

## Male parental care and monogamy in snow buntings

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**Summary.** We experimentally removed males from a random sample of 14 snow bunting (*Plectrophenax nivalis*) pairs to determine the influence of male parental care on reproductive success. Widowed females increased their rate of food delivery to nestlings by increasing their feeding visit rate but not their load size. However, Widows were only able to achieve 73% of the food delivery rate of Control pairs and, as a result, they raised fewer offspring of lower quality (i.e. lower mass at fledging). Total brood mass raised by Widows was only 55% of that of Control pairs. Thus, in the year of our experiment, male parental care in the nestling period almost doubled the reproductive success realized from a brood. Our experiment, however, was done in a year of poor food availability and data from the previous year, when food supply was higher, indicate that males may not always be so important. Since nestling food supply appears to be unpredictable at the time of pair formation, we suggest that monogamy is a bet-hedging strategy in case of poor food availability. As a consequence the importance of male parental care in some years may explain why snow buntings are almost always monogamous.

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### Introduction

Monogamy is the common avian mating system (exhibited by 90% of bird species; Lack 1968), in striking contrast to all other animal taxa in which monogamy is exceptional (Lack 1968; Trivers 1985). Wittenberger and Tilson (1980) outlined 5 hypotheses for the evolution of monogamy, and

reviewed the available evidence in their support. Although they discussed other factors that may favour its evolution (e.g. skewed sex ratios), they concluded that male parental care has been an important force in the evolution of monogamy in most avian species, as suggested earlier by Lack (1968).

Although there is a correlation between monogamy and male parental care in birds, it is possible that male care in some species may be a *consequence* of monogamy, rather than a cause. For example, if some factor other than male care imposes monogamy, then the cost of male parental care with respect to the loss of additional matings (Trivers 1972) may be greatly reduced. Thus, the simple observation that male parental care occurs in a monogamous species does not confirm that it enhances reproductive success sufficiently to account for the evolution of monogamy. Only experimental studies can reveal whether male parental care has an important influence on reproductive success and, therefore, whether or not females are able to completely compensate for the loss of male care if their mates desert them.

The few experimental studies done to date have relied on male removals to assess the importance of male parental care in birds, and the results have varied. In one study, male parental care was found to be *essential* for any reproductive success (Erckmann 1983), while in others, male care was not essential, but was *useful* in that it had a positive effect on reproductive success by reducing the risk of nest predation (Hannon 1984) or increasing the number and quality of offspring produced (Weatherhead 1979; Smith et al. 1982). Interestingly, studies of some species have found that removal of the male had no detectable influence on a female's reproductive performance (Gowaty 1983 and references therein). Thus factors other than male paren-

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tal care may have played a role in the evolution of monogamy in these species. As Mock (1986) points out, there is a need for similar experiments on a variety of bird species living in different ecological situations.

In this study, we examine the significance of male parental care in the snow bunting (*Plectrophenax nivalis*), a monogamous finch that breeds in the high arctic. We first compare the relative effort devoted to raising offspring by male and female buntings in a natural situation by examining nestling feeding rates and load sizes brought in by each sex. We then present the results of a removal experiment designed to reveal the influence of male parental care on reproductive success and we discuss the potential effects of year-to-year variation in food supply on monogamy in general.

## Methods

### *Animals and study area*

We studied parental care in snow buntings at Sarcpa Lake (68°33' N, 83°19' W) on the Melville Peninsula of Canada's Northwest Territories in 1982 and 1983. Buntings are normally monogamous at Sarcpa Lake, but as in other areas (Tinbergen 1939), some males (up to 5% of the population) are polygynous in some years, almost certainly as a consequence of a slight female bias in the sex ratio (Lyon and Montgomerie 1987). As a result of the short snow-free season, breeding is highly synchronous with all pairs beginning egg laying within the same 2-week period each year (Lyon and Montgomerie 1987). Both sexes provide parental care throughout the nesting cycle; females incubate the eggs and brood young chicks, males feed females during incubation (Lyon and Montgomerie 1985) and both sexes feed the chicks until independence. Thus, given the high degree of nesting synchrony, a male mated to two females would be forced to feed nestlings at both nests. We have described the general breeding biology of this species at Sarcpa Lake elsewhere (Montgomerie et al. 1983; Lyon and Montgomerie 1985).

### *Experimental removals*

In 1983 we created 14 Widow females by removing their mates either at the onset of incubation ( $n=7$ ) or at hatch ( $n=7$ ). In an earlier analysis of these data, we found no differences between these 2 sets of Widows in any post-hatch indices of reproductive success (see Table 2 in Lyon and Montgomerie 1985) so the data are pooled for analysis here. Widows were chosen randomly from the study population in 1983, leaving 11 Control nests for comparison. Widows and Controls did not differ in either clutch size (Mann-Whitney  $U=68.5$ ,  $P=0.63$ ,  $n=14$ , 11) or date of clutch completion (Median test,  $\chi^2_1=0.62$ ,  $P=0.44$ ,  $n=14$ , 11). For some of the variables measured in this study, our sample size was lower than the total number of birds in the Widow and Control groups because of either predation or inaccessibility of the offspring for measurement.

