicapillus*, *R. satrapa* and *R. calendula* are partially migrants (Figure 1): some populations are migratory, but small wintering populations of them remain at northern latitudes and tolerate extreme cold, long nights (ca. 17 h) and very short days. Normally they roost in the open, never in cavities, but sometimes under the snow.

Because they are small, the kinglets might be expected to utilize controlled hypothermia or torpor to ensure that their energy reserves suffice for the night, as do several small wintering passerines, e.g. *Parus atricapillus* (Reinertsen 1986). However, preliminary studies of their energetics showed clearly that kinglets are able to balance their nocturnal energy budget, even under severe weather conditions, at normothermic body temperatures (Reinertsen et al. 1988, Thaler-Kottek 1988, 1990). This implies that they must utilize other strategies within the framework of their behavioural patterns in adapting to cold climates. I shall try to point out the most important of these:

- a) Feeding behaviour, feeding strategies, temperature-dependent changes in locomotory patterns and vocalisation (Thaler 1973), kinds of food (Thaler 1990).
- b) Social behaviour; contact sleeping (huddling).
- c) Avoidance of predators.

Preliminary studies provide some clues about the predator's behaviour: during winter, the Pygmy Owl *Glaucidium passerinum* chooses larger prey in preference to *Regulus*.

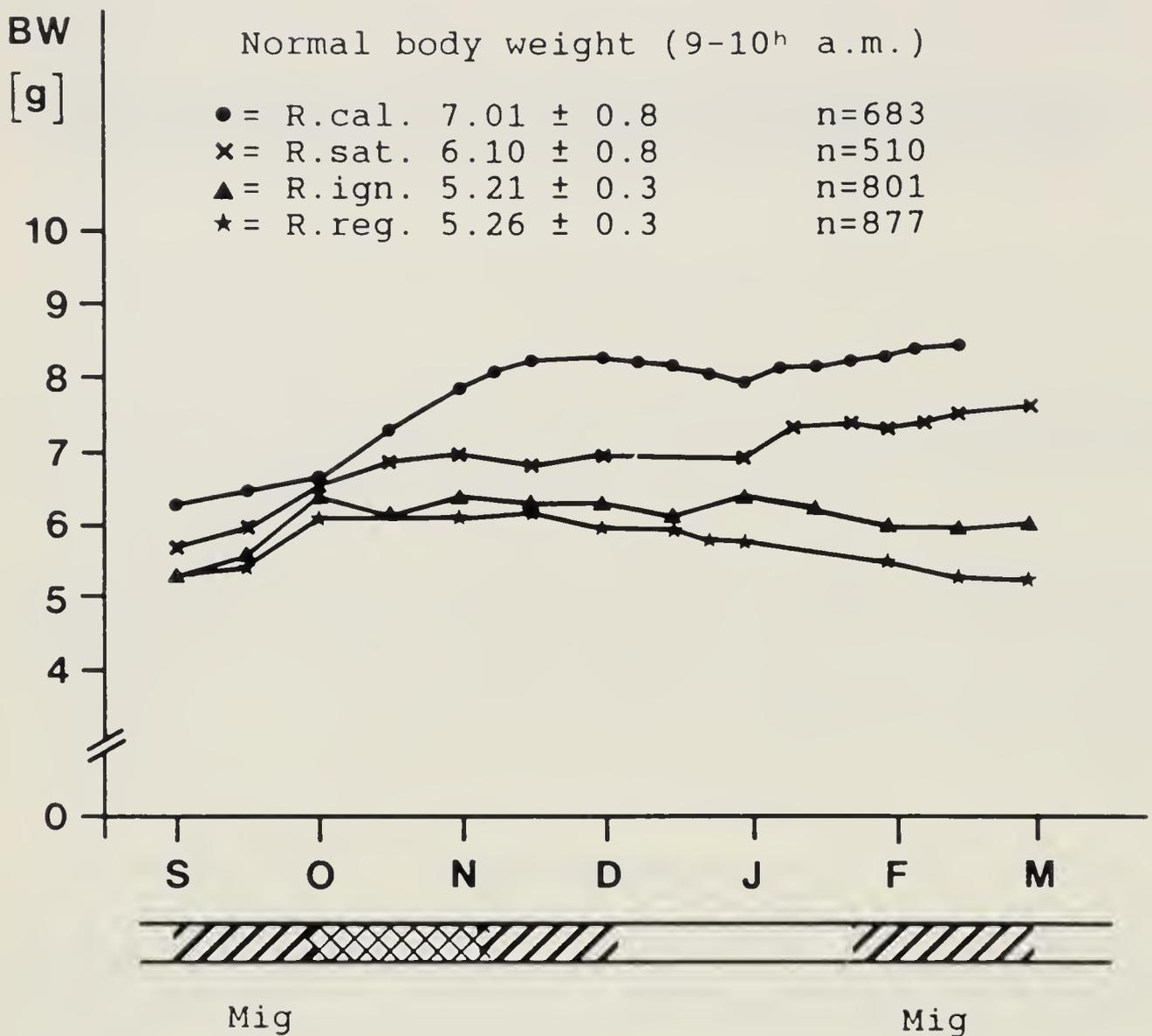


FIGURE 1 - Body mass of *Regulus regulus*, *R. ignicapillus*, *R. satrapa* and *R. calendula* during fall, wintering and spring migration (September - March). The shape of the curves provides an indication of their migration status. Whereas *R. calendula* and *satrapa* are well-adapted for migration, with a good fat deposit, *R. regulus* is less well prepared. All species have a higher body mass (0.8-2.0 g) in the late afternoon.

METHODS

Four species of kinglets (*Regulus regulus*, *R. ignicapillus*, *R. satrapa*, *R. calendula*) were studied for several years in the field as well as in aviaries (for details see Thaler-Kottek 1979, 1990); behavioural patterns were observed and documented in aviaries by the usual methods (recorder, video, photo/film). As far as possible the same techniques were employed in the field. For feeding strategies and nutrition see Thaler & Thaler (1982) and Leisler & Thaler (1982). Data on huddling behaviour were obtained by direct measurements in the plumage of contact-sleeping kinglets at their normal sleeping sites (branches), using a highly sensitive thermistor (Thaler 1988). The weights of the birds were obtained with a METTLER balance, used as a feeding dish throughout the day.

The reactions of Pygmy Owls to Goldcrests and Coal Tits *Parus ater* were tested in aviaries with three compartments (80x40x40 cm); captive Pygmy Owls were placed

in the middle and the "prey" on either side. The partitions between the compartments consisted of soft plastic-covered double net, mesh size 1 x 1 cm. The reactions of the owls were observed continuously for 60 min/day, the positions of *R. regulus* and *P. ater* being reversed at irregular intervals. During the tests the owls were provided with their accustomed food (mice) so that their choice was not influenced by hunger.

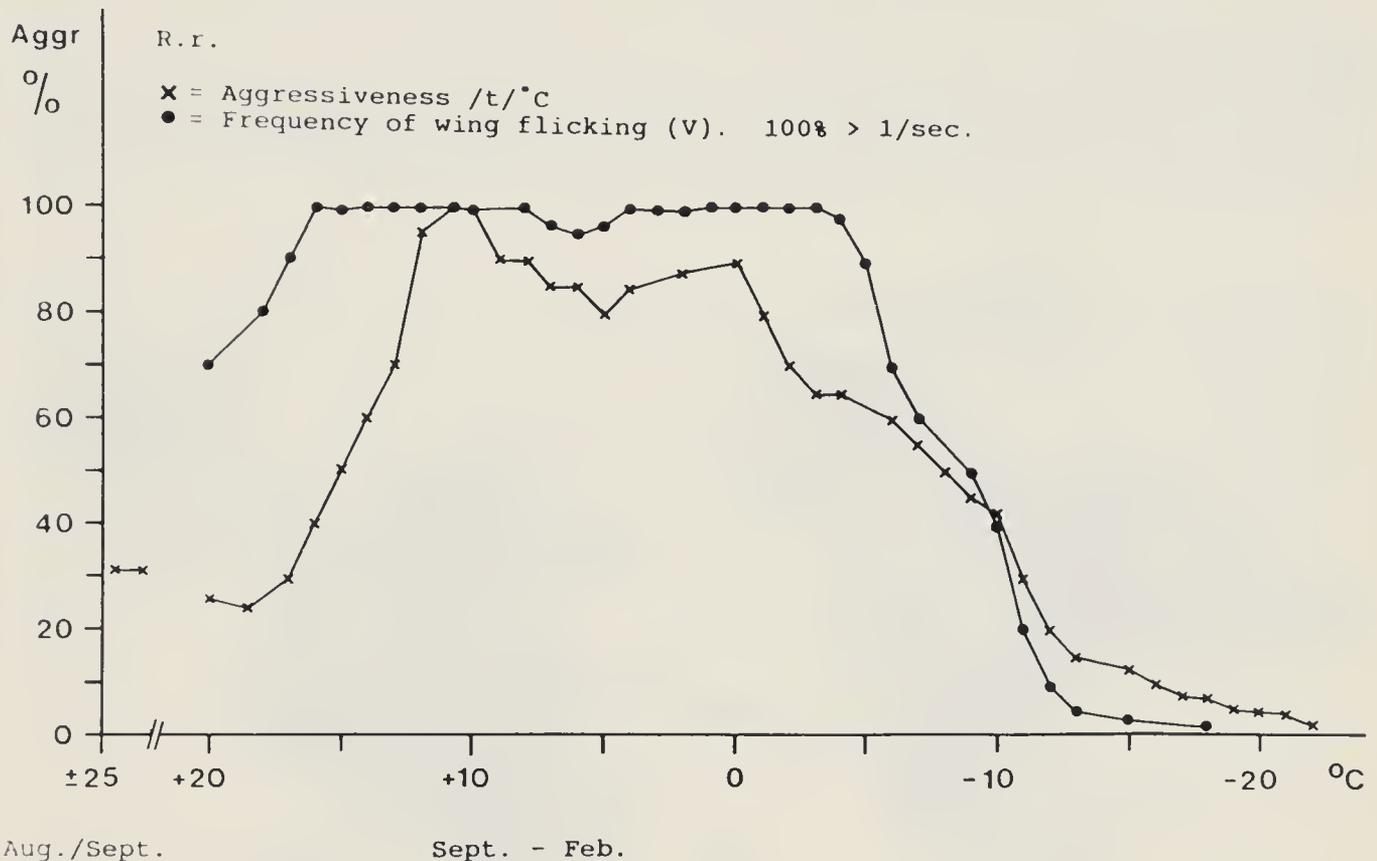


FIGURE 2 - Decrease of aggressive behaviour and wing flicking at low temperatures, for details see text. 100% wing flicking = >1 movement/sec. (V) = tested in aviaries.

RESULTS

Feeding behaviour, feeding strategies and diet

Kinglets feed exclusively and at a very high rate on small arthropods; they need at least their own body mass/day, although under severe winter conditions they require even twice this quantity (Thaler & Thaler 1982). Short days and long cold nights necessitate a number of adaptations, the majority of which are found within the "normal behaviour" of the kinglets. Most of the following observations were made on Goldcrests, but the few data obtained from other species are similar.

- The speed of food searching is reduced in the cold: decreasing temperature brings about a decrease in the speed of feeding activity. The Goldcrests advance slowly, search accurately, fly rarely and then only over small distances (e.g. Thaler 1973, Leisler & Thaler 1982: normal speed for the Goldcrest at 15°C: 8 m/min; Firecrest: 22 m/min; at -18°C: 0.71 m/min, and 13 m/min respectively).
- In the cold they reduce or avoid movements which are normally very characteristic for the species, e.g. wing flicking and hovering. At temperatures above 0°C the birds perform these two movements continuously (see Figure 2).
- Goldcrests feed principally on Springtails (*Collembola Entomobrya* sp.). These primitive insects are highly resistant to frost and are very abundant on twigs and between needles of spruce and pine trees. They are rich in fat and thus represent

a food resource of high energetic value. If need be, Goldcrests also catch larger prey such as flies, moths, and Hymenoptera (Thaler & Thaler 1982), which they would not consider in the warmer seasons. Such large food items were swallowed immediately on cold days, without the careful removal of legs, wings etc. that otherwise precedes their ingestion.

Social behaviour

Kinglets are territorial birds, and only during the non-reproductive periods do they form small flocks. Goldcrests, especially, maintain individual distance from each other, even within flocks, and also exhibit distinctly aggressive behaviour.

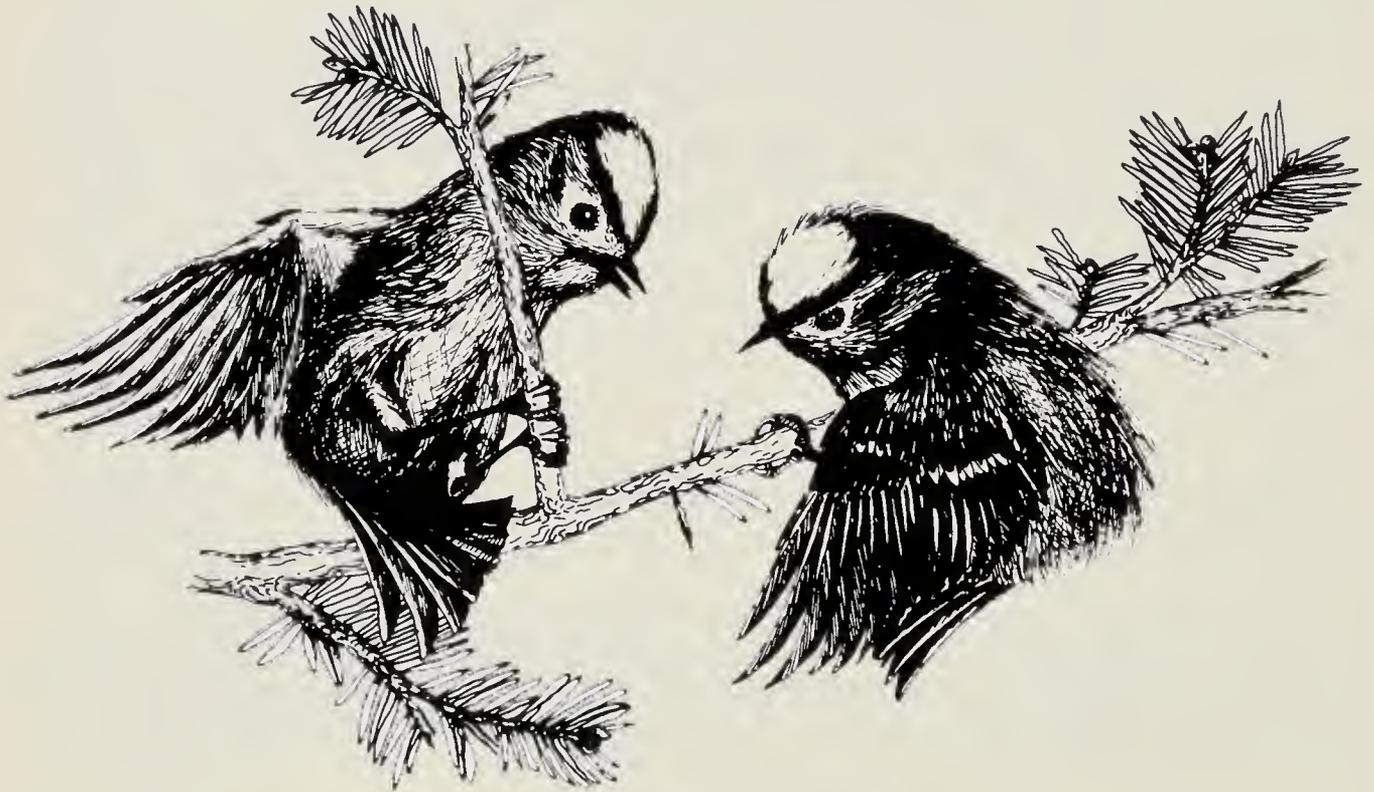


FIGURE 3 - Goldcrests *Regulus regulus*, two females: Aggressive behaviour.

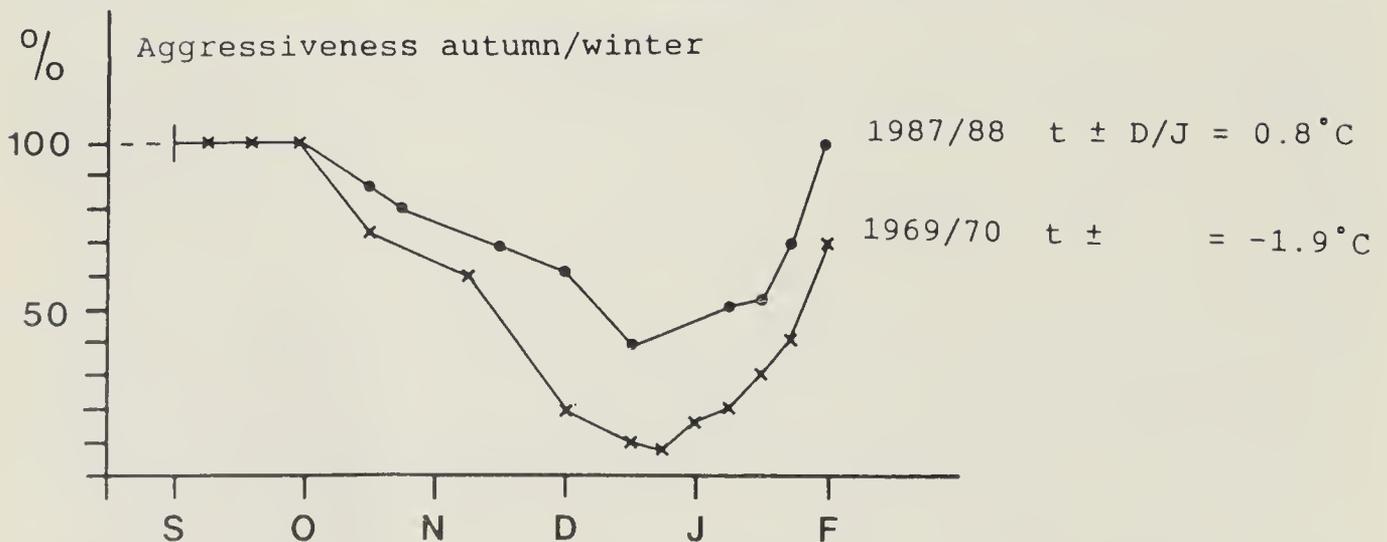


FIGURE 4 - Relation between low temperatures and aggressiveness of *R. regulus* in two seasons (Sept.-Feb.).

Decreasing temperature dramatically changes this behaviour (Figure 3): the distance between individuals decreases in proportion to the drop in temperature, i.e. the cooler the weather the closer are the birds to one another (Figure 2, 4). Between 0°C and

10°C, kinglets are aggressive toward each other, presenting a forward display (Figure 3) and emitting aggression calls if another individual comes within a distance of 1 m. They invest about 5-10% of their daily activity in chasing each other away. At -18°C the forward displays and aggression calls disappear completely and individuals may even come within 10 cm of each other. In this case they only “face away” (as shown in Figure 5). The normally loud contact call can scarcely be heard at temperatures of about -18 to -20°C: instead, the birds emit a continuous, very weak and gentle piping, audible only over short distances (<1m). This may serve to ensure close contact within the wintering groups and that the flock remains in close contact overnight when roosting.

Huddling behaviour

Goldcrests minimize heat loss behaviourally by selecting favorable microclimates, huddling in dense branches or in snow holes beneath snow-covered branches, never in true holes or cavities. Kinglets huddle in groups of three to five in their roosts (Thaler 1972). Huddling behaviour is exhibited by other small bird species such as the Brown Creeper *Certhia familiaris*, Wren *Troglodytes troglodytes* and Long-tailed Tit *Aegithalos caudatus* (Löhrl 1955), and its energetic significance has been demonstrated for the Common Bush Tit *Psaltriparus minimus* (Chaplin 1982). At -20°C Goldcrests even dispense with their ritualized appeasing behaviour (Figure 5) and calls prior to huddling; they make close contact within seconds and without emitting a sound.

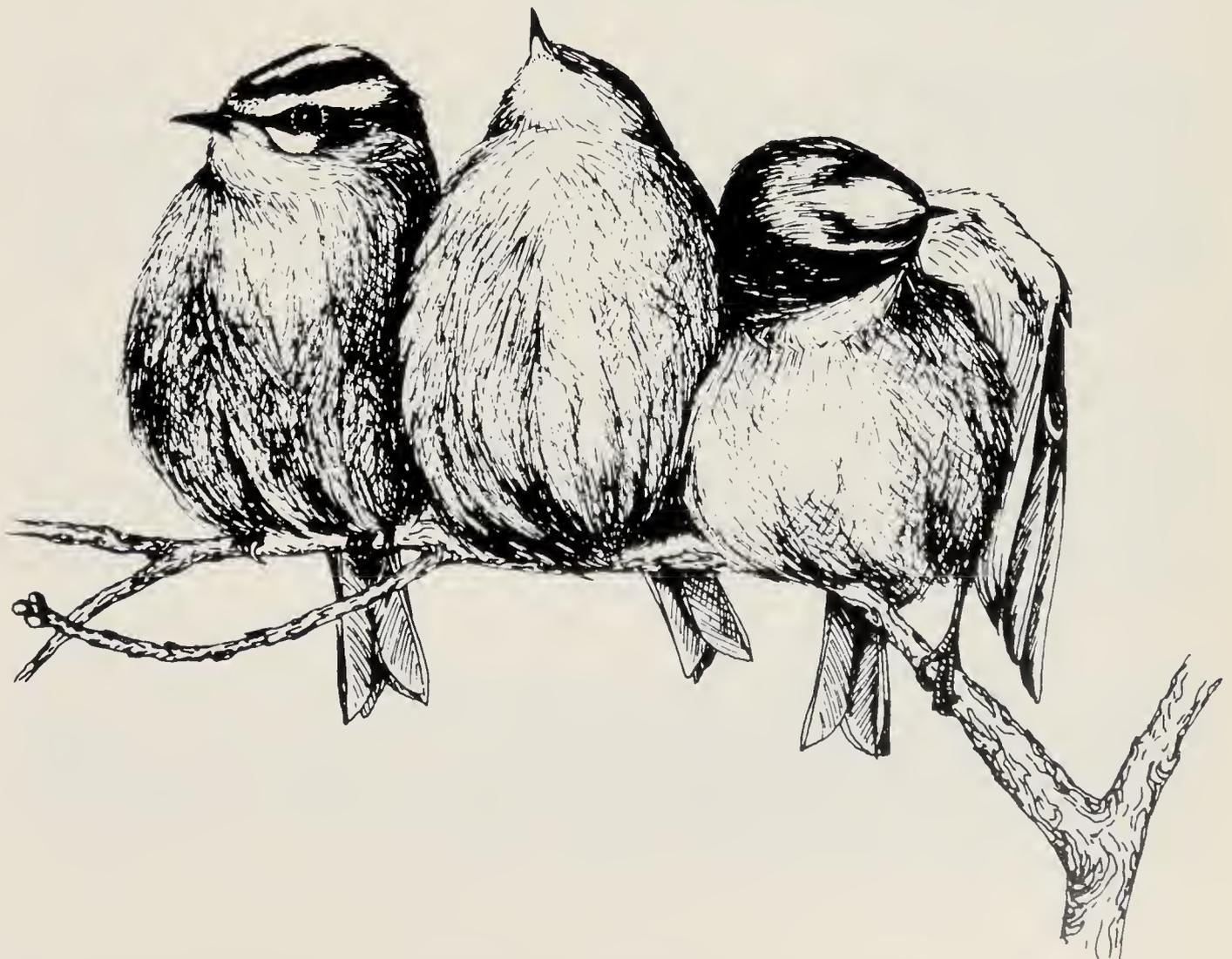


FIGURE 5 - Firecrests *R. ignicapillus*, huddling. The bird on the right shows ritualized preening, middle: “head up” posture, left: “face away” posture.

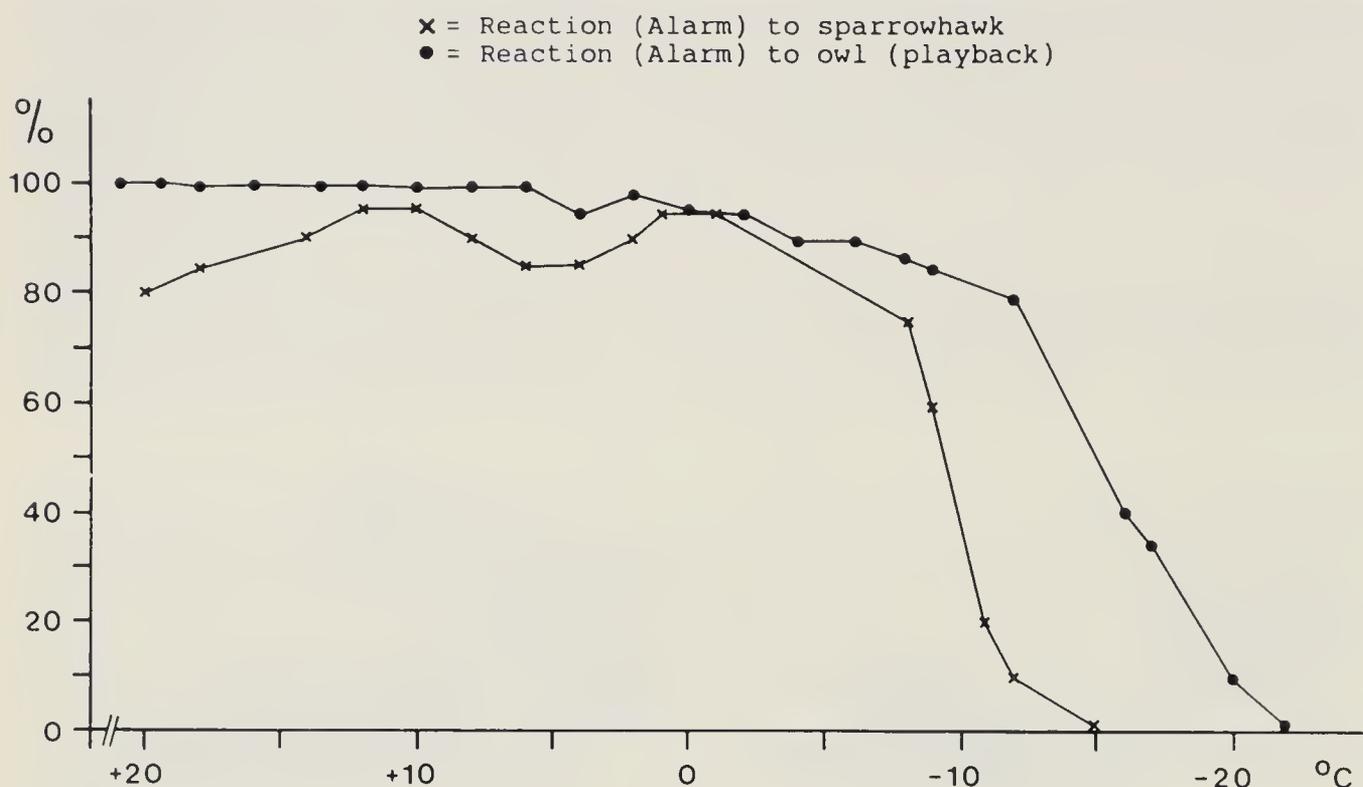


FIGURE 6 - Alarm reaction to a sparrow hawk and to the playback of the Pygmy Owls call at decreasing temperatures during the winters 1972-76 and 1987/88; n days = 93 (Sparrow Hawk), 81 (Pygmy Owl).

Avoidance of predators

As the temperature decreases, Goldcrests pay less attention to any predators. They ignore Sparrow Hawks at temperatures below -20°C , and their reaction to even their main predator, the Pygmy Owl, strongly decreases (see Figure 6). Such behavioural adaptations are also suggested by Gibb (1960). Humans are allowed to come near enough to touch kinglets at this temperature. The birds do not even react if a predator attacks a conspecific in their vicinity.

Observations in the field show that predators such as Sparrow Hawks or Pygmy Owls are more interested in larger prey during cold periods. This is also shown by the findings of Hilden (1982), and Kellomäki (1977), in Finland: among the 147 birds killed and deposited by *G. passerinum* only two Goldcrests were found. This suggests the following hypothesis: the risk run by a Goldcrest in ignoring such birds of prey during periods of cold is less, because the raptor itself is less interested in prey as small as the Goldcrest.

A series of tests made in aviaries showed up this tendency even more clearly. Two Pygmy Owls (1 male, 1 female) were tested for their food preference: In a double choice test with *Regulus regulus* and *Parus ater* over 1 h/d every owl showed initially a small, but in the course of the experiment increasing preference for the larger tit. (*R.r.* 6 g, *P.a.* 11 g). The two birds were equally attractive to the owls with respect to behaviour since both species were in constant motion (Figure 7).

DISCUSSION

Observations on overwintering kinglets, and especially the Goldcrests, show the presence of well-defined behavioural adaptations to cold. Since kinglets must feed continuously during the short and cold winter days, most adaptations are found in connection with the normal feeding behaviour:

- 1) They lose no time on aggressive behaviour or avoidance of raptors during food-searching.
- 2) Feeding flocks of kinglets must move in close formation to ensure a common roosting place for the night (huddling).
- 3) They reduce their activity: no flights are made over longer distances, wing flicking is reduced or absent, and they no longer hover.
- 4) They feed mainly on springtails, a high-energy food source that is invariably available.

Attacks of *G. passerinum* within 60 min.

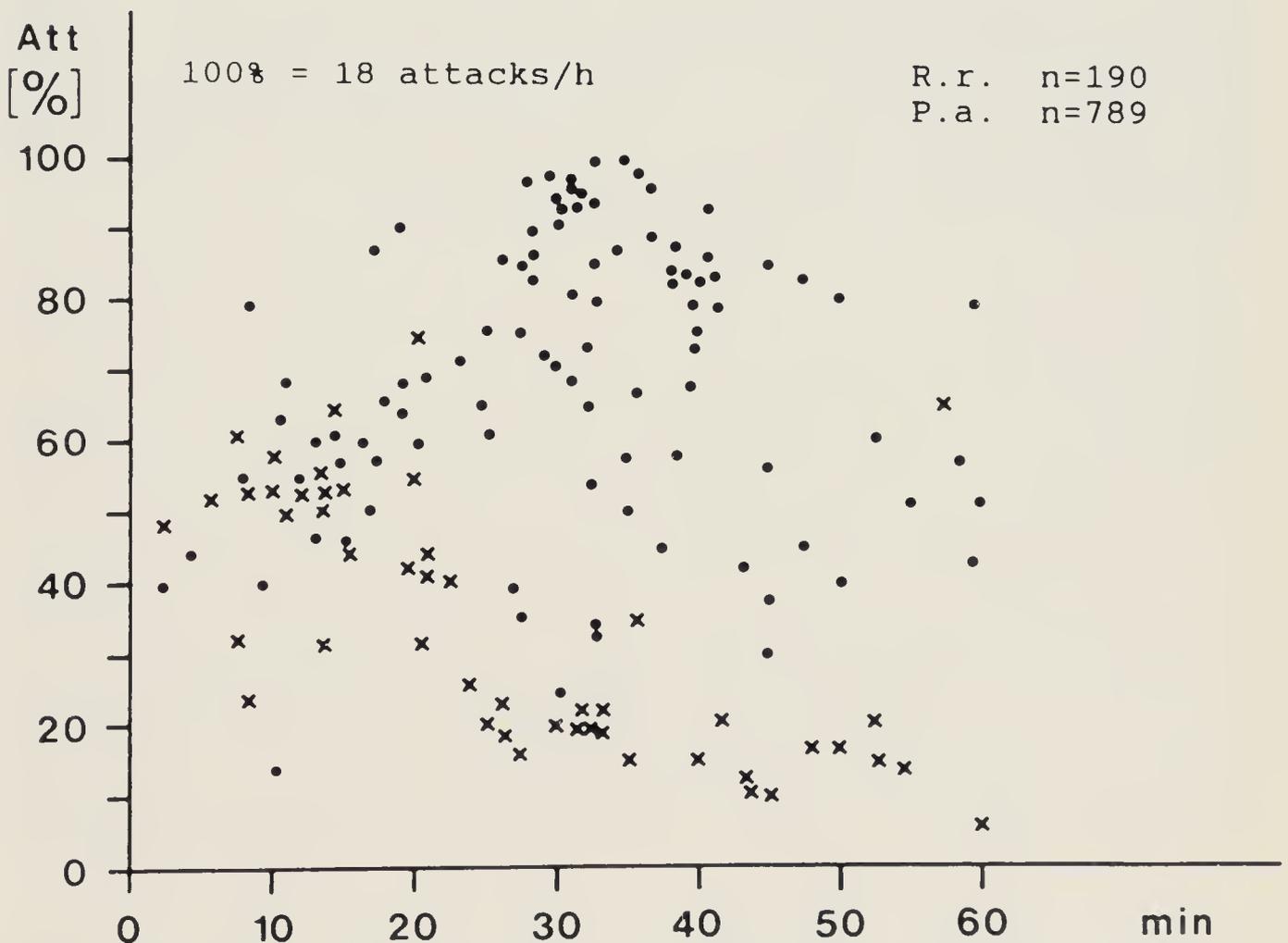


FIGURE 7 - Attacks by two Pygmy Owls (male, female) on *R.r.* (x) and *P.a.* (o) in a double choice test; (*R. regulus* on the one side and *P. ater* on the other). At first the owls show no clear preference, but after 15 min. they more often choose *P. ater*.

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CONCLUDING REMARKS: ADAPTATIONS TO EXTREME ENVIRONMENTS

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The intent of this symposium was to elucidate avian physiological and behavioural adaptations to environmental challenges such as extreme cold and hot climates, water shortage and chronic salt load. Since small body size makes it especially difficult to cope with extreme environmental conditions, the symposium has also focused on survival strategies of smaller versus larger birds.

Webster reviewed recent advances in the study of avian adaptations to arid, hot climates. Desert birds must cope with the conflicting demands of heat defence and conservation of water. It seems that the role for cutaneous evaporation in heat defence should be re-evaluated since evaporation from the skin is now known to comprise 40-75% of total evaporative water loss in the several avian species measured. Birds obtain water by drinking, from water contained in food, and from oxidative metabolism of foodstuffs. Water is conserved by adaptive reduction of excretory water loss. Recent research has provided improvements in the understanding of the roles of lower intestinal and caecal epithelia in osmotic and ionic regulation and also more precise estimates of kidney function and comparative structure. Some desert bird species utilize nasal glands to secrete concentrated salt solutions and thereby spare body water. Such glands are, however, particularly useful for sea and shore birds exposed to high chronic salt intake. The nasal glands of Pekin ducks can concentrate salt to more than three times body fluid osmolality. Previous observations have suggested that chronically salt-loaded ducks reduce rather than elevate blood pressure. Brummermann presented an investigation on the development of differences in blood pressure between "salt" and "water" ducks. Her results suggest that decreased cardiac output is responsible for the hypotensive circulatory adjustment observed in salt-water-acclimated ducks. The depressed cardiac function was not due to changes in sensitivity to adrenergic transmitters but rather to a decrease of circulating norepinephrine concentration in the salt-ducks, leading to a stronger vagal inhibition of cardiac performance.

Thomas described marked interspecific differences in energy metabolism and thermoregulatory physiology in three sandgrouse species, despite the general similarities of size, shape and ecology between the various species. They face problems of high environmental temperatures, water shortage and also low biological production. The solutions to these problems may often be conflicting and require trading benefits against risks, as in the dilemma of conserving water in defense of physiological fluid composition and using it in defense of body temperature. By tolerating both hypothermia and hyperthermia sandgrouse can save both water and energy through a reduction of the temperature gradient between the body and the environment.

Though several avian species utilize hyperthermia as an adaptation to high environmental temperatures, thermal lability in birds is most thoroughly studied as an adaptation to cold in birds that utilize hypothermia on a diurnal basis. Hypothermia and hypometabolism in smaller versus larger birds was thoroughly reviewed by Le Maho, together with a description of hypometabolism without torpor. Body fuel reserves seems to be integrated in the processes that trigger torpor since the depth of hypothermia is inversely correlated to body weight. The crucial question is how the birds are able to evaluate the availability in body fuel reserves. Furthermore, how a critical depletion of the reserves is anticipated by a signal triggering refeeding, has yet to be established. It seems that a concept of a seasonal change in a set point for regulation of the amounts of energy reserves is an important factor in the regulation of energy expenditure.

Although the metabolism may be reduced by 60-90% in hypothermia compared with normothermia, this mechanism of energy saving is not used by all birds living in cold climates. Since the energetic significance of hypothermia depends strongly on both body size and body - ambient temperature gradient, it may not be surprising that Goldcrests and Firecrests are able to survive winter conditions in northern regions without entering hypothermia, but rather rely on behavioural adaptations. Since they must feed continuously during the short and cold winter days, most adaptations are found in connection with the normal feeding behaviour. Thaler has studied four species of Kinglets for several years in the field as well as in aviaries and presented a review of the results from these remarkable studies. By comparing measurements and observations in aviaries with observations in the field, a thorough documentation of the behavioural patterns of these birds was obtained. Only through such field observations and measurements can behavioural adaptations to extreme environments be revealed. Since field conditions expose the individual birds to the cost of increased predation risk in addition to the energetic cost of e.g. thermal and osmotic homeostasis, this may influence to what extent priority is given to the utilization of different physiological and behavioural adaptive mechanisms.

SYMPOSIUM 32

SENSORY BASIS OF ORIENTATION

Conveners W. WILTSCHKO and R. C. BEASON

SYMPOSIUM 32**Contents**

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INTRODUCTORY REMARKS: SENSORY BASIS OF ORIENTATION

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Birds are well known to be excellent navigators: year after year, myriads of birds migrate over hundreds or even thousands of kilometers to their species-specific winter quarters and, a few months later, return to their breeding grounds, very often settling in the immediate vicinity of the previous year's nest site. Many species have been shown to return to their home after displacements over considerable distances, some sea birds even from distances of more than 4000 km. Ornithologists have always been fascinated by these outstanding performances, and have marvelled about how the birds managed to find their way. Although a 'sense of direction' is a familiar term in everyday language, it became obvious that such a 'sense of direction' or 'sense of location' ('Ortssinn', Stresemann 1935) as a separate sensory quality does not exist in birds. Instead, birds are able to derive directional and spatial information from a great variety of environmental cues.

In nature, factors containing potential orientational information are not scarce: celestial cues like the sun, the stars and the pattern of polarized light in the sky have been shown to provide directional information. The magnetic field of the earth is another source of directional information, while the spatial distribution of magnetic parameters such as total field intensity and inclination show gradients from the poles to the magnetic equator which represent a potential source of positional information on the earth. The same is true for the Coriolis force, a force associated with the rotation of the earth (see Yeagley 1947). Gravity also forms distinct geographical patterns which could be used for orientation.

The list of potential orientation cues need not be restricted to world-wide gradients, however. Factors distributed on a smaller scale might provide spatial information on a regional basis. The displacement experiments with migrants by the Dutch bird banding station suggest that the area in which a bird is able to home might be limited: Baltic Starlings were caught in great numbers as transmigrants near The Hague in the Netherlands and displaced roughly perpendicular to their normal migration route. Subsequent banding recoveries show that the birds released in Switzerland, ca. 600 km from The Hague, were able to return to their normal breeding areas in the Eastern Baltic (Perdeck 1958), whereas most of the starlings displaced ca. 1200 km to Barcelona, Spain, apparently could not do so. The majority of the recoveries of these birds in spring and summer lay in southern France and northern Italy (Perdeck 1967). A similar limitation on the spatial range of navigation was suggested by loalé et al. (1983) for homing pigeons. In view of these findings, factors of more local nature become potential orientation: odors, infrasound, topography and prominent landmarks, to name just a few proposed in this role.

This leads to the crucial question: Which of the potential orientation cues are available to birds and how are they utilized? When orientation research began, most authors either tended to assume that the sensory world of birds was comparable to our own, or they were inclined to attribute birds with various mysterious sensory capacities that greatly exceed our own human sensing abilities. Although many of these exaggerated assumptions proved false, research in the past decades has revealed that the sensory world of birds is surprisingly rich and encompasses many unexpected qualities: birds are able to perceive factors that are inaccessible to humans, such as the magnetic field and barometric pressure. In the more familiar sensory modalities like vision and audition, birds may have larger ranges and/or can use aspects that we cannot perceive, like ultraviolet and polarized light and infrasound (see Delius & Emmerton 1978, Kreithen 1980). It is the aim of this symposium to ask the sensory physiologists to share their knowledge on the various sensory capabilities of birds with us. This should lead to a better understanding of the birds' sensory world and, consequently, of their orientation abilities.

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AVIAN HEARING MECHANISMS AND PERFORMANCE FROM INFRASOUND TO THE MID-FREQUENCY RANGE

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ABSTRACT. The acoustic signal initiates a travelling wave along the avian basilar membrane, which stimulates the hair cells. The frequency selectivity of the mechanical response is insufficient to explain the frequency selectivity of primary afferent fibres, however. Additional hair cell filter processes have to be postulated. This view is supported by the temperature dependence of primary afferent frequency tuning, the oscillations in the hair cell membrane potential and the existence of preferred intervals in the spontaneous activity of the nerve fibres. In addition to sound in the audio frequency range pigeons and possibly other birds, also respond to infrasound behaviourally. In the auditory nerve, fibres responding to infrasound have been found. These originate in the papilla basilaris. However, the biological importance of avian infrasound hearing is still unclear.

The highly developed vocal communication of birds requires an elaborate hearing organ and, in fact, the performance of the avian inner ear is comparable to that of the mammalian cochlea. Although many mammalian species can hear in the ultrasonic range the bird's ear shows more sensitivity at infrasonic frequencies. Despite their similar capabilities mammalian and avian (or submammalian) basic transduction processes may show substantial differences - as we shall see. The present review cannot include the avian outer ear, although in some species (e.g. owls) its configuration contributes substantially to spatial discrimination (Knudsen 1980). Furthermore the middle ear transfer characteristics cannot be considered in detail (see Gummer et al. 1989a, b). A more comprehensive survey of reptilian and avian hearing may be found in Manley's (1990) recent monograph and psychophysics of bird hearing in Dooling (1982).

The avian inner ear has a basilar papilla which is boomerang-shaped and between 3 mm (Starling) and 11 mm (Barn Owl) long. The basilar membrane (BM) extends between two cartilaginous plates. As in the mammalian ear, there are three fluid-filled spaces, the scala tympani, the scala media and the shallow scala vestibuli (Figure 1). Unlike the mammal, the scala media and scala tympani are separated by the thick tegmentum vasculosum, a tissue which is thought to produce the endolymphatic fluid to generate the endo-lymphatic potential (EP), and to be analogous to the mammalian stria vascularis. However, biochemical differences obviously exist. The avian EP is only between 10-20 mV and is not affected by diuretics which are ototoxic in the mammals (Schermuly et al. 1990). This suggests different ionic mechanisms for the generation of mammalian and avian EPs.

The sensory hair cells (HCs) are located on the basilar membrane. Depending on species there are some 6000-11,000 of them. As the avian BM is short, there are between 10 and 50 HCs in one cross-section, an arrangement quite different from that in mammals. The HCs are embedded in supporting cells and again unlike the mammal, there are no empty fluid spaces like the tunnel of Corti separating them. At least

two types of HCs are present, the tall (THC) and short (SHC) hair cells. In some species there is also an intermediate type. They are classified primarily according to their morphology; their respective functions are only slowly beginning to emerge. Most of the THCs lie over the cartilaginous plate, whereas the short and intermediate hair cells (SIHCs) are located over the free basilar membrane and thus possibly experience more basilar membrane motion than the THCs. The HCs carry stereovilli on their free surfaces, something between 200 at the basal and 50 in the apical end of the papilla. Unlike mammalian auditory HCs, a kinocilium is also present. The villi are short in the basal and long in the apical region.

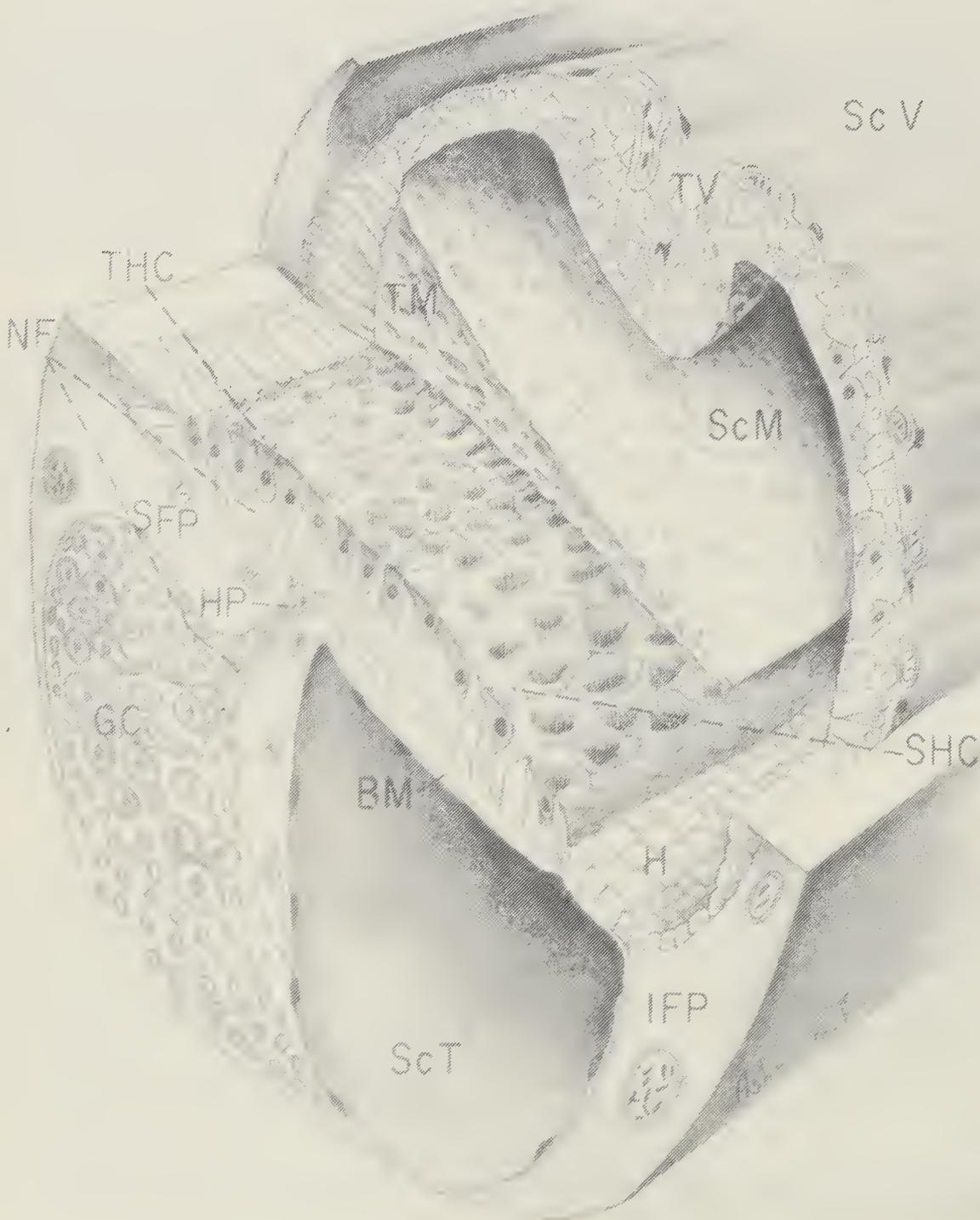


FIGURE 1 – Transverse section through the pigeon's cochlear duct (Takasaka & Smith 1971). TV: Tegmentum vasculosum; TM: Tectorial membrane; ScM: Scala media; THC: Tall hair cell; SHC: short hair cell; BM: Basilar membrane

As in the mammal the HCs are covered by a tectorial membrane. There is, however, no subtectorial space. The stereovilli protrude into honeycombed structures in the tectorial membrane.

The innervation pattern of the HCs has unfortunately not been sufficiently elaborated yet. There are afferent and efferent fibres. All afferent fibres are myelinated. THC-afferents do not branch or innervate only two THCs whereas fibres to SIHCs branch and supply up to 10 hair cells (Rebillard & Pujol 1983, Whitehead & Morest 1985, von During 1985, Schermuly & Klinke unpublished) as in the mammal. Nevertheless the question of whether or not mammalian inner and outer hair cells (IHC, OHC) are equivalent to avian THC and SIMC respectively is entirely unresolved and there are strong arguments against this contention (see later).

Neurophysiological data on auditory afferents are available from the Pigeon *Columba livia*, the Starling *Sturnus vulgaris*, the Red-winged Blackbird *Agelaius phoeniceus* and the chicken *Gallus domesticus*, admittedly hardly representative of songbirds. All the auditory afferents show an irregular spontaneous discharge rate of between 20-180 imp/s (see Manley 1990 for review, Smolders et al. unpublished). In a proportion of the fibres the inter-spike intervals during spontaneous activity are not distributed in a Poisson-like manner but certain "preferred intervals" prevail (Manley 1979). These intervals are related to the frequency the fibre is tuned to, the characteristic frequency (CF), and their duration is close to $1/CF$. "Preferred intervals" have never been reported from mammalian auditory afferents, but have been from many non-mammalian species. It is assumed that the preferred intervals reflect intrinsic properties of the avian frequency tuning mechanism.

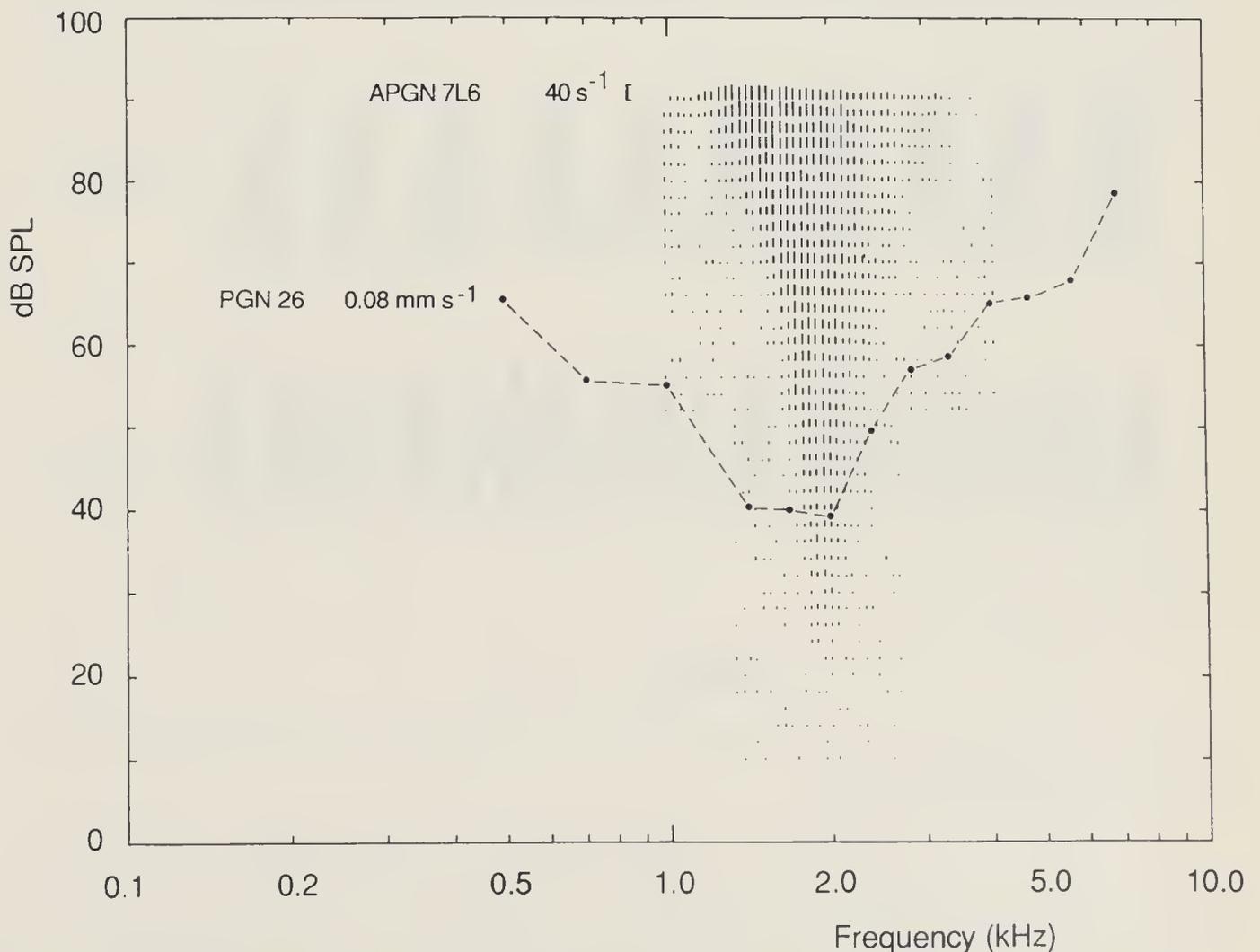


FIGURE 2 – Iso-velocity response of a discrete point of the pigeon BM (broken line) to sound stimuli of various frequencies compared to the neuronal response of a single fibre. Bar length signifies number of action potentials per tone stimulus.

When acoustically stimulated with frequencies between 30 Hz and 6 kHz, avian auditory afferents will be activated and increase their discharge rate. The response of each fibre is frequency-specific in that a certain frequency, termed the CF will activate that fibre at a lower sound pressure (see Figure 2) than other frequencies. This frequency tuning is generally sharper in units with high CF but a considerable scatter is found. The thresholds near CF are likewise scattered over a wide range. These differences must of course originate in the sensory cells and cannot be attributed to the fibres themselves.

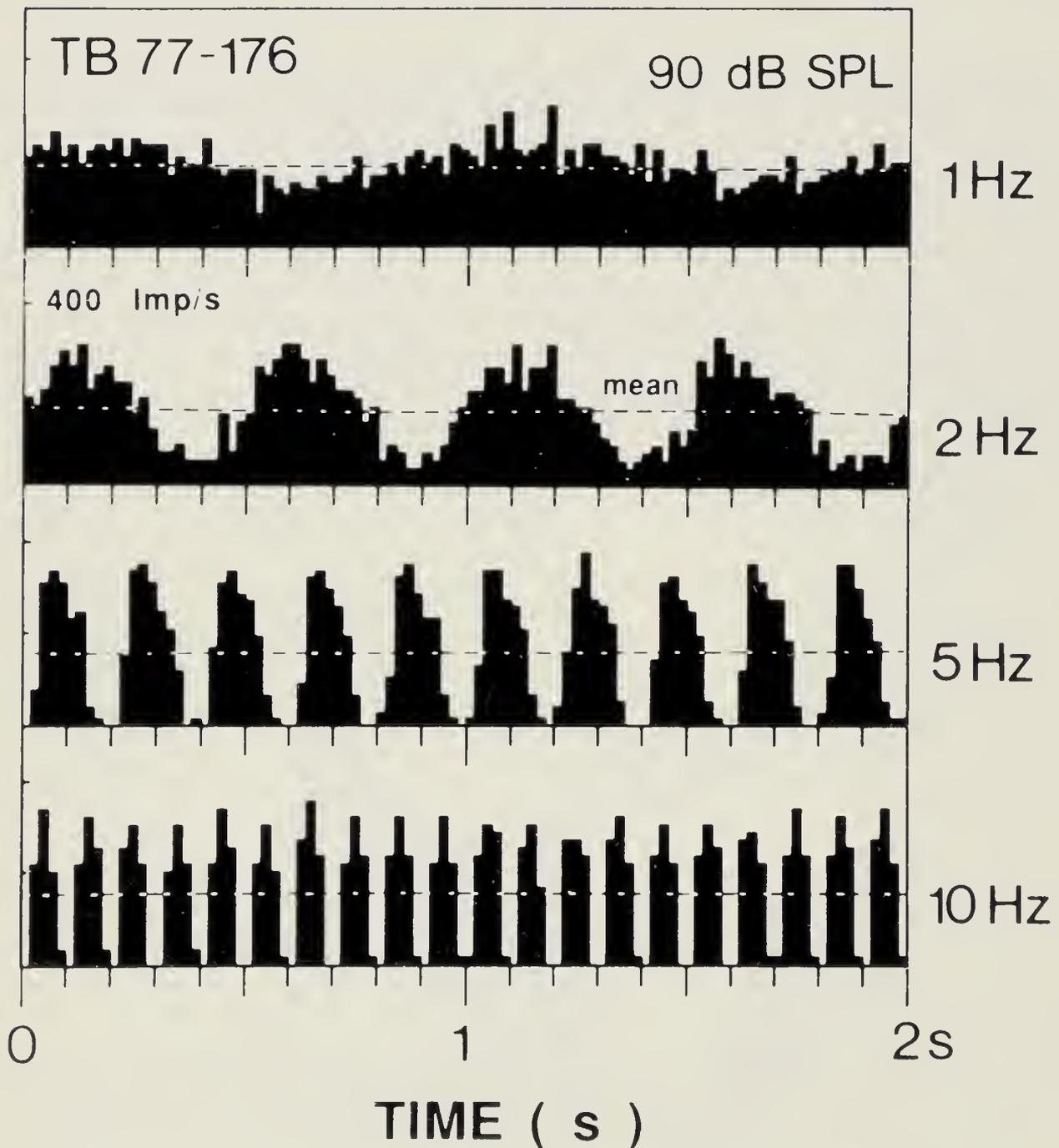


FIGURE 3 – Modulation of the neuronal activity of a pigeon infrasound fibre by sound stimuli in the infrasound range.

However, among the fibres coming from the pigeon basilar papilla there are some that cannot be activated by acoustic stimuli in the audio-frequency range. These are influenced by infrasound stimuli (Schermuly & Klinke 1990). They possess a high spontaneous discharge rate that is modulated by the sound stimulus (see Figure 3), whereby the mean spontaneous rate remains fairly constant over a wide range of sound intensities. These fibres are not normally frequency-tuned; if they are, tuning

is extremely poor. As the infrasound fibres do not increase their discharge rate during stimulation, a rate threshold, as in ordinary auditory afferents cannot be defined. Instead a threshold for modulation of their discharge rate can be used. Modulation thresholds neatly match the behavioural thresholds for pigeon infrasound detection as determined by Kreithen & Quine (1979). These infrasound fibres are therefore likely to be the physiological correlate of pigeon infrasound perception.

The described modulation of auditory afferents to the sound frequency is not a unique property of infrasound fibres. Most or all afferent fibres lock their discharges to a certain phase of the acoustic stimulus, at least up to about 4 kHz (Gleich & Narins 1988, Hill et al. 1989), in the owl up to 9 kHz (Sullivan & Konishi 1984). This phase-locking of discharges is common in all species so far studied, in mammals (Rose et al. 1967) as well as in lower vertebrates e.g. caiman (Solders & Klinke 1986). Most importantly, it occurs at intensities of 10 dB and less below the activation threshold of a fibre. Phase-locking can even be found in suppressive sidebands to the fibres' response area (tuning curve) where the spontaneous activity of the fibre is reduced by the presence of an acoustic stimulus (Hill et al. 1989). Thus phase-locking is a reflection of hair cell processes and transmits the fine time structure of the acoustic stimulus to the brain.

Surprisingly the CF of bird (pigeon) auditory afferents depends on skull temperature. With lower temperature the CF shifts to lower values (Schermuly & Klinke 1985). Below 30°C a slope of about one octave/10°C has been determined. This effect of temperature on tuning has also been described for reptiles, e.g. the Tokay gecko *Gekko gecko* (Eatock & Manley 1981) or the caiman *Caiman crocodilus* (Smolders & Klinke 1984). In contrast, it has not been found in mammals (cat, Klinke & Smolders 1977; guinea pig, Gummer & Klinke 1983). This is another indication that basic tuning properties in birds and mammals may be different.

Evidently the properties of auditory afferents reflect processing of the acoustic stimulus in the outer and middle ears, the cochlear mechanics and the hair cell transduction process. Here we have to concentrate on inner ear mechanisms.

With acoustic stimulation a travelling wave runs along the avian basilar membrane (Gummer et al. 1987) as in the mammalian cochlea. Amplitude maxima of these travelling waves tonotopically map sound frequency along the BM, high frequencies being represented at the basal end. Thus each location on the BM is tuned to a certain frequency, as afferent fibres are tuned to their CF. If, however, sharpness of mechanical tuning is compared to neuronal tuning (see Figure 2) a major difference becomes obvious: Primary afferents are much more sharply tuned than the mechanical tuning of the BM. The above measurements were made under the same conditions which result in virtually identical mechanical and neuronal tuning curves in mammals (Sellick et al. 1982). Thus it is likely that the difference is not an artefact and that processes additional to the mechanical BM tuning, e.g. HC properties, are responsible for the final frequency selectivity and low thresholds.

This is supported by closer inspection of Figure 2. The fibre's neuronal response appears to be composed of a sharply tuned (narrow) low threshold portion and a less sharply tuned portion in the high intensity range. The slopes of this latter segment resemble those of the mechanical tuning curve (broken line, Figure 2).

The hair cells are the transducers proper. Bending of the stereovilli opens ionic gates on their tips (Hudspeth 1989) and a transduction current is generated, driven by the potential difference between scala media endocochlear potential (EP) and the interior of the HC. Experimental variation of this potential difference (Voßieck & Klinke 1990, unpublished) influences the sensitivity and frequency selectivity of afferent fibres but the CF and mean spontaneous discharge rate remain the same. However, the probability of preferred intervals is increased if the EP is increased and preferred intervals may completely disappear, if the EP is lowered.

Recent results from mammals (Ashmore 1987, Brownell et al. 1985, Zenner et al. 1985, Zenner 1986) led to the conclusion that mammalian IHCs and OHCs are specialized for separate functions. Mammalian OHCs can actively oscillate under certain conditions, e.g. in an electric field. It is thus assumed that the OHCs provide narrow band amplifiers for the minute sound energies that enter the inner ear. The mammalian IHCs are consequently supposed to be the receptors for the locally amplified acoustic signal, transducing the signal, releasing transmitter and activating auditory afferents. The view that the IHCs are the cells that send the information to the brain seems acceptable as more than 90 % of the afferent fibres contact IHCs (Spoendlin 1972). It also seems that mammalian OHCs do not send auditory information to the brain as the few afferents contacting these cells are unmyelinated, thus having a low conduction velocity. These fibres would therefore be of little value for the transmission of rapidly varying sound signals. All marked mammalian afferents responding to sound could be traced to IHCs (Lieberman 1988) and the only fibre ever traced to OHCs by means of horseradish peroxidase was unresponsive to sound (Robertson 1984).

This revolutionary insight into the mammalian inner ear transduction process prompts the question whether a similar division of labour exists in the avian cochlea.

We, thus tested whether avian HCs are contractile as well. Attempts to show such active movements have thus far been unsuccessful (Zimmermann et al. 1989). Although this negative result should be viewed with caution, one has to add that mammalian OHCs are only loosely held by the Deiters' cells, whereas all avian hair cells are uniformly embedded in supporting cells. Thus from a morphological point of view it seems hard to conceive that avian HCs can move in a similar way to mammalian OHCs.

In contrast to mammals, all fibres in the avian auditory nerve are myelinated. Horseradish peroxidase stains of physiologically characterized single auditory fibres responsive to sound stimuli are available from the Chicken, the Starling and the Pigeon (Manley et al. 1989, Schermuly & Klinke 1990, Smolders et al. 1990). Manley et al. (1989) report, that except for two unusual fibres, only afferents to THCs were stained in their sample and that each fiber stained contacted a single HC. However, Schermuly & Klinke (1990) reported that their infrasound sensitive fibres contacted more than two short or intermediate HCs in the pigeon apical, abneural region of the BM. Smolders et al. (1990) extended these marking studies and found that the tonotopy of the CFs matches well with the mechanical data of the pigeon BM (Gummer et al. 1987), and that fibres to avian SIHCs do certainly respond to sound stimuli. The frequency tuning of these fibres can be as sharp as that of THC-fibres. Furthermore their thresholds can be very low and some were found to be among the most sensitive fibres recorded.

Preliminary data in the low frequency range suggest that there may be a continuous transition from "ordinary" tuned fibres of low CF to the infrasound fibres with no frequency tuning at all (Schermuly pers. comm., Smolders pers. comm.). It may well be that Manley et al. (1989) two fibres having an unusually high threshold belong to this "continuum".

More experiments appear necessary before the exact functional role of the three avian HC-types becomes clear. However, the staining experiments described have revealed differences between avian and mammalian transduction processes in as much as fibres responsive to sound can also be found from hair cells other than the inner (tall) hair cell type.

Nevertheless there are also contradictory data. Kemp (1978) first reported acoustic energy coming *out* of the ear, which can be recorded shortly after an acoustic click has struck the tympanic membrane. These mammalian otoacoustic emissions are widely considered as a correlate to the postulated OHC amplifier.

However, such emissions have also been found in birds (Starling, Manley et al. 1987) and lower vertebrates (e.g. caiman, Strack et al. 1981). If these emissions do originate from the OHC amplifier, such an amplification should also theoretically be postulated for the bird.

However, in order to increase frequency selectivity beyond that obtained by the mechanical filtering of the BM, active mechanical processes, as assumed to occur in the mammal, are not a necessary prerequisite. In turtle HCs Crawford and Fettiplace (1981) demonstrated that the membrane potential may show oscillations and suggested that an electrical tuning mechanism intrinsic to the single HC may be present. Direct evidence for electrical tuning of chicken HCs has been put forward by Fuchs et al. (1988). Indirect evidence comes from the temperature sensitivity of the tuning mechanism (Schermuly & Klinke 1985) and the existence of preferred intervals (Manley 1979) in the spontaneous activity of afferent fibres, which are thought to reflect oscillations of the HC membrane potential.

Additional filter mechanisms, based on the micromechanics of the stereovilli have been proposed by Nielsen & Turner (1983) and Frishkopf & DeRosier (1983) for reptilian HCs (see also Freeman & Weiss 1990). At present there is no evidence for such a mechanism in the avian inner ear. However, as the length of the stereovilli varies systematically over the length of the BM this may still be possible.

The ornithologist may ask the question: Are there specializations in the avian inner ear that improve perception of species-specific calls or serve to preprocess these stimuli? Apparently this is not the case, although the anuran inner ear obviously serves such a purpose (Capranica & Moffat 1975, Narins & Capranica 1980). Within the hearing range of a given bird no further inner ear specializations have been described as yet. Thus feature extraction and signal detection seems to be the exclusive domain of central nervous processing, as is the case in mammals. An outstanding avian example is imprinting, the underlying central mechanisms of which have been described by Scheich (1987).

ACKNOWLEDGEMENTS

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TWO DIFFERENT MAGNETIC SYSTEMS IN AVIAN ORIENTATION

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ABSTRACT. Behavioral evidence indicates that birds may use a two step process, such as a map and a compass, to orient within the earth's magnetic field. Neuronal correlates of the magnetic compass may be in the visual system, with the retinal photoreceptors functioning as magnetoreceptors. Cells in different parts of the visual projections respond to magnetic direction changes, as would be expected from a compass, but do not respond to pure intensity changes. In contrast, the activity of ophthalmic nerve fibers, which come from the upper beak area, can be influenced by small (200 ntesla) changes in magnetic field intensity; the type of sensitivity needed to detect components of a magnetic map. Although there is no direct evidence, these fibers may be associated with ethmoidal magnetite deposits. Magnetically sensitive fibers in the ophthalmic nerve responded to magnetic field changes even after destruction of the retina, and visual cells responded to magnetic stimulation even after severing both ophthalmic nerves. Therefore, it appears that birds possess two different magnetic systems, one sensitive to magnetic compass features and one sensitive to magnetic "map" features.

Keywords: Magnetic, ophthalmic nerve, visual system, sensory receptors, orientation.

INTRODUCTION

In spite of the amount of data indicating that birds and other taxa are capable of perceiving the Earth's magnetic field (MF) and can extract useful information from it, we do not know the structure of the magnetoreceptor organ, or even its location. This is one of the few examples of a sensory modality in which the ability to perceive information has been established before its neuronal basis is understood. For most sensory stimuli to which humans are blind, the sensory organs were described before their function was identified.

Researchers studying avian magnetic sensitivity have reported two ranges of sensitivity: large MF changes (30 - 100 μ T) and small MF changes (20 - 500 nT). There is no a priori reason why the same receptor should be used for both types of sensitivities. In fact, it has been proposed that birds may have two independent magnetoreceptor systems (Beason & Semm 1987), which could be the neuronal basis of the magnetic compass system (sensitive only to large changes) and the magnetic map (sensitive to small changes).

Several candidate magnetic transducer schemes have been proposed: biological radicals (Schulten & Windemuth 1986), magnetite (Kirschvink & Gould 1981), melanin (Leucht 1987), photopigments (Leask 1977), and perhaps free nerve endings (Semm & Beason 1990). Of these, most of the data support the use of photopigments and/or a magnetic material, probably magnetite, to transduce magnetic information to the avian nervous system.

MECHANISMS

Sensitivity to large changes

Most of the work on the sensitivity of birds to large magnetic field changes has been focused on the use of the geomagnetic field as a type of compass for homing or migratory navigation (Wiltschko & Wiltschko 1988). Unlike the human technical compass, behavioral studies indicate that the avian compass is an inclination compass in which birds perceive the magnetic field as a total vector and cannot distinguish its polarity (Wiltschko & Wiltschko 1972). By using the relationship between the magnetic vector and gravity, the birds can distinguish between "equatorward" and "poleward," not north and south. Although the magnetic compass receptor can adapt to different intensities with time, it operates within a range of intensities similar to that of the natural magnetic field (Wiltschko 1968).

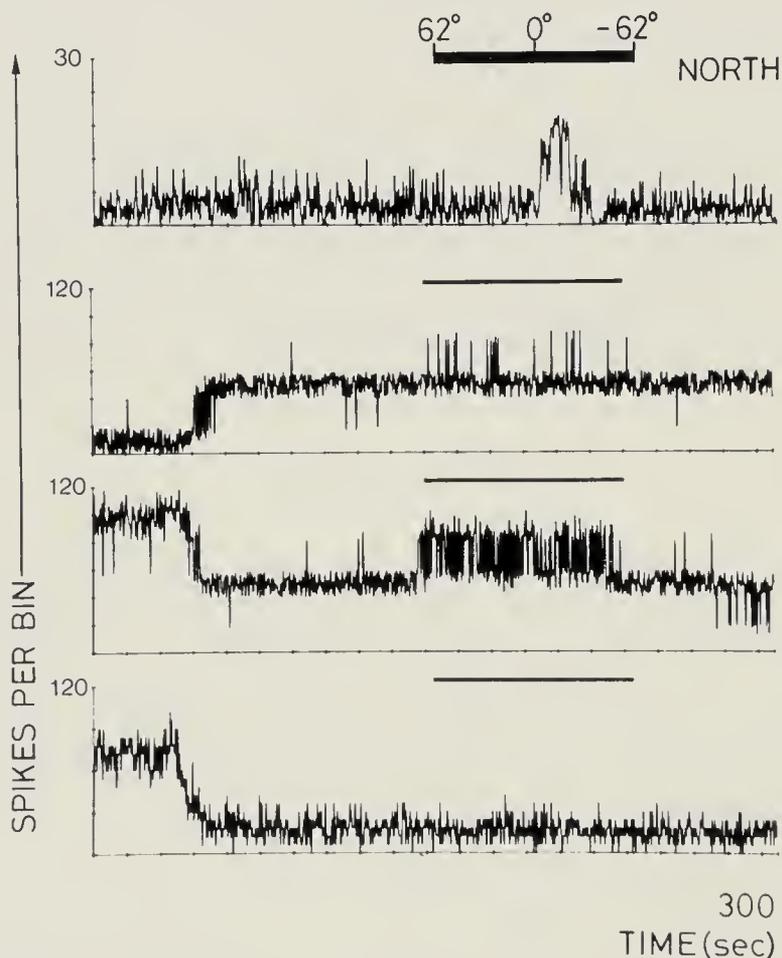


FIGURE 1 - Peristimulus time histograms of the electrical activity of single units in the visual system tested with magnetic stimulation (gradual inversion of the vertical component of the natural magnetic field). The period of stimulation is indicated by the scaled bar. a. A direction-selective cell in the optic tectum, the firing frequency of which was augmented during a distinct portion of the range of magnetic field inversion. b + c. A unit in the superior vestibular nucleus, which responded to magnetic stimulation after tilting the animal out of the horizontal plane. The record shows the alteration in spontaneous activity which occurred during and immediately after tilting. Under these conditions, the units increased their firing rates while the magnetic field was changing. d. The activity of a third unit in the vestibular nucleus of the same animal following contralateral enucleation. The cell shows a clear response to the horizontal tilt but failed to respond to magnetic stimulation.

The mechanism of the inclination compass requires the animal to simultaneously detect both gravity and the magnetic field, and to integrate the information. Such a

requirement means that the magnetic receptor has connections with the vestibular system. Semm et al. (1984) reported the presence of units in the vestibular nuclei of the pigeon that responded to magnetic stimulation only after the animal was tilted from the horizontal position, indicating that the nuclei are receiving input from a magnetic receptor system as well as the vestibular nuclei. A likely candidate for the location of the magnetic receptor is the visual system in which the integration of magnetic and vestibular information could be achieved through known visual-vestibular projections within the brain. One area that projects to the vestibular system is the nucleus of the basal optic root (nBOR). Neurophysiological recordings by Semm and his colleagues (Semm et al. 1984, Semm & Demaine 1986) from the nBOR demonstrate the presence of some units that responded to a gradual inversion of the vertical component of the magnetic field with gradual augmentation of activity. The nBOR receives input from displaced ganglion cells distributed throughout much of the retina (Karten et al. 1977, Reiner et al. 1979). Individual neurons within the nBOR and stratum griseum et fibrosum superficiale of the optic tectum, which also contains visually direction-selective cells, responded selectively to magnetic stimulation only within a distinct part of the total range (Figure 1). These nerve cells also were direction-selective for visual stimulation, and most of them exhibited an axial specificity to light (Semm et al. 1984, Semm & Demaine 1986). Whether or not there is a correlation between the magnetic directional selectivity and the visual directional selectivity is unknown.

The ability of the visual and vestibular systems to respond to magnetic stimulation depended upon input from intact photoreceptors that were illuminated. When recordings were made from the optic tectum and nBOR with the bird in total darkness (Semm & Demaine 1986) or from the vestibular nuclei with the contralateral optic nerve severed (Semm et al. 1984), sensitivity to magnetic stimulation was abolished (Figure 1). Recordings from the vestibular nuclei with the contralateral eye intact and the connection to the ipsilateral eye severed showed no change in responses to magnetic stimulation. Such results indicate that either (1) light is necessary for transduction of the magnetic field, or (2) light is necessary for gating information from the magnetic receptor to the central nervous system (CNS) or for processing that information. While the animal may need light to spatially integrate the magnetic information with its surrounding (Semm & Beason 1990), such a requirement should not affect the sensory input to the CNS.

Leask (1977) proposed that the photopigment rhodopsin in vertebrate photoreceptors could serve as a magnetic transducer through the physiochemical mechanism of optical pumping, which depends on the excitation of the molecules by visible radiation. The proposed mechanism involves an optical/r.f. double resonance, dependent on the presence of light. Although the response from a single photopigment molecule would be weak, the well-ordered array of molecules within the photoreceptor and the similar arrangement of photoreceptors within the retina enhance the sensitivity of the mechanism. A predicted characteristic of such a receptor mechanism is that its response to the magnetic field would be axial rather than polar; showing a sensitivity to dip angle rather than N-S. Leask further predicted that this mechanism would be most sensitive in earth-strength magnetic fields (ca. 50 μ T), and respond only to large (20%) changes in the intensity of the field. Interestingly enough, these are the very characteristics of the avian magnetic compass (Wiltschko & Wiltschko 1988).

The necessity of light for the avian magnetic compass to function was tested by Wiltschko & Wiltschko (1981) by transporting young, inexperienced homing Pigeons

Columba livia to a release site in total darkness. The effect of total darkness on these birds was the same as the effect of being transported in a distorted magnetic field: random orientation by the experimental birds. In both instances, the control birds were significantly oriented, and oriented towards home.

One interpretation of the physiological and behavioral data is that the avian magnetic compass is based on detection of the magnetic field information by the light-excited photopigments in the photoreceptors of the retina, and transduced to the visual portion of the CNS where it is integrated with vestibular information. While these results are in agreement with the Leask model, they do not provide direct support for any mechanism of magnetic field detection. There have been no published records of recordings from individual vertebrate photoreceptors responding to magnetic stimulation, although Phillips (1987) reported such sensitivity in the blowfly.

Sensitivity to small changes

A second potential receptor mechanism involves a magnetic material, such as magnetite, transducing the ambient magnetic field to the nervous system. Iron deposits, some of it probably magnetite (Fe_2O_3), occur in the avian ethmoidal region and the Harderian (lacrimal) gland (Walcott et al. 1979, Walcott & Walcott 1982, Beason & Nichols 1984, Beason 1989). The most conspicuous concentrations are around the olfactory nerves and in the ethmoidal turbinates (Beason & Nichols 1986, Holtkamp & Semm unpub. data, Wheeler & Beason unpub. data). The magnetic characteristics of avian heads is consistent with the presence of single-domain magnetite within the tissue (Walcott et al. 1979, Beason & Brennan 1986, Edwards et al. 1990). Magnetic material which was extracted and examined with x-ray diffraction and TEM, proved to be particles of magnetite less than 0.1μ in diameter (Beason 1989).

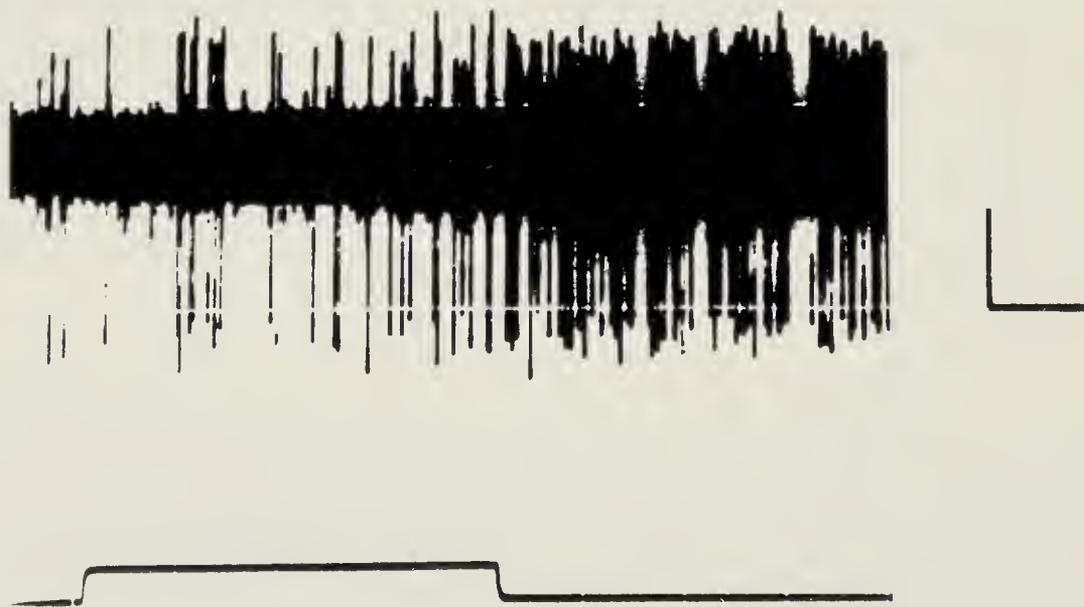


FIGURE 2 - Response of a trigeminal nerve cell to a 200 nT decrease in the vertical component of the magnetic field. The stimulus is shown in the bottom trace. Vertical scale = 2 mV, horizontal scale = 1 sec.

Although the actual structure of a magnetite-based magnetic receptor organ has not been worked out, the amount of material which has been reported in birds, if it is single-domain magnetite, may be sufficient to permit the sensitivity needed to function as a receptor for the magnetic map (Yorke 1979, 1981). Obviously, such sensitivity would not preclude its use as a compass.

Because the region of the deposits is associated with fibers from the ophthalmic branch of the trigeminal nerve, Beason and Semm (1987) investigated the responses of individual units of this nerve to alterations in the ambient magnetic field. Their results indicate that approximately 15% of the spontaneously active units in the nerve responded to the magnetic stimulation of reversing the vertical component of the natural magnetic field or rotating the horizontal component by 90°. These large changes are similar to those expected of a magnetic compass, but left unresolved the source of the greater sensitivity needed to detect features of a magnetic map.

Subsequent work by the same researchers examined the question of the minimum sensitivity of the ophthalmic nerve fibers. Semm & Beason (1990) report finding spontaneously active units in the ophthalmic nerve and the trigeminal ganglion that responded to alterations of the ambient magnetic field as small as 200 nT (Figure 2). This sensitivity is similar to the sensitivities required to account for the behavioral responses of pigeons to daily magnetic field variations (50-150 nT: Keeton et al. 1974, Wiltschko et al. 1986) and when released at magnetic anomalies (500 nT: Walcott 1978). Because these behavioral responses are thought to be associated with a magnetic map, they may indicate the realm of sensitivity needed to detect components of such a map.

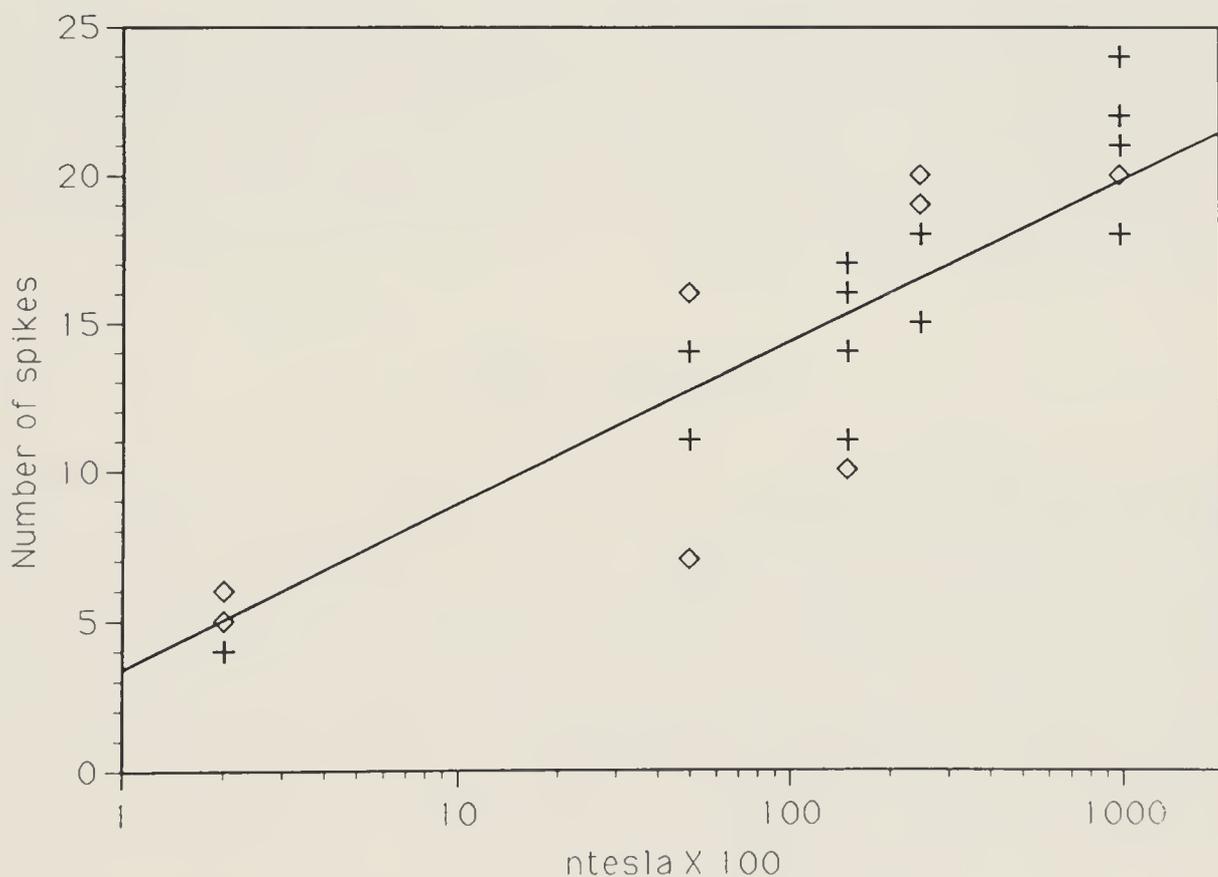


FIGURE 3 - Response of a trigeminal ganglion cell to different changes in the intensity of the magnetic field. The fitted regression for the mean fit is $S = 4.5 \times MF^{0.23}$, where S = no. of spikes, MF = magnetic field (nT). The crosses indicate single values and the diamonds indicate multiple values with $N = 6$ for each intensity. (Based on data from Semm & Beason 1990).

Some of the cells that were recorded responded to large as well as small changes of the magnetic field (Semm & Beason 1990). One response was a logarithmic increase in the number of nerve impulses produced with stronger magnetic fields (Figure 3). This type of logarithmic response is typical for many sensory receptors and, therefore,

not surprising. Magnetically responding cells that were tested, also responded to movement of a hand-held magnet.

Although these results suggest that some units of the ophthalmic nerve could be involved in detecting features of the magnetic map, there is no evidence that the magnetic information detected by the trigeminal system is used at all for navigation. Results from experiments on impulse magnetized Bobolinks (Beason et al. 1990) and Pigeons (Wiltchko & Beason 1990) support the use of a magnetizable material, such as magnetite, in the magnetic map system of these species. Because previous attempts at affecting orientation of Pigeons (Lednor & Walcott 1988) and Bobolinks (Beason unpub. data) were unsuccessful, the method of applying the magnetic field is important. These results taken together may indicate that the receptor involves a magnetic material such as magnetite to transduce the magnetic map information to the nervous system, but the material is able to rotate when the external magnetic field is modified relatively slowly.

CONCLUSIONS

There is support for two of the proposed methods of magnetoreception in birds. We can propose that the photoreceptors and the visual system may be the neural correlate of the magnetic compass, with the photopigments in the retina transducing features of the magnetic field to the system; and the ethmoidal magnetite deposits, possibly associated with the ophthalmic branch of the trigeminal nerve, may serve to transduce features of the magnetic field used for a magnetic map, although the mechanisms of such a map are unclear.

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OLFACTORY ABILITIES OF BIRDS

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ABSTRACT. From the earlier denial that birds could smell to the current recognition that all birds almost certainly have functional olfactory tissue has been a dramatic change in our understanding, with important implications for the study of avian behavior. The amount of such tissue varies markedly across species and presumably relates directly to the degree of dependence on olfactory information. As a discrete structure visible on the brain surface, the olfactory bulb has been convenient to quantify. Growing evidence supports odor reliance in certain natural behavior patterns both in species with large olfactory systems, such as apterygiforms and procellariiforms, and in species with small ones, such as passerines. A key concept is that olfactory usage by some species is specialized for one or two limited functions but may be more general in others. Such results emphasize the importance of attending to olfaction when studying avian behavior.

Keywords: Olfaction, olfactory, foraging, odor-reliance.

INTRODUCTION

For the first time in biology's history, sustained attention is being directed to the avian olfactory system. Sporadic reports, of mixed quality and with mixed results, had appeared for more than a century. For the last three decades, however, a small but continuous series of investigations has been conducted on all aspects of olfaction in birds. The critical initiating stimulus for this new era was Cobb's interest in comparative brain anatomy and his quantification of olfactory bulb size so that different species could be compared (1960a, b). He emphasized that avian species varied widely in bulb size and his ratio of olfactory bulb diameter to ipsilateral cerebral hemisphere diameter has become the standard measure. In collaboration with Bang, the measurements were extended to over 100 species (Bang & Cobb 1968). The basic principle of marked variation across species from very large to very small olfactory bulbs was established and it was argued that such variation should be related to function. Bang, meanwhile, studied the nasal anatomy of these species and found impressive evidence for adaptations favoring olfactory function in many of them (Bang 1960, 1964, 1965, 1966, 1971). Cobb had also stimulated Michelsen, a student of B. F. Skinner and highly skilled in sophisticated techniques for training animals, to teach Pigeons *Columba livia*¹ to discriminate between two pure odors that could be presented in different controlled intensities (1959). At about the same time, Neuhaus (1963) recorded changes in the respiratory rate of untrained Graylag Geese *Anser anser* L. on presentation of odors. None of these studies asked a new question; their significance lay in an open-minded approach and the use of more effective techniques than those used previously.

¹ Common and scientific names follow the AOU Check-list of North American Birds, 1983 or the names as given in the references cited. The common name, Pigeon, rather than Rock Dove, was used in almost every reference.

The data reported subsequently, though scattered and notably incomplete, raise many provocative questions that point toward further research. Several reviews have appeared recently and can be consulted for detailed discussion of selected topics (Bang & Wenzel 1985, Kare & Mason 1986, Waldvogel 1989). My purpose here is to outline our present understanding based on the completed studies - behavioral, physiological, and anatomical - and the challenges their results present to ornithologists.

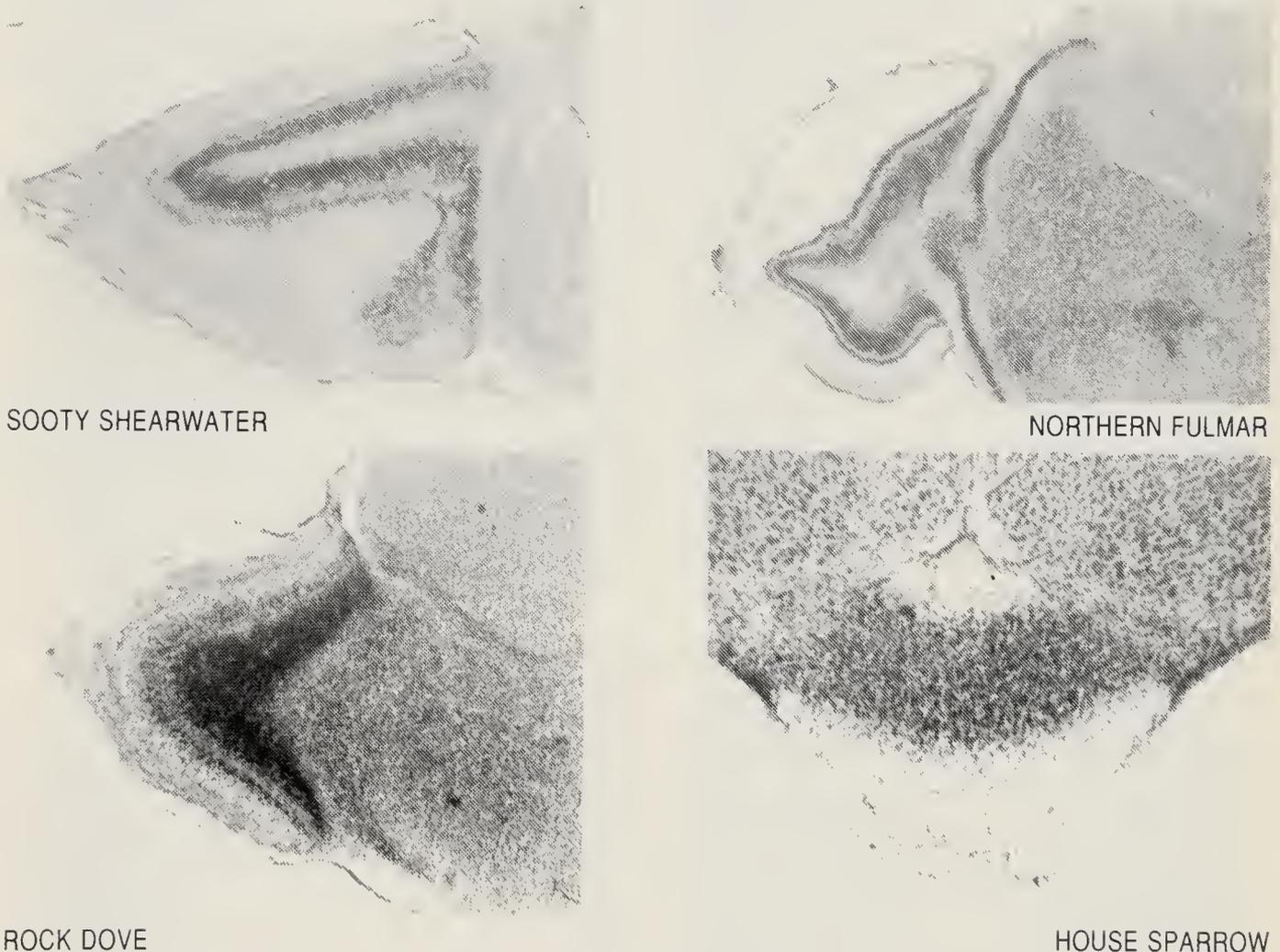


FIGURE 1 – Parasagittal photomicrographs of the olfactory bulb in four species with widely varying olfactory bulb dimensions. In all but the sparrow, which has a medially-placed fused bulb, the layers characteristic of vertebrate bulbs are visible. Bang's (1971) ratios of bulb diameter to hemisphere diameter are .27 for the Northern Fulmar, .18 for the Rock Dove, and .04 for the House Sparrow; her value for two other shearwaters (*Puffinus* sp.) is .30. Magnifications (clockwise from upper left) are 13.5X, 17X, 80X, and 29X. (From Wenzel 1986 with permission of the publisher.)

OLFACTORY ANATOMY

Central to an understanding of avian olfactory capability is the fact that every species examined has olfactory tissue - a sheet of receptor cells in the nasal cavity, an olfactory nerve, an olfactory bulb on the anterior surface of the brain, and central projections to other brain regions - albeit in varying amounts. In addition, the first evidence for an avian terminal nerve, which accompanies the vertebrate olfactory nerve and is hypothesized to subservise chemoreception, has been presented recently for the Mallard Duck *Anas platyrhynchos* (von Bartheld 1987) and the domestic Chicken *Gallus gallus* (Wirsig-Wiechmann 1990). No accessory olfactory system - vomeronasal nerve

and accessory olfactory bulb - has been found in any bird. Trigeminal innervation of the nasal cavity is present and has chemoreceptive sensitivity (Walker et al. 1979), which is less acute than that of the olfactory receptors (Walker et al. 1986). In all but the very smallest olfactory bulbs, the histological structure closely resembles that of reptiles and mammals (Figure 1). Detailed examination of the "domestic duck's" *Anser cinereus* [sic] olfactory membrane (Graziadei & Bannister 1967) and of the Northern Fulmar's *Fulmarus glacialis* olfactory bulb (Wenzel & Meisami 1987, in press) has revealed structures basically similar to those of other vertebrates (Andres 1970) but quantitative analysis has shown some differences in organizational patterns, which imply functional differences (Wenzel & Meisami in press). Reports on the course of central projections from the olfactory bulb are somewhat contradictory (Rieke & Wenzel 1978, Reiner & Karten 1985) and deal only with the Pigeon, but it is clear that connections are made with several forebrain sites. Neurophysiological studies have shown that odor stimuli elicit characteristic electrical responses of the olfactory nerve and bulb in all species studied (Tucker 1965, Sieck & Wenzel 1969, Hutchison & Wenzel 1980b, Clark & Mason 1987). The possibility of "the existence of an olfactory organ without any demonstrable function" (Neuhaus 1963, p. 117) is hardly acceptable. The challenge, therefore, is to describe the functional significance of such tissue for individual species. The report (Healy & Guilford 1990) of a positive correlation between bulb size and the evolution of nocturnality is one example of research to meet this challenge.