### *Food delivery rates*

In both 1982 and 1983, almost all nests were found before clutch completion and most nests were monitored every second

day through to fledging. To quantify male and female parental care, we observed nests for 1-h observation periods to document both the rate of feeding visits to the nest and the amount of food delivered by each sex. Each nest was watched for at least three 1-h sessions on different days during the nestling period. We observed males and females at 4 Control nests in 1982, and at 5 Control and 11 Widow nests in 1983.

To quantify the load sizes brought to nestlings, we assigned loads to 3 size categories relative to the number of crane-flies carried: small = 1, medium = 2 or 3, and large = 4 or more crane-flies. The diet of nestling buntings at Sarcpa Lake was comprised almost entirely of crane-flies (Tipulidae). For all but 3 parents, we observed at least 3 loads; for the others we observed only 2 loads ( $n=1$ ) or 1 load ( $n=2$ ). We used the product of feeding visit rate and our load size index as an estimate of the overall rate of food delivery for each parent studied. For analysis of both load sizes and feeding rates we used the mean values for each individual to avoid potential problems with pseudoreplication (Hurlbert 1984).

### *Reproductive success*

We used several indices of reproductive success to examine the consequences of male parental care; number of chicks fledged, absolute growth rate (g/d), fledging mass (g), brood mass (g), length of nestling period (d). Chicks were weighed every second day to the nearest 0.1 g on a Pesola spring balance. From these data we calculated the absolute growth rate (KA/4) of each chick that survived to fledging. KA/4 is not nearly as sensitive to a variable asymptote (A) as the relative growth index, K (Hussell 1972; see Lyon and Montgomerie (1985) for details on our calculations of absolute growth rate). The length of the nestling period is the time from the hatching of the first egg to the fledging of the first chick in each nest. Because nests were sometimes visited every other day, there could have been as much as 48 h error in the calculation of nestling period for an individual nestling. To minimize this error in analysis, we used the average of the minimum and maximum estimate of nestling periods for each nest.

For analysis we used the mean chick growth rate for each nest. We have shown elsewhere that there was a significant effect of 'nest' on offspring growth in snow buntings (Lyon and Montgomerie 1985). Thus the growth rates of young within a nest were not independent.

We also weighed as many of the adult females as possible just prior to fledging to determine whether loss of male care affected their condition. Because Widows were selected at random, we assume that there was no difference in the body mass (or condition) of Widows and Controls at the start of incubation in 1983.

For statistical comparisons between Widows and Controls, we used one-tailed tests. Because we expected Widows to try to compensate for the loss of their mates, we predicted that their rates of food delivery would be higher than those of Control females but lower than those of Control pairs. We also expected a decline in the condition of Widows, a reduction in both the number and quality (growth rate and fledging mass) of their chicks, and a lengthening of their nestling period.

### *Food availability*

As part of a longer term study, we have monitored the insect food available to birds for 5 years (1981–1985) at this study site. To sample insects, we used 0.1 m × 1.0 m boards covered by plastic sheets coated with a sticky resin (Tanglefoot®; see also Hussell 1972). We used 8 such boards in 1981 and 20 boards in the subsequent 4 years. In each year we placed boards in all of the habitats visited by foraging finches. Crane-flies

**Table 1.** Feeding visit rates (feeds/h), load sizes (food units), and food delivery rates (food units/h) of male and female buntings feeding nestlings. Load sizes are expressed as food units where 1 = small, 2 = medium, and 3 = large loads (see Methods)

	Female		Male		Com- parison <sup>a</sup>	
	Mean	Range	Mean	Range	<i>z</i>	<i>P</i>
1982 ( <i>n</i> = 4 pairs)						
Feeding visit rate	8.5	5.8–10.9	6.6	5.1–7.1	1.46	0.14
Load size	1.9	1.7–2.1	2.2	2.0–2.4	1.83	0.06
Food delivery rate	15.7	9.8–19.5	14.4	11.8–16.8	0.73	0.47
1983 ( <i>n</i> = 5 pairs)						
Feeding visit rate	4.5	3.3–6.0	4.6	3.0–7.0	0.00	0.30
Load size	1.9	1.0–2.4	2.7	2.2–3.0	2.02	0.04
Food delivery rate	9.0	4.0–14.6	13.2	9.0–18.6	0.94	0.35

<sup>a</sup> Wilcoxon matched-pairs signed ranks tests (2-tailed)

captured on the boards were counted every 4 d, at which point the resin-covered plastic was replaced.

## Results

### Parental effort

The feeding visit rates of males and females at Control nests did not differ significantly in either 1982

or 1983 (Table 1). Males, however, brought in larger loads than females but this did not result in significantly higher food delivery rates in either year or for both years combined (Table 1). Thus paired males and females delivered approximately equal amounts of food to their nestlings. Overall, females that had male help delivered 48% of the food taken to their nestlings.