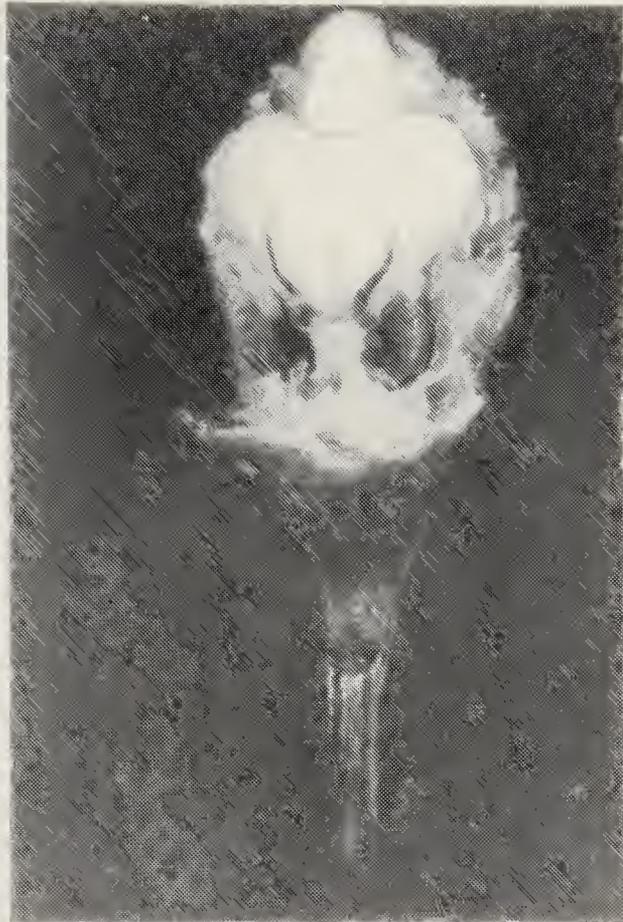
ODORS AND NATURAL BEHAVIOR

To most writers through the centuries, "smelling" has meant regulating behavior in response to odors under natural conditions. For experimentation, however, the "ability to smell" must be specifically defined (Wenzel 1966). It has at least three aspects, viz., (1) ability to perceive olfactory stimuli, (2) regulation of natural behavior according to odor cues, and (3) ability to learn to regulate behavior by odor cues; all of them have been addressed among the various studies reported.

Foraging

The oldest, and for many years the only, strong case of a bird's natural reliance on smell, specifically in foraging, is the Brown Kiwi *Apteryx australis*. Its alleged ability to find earthworms by smell was described as early as 1906 (Benham 1906) but systematic study was not completed until 1968 (Wenzel 1968). Five captive Brown Kiwis, in large outdoor enclosures with natural vegetation and features, were completely accurate in various tests requiring them to uncover buried containers of giant earthworms or of the redolent dietary mix regularly given them. No unbaited container was ever opened and no baited container failed to be opened. Kiwis possess easily appreciated, special characteristics that implicate olfaction as a useful sense, viz., unique placement of the external nares at the tip of their long, probing beak, a snuffling sound as they rummage through forest litter for food, and poor eyesight despite nocturnality. Less obvious are their elaborate olfactory membrane in the nasal cavity and very large olfactory bulb in the brain (Bang 1971).

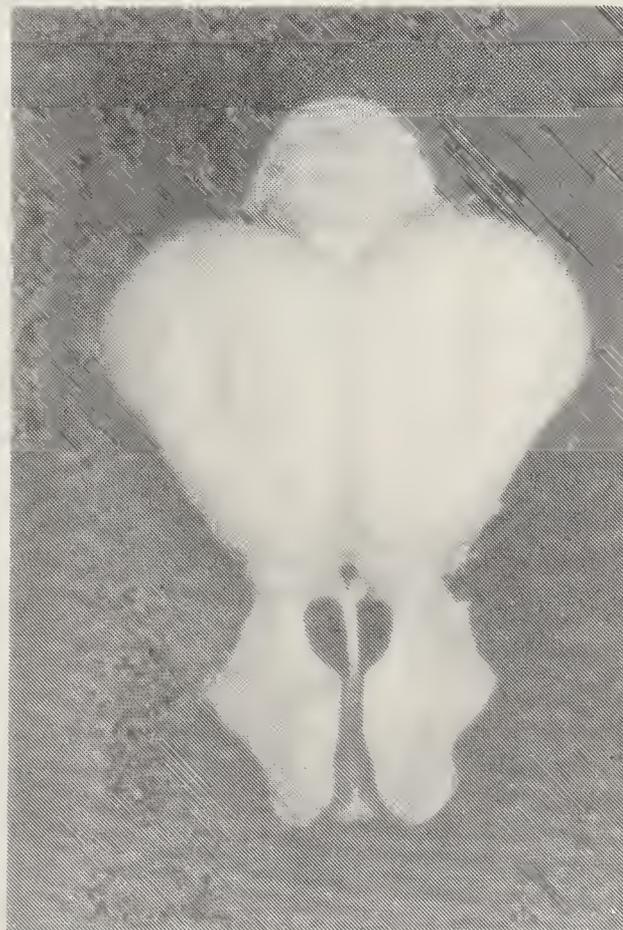
The smelling ability of an entire order of birds, Procellariiformes, has been a persistent topic of interest and speculation since their habits came under close observation from whaling stations and vessels in the Antarctic and Subantarctic where these birds are



SOOTY SHEARWATER



SOUTHERN GIANT PETREL



SNOW PETREL



ANTARCTIC PETREL

FIGURE 2 – Dissected brains and proximal portion of nasal cavities in four procellariiform birds showing the olfactory bulbs on the anterior pole of each hemisphere and the olfactory conchae in the nasal cavities. The conchae are lined with the olfactory membranes, sheets containing the olfactory receptor cells, the axons of which form the olfactory nerve. (From Wenzel 1986 with permission of the publisher.)

very numerous (Wenzel 1980). Of the four procellariiform families, all but Pelecanoididae are characterized by large olfactory bulbs and extensive olfactory membranes (Bang 1966) (Figure 2). In one study (Jouventin 1977), two Snow Petrels *Pagodroma nivea*, a species that not only feeds but also breeds below the Antarctic Circle, found pieces of fish hidden on the laboratory floor or in snow outside with an accuracy comparable to that of the kiwis described above. Later experiments in the Antarctic and Subantarctic (Jouventin & Robin 1983, Lequette et al. 1989) on attraction to cod liver oil released from a small raft offshore found that several procellariiforms approached the fish odor significantly more often than the seawater control and were more likely to approach from downwind, even changing flight direction to do so, and to approach very closely; nonprocellariiforms in the area, however, did not approach it more often than they did the control. These observations agreed with earlier work in the temperate Northern Hemisphere (Grubb 1972, Hutchison & Wenzel 1980a, Hutchinson et al. 1984).

Finally, the Turkey Vulture's *Cathartes aura* behavior has invited speculation about odor dependence in foraging for a very long time. These birds also have impressive olfactory equipment (Bang 1964). In field experiments they followed a controlled odor trail of ethyl mercaptan (Stager 1964) or one released by one-day-old chicken carcasses (Houston 1986); they rarely found fresh carcasses and usually rejected four-day-old ones. The Black Vulture *Coragyps atratus*, with a smaller olfactory system (Bang 1964), is said to find food by following the Turkey Vulture (Houston 1986). Alone among the vultures, the Turkey Vulture's olfactory bulb is as large as that of several of the procellariiforms (Bang & Cobb 1968) and its nasal cavity is well arranged for olfaction (Bang 1964). Food-finding tests in captivity were failed by King Vultures *Sarcorhamphus papa* (Houston 1984), and by three species of Old World vultures (Ben Moshe & Yom-Tov 1978).

In contrast to the consistently large procellariiform olfactory bulbs, the bulbs of passerine species are consistently small. Nonetheless, some instances of untrained reliance on odors have been documented. Common Ravens *Corvus corax* were highly accurate in locating fresh ground fish concealed under gravel; performance was correlated with the amount and depth of the fish (Harriman & Berger 1986). Black-billed Magpies *Pica pica* uncovered caches of cod liver oil-scented raisins or suet almost exclusively, ignoring unscented ones (Buitron & Nuechterlein 1985). The Great Tit *Parus major* avoided maggots treated with bitter almond oil without actually tasting them; in the absence of any visual differences discernible to the experimenters, odor was proposed as the distinguishing cue (Jarvi & Wicklund 1984).

Head-shaking to odors of plants that adult Graylag Geese do not eat occurred in juvenile geese between the 11th and 20th hours after hatching before any opportunity for tasting, and in 4- to 9-day-old domestic goslings *Anser domesticus* when favorite grasses were impregnated with odors of other plants (Wurdinger 1979). Olfactory bulb size has not been reported for either species but that of other anseriforms is above average.

Non-foraging

The best known example must be the Pigeon's proposed use of odors for orientation to the home loft (Waldvogel 1989). The issues involved in this hypothesis are too complex and the literature is too extensive for discussion here. The direct involvement

of the olfactory system is increasingly accepted but how to interpret the data remains uncertain (see final section below).

Goslings (*Anser* and *Branta* sp.) raised in warming boxes with different odors, when tested at 5-10 days of age, chose the box with the odor they had been exposed to since hatching (Wurdinger 1982). Similar results have been reported for female domestic chicks (Jones & Gentle 1985). The possibility of a female uropygial pheromone in Mallard Ducks is supported by evidence that the gland's chemical composition differs between the breeding and nonbreeding seasons and male reproductive behavior is inhibited after olfactory nerve section (Balthazart & Schoffeniels 1979).

In addition to odor-based foraging, Grubb (1974, 1979) also reported that breeding Leach's Storm-petrels *Oceanodroma leucorhoa* located their islands and burrows by smell, but Shallenberger's (1973) experiments with the Wedge-tailed Shearwater *Puffinus pacificus* found little supporting evidence for olfactory burrow location nor did James's (1986) work with the Manx Shearwater *Puffinus puffinus*. Neither of the latter two species was nesting in areas of such extremely low illumination as that of the Leach's Storm-petrels' heavily wooded breeding island in Grubb's study.

European Starlings *Sturnus vulgaris* select fresh biocidal foliage to line nests in secondary use. They were readily trained to discriminate between the volatiles from different plant species, lost the discrimination when their olfactory, nerves were cut (Clark & Mason 1987), and showed seasonal changes in olfactory sensitivity with the peak during the time of nest construction and the trough in late summer and early fall (Clark & Smeraski 1990). This research exemplifies the benefit of carefully observing natural behavior patterns without bias against olfaction as a partial mechanism. When this type of approach is applied more widely, more examples of specialized odor usage are likely to be discovered.

OLFACTORY PERCEPTION, TRAINING, AND SENSITIVITY

The task of describing a nonverbal animal's sensory experiences is a necessary part of understanding how a sensory system works but can be perilous. Perhaps the most secure way to reveal an animal's awareness of a given stimulus is to "ask" its autonomic system, which is relatively free of voluntary control. Heart and respiratory rates, for example, have been monitored for indication of perception (e.g., Neuhaus 1963, Wenzel 1966, Wenzel & Sieck 1972, Walker et al. 1986); by recording continuously under relaxed conditions and including odorous stimuli for short periods in the steady flow of background air, changes in cardiac or respiratory rate during odor presentations are evidence of altered, odor-related, central neural activity. This technique is especially convenient for assessing the significance of given odors for a given species - for example, in preparation for a study of olfactory sensitivity (Snyder & Peterson 1979) - but it should be realized that species differ in the relative consistency of their cardiac and respiratory rate changes (Wenzel 1966) and the more reliable response index should be chosen after preliminary testing. The procedure can be made more complex by converting it into a conditioning task, i.e., by pairing an odor stimulus with a stimulus that naturally elicits a pronounced change in heart rate, such as an electric shock to the leg (Snyder & Peterson 1979, Walker et al. 1986, Clark & Mason 1989).

Other training techniques have been used to provide evidence for odor perception. Under natural conditions, both the Black-chinned Hummingbird *Archilocus alexandri* and the White-vented Violetear *Colibri serrirostris* learned to approach nectar-containing feeders according to associated olfactory stimuli (Goldsmith & Goldsmith 1982, loale & Papi 1989). Operant conditioning procedures in the laboratory using either positive (Walker 1983) or negative (Henton 1969) reinforcement have been successful in training pigeons to respond on the basis of odor. No other avian species has been tested with these paradigms.

Negative results in any learning experiment do not necessarily mean that the bird involved is unable to smell. Perhaps the stimulus odor is simply irrelevant or the task is too difficult. Such precautions are especially important for comparative studies. It is inaccurate to conclude poorer sensitivity for one species compared to another on the basis of tests with a single odor or a single testing procedure. Snyder and Peterson (1979) have made the cogent point that the olfactory bulb/cerebral hemisphere ratio changes if the diameter of the cerebral hemisphere differs without any difference in olfactory bulb diameter. Because hemisphere size is probably related to learning ability, two species with the same absolute bulb size might perform differently in an olfactory learning task if their hemispheres differ. Until the basic mechanism of olfactory stimulation is understood so that a universally appropriate "pure" stimulus might be devised, analogous to the pure tones used to study auditory function, meaningful measurements of olfactory acuity will be elusive. This is not to say that no generalities are possible; on the contrary, we can say that all birds perceive at least certain odors, that absolute thresholds vary across species by several orders of magnitude and are probably higher than those of macrosmatic mammals (for summary, see Waldvogel 1989), and that discrimination between odors may be fairly good (Davis 1973). As data accumulate on birds' odor reliance in the field, interest in thresholds for odor detection will increase. Smith and Paselk (1986), for example, could not reconcile the Turkey Vulture's ability to follow an ethyl mercaptan trail in the field (Stager 1964) with their measurement of its sensitivity for the compound in the laboratory. A great deal of such research will be needed for a clear understanding of avian olfactory function to emerge.

SPECIAL FUNCTION OF OLFACTORY SYSTEM; RELEVANCE TO PIGEON HOMING

Abundant evidence has been reported for involvement of the olfactory system in pigeon homing (Papi 1989, Wiltschko & Wiltschko 1989, Wallraff 1990) although the mechanism remains unexplained. Wiltschko and Wiltschko (1989) have suggested that the critical factor might be related to a non-cue function of the system rather than the cue, i.e., odor discrimination, function. It has been known for some time that anosmic pigeons differ from normal ones in more ways than their inability to smell (Wenzel & Salzman 1968, Wenzel et al. 1969, Hutton et al. 1974, Wenzel & Rausch 1977). The effects of such olfactory deprivation appear in motivational or affective aspects of behavior rather than in cognitive or problem-solving ones. These effects are not limited to pigeons but have also been found in several mammals (Wenzel 1974) and are thought to be characteristic of the olfactory system, at least in higher vertebrates. They represent an alternative hypothesis for the relation between this neural system and the behaviors of orientation and homing, one that will require much ingenious experimentation before it can be accepted or rejected.

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ASPECTS OF AVIAN VISION AND ORIENTATION

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ABSTRACT. Three aspects of avian vision are discussed (1) The visual fields of lateral eyed birds are extensive. In some species they provide near comprehensive visual coverage of the celestial hemisphere as well as extensive coverage of the world below. The implications of such comprehensive vision for the perception of celestial orientation cues are discussed. (2) Some avian retinae, especially those of species which use habitats largely devoid of distinctive topographical features, contain linear areas. These areas could aid the perception of the horizon and provide a stable coordinate base from which to determine the position of celestial features. (3) The use of orientation cues derived from the polarization pattern of sky light has seemed well established. It is now questioned by experiments which have failed to replicate the original demonstrations of polarization sensitivity in birds.

Keywords: Vision, visual fields, linear areas, retinal topography, polarization sensitivity, orientation, migration.

INTRODUCTION

In 1943 Rochon-Duvigneaud defined a bird as, "a wing guided by an eye". Although since that time it has been shown that some birds may guide their behaviour by odours (Wenzel, this symposium), sounds (Klinke, this symposium) or magnetic field cues (Beason, this symposium), the primacy of visual cues in the orientation of most birds' behaviour, even in species migrating at night, is still valid (Martin 1990a).

This review briefly discusses some aspects of the visual capacities, anatomy and physiology of the visual systems of birds which exhibit features that are likely to be of particular importance in orientation behaviour. It is not a comprehensive review. The aim here is to draw attention to specific aspects of avian vision which may facilitate the detection of cues that enable a bird to monitor its position and determine the direction in which it should travel. It seems that there are no aspects of avian vision which can be linked uniquely with orientation behaviour.

VISUAL FIELDS

The volume of space around an animal's head in which visual information can be detected is referred to as the cyclopean visual field. The cyclopean fields of birds are complex and show marked interspecific variation. These variations have been attributed to differences in both ecology and behaviour (Martin 1984, 1986a,b).

Cyclopean fields are composed of the two monocular fields and, where these overlap, the region of binocular vision. The size and shape of a monocular field is determined by the optical structure of the eye and the size of the retina. While the optical field typically exhibits radial symmetry about the eye's optic axis the retina usually

serves only part of the optical field and is not symmetrical (Martin 1984). The dimensions of the cyclopean and binocular fields depend upon the features of the monocular fields and upon the position and movements of the eyes (Martin 1986b).

Table 1 shows the angular extent of the visual fields in an approximately horizontal plane in four bird species which have their eyes placed laterally in the skull and in one species with more forward eyes (an owl). For comparison data for the human visual fields are also shown. [N.B. Owl eyes do not face directly forward as in man. In the Tawny Owl eye axes diverge by 55 degrees.] Data refer to the visual fields measured when the eyes have adopted a natural resting position. In the Starling an indication of the way in which eye movements alter the extent of visual fields is also given. For details of the three dimensional structure of these visual fields see the references given in the Table legend.

TABLE 1 - Retinal visual field widths (degrees) in an approximately horizontal plane in five species of birds and man. The width of the blind sector behind the head is also shown. In all cases data refer to the situation when the eyes have adopted a resting position. In the Starling, cyclopean and binocular field widths produced as the result of achieving maximum convergence (1) and divergence (2) of the eyes are also shown. Data from the following sources: Pigeon, Martin & Young (1983); Starling, Martin (1986b); Mallard, Martin (1986a); Manx Shearwater, Martin and Brooke (1991); Tawny Owl, Martin (1984); Human, Vakkur & Bishop (1963).

Species	Cyclopean	Binocular	Monocular	Blind Sector
Mallard Duck <i>Anas platyrhynchos</i>	360	16	191	0
Pigeon <i>Columba livia</i>	316	22	169	44
European Starling <i>Sturnus vulgaris</i>	296 (1) 328 (2) 286	26 6 36	161	64 32 74
Manx Shearwater <i>Puffinus puffinus</i>	285	11	148	75
Tawny Owl <i>Strix aluco</i>	201	48	124	159
Human	200	140	170	160

In all bird species, except the owl, the lateral visual field is extensive and the binocular field a relatively small proportion of the total cyclopean field. In the Mallard Duck *Anas platyrhynchos* there is complete visual coverage in the horizontal plane, that is, there is no blind area behind the head. It is important to note, however, that associated with such wide horizontal visual fields there is also extensive coverage both above and below the horizontal. In all species, except the owl, visual coverage in the frontal field extends at least to directly above the head.

In the Mallard Duck visual coverage reaches its maximum possible extent in that binocular overlap extends from the bill to directly behind the head. Thus with the eyes in their resting position the Mallard always has comprehensive visual coverage of the celestial hemisphere. In the Starling nearly comprehensive visual coverage of the celestial hemisphere can be achieved by virtue of eye movements. These are of maximum amplitude in a plane passing approximately 50 degrees below the bill and permit the bird to alternate between having a relatively wide (43 degrees) binocular field below the bill and abolishment of that field in favour of extensive visual coverage above and behind the head (Martin 1986b). Eye movements may produce similar alterations to the visual field of the Pigeon (Nalbach et al. 1990).

It has been argued that the different shaped visual fields found in birds have evolved primarily in response to two competing demands; (1) frontal vision for the control of bill position during foraging and, (2) comprehensive visual coverage to facilitate the detection of predators and conspecifics (Martin 1986a,b). However, extensive visual coverage of the kind found in lateral eyed birds also has important implications for the detection of orientation cues and the requirement to detect these may also have influenced the evolution of visual field size. Thus, in animals with frontally placed eyes (including man), perception of the celestial hemisphere requires conspicuous effort and a change of head position. However, for birds with lateral eyes, celestial orientation cues [sun, moon and star patterns (Schmidt-Koenig & Keeton 1978, Papi & Wallraff 1982, Wiltschko & Wiltschko 1988, Wiltschko & Balda 1989)] will always be a conspicuous, indeed unavoidable, part of the animal's visual world. In other words, celestial compass and position cues are likely to be continually available to birds with laterally placed eyes whenever they are active.

Furthermore, extensive visual coverage is not restricted to the celestial hemisphere. As Table 1 indicates, visual coverage in a horizontal plane (which corresponds approximately with the horizon in a flying bird) is often extensive as also would be coverage of the terrain below.

There is evidence that both day- and night-flying migrating birds are influenced in their orientation by visual (topographical) cues from the landscape below (Bingman et al. 1982, Bruderer 1978, 1982, Martin 1990b). [However, the extent to which this is true in Pigeons *Columba livia* homing to a loft is not clear (Schmidt-Koenig & Keeton 1978, Papi & Wallraff 1982)]. Consideration of the extensive visual fields of lateral eyed birds indicates that when flying, the position of a particular topographical feature ahead could be constantly monitored with respect to other features at the side and possibly behind, *and* also to the orientational cues available in the celestial hemisphere above the bird. This means that for a night-migrating bird under a cloudless sky the star pattern of the whole, or a substantial portion of, the celestial hemisphere will be continually available and can be related to the horizon and to virtually the complete landscape below the bird. Similarly, during day-time, birds would be able to continually monitor the position of the sun in relation to the horizon and to landscape features below.

It is not argued that the extensive visual fields found in many birds are essential for the exploitation of celestial orientational cues. However, the constant and comprehensive visual coverage of the world which these fields provide, is likely to facilitate both reference to celestial orientation cues and the linking of those cues to topographical features.

RETINAL TOPOGRAPHY

Avian retinae are far from uniform (for reviews see Meyer 1977, Martin 1985). Within a single retina the distribution and abundance of receptor types and ganglion cells varies markedly. At specific locations there may be particularly high concentrations of particular cell types (Areae).

The functions of many features of retinal topography are not well understood but Areae which contain high concentrations of small photoreceptor and ganglion cells are almost certainly correlated with sectors of the visual field where spatial resolution is enhanced. There are also marked interspecific differences in retinal topography but the ways in which many of these are related to differences in ecology and behaviour are not clear (Meyer 1977, Martin 1985).

A particular retinal feature which may serve an important function in the orientation behaviour of some birds is the *Linear Area*. This is a ribbon-like region extending across the full width of the retina. Within a linear area the density of all retinal cells is locally increased and there may be an elongated fovea-like depression (Duijm 1958). Functionally the area probably represents an elongated region of increased spatial resolution.

The most comprehensive surveys of the occurrence of linear areas have been those of Duijm (1958) and Pearson (1972). In general, linear areas seem to be found in birds which live in open habitats, such as sparse scrub, deserts, marshes and open water, particularly the sea. These are all flat habitats which are largely devoid of distinctive topographical features.

Duijm (1958) concluded that when the bird is at rest the linear area is maintained in a horizontal position similar to that occupied by the horizontal semicircular canals. Certainly a recent study of the visual fields and retinal topography in the Manx Shearwater *Puffinus puffinus* (Hayes et al. 1991) indicated that in level flight the visual streak would be oriented parallel with the horizon.

Many functions have been attributed to the linear areas but none have been experimentally verified. Proposed functions include movement detection (Pumphrey 1961), localisation of the visual horizon (Pennycuick 1960), and spatial orientation (Duijm 1958). Clearly all of these functions could be important in the orientation behaviour of these birds. In open habitats which are largely devoid of conspicuous features that could provide topographical or landmark cues for orientation, visual fixation of the horizon may be particularly important. Such fixation could provide a stable co-ordinate base from which small changes in the position of celestial features could be accurately assessed. The ability to do this might be particularly important when celestial cues provide the sole basis from which position and compass direction can be determined, as might be the case in seabirds. It is worth noting that linear areas are found only in birds with laterally placed eyes and presumably extensive visual coverage of the celestial hemisphere (see above).

SENSITIVITY TO THE PLANE OF POLARIZATION OF LIGHT

There have been many investigations of the ways that birds can use the sun's position as a means of orientation (for reviews see, Schmidt-Koenig 1979, Papi & Wallraff 1982, Baker 1984, Wiltschko & Wiltschko 1988). However, to function as an orientation cue the sun does not need to be perceived directly since a patch of skylight contains a pattern of polarization which is unambiguously related to the sun's position (Brines 1980, Kirschfeld et al. 1975). Both psychophysical studies of visual capacity (Kreithen & Keeton 1974, Delius et al. 1976) and studies of orientation behaviour (Able 1982, Moore 1987, Moore & Phillips 1988, Phillips & Waldvogel 1988, Helbig & Wiltschko 1989) have supported the notion that birds have polarization sensitivity and that polarization cues influence orientation behaviour. However, a recent series of experiments has questioned whether birds can in fact detect the plane of polarization (Coemans et al. 1990).

The principal weakness of work on polarization sensitivity in birds has been the failure of investigators to find a satisfactory mechanism whereby lights with different planes of polarization could be discriminated. Satisfactory mechanisms have been described in certain fish retinæ (Hawryshyn & McFarland 1987) and in various invertebrate eyes (Waterman 1981, Fent & Wehner 1985), but not yet in birds. Mechanisms have been proposed for polarization detection in birds involving the fovea (Kreithen & Keeton 1974) and double cones and their associated oil droplets (Young & Martin 1984), but these have never been substantiated experimentally.

The major problem in handling polarized light is that it is easy to translate a differentially polarized stimulus into a source of differential brightness. Light from many common sources is already partly polarized so simply putting it through a polarizing filter can induce subtle brightness patterns as well as alter the plane of polarization. These brightness patterns would change with the orientation of the filter and if a rotating polarizing filter is used, then the light pattern can become one that flickers. It seems well established that birds are very sensitive both to brightness differences and to flickering lights (Emmerton 1983).

Furthermore many common surfaces, including mat black ones, can reflect light polarized in different planes unequally. Thus a surface uniformly illuminated with polarized light can become one containing subtle brightness differences. Coemans et al. (1990) have argued that both sources of contamination could have crept into previous studies of polarization detection in birds. When these possible artefacts were controlled Coemans et al. (1990) failed to replicate the evidence of Kreithen & Keeton (1974) and Delius et al. (1976) for polarization sensitivity in the Pigeon.

Field experiments have used polarizing filters to manipulate the plane of polarization of light presented above passerine birds which were in a state of migratory restlessness (Able 1982, Moore and Phillips 1988, Helbig & Wiltschko 1989). There is no doubt that the birds' orientation behaviour was influenced by the orientation of such filters. However, just what factors the birds were responding to would now seem to need further study.

CONCLUDING REMARKS

This review has briefly considered just three aspects of avian vision in relation to orientation behaviour. It has been argued that features of avian visual fields and of retinal topography, especially linear areas, would seem to facilitate the acquisition of information from celestial cues. Extensive visual fields might also facilitate the ability of birds to relate celestial orientation cues to topographical ones. However, the evidence for all of these proposals is circumstantial and requires experimental investigation. Whether birds really do have access to celestial orientation cues through the perception of polarized light is an important question. It now seems necessary to find better evidence for polarization discrimination in birds either by way of psychophysical investigations or by providing predictable results from orientation experiments.

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COGNITIVE PROCESSES AND VISION IN THE HOMING PIGEON

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ABSTRACT. This paper reviews some of the recent literature on visual perception and cognition in the homing Pigeon *Columba livia*. Field studies of this animal's homing abilities suggest that it might use visual landmarks as orientation cues mainly in the vicinity of the loft. Laboratory studies of the pigeon's discrimination of landscape slides show that these birds can form a concept of a particular location. They also have an extensive long term memory for complex pictorial stimuli. Experiments on perceptual invariance suggest that pigeons still recognize specific objects in spite of various changes in their visual characteristics.

Keywords: Pigeon, *Columba livia*, homing, landmarks, visual perception, location discrimination, concept learning, long term memory, perceptual invariance.

INTRODUCTION

Laboratory studies of behaviour in the homing pigeon attest to the general importance of vision in guiding this animal's actions. Analysis of neural function also indicates that a large proportion of its brain is allocated to processing visual stimuli. Indeed, the anatomical evidence is that vision is likely to be the dominant sensory system. Yet, in the context of its ability to home and navigate over long distances, the pigeon's visual sense is only one of many that are used. While they use vision to detect celestial cues, such as the sun and skylight polarization patterns, they also obtain directional information from olfactory cues and from sensing the earth's magnetic field (see Keeton 1979). However, the recognition of complex patterns offered by optical landmarks seems to be of secondary importance.

VISUAL LANDMARKS AND HOMING

Although Griffin (1955) argued that pigeons could use landmarks to pilot a course home, when pigeons' vision was severely restricted by translucent contact lenses, they were still able to orient at the release site in the direction of home and often landed in the vicinity of the loft (Schmidt-Koenig & Schlichte 1972). Recognition of visual landmarks is therefore not essential for long distance orientation. Nevertheless, peculiarities were reported in the way these animals flew home and subsequently landed, suggesting that pigeons are reluctant to fly without being able to maintain sight of the ground. Pigeons, as well as migrating birds (Emlen 1975), are also known to follow topographical features like coastlines, rivers, or valleys, where these do not deviate greatly from the homeward orientation. In alpine topography, homers have difficulty finding the loft site when they are forced to fly over, rather than under, stratus cloud (Wagner 1978).

Whereas visual landmarks may not be of primary importance in direction finding, a subsidiary role for such cues in orientation has not been eliminated entirely. Experiments in which pigeons were clock-shifted give somewhat contradictory results. Foa

and Abonetti (1980) found only a small deflection in clock-shifted homing pigeons' orientation when they were already familiar with the release site. At unfamiliar sites, orientation of clock-shifted birds that were repeatedly released from the same site improved. This was interpreted as being due to an increased reliance on release site stimuli. In contrast, release site familiarity did not diminish the amount of deflection in pigeons' initial orientation in another study by Fuller et al. (1983). Tracking the flight paths of pigeons to see when they correct their homeward path has suggested that they only begin to use visual landmarks within 15 to 20 km of the loft (see Emlen 1975). One difference in the clock-shift studies was that the pigeons were released from short distances in the first study and from longer ones (> 40 km) in the second. But elsewhere it has been reported that, even when pigeons are within sight of the loft, their orientation is altered by clock-shifting them rather than it depending on visual cues (see Keeton 1974).

Nevertheless, visual recognition of the landscape seems to become important mainly in the vicinity of the home loft. This conclusion is supported by results from brain lesion experiments. Pigeons in which the dorsomedial forebrain was ablated were homeward oriented on release from sites over 30 km from the home loft but very few were successful in returning to it. This seemed to be due to their failure to recognize it visually, even when released within half a kilometre and in full sight of the loft (Bingman et al. 1984).

The use of landmarks in orientation, even when these are limited to ones in the vicinity of the home site, requires both sophisticated perception of complex patterns and the ability to memorize these patterns in order to recognize them over long time delays.

PATTERN PERCEPTION AND LOCATION CONCEPT

There have been several experimental studies of pigeons' ability to discriminate complex naturalistic pictures in a concept-like way. In most of these experiments, a series of slides is projected in a randomized sequence onto a screen or a pecking key. Half of the pictures are designated positive: responses to them during a set time period (e.g. 20 sec) are rewarded with food. The other half of the pictures are the negative stimuli. Pecks towards these stimuli during an equivalent presentation period are either not rewarded or the animal's incorrect response is signalled and mildly punished by sounding a tone or lengthening the stimulus period.

The discrimination experiments with naturalistic stimuli that are most relevant to the question of what perceptual and cognitive abilities might underlie the recognition of landmarks are those in which slides of landscapes or locations have been employed.

In an early experiment on concept formation in pigeons, Lubow (1974) initially trained the birds to discriminate 80 slides taken from black and white aerial photographs. The positive slides included man-made objects such as city buildings, roads, orchards and ploughed fields. The negative ones depicted natural terrain such as mountains, valleys, forests and water. Three out of four birds learned to differentiate these aerial scenes correctly. They also transferred or generalized their differential responding to new instances of the positive and negative stimuli. From their ability to discriminate novel slides in the same way as they had the familiar training scenes (which they could have learned simply by "rote"), Lubow concluded that pigeons had formed a

concept of scenes containing man-made objects. The main features they seemed to rely on for this concept formation were straight lines or right-angles in the man-made scenes.

More recently, pigeons have been trained to discriminate locations shown in colour slides. Honig and Stewart (1988) presented pigeons photos showing various views of two different locations on a university campus. They suggested that pigeons in the real world have to learn to integrate different views of their environment in order to have a concept of a particular location. They trained two groups of birds. One group had to discriminate stimuli on the basis of the location they depicted. The other group received the same slides but each stimulus was arbitrarily designated correct or incorrect, irrespective of which location it showed. Therefore one group could have formed a concept of location, the other one could have memorized only individual views of places. Discrimination learning took place more rapidly when the task was to learn a location.

The animals trained on location discrimination were tested for their transfer to new views of the locations (pictures taken from the original standpoints but looking in a different direction), to slides taken from new standpoints within these locations, and to inverted slides. In all these tests the birds transferred well to the new conditions. Only the inversion test was performed with birds in the second group and their discrimination performance dropped to a chance level. Honig and Stewart suggested that pigeons based their discrimination of location not on any single defining characteristic but rather on an aggregate of varied features. They suggested that a whole location is memorized or represented for a bird not in the form of an integrated template of the surroundings but instead as a set of specific features, and that different "snapshots" of a location are internally linked up by generalization - a process based on stimulus similarities - amongst these snapshots.

In Honig and Stewart's study the birds did not have direct experience of the locations that they were required to discriminate in pictorial form. The effect of such experience on discrimination was tested by Wilkie et al. (1989). One group of pigeons (the "homers") was given flight training from the roof of the psychology department building. Another group (the "non-homers") were kept in the laboratory. Two sets of colour slides were used as stimuli. Some slides ("home") were taken in the vicinity of the psychology building or from its roof. Others were taken at a location ("away") that had never been seen by the "homers" but that contained some landscape features similar to those depicted in the "home" slides (e.g. buildings, trees, etc.). Responding to the "home" slides was rewarded in discrimination training.

"Homers" were slightly, but non-significantly, better at discriminating the initial training slides. New slides (half "home" and half "away") were added in each of 10 transfer sessions. During the first three transfer tests when "homers" were still receiving outdoor flight experience in the "home" environment, their discrimination of these new slides was significantly better than that of the "non-homers". Subsequent discrimination performance, when both groups were housed in the lab, did not differ statistically between the two groups, but in most of the tests the "homers" tended to be slightly better than the "non-homers". Successful transfer to these and other new stimuli provided evidence for conceptual discrimination of location as shown in slides, although it was not possible to define which features went to make up the concept of a place. The discrimination advantage of pigeons with actual experience of the location

suggests that birds perceived the slides as two-dimensional representations of the three-dimensional world. This is supported by data from Honig and Ouellette (1989) that birds trained to discriminate pictures of different ends of a lab room transferred their search for food in the room itself almost immediately when food was in that half of the room that had been shown in the "correct" pictures but the birds that had to seek food in the previously "incorrect" end of the room made many errors before they mastered the real-world discrimination. Also, tests by Wilkie et al. for the retention of slide discrimination following a pause for 60 days showed that the pigeons were able to memorize differences between locations for a fairly long time period.

Slides of locations showing two different buildings were employed in another study of concept formation by von Fersen and Lea (1990). Rather than analysing on a purely post hoc basis which features of locations might have been learned by the animals they instead prepared slides that varied along five different bipolar dimensions: views from nearby or far away, a sunny or cloudy scene, a horizontal or obliquely tilted picture, a perspective from the ground or a rooftop, and the site of the building itself (the university or a pub). For each dimension one alternative was designated positive, the other negative. "Correct" slides contained three or more of the positive alternatives. First the birds were trained to discriminate these stimuli. Tests then involved partial reversal, i.e. the positive alternative on one dimension was declared negative. This reversal failed to generalize to the other dimensions in the picture however. Von Fersen and Lea argued that pigeons do not learn an integrated concept with these naturalistic pictures but instead learn a collection of separate features, each of which is itself quite complex. Also, the more "positive" features a picture contained, the more the pigeons responded to the picture as correct. The conclusion that pigeons learn a set of independent features is similar to Honig and Stewart's idea that pigeons distinguish a location as an aggregate of features.

These experiments indicate that pigeons can use various visual features to discriminate specific locations and can also use these features to, in some sense, form a concept of that location. Other experiments show that these birds can memorize specific pictures for long periods of time.

VISUAL LONG TERM MEMORY

Long-term memory in discrimination tasks involving complex visual stimuli was first tested by Vaughan and Greene (1984). In all their experiments, it was arbitrarily decided which stimuli were associated with reward or non-reward, rather than the stimuli being allocated to conceptual groups. Initially they trained pigeons to discriminate a series of slides showing one or two abstract squiggles. When the pigeons' retention of discrimination was tested 490 days after completion of training with 80 of the original 160 training stimuli, their ability to differentiate these random stimuli correctly was only slightly poorer than at the end of training. New pigeons were trained in other experiments with naturalistic colour slides that proved easier for them to learn than the abstract squiggles. Only when positive and negative stimuli differed minimally (e.g. the same scene photographed from slightly different angles or in quick succession so that shadows had changed) did the birds have difficulty learning which one was the positive and which the negative stimulus. Memory for whether 80 or else 160 slides of outdoor scenes (depicting houses, trees, road signs, cars, etc.) had been assigned to the rewarded or non-rewarded group in training was barely disrupted by pauses of

490 and 629 days respectively. When underwater scenes were used as training material, the reward and non-reward contingencies were sometimes changed along with mirror-image reversals of the pictures. This time there was a pause of two years before the training stimuli were shown again. The birds seemed to have had difficulty remembering which orientation of the stimulus went with reward, but their long-term memory for the stimuli themselves was hardly affected. They very quickly relearned which orientation of a particular stimulus was the correct one during several days of testing that included further mirror-image reversals.

Several tests were also performed with pictures in different orientations. Although they could learn to differentiate mirror-image reversed pictures when specifically trained to do so, left-right reversals that were suddenly introduced in test sessions had little effect on their ability to discriminate the pictures. However, performance dropped to a chance level when scenes were shown upside down. This is similar to Honig and Stewart's (1988) findings for inversion of individually learned scenic pictures as compared with pictures that were grouped on the basis of location. Although this is an orientation change that a pigeon would not frequently experience in its natural environment, the disruption in slide discrimination may have had more to do with the fact that the animals in Vaughan and Greene's study seemed to learn more about the upper half than the lower half of the pictures. When the bottom half of the pictures was covered, test performance was almost as good as training performance but discrimination of the pictures was poorer in tests when only the bottom half of the pictures was visible. Covering the right or else left side of the pictures had little effect on discrimination.

Another study of the pigeon's long-term memory for an even larger number of visual stimuli employed abstract geometric patterns (von Fersen & Delius 1989). Pigeons were first trained to discriminate pairs of stimuli chosen from a set of 725 shapes: 100 of these (the "few") were associated with food reward and were gradually introduced in subsets during the course of training. The non-rewarded stimuli were mixtures of all the other 625 patterns (the "many").

Thus, by the end of training the birds had seen the "few" stimuli more often than the "many". Tests in which either the "few" or else the "many" patterns were replaced by novel ones showed that birds had learned to recognize all 725 shapes and had additionally categorized them as belonging to the rewarded versus non-rewarded groups on the one hand and to the frequently versus less frequently seen groups on the other. Tests in which the orientation of some of the stimuli was altered showed little effect of this change, although discrimination was slightly worse when patterns were shown upside down than when mirror-image alterations were made.

The pigeons' extensive memory for visual patterns was confirmed when 645 of the original patterns were shown to the birds after a pause of over six months. Although their discrimination performance was poor initially, they rapidly relearned the discrimination. This, together with the good discrimination of the remaining 80 patterns in a later session, showed that the birds had not forgotten the shapes themselves but needed to be reminded whether it was reward or non-reward that was associated with the patterns they had seen more or else less often.

These experiments, employing either arbitrary, highly artificial patterns or else naturalistic pictures, indicate that pigeons have an extensive long-term memory for

complex visual scenes. A large memory capacity, which probably has not been tapped exhaustively in these studies, is one of the prerequisites if pigeons are to form an effective "mosaic map" in which visual information about landmarks is utilized to orient to the home loft. According to the "mosaic hypothesis" (Wiltschko & Wiltschko 1978, Wallraff 1984), a bird would have piecemeal knowledge about at least a limited area near the home loft through memorizing a number of different landmarks or previously visited locations, together with the compass direction connecting each of these locations with the loft. On re-encountering a familiar site, rather than having to pilot home via a series of landmarks, the animal would "know" the direct route from that specific landmark to the loft. As a means of short-range homing by visual cues, the mosaic map would become more efficient if a large number of landmarks or locations could be remembered. Laboratory experiments suggest that pigeons have the capacity to do this.

PERCEPTUAL INVARIANCE

There are a number of ways in which the appearance of a location may change. Depending on a bird's angle of approach to a location, the relative orientation of the scene may differ for the bird from one time to the next one on which it flies over the same terrain. There are also seasonal changes - in the colour of foliage, for instance. During low flight, the bird's movement through a location may lead to some structures being temporarily occluded by others. Some studies of perceptual invariance give clues to the extent to which pigeons could recognize that an object remains one and the same thing in spite of changes in its optical properties.

Pigeons' perceptual invariance has been investigated by training them to discriminate oddity from sample. A sample stimulus (an arbitrary pattern) is first projected onto a central key. After they respond to this sample, two comparison patterns are shown on keys to the right and left of the sample. One of these patterns is the same shape as the sample. The other pattern, to which responding is rewarded, differs in shape. When small shapes are used, pigeons can detect pattern differences (Lombardi 1987) or mirror-image reversals of shape (Hollard & Delius 1982) in spite of orientation discrepancies between the comparison and sample stimuli. Recognition of shape and detection of pattern oddity is also unaffected when sample and comparison patterns are of different colours (Lombardi & Delius 1988).

There is indirect evidence that pigeons could use movement cues to recognize where an object that is momentarily occluded by another should reappear in view. Neiwirth and Rilling (1987) trained pigeons to observe a computer-displayed clock hand rotating at constant speed. The stimulus briefly disappeared and reappeared at one of two other locations. The birds then had to indicate whether the reappearance position of the clock hand was correct or incorrect for the amount of time it had been occluded, i.e. for the distance it could have continued moving at constant speed during that time. They also discriminated between correct and incorrect reappearance of the moving bar when a novel reappearance location and new occlusion times were tested. This experiment suggests that birds have the sort of imagery processes necessary to recognize the unity of an object that perceptually is briefly hidden behind another one as the animal flies through its environment.

CONCLUDING REMARKS

Given the richness of pigeons' visual perception, it is perhaps surprising that they do not rely more on pattern vision to orient in their environment. But what reliance they do place on the perception of objects and locations seems to be restricted to their orientation within a short range of the loft, a range that may also be important to them when foraging. Laboratory studies indicate that these birds have the perceptual mechanisms to process information about different locations in a flexible way. Their visual memory capacity is also extensive but reliance on storing a large amount of information that itself consists of complex and multiple cues may not be the most efficient means of orienting over large distances as long as alternative sensory mechanisms are available.

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CONCLUDING REMARKS: SENSORY BASIS OF ORIENTATION

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Although our knowledge of how the various environmental cues are perceived and processed has greatly increased in recent years, we are still far from understanding how these different types of information are utilized by migrating and homing birds. The relationship between stimuli and behavior is highly complex because of two reasons: (1) birds make use of multiple cues, and (2) the ranking of these cues may vary.

»MAP«

»COMPASS«

→ goal direction as compass course

external reference

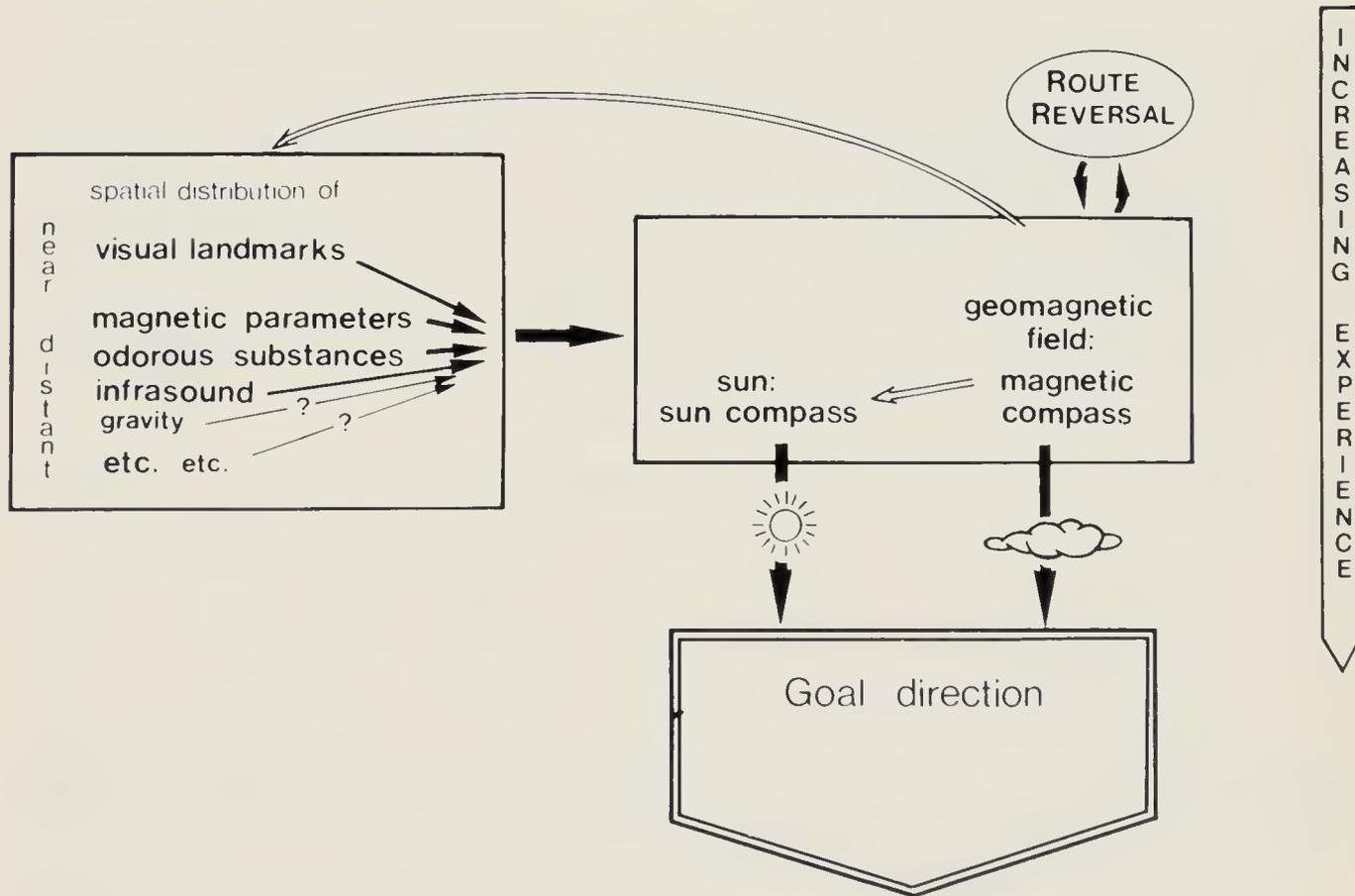


FIGURE 1 – The modern ‘map and compass’ model which looks upon bird navigation as a multifactorial system. Light arrows indicate learning processes and transfer of information during ontogeny; dark arrows indicate the actual use of information during homing.

A MULTIPLE CUE SYSTEM

Early attempts to analyze bird orientation often started with the assumption that orientation was controlled by just one or two major cues. The classic hypotheses like the ones forwarded by Viguier (1882), Yeagley (1947) and Matthews (1953) are examples for this; the olfactory hypothesis advanced by Papi (1976) is likewise centered around

one dominant cue. Yet, in spite of considerable experimental efforts, no one factor was found that alone could explain bird orientation; it always became evident that additional factors were involved. This is not surprising at all. In nature, birds live in a highly complex environment offering a multitude of cues, and we must expect that birds take advantage of all available cues that provide useful information.

The modern version of the 'map and compass' concept of bird navigation (Figure 1) takes this into account. The concept was first proposed by G. Kramer (1953) and originally assumed the sun compass as a sole compass mechanism and a 'map' based on unknown factors. The crucial point of Kramer's model is the idea that orientation is established via an *external reference*, i.e. the first step is to use a set of factors to determine the home direction as a compass course, and the second step is to plot this course using a compass to transfer it into an actual flying direction. In this sense, the model represents an open concept, which later was extended to include more than one factor for the 'map' step as well as for the compass step (see Wallraff 1974, Wiltschko & Wiltschko 1982). These factors interact in complex ways, replacing as well as supplementing each other.

In the compass step, the sun compass can be replaced by the magnetic compass on overcast days. The two compasses are not independent of each other, because the sun compass is calibrated against the magnetic compass when it is first established during ontogeny, a process that ensures that the mechanisms of compensating the sun's movements are adapted to the local situation. Night-flying birds are known to make use of the star compass which is also controlled by the magnetic compass. Theoretically, other factors that are spatially and temporally relatively constant could also be calibrated so that they could serve as additional sources of directional information (see Wiltschko & Wiltschko 1988).

For the 'map' which encompasses the mechanisms used to determine the homeward course, a variety of factors has been suggested. Landmarks seem to play an important role only in the immediate vicinity of the loft (Schlichte 1973). For orientation from greater distances, factors like magnetic parameters, odors, infrasound and gravity have been proposed. The use of the first three is supported by experimental evidence (see Wiltschko & Wiltschko 1988, Papi 1982, Schöps 1990), even if many questions about their role in the orientation system remain unsolved. The birds acquire knowledge about the spatial distribution of these factors through experience during the first months of their life. Later, when they are released at an unknown location, they can interpret the local navigational factors on the base of this knowledge and thus determine their home course (see Wallraff 1974, Wiltschko & Wiltschko 1982). Their 'map', however, need not be restricted to the factors mentioned above; other, still unknown factors might be incorporated in a similar way.

Consequently, for the 'map' as well as for the compass, the birds seem to have more than one option. The orientation system is not dependent on any one factor alone and because of this, is less susceptible to disturbances. The multitude of factors involved, however, renders the analysis of the system much more difficult.

THE WEIGHING AND RANKING OF CUES

The use of multiple cues is not the only obstacle that has to be overcome to understand bird orientation. In recent years, a growing body of evidence indicates that the various navigation factors are not rated in a constant manner. At least as far as the 'map' is concerned, there is no fixed hierarchy of cues. The relative importance of any cue may vary, as the birds seem to make use of individual cues in a highly flexible way. This first became obvious when results obtained with homing pigeons from one loft could not be reproduced with birds from another. The controversies between Papi and Keeton in the late 1970s provides a well-known example (see Keeton 1980). Later experiments using identical methods of olfactory deprivation with birds of lofts in three different countries (Italy, USA and Germany) demonstrated that these differences were not caused by different techniques, but reflected true differences in the pigeons' behavior (Wiltschko et al. 1987). Varying results were also obtained in tests involving different routes of the outward journey (Hartwick et al. 1978), treatments with oscillating magnetic fields (Wallraff et al. 1980), and the behavior at magnetic anomalies (Walcott 1988).

Orientation at Jersey Hill, New York:

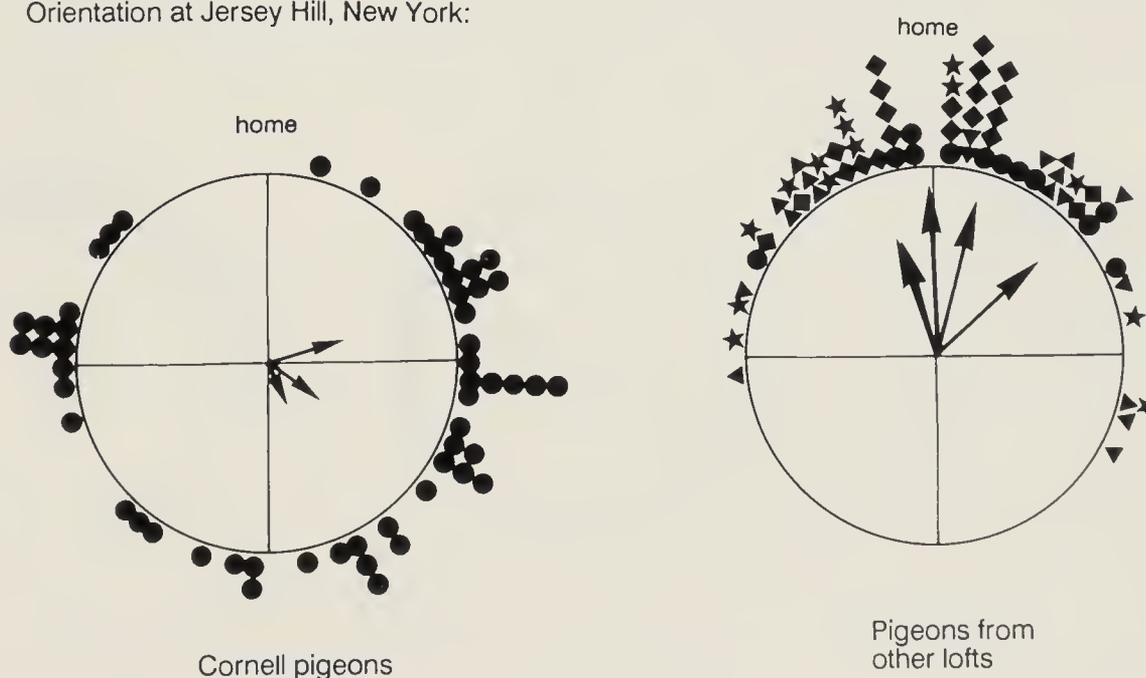


FIGURE 2 – Pigeons from different lofts behave differently at a specific site in upstate New York. The symbols at the periphery of the circle give the vanishing bearings of individual birds in relation to home (= upward), the bearings of birds from five lofts in the left diagram marked with different symbols. The arrows represent the mean vectors of releases (data from Walcott & Brown 1989).

There are three possibilities discussed as the basis of these differences in behavior: (1) Regional differences in the distribution and availability of potential navigational cues, (2) genetic differences in the experimental pigeons used and (3) differences which might be induced by different methods of raising, housing and training the birds and which can be grouped as 'caused by individual experience'. Recent findings indicate that all three causes might equally contribute the variability of behavior.

An effect of the regional distribution of available 'map' factors is indicated by the orientation at Jersey Hill, New York (Figure 2): Pigeons from the Cornell loft at Ithaca, New York, 120 km east of the site, do not depart homeward oriented; in fact, their

vanishing bearings do not show any directional preference at all (Walcott & Brown 1989). Yet pigeons from five other lofts in four different towns, between 100 and 350 km in various directions from the test site, show oriented behavior in or close to the home direction. Apparently, these pigeons were able to interpret the local navigational cues and determine their respective home courses, whereas Cornell birds, for reasons unknown, were unable to do so. Subsequent experiments with pigeons of different origins, raised together, clearly showed that it was not the genetic stock, but rather the location in which the pigeons grew up that is crucial for their oriented or disoriented behavior at Jersey Hill (Walcott & Brown 1989).

Genetic differences, on the other hand, were found to affect the pigeons' reaction to treatments with oscillating magnetic fields. After the differences between Italian and German birds had been described (Wallraff et al. 1980), young pigeons from Wallraff's loft in Germany were transferred to Italy and raised at a loft in Tuscany together with a group of young Italian birds. In the critical tests (Figure 3), when the birds were treated with oscillating magnetic field for 3 h prior to the release, the Italian pigeons showed larger deviations from the home direction and an increase in scatter, whereas the birds of German origin remained unaffected (Benvenuti & Ioalé 1988).



FIGURE 3 – Pigeons from different genetic stock react differently to being treated with oscillating magnetic fields. Symbols as in Figure 2 (from Benvenuti & Ioalé 1988).

In addition to genetic differences and regional differences in cues available, the way young pigeons are raised and maintained might be crucially important in determining their later use of orientation cues. This is demonstrated by a series of experiments with pigeons from our Frankfurt loft, in which birds living in the normal, wind-protected loft in the garden were compared with birds from a wind-exposed loft at a roof (Wiltschko & Wiltschko 1989). Although the two groups were housed only about 50 m apart and were exposed to identical conditions during all their free flights, their reaction to olfactory deprivation differed markedly: In the birds from the wind-exposed loft, this treatment regularly induced large deviations from the directions chosen by the controls, whereas the birds from the loft in the garden were mostly unaffected (Figure 4).

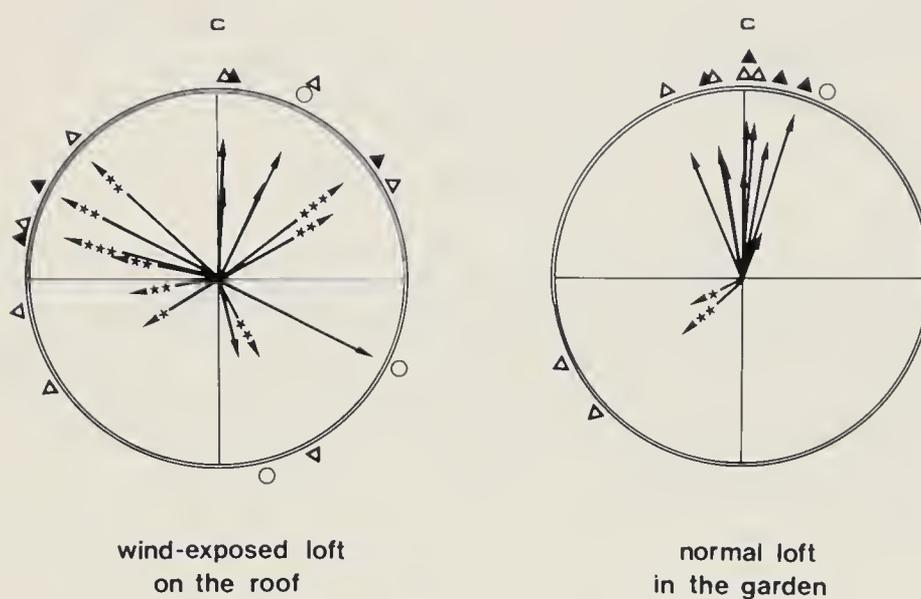


FIGURE 4 – Pigeons raised at the Frankfurt loft in different ways react differently to olfactory deprivation. The arrows represent the mean vectors of anosmic pigeons given in relation to the mean direction of the controls (= upward). The symbols at the periphery of the circle mark the mean directions and indicate whether the respective controls were home-ward oriented (open triangle), showing a release site bias (solid triangle) or were not significantly oriented (open circle). From Wiltschko & Wiltschko (1989).

In all three examples given above, the pigeons were released at the same site on the same day, alternating birds of the various groups, i.e., the environmental factors were identical for all birds. Nevertheless, the birds behaved differently. This clearly shows that bird orientation cannot be understood on the basis of sensory input alone. Birds are not automatons that react in the presence of a given set of factors in a quasi standardized way. The examples seem to indicate that the different groups were relying on different navigational cues. Apparently, the orientation system provides more possibilities than are used by a bird in a given situation - it is at least partly redundant, with different groups of birds selecting different sets of cues. Thus the available orientation factors are not the only determinants of behavior, because the birds apparently can weigh and rank the factors very differently, preferring some over others.

The relative importance of available information depends, as our examples show, on genetic factors as well as on the previous experience of the birds. Especially the latter is not surprising in view of the fact that the distribution of the navigational factors is learned during ontogeny (see light curved arrow in Figure 1) - it is easily seen how individual experience might shape the navigational system. We can expect that birds tend to prefer the factors that have proven to be the most suitable and most reliable during the establishment of the 'map'. This leads to a 'map' which is well adapted to the specific local situation in which the bird has to orient, especially, if it continues to be updated by new experiences. The choice of a specific set of cues would reflect the individual experience of the bird, yet, on the long run, the regionally most appropriate factors might also be supported by a genetic disposition which favors just these cues, thus optimizing the adaptation of the orientation system.

Our knowledge of these interrelations is still rather limited; an analysis of the ontogenetic development of the orientational systems has only just begun. To find out how the different factors are weighed and rated in given situations, and what deter-

mines their relative importances will be one of the great challenges of orientation research in the years to come.

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SYMPOSIUM 33

PHYSIOLOGY OF DIVING BIRDS

Conveners P. J. BUTLER and D. R. JONES

SYMPOSIUM 33

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THE BEHAVIOUR OF DIVING BIRDS

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ABSTRACT. Birds diving to forage use aerial plunges or wing or foot-propulsion to submerge. Dives are either bounce-dives, in pelagic foragers, or flat-bottomed dives, in benthic and pelagic foragers. Diving birds alter dive depth, swimming speed, heading and duration according to biotic and abiotic environmental parameters; prey distribution and size, water temperature, water visibility and depth, light availability, bottom topography etc. Changes in dive parameters are a physiologically-tailored response by the bird to the environment so as to maximise hunting efficiency.

Keywords: Dive duration, speed, heading, depth, diving birds, optimisation.

INTRODUCTION

Birds that dive to feed have very special foraging constraints. Being air-breathing they must obtain their food from an environment that can be only exploited for short periods (cf. Kramer 1988, Ydenberg 1988). Diving in birds is an energetically costly activity (Butler & Woakes 1983, Nagy et al. 1984), which in turn uses body oxygen stores fast and limits dive duration. It is thus particularly important that diving birds feed in the most efficient manner possible.

Due to the difficulties of directly observing birds underwater, much work on the diving behaviour of birds has centred around the length of time that birds remain underwater, here termed dive duration (Dewar 1924, Dow 1964, Cooper 1986, Trayler et al. 1989). Although dive duration is interesting in that it generally indicates the oxygen store status of the bird, it is actually an integrated end product resulting from various underwater behaviours adopted by birds in response to environmental variables so as to maximise foraging efficiency.

Work to determine the behaviour of diving birds when underwater has only relatively recently begun. Apart from visual observations in the wild (e.g. Roberts 1951, Grover & Olla 1983), and in captivity (e.g. Duffy et al. 1987, Tome 1988) authors have used new technology (e.g. Gales et al. 1990) and ecological models (e.g. Wilson & Wilson 1988) to this end. In this paper I present information on how birds forage underwater and examine variability in foraging parameters and how this relates to maximizing foraging efficiency.

BACKGROUND

For the purposes of this paper I will define diving as complete body submergence (Cramp & Simmons 1983). This eliminates all species that only engage in surface seizing or head-ducking (*sensu* Cramp & Simmons 1983) (e.g. swans) where breathing is curtailed during food acquisition.

TABLE 1 – Foraging paramets of major diving bird groups.

Group	Propulsion					Max dive depth	Max dive duration	Dive types		Source
	Plunge	Feet	Wings	Pelagic	Benthic			Bounce	FI-bot	
Penguins Spheniscidae	•	•	X	X	x	>400 m	1080 s	X	X	1,2
Divers Gaviidae	•	X	•	X	•	60 m	>120 s	•	X?	3,4
Grebes Podicipedidae	•	X	•	X	•	22 m	?	•	X?	5
Petrels/ Shearwaters Procellariidae	X	•	X	X	•	60 m	?	X	X?	6,7
Diving Petrels Pelecanoididae	•	•	X	X	•	?	24 s	?	?	8
Gannets / Boobies Sulidae	X	x	x	X	•	10 m	11 s	X	•	9
Cormorants Phalacrocoracidae	•	X	•	x	X	125 m	380 s	?	X	10,11
Terns / Noddies Sternidae	X	•	•	X	•	1 m	1 s	X	•	12
Auks Alcidae	•	x	X	X	x	180 m	202 s	X	X	2, 13, 14, 15
Ducks Anatidae	•	X	x	x	X	55 m	180 s	•	X	4, 16
Anhingas Anhingidae	•	X	•	X	•	?	45 s	•	X	17

X indicates major usage, x indicates occasional usage or extensive usage by relatively few species.
FI-bot = Flat-bottomed dive.

Sources: (1) H. Burton in litt, (2) Summarised by Burger (in press), (3) Schorger (1947), (4) Kooyman (1975), (5) T. Piersma in litt, (6) Harrison (1983), (7) Prince & Morgan (1987), (8) T. Chauraud (pers. comm.), (9) Percy FitzPatrick Institute (unpubl. data), (10) Wanless et al. (in press), (11) Wanless in lit, (12) Duffy (1983), (13) Wanless et al. (1988), (14) Jury, (1986), (15) Piatt & Nettleship (1985), (16) Reynolds (1987), (17) Unpubl. data.

Twelve bird families contain appreciable numbers of habitual divers (Table 1). Birds may submerge for a variety of reasons including escape from predators (Butlin & Burke 1988), travel (e.g. Trivelpiece et al. 1986), to pick up material from the bottom (Levick 1914), to play (Bartlett 1988) and to forage. This paper will only consider diving behaviour associated with foraging since it constitutes the main function of diving for most species.

DIVING BEHAVIOUR

Diving behaviour is usually confined to bouts which may last several hours as the birds hunt and capture prey (Kooyman 1989). Kooyman describes bouts as "a series of dives, usually to a consistent depth, with a short surface interval between each dive for gas exchange". Essentially, this means that diving birds partition their day so that certain periods are exclusively used for intense foraging rather than engaging in low-level foraging throughout the day. Bout-diving may be initiated by light levels (Piersma et al. 1988), local prey abundance (Hobson & Sealy 1985), tidal cycle (Ryan et al. 1988) etc. and presumably occurs when the probability of prey capture is highest. Dive bouts may be terminated by a decrease in prey availability (Piersma et al. 1988), satiation or by lactic acid build up (Kooyman 1989).

Submergence.

Due to large quantities of air in the feathers, lungs and air sacs, birds are highly positively buoyant (Butler & Woakes 1984, Stephenson et al. 1989). Different mechanisms are used to enable birds to submerge and to remain submerged.

PLUNGING. Species such as terns, gannets and some pelicans fly above the water's surface and then, by plunging down, convert their potential energy into kinetic energy which is used to drive them underwater (Schreiber & Clapp) 1987). This method of submergence may even be used by species that do not habitually dive to enable them to reach submerged prey e.g. herons (Morey & Smits 1987).

FOOT-PROPELLED DIVERS. Foot-propelled species (Owre 1967) include most ducks, cormorants, divers and grebes (Table 1). These birds often engage in a pre-dive leap before descent (Nuechterlein & Buitron 1989).

WING-PROPELLED DIVERS. Wing-propelled species (Livezey & Humphrey 1984, Hui 1988) include some petrels and shearwaters, penguins, diving petrels and auks (Croxall 1987) (Table 1). These species never engage in a pre-dive leap.

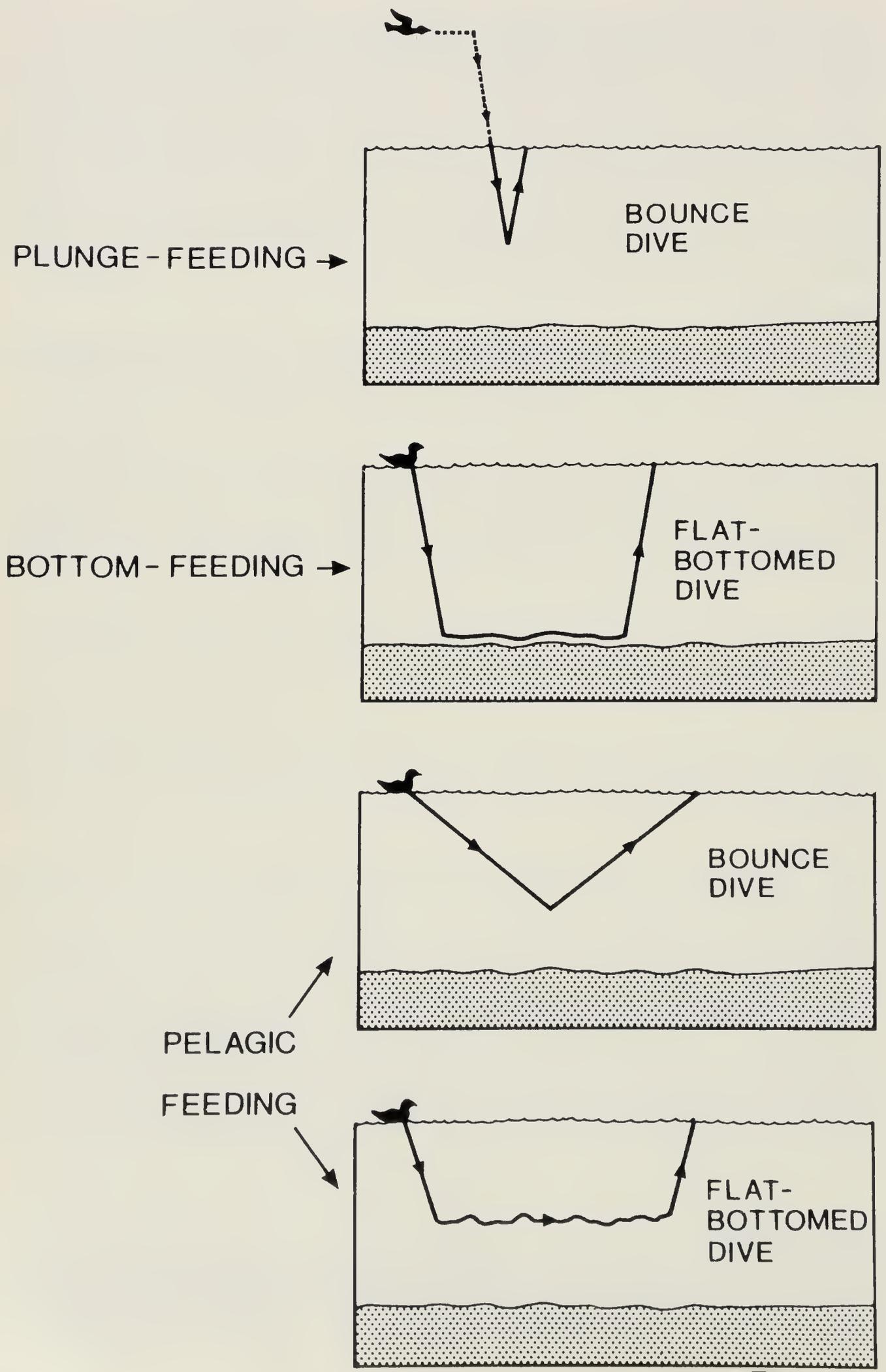
Dive types

In 1971, Ashmole (1971) proposed a classification of seabird feeding methods which included various categories of diving. This scheme has been variously modified by Cramp & Simmons (1983) and Harper et al. (1985). In essence, two categories of diving plunge are recognised; plunging, where an aerial dive allows the bird to penetrate the water and pursuit-plunging, where a bird in flight plunges into the water, then pursues prey by active swimming underwater. Two categories of dive are listed; surface dives, where a bird settled on the water submerges momentarily directly onto prey with little or no pursuit swimming; and pursuit diving, where a bird settled on the water dives and pursues its prey underwater by pursuit swimming. Such classifications tend to become more complex with time (Cramp & Simmons 1983) since boundaries between the various categories are indefinite.

Dive profiles

Bird dive type could also be conveniently classified according to dive profile (cf. Le Boeuf et al. 1988). Each profile may be further divided into phases according to function.

FIGURE 1 – Schematic diagram showing the major dive profiles of foraging diving birds.



PASSIVE-PLUNGERS. Birds that dive uniquely using momentum derived from an aerial plunge (e.g. terns) have a bounce-dive profile. There is a short, steeply-angled descent phase followed immediately by the ascent phase. The prey is almost invariably caught at the deepest part of the dive (Figure 1). The function of the dive is transit, since search for prey occurs above the surface and a dive is only executed when prey is sighted. Dive times are typically less than 5 s (e.g. Duffy 1983) although during longer dives birds may dive as deep as 10 m (Percy FitzPatrick Institute unpub. data). This type of dive will not be discussed further.

ACTIVE SWIMMERS. (i) Bottom foragers: Species that forage on benthic or demersal prey exhibit a three-phase, flat-bottomed dive (e.g. Wilson & Wilson 1988) (Figure 1). This consists of a descent phase where the bird is in transit between the surface and the bottom, a flat-bottom phase where time is spent searching for and capturing prey and an ascent phase which is again a transit period between the bottom and the surface. Almost all bottom foragers (most ducks and cormorants) are foot-propelled (Table 1), possibly because this method of propulsion interferes less with activity on the bottom than forward-placed wings. It is notable that the normally wing-propelled auks use their feet for propulsion when feeding on the bottom e.g. Pigeon Guillemots *Cephus columba* (Duffy et al. 1987). (ii) Pelagic foragers: These species exhibit essentially two dive types, either bounce dives or flat-bottomed dives. Bounce dives are two-phase and consist of a descent phase during which prey search occurs. Dive angles are shallow and are reported to vary between 3° and 45° (Naito et al. 1990, Wilson et al. 1990). After a momentary turn at the deepest part of the dive, prey search continues in an ascent phase which is very similar to the descent phase (Wilson et al. 1989, Naito et al. 1990) (Figure 1). Pelagic flat-bottomed dives are very similar to demersal flat-bottomed dives except that limited prey search and capture may also occur during the descent and ascent phases (Figure 1). The bottom phase may also be less flat since it is not dependent on bottom topography. It is likely that the bottom phase in pelagic foragers may turn out to be variously undulating, rising (cf. Hobson 1966), sinking or U-shaped (cf. Kooyman 1989), as has been noted for seals (Plotz pers. comm.), according to species or environmental conditions.

Optimisation

It is to be assumed that diving birds, like other animals, maximise hunting efficiency, ultimately so as to maximise reproductive success (Krebs 1978), perhaps via individual survival (Houston et al. 1988). A number of authors have attempted to consider how diving birds should maximise hunting efficiency, looking at particular parameters to be optimised e.g. time (Wilson & Wilson 1988, Ydenberg & Clark 1989), energy (Tome 1988) or prey ingestability (Draulans 1984). Perhaps the simplest reasonable view is to consider that diving birds should attempt to maximise energy gain with minimum energy expenditure in the minimum time (net energetic gain per unit time; Stephens & Krebs 1986). The bird can essentially alter four dive parameters which constitute dive behaviour: swimming depth, heading, duration and speed, in response to variability in environmental factors such as light availability, prey distribution, prey size, bottom topography, water visibility, water temperature and water depth. Below I will consider environmental factors that are thought to alter dive parameters.

LIGHT AVAILABILITY. Most diving birds are visual hunters (Baker & Parker 1979) so it is to be expected that foraging parameters vary with light availability. Light availability varies throughout the circadian cycle and decreases with increasing depth. Due to the limits of vision, we expect birds to dive less deep at night than during the day and this

has been reported in numerous species (Croxall et al. 1988). However, whether this behaviour is due to visual limitations or changes in vertical prey distribution, due itself to circadian light changes, is unclear and must yet be demonstrated (Wilson et al. 1989c, but see Piersma et al. 1988).

WATER VISIBILITY. To my knowledge there is only one study on the effect of water visibility on the foraging behaviour of actively-swimming diving birds (Eriksson 1985) (but see Ainley (1977) and Haney and Store (1988) for plunge-divers). Since birds are primarily visual hunters, water visibility is expected to effect foraging behaviour (cf. Breitburg 1988) e.g. swimming speed, since prey detection rates are altered (Vinyard & O'Brian 1976).

PREY DISTRIBUTION. Variability in prey distribution is crucial in determining foraging strategies. This is a complex topic and changes in all foraging parameters are expected according to prey density, prey patchiness, prey patch size, prey depth distribution etc (cf. Stephens & Krebs 1986). Some work has been carried out examining aspects of prey distribution (e.g. Wood & Hand 1985, Tome 1988) but this field is poorly covered in diving birds.

PREY SIZE. Although it is usual for many diving species to swallow prey underwater, large prey items are generally brought to the surface (Rand 1960). Dive duration can thus be immediately curtailed by large prey capture. The extent to which this modifies the frequency distribution of dive durations depends on the probability of prey encounter in relation to the dive duration (Wilson & Wilson 1988).

Dive parameters

Below I consider the dive parameters and the extent to which they may be modified by environmental factors.

SPEED. Oxygen utilisation by a bird swimming underwater increases as a function of the speed cubed (Kooyman & Davis 1987) which correspondingly reduces maximum dive duration. The speed at which a bird should swim will depend on its activity.

(i) Pelagic-foraging, bounce-diving birds should swim at a speed concomitant with the lowest cost of transport (Kooyman & Davis 1987) which would enable them to search the greatest water volume with least energy utilisation. This solution is probably also optimal for bottom speeds in pelagic-foraging birds exhibiting flat-bottomed dives (Naito et al. 1988, Wilson et al. 1989a, 1990) and have essentially invariant swimming speeds ranging between 1.9 and 2.4 m/s (for 10 species reviewed in Wilson et al. 1989b, cf. Gales et al. 1990). Free-living Adelie *Pygoscelis adeliae*, Gento *Pygoscelis papua* and Chinstrap *Pygoscelis antarctica* Penguins all have mean swimming speeds of 2.2 m/s (Wilson et al. 1989b) which correspond well to their lowest costs of transport (Adelie - 2.1 m/s, Gento - 2.2 m/s, Chinstrap 2.4 m/s; Culik & Wilson unpub. data).

Very high speeds may be used when prey has been sighted in order to secure capture. For example, pelagic-fishing Cape Cormorants *Phalacrocorax capensis* may achieve speeds of 3.8 m/s when lunging into schools of mullet although normal pelagic search speeds are ca. 2 m/s (unpubl. data). Although energetic costs are high, the probability of prey capture is also high and not dependent on encounter rates as during searching.

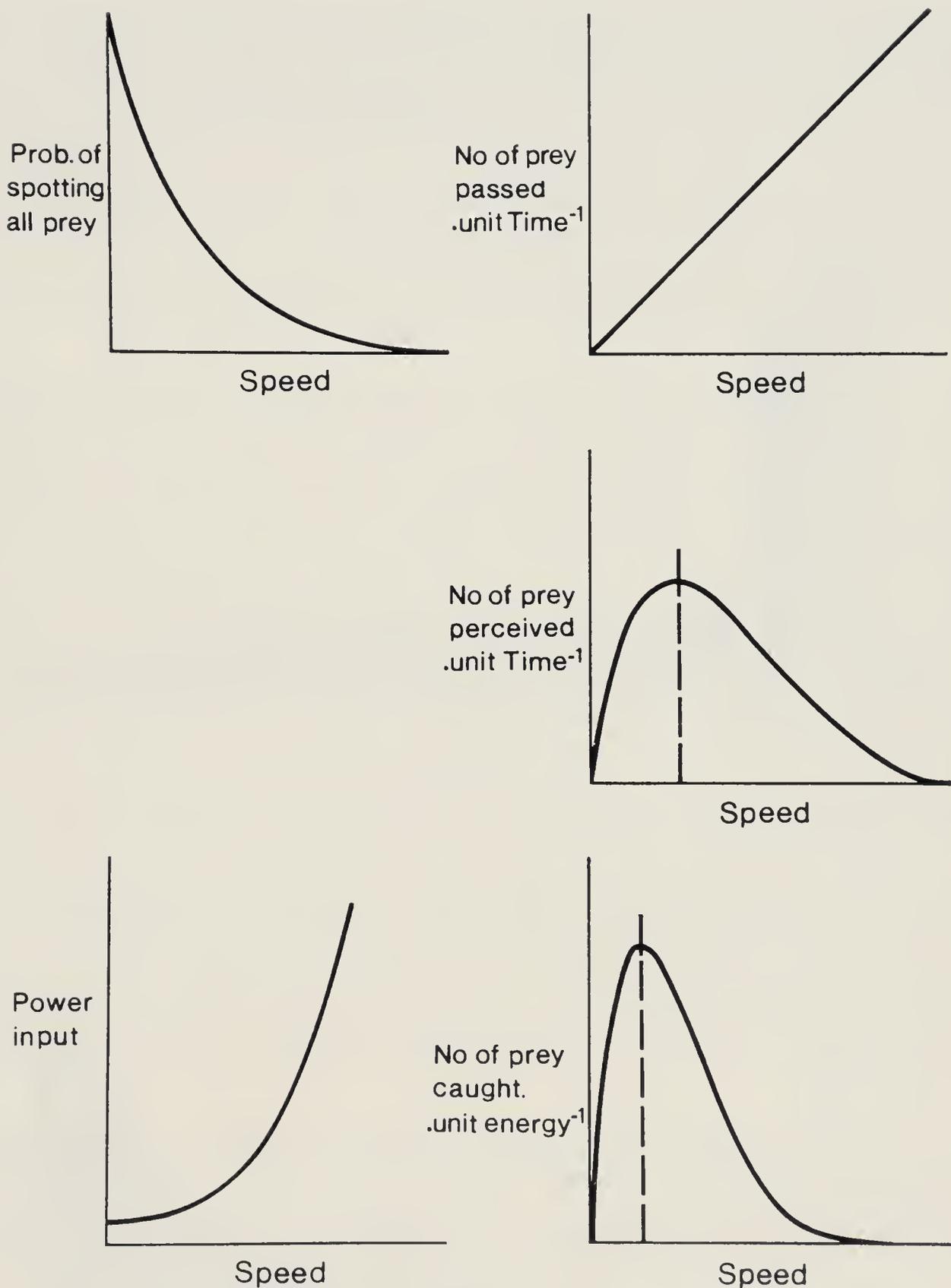


FIGURE 2 – The probability that a benthic-foraging bird will perceive all prey within its sensory range will decrease (according to some function determined by the bird's sensory capabilities and the way the prey is hidden) with increasing bottom speed (upper left). Birds will bring more prey into their sensory range as a linear function of swimming speed (upper right). The overall number of prey actually perceived by the bird per unit time will depend on these two functions and have an optimum value (centre right). However, since power input values rise as a function of the swimming speed cubed (bottom left), the number of prey perceived per unit energy as a function of bottom speed (bottom right) can be obtained by dividing the number of prey seen with respect to speed by the power input for that speed. The optimum speed for maximised net energetic gain is thus always lower than the optimum speed for maximising prey perception.

(ii) In benthic-foraging birds, transit time between the surface and the bottom is unprofitable so this period should be minimised although, in order to maximise time available underwater, descent speeds should be at the lowest cost of transport. This should be invariant of dive depth (cf. Houston 1986). Mean descent rates for benthic-foraging birds have been noted at between 0.66 and 1.9 m/s for various cormorant species (Wilson & Wilson 1988, Wanless et al. in press), and are approximately 1 m/s in auks, but may be as high as 3 m/s (Croll, cited in Burger in press). There are no cost of transport data for the relevant species. Generally, the ascent to the surface is similarly fast (pers. obs) although passive (Jones & Butler 1982, Duffy et al. 1987) as a result of air-induced buoyancy. Non-active surfacing may help extend dive durations by lowering metabolic rate to resting levels at this time.

Optimum bottom speed in benthic-foraging birds is complex and bottom topography-dependent. Bottom topography and type presumably affect prey visibility and accessibility. Bottoms with more relief are more likely to hide prey so swimming speeds should be correspondingly slower. Crowned Cormorants *Phalacrocorax coronatus* foraging over sand swim faster than when foraging over rocks (means of 1.38 m/s and 0.33 m/s, respectively) (Wilson & Wilson 1988). Two prey-dependent processes are pertinent in determining bottom speeds. Firstly, more prey will be brought within the bird's sensory range per unit time as speed increases (Figure 2) and second, birds are more likely to miss a higher percentage of cryptic prey with increasing speed (Figure 2). These processes must be equated with the higher metabolic cost, and therefore decreased available search time, incurred with higher swimming speeds (Figure 2). In general, large, widely-spaced and easy-to-perceive prey should be searched for at higher speeds whereas small, dense, cryptic prey should be searched for slowly (cf. White-breasted Cormorants *Phalacrocorax carbo* foraging for prey with a mean mass of 212 g (Rand 1960) at a mean bottom speed of ca 1.7 m/s (Wilson & Wilson 1988) and Cape Cormorants foraging for prey with mean mass 1.5 g at a mean bottom speed of 0.3 m/s (Wilson & Wilson 1988)). Bottom speeds may also be slower when birds feed on non-mobile prey since the 'element of surprise' is less important. Four species of diving duck, Canvasback *Aythya valisineria*, Ringneck *Aythya collaris*, Scaup *Aythya affinis* and Redhead *Aythya americana*, have minimum bottom speeds of 0.02, 0.06, 0.42 and 0.02 m/s, respectively (calculated from data in Alexander & Hair 1980).

DEPTH. It has been proposed that larger bird species should be able to dive deeper (Stonehouse 1967) and this appears to be the case (Butler & Jones 1982, Piatt & Nettleship 1985, Prince & Harris 1988). Maximum diving depth in alcids and penguins varies allometrically with body mass (kg) according to: Max depth = $75.905 \text{ Mass}^{0.316}$ (Burger in press) and in penguins percentage time spent per metre depth = $[29.9 \text{ Mass}^{-0.888} - 12.5 \text{ Mass}^{-1.229} (\ln \text{ Depth})]$ (Wilson et al. 1990). It is unclear whether large masses enable an animal to dive deep by conferring advantages with respect to pressure tolerance per se or whether larger animals can dive deeply because body oxygen stores scale approximately isometrically as a function of body mass (Lasiewski & Calder 1971, Hudson & Jones 1986) while metabolic rate scales as a $\text{Mass}^{0.75}$ (Peters 1983) function so that larger animals have more time to go deeper (Burger in press). The situation is further complicated because birds have a large quantity of air in the feathers, air sacs and lungs (Butler & Woakes 1984, Stephenson et al. 1989) which reduces in volume with increasing depth. The upthrust, against which the bird must swim, correspondingly decreases which means that the bird expends less en-

ergy at deeper depths and can thus theoretically extend the dive duration (unpub. data). Conversely, the pressure-mediated decrease in air volume in the feathers results in reduced insulation which may necessitate an increase in metabolic rate to maintain body temperature. An increment in metabolic rate would increase oxygen consumption and decrease dive duration.

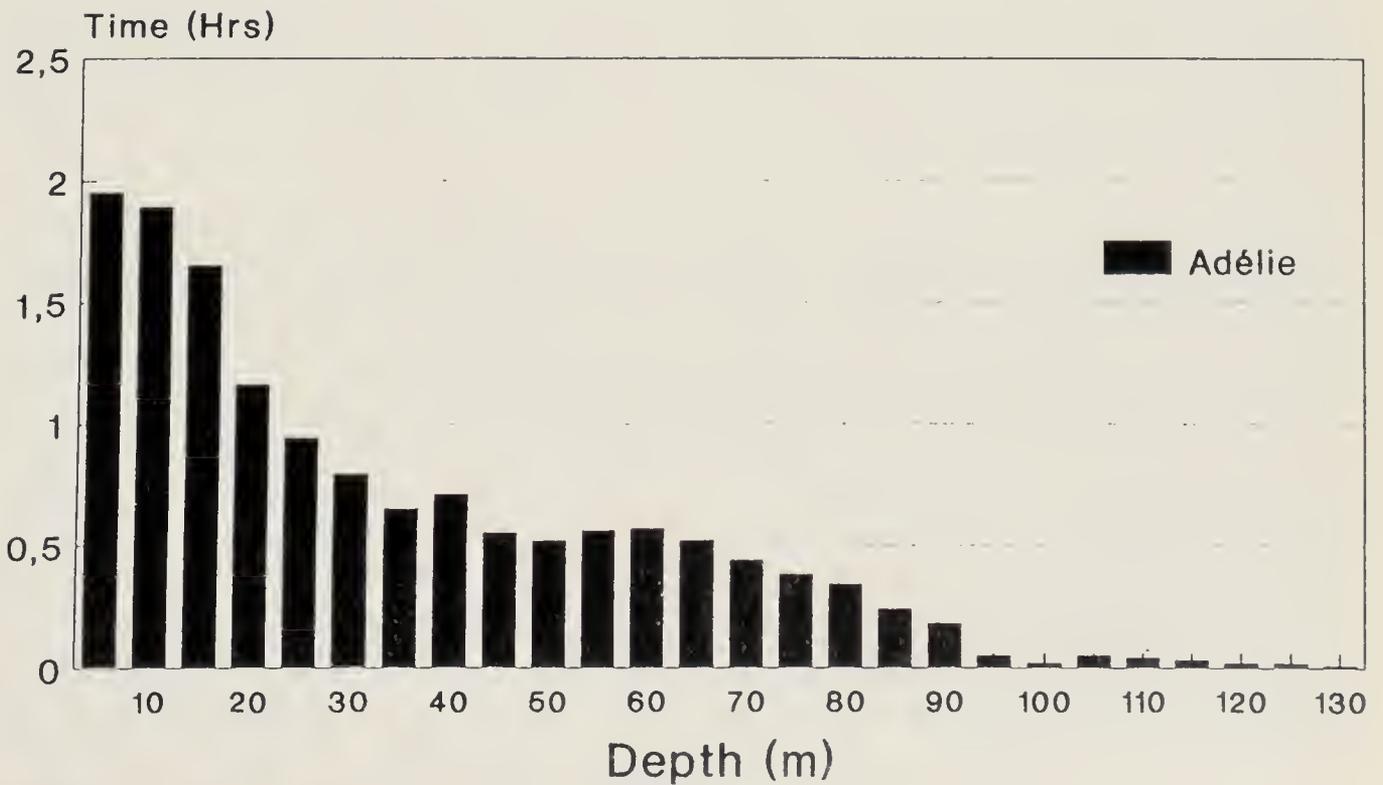
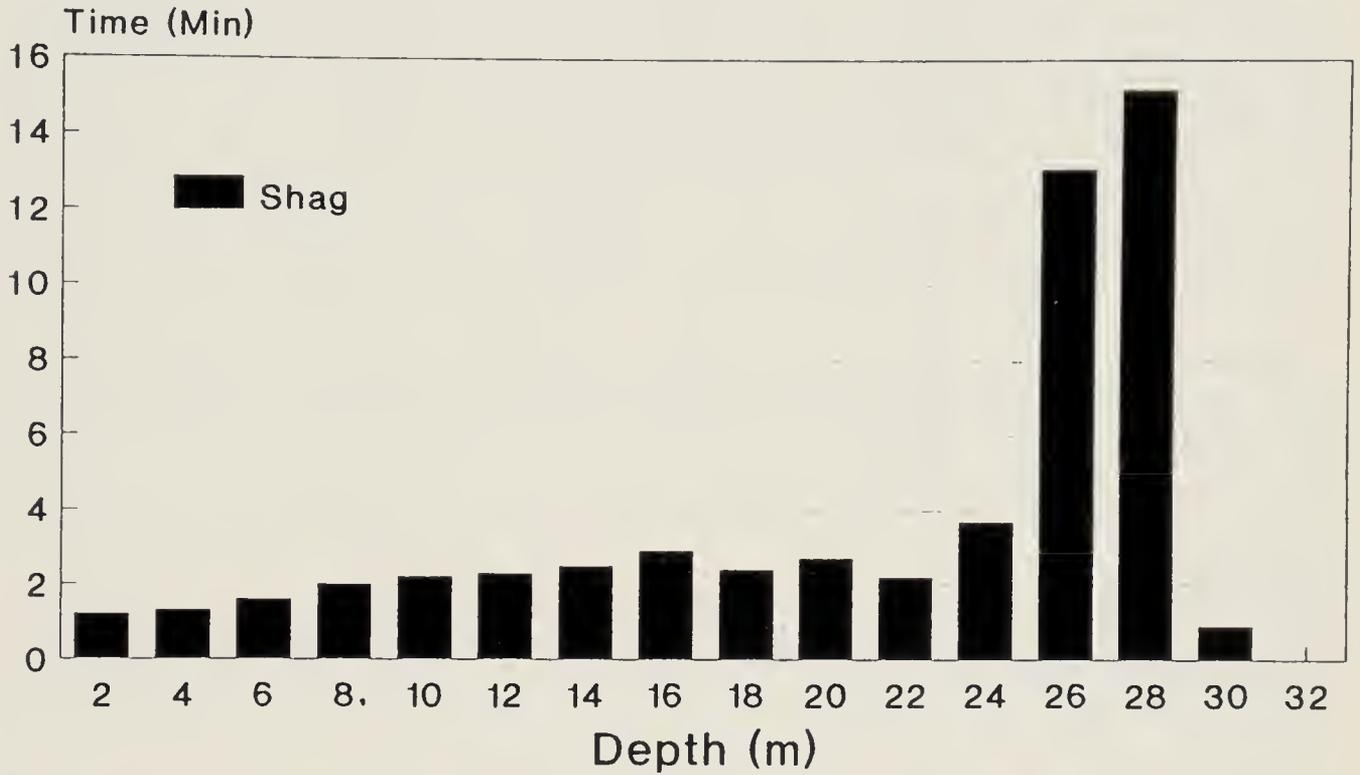


FIGURE 3 – Cumulative time-at-depth for (a) a benthic foraging seabird, the Shag *Phalacrocorax aristotelis* (modified from Wanless et al. in press) and (b) a pelagic foraging seabird, the Adélie Penguin (unpub. data).

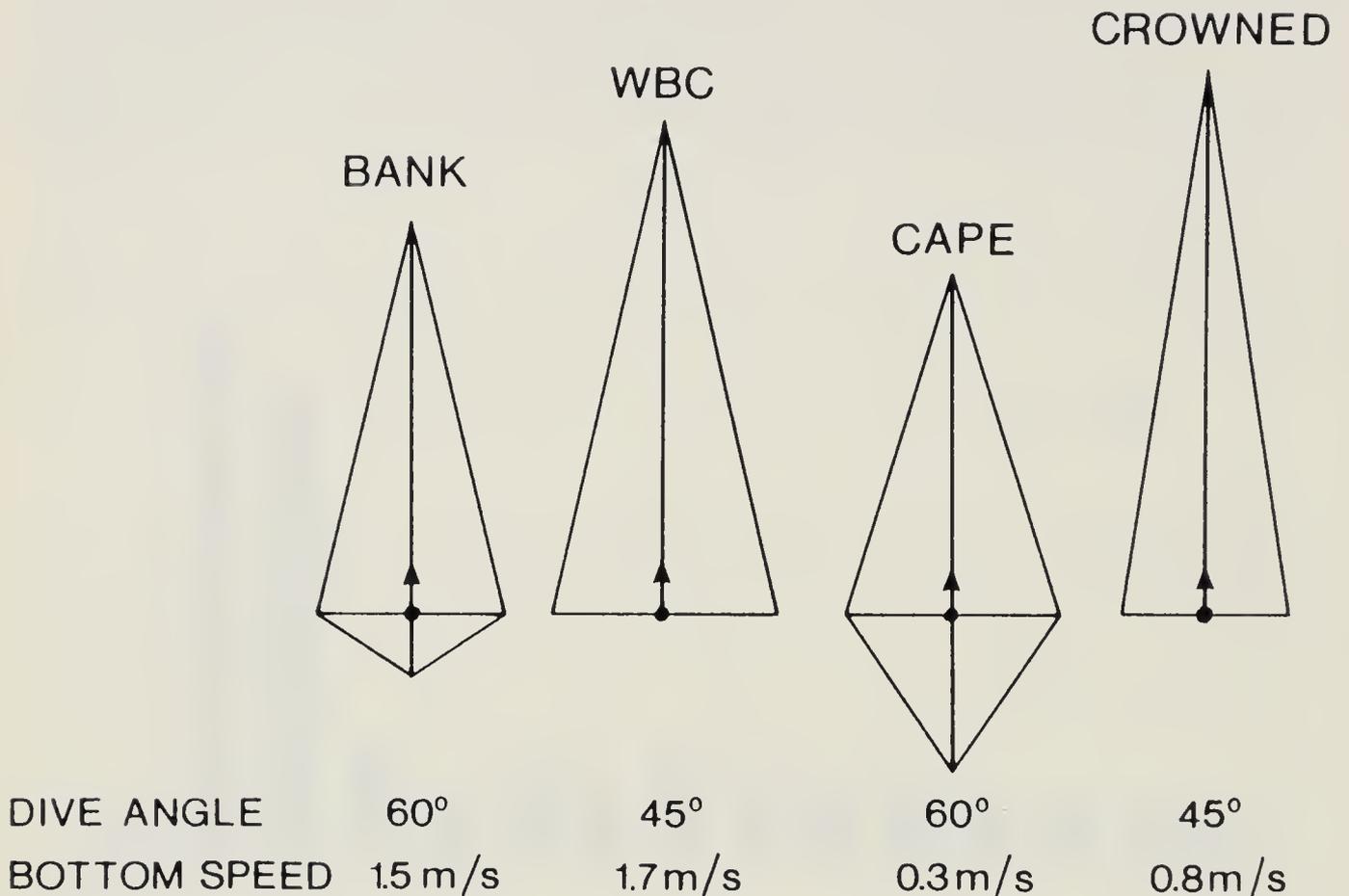


FIGURE 4 – Directionality during benthic foraging in four species of cormorant; Bank *Phalacrocorax neglectus*, White-breasted (WBC), Cape, and Crowned. The frequency distribution, expressed as a percentage, of post-dive positions of birds in relation to the pre-dive position (depicted by dots) and heading (arrows) is shown. Bird post-dive position was classified as either 'ahead of', 'behind' or 'to the side of' the start position and is represented by the length of the axes emanating from the central dots (unpub. data for a minimum of 31 dives from each species).

Overall, few birds dive regularly in excess of 100 m (Table 1). The distribution of cumulative time-at-depth depends on dive profiles. Bottom foragers (Figure 3a) generally have a constant time-at-depth down to the deepest part of the water column exploited where a large peak in time at depth occurs (Wilson et al. 1990, Wanless et al. in press). This peak corresponds to the cumulative bottom time while other values are accumulated during transit between the surface and the bottom. Pelagic-foraging divers (Figure 3b) are characterised by decreasing time spent at increasing depths. This presumably occurs as a result of bounce-diving behaviour where the distribution of depth maxima determines the form of the decrease since during any single dive the time spent between the surface and the deepest part of the dive is constant per unit depth interval (Wilson et al. 1990). This may, however, be modified by peaks at certain values (Burger & Powell 1989, Wilson et al. 1990) which probably stem from flat-bottomed dives at depths of particular interest. Occasionally, pelagic-foraging birds make single exceptional dives to much greater depths than those normally exploited (Burger in press) although why they do this is unclear.

HEADING. The direction the bird chooses to swim when underwater does not directly affect its energetic expenditure and therefore have a bearing on dive duration. However, heading is crucial in determining the likelihood of prey encounter since, in general, birds will not benefit by covering the same area twice although they should remain in the most profitable foraging areas (Smith 1974). There are almost no data on this aspect of diving behaviour. However, Wilson et al. (in press) have shown that African Penguins *Spheniscus demersus* stop the highly directive diving indicative of travelling when they reach certain areas. When foraging, these birds concentrate diving in these areas so that approximately half the time they are doubling back on their tracks, presumably searching a body of water parallel to their initial course (Wilson et al. in press). Data from four species of bottom-foraging cormorant show that between 48% and 77% of all dives terminate with birds surfacing in an area directly ahead of their initial dive position (Figure 4) indicating highly directional searching.

DURATION. Duration as a dive parameter is relevant in that the total energetic component of the dive, which determines the maximum dive duration, is the sum of the durations of particular activities multiplied by their energetic costs. Overall dive duration in birds has been reported as long as 18 min in Emperor Penguins *Aptenodytes forsteri* (Kooyman et al. 1971) although this is exceptional. Dives in excess of ca 2 min are common in most penguin species (Kooyman 1975, Trivelpiece et al. 1986, Davis et al. 1988), occur in some cormorants (Wanless in litt.) and also occur in auks (Bradstreet 1982, Wanless et al. 1988). Otherwise, most species appear to have dive durations of less than 1 min (Dewar 1924), although dive durations determined by visual observation are likely to be biased shorter due to difficulties in verifying long dives. Future work using bird-attached devices to species other than auks (Wanless et al. 1988), penguins (Trivelpiece et al. 1986) and cormorants (Wanless et al. unpub. data), will give a better idea of diving capacities in all bird families.

Dive duration also affects recovery duration which itself affects subsequent dive duration. Recovery duration may be very brief after short aerobic dives, but disproportionately prolonged following long anaerobic dives (Jones & Furilla 1987). Although birds generally appear to dive aerobically so that dive durations appear linearly related to recovery durations (e.g. Hobson & Sealy 1985, Cooper 1986, Wanless et al. 1988), after extended durations underwater it appears that dive durations are related to recovery durations by a power function (Ydenburg 1988, Wilson & Wilson 1988). When infrequently-encountered patchy prey can only be exploited during single dives, it may be more profitable for birds to engage in long anaerobic dives before the patch is lost (Ydenburg & Clark 1989, see also Burger in press). African Penguins, feeding on large fish schools which can be relocated after surfacing to breathe, have mean dive: recovery durations of 105 s and 19 s, respectively, whereas birds feeding on small schools which cannot be relocated after surfacing have mean dive: recovery durations of 147 s and 420 s, respectively (Wilson & Wilson 1990). Alternatively, birds exploiting a prey resource may dive anaerobically but maintain short inter-dive periods by accumulating lactic acid with each dive until they are obliged to stop (Kooyman 1989).

Many birds have increased dive durations when diving to greater depths (Dewar 1924). This is partly due to increased transit time, but is also because many species increase bottom time with increasing transit time (Wilson & Wilson 1988), presumably to maintain efficiency. As foraging depth increases, dive duration eventually stabilises at a particular value, because birds have reached their dive limit. Here, increases in

foraging depth result in a decrease in bottom time (A. Burger pers. comm.) which is presumably compensated by increased prey availability.

Dive duration is also influenced by water temperature (J. de Leeuw in litt.). When water temperature is low, heat loss is higher in diving birds necessitating increased metabolic rates (Butler & Stephenson 1987). This is likely to be exacerbated when birds dive deep (see above). This may force dive durations to be shorter because resultant energy expenditure quickly uses body oxygen stores or, when temperatures are particularly low, birds may be physiologically incapable of maintaining body temperature for long periods underwater. Tufted duck *Aythya fuligula* dive for shorter periods when water temperatures are lower (J. de Leeuw in litt.).

When underwater, diving birds show considerable variability in foraging parameters (swim speed, depth, duration, heading). This variability is a physiologically-tailored response by the bird to the environment so as to maximise hunting efficiency. Optimal hunting solutions are made considerably more complex by the interdependent nature of the foraging parameters. Our understanding of the optimal hunting strategy is, perhaps in their field more than any other, also dependent on a comprehensive understanding of the bird's diving physiology. Future studies examining why birds behave as they do when foraging underwater will have to consider both ecological and physiological aspects as important.

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MECHANICS OF UNDERWATER SWIMMING IN FOOT-PROPELLED DIVING BIRDS

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ABSTRACT. Data on buoyancy, hydrodynamic drag, and acceleration during swimming strokes are used to develop a biomechanical model of underwater locomotion in diving ducks (*Aythya* spp.). Results indicate that buoyancy is far more important than drag in determining energy costs of diving. Inertial (accelerational) effects substantially increase costs of descent. Power requirements for descent are at least three times higher than for bottom foraging, and this difference increases with decreasing body size. Maximum changes in body fat affect dive costs only slightly, and can probably be offset by adjusting air volumes in the respiratory system and plumage. Effects of pressure with depth on buoyancy and dive costs are substantial and depend on body size. The most critical need in studies of underwater locomotion in birds is devising means for measuring respiratory and plumage air volumes during unrestrained dives. Foot-propelled divers exhibit diverse variations in submergence mode, buoyancy control, stroke patterns, and use of wings. This variation limits use of a general biomechanical model for all species.

Keywords: Biomechanics, locomotion, kinematics, hydrodynamic drag, buoyancy, accelerational swimming, diving.

INTRODUCTION

Several workers have investigated the biomechanics of wing-propelled diving in penguins (Clark & Bemis 1979, Hui 1988), but only recently has underwater swimming in foot-propelled divers been analyzed (Stephenson et al. 1989, Lovvorn et al. 1990). Major determinants of the energy costs of foot-propelled diving are hydrodynamic drag, buoyancy, and inertial work in unsteady (accelerational) stroking. In the diving duck genus *Aythya*, body drag, buoyancy, and patterns of acceleration during strokes are predictable from body mass (Lovvorn et al. 1990). However, the applicability of these relations to other species has not been explored. Here, I review a biomechanical model of locomotion in *Aythya*, and its implications for measuring energy costs and estimating aerobic efficiency of diving. I then identify locomotor variations in other foot-propelled divers that limit the model's generality. Finally, I discuss several lines of investigation that might reveal basic constraints on strategies of underwater locomotion in birds.

MODEL OF LOCOMOTION IN AYTHYA

Lovvorn et al. (1990) developed a model for underwater locomotion based on data for Canvasbacks *Aythya valisineria*, Redheads *A. americana*, and Lesser Scaup *A. affinis*. These species spring upward from the water surface before submerging, stroke their feet synchronously during descent and at the bottom, keep their wings appressed to the body throughout the dive, and ascend passively by means of buoyancy.

Hydrodynamic drag of ducks frozen in a diving posture was measured in a tow tank (Lovvorn et al. 1990). Buoyancy was calculated as the difference between body weight and the weight of water displaced by restrained ducks submerged in a water-filled pipe. Ducks descending in a tank 2 m deep were filmed at 100 frames s^{-1} to determine linear displacement at 0.01s intervals during a stroke cycle (including power and recovery phases). Work during these intervals was calculated by multiplying drag and buoyancy by displacement, and then adding inertial work done in accelerating the body and the added mass of entrained water. Work during all intervals was then integrated over the entire stroke. Similar calculations were made for strokes by birds at the bottom. Counts of strokes (from video films) required to reach the bottom and remain there allowed estimates of total work during dives.

BODY DRAG

The allometric equation relating drag coefficient C_D to Reynolds number Re in *Aythya* yielded far less accurate estimates of drag than a second-order polynomial regression relating drag to body mass and speed ($r^2 = 0.95$) (Lovvorn et al. 1990). Foot-propelled diving birds span a relatively small size range (Table 1), so allometric $C_D - Re$ equations may be less suitable than regressions of drag versus mass and speed for foot-propelled divers in general. Values of underwater drag for frozen Humboldt Penguins *Spheniscus humboldti* (body mass about 3.78 kg) and for a stuffed Common Murre *Uria aalge* (about 0.89 kg) resemble drag of *Aythya* at the same speeds (Eliassen 1960, Hui 1988). However, the penguins are much larger, so their mass-specific drag is lower than that of diving ducks or murre.

BUOYANCY

Most past studies of underwater swimming have focused on hydrodynamic drag as the primary determinant of locomotor cost. However, if such studies are to be relevant to a natural context of vertical diving, they must consider buoyancy. Factors potentially affecting buoyancy include molt, body mass or composition, pressure with depth, and variations in respiratory or plumage air volumes. Comparison of diving ducks in late summer that were flightless versus those that had complete remiges showed that wing molt has no effect on body volume or buoyancy. However, body volumes relative to mass are higher in winter than summer, probably because a thicker plumage air layer is maintained during winter for thermal insulation.

In scaup, maximum gain of body lipid from 35 to 190 g increases energy costs of descent more through inertial effects of higher mass and added mass of entrained water (82.8% of change) than through greater work against drag (12.0%) or buoyancy (5.2%). Costs of foraging at the bottom are 20% lower in the fatter birds, because increased inertial resistance to the buoyant force is greater than the increase in buoyancy. Maximum changes in body lipid and associated hypertrophied muscle increase overall costs of diving to a depth of 2 m by only 2%. Such effects can probably be offset by altering respiratory and plumage air volumes (+15 mL for 155 g lipid increase) or relative time spent at the bottom. Fresh adipose tissue has a higher buoyancy than muscle (0.52 versus -0.69 $N L^{-1}$), but both have much lower buoyancy than air (9.79 $N L^{-1}$ for vapor-saturated air at 35°C). Thus small changes in air volume can compensate for relatively large changes in the volume or composition of tissues.

TABLE 1 – Locomotor types in foot-propelled diving birds.

Submergence	Descent	At bottom	Ascent	Foot stroke	Genera
Level; sink	Feet only	Feet only	Passive or feet only	Synchronous	<i>Gavia</i> ^{a,b}
"	"	"	Feet only	Alternate	<i>Anhinga</i> ^{c,d}
"	"	"	No data	No data	<i>Biziura</i> ^e
Spring; level; sink	Feet only	Feet only	Passive	Synchronous	<i>Aechmophorus</i> ^{d,f} <i>Podiceps</i> ^a <i>Podilymbus</i> ^a <i>Tachybaptus</i> ^d
Spring; level	Feet only	Feet only	Passive	Synchronous	<i>Phalacrocorax</i> ^{a,g} <i>Mergus</i> ^{d,i}
Spring	Feet only	Feet only	Passive	Synchronous	<i>Aythya</i> ^{i,k} <i>Bucephala</i> ^{h,i} <i>Oxyura</i> ^{e,j}
Spring; wing-lunge with feet	Feet only; feet with alula out; feet and stroking alula	Feet only; feet with alula out; feet and stroking alula	Passive	Synchronous	<i>Melanitta</i> ^{l,l}
Wing-lunge with feet	Feet and stroking alula	Feet with alula out	Passive	Alternate	<i>Somateria</i> ^{d,h}
"	"	No data	No data	No data	<i>Histrionicus</i> ^{d,h}
"	Feet with alula out	Feet with alula out	Passive	Alternate	<i>Tachyeres</i> ^m
Wing-lunge	Wings only	Wings & feet	Passive	Variable	<i>Cephus</i> ^{n,o}
"	"	No data	Wings	No data	<i>Clangula</i> ^p

^a Townsend (1924); ^b J. Barr, underwater observations of tame birds; ^c Owre (1967:61); ^d Townsend (1909); ^e Frith (1967); ^f Nuechterlein and Buitron (1989); ^g Ross (1976); ^h Humphrey (1958); ⁱ Brooks (1945); ^j Tome and Wrubleski (1988); ^k Lovvorn et al. (1990); ^l Humphrey (1957); ^m Livezey and Humphrey (1984); ⁿ Duffy et al. (1987).; ^o J. R. Lovvorn, unpubl. data. ^p Snell (1985).

Artificial compression of the plumage indicates that reduction of the plumage air layer by ptilosuppression reduces buoyancy by <6% (Stephenson et al. 1989). Plumage air volume in Lesser Scaup is 325 to 360 mL of which 6% is about 20 mL. Tufted Ducks *Aythya fuligula* habitually diving 6 m versus 0.6 m for food decreased their respiratory volumes by about 26 mL, while increasing non-pulmonary oxygen storage (mainly in blood) by a compensatory amount (Stephenson, Turner & Butler 1989). Tufted Ducks use only about 30% of oxygen stored in their bodies during voluntary dives to 1.7 m (Woakes & Butler 1983). Given the size and flexibility of oxygen stores, most buoyancy variations resulting from molt or changes in body mass or composition can probably be countered by adjusting air volumes. This finding contrasts with the energetics of flight, which are strongly affected by body mass changes.

Reduced buoyancy from compression of air spaces with depth lowers costs of bottom foraging in scaup by 24% at 1.2 m and 36% at 2 m. Plumage air volume decreases with increasing body mass, and body tissues are essentially incompressible relative to air. Therefore, buoyancy decreases faster with pressure in smaller birds, and they become negatively buoyant at shallower depths (about 43 m for Oldsquaws *Clangula hyemalis*). Ducks such as eiders (*Somateria* spp.) weighing over 1200 g and diving to less than 60 m probably never become negatively buoyant.

Some penguins dive upon inspiration (Kooyman et al. 1971), but most other species studied such as cormorants and ducks dive upon expiration (Ross 1976, Butler & Woakes 1979, Tome & Wrubleski 1988). Small changes in air volume have large effects on buoyancy, but to date no one has measured respiratory or plumage air volumes in freely diving birds. Devising means for making such measurements is a critical need in studies of the locomotor energetics of diving.

ACCELERATION

The degree of acceleration and deceleration during a stroke increases with decreasing body size (decreasing inertia) among species of *Aythya*. The power phase lasts 66-70% of stroke duration, and the ducks accelerate for the first 84% of this phase (Lovvorn et al. 1990). Stroke acceleration patterns have not been described for other foot-propelled divers, but probably vary with body size, buoyancy, and alternate versus synchronous stroking.

UNSTEADINESS, COSTS OF DIVING, AND AEROBIC EFFICIENCY

During the power phase in *Aythya*, work against drag is 10-12%, work against buoyancy 36-38%, and inertial work in acceleration 49-54% of total mechanical work done (Lovvorn et al. 1990). Costs of descent based on this unsteady model are 47-75% higher than estimated by a steady model including only work against drag and buoyancy at constant speed (e.g. Stephenson et al. 1989). Effects of accelerational stroking on descent costs increase as body size decreases from Canvasbacks to Lesser Scaup.

According to the unsteady model (Lovvorn et al. 1990), mechanical energy costs of descent are about three times the costs of staying at the bottom. The relative difference between costs of descent and bottom phases increases with decreasing body size. Because of large differences between mechanical costs of descent and bottom phases in *Aythya*, "costs of diving" measured as oxygen consumption between dives are strongly affected by relative times spent descending and at the bottom. Estimates of the aerobic efficiency of locomotion during dives (mechanical power output/oxygen consumption rate) must consider these dive-phase differences in mechanical power required.

DIVERSITY OF LOCOMOTOR TYPES

Foot-propelled divers exhibit a variety of methods for overcoming buoyancy (Table 1). Loons (*Gavia*), anhingas (*Anhinga*), Musk Ducks *Biziura lobata*, and grebes

(*Aechmophorus*, *Podiceps*, *Podilymbus*, *Tachybaptus*) reduce buoyancy by lowering air-sac volumes, and can sink without apparent effort or dive from a level position without first springing upward. Diving ducks of the genera *Aythya*, *Bucephala*, and *Oxyura* spring upward from the water surface to gain momentum for descent; grebes (*Aechmophorus*), cormorants (*Phalacrocorax*), mergansers (*Mergus*), and scoters (*Melanitta*) commonly do this also. Several sea ducks (*Melanitta*, *Somateria*, *Histrionicus*) and steamer ducks (*Tachyeres*) submerge by pulling themselves under with their wings ("wing-lunge" in Table 1) while thrusting with the feet. Guillemots (*Cepphus*) and Oldsquaws, the latter included in Table 1 because all other diving ducks are foot-propelled, submerge by wing action alone.

During descent, several species extend the alulae and use them for stabilization or stroke them to supplement propulsion by the feet (Table 1). Oldsquaws reportedly descend by wing propulsion only. These patterns during descent generally continue at the bottom (Table 1), except when extended alulae are no longer stroked and are held rigid to oppose buoyancy by increasing vertical drag. No data exist on locomotion of Oldsquaws at the bottom, but guillemots (*Cepphus*) begin using feet as well as wings in complex combinations. Foot-stroking is synchronous in most species, although observations in aquaria have revealed alternate stroking by large-bodied eiders *Somateria mollissima* and steamer ducks *Tachyeres brachypterus* (Table 1).

The relation between body mass and buoyancy of restrained birds does not differ among dabbling ducks or most diving ducks ranging in size from Buffleheads *Bucephala albeola*, (mean body mass = 0.34 kg) to Black Ducks *Anas rubripes*, ($x = 1.34$ kg) (Lovvorn and Jones, unpubl. data). However, Common Eiders *Somateria mollissima*, ($x = 1.56$ kg) and White-winged Scoters *Melanitta fuscus*, ($x = 1.26$ kg) have higher buoyancies (28 and 22%, respectively) than predicted by the relation for other ducks. Double-crested Cormorants *Phalacrocorax auritus* ($x = 2.32$ kg) have 36% lower buoyancies than predicted by the duck equation. Buoyancies of Rhinoceros Auklets *Cerorhinca monocerata* ($x = 0.49$ kg) are the same as for ducks of similar mass.

Some of these locomotor variations will affect the energetics of underwater swimming. The mechanics of submerging by various means have not been investigated in any species, but probably influence momentum and acceleration patterns early in descent. Extreme manipulation of air-sac volume in species like loons and grebes makes measuring buoyancy difficult and estimates unreliable. Effects of stroking alulae or wings on acceleration patterns must be measured to calculate inertial work. Enhancement of vertical drag by extended alulae or wings will lower costs of staying at the bottom. Alternate versus synchronous stroking by a few species during descent (see below) have as yet unquantified effects on stroke acceleration patterns and inertial work.

ALTERNATE VERSUS SYNCHRONOUS STROKING

Alternate stroking while submerged is rare among foot-propelled divers, but does occur in several species (Table 1). Why do most diving birds stroke their feet synchronously when underwater, but almost invariably stroke alternately when swimming

at the surface? This question is not trivial, given the strong effect of stroke acceleration patterns on locomotor costs.

In diving ducks (*Aythya*), costs of descent calculated as work against drag and buoyancy at constant speed are far less than when augmented by inertial work during accelerational stroking (see above). In ducks there is no glide phase between strokes when drag is reduced by suspension of limb movements. Consequently, synchronous stroking merely leads to greater acceleration and thus inertial work than does alternate stroking at the same average speed. Because body drag increases rapidly with speed (Stephenson et al. 1989, Lovvorn et al. 1990), synchronous stroking also incurs greater drag costs because more time during a stroke is spent at higher speeds. Thus, if body drag, buoyancy, and acceleration are the only significant factors, alternate rather than synchronous stroking should be used during descent as well as at the surface. Why is this pattern not usually observed?

The combined resistance of drag and buoyancy during descent is at least 4-7 times higher than drag during surface swimming (Stephenson et al. 1989). Therefore, the force exerted by each foot to move the same distance per stroke cycle (including alternate strokes by both feet) must also be greater during descent. If the feet are stroked alternately with increased force or frequency, pitching and yawing probably increase. Such oscillations substantially enhance hydrodynamic drag (Blake 1983), perhaps enough to offset inertial benefits of alternate stroking. Resolving this question will require kinematic data and drag measurements during both descent and surface swimming, as well as measurement of pitch, yaw, and associated drag from alternate versus synchronous strokes.

FOOT-PROPELLED VERSUS WING-PROPELLED DIVING

In general, foot-propelled divers are found in inshore or inland habitats, whereas wing-propelled divers are restricted to open marine areas. There are exceptions. Oldsquaws, which use mostly their wings underwater (Table 1), are often found inland but dive as deeply as 60 m (Schorger 1947) and prefer large water bodies. Pigeon Guillemots *Cephus columba*, which unlike other alcids intersperse propulsion by wings and feet when at the bottom, also differ from other alcids in being mainly inshore benthic feeders. Wing-propelled diving in Oldsquaws apparently does not compromise their flying ability relative to other diving ducks, but still no other inland divers have adopted wing propulsion as principal means of underwater swimming. Analysis of wing structure and performance in foot-propelled versus wing-propelled divers (c.f., Pennycuik 1987a,b) might reveal important trade-offs in wing adaptations for aerial versus underwater flight.

Generation of thrust on both upstroke and downstroke in lift-based wing propulsion (Hui 1988) might reduce inertial work relative to more unsteady foot propulsion with high drag during recovery. However, streamlining of tarsometatarsi (in Eared Grebes *Podiceps nigricollis* width is only 30% of depth) undoubtedly reduces recovery-stroke drag substantially. Comparing locomotor efficiencies of penguins and alcids versus those of highly adapted foot-propelled divers such as loons and grebes would reveal whether wing propulsion is inherently more efficient than foot propulsion during sustained swimming underwater.

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PHYSIOLOGY OF DIVING IN DUCKS AND OTHER AQUATIC BIRDS (EXCLUDING PENGUINS)

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ABSTRACT. Although ducks are not the most accomplished of diving birds, they are, with the exception of the penguins, the most widely studied from the physiological point of view. They do not normally remain submerged for excessively long periods when feeding but, because of their positive buoyancy, they have to work hard to become submerged and to remain at the bottom of the water column. In fact, mean oxygen uptake of Tufted Ducks at a mean dive duration of 15 s is not significantly different from that when they are swimming at maximum sustainable velocity at the surface. It has been suggested that the cardiovascular response to normal feeding dives in ducks is a balance between the classical, Scholander-type response to breath-hold diving (bradycardia, selective peripheral vasoconstriction) and the exercise response (tachycardia, peripheral vasodilatation), with the bias towards the latter. Details of this response are described and deviations from it, as seen when the animals have to swim long horizontal distances under water or when they are temporarily unable to surface, will be discussed. Seasonal metabolic requirements are also considered.

Keywords: Diving, ducks, behaviour, aerobic metabolism, cardiovascular.

INTRODUCTION

Most of the earliest work on the physiology of diving in air breathing vertebrates was performed on birds and the most common bird used was the European domestic duck (Andersen 1966). More recently, the wild form of the Domestic Duck, the Mallard *Anas platyrhynchos*, has been used (Butler & Jones 1968), but until the use of radio-telemetry, none of these studies were performed on freely diving birds.

The first account of physiological adjustments during free diving in ducks was that of Butler & Woakes (1976a) who found that, unlike the situation during enforced submersion, there is no maintained reduction in heart rate (bradycardia) in the Pochard *Aythya ferina* during voluntary diving. The birds performed a number of dives in relatively quick succession (bout) and several seconds before the first dive of a bout, heart and respiratory frequency increased. Just before the nostrils were submerged (Butler & Woakes 1982a) and before ventilation ceased (Butler & Woakes 1976b), there was a dramatic reduction in heart rate, which then increased over the next few seconds to reach a relatively steady rate. This was close to that recorded when the bird was swimming on the surface (i.e. before the pre-dive tachycardia). Heart rate began to increase before the bird reached the surface (Butler & Woakes 1982a) and remained well above the resting level until the next dive in the bout (Figure 1).

This lack of bradycardia during voluntary diving has since been shown to be the case in other species of bird, e.g. Tufted Duck *A. fuligula* (Butler & Woakes 1979), Double Crested Cormorant *Phalacrocorax aurita* (Kanwisher et al. 1981), Redhead *A. americana* (Furilla & Jones 1986).

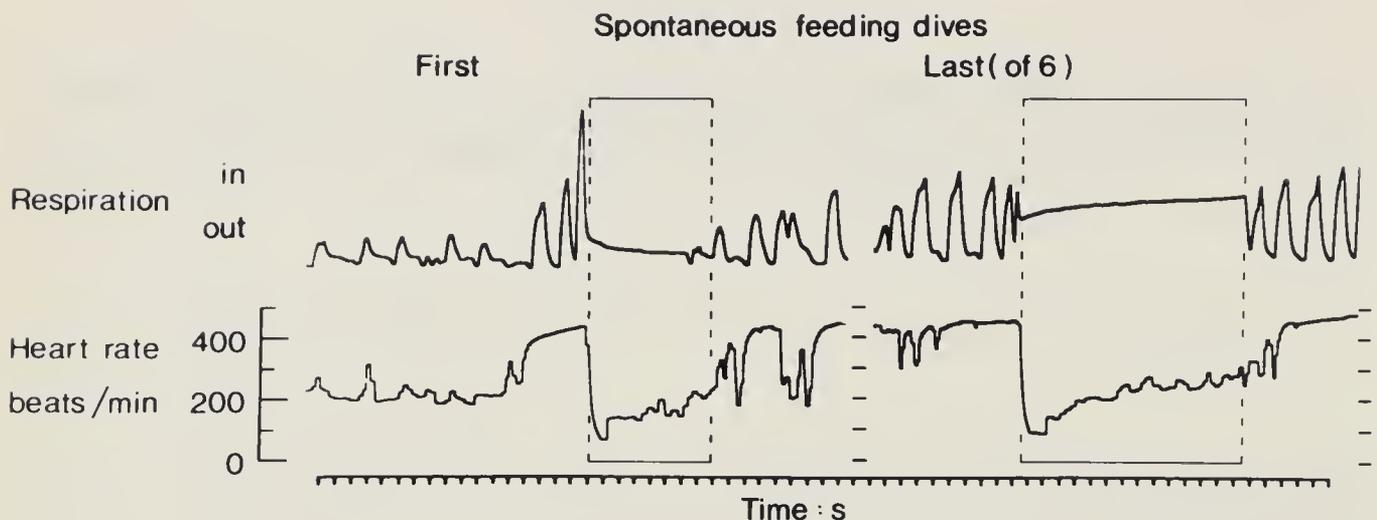


FIGURE 1 – Traces showing heart rate and respiratory frequency associated with the first and last spontaneous dives of a bout performed by a male Tufted Duck. In each case the period of submersion is indicated by the dashed vertical line joined by horizontal bars (From Butler 1979).

The earlier studies, using restrained birds that were forcibly submerged, demonstrated that the clear bradycardia is related to other dramatic cardiovascular and metabolic adjustments. There is vasoconstriction and large reductions in blood flow in virtually all vascular beds, except the brain, heart and adrenal glands (Jones et al. 1979). Blood pressure is maintained as a result of a large reduction in cardiac output, which is virtually in direct proportion to the fall in heart rate (Jones & Holeton 1972). These profound cardiovascular adjustments mean that only the oxygen-dependent tissues, CNS and heart, (plus the adrenal glands) are perfused and, therefore, supplied with oxygen, the rest of the body reduces its metabolism and/or metabolises anaerobically, producing excess amounts of lactic acid (Scholander 1942, Pickwell 1968).

The bradycardia is the typical element of these cardiovascular and metabolic adjustments to submersion asphyxia and is often taken as an indicator of the remainder of the response taking place (Blix & Folkow 1983). The total oxygen conserving response, described above, has been termed the classical response to submersion (Butler 1982). The question is, to what extent does this response occur during natural submersion in ducks and other (volant), diving birds?

BEHAVIOUR

Before looking at the physiology of diving in birds, it is perhaps worth spending a short time discussing their behaviour. For many birds which feed on benthic organisms, dive duration is related to the depth of the water (Dewar 1926), at least to a depth of 4m (Draulans 1982). At a depth of 2m, Tufted Ducks, Pochards, and the White-headed Duck *Oxyura leucocephala*, dive, on average, for 20 - 25 s (Butler & Stephenson 1987) with a maximum duration of 45 s (Stephenson et al. 1986). A number of birds such as Grebes, Divers, Cormorants and a range of Auks are, to a greater or lesser extent, active predators of fish and remain submerged for an average of 20 - 70 s, with the Guillemot *Uria aalge* having a reported maximum dive duration of 202 s (Wanless et al. 1988) and the Imperial Cormorant (Blue-eyed Shag) *P. atriceps* of

312 s (Naito et al. 1991). The latter species has been monitored diving to a maximum depth of 116 m, whereas other birds have been trapped in nets at 180 m (Guillemots), 120 m (Razorbills *Alca torda*) and 60 m (Great Northern Diver *Gavia immer*) (Schorger 1947, Piatt & Nettleship 1985). These dive durations and depths compare very favourably with those of the smaller penguins (Butler 1990). Unfortunately, physiological studies have only been performed, so far, on species of ducks.

AEROBIC METABOLISM DURING DIVING

Mean oxygen uptake at mean dive duration has been estimated for freely diving Tufted Ducks (Woakes & Butler 1983). Oxygen consumption was measured between dives by way of an open-circuit respirometer and a fast-responding mass spectrometer. A linear multiple regression analysis was performed between dive duration, the succeeding duration at the surface and oxygen uptake during the surface period. The regression coefficients represent the mean oxygen uptake at mean dive duration and at mean duration at the surface. At a mean dive duration of 14.4 s (water temperature 13.5°C), mean oxygen uptake (V_{O_2} , STPD) was 57 ml kg⁻¹ min⁻¹ and not significantly different from the value (63 ml kg⁻¹ min⁻¹) obtained from the same ducks swimming at maximum sustainable speed on the surface. These values are some 3.5 - 3.8 times resting oxygen consumption, respectively, and indicate that, rather than aerobic metabolism being reduced during diving in ducks, feeding under water is, in energetic terms, a very costly business for these animals.

On the basis of the usable oxygen stores in the Tufted Duck (Keijer & Butler 1982), this species should be able to remain submerged and metabolise aerobically at the level given above for approximately 50 s. This is some 2.5 times longer than the preferred dive duration of these animals on a 1.9 - 2.8 m deep pond (Stephenson et al. 1986), and would suggest that they metabolise completely aerobically during most voluntary dives, using the oxygen stored in the body and replacing it upon surfacing. It could be, however, that oxygen consumption actually decreases as dive duration progresses beyond 15 s (Bevan et al. 1990). Certainly, observations on individual ducks indicate that mean oxygen consumption at mean dive duration is lower in those that perform longer dives (Figure 2). This could result from reduced buoyancy as the dive progresses, [in those birds that perform longer dives it could be the result of reduced volume of the respiratory system (Stephenson et al. 1989 a, b)] and/or it could indicate that aerobic metabolism declines as a dive proceeds with, perhaps, increasing anaerobiosis. This latter suggestion would imply associated cardiovascular adjustments.

As the energetic cost of feeding under water is so high for aquatic birds such as Tufted Ducks, an important question is what happens in winter when they are on cold water? When at rest on water under winter conditions (air temperature 6°C, water temperature 7.5°C), oxygen consumption in Tufted Ducks is twice that under summer conditions (26°C and 23°C respectively), and deep body temperatures are similar. However, mean oxygen consumptions at mean dive durations are not significantly different under the two conditions (Bevan & Butler 1989), whereas mean oxygen consumption at mean duration at the surface is some 50% higher under winter conditions. Deep body temperature is a full 1°C lower after a bout of diving in winter conditions compared with that at summer temperatures (Figure 3). It would appear that while

actually feeding under water the "wasted" heat from locomotor activity is insufficient to maintain core temperature but the ducks do not enhance metabolic heat production during this period. On the other hand, while at the surface between dives, aerobic metabolism is higher during winter, but is still insufficient to prevent a reduction in body temperature over a complete bout of diving. The outcome is that overall, feeding in winter is metabolically more expensive (approximately 40% in the present study) for Tufted Ducks than that in summer, but not as great as might be expected from the elevation of oxygen uptake seen in ducks resting on water in winter conditions.

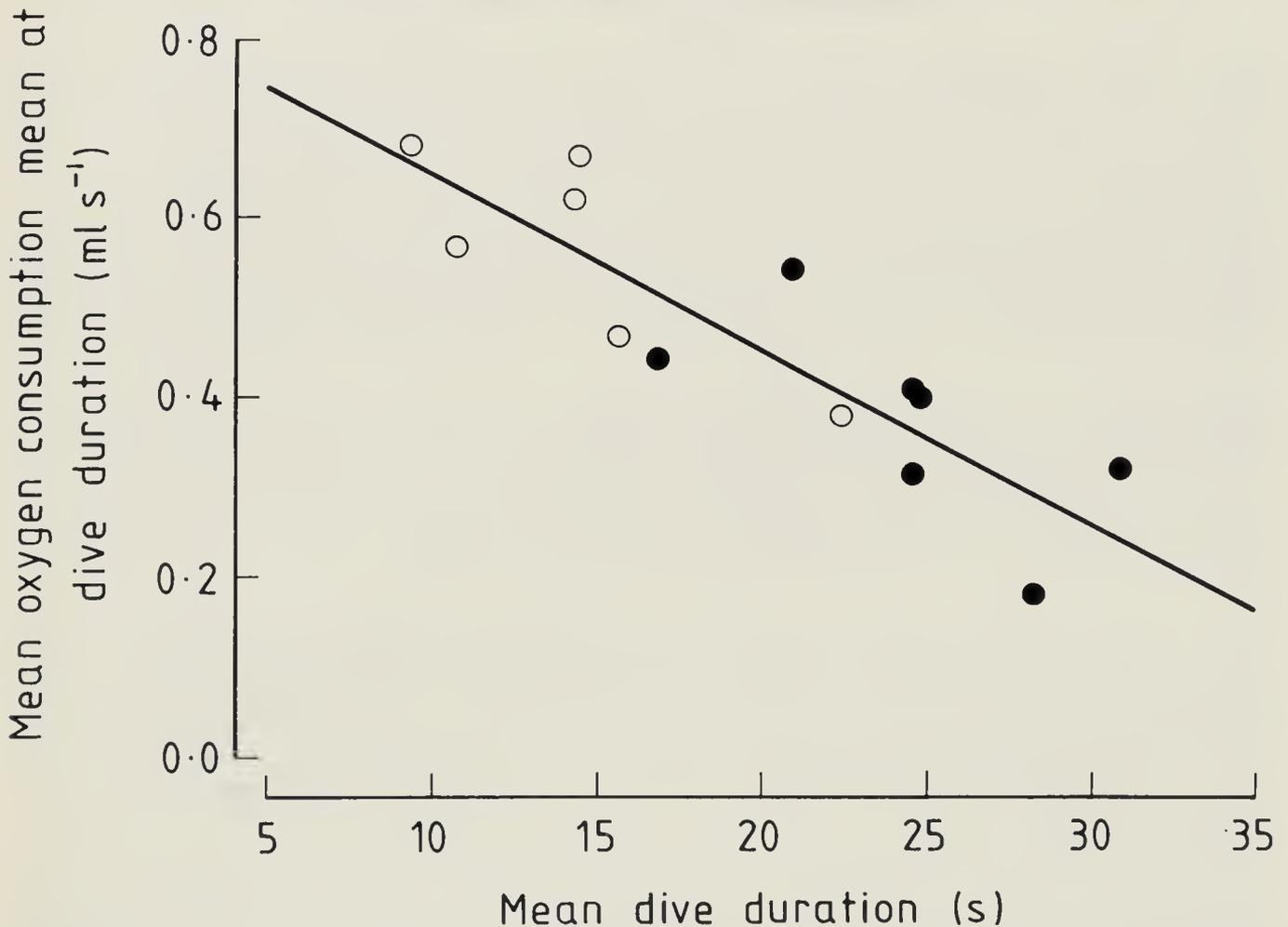


FIGURE 2 – The relationship between mean oxygen consumption at mean dive duration and mean dive duration from individual Tufted Ducks. o, data from 6 ducks diving freely in a tank 1.7m deep (Woakes & Butler 1983). •, data from 7 ducks trained to dive for different durations in a shallow (0.6m) tank (Bevan et al. 1990). The regression line through all of these data points is described by the equation $y = 0.838 - 0.019x$, $r^2 = 0.87$.

CARDIOVASCULAR ADJUSTMENTS AND THEIR CONTROL

With oxygen consumption during dives of approximately 15 s duration being similar to that at maximum sustained swimming speed, similar cardiovascular adjustments might also be expected. However, Woakes & Butler (1983) discovered that mean heart rate just before surfacing from dives of approximately 15 s duration is significantly lower than that recorded from the same animals when they are swimming at the surface and consuming oxygen at the same level (Figure 4). Assuming that heart rate is an indicator of the degree of peripheral vasoconstriction (and thus, of anaerobic metabolism), it has been suggested (Butler 1982) that during most dives, perfusion (and hence aerobic metabolism) of the active muscles (heart, legs) and of the

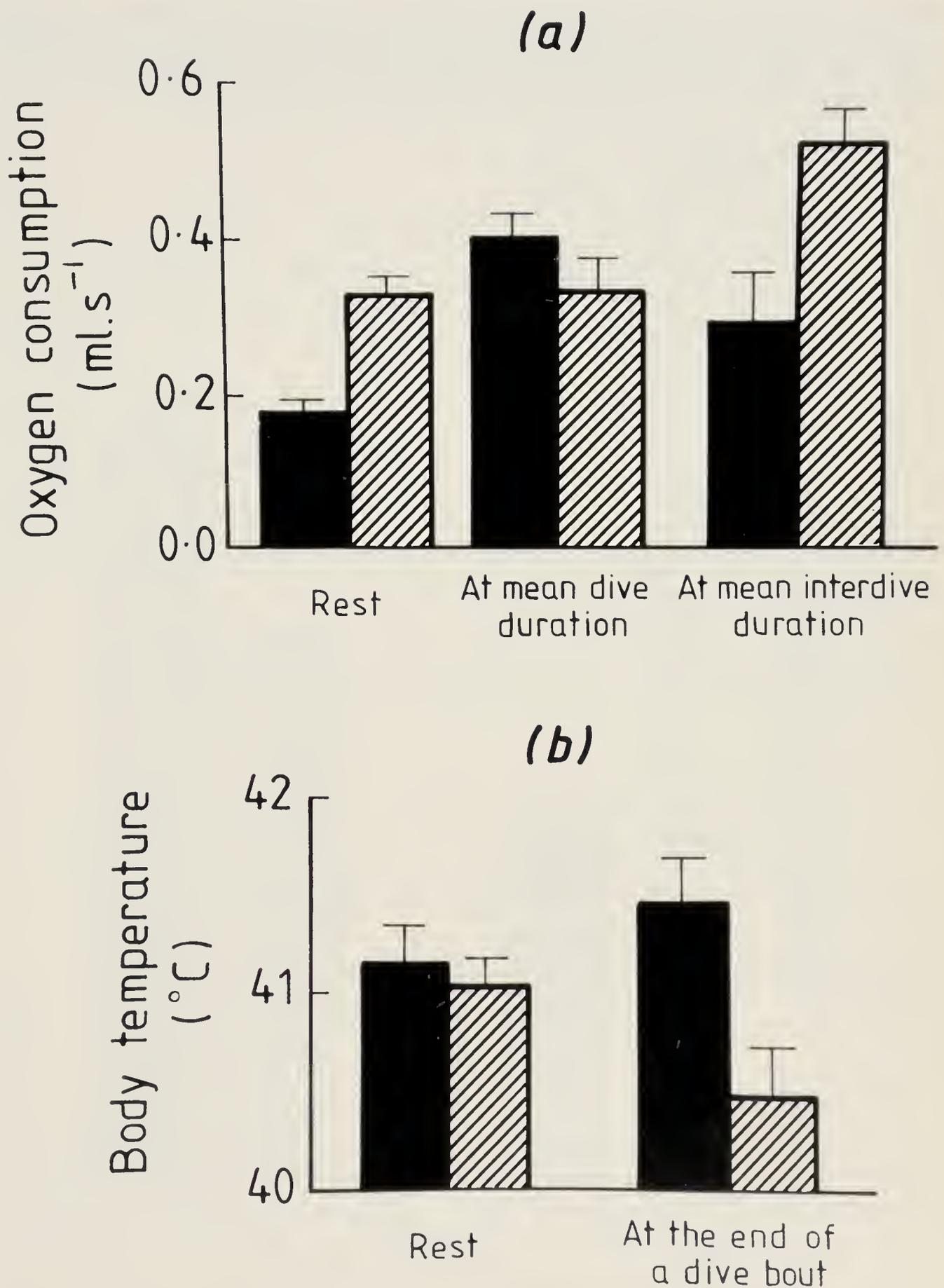


FIGURE 3 – (a) Histogram showing mean oxygen uptake (+ S.E.) in Tufted Ducks at rest, at mean dive duration and at mean interdiving duration. The birds were acclimated to summer (air temperature 26°C, water temperature 23°C - solid columns) or winter (air temperature 6°C, water temperature 7.5°C - hatched columns) conditions.

(b) Histogram showing mean deep body temperature (+ S.E.) in Tufted Ducks at rest and at the end of a bout of dives. The birds were acclimated to summer (solid columns) or winter (hatched columns) conditions - see above. (From R.M. Bevan & P.J. Butler unpubl.)

FIGURE 4 – Mean heart rate (\pm S.E.) for Tufted Ducks at rest, 15 s after enforced submer-
sion of the head (from Butler & Woakes 1982b), during voluntary dives of 14.4 s mean
duration and while swimming. Oxygen consumptions ($\dot{V}O_2$) at mean dive duration and while
swimming were the same, $57 \text{ ml kg}^{-1} \text{ min}^{-1}$ (From Woakes & Butler 1983).

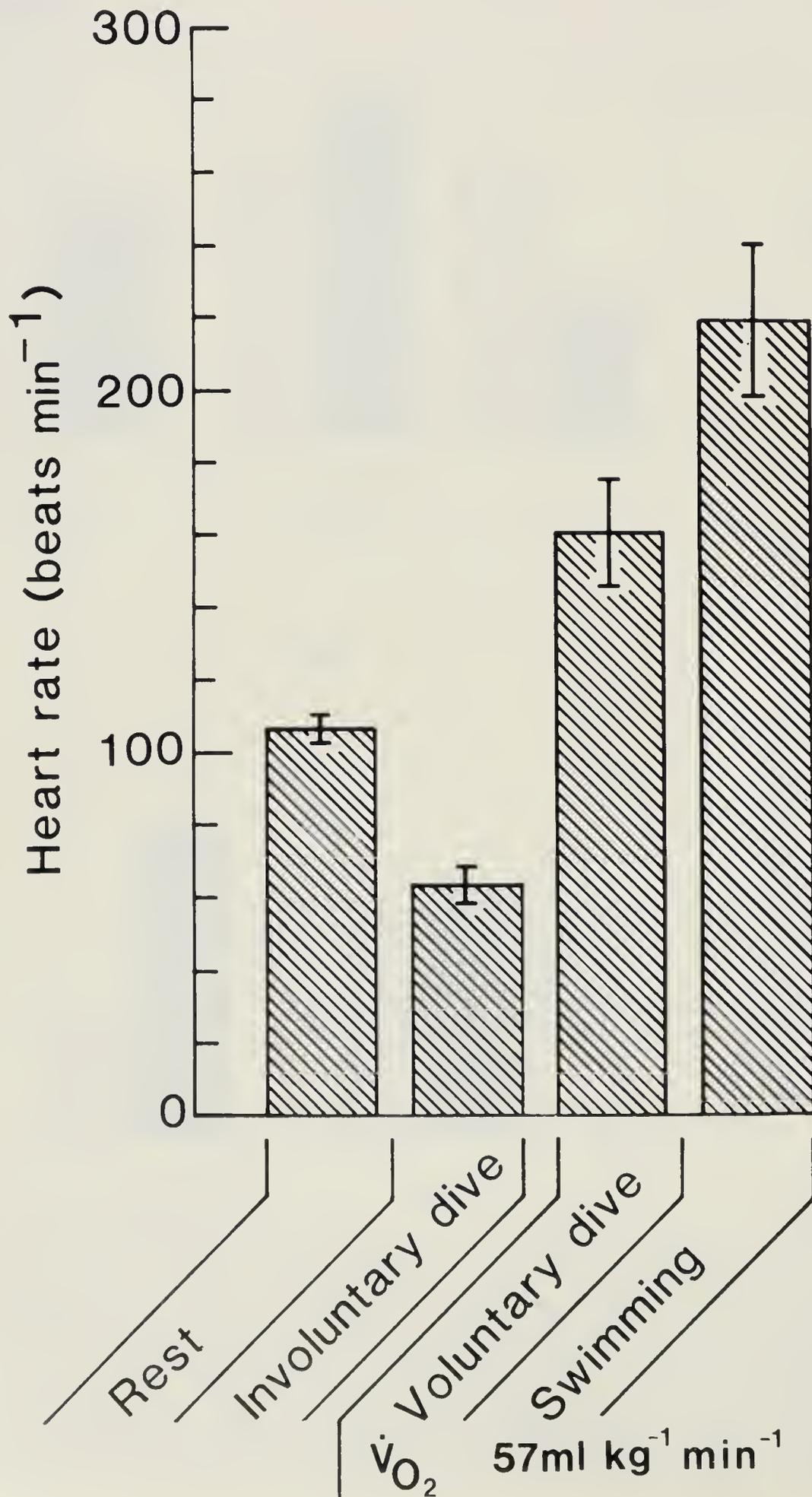
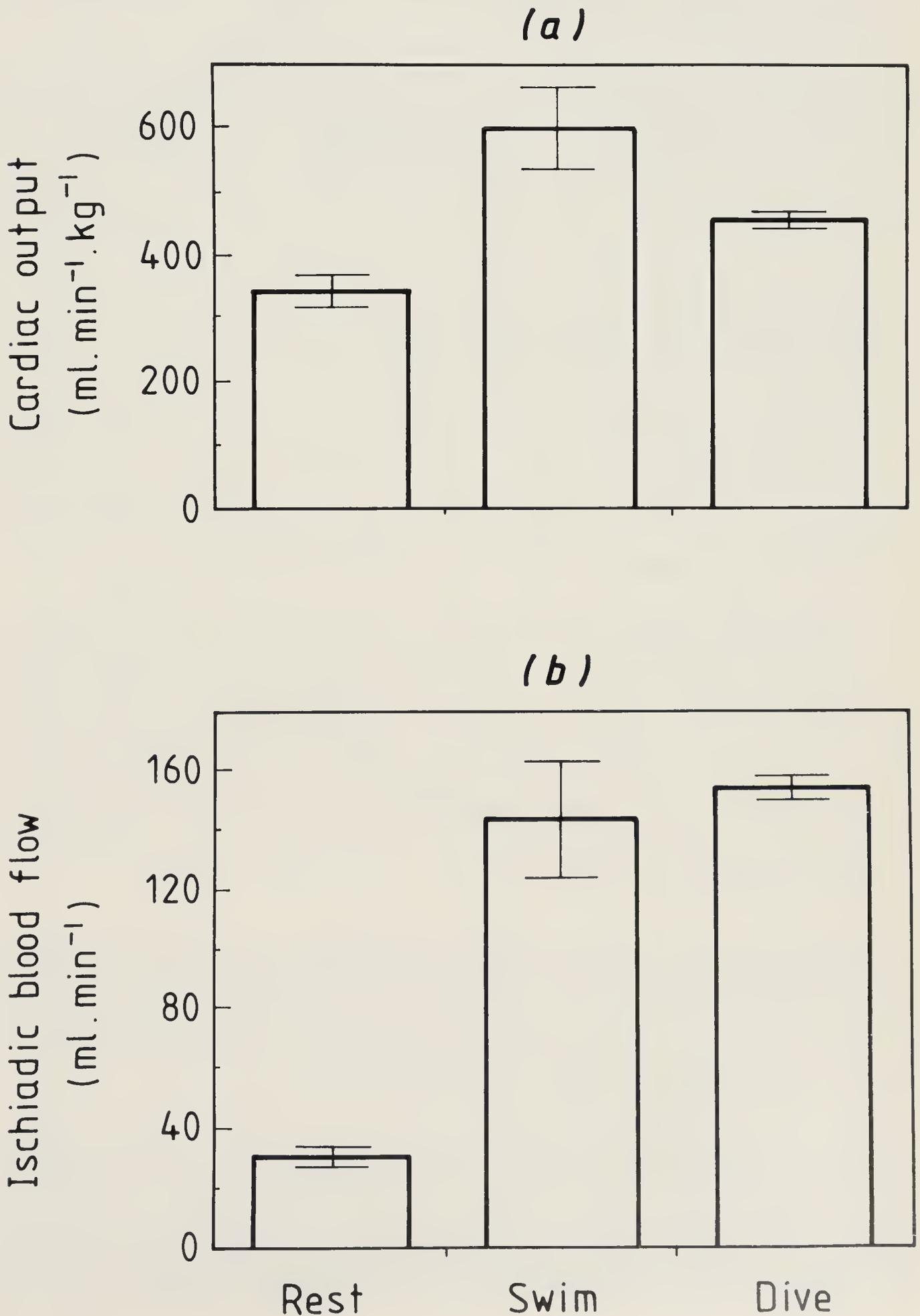


FIGURE 5 – Histogram showing mean values (\pm S.E.) of (a) cardiac output and (b) blood flow through the ischiadic arteries in Tufted Ducks at rest, while swimming at a speed of 0.75 m s^{-1} and during the last 5 s (excluding the second prior to surfacing) of dives with a mean duration of 15.5 s (From R.M. Bevan & P.J. Butler unpubl.)



central nervous system is similar to that during exercise in air, whereas the viscera and inactive muscles (which, of course, includes the large pectorals in these birds) may be perfused less than during exercise in air. This hypothesis has gained some support from qualitative studies using micro-aggregated albumin labelled with ^{99m}Tc (Jones et al. 1988), and from direct measurements of blood flow through major arteries (R.M. Bevan & P.J. Butler unpubl.).

Blood flow through the right pulmonary, left brachiocephalic, left carotid and right ischiadic arteries have been continuously monitored in resting, diving and swimming Tufted Ducks. Cardiac output was assumed to be twice the flow through the right pulmonary artery and brachial flow (to the breast muscles) was estimated by subtracting flow through the carotid from that through the brachiocephalic. Resting cardiac output was $342 \text{ ml min}^{-1} \text{ kg}^{-1}$. It increased by 74% when the ducks were swimming at 0.75 m s^{-1} and by 33% during the last 5 s (excluding data over the final second) of dives with a mean duration of 15.5 s (Figure 5a). Under similar conditions, blood flow through both ischiadic arteries was 30 ml min^{-1} at rest, increasing by 4.8 times during swimming and 5.1 times during diving (Figure 5b). Thus the proportion of cardiac output flowing through the ischiadic arteries was greater during diving than during swimming and this inevitably means that the rest of the body was perfused by less blood during diving than during swimming. This is, unfortunately, not clearly reflected in the estimated blood flow through the brachial artery. Although flow through the brachial arteries, at 26 ml min^{-1} , was significantly lower during diving than that in the resting birds (66 ml min^{-1}), it was not, however, significantly lower than that during swimming (42 ml min^{-1}). A region of the body which could well receive less blood during diving than during swimming is, of course, the respiratory muscles.

Mean arterial blood pressure varied in much the same way as heart rate before, during and after a dive. During dives of 18 s mean duration, partial pressure of oxygen in arterial blood (PaO_2) fell from 11.8 to 9.4 kPa, PaCO_2 changed little from 3.15 to 3.21 kPa, whereas pH_a fell from 7.55 to 7.48. This acidosis resulted mainly from an increase in blood lactate from 1.7 to 3.0 m mol l^{-1} (R.M. Bevan & P.J. Butler unpubl.). The latter value is only slightly higher than that recorded in ducks swimming at 0.7 m s^{-1} (Woakes & Butler 1986). It would be interesting to know whether there is a progressive accumulation of blood lactate during bouts consisting of dives of less than approximately 20 s duration, or whether the level quoted above is the new steady-state during such bouts.

It would appear, therefore, from the evidence presented so far, that Butler's (1982) hypothesis is correct, i.e. diving in ducks is a modified exercise response, with the legs, as well as the heart and CNS, being perfused adequately to maintain overall aerobic metabolism. Other, inactive parts of the body are, however, less well perfused than during surface swimming. Under certain circumstances, however, the balance may tip towards more of an oxygen conserving response.

Stephenson et al. (1986) found that when Tufted Ducks swim long horizontal distances under water for their food (e.g. under ice in winter), heart rate progressively declines after approximately 10 s, so that by approximately 30 s it is significantly below the resting value (Figure 6a). During these dives the birds actively swim to and from the food. However, during normal vertical dives of similar duration and when the birds surface passively, heart rate remains elevated above the resting level. If, as

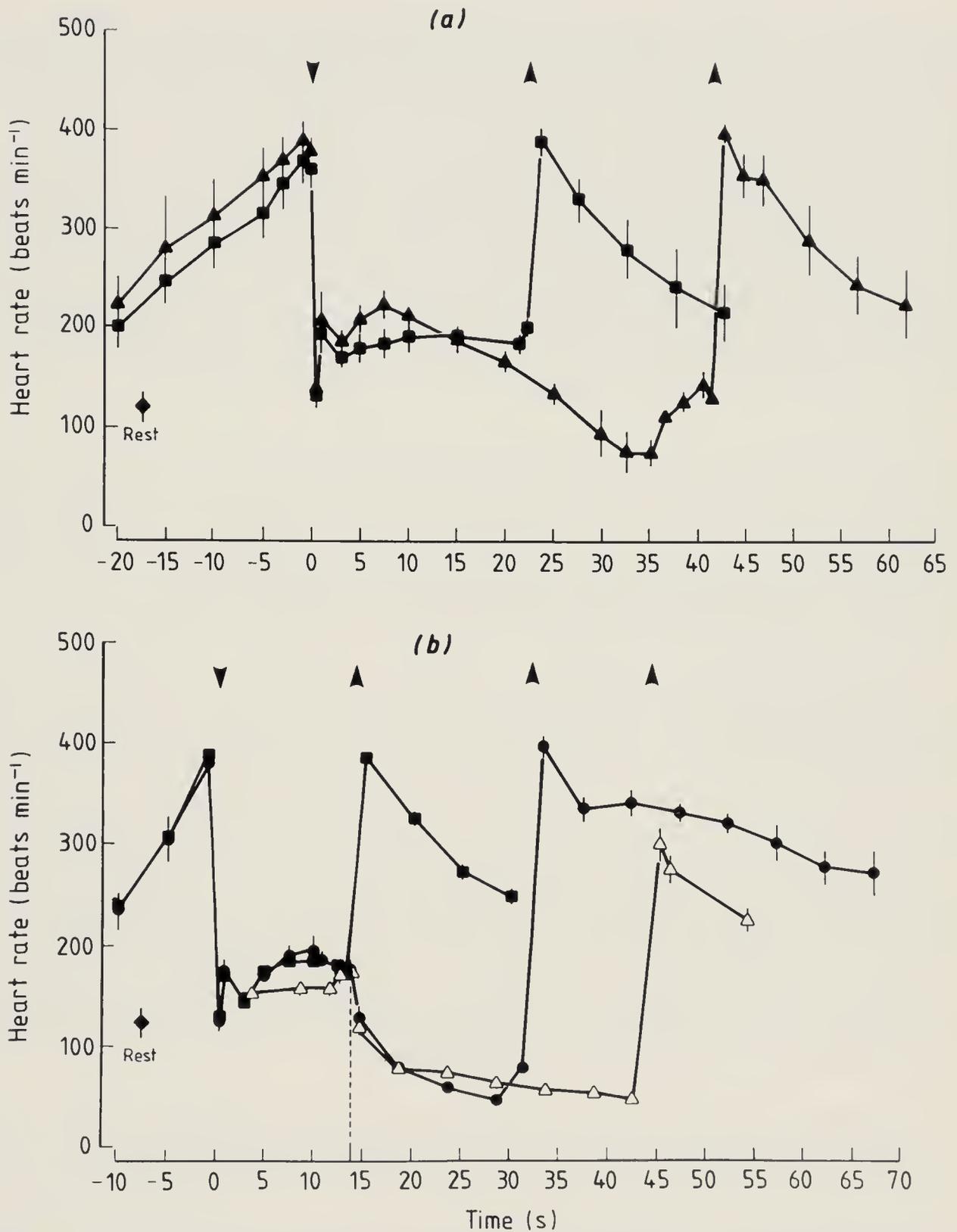


FIGURE 6 – (a) Mean heart rate (\pm S.E.) of Tufted Ducks before, during and after normal vertical dives (\blacksquare) and extended, “horizontal” dives (\blacktriangle). Downward pointing arrowhead (time zero) represents point of immersion and upward pointing arrowheads represent mean points of emersion for “normal” dives (22.4 s) and “horizontal” dives (41.4 s). \blacklozenge , resting heart rate. (b) Mean heart rate (\pm S.E.) of Tufted Ducks before, during and after normal, vertical dives (\blacksquare), normal dives from which the ducks were temporarily unable to surface, “trapped” (\bullet) and involuntary submersion (\triangle ; data from Butler & Woakes 1982b). Downward pointing arrowhead represents the point of immersion in normal feeding dives and “trapped” dives (but *not* involuntary submersions). Upward pointing arrowheads represent points of emersion for all dives. The vertical dashed line represents the point at which the ducks apparently became aware that they were temporarily unable to surface during “trapped” dives (after 13.8 s mean duration of submersion) and it also represents the point of head immersion in the case of involuntary submersion. \blacklozenge , resting heart rate. (After Stephenson et al. 1986).

indicated by the sub-resting heart rate, blood lactate does accumulate during a long horizontal dive, it does not have a large inhibitory effect on exercise, because the birds are still able to perform a number of dives in succession. There may, however, be a cumulative effect since the number of dives in a bout is lower than normal.

If a duck is temporarily unable to surface from a voluntary dive, e.g. if it is disoriented under ice, there is an immediate reduction in heart rate as soon as the bird becomes aware of the situation. Heart rate follows the same time course and reaches a similar level to that seen during involuntary submersion (Figure 6b), when selective vasoconstriction, a reduction in aerobic metabolism and increased lactate production are known to occur (Butler & Jones 1982). This intense bradycardia occurs in "trapped" ducks, despite the fact that they are still active under water.

It is clear that the cardiovascular response to diving in ducks is highly labile. On the basis of the cardiac response, it does appear as if, under certain circumstances, the cardiovascular and metabolic responses during voluntary dives can shift progressively or more immediately to those of the "classical" diving response, i.e. relatively more intense peripheral vasoconstriction and increased lactate production in some tissues and organs, maybe even in the legs themselves in "trapped" ducks.

Although physiologically expedient, in as much as oxygen is conserved, it appears that such a shift affects the feeding behaviour of the birds. At one extreme, it is usual for a bird to remain at the surface for an hour or more before making another dive after temporarily being unable to surface from a voluntary dive. Also, the time spent feeding during each dive decreases as horizontal distance to the food increases (Stephenson et al. 1986). This is contrary to the predictions of optimal foraging theory, which suggest that if more energy is expended in reaching a source of food, more time would be spent in obtaining (more) food (Charnov 1976). This apparent contradiction in aquatic birds may result from the opposing time constraint imposed by physiological factors associated with the maintenance of aerobic metabolism, at least in the active muscles, CNS and heart. It appears that under such conditions, the physiological adjustments allow optimization of feeding behaviour, but that these adjustments impose their own constraints upon that behaviour.

The lability of the cardiovascular response to voluntary diving indicates that the control processes must be complex, involving higher regions of the brain as well as peripheral sense organs and simple reflexes. However, studies so far have been restricted to investigating the role of the latter. Arterial baroreceptors appear not to be involved in the cardiac response to voluntary diving at all (Furilla & Jones 1987). The carotid body chemoreceptors do contribute to, but are not solely responsible for, the bradycardia seen during extended horizontal dives and when Tufted Ducks are temporarily unable to surface from a voluntary dive (Figure 6, Butler & Stephenson 1988). They also have a slight inhibitory effect on heart rate towards the end of 'normal' vertical dives of approximately 20 s duration (Butler & Woakes 1982b). In the latter study, there was a significant increase in dive duration following bilateral denervation of the carotid bodies. Thus, these sense organs do not appear to play a dominant role in cardiac control during voluntary diving in ducks and are not involved at all in the immediate reduction in heart rate seen when "trapped" ducks become aware of their predicament (Figure 6b). Inactivation of receptors in the nasal passages with local anaesthesia prevented voluntary diving in some Redhead Ducks and heart rate was

10-30% higher than in untreated ducks during the first 12-5 s of submersion when the animals dived in response to being chased (Furilla & Jones 1986).

Thus, it seems that receptors in the nasal passages have an inhibitory effect during the first few seconds of voluntary submersion and that the carotid body chemoreceptors have a similar influence after 10-15 s of submersion. However, it is clear that the dramatic reduction in heart rate, from the elevated pre-dive level, occurs before the nasal areas contact the water (Butler & Woakes 1982a) and is probably centrally mediated. The motor side of the cardiac response resides entirely in the vagal branches to the heart (Butler & Woakes 1982a, Furilla & Jones 1987). It is clear from this brief discussion that the neural control of the cardiac response in freely diving birds is very complex and well worthy of further study.

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DIVING PHYSIOLOGY OF PENGUINS

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ABSTRACT. Behavioral data (dive depth, duration, and frequency) collected by remote recorders and telemetry demonstrate the diving capabilities of penguins. Most diving physiology studies of penguins, while yielding valuable information on cardiovascular responses and the effects of pressure, have been either under forced submersion conditions or in relatively confined pools. They have not addressed the physiology of free-diving penguins, especially such deep divers as Emperor and King Penguins. Microprocessor technology allows examination of this topic, and some results of recent field work on Emperor Penguins are presented. Much is still unknown about the cardiovascular responses, magnitude and utilization of oxygen stores and effects of pressure in free-diving penguins.

Keywords: Penguin, heart rate, diving physiology.

The diving abilities of penguins have been determined in the past by surface observations, and, more recently, by the use of miniaturized depth recorders. Feeding dive durations of the smaller penguin species are one to two minutes (min) (Kooyman 1975, Lishman & Croxall 1983, Trivelpiece et al. 1986), while durations as long as 9 min have been reported for the larger Emperor Penguins *Aptenodytes forsteri* (Kooyman et al. 1971). Dive depths are also species-dependent, ranging from <20 meters (m) for Macaroni Penguins *Eudyptes chrysolophus* to in excess of 240 m for King and Emperor Penguins (Croxall et al. 1988, Kooyman et al. 1971, Kooyman et al. 1982). While such dive behavior is remarkable and continues to be the subject of much research, relatively little is known about the physiological—in particular, cardiovascular—responses underlying these abilities.

In this paper, we will summarize past work on the cardiovascular physiology of penguins and compare it to our knowledge of cardiovascular responses during diving in other birds and in pinnipeds. We will then present a preliminary analysis of our work on heart rate responses in diving Emperor Penguins.

Scholander (1940) was the first to examine cardiovascular responses to forced submersions in penguins when he studied Macaroni and Gentoo Penguins *Pygoscelis papua*. There have been almost no further studies of forced submersions since these first works. His most noteworthy observations were a bradycardia (Table 1), a lack of bleeding from pectoral muscle biopsies, and an inability to draw blood from toe arteries during forced submersions of 3 to 3.5 min. Muscle oxygen content dropped from 4.1 vol % to 0 by the end of the submersion and, interestingly, remained at 0 vol% for the first 5 min after the end of submersion. Similarly, muscle lactate increased by 3 to 22 millimoles/kg muscle wet weight (mM/kg w.w.) by the end of submersions, and it again increased by an additional 3 to 10 mM/kg w.w. during the first 5 min afterwards. Blood lactate increased during submersions by 3 to 11 millimoles/liter (mM) and always increased significantly after the submersion (highest concentrations reached - 17 to 22 mM). In comparison, similar experiments on seals revealed peak post-submersion blood lactates of 8-18 mM and muscle lactates of 12-42 mM/kg w.w.

(Scholander et al. 1942). Scholander concluded that these data supported Irving's concept of a differential and restricted blood flow distribution as part of a mechanism for prolonged submersion. No explanation was given for the continuance of muscle in the reduced state for several minutes after the dive. He also noted that these forced submersions were considerably longer than the duration (< 1 min) of voluntary dives exhibited by these birds in a lake during their captivity.

No penguin cardiovascular physiology research was conducted since this original work by Scholander until the early 1970s. During gas exchange studies of Adelie *Pygoscelis adeliae* and Gentoo Penguins, Kooyman reported presubmersion heart rates of 80-100 beats/min, and a bradycardia in the 20 beats/min range during submersion to 4 and 7.8 atmospheres absolute (Kooyman 1975). This is similar to what Scholander saw in his studies of the Gentoo Penguin.

Millard et al. (1973) placed monitors on Gentoo and Adelie Penguins with either a nylon jacket (on land) or leather harness and tether (in water), and recorded heart rate and femoral blood flow during walking, swimming, voluntary dives, and forced submersions. Interpretation of the forced submersion data (Table 1) was limited due to struggling by the birds. Although the sample size was small, the use of telemetry and remote acquisition of data was a first in the field, and heralded research efforts of the future. Treadmill or provoked exercise on land resulted in high heart rates (180-280 beats/min) and increased femoral flow (+100-400%). During surface swimming, heart rate averaged 227 beats/min, and during voluntary dives of 30-60 seconds, it decreased to 1/3 to 1/2 that value (or to about the resting rate on land—see Table 1). Onset of this decrease was rapid, and a presurfacing tachycardia was noted. Whereas femoral flow increased during surface swimming (100% greater than at rest on land), it decreased during voluntary dives (to about 50% that at rest on land). The authors concluded that blood flow to muscle was reduced but maintained during voluntary dives, and that the assumed reduction in cardiac output was less than in forcibly submerged ducks.

No further work on penguin diving physiology occurred until the 1980s when Butler and Woakes (1984) published their studies of free swimming Humboldt Penguins *Spheniscus humboldti*. Here the penguins were truly unrestrained with implanted heart rate telemetry transmitters; data were obtained while they swam in a 9x4.6x2.7 m deep pool. Once again, running resulted in the highest heart rate (245 beats/min) observed. While swimming on the surface with the bill and eyes submerged, the heart rate was reported to become steady at 119 to 125 beats/min, and during voluntary dives of about 30 seconds duration, it remained in this range. Frightening or forcing a penguin to stay submerged beyond 50 seconds did result in a decrease in heart rate down to 78 beats/min. A presurfacing increase in heart rate was seen in all voluntary dives.

There was apparently no tachycardia prior to the first dive of a series. After a dive, there was a pronounced tachycardia with a mean of 231 beats/min during the first exhalation. Heart rate was reported to remain elevated above resting levels until the next dive occurred.

Oxygen consumption was also measured; calculated diving metabolic rates were higher, but not significantly, than that measured during rest. Butler and Woakes stated

that the physiological responses to diving in penguins were similar to diving ducks and that penguins were able to remain submerged longer due to the efficiency of their underwater locomotion. They apparently concluded that no redistribution of blood flow of any degree occurred during these short voluntary dives in a pool of less than 3 m depth but stated that, like ducks, penguins could probably switch to "an oxygen-conserving 'classical' response" during dives in the wild.

TABLE 1 – Penguin heart rate (HR) data (beats/min) available in the literature. Sources include mean values reported and estimates taken from figures and rates in the cited references.

	Species			
	Gentoo/ Macaroni ¹	Gentoo/ Adelie ²	Gentoo/ Adelie ³	Humbolt ⁴
Resting or presubmersion HR	140-180	80-100	90-100	121
Forced submersion HR	30-48	20	60-240	78*
Surface swimming HR	–	–	227	119-125 139, 200**
Diving HR	–	–	70-110	119-125

¹ Scholander 1940; ² Kooyman 1975; ³ Millard et al. 1973; ⁴ Butler & Woakes 1984.

* Observed when forced beyond a 50-second submersion.

** 139-resting in water; 119-125 – surface swimming; 200 – range observed after dives but not prior.

These four papers represent all the available research on diving cardiovascular physiology in penguins. It is noteworthy that, although only addressing forced submersions, Scholander's original work is still (50 years later) the most extensive study of penguin cardiovascular physiology. The heart rate data available for voluntary dives of penguins are limited to dives of 30- to 60-second durations and, where observed, to a maximum depth of 3 m. Only Adelie, Gentoo, and Humboldt Penguins have been examined. These species or at least penguins in this size range, commonly dive to depths of 15-100 m and stay submerged for 1 to 2 min (Croxall et al. 1988, Kooyman 1975, Lishman & Croxall 1983, Trivelpiece et al. 1986, Wilson et al. 1989). Such dives most certainly include greater distances travelled, and probably higher swim velocities and overall energy consumption than those reported in the physiological studies.

Indeed, the diving and interdive metabolic rates measured by Butler and Woakes are 1.9 and 2.6 times the standard metabolic rate (SMR) calculated from the active phase allometric equation of Aschoff and Pohl (1970). This is less than the doubly labeled water determinations of metabolic rates at sea for King, Gentoo, Macaroni, and Jack-ass Penguins (2.8-7.3 times SMR) (Davis et al. 1989, Kooyman et al. 1982, Nagy et al. 1984). Thus, the "dives" in these two physiological studies of penguins (Millard et al. 1973, Butler & Woakes 1984) may represent more a modification of surface swimming than actual diving.

The tachycardia associated with increased oxygen consumption is well documented in exercising terrestrial mammals and flying birds (Taylor et al. 1987, Berger et al. 1970, Butler et al. 1977). Butler has suggested that the overall heart rate response to diving in Tufted Ducks *Aythya fuligula* is a mixture of the classical exercise response and the forced submersion response (Butler 1982). More recently, Butler and Stephenson (1987) suggest that the latter response may predominate in natural dives of the Tufted Duck. They have observed that, although heart rate remains above resting levels during vertical dives of the Tufted Ducks, it declines below resting levels during horizontal dives of similar duration (Stephenson et al. 1986). In either case, submerged heart rate was below pre- and post-dive heart rates as well as below surface swimming heart rates. The data available for free-diving penguins at this time are too limited to interpret.

The ability of an animal to make active dives during which its heart rate and presumably muscle blood flow decrease has been a paradox. As recently reviewed by Baldwin (1988), greater anaerobic capacities (more buffering capacity, higher % M subunits of lactate dehydrogenase and lower lactate dehydrogenase pyruvate inhibition ratios) are found in Adelie, King, and Emperor Penguin muscle than are found in muscle of Little *Eudyptula minor*, Royal *Eudyptes schlegeli*, Rockhopper *Eudyptes chrysocome* and Gentoo Penguins. These different capacities may reflect varied biochemical and associated cardiovascular diving strategies among the penguin species. Such variability suggests that several species will need to be studied before a comprehensive understanding of penguin physiology will be attained.

Kooyman (1985) considered models of circulatory regulation in pinnipeds and has re-emphasized the potential role of myoglobin as an oxygen store regardless of whether there is no blood flow, intermittent flow, or continuous, low flow to muscle during dives. Elsner (1989) has also emphasized myoglobin's function as an oxygen store in seal myocardium during coronary blood flow oscillations observed during forced submersions. The elevated myoglobin levels found in penguins (Weber et al. 1974, Mill & Baldwin 1983) may serve a similar role. The extent and nature of peripheral circulatory adjustments during diving in both pinnipeds and penguins are still unknown. Examination of heart rates and such indicators of peripheral blood flow as blood and/or muscle pO_2 or oxygen saturation are required in order to further define cardiovascular responses to diving.

In order to examine heart rate responses in the larger penguins, we are pursuing studies of Emperor Penguins swimming at controlled rates in a flume as well as diving from an ice hole. Only the latter will be discussed here. Animals were anesthetized with isoflurane the previous day, and mounted with subcutaneous EKG electrodes connected to a microprocessor equipped with an R-wave detector and pressure transducer (Micromonitors, 1348 Shasta Avenue, San Jose, California 95126). The recorder was clamped to the feathers between the wings. A preliminary analysis of a typical record of an Emperor Penguin is as follows: 1) Resting heart rates were recorded overnight (between anesthesia and the dive study) while the penguins rested and walked about in a corral; the mean was 77 beats/min with a range of 50 to 125. 2) During dives, heart rates quickly decreased and remained in a range of 50-80 beats/min. 3) Upon surfacing, a tachycardia (>100 beats/min) occurred. Dive durations ranged from 2 to 10 minutes; maximum depths from 10 to 80 meters.

The inter-dive tachycardia of the Emperor Penguin was maintained throughout the period at the surface, even when birds exited the water and stood on the ice. When they dived there was a conspicuous decrease in heart rate, although heart rate only fell to resting levels. This situation is reminiscent of phocid seal exercise and dive studies where heart rate is low during submersion, and elevated at the surface (Fedak 1986, Fedak et al. 1988, Hill et al. 1987, Jones et al. 1973, Kooyman & Campbell 1973, Williams et al. in press). The decreased heart rates observed during these dives in pinnipeds and Emperor Penguins were not as low as in forced submersions.

In summary, only basic and limited measurements of diving physiology in penguins have been published. These measurements include heart rate and metabolic rate while the birds rested or swam in a small pool, or just offshore on a tether. Initial analysis of heart rate data from Emperor Penguins diving from an ice hole suggests a heart rate response during diving similar to phocid seals. Further investigation of the intensity of heart rate and vasoconstriction responses during diving is required.

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EVOLUTION AND ADAPTATION OF THE DIVING RESPONSE IN BIRDS

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ABSTRACT. The phylogenetically ancient forced diving response of bradycardia and vasoconstriction is seen in both aquatic and non-aquatic birds during forced submergence although it is far better developed and sustained in the former. In voluntary diving, however, heart rate and vasoconstrictor responses are greatly modified but a "forced" dive response is seen in all birds when they are trapped underwater even if they are free to move around. Hence, the forced dive response lurks just beneath the surface of the voluntary diving adjustments. In fact, in diving ducks there is a strong relation between pre-dive and dive heart rate which can be explained by assuming that all diving manoeuvres elicit an increase in cardiac vagal activity of some 50% of maximum. However, changes in sympathetic vasomotor activity vary depending on the type of dive. Nevertheless, at least for diving ducks, the response to diving in terms of efferent vagal activation is the same under all conditions including dabbling.

Keywords: Aquatic birds, non-aquatic birds, ducks, bradycardia, vasoconstriction, cardiac control, forced submergence, voluntary dive.

INTRODUCTION

Marked cardiovascular adjustments (bradycardia and vasoconstriction) are displayed by all vertebrates in response to breath-hold asphyxiation. Their purpose is to conserve stored oxygen for those tissues such as the heart and brain which are irreversibly damaged by oxygen lack and close down the circulation in those tissues which can survive prolonged anoxia (i.e. muscles and gut). In lower vertebrates blood shunts are effected both centrally and peripherally whereas in those vertebrates with divided hearts and separate pulmonary and body circulations, shunts are achieved by selective peripheral vasoconstriction. Nevertheless, there are sufficient similarities in the response in all vertebrates to confirm our view that it is phylogenetically ancient and was justifiably described by Scholander (1963) as "the master switch of life".

The ability to endure forced submergence is seldom tested in voluntary diving. Voluntary dives are usually short and seldom longer than one-third of maximum underwater endurance. Furthermore, the animal is exercising vigorously and there is an obvious conflict between the circulatory and metabolic demands of exercise compared with those seen in forced submergence. Exercise calls for elevated heart rates and enhanced perfusion of working muscles to provide for increased aerobic metabolism and greatly increased rates of lactate recycling. These responses are diametrically opposed to those seen in forced dives which include bradycardia, reduced cardiac output, vasoconstriction, mixed aerobic and anaerobic metabolism, lactate accumulation at sites of formation (with low recycling rates) and, overall, reduction in metabolism. In view of this Millard et al (1973) suggested for penguins (*Pygoscelis papua* and *P. adeliae*) the response to voluntary diving represented a composite of responses to

exercise and forced submergence, and Butler (1982) elaborated on this to suggest that in diving ducks the exercise response is emphasised. Hence factors such as drag and buoyancy, due to their influence on metabolic rate during diving, are likely to be much more important in influencing cardiovascular adjustments than any presumed evolutionary relationships between birds.

EVOLUTIONARY RELATIONSHIPS OF AQUATIC BIRDS

Avian phylogeny is beset with pitfalls for the non-specialist. These spring from attempting to reconcile palaeontological records of extant and extinct species with comparative studies in the ecology, behaviour, morphology, physiology, biochemistry and genetics of living species. However, the early evolutionary history of birds is based, almost exclusively, on the fossil record and it is clear that aquatic birds arose fairly early in avian evolutionary history with *Gansus* from the lower Cretaceous period being coeval with *Archaeopteryx* and probably representing the common ancestor of all shorebirds and waterbirds (Hou & Li 1984). In this case it seems likely that the toothed diving birds of the Cretaceous such as *Enaliornis*, *Hesperornis* and *Ichthyornis* are separate phyletic lines (Olson 1985). Hence, development of an aquatic lifestyle appears to have arisen a number of times in avian evolutionary history and convergent evolution is a possible explanation for challenges presented to the fossil record by phylogenies based on molecular and genetic affinities (Patton & Avise 1986, Sibley et al. 1988).

Among aquatic birds, diving and dabbling ducks are the most well studied and there is general agreement that they are a monophyletic group which, along with the ratites and gallinaceous birds, are among the oldest groups with present day representatives. Furthermore, ducks are quite distinct, evolutionarily, from other diving and dabbling birds such as coots, cormorants, penguins, puffins and murres. In fact, DNA-DNA hybridisation studies by Sibley et al. (1988) suggest that all the later are a sister group of the Passeriformes which itself contains one diving representative, the dippers *Cinclus* spp.

CARDIAC RESPONSES TO SUBMERGENCE IN BIRDS

Diving as a mode of life is very old and in the 100 million years or so that birds have been making their living underwater considerable divergence in anatomical and physiological traits might be expected. However, with respect to the latter, differences appear to be at the subtle rather than fundamental level. The phylogenetically ancient response of bradycardia to enforced submergence is retained in all birds. Non-divers such as the Chicken *Gallus domesticus*, Pigeon *Columba livia*, Quail *Colinus virginianus*, Pheasant *Phasianus colchicus*, Hawk *Buteo lineatus* and Robin *Turdus migratorius* show a fall in heart rate during immersion although heart rate usually remains above 100 min⁻¹ and is less well sustained than in diving or dabbling birds during submergence (Figure 1; Bond et al. 1961, Murrish 1970). Interestingly, in diving ducks *Aythya* sp., bradycardia develops equally well in both restrained and unrestrained birds. The faster the oxygen conserving response can be effected in both restrained and free animals the longer will be underwater survival. Diving ducks *Aythya* sp. develop bradycardia quicker than dabblers (*Anas* sp.; Catlett & Johnston

1974, Butler & Woakes 1982, Furilla & Jones 1986). Bradycardia is also rapid in the Cormorant *Phalacrocorax auritus*, Dipper, Shag *P. aristoleles* and Guillemot *Uria aalge* but, surprisingly, is slow in the Penguin *Eudyptes chrysolophus* and *P. papua* (Figure 1; Scholander 1940, Eliassen 1960, Murrish 1970, Mangalam & Jones 1987, Jones & Larigakis 1988). In diving ducks *A. americana*, bradycardia is initiated by nasal receptors stimulated by immersion (Furilla & Jones 1986) whereas in dabblers *A. platyrhynchos* bradycardia is brought about by stimulation of arterial chemoreceptors by blood which is low in oxygen and high in carbon dioxide (Jones & Purves 1970). Consequently, the mechanism in the dabbling duck is inefficient since oxygen must be consumed before the arterial chemoreceptors will be stimulated yet, even so, the dabbling duck has one of the best underwater tolerances of all forced dived birds (Hudson & Jones 1986).

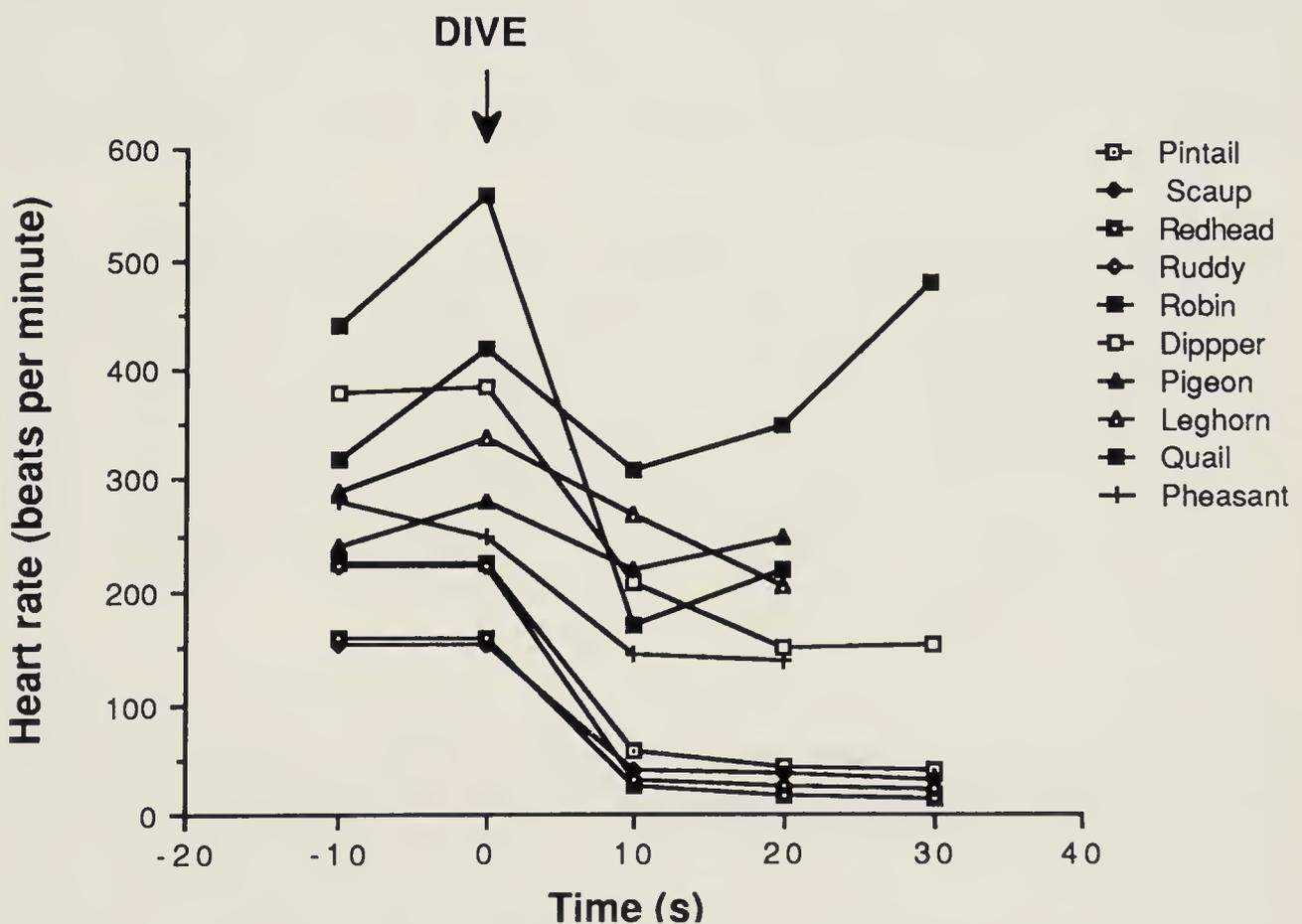


FIGURE 1 – Bradycardia in response to forced submergence of aquatic and non-aquatic birds (data from Bond et al. 1961, Murrish 1970, Catlett & Johnston 1974, and Jones & Larigakis 1988).

In voluntary diving the picture is very different. Low heart rates characteristic of forced dives by diving birds do not occur and diving rates are seldom below 100 min^{-1} . This is the case in penguins, ducks, dippers, cormorants and even in dabbling ducks which have been trained to dive for their food (Butler & Woakes 1984, Murrish 1970, Kanwisher et al. 1981, Furilla & Jones 1987b). In cormorants and diving ducks there is a noticeable pre-dive tachycardia which is not seen in penguins, dippers and dabbling ducks. In cormorants, dippers and diving ducks, heart rate falls rapidly to the diving level whereas in dabblers diving heart rate is around 250 min^{-1} and heart rate is rapidly adjusted up or down to that rate, depending on the pre-dive rate. In penguins there is little change in heart rate on submergence. However, in cormorants, diving ducks and penguins a full blown diving response lurks just below the surface

because marked bradycardia occurs if they are prevented from surfacing at the end of a voluntary dive. If the oxygen conserving response is to be effective then marked bradycardia implies an equally rapid and effective peripheral vasomotor response. In a recent series of experiments using macro-aggregated albumin labelled with 99m Technetium (Heieis & Jones 1988) we monitored blood flow distribution in diving ducks at rest, during swimming at the surface, during voluntary diving, after trapping the duck underwater and during forced dives. Organ trapping of the labelled protein, visualised using a gamma camera, gives a qualitative picture of blood flow distribution. Compared with the generalised distribution at rest we found that during swimming and voluntary diving blood flow was preferentially directed towards the active muscles of the hind limb whereas after trapping, or in forced dives, blood flow distribution was preferentially directed to the head and brain (Stephenson & Jones in preparation). We found little overt difference in blood flow distribution in trapped compared with forced dives even though the animal was actively moving around, seeking the surface, in trapped dives. In fact, this pattern of flow distribution confirms what was expected from heart rate determinations alone (Furilla & Jones 1986, Stephenson et al. 1986).

In voluntary dives, diving ducks *A. fuligula* work quite hard against buoyancy and diving oxygen consumption is considerably elevated above the resting level (Woakes & Butler 1983). Penguins have a low drag coefficient and are close to neutral buoyancy so it is no surprise that their diving oxygen uptake is much lower than that of ducks (Butler & Woakes 1984). Nevertheless, for both species, there is enough oxygen in the body oxygen stores to provide for diving metabolism so that marked cardiovascular adjustments, with the implication that muscle metabolism is fueled anaerobically, are not required. Even so, it is not clear how the cardiovascular responses seen in forced diving are inhibited or overruled particularly when they can be evoked so readily by trapping a voluntarily diving bird underwater.

If the exercise response is indeed overruling the dive response then it should be possible to affect forced diving brachycardia by evoking activities associated with exercise or by simulating input from peripheral receptors (i.e. muscle and joint receptors) which are stimulated during muscular movement. Rhythmic passive hind limb beating, at the same frequency as occurs in diving, or electrical stimulation of spinal dorsal roots has no effect on bradycardia. Furthermore, stimulation of the central nervous system in areas that promote walking also has no effect on forced diving bradycardia (Jones, Butler, West & Funk unpubl.).

The forced dive response, however, in both dabbling and diving ducks can be habituated and the stimulus of being trapped may dishabituate the oxygen conserving response and allow its full expression (Gabrielsen 1985, Gabbott & Jones 1986, 1987). This raises the spectre of "stress" or "fear" as being a major component of the forced dive response and that the perception of "fear" is an important agent for its release (Kanwisher et al. 1981). However, it has been shown repeatedly, most recently by Gabbott & Jones (1986), that decerebrate ducks develop an identical cardiovascular response to forced diving as their intact fellows and as Blix & Folkow (1981) point out "decerebrate ducks are rather difficult to scare". Brain transection just in front of the brainstem also fails to prevent marked bradycardia in forced dives. Hence, the extreme cardiovascular responses to forced diving are reflexogenic and are integrated at the brain stem level. Furthermore, the dive response can be habituated even in

decerebrate ducks. However, the response to being trapped does not appear to habituate in intact diving ducks (Stephenson 1987) and it could well be that the elicitation of a dive response by trapping is, by itself, a conditioned response evoked by intense psychogenic stimulation.

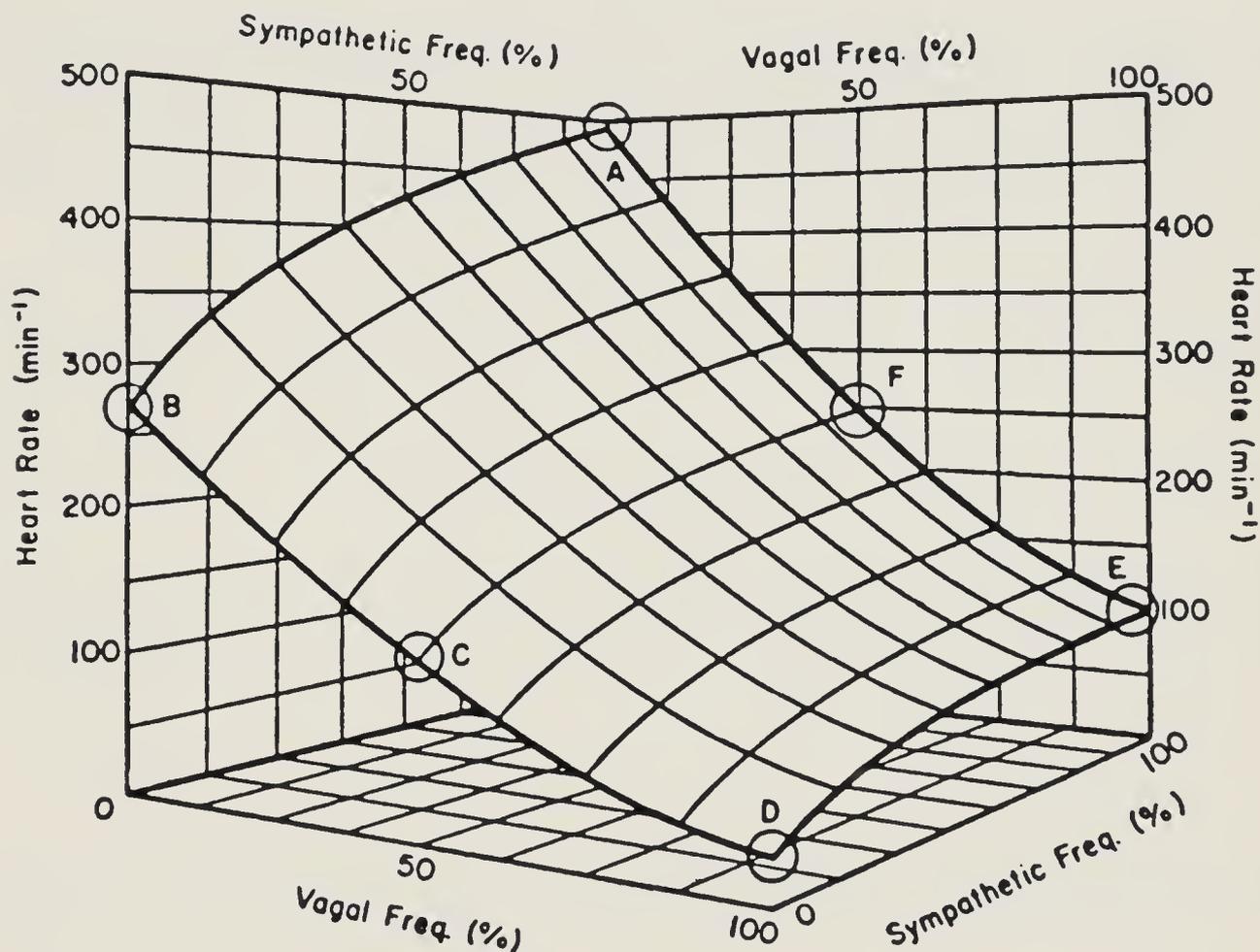


FIGURE 2 – The relationship of heart rate to bilateral stimulation of the distal cut ends of the vagus and cardiac sympathetic nerves of the Pekin Duck *A. platyrhynchos*. 100% represents the frequency of stimulation above which no further changes in heart rate occurred. The heart rate resulting from a given level of vagal and sympathetic stimulation was plotted on “perspective” graph paper and the surface was drawn, by eye, to encompass all heart rates obtained in the stimulation experiments. Area B represents complete cardiac denervation, and area E maximal vagosympathetic stimulation. The effect of sympathetic stimulation at minimal and maximal vagal activity are represented by the lines A-B and D-E, respectively. Similarly, the effect of vagal stimulation at minimal and maximal sympathetic activity are represented by the lines B-D and A-E, respectively. See text for an explanation of points A-F relative to diving. (Reprinted from Furilla and Jones 1987a.)

HEART RATE IN FREE AND FORCED DIVES: A MECHANISTIC EXPLANATION

A mechanistic explanation of the heart rate responses during forced and voluntary diving has been presented by Furilla & Jones (1987a). They observed a strong correlation between pre-dive (or pre-trapped) heart rate and heart rate some 2-5 s after diving (or trapping) in Redhead Ducks and Lesser Scaup *A. affinis*. The relation held for voluntary diving, for forced diving in restrained ducks and even held for ducks dived while exercising on a treadmill. Further, the relation also described pre-dive:dive heart rate relations in Tufted Ducks *A. fuligula* studied by Butler & Woakes (1979).

Finally, the relation even applied to diving ducks dabbling. This latter observation is significant because metabolic rate of dabbling ducks must be well below that when diving and therefore contradicts the idea that diving heart rate bears any relation to the level of exercise in ducks diving voluntarily (Butler 1982). Furilla and Jones (1987a) were able to identify regions on a perspective plot of heart rates, resulting from vagal and cardiac sympathetic nerve stimulation in *A. platyrhynchos*, which corresponded to their empirically established pre-dive:dive heart rate relation (Figure 2). In essence, Furilla and Jones (1987) argue that, regardless of the level of cardiac sympathetic excitation, all diving (or trapping) is accompanied by an increase in vagal activity to the heart of some 50% of the maximum possible activation (Figure 2).

For example, in the first dive of a series heart rate increases from the resting rate (C in Figure 2, $100-120 \text{ min}^{-1}$) to around 300 min^{-1} (B). This increase must be due to a reduction in vagal activity because it occurs too rapidly for the cardio-acceleration to be due to increased sympathetic nerve activity (Furilla & Jones 1987a). When the duck dives heart rate falls to around 100 min^{-1} representing an increase in vagal activity of some 50%. At the end of a voluntary diving bout pre-dive heart rate, due to increased sympathetic outflow to the heart, will be around 500 min^{-1} (A) and during dives heart rate will fall to about 250 min^{-1} (F) representing an increase in vagal activity of 50% of maximum. If this animal is prevented from resurfacing heart rate will fall from 250 min^{-1} to around 100 min^{-1} (E) and vagal activity will now be maximal. On the other hand, if the bird is prevented from surfacing after the first dive of a bout then heart rate will fall from 100 min^{-1} (C) to 20 min^{-1} (D) and vagal activation will again be maximal. Other pre-dive:dive heart rates can also be recognised on Figure 2. In the laboratory, pre-dive heart rate is low (about 100 min^{-1}) and is unaffected by blocking the adrenergic receptors on the heart (β -blockade) so the vagal:sympathetic interplay producing this point must be at C. Hence, a 50% increase in vagal activity will give a rate of 20 min^{-1} (D) which is common in laboratory dives. Finally, pre-dive heart rate in β -receptor blocked ducks diving voluntarily never exceeds 300 min^{-1} and is described by point B. During dives, heart rate in β -blocked ducks falls to around 100 min^{-1} (C) which, again, represents an increase in vagal activation of 50% of maximum.

The simplest explanation for this relation would be that a single group of receptors, whose afferent input causes a 50% increase in vagal activity, are excited by water immersion under all conditions. The most likely candidates are the nasal receptors which cause about 80% of cardiac deceleration in forced dives. However, in voluntary dives only 10-30% of the fall in heart rate can be attributed to their stimulation (Furilla & Jones 1986). Nevertheless, nasal receptors could still be involved because it is a possibility that the ducks condition on their input to give a stereotyped vagal output pattern in all dives. Extreme stimulation, occurring in forced and trapped dives, evokes maximal vagal output which is unconditioned and may represent dishabituation of the response to nasal stimulation. If this seems complicated consider for a moment the vasomotor response to free or forced diving. In voluntary diving there is anterior constriction and posterior dilatation while in forced dives total vasoconstriction occurs.

CONCLUSION

The dive response of bradycardia and vasoconstriction is phylogenetically ancient and birds, like all other air-breathing vertebrates, display the response when forced underwater. However, most diving birds show a more marked and sustained response than

that in non-aquatic birds. In voluntarily diving ducks, heart rate, if not blood flow, differs from that seen when birds are swimming on the water surface at the same speed (Woakes & Butler 1983) but a typical dive response is rapidly evoked if the bird is trapped underwater. Even birds such as penguins (*Spheniscus humboldti*, Butler & Woakes 1984) which show no overt cardiac response to voluntary submergence develop a marked bradycardia when denied access to the surface. Hence, the evolutionarily ancient dive response lurks just beneath the surface of the voluntary dive response. In fact, in diving ducks, there is a good correlation between pre-dive and dive heart rate in all types of dive, and even in dabbles, which can be explained by assuming that all dives promote an increase in cardiac vagal activity of some 50% of maximum (Furilla & Jones 1987a). The genesis of this burst of vagal activity is unclear although it seems that psychogenic factors are more important than any change in afferent neural input from neuro-, chemo- or baro-receptors on submergence (Jones et al. 1988).

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SYMPOSIUM 34

PAIN AND STRESS IN BIRDS

Conveners A. ELZANOWSKI and M. ABS

SYMPOSIUM 34

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INTRODUCTORY REMARKS: PAIN AND STRESS IN BIRDS

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To minimize stress of free-living, captive and domestic birds, we have to learn to diagnose it from physiological and behavioural symptoms. The last decade brought substantial progress in this area of knowledge, providing a number of physiological and behavioural indicators of stress.

The plasma concentration of corticosterone is the most widely used physiological measure of stress. It can be easily used for wild birds upon their capture (Wingfield 1988). Capturing procedures are known to impose a considerable stress upon free living birds. Willow Tits *Parus montanus* showed a linear correlation between time spent entangled in a mist net and plasma corticosterone levels (Silverin et al. 1989). The capture stress may be dependent on sex, age and season (Schwabl et al. 1988).

Immobilization may have comparable effects to those of capture in nets. Immobilization is followed by an enduring rise of the corticosterone levels in cockerels (Wodzicka-Tomaszewska et al. 1982). Anaesthesia reduces stress, but acts as a stressor itself and elevates the corticosterone levels in cockerels (Cheung et al. 1988).

The capture stress can be measured also by the loss of body weight. Dunlins *Calidris alpina* and Knots *Calidris canutus* captured for ringing procedures and kept for 24 h lost, respectively 19% and 23% of their body mass. The weight loss is caused by an elevated body temperature and an increased metabolic rate. It occurs primarily at the expense of water, fat, and the tissue of the pectoralis muscles (Davidson 1984). Along with the endocrinological data, such a dramatic weight loss reveals a rather heavy stress experienced by birds upon capture. This calls for more consideration in planning and conducting research involving capture of wild birds. Imperative, at the very least, is the minimization of the capture time!

A major issue in the assessment of stress in animals is the distinction of stress from other forms of arousal, which may be elicited by appetitive or biologically neutral stimuli. Heart-rate may measure a general arousal rather than stress (Patton et al. 1985). Such an arousal may be difficult to distinguish between the two causes of increased heart-rate (Patton et al. 1985). Such an arousal may be difficult to distinguish endocrinologically from the stress proper, e.g., the concentration of catecholamines and their metabolites may be raised to equal levels through either an aversive situation or a pleasant excitement in human subjects (Frankenhaeuser 1976). For that reason, physiological parameters may not be reliable as indicators of a short-lasting stress unless the nature of the stimulus is unequivocally aversive. Behaviour, in particular escape behaviour, has to be used as the indicator of stress in such cases. Also the tonic immobility response is used as a measure of anxiety, especially in

domestic birds. After exposure to stressors, such as electroshocks, the chickens remain longer in the tonic immobility than unstressed controls (Gallup 1977).

Interestingly, birds tend to intensify comfort behaviour, e.g., preening, after being exposed to a potential stressor (Delius 1988). Such comfort behaviour may be used as an additional indicator of the preceding stressful experience. Aside from its likely adaptive significance, this behaviour appears to reflect a positive secondary affective state, which follows a negative affective state evoked by a stressor and thus provides a new evidence for the succession of affective states. A stimulus elicits the primary affective state and determines its positive or negative hedonic value. After the cessation of the stimulus, an animals falls into the secondary affective state with the opposite hedonic value instead of returning immediately to the original state of neutrality. Good evidence for the effective contrast in birds has been presented for the opponent process theory of acquired motivation (Solomon 1982).

This brief review points to an urgent need of a synthetic approach to such complex phenomena as pain, stress and various forms of suffering. It is the compartmentalisation of knowledge that is largely responsible for a certain helplessness of science in this area. A major objective of this symposium is to promote a thoughtful and considerate rather than dogmatically mechanistic study of birds and a more responsible treatment of these animals in industrial practice and elsewhere.

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STRESS IN BIRDS

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ABSTRACT. An understanding of the responses of birds to stressors is critical in order to assess their welfare status. The initial stage of the stress response is activation of the sympathetic nervous system, leading to increased heart rate, glycogenolysis, peripheral vasoconstriction, bronchiodilation, and behavioral arousal. These "fight or flight" responses are potentiated and prolonged by the release of adrenal catecholamines. Pituitary ACTH secretion then stimulates the release of adrenal glucocorticoid hormones (principally corticosterone), resulting in increased gluconeogenesis. Although these responses are adaptive in the short term, persistent glucocorticoid secretion can have a number of deleterious effects, including impaired immunocompetence and the suppression of growth and reproduction. Animals under chronic stress may also display behavioral abnormalities. Wild and captive birds may experience a number of stressors, including feed and water restriction, social interactions, and handling and transport. These stressors are discussed, as are the problems involved in defining and measuring stress in birds.

Keywords: Stress, corticosterone, handling, social behavior, feed restriction, transport.

INTRODUCTION

Stress is rather like the weather as described by the American novelist Mark Twain. "Everybody talks about it", said Twain, "but nobody does anything about it." Publications about stress, both scientific and popular, have proliferated since Hans Selye first used the term in 1950 to describe the physiological phenomena associated with physical insult to mammals. Since then the usage of the term has been extended to encompass all of the traumas of modern life. Stress, however, is not only something that everyone experiences and has an opinion about, but is also something that is not easily defined, measured or controlled. Nevertheless, an understanding of stress is crucial not only to the assessment of the welfare of confined birds, but is also key to determining the adaptive significance of the behavior of wild birds.

STRESS: AN OVERVIEW

The physiological mechanisms of the stress response in mammals were first elaborated by Walter Cannon (1929) and Hans Selye (1950). Exposure of an animal to a physical or psychological stimulus which is perceived as a significant threat to homeostasis (a "stressor") causes activation of the sympathetic nervous system, resulting in increased respiratory and heart rates, bronchiodilation and peripheral and visceral vasoconstriction. These "fight or flight" responses are potentiated and prolonged by the release of catecholamines (epinephrine and norepinephrine) from the adrenal medulla. Shortly thereafter, corticotropin releasing factor (CRF) from the hypothalamus stimulates the anterior pituitary to release adrenocorticotrophic hormone (ACTH), which in turn induces the secretion of glucocorticoid hormones from the adrenal cortex. Glucocorticoid hormones have a number of metabolic effects, but serve

principally to increase glucose availability at a time when the animal has an increased energy requirement.

Selye (1950) viewed these physiological responses as non-specific events that were initiated after exposure to any stressor. They are also beneficial, enabling the animal to cope either by eliminating the source of stress or by adapting to the stressor physiologically and behaviorally. Selye thus used the term General Adaptation Syndrome (GAS) to refer to these physiological events. In Selye's scheme, the GAS occurs in three stages: an initial stage of "alarm"; a stage of "adaptation" during which the adrenal gland hypertrophies and corticosterone is secreted; and lastly, if the stressor persists, a stage of "exhaustion", wherein the depleted adrenal atrophies and the animal develops stress-related pathologies.

A COMPARISON OF STRESS IN BIRDS AND MAMMALS

The basic physiological processes underlying the stress response appear to be similar in birds and mammals. However, both adrenal histology and patterns of hormone secretion do demonstrate some taxonomic differences (Draper & Lake 1976, Holmes & Phillips 1976). Avian species in general have a lower ratio of cortical (glucocorticoid-secreting) to chromaffin (catecholamine-secreting) tissue in the adrenal gland than do mammals, and cell types are intermingled rather than arranged in discrete zones. Basal corticosteroid secretion is generally lower in birds than in mammals, while the catecholamine content of the adrenal gland is higher. Draper and Lake (1976) have suggested that catecholamine-related responses to stress may thus be of more significance in birds than responses related to the glucocorticoid axis. The control of glucocorticoid secretion may also differ from that found in mammals, since there seems to be less hypothalamic control of the pituitary and less pituitary regulation of the adrenal cortex in birds (see reviews in Holmes & Phillips 1976, Siegel 1980).

OTHER INDICATORS OF STRESS

Since Selye's pioneering work, a number of other hormones and neurochemicals including prolactin, glucagon, the thyroid hormones, dopamine, serotonin and central catecholamines have been found to be strongly influenced by stressors (Freeman 1971, 1976). Recent research has also focused on determining the behavioral indicators of stress, particularly in Domestic Fowl *Gallus domesticus* (to be referred to hereafter as Fowl), since there is growing concern about the housing, transport and slaughter of commercially-raised poultry (Mench & van Tienhoven 1986). Behavioral indicators of stress in Fowl include increased attention, fear-related responses, stereotypies, displacement grooming, heightened aggression, cannibalism and an increased duration of tonic immobility (Hill 1983, Williams 1984, Jones 1987).

Persistent corticosterone secretion associated with chronic stress in birds may have a number of other deleterious effects which can be observed at the whole-animal level. These include the suppression of humoral and cell-mediated immunity and a resultant increase in morbidity and mortality (Siegel 1985, Gross & Siegel 1988) as well as decreased growth in maturing birds and weight loss in adults (Bartov et al. 1980). The secretion of other steroid hormones is also affected, thus influencing both physiological and behavioral aspects of reproduction (Edens 1983, Ottinger & Mench

1989). Long-term administration of corticosterone to birds causes the cessation of egg production, the inhibition of gonadal growth and gonadal atrophy (Flickinger 1966, Gross et al. 1980, Williams et al. 1985) and the abandonment of nestlings (Silverin 1986).

CAVEATS

There are a number of theoretical and methodological problems associated with interpreting changes in the secretion of stress hormones as a measure of welfare in birds. Basal corticosterone levels, for example, can be influenced by a variety of factors which are independent of the stressors under consideration (Figure 1). Methodological problems can be partially overcome by careful experimental design and technique, such as using implanted radiotransmitters to measure responses without disturbing the animal (Duncan 1983). The theoretical questions, however, are not so easily resolved (Rushen 1986). As previously mentioned, increases in stress hormones are physiologically adaptive for the animal. Indeed, a certain amount of stress is probably even imperative for optimal functioning (Gross & Siegel 1981). Are elevated levels of corticosterone therefore reliable indicators of reduced welfare? Moberg (1987) and others have argued that other measures (e.g. immunosuppression prior to the appearance of morbidity) are better indicators of "distress", since they mark the borderline between adaptive responses and the development of pathologies.

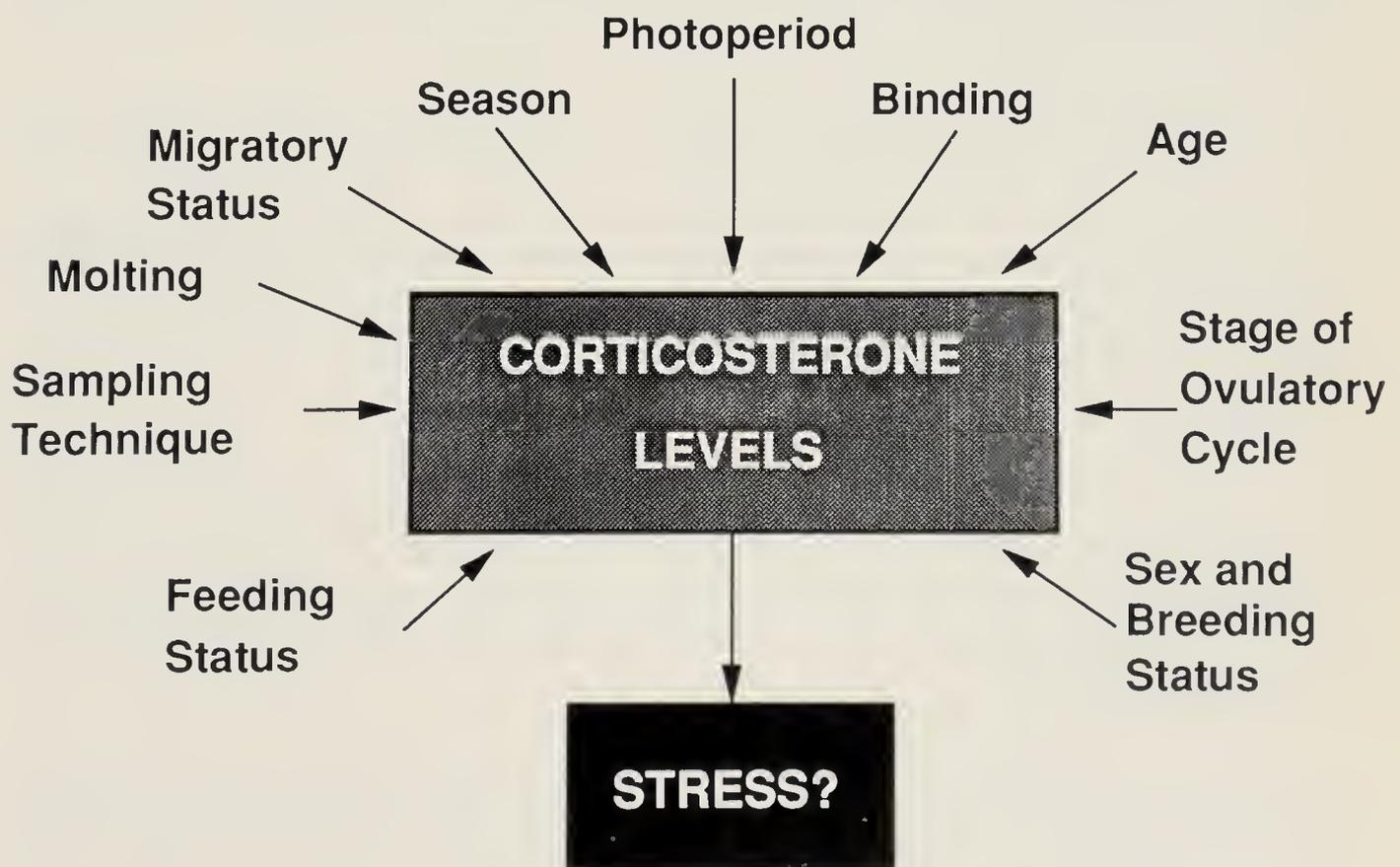


FIGURE 1 – Factors which can affect basal corticosterone secretion in birds.

Perhaps most significantly, Selye's (1950) concept of a generalized physiological response has undergone considerable revision since it was first elaborated. Mason's work with primates (1971) made researchers cognizant of the influence of psychosocial and experiential factors on manifestations of stress (Dantzer & Mormede 1983). There is now abundant evidence that physiological responses in mammals are

strongly influenced by factors such as prior exposure to the stressor or similar stressors, genetics, sex, age, social context in which the stressor is encountered, predictability and the animal's ability to control the source of stress (Henry & Stephens 1977). However, there is little information on the role of these cognitive factors in birds.

STRESSORS IN BIRDS

The physiological and neurochemical effects of physical stressors such as heat, cold, anesthesia and surgery, noise and exercise in birds have been reviewed elsewhere (Freeman 1971, 1976, Siegel 1980, Harvey et al. 1984). In this paper I will concentrate on several potential stressors to which captive and domesticated birds are often exposed, namely social interactions, handling and transport, and feed and water restriction. The corticosterone response will be emphasized, since this has been the most widely-studied stress response in birds.

Social interactions

Chickens reared for commercial poultry production are often housed in social environments where there are high population densities and/or large group sizes, and where unfamiliar animals are introduced into the social group. These factors can lead to heightened aggression and social instability and thus impact the welfare of the animal. A consideration of social factors is also important in the treatment of birds used for research and as pets.

SOCIAL DISRUPTION. Isolating Fowl chicks from companions results in a rise in corticosterone within 30 minutes (Gibbs & Ng 1984). Similarly, increases in corticosterone, followed by behavioral indicators of stress including reduced feeding, peeping, defecation and jumping are seen as the size of the social group is progressively decreased by removal of chicks (Jones & Harvey 1987). In adult birds, however, removal of the alpha male from a long-established rooster groups has little effect on plasma corticosterone (Mench & Ottinger, 1991).

Mixing unfamiliar animals also results in heightened stress responses. Corticosterone levels increase in juvenile Fowl during the first week after unfamiliar males are mixed (Williams et al. 1977), although they decline to normal levels thereafter. Daily introduction of unfamiliar animals results in immunological and reproductive suppression in both Fowl and Japanese Quail *Coturnix japonica* (Gross & Siegel 1981, Edens et al. 1983, Edens 1987).

Although these studies would seem to suggest that the agonistic encounters associated with mixing are a source of stress, there is in fact little evidence that aggression in birds is associated with elevated corticosterone levels (Harding 1981, Ramenofsky 1985, Mench & Ottinger 1991). Corticosterone may even suppress aggressive behavior, since corticosterone-implanted male Song Sparrows *Melospiza melodia* fail to defend their territories against simulated intruders, an effect which is independent of changes in the levels of gonadal hormones (Wingfield & Silverin 1986).

SOCIAL DOMINANCE. Social subordination in animals may be associated with reduced access to feed, water, breeding territories and other important resources as well as the receipt of aggression. The effects of social subordination on reproduction may be

pronounced, and include delayed sexual maturation and/or the suppression of egg laying, fertility and reproductive behavior in adult birds (see reviews in Edens 1983, Ottinger & Mench 1989).

Whether these reproductive effects are mediated through corticosterone secretion, however, is less clear. In several species, subordinate birds have been found to have hypertrophied adrenals (Flickinger 1961, Fretwell 1969, Murton et al. 1971). Corticosterone and social status are inversely correlated in Harris' Sparrows *Zonotrichia querula* (Rohwer & Wingfield 1981). In other studies, however, no correlation between adrenal weight and status (Siegel & Siegel 1961) or status and basal corticosterone levels (Williams et al. 1977, Marsteller et al. 1980, Cunningham et al. 1987, 1988, Mench & Ottinger 1991) is apparent. This may be either because stress does not impact animals in a strictly linear fashion within a hierarchy (Gross & Siegel 1983) or because subordinate animals adapt physiologically when they are maintained in stable social groups, although they may show an impaired or exaggerated hormonal response after exposure to a stressor; this phenomenon has been observed in primates (Kaplan 1985).

POPULATION DENSITY. In Fowl, crowding and/or enlarged group sizes (two variables which are confounded in most studies) are associated with adrenal hypertrophy and elevated corticosterone levels (Siegel 1958, 1960, Flickinger 1961, Koelkebeck & Cain 1984, Mashaly et al. 1984, Craig et al. 1986). A depression in egg production is also common with increasing hen density (Adams & Craig 1985) and is most pronounced in subordinate females (Cunningham & van Tienhoven 1983), although it is not clear that these effects are mediated through increased corticosteroid secretion (Koelkebeck and Cain 1984, Craig et al. 1986, Davami et al. 1987, Cunningham et al. 1988).

Capture, handling, immobilization and transport

There are significant welfare issues regarding the treatment of both wild birds destined for the pet trade and commercial poultry prior to slaughter with regard to capture and transport. The physiological and behavioral responses to transportation have, however, received comparatively little systematic research attention, probably because there are many confounding factors (such as social disruption and feed and water deprivation) involved.

Corticosterone levels begin to increase significantly in Fowl within a few minutes after handling (Beuving & Vonder 1978, Freeman & Flack 1980). Hens show elevations in heart rate, respiration rate and corticosterone when removed from their enclosures and carried by an experimenter which may persist for 2 h (Howard 1971, Broom et al. 1986). Handling by humans may be particularly stressful primarily as a result of the predatory overtones associated with the human presence. Duncan et al. (1986) found that heart rates and tonic immobility durations increased in chickens when they were captured either by or and with a purpose-designed machine, but both returned to normal more quickly in the machine-caught birds.

Early handling which results in the socialization of birds to humans, however, can be beneficial. Fowl chicks handled during the brooding period have been shown to have improved disease resistance and a stronger immune response to antigenic challenge. Conversely, immune competence is particularly poor in birds exposed to negative

human contact (Gross & Siegel 1982). Habituating hens to handling can result in a reduction in the corticosterone response (Webb & Mashaly 1984).

Lengthy immobilization also causes increases in corticosterone which persist throughout the immobilization period. This is true whether birds are immobilized by hand (Beuving & Vonder 1978), by tying their legs together (Wodzicka-Tomaszewska et al. 1982) or by tightly confining them in a shipping crate with other birds (Beuving & Vonder 1978).

A number of physiological indicators of stress increase in laying hens after they are handled, crated and transported for two hours (Broom et al. 1986). In White-crowned Sparrows *Zonotrichia leucophrys*, the stress associated with capture and transport may persist for up to three weeks depending on the numbers of birds housed together after transport (Wingfield et al. 1982).

Feed and water restriction

In the wild, birds may experience periods of varying length during which feed and water are scarce or unavailable. Feed and water restriction or deprivation are also commonly employed in commercial poultry management in order to induce molt in laying hens and to restrict growth in meat-type birds used for breeding stock.

Several studies have assessed the impact of feed and water restriction on stress responses in birds. Fasting birds for as little as 10 to 24 h results in persistent increases in corticosterone secretion and adrenal hypertrophy (Nir et al. 1975, Freeman et al. 1980, Harvey et al. 1980, Scanes et al. 1980, Scott et al. 1983), as does restricting total energy intake to 75% of ad libitum during maturation; in the latter case, birds appear to accommodate to the feed restriction regimen within five weeks (Freeman et al. 1981). In a study of simultaneous feed and water restriction comparable to that used commercially to induce molt in laying hens, however, Beuving and Vonder (1978) found that corticosterone levels declined after 2.5 days when water was provided even though feed was still unavailable. Since water restriction and water deprivation are both potent stressors in birds (Tome et al. 1985), the separate and combined effects of feed and water deprivation require further investigation.

The results of several feed restriction studies indicate the importance of psychogenic factors with regard to stress responses in birds. Fasting-induced rises in corticosterone are attenuated in chicks previously accustomed to repeated shorter fasts (Rees et al. 1985). When fasted chicks are refed, corticosterone levels drop to normal within 30 minutes. This decline occurs not only when chicks are allowed to feed freely, but also when they are provided only a small amount of food or permitted to feed for a few seconds, although the length of time that corticosterone levels are decreased is proportional to the feeding time and amount ingested (Harvey & Klandorf 1983). Interestingly, corticosterone levels also decrease in fasted chicks that are simply shown food or provided with a nutritionally inert substance to eat, indicating that the stress associated with feed restriction is only due partly to metabolic effects (Harvey et al. 1983).

In an unpublished study, we examined the effects of commercial feed restriction programs on behavioral and physiological indicators of stress in poultry. Male Fowl were placed on one of two feed restriction programs commonly used in commercial

poultry production throughout development. Both of these feeding programs are designed to retard body weight gain to approximately 45% of that of ad libitum fed birds. On one of the programs measured amounts of feed are delivered daily, while on the other feed is delivered only on alternate days. Although both programs resulted in an increase in aggression, corticosterone was elevated only in those birds receiving feed on alternate days (Figure 2). Thus even though both groups were receiving an identical amount of feed, feeding at shorter intervals was less stressful, perhaps because it decreased the perception that feed delivery was unpredictable. These studies indicate that the cognitive and perceptual factors associated with physiological stress responses may be of great significance in birds, although they have received little research attention.

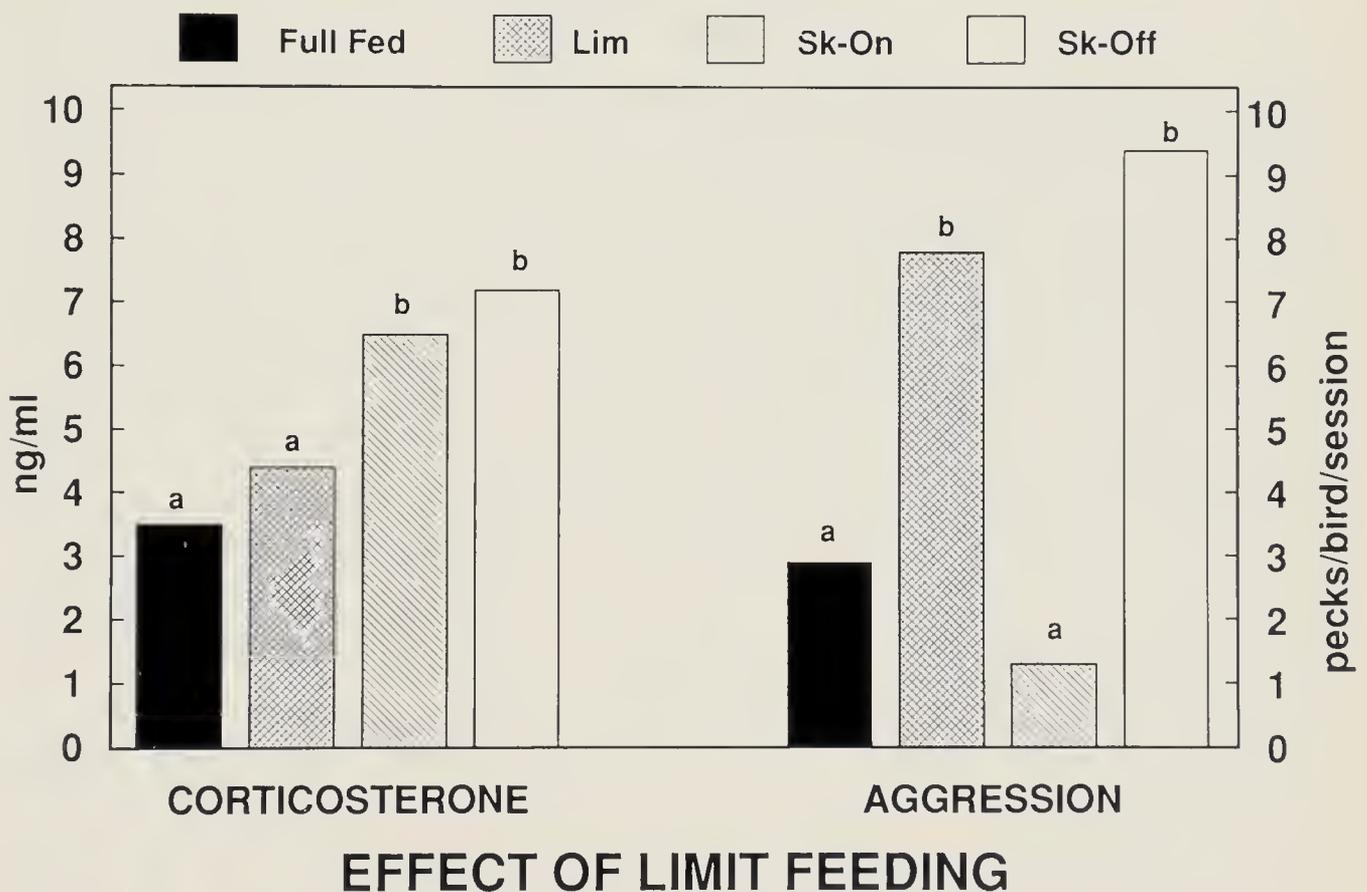


FIGURE 2 – Aggression and corticosterone levels in male Fowl either fed ad libitum (AD) or placed on commercial feed restriction programs where feed was delivered either daily (LIM) or on alternate days (SK). Corticosterone levels were significantly higher in the SK birds, even though they received an amount of feed equivalent to the LIM birds. Aggression was elevated in both feed restricted groups.

CONCLUSIONS

Birds in both wild and captive situations may experience a number of psychogenic and physical stressors. An understanding of physiological stress responses is critical to the assessment of the welfare of domesticated and captive birds. Assessing physiological stress in birds is not, however, an endpoint unto itself. Hormonal and immunological measures strongly suggest that handling, transportation, feed and water restriction and certain types of social encounters with conspecifics are stressful to birds. In order to provide adequate answers to the questions that are currently being posed about the welfare of birds, however, additional information is required. In

particular, research attention should be directed toward behavioral indicators of stress as well as the role of cognitive and perceptual factors in the stress response.

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BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES TO PAIN IN THE CHICKEN

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ABSTRACT. Pain can be divided into acute pain lasting for minutes, hours or days and chronic pain lasting for weeks, months and even years. Both of these aspects of pain have been investigated in the chicken. Acute noxious cutaneous stimulation activates nociceptors resulting in characteristic changes in behaviour together with increases in blood pressure and heart rate. Following major trauma, such as partial beak amputation, there is anatomical, behavioural and physiological evidence of persistent chronic pain. The behavioural and physiological responses of birds to noxious stimuli are essentially similar to those shown by mammals and so the same ethical considerations that are applied to mammals should be extended to birds.

Keywords: Chicken, *Gallus gallus*, pain, trauma, behaviour, heart rate, blood pressure, beak amputation, nociceptors.

INTRODUCTION

Pain is a subjective unpleasant, emotional experience. Whereas verbal communication is essential in defining pain in humans, a definition of pain in animals must rely on behavioural expression. Zimmermann (1986) has proposed a definition of pain which can be adopted for animals: "Pain in animals is an aversive sensory experience caused by actual or potential injury that elicits protective motor and vegetative reactions, results in learned avoidance behaviour, and may modify species specific behaviour, including social behaviour". This, as Zimmermann has stressed, is not a comprehensive definition, as it does not help us to unambiguously decide whether or not an animal is in pain. There is no reliable or universal indicator of pain in animals but this definition does provide a framework on which to decide whether or not an animal is in pain.

In this paper I will briefly review some of the work performed in our laboratory to try not only to detect and assess pain in the Chicken *Gallus gallus* but also to try and answer the question: does the pain-system of birds differ from that of mammals? The work falls into three main areas. Firstly, because pain is a sensory experience, we have investigated the cutaneous sensory receptors which signal actual or potential tissue injury, the nociceptors. Secondly, the protective motor (behavioural) and vegetative reactions (autonomic cardiovascular changes) were investigated following nociceptive stimulation. Thirdly, anatomical, behavioural and physiological evidence was collected to determine the chronically painful consequences of major trauma.

NOCICEPTORS

Three types of nociceptors have been identified in birds. Thermal nociceptors without mechanical sensitivity have been reported in the Chicken (Beward 1985) and the

Pigeon *Columba livia* (Necker & Reiner 1980). Mechano-thermal (polymodal) nociceptors which responded to thermal and mechanical stimulation were identified in the Pigeon feathered skin (Necker & Reiner 1980) and have been extensively investigated in the Chicken beak (Gentle 1989). Finally, there are a group of high threshold mechanical nociceptors reported in the Chicken (Roumy & Leitner 1973, Holloway et al. 1980) and other birds (Gregory 1973, Gottschaldt et al. 1982) which have been investigated quantitatively only in the Chicken (Gentle 1989).

Mechano-thermal (polymodal) nociceptors

These receptors showed no spontaneous activity and responded to heating of the receptive field with thresholds above 40°C. They also responded to mechanical stimulation but not to cooling down to 0°C. The units identified had receptive fields which were circular or elliptical about 1 to 2 mm in diameter. The response thresholds to thermal stimulation ranged from 41°C to 52°C (mean 44.5°C). Mechanical thresholds, using a 0.5 mm diameter probe, ranged from 2 to over 50 g (median 25 g). Conduction velocities ranged from 0.4 to 1.86 m/s so that the fibres were in the C-fibre range. The discharge pattern of the majority of the chicken mechano-thermal nociceptors during sustained supra-threshold heat stimulation consisted of an irregular continuous discharge. Increasing the stimulus magnitude resulted in an increase in the number of responses. Some of the fibres continued to show an increase in response up to the highest temperature tested (56°C). Other fibres showed a clear peak in response at a lower temperature and increasing stimulus intensity beyond this temperature resulted in a reduced response.

High threshold mechanical nociceptors

These receptors showed no spontaneous activity and only responded to high threshold mechanical stimulation. Response thresholds ranged from 5 to over 50 g (mean 25 g). Conduction velocities were measured and ranged from 1 to 5.5 m/s (mean 2.4 m/s) which would indicate small myelinated A-delta and unmyelinated C-fibres. Receptive fields for most of the units identified were similar to the polymodal nociceptors but some units had larger receptive fields. Increasing stimulus strength over the threshold produced an increase in response: in some units the stimulus-response curves were linear, whereas in others it was positively accelerating, i.e. the slope of the curve at any point gets bigger as the stimulus gets bigger. In response to a maintained mechanical displacement the units adapted relatively rapidly at low stimulus intensities but the length of response increased with increasing stimulus magnitudes.

In terms of discharge patterns and receptive field sizes, the nociceptors found in the Chicken are similar to those found in a variety of mammalian species (Iggo 1959, Bessou & Perl 1969, Beitel & Dubner 1976, Torebjork et al. 1984). Birds therefore have a well developed sensory system to monitor very precisely external stimuli which result in actual or potential tissue damage.

BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES TO NOCICEPTIVE STIMULATION

Having identified and characterised nociceptors, the next important step was to determine the behavioural and physiological changes which follow nociceptive stimulation. A number of different nociceptive stimuli have been investigated and have

included electric shock (Gentle & Richardson, unpublished observations), comb pinch (Woolley & Gentle 1987), cutaneous thermal stimulation (Woolley & Gentle 1987), algogenic substances (Gentle & Hill 1987) and feather removal (Gentle & Hunter 1990). These nociceptive stimuli produced a rapid increase in heart rate and blood pressure, the magnitude and duration of the response depending on the strength of the stimulus. After simple comb pinch the heart rate had returned to normal within 35 s whereas following a 1 s of 0.25 mA electric shock it took 2 min to return to normal. It would also appear that heart rate is a more variable measure of nociceptive stimulation than blood pressure. In one experiment the heart rate and blood pressure were recorded while single feathers were removed at regular intervals. Feathers were removed from different regions of the body and this was repeated in nine birds. While there was a clear increase in blood pressure after each feather removed in all birds not all feather removals gave a sustained increase in heart rate.

Two different behavioural patterns were observed following nociceptive stimulation. Following electric shock or comb pinch, active avoidance behaviour was observed and the birds showed vigorous escape attempts involving jumping, wing flapping and occasionally calling. Following cutaneous thermal stimulation or after the oral presentation of algogenic substances, the birds showed passive immobility but no escape attempts or vocalisations. The passive immobility was characterised by a crouched posture with the head pulled into the body and the eyes partially or fully closed. Both the active and passive behavioural changes were observed following feather removal. A single feather was removed from adult hens every three minutes and the behaviour and electroencephalogram recorded (Gentle & Hunter 1990). The first feather removed resulted in the birds becoming agitated with jumping, wing flapping and/or vocalization. The continual removal of feathers did not produce an exaggerated escape response; instead they were observed shortly after feather removal to crouch in the cradle with the tail feathers and head lowered in an immobile state. During this period of immobility following feather removal, the EEG showed a characteristic high amplitude low frequency activity similar to that seen in sleep (Van Luitjelaar et al. 1987, Tobler & Borbely 1988) or catatonic states such as tonic immobility (Silva et al. 1959; Klemm 1966, Ookawa 1972, Carli 1974, Gentle et al. 1989).

Birds, like mammals, have therefore two basic modes of response to external noxious stimulation. There is the flight-fight response and the conservation-withdrawal response. The flight-fight response is seen typically after a comb pinch stimulus and the animal struggles to escape. The comb pinch would activate a variety of cutaneous mechanoreceptors but it seems likely that it is the activation of the A-delta high threshold mechanical nociceptors which initiate the behaviour.

The conservation-withdrawal system is typified by the crouching immobility seen after noxious cutaneous thermal stimulation. Noxious thermal stimulation would produce activity primarily in unmyelinated C-fibre polymodal nociceptors and it is the activation of these receptors which initiates this behaviour. The change from active escape to crouching immobility following repeated feather removal is of interest and may be related to learned helplessness. Learned helplessness is a behaviour pattern which develops when an animal experiences traumatic events which are aversive and which continue to occur independently of any attempts by the animal to reduce or eliminate

them. A similar immobility has been observed by birds being feather pecked when the pecked bird showed little or no behavioural response to indicate that the removal of feathers is painful.

PAINFUL CONSEQUENCES OF TRAUMA

Although acute pain is important to the animal, it is chronic pain which may last for weeks, months or even years which presents a major welfare problem. We have been trying to evaluate the painful consequences of major trauma using partial beak amputation (beak trimming) as a model. Partial amputation of the beak is a common agricultural practice and involves the partial removal of the upper and/or lower beak in order to prevent or control feather pecking and cannibalism in intensively reared poultry. The amputation is accomplished by a combination of cutting and cautery. From the work on nociceptive stimulation it seems likely that there will be pain associated with the initial trauma of amputation. Recordings from the sensory nerves innervating the beak have demonstrated massive injury discharges which can persist for as long as 48 s (mean 15 s) immediately after amputation. An analysis of the responses of these primary sensory beak afferents failed to show any abnormal neural activity for at least 4.5 h after amputation. Behavioural analysis of the birds after amputation also failed to show any pain related behaviours such as guarding behaviour of the beak or increased inactivity. It seems likely therefore that for the first few hours after amputation the birds experience a pain-free period similar to that sometimes experienced by humans following major trauma (Ty et al. 1984). By approximately 24 h after amputation the birds were showing pain related behavioural changes with the birds unwilling to peck at the environment, reduced food and water intake, together with long periods of sitting and dozing. The behaviour of the bird changes over the next six weeks and food and water intake increases up to preoperative levels. A number of behavioural patterns do not, however, change and the bird shows a reluctance to use the beak for unessential activities such as exploratory environmental pecking, head shaking, beak wiping, and preening (Gentle et al. 1990). This reduced usage of the beak can be interpreted as guarding behaviour so commonly seen in humans and other mammals following painful injuries. Dozing and general inactivity were observed by Eskeland (1981) in birds over a 56 week observation period. Increases in inactivity are common in humans suffering from chronically painful conditions.

In addition to this behavioural evidence there is anatomical and physiological evidence for chronic pain following amputation. In an anatomical study of the nerves in the beak of the chicken from 1 h to 70 days after amputation (Gentle 1986) it was found that the beak had a limited ability to regenerate normal beak structure. By 15 to 30 days after amputation the stump had healed. The beak then continued to grow and retained a similar general external conformation to the normal beak, the normal dermal structure, however, did not regenerate. The healed stump contained a continuous layer of epithelium with outer keratin sheath overlaying an extensive area of scar tissue. Adjacent to the scar tissue, the damaged and regenerating nerve fibres formed extensive neuromas. Electrophysiological recordings from the nerve fibres innervating these neuromas showed abnormal features not seen in normal trigeminal afferent fibres (Beward & Gentle 1985). The most characteristic abnormality encountered in the beak stump was the presence of large numbers of spontaneously active units. The

pattern of spontaneous discharge was basically either regular, irregular or bursting. The effects of heat, cold and mechanical stimulation on the rate of response varied from unit to unit. For some units, all stimuli produced an increase in discharge whereas others were totally unaffected by external stimulation. These abnormal units were recorded from the beak stump at 5 - 83 days after initial amputation with their receptive fields located on the distal tip of the stump and at varying distances (up to 12 mm) proximal to it. This spontaneous activity seen in the amputated stump of the beak is markedly similar to that observed in the experimental neuroma preparation developed initially by Wall, Devor and coworkers (Wall & Gutnick 1974, Govrin-Lippmann & Devor 1978, Devor & Bernstein 1982) in the rat and later extended to the mouse (Scadding 1981) and cat (Blumberg & Janig 1984). These studies on peripheral nerve injury and subsequent neuroma formation in mammals have suggested that abnormal activity arising from regenerating axons is implicated in post-amputation stump pain (Wall 1981).

CONCLUSIONS

The presence of nociceptors which signal actual or potential tissue damage, the behavioural and physiological changes resulting from nociceptive stimulation together with the physiological and behavioural changes following trauma satisfy the definition proposed for pain in animals (Zimmermann 1986). The close similarity between birds and mammals in their physiological and behavioural response to painful stimuli argues for a common sensory and emotional experience. It is therefore essential that the ethical considerations normally granted to mammals be extended to birds.

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MOTIVATION AND SUBJECTIVE EXPERIENCE IN BIRDS

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ABSTRACT. Self-stimulation of certain brain sites and the operant avoidance of stimulation of others, drug dependence, play and the evidence for subjective value perception in the appetitive and avoidance behavior of birds and mammals all point to a motivation system based on positive and negative affective states having similar neural mechanisms and the same biological functions as our human good and bad feelings associated with sensory experience. Affective motivation evolved largely independently in mammals and birds, in correlation with the parallel evolution of their cognitive capacities. It is proposed that a prerequisite for the independent evolution of play in birds and mammals was the capability of deriving a subjective reward from activities per se, in addition to the reward derived from an external stimulation. As beings capable of experiencing positive and negative affective states, birds ought to be treated as moral patients, i.e. as appropriate objects of human moral concerns.

Keywords: Motivation, affective state, emotion, subjective experience, brain stimulation, intracranial self-stimulation, reward, punishment, play, values, morals, ethics.

INTRODUCTION

We humans have evolved on this planet and, as a species, still have many close relatives. This fact is of some importance for understanding the behavior of both ourselves and our vertebrate relatives. The motives for our actions are certainly more complex than that of any other animal, which is due to the development of uniquely human forms of thought and speech. However, some human motives are clearly independent in their biological function and largely independent in their action of any specifically human attributes. This part includes rewarding feelings that accompany consummatory acts such as eating, drinking, and sex, and negative feelings such as pain, fear and anxiety, hunger, and thirst. An obvious biological function of these feelings is to motivate adaptive behavior. Even though humans have learned to some extent to manipulate their feelings, it remains true that the primary function of hunger and thirst is to ensure the satisfaction of metabolic needs, the primary function of pain and fear is to prevent injury and death, and the primary function of sexual pleasure is to promote reproduction. Motivation constitutes the primary, if not the only, biological function of subjective experience. Therefore, it seems reasonable to expect that the analysis and comparison of motivational systems will provide evidence for the presence of subjective experience in animals and reveal some of its functional characteristics.

THE NEURAL BASIS OF MOTIVATION

Mammalian behaviors indicative of fear and aggression, hunger, satiety, sexual pleasure and euphoria are under the control of fairly well-localized nuclei in the limbic system, which includes primarily the hypothalamus and the phylogenetically oldest parts of the forebrain. Pain reactions defy localization to a well-defined center or region although parts of the limbic system are involved. The avian forebrain is very different from that found in mammals in that it is dominated by the striatal rather than the

cortical parts and has no distinct neocortical layering. However, birds do have an equivalent of the limbic system, which includes the caudal and medial divisions of the archistriatum (Cohen & Karten 1974, Breazile & Hartwig 1989). Avian behaviors indicative of fear and aggression are controlled by the septal region, archistriatum and paleostriatum augmentatum, tracts connecting the forebrain with the diencephalon and mesencephalon (septo- and the occipito-mesencephalic tracts, anterior commissure and parts of the lateral forebrain bundle), dorsal thalamic nuclei, intercollicular and dorsolateral mesencephalic nuclei, and anterior hypothalamus (Vowles & Beasley 1974). The paleostriatum augmentatum is also known to support self-stimulation (see below) and thus seems to be the prime candidate for a substrate of gratifying aggressive motivation, which is also known in mammals (Doty 1969); indeed in one pigeon the same site in the paleostriatum augmentatum was reported to be self-stimulated and to evoke aggression when experimenter-stimulated in the presence of another, normally dominant bird (Goodman & Brown 1966).

Two kinds of behaviors can be elicited by electrical brain stimulation (ESB): ESB-imposed behaviors which are automatic reactions limited in duration to the time of stimulation, e.g. reactions elicited by stimulation of the mammalian neocortex (Doty 1969), and ESB-motivated behaviors which include self-stimulation (known as the intracranial self-stimulation, ICSS) and the avoidance of stimulation. Mammals and birds with electrodes implanted in specific brain sites quickly learn to press a lever or peck a key to self-stimulate, sometimes to complete exhaustion, while animals with electrodes in other sites, some of which are known to evoke aversive reactions, will desist from actions that result in brain stimulation (Stellar 1982). There is extensive evidence for self-stimulation from several forebrain sites including the nucleus basalis, fronto-archistriate tract, and paleostriatal complex (Zeigler et al. 1978, Delius & Pellander 1982) and some evidence for the avoidance of stimulation (Goodman & Brown 1966, Macphail 1967) in birds. Stimulation of some sites apparently acts as a reward, often more powerful than natural consummatory acts, while stimulation of others acts as a punishment. There is a general consensus that brain self-stimulation involves an artificial activation of a natural mechanism (Gallistel et al. 1981, Halperin & Pfaff 1982, Olds & Fobes 1981, Stein & Beluzzi 1987) and the same can be assumed for the avoidance of stimulation.

The comparative evidence does not leave any reasonable doubts that ESB-motivated behavior is indeed motivated through affective states (see also Gray 1988), which is the only known alternative to automatic behavior (Epstein 1982). Human patients with electrodes implanted in appropriate brain sites report pleasurable or unpleasant effects of ESB and some patients may spontaneously self-stimulate, e.g. for sexual excitement (Delgado 1976). Together with our common hedonic experience, such as pain, taste, or sex, this demonstrates that stimulation of certain brain sites translates into positive or negative affective states and that this translation is automatic and largely independent of human thinking or will. Since ESB-motivated behavior in other mammals is based on homologous substrates and reveals all characteristics of affective behavior (Epstein 1982), it is rather obvious that its motivation involves positive and negative affective states. Since birds parallel mammals in many other brain capacities, the commonality of the motivational principle provides the only acceptably parsimonious explanation.

As the obvious function of subjective reward is to promote consummatory acts and that of subjective punishment to promote avoidance of actual or potential harm, ESB-

motivated behavior provides strong evidence that the natural appetitive and avoidance behavior in mammals and birds is voluntary rather than a part of any automatism, homeostatic or otherwise. Indeed, some sites supporting self-stimulation are known to control natural appetitive and consummatory behaviors and the avoided sites are known to control behavior indicative of fear. This is not to say that every behavioral act in an appetitive or avoidance sequence must be voluntary. Complex natural behaviors may and commonly do incorporate some partial automatisms, innate or learned, which may obscure their emotional causation and provide grounds for mechanistic interpretations.

Another way to artificially stimulate the natural reward mechanism is the administration of drugs (Kornetsky & Bain 1990). In fact, most drugs of abuse enhance the rewarding effects of brain self-stimulation (Kornetsky & Bain 1990). Therefore, dependence and/or withdrawal symptoms are good evidence of true affective motivation. Using methadone and its antagonist naloxone, Bronson and Sparber (1989a,b) demonstrated acute opioid dependence and withdrawal symptoms in the embryos and hatchlings of the chicken. The rewarding effects of apomorphine, a dopaminergic drug which is self-administered by mammals, have been demonstrated in pigeons, which showed a persistent preference for the place where this drug was administered by the experimenters (Burg et al. 1989).

SUBJECTIVE VALUE PERCEPTION

Adaptive behavior entails avoiding interactions that impair fitness, pursuing interactions that enhance fitness and, at least for some animals including the higher vertebrates, doing this in some proportion (in terms of time, energy, speed or other parameters) to actual fitness costs and gains of incurring the present situation and to potential costs of failing to reach or to avoid an expected situation. Therefore, if adaptive behavior is motivated through affective states, these must be consistent with and proportional to the present or expected impact of the incentive situation on fitness. Affective motivation of adaptive behavior implies subjective perception of the costs (Dawkins 1990, Hughes & Petherick 1990) as well as gains in the common currency of fitness, which amounts to a subjective perception of objective biological values. This is amenable to experimental verification since the dynamics of affective states has its characteristic observable concomitants and the biological value of many incentives, such as food or predators, can be and commonly is estimated on objective grounds.

In accordance with the evidence from ESB-motivated behavior, the appetitive and avoidance behavior of higher vertebrates reveals a basic division between motivational states, which corresponds to the good-bad polarization of human hedonic experience. States elicited by either appetitive or aversive incentives enhance one another while the states elicited by incentives with opposite biological values inhibit one another (Toates 1986, 1988 and references therein). In the typical case of conditioned suppression, which is well known from experiments with mammals, a signal for an aversive event interferes with bar-pressing for food; the conditioned suppression was also demonstrated in birds (Hoffman 1965). Even more importantly, a signal for food inhibits bar-pressing to avoid shock even though in each case the food and an aversive event are delivered independently of each other. Inasmuch as affective

states are mental and involve the whole body, interference is what one should expect between two affective states with opposite value perceptions. This is in marked contrast to the automatic behavior as observed in insects, which will continue with normal activities even after severe injury or removal of body parts (Eisemann et al. 1984).

There are exclusively value-dependent similarities in reactions on otherwise dissimilar appetitive or aversive situations, amounting to value-dependent categorization. For example, rats tend to bury such disparate aversive objects as shock electrodes and poisoned food. Another form of value-dependent categorization is the value extension to accompanying events, as shown by rats who greet another rat that has been used as a signal of food (for discussion and references see Walker 1987) and is therefore perceived as something pleasant; and pigeons who peck a key to extinguish another key that signalizes no food (Rilling et al. 1973) and thus has apparently acquired a negative value. A spectacular example of value-dependent categorization has become known through behavioral research (Mackintosh 1983, p. 123): animals tend to react in a similar way to a punishment and an omission of the reward in the fixed schedule conditioning.

Both birds and mammals show the phenomenon of affective contrast (Solomon & Corbit 1974, Solomon 1982), wherein a primary affective state, aroused by an incentive stimulus, is followed by a secondary, opposite affective state, rather than a return to neutrality after the stimulus is removed. In the well-known imprinting process, newly hatched ducklings become attached to any moving object: when presented with such an object, the ducklings show interest and follow it; when the object is removed the ducklings react with distress calls. The appearance of the object acts as a reward and the disappearance as a punishment, since ducklings will perform various operant responses, such as pecking a pole, both to make the object appear and to prevent it from disappearing (Bateson 1973, Solomon 1982). There is a correlation between the reaction with the quality of reinforcement: the ducklings emit even more distress calls after the disappearance of the object when its presentation has been paired with a honking sound (Starr 1978). This experimental work demonstrates that the observed sequence of reactions is caused by the sequence of affective states rather than an innate automatism and that cessation of stimulation perceived as pleasant or unpleasant can be perceived as being of opposite value.

In addition to direct behavioral evidence, the subjective perception of values is implicit in the current views on associative learning in higher vertebrates, which recognize the leading role of mental expectancy in instrumental and even in classic (Pavlovian) conditioning (Mackintosh 1983, Walker 1983, 1987). Expectancy involves the concentration of attention on a mental representation of something absent. While the present events may be neutral and still attract attention, the only reason for an animal (and in fact most if not all people) to concentrate on something absent is its being either attractive or aversive. Expectancy in instrumental learning implies subjective value perception. This concurs with Epstein's (1982) idea of expectancy being one of the major criteria of affective motivation.

PLAY

Play is a natural behavior of mammals and birds, which makes affective motivation particularly manifest. As a voluntary, casual, in detail unpredictable activity (Millar

1987) play constitutes a true opposite of automatic behavior (Hediger 1980), although play commonly incorporates variably modified elements of other behaviors, some of which may be automatic. The combination of our human self-knowledge of play and the similarity in the basic forms and rules of this behavior in humans and other mammals, which is attested by the human empathic ability to spontaneously recognize animal play (Martin and Caro 1985), supports the commonsense perception of play as a voluntary, pleasing, autotelic activity, rewarding for its own sake (Young 1961, Baldwin 1982). This has been confirmed by demonstrating that play acts as a reward in instrumental learning and that deprivation of play is followed by a rebound (Fagen 1981).

Rewarding effects account for the repetitive and exaggerated behaviors characteristic of play (Millar 1987), as some movements and actions are likely to stimulate the reward-releasing neurons more than others. This hypothesis can be tested by recording the brain activity, inasmuch as the rewarding process has its correlate in the firing of neurons in specialized sites. The rapid progress in brain imaging techniques will certainly make such testing feasible without using invasive techniques.

Play is absent in reptiles. Its independent evolution in birds and mammals thus provides a spectacular example of behavioral homoplasy extending to the independent appearance of the three basic forms of play, locomotory, object-oriented, and social play (Fagen 1981). In both classes play, and in particular social play, is best developed in altricial groups (Ortega & Bekoff 1987). How can one then explain the independent emergence of play in the higher vertebrates?

Burghardt (1982) hypothesized that birds and mammals can play because of being endothermic and thus having a surplus of energy in comparison to reptiles. However, there is no evidence for such a difference in energy budgets; both endotherms and ectotherms may have relatively cheap energy available at certain times and under certain circumstances. An important compounding variable is time, which is in part exchangeable with energy and which seems to be as limiting as energy is for play behavior. The active lifetime is energetically cheaper in ectotherms, which, if anything, would favor the development of play in reptiles. Contrary to the previous argument, Byers emphasized the high energy costs of endothermy and proposed that play developed for better shaping of the muscles in ontogeny, which should help to conserve energy (Bekoff & Byers 1985). While play may well be credited with providing benefits of physical exercise, there is no evidence for the impact of such an improvement on the energy budget and no reason to believe that shaping and training muscles would not be important enough for reptiles. Both the benefits and costs of play are considered to be very minor by Martin and Caro (1985). This opinion probably reflects immense difficulties in the assessment of long-term, multifunctional effects rather than their absence.

I propose that the independent evolution of play in birds and mammals is a direct consequence of the independent evolution of their reward system. The primary function of the reward system is to translate the sensory input from incentive objects (e.g., during consummatory acts) into a positive affective state and thus to promote immediate biological benefits. It seems impossible to derive play from this stage since the irrelevance of consummatory acts is one of the most distinctive characteristics of play. To account for the origin of play it is necessary to postulate a stage at which

activities would be rewarding per se, in addition to the reward from the external stimulation. There is indeed good evidence that the animal's own activity provides a component of the reward from consummatory acts (Toates 1986). For example, rats, pigeons, Chickens *Gallus gallus* and Starlings *Sturnus vulgaris* prefer earned in comparison with free food (Inglis & Ferguson 1986 and references therein, Dawkins 1990 and references therein). Rats self-stimulate more vigorously if they have something available for chewing and prefer self-stimulation over an identical stimulation administered by the experimenter (Ettenberg et al. 1981). In pigeons the activation of dopaminergic neurons in the nucleus basalis with a dopamine agonist, apomorphine, elicits pecking independent of food intake (Lindenblatt & Delius 1988). The nucleus basalis supports self-stimulation, which is known to be dopamine dependent. Therefore, the same structure is involved in the apomorphine-induced pecking and self-stimulation, which suggests that the apomorphine-induced pecking may be rewarding. This provides an indirect support to a long held view that pigeons' anticipatory pecking at keys known as autoshaping is self-reinforcing (Herrnstein 1977).

Play is known to be best expressed in young mammals and birds who, when very young, may perform activities detached from their functional effects (Toates 1986). For example, infant rats at 10-21 days show no preference for suckling that yields milk over suckling that does not, and will learn an instrumental task for the reward of a non-lactating nipple. A similar situation has been demonstrated in fowl chicks, who at first peck equally at food and at sand. Only later does the pecking become associated with the hunger system (Hogan 1977). If the behavior alone is the first source of reward in the individual development (Toates 1986), then play probably derives from such detached behaviors.

The proposed derivation of play from behavior rewarded for its performance, in addition to its immediate effects, predicts the absence of activity-derived reward in reptiles. The evolutionary appearance of play opened up a new sphere of rewarding experience, particularly for young animals, and thus increased the intrinsic value of their lives. With the appearance of object and social play some neutral objects became toys and other individuals turned into play partners. This provides a substantial enrichment of an animal's emotional bonds with the environment beyond those established by consummatory acts.

THE PHENOMENON OF HIGHER VERTEBRATES

Play is just one example of a stunning array of behaviors and cognitive abilities that have developed independently in birds and mammals. "In most cases where it is possible to suggest a form of mammalian superiority, the mammalian characteristic is seen in birds as well" (Walker 1983, p. 236). This applies to such diverse phenomena as sleep with a distinct phase of paradoxical (active) sleep, complex vocalizations, complex social organization, flexible goal-directedness in appetitive and avoidance behavior resulting in an unmatched ability to learn arbitrary operants, learning by imitation, latent learning, food storing, and complex parental care with feeding of the young. There cannot be better proof of the reality of the resulting higher vertebrate grade than play between a bird and a mammal, e.g. between a corvid and a dog or a cat (Fagen 1981), which clearly involves some level of understanding between descendants of two phylogenetic lines, archosaurs and therapsids, that split some 300 m.y.a.

The key for understanding the unique development of affective motivation in higher vertebrates (Leeper 1970) lies in the functional and evolutionary interdependence of motivation and cognition (Livesey 1986). Affective motivation permits a great adaptive flexibility of behavior (Scherer 1984) but this can be achieved only with sufficient cognitive equipment. The evolution of avian and mammalian behavior certainly involved positive selective feedbacks between motivation and cognition, as new motivated behaviors open up new possibilities for exploration, which in turn put new demands on the refinement of motivational control. A better understanding of this interdependence will certainly shed new light on the evolution of both intelligence and subjective experience.

Emphasizing the high development of subjective experience in mammals and birds does not mean denying its very presence in other vertebrates. Based on the occurrence of endogenous opiates and benzodiazepine receptors in all gnathostome vertebrates, Green (1987) remarked that "there is clearly something about being a vertebrate that involves a lot of pain and anxiety". In fact teleost fishes give strong indications of pain and psychogenic stress (Klausewitz 1989) and may possess a brain reward mechanism although the only record of self-stimulation in fishes has been criticized for the lack of convincing behavioral data (Walker 1983: 224). More convincing in this respect is the well developed play of the tapir snout fishes (Mormyridae), which is the only unquestionable case of play in vertebrates other than birds and mammals (Fagen 1981). Being clearly isolated and derived, this case provides independent evidence for the pervasiveness of parallelism in the concerted evolution of cognition and motivation. In many features of general adaptive significance, such as encephalization, partial endothermy and social behavior, some teleost fishes seem to be closer to higher vertebrates than are living reptiles and thus are of little value as a source of information about the primitive tetrapod or reptilian condition. Even if some of the higher vertebrate features of cognition and motivation prove to be incipiently developed in some reptiles, the distance to higher vertebrates is unlikely to disappear.

CONCLUSION

The combined evidence for the subjective control of the ESB-motivated behavior and play and the role of subjective value perception in the motivation of adaptive behaviors does not permit reasonable doubts that birds do experience positive and negative affective states. To perform their motivational function, the affective states must be experienced in some proportion to the biological significance of the stimuli in terms of their impact on fitness. Therefore, there is no reason to consider subjective experience to be negligible if the biological impact of a stimulus is not negligible. It follows that, at the risk of accepting arbitrary limits to the execution of morals, birds should be granted the status of moral patients, as defined by Regan (1983), i.e. recipients of moral actions from human moral agents.

As beings capable of experiencing pleasure and suffering for a part of the same reasons as we do, the higher vertebrates share a part of our values. We have inherited these values from our mammalian ancestors and categorized them as hedonic. After doctrinal wars against some of them, they have been fully validated in our civilization. Hedonic values are an integral, legitimate part of the human system of values. If our morals are to be set on a solid, rational basis, we should start respecting legitimate values wherever they obtain.

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A PRELIMINARY STUDY OF SKELETAL PATHOLOGY OF BIRDS IN ZOOS AND ITS IMPLICATIONS

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ABSTRACT. Skeletons of birds derived from zoological parks are known to have a large percentage of pathologic bones when compared with skeletons derived from wild birds. These lesions and deformations are sufficiently severe and numerous that workers in paleobiology have traditionally avoided skeletons of captive birds in comparative osteological studies. Coarse osteotic and osteoarthritic lesions are thought to be the result of restricted space or flight room and/or tenotomy, artificial diet, and may also be age related. It may be possible by examining skeletal collections of birds derived from zoological parks, in comparison with skeletons of wild birds, to assess what types of birds are the most (and least) susceptible to these pathologies. Such studies may provide clues as to which birds are most appropriately housed in captivity.

Keywords: Exostoses, osteoarthritis, parrots, pathology, ratites, skeleton, zoological parks.

INTRODUCTION

Zoological parks and similar institutions have traditionally served in multifarious roles. Not only do they educate the public as to the diverse nature of life on earth and its conservation, but they also provide a setting for much needed research in animal behavior and other aspects of biology, and they provide an arena for breeding endangered animals, predominantly mammals, which often breed effectively in captivity. Thus, in a sense they have become in the minds of some, "Noah's Arks" (Johnson 1971, Luoma 1982), so that Johnson (1971 p. 5) could state: "The average zoo animal is always healthier than the average animal in its wild habitat."

Given the current importance of zoological parks and aviaries, it is important to ask what types of animals, and for the purpose of this paper, birds, can be housed effectively and appropriately in such captive settings. And, just what are the consequences of captivity for the individuals so housed?

I was first introduced to the problem indirectly some twenty years ago when I was comparing the bones of living species of birds in the skeletal collections of the Smithsonian Institution with those of fossils. The late Alexander Wetmore, then Director Emeritus of the Smithsonian, admonished me never to use skeletons of birds from zoological parks in my comparisons because of the widespread osteologic pathologies and bony deformations exhibited by such specimens. Because so many skeleton collections have depended on zoological parks extensively for their collections of exotic birds, many errors in the proper allocation of fossil specimens have no doubt found their way into the literature.

During the past several years the idea occurred to me that skeletal collections might, in combination with other information, be an excellent source of information to: 1) ascertain the extent of the problem; 2) properly assess what types of birds might be

most appropriately housed in captivity; and, 3) determine if it is at all appropriate to use "zoo" skeletons for more than ordinal or familial diagnosis of fossil birds.

The first question, and that posed by this paper, therefore, is, can examination of museum skeleton collections give us some idea of the relative extent of bone pathology in captive birds? In this preliminary study, skeletons obtained from captive birds were examined to determine if, indeed, pathologic bony lesions were present, and a more thorough examination of ratite birds was undertaken.

METHODS

In order to ascertain if this general approach might be profitable, skeletons of captive birds from zoological parks, as well as comparable "wild" skeletons, were examined in the collections of the Division of Birds, National Museum of Natural History, Smithsonian Institution, as well as other collections. In this preliminary study, skeletons of captive birds were examined representing each major living group commonly housed in zoos or aviaries. In this case specimens were examined only to see if coarse pathologic bone lesions were present. Because lesions were usually found by examining five or so specimens, ten skeletons of wild birds of the same species were also examined. No coarse pathologic lesions were located in the "wild" skeletons. Second, a large number of skeleton specimens of large ratites, primarily in the National Museum of Natural History, were examined in order to determine the extent of bone pathology in both captive and wild birds. Among the common types of bony lesions encountered in skeletal preparations are fractures that have healed, either with or without excess bony growth or exostoses. Since the purpose of this study was to search for pathologies that were the result of captivity or disease, healed fractures and similar wounds (see Goodman & Glynn 1988), with or without exostoses, were generally ignored, as they are not indicative of disease or degenerative processes. Also, very minor lesions that might be the result of artifact were ignored. Indeed, only bony lesions that were clearly visible to the naked eye were recorded.

Many bone pathologies appear similar in skeletal preparations, and there is very little literature on this subject (Griner 1983, Hofstad et al. 1984, Petrak 1982, Seneviratna 1969, Wise 1975). In general, bone disease usually takes on the form of osteitic (inflammation of the bone), or osteomyelitic (inflammation of the marrow), lesions. Such lesions often appear to be the result of a degenerative process, and often appear as chronic degenerative joint disease, osteoarthritis. However, *Mycobacterium avium*, which causes avian tuberculosis (ATB) as well as other microorganisms, can also produce bone and joint lesions, often characterized by acute swelling and porosity of bone (Montali et al. 1976). Also, gout, a metabolic disorder in which urates are deposited around tendons and articular surfaces may be commonly seen (Altman 1986). Bumblefoot, which causes extensive foot lesions and swelling, generally in "heavy, inactive birds, constantly standing on the same diameter perches so that their feet get little exercise," (Coles 1985), is a common disease of raptors, and is usually associated with the bacterium *Staphylococcus aureus* (Fowler 1986). Osteoporosis is also common (Altman 1982), in, but not restricted to, raptors, and results from animals not having received a balanced calcium phosphorous intake, which should be about 1.5:1.0 (Coles 1985). Frequently, bone lesions will produce distinctive exostoses, or growth projecting outward from the surface, and these growths as well as degenerative or myelomic growths are difficult to properly

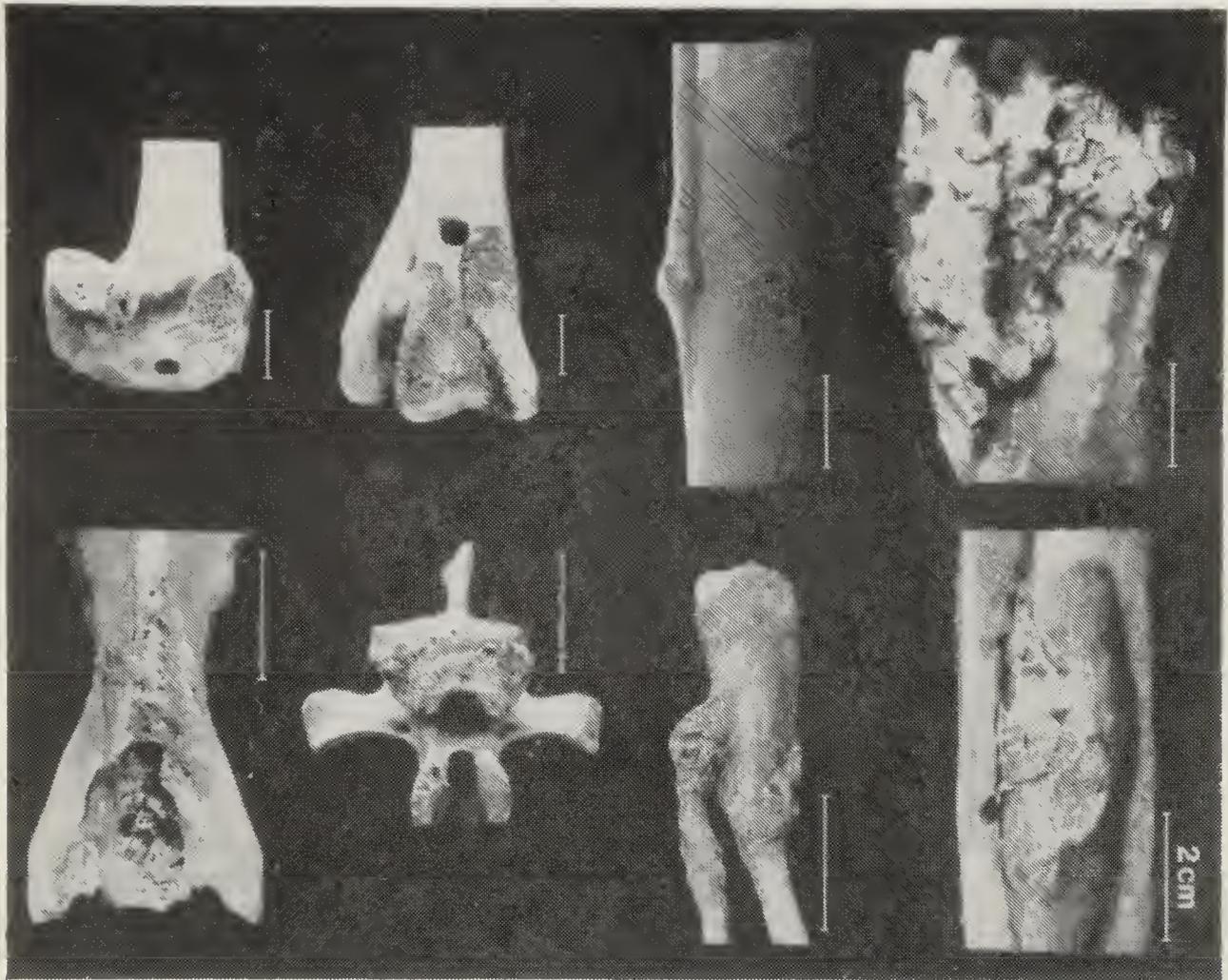


FIGURE 1 – Osteological lesions in a variety of captive ratites. Specimens in this figure and Figure 2 from private collection of author, unless otherwise indicated. Upper, left to right. Ostrich *Struthio camelus* (USNM# 343621), bone erosion, osteoporosis, distal tibiotarsus; Ostrich (USNM# 343621), same, distal tarsometatarsus; Double-wattled Cassowary *Casuarius casuarius* (USNM# 320946), exostosis of fibula; Emu *Dromaius novaehollandiae*, osteoarthritis of proximal tibiotarsus; Lower, left to right. Greater Rhea *Rhea americana*, (USNM# 19915), pathological vertebra, possibly osteomyelitis; Greater Rhea, same; Greater Rhea, osteoporosis of the carpometacarpus, possibly caused by avian tuberculosis; Greater Rhea, exostosis along the shaft of the tarsometatarsus.

diagnose in skeletal preparations. Distal extremity necrosis (DEN) is still another condition seen usually following trauma or frostbite, and may be visible in skeletal preparations (Calle et al. 1982).

RESULTS

Bone pathologies were found in representatives of all major living groups of birds that are commonly housed in zoological parks. These represented bony lesions that were not the result of broken bones or other trauma-induced bone injury (see Goodman & Glynn 1988), but were rather interpreted to have resulted predominantly from inactivation of the flight or pectoral apparatus, and/or hind limbs, and therefore lack of

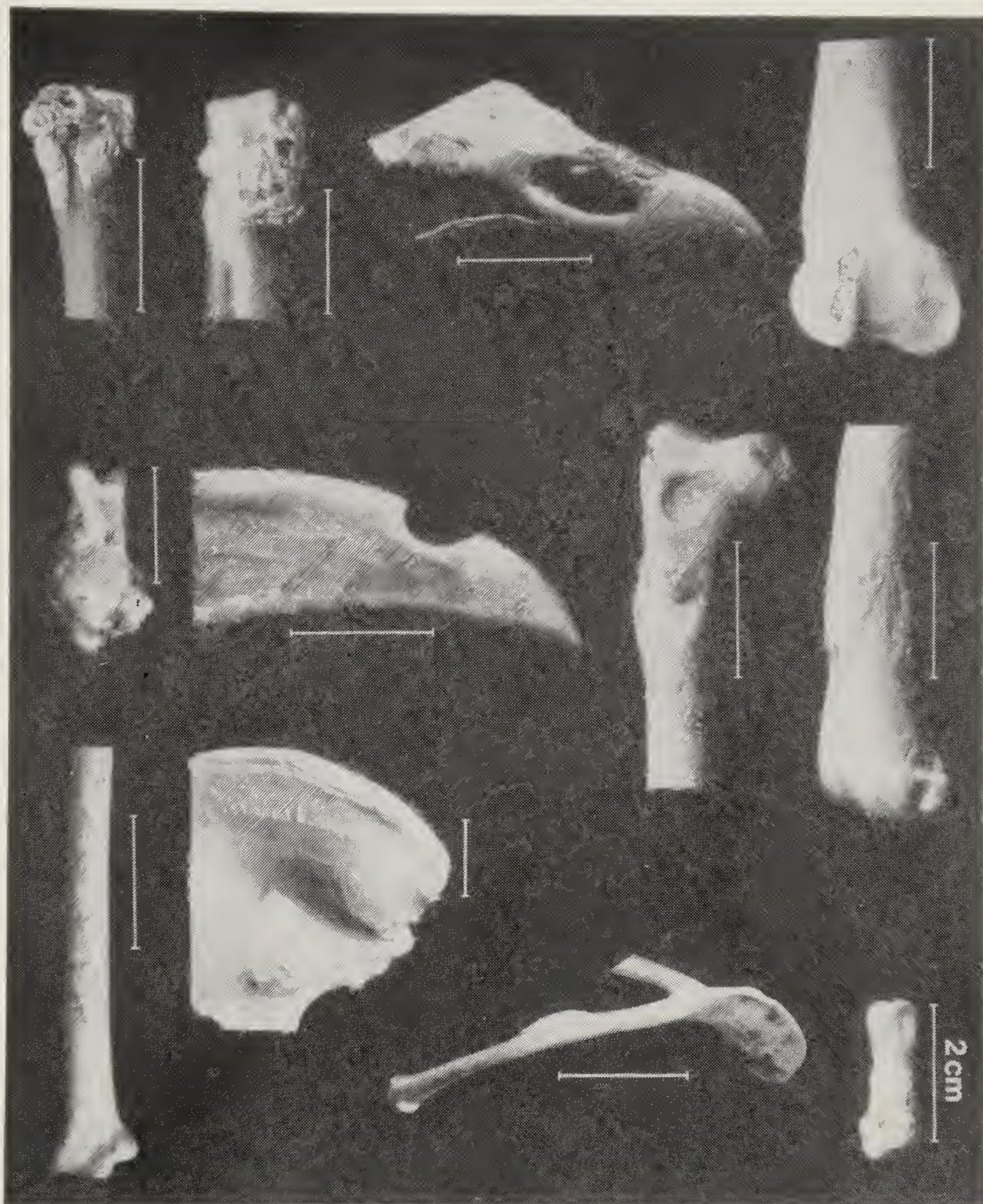


FIGURE 2 – Osteological lesions in a variety of captive birds. Upper, left to right. Turkey Vulture *Cathartes aura*, osteoarthritis of the distal tibiotarsus; Turkey Vulture, osteoarthritis of the distal carpometacarpus; Turkey Vulture, exostosis of the bill; Common Turkey *Meleagris gallopavo*, osteoporosis of the distal tibiotarsus; Middle, left to right. Hyacinth Macaw *Anodorhynchus hyacinthinus*, deformed carpometacarpus, with bulbous exostosis, probably resulting from cutting distal wing; Collared Aracari *Pteroglossus torquatus*, bill deformation; Great Indian Hornbill *Buceros bicornis*, exostoses (osteomyelitis) of the shaft of the femur; Boat-billed Heron *Cochlearius cochlearius*, exostoses (osteomyelitis) of the shaft of the femur; Lower, left to right. Hyacinth Macaw, exostoses of the ulna; Jabiru Stork *Jabiru mycteria*, bulbous, deformed sternal carina; Silver Pheasant *Lophura nycthemera*, exostosis of the furcula; Magellan Penguin *Spheniscus magellanicus*, toe with exostoses, possibly gout.

normal activity, or disease resulting from micro-organisms, such as *Mycobacterium avium* tuberculosis (Montali et al. 1976). Figures 1 and 2 illustrate a variety of these pathological bony lesions. Other lesions were interpreted to have been the result of abnormal activities, such as climbing cages in parrots (Coles 1985). Still other cases involving acute osteoarthritis, degenerative joint disease, were noted. Although this study is still somewhat in its infancy, my first impression is that the larger birds tend to be more susceptible to bone disorders, and rarely does one locate such pathology in small passerines.

A total of sixty ratites (including tinamous) were examined, 29 captive, and 31 from the wild. Of the 29 captive specimens, 24 had pathologic bone lesions, with a total of 80 lesions recorded. Of the 31 wild specimens examined, only one had a single lesion which appeared to be an exostosis caused by a natural injury to the anterior mid-shaft of the tarsometatarsus. Representative bony lesions are illustrated in Figure 1. The large ratites seem to be particularly susceptible to bone pathology. The smaller kiwis and tinamous do not seem to be as susceptible, although some pathology was noted, and Elzanowski (pers. comm.) noted numerous pathological skull deformations in the skeletons of captive tinamous he studied. These results, which coincide with the study of ratite skeletons by Coulon (1966), seem to confirm that this represents a fertile field for further investigation.

An unfortunate aspect of this study is that many skeletons of "zoo" ratites date back in time, most earlier than the 1960's, and there are fewer recently acquired specimens. Also, most current "zoo" ratites are now acquired from domestic breeding stock, from so-called ratite farms (pers. comm., various zoo curators). However, this study still points to a rather dramatic problem in keeping these large birds captive. In addition, ratites are difficult birds to handle in captivity, and there are numerous reports of ratites dying from trauma. Whole collections of Rheas have been lost in a single night by the presence of feral dogs causing them to run into fencing (Fowler, 1986, p. 287). Some bone deformations may be the result of injury.

DISCUSSION

The approach utilized in this study suffers from some substantial drawbacks, and the problem itself is not an easy one. For example, one has no data as to the age of the bird at time of death, or the actual time the bird resided in captivity. Nor does one know from what disorder the bird died. Birds with coarse osteotic pathologies may die from an unrelated disorder. An example is a penguin, a toe from which is illustrated in Figure 2. Although the toe is pathological, the bird actually died from cancer and had numerous tumors within the lungs and abdominal cavity. Further, mortality records are insufficient to make the point because birds may suffer in zoos for literally decades with bone disorders before succumbing to some other disease, and therefore the autopsy records would not normally indicate bone pathology. Autopsies are now so thorough, at least with respect to soft anatomy, that specimens are typically destroyed and do not find their way to skeletal collections. Such autopsies, without radiographs, are incapable of detecting the types of bone pathology visible in skeletal preparations. It is hoped that museum skeletal preparations represent a more or less random sampling of captive birds over a long period of time, with no real bias, although it is impossible to estimate the rates of disease in wild populations of birds,

that is, they die. What this type of study can and does illustrate is that birds are difficult animals to keep in captivity free of metabolic and infectious bone disorders.

When one considers the anatomy of birds, these bone lesions are certainly not unexpected. Ratites, with their massive hind limbs, are designed for running, yet they are generally restricted to small areas of zoological parks. Volant birds, which constitute the vast majority of those housed in captivity, have a considerable portion of their anatomies devoted to the flight apparatus. The two pectoral muscles, *M. pectoralis major*, and *M. supracoracoideus*, range in total body weight from 7.8% in the Whitethroated Rail *Laterallus albigularis*, to 36.7% in Cassin's Dove *Leptotila rufinucha* (George & Berger 1966, Hartman 1961). Yet, unless birds are kept in large, open aviaries, it is necessary to immobilize them by either pinioning and wing feather cutting, or tenotomy, in which the extensor tendons on the anterior edge of the metacarpal bone are cut (Coles 1985).

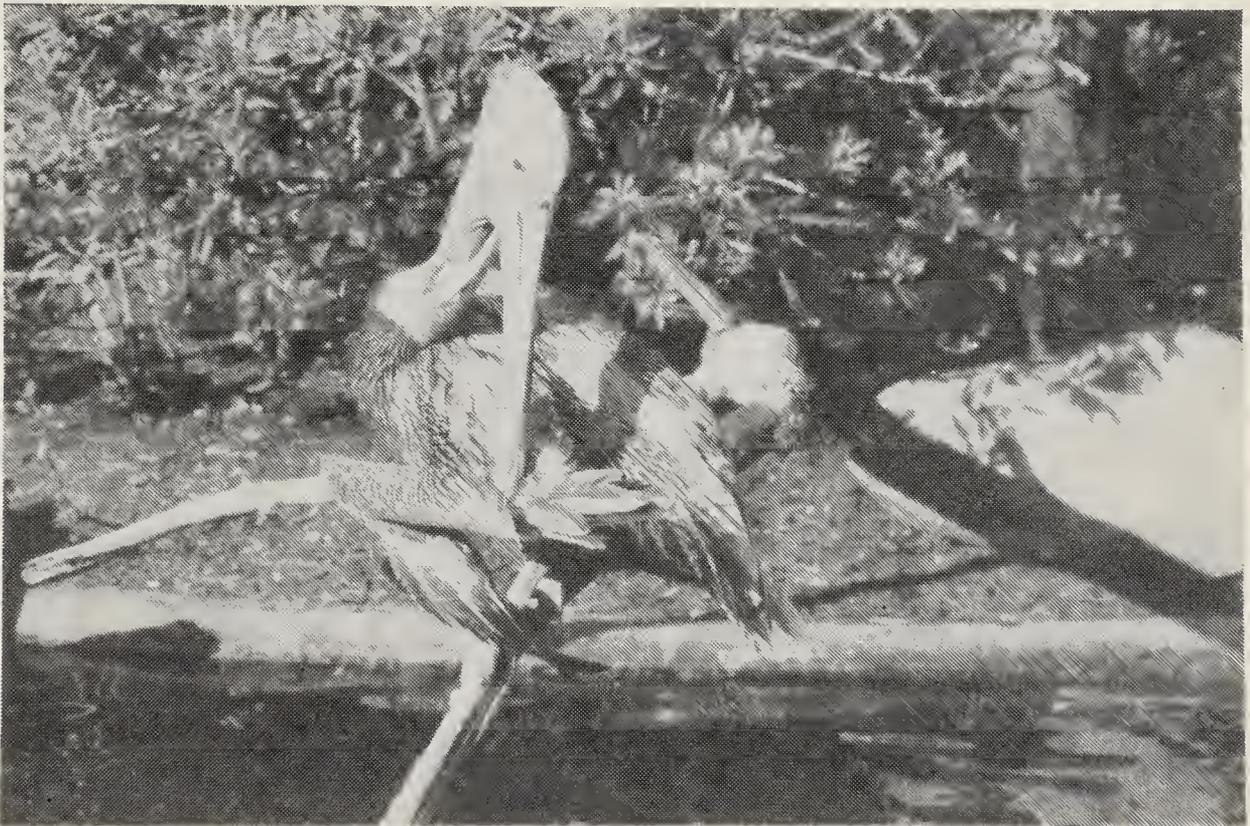


FIGURE 3 - Brown Pelican *Pelecanus occidentalis* with drooping left wing due to tenotomy or cutting of the extensor tendons of the wing, in a major zoological park, May 1990. This bird sat on the same branch in the same position all day. Photo by the author.

An example of the result of tenotomy is illustrated in Figure 3. Typically the wing droops, and is rendered immobile. The bird pictured in Figure 2 was photographed at 0800, at which time it was preening the mutilated affected wing. The bird remained on the same perch all day, immobile. This particular case dramatically illustrates one of the main problems in keeping birds, particularly large ones, in zoological parks. Generally, at least one fourth of the bird's bone and muscle mass is rendered immobile, and the individual sits and undergoes long-term atrophy.

Still another problem attends the fact that mortality rates are quite high in zoological parks. As one of many examples, from 1972 through 1977, 229 young Rheas and 33 adults were received for pathologic examination at the San Diego Zoo (Griner 1983). Most had died from infectious diseases, but within the 33 adults, "Trauma and evi-

dence of stress and shock from capture, restraint or surgical procedures were observed in 26." (Griner 1983, p.112). And, while mortality rates in zoos are high, the death rate in transport may be even higher: see Bruning (1985) and James (1990), for description of the horrendous trade in parrots. It is hoped that a definitive pattern as demonstrated in the ratites will emerge from the continuation of this study, and this information will aid in enabling one to compose a list of the types of birds that are most appropriately housed in zoological parks with the least chance of developing pathology.

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AVIAN INTELLIGENCE AND SUFFERING?

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ABSTRACT. Research from laboratory experiments provides evidence for avian cognitive abilities, including category formation, as well as significant communicative capacity. Field research yields results strongly suggestive of purposive behaviour by birds and an ability by at least some parent birds to learn rapidly to distinguish between dangerous and benign intruders onto their territory. Given these substantial cognitive abilities, one is led to inquire into the nature of avian suffering. In addition to a capacity to experience pain, might a bird also be able to anticipate pain and to experience other forms of suffering? Does intelligence affect the capacity to suffer? The concept of suffering is discussed, particularly as it relates to avian and other non-human animals. A caveat to those who venture into such difficult areas: only for oneself can one find direct evidence for conscious experience, be it colour, pleasurable experience or suffering. Yet based on ethological and neurophysiological evidence, one can make reasonable statements about likely distress or well-being of an organism.

CONCLUDING REMARKS: PAIN AND STRESS IN BIRDS

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The evidence presented at this symposium, in particular for pain by Michael Gentle and the psychogenic nature of stress by Joy Mench, leaves little doubt that birds are capable of suffering, which is best defined as a collective term covering "a wide range of unpleasant emotional states" (Dawkins 1980). And the ample evidence for the affective motivation of appetitive and avoidance behavior demonstrates that avian selfish genes employed the carrot as well as the stick to manipulate their ephemeral vectors.

Research on the well-being of birds has been initiated (Dawkins 1980) and successfully developed on poultry (Dawkins 1990, and as presented by Gentle and Mench in this symposium). This work demonstrates that the assessment of animal suffering constitutes a fully scientific endeavor that requires asking specific questions and employing specific methodology. So far the best approach seems to be a combination of behavioral and physiological experiments.

Yet the question of subjective experience in birds continues to be avoided in ornithological basic research. Why do ornithologists seem to be interested in everything about birds except for their emotional experience? The usual answer, which is a lingering popular version of behavioristic agnosticism, is that it is virtually impossible to know the private states of other beings and therefore it is unscientific to consider them. In fact, if "knowing" means "feeling" or "experiencing", this answer is trivial. If "knowing" refers to any form of scientific knowing, the answer is plainly wrong. The popular agnosticism has been recently refuted by many scientists (e.g., Walker 1973, Plutchik 1980, Toates 1986, Dawkins 1990), philosophers (e.g., Singer 1990, Regan 1983, Rollin 1989) and a mixed team (Bekoff & Jamieson 1990). This reasoning is no longer valid as an excuse for denying subjective experience in animals.

By their very nature, the subjective experiences of other human or animal individuals must be inferred from observable phenomena rather than observed directly. There is nothing unusual about that. It is a routine scientific procedure to explain observable phenomena with reference to nonobservable factors, as long as these permit testable predictions. This condition is fulfilled in the explanation of behavior through subjective states since these have their objective observable behavioral and physiological concomitants that permit direct experimental predictions (Epstein 1982, Stellar 1982, Toates 1986).

Subjective experience depends on the brain's ability to translate the biological values of incentive objects into positive or negative affective states. Inferring this capability is as valid scientifically as inferring the capability of performing a cognitive operation

(Byrne 1990). Both are inferred from the combination of behavioral observations, brain organization, and our human self-knowledge. Using our own intelligence as a reference is only reluctantly admitted, but is inevitable in cognitive studies of animals. We could never ask if a bird is capable of category formation if we had not this capability ourselves. And both inferences equally command a healthy skepticism (Bekoff & Jamieson 1990) as the brain mechanisms of either affects or cognitive operations are at present beyond our understanding.

If one agrees that moral standards should be single and applied consistently, rather than double and applied depending on the interests of the arbiter, then subjective experience should be respected wherever it occurs. In reality the subjective experience of most birds, whose fate depends on the human combination of intelligence and morality, is not even considered, let alone respected. Billions of factory-farmed birds (five billion in the US alone) are processed worldwide every year and exposed to inhumane treatment in transport, slaughter and factory farming practice (Mason & Singer 1980, Zimmer 1983, Eimler & Kleinschmidt 1987, Druce 1989, Birchall 1990, Singer 1990). Birds categorized as a nuisance or as pests are exterminated like vermin by all available means, including poison gas, surfactants, explosives and flame throwers (Dolbeer 1988, Briggers & Elliot 1990). Overall, these practices seem to be condoned by the general public and ornithologists, and some ornithologists even support the most inhumane extermination campaigns. Only the horrors of the cage bird trade (Nilsson 1980) have attracted some attention among the general public and ornithologists, the latter, however, being primarily concerned with the conservation of threatened species rather than with treatment of individual birds.

The question of direct moral responsibility of science is too complex to be addressed here at any length. Instead, I shall briefly address the primary obligation of each scientific community, which is to provide other interested people including the general public, politicians, and other scientists with a realistic picture of the explored aspect of the world. It is my contention that ornithologists do not even try to fulfill this obligation with respect to one of the most consequential aspects of avian organization, that is the motivational system and subjective experience. We ornithologists have been interested so far in almost every aspect of the life and death of birds except for the question of what life might mean for them. The consequences of this neglect are two-fold. Firstly, it makes our vision of a bird consistent with the commercial vision of a poultry bird as a raw product composed of meat and feathers. Secondly, it leads to a bias in research that has been best expressed by the prominent student of play in animals, Robert Fagen: "If play were as interesting to certain field biologists as infanticide, we would have plenty of information about survivorship costs of play - and this information would be just as hotly contested" (Martin & Caro 1985). It is a truism in the philosophy and history of science that scientists see what they are prepared to see due to their background, theoretical and otherwise.

In conclusion, it is time to start looking more realistically at the proximate causes of avian behavior, which will certainly lead to considering and respecting birds as beings with their individual stakes in life. One consequence of such a change of attitudes will be an enhanced self-discipline in dealing with living birds, resulting in technical and intellectual refinement rather than restrictions on research. The other consequence will be a contribution of ornithology to a more rational and equitable ethic of the future, resulting in a gain of new significance and public recognition for our science.

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THIOLLAY J-M	1489	WIERSMA P	761
THIOLLAY J-M	1576	WILEY J	2417
THOMAS D H	1757	WILLIAMS J B	1964
THOMAS D H	2122	WILLIAMS M J	841
THOMAS N J	2331	WILLIAMS M J	860
THORNHILL R	1361	WILLIAMS M J	876
TIEBOUT H M III	1175	WILLIAMS T D	1393
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
UTTLEY J D	2257	WILSON A C	2441
VAN HORNE B	2313	WILSON J B	1617
VAN DEN ELZEN R	459	WILSON R P	1853
VAN NOORDWIJK A J	2433	WILTSCHKO W	1803
VAN NOORDWIJK A J	2462	WILTSCHKO W	1845
VAN NOORDWIJK A J	2469	WILTSCHO R	1803
VAUK G	2365	WILTSCHO R	1845
VELTMAN C J	860	WINGFIELD J C	2055
VERHEYEN R F	1003	WOBESER G	2325
VERMEER K	2378	WOBESER G	2356
VICKERY J A	2494	WOLF L	1229
VUILLEUMIER F	327	WOOLLER R D	1657
VUILLEUMIER F	354	WOOLLER R D	2390
VUILLEUMIER F	553	WORTHY T H	555
VUILLEUMIER F	578	YAMAGISHI S	1195
VUILLEUMIER F	587	YAMAGISHI S	1220
WALLACE M P	2417	YAMAGISHI S	1240
WATTS C	1012	YOUNG B E	1605
WEATHERS W W	1957	YUILL T M	2338
WEBSTER M D	1765	ZACK S	1301
WENZEL B M	1820	ZIEGENFUS C	1229
WETTON J H	2435	ZINK R M	591
WHITEHEAD M D	1384	ZINK R M	629
WHITELEY P L	2338	ZWEERS G A	897

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