Widows, on the other hand, significantly increased their feeding visit rate above that of Control females (1983 data), although they did not change the size of loads brought to the nest (Table 2). As a result of the increase in feeding visit rate by Widows, they delivered more food to the nest than Control females but still significantly less than Control pairs (Table 2). Thus, although Widows increased their feeding visit rate from 49% (i.e. Control female rate) to 77% of the rate of Control pairs, this resulted in an increase in actual food delivery rate to only 62% of that of pairs (Table 2). This increase in effort by Widows apparently did not affect their overall condition as Widow and Control females did not differ in body mass at the end of the nestling period (Table 2).

### Reproductive success

The loss of male parental care had a striking effect on both the quantity and quality of offspring fledged. Widows fledged an average of 2.7 chicks

**Table 2.** Indices of parental effort, female condition and reproductive success for Widow and Control buntings during the nestling period. For analyses of feeding rates and load sizes, we used mean values for each individual; for growth rates and fledging masses, we used the mean value per nest. Total feeds per hour is the pooled feeding rate of males and females at Control nests

	Widows			Controls			Comparison <sup>a</sup>	
	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>	<i>U</i>	<i>P</i>
Parental effort								
Feeds/h (females only)	7.1	4.3–11.8	11	4.5	3.3–6.0	5	6.5	0.008
Feeds/h (total)	7.1	4.3–11.8	11	9.2	6.7–10.6	5	13.0	0.05
Load size	1.8	1.3–2.3	10	1.9	1.0–2.4	5	18.0	0.20
Food delivery rate:								
females only	13.3	5.9–21.3	9	9.0	4.0–14.6	5	12.0	0.04
total	13.3	5.9–21.3	9	21.3	15.6–26.8	5	4.0	0.01
Female condition								
Female mass (g)	32.1	29.6–35.2	7	32.2	29.7–34.6	5	15.0	0.38
Reproductive success								
Growth rate (g/d)	3.9	2.3–5.9	11	4.4	3.1–5.7	9	35.0	0.19
Fledging mass (g)	24.9	20.8–29.7	11	30.4	22.6–35.2	9	8.0	0.001
Brood mass (g)	75.1	43.5–148.5	11	135.4	90.5–181.3	9	8.0	0.001
Nestling period (d)	12.6	10.5–14.2	7	12.4	11.0–13.7	8	24.0	0.35

<sup>a</sup> Mann-Whitney *U*-tests (one-tailed)

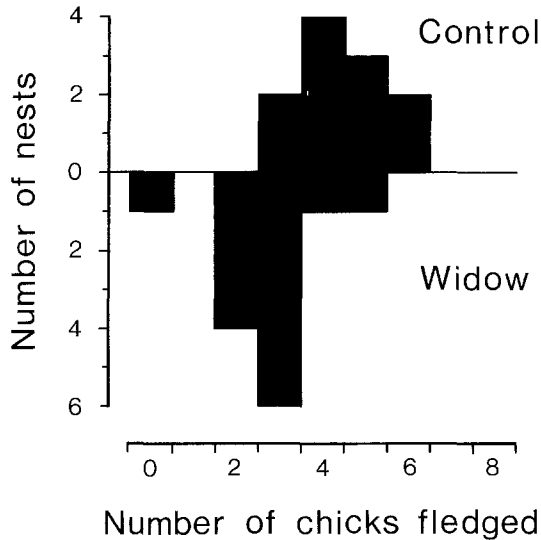


Fig. 1. The number of chicks fledged by 13 Widow females and 11 Control pairs in 1983

per nest versus 4.5 chicks per nest fledged by Control pairs (Fig. 1) and this difference is highly significant (Mann-Whitney  $U=17.5$ ,  $P<0.002$ ,  $n=13, 11$ ). Since there was no difference in the clutch sizes laid by Widows and Controls (see Methods), this difference must have been the result of brood reduction due to the nestling starvation that we observed. In addition, the mean fledging mass of chicks from Widow nests was only 82% of that of chicks fledged by Control pairs. As a result, the total brood mass fledged by Widows was, on average, only 56% of that of Controls (Table 2). Growth rates of Widow chicks were also lower than those of Controls, but not significantly so, and the 2 groups of females did not differ in nestling period (Table 2).

#### Food availability and clutch size

If females adjust clutch size to food availability during the nestling period, then male parental care should always be useful (Lack 1968). However, if clutch size is determined by factors other than the food supply for nestlings then male parental care may have little effect on reproductive success in years of abundant food. By chance, our male removal experiments were done in the year with the lowest availability of craneflies during the 5 years that we have been monitoring food supply. As an index of the availability of food for nestlings, we calculated the average number of craneflies captured per sticky board for the 4 sampling days during the nestling period each year (Fig. 2). During these 5 years, this index of cranefly availability varied 30-fold from a low in 1983 to a high in 1982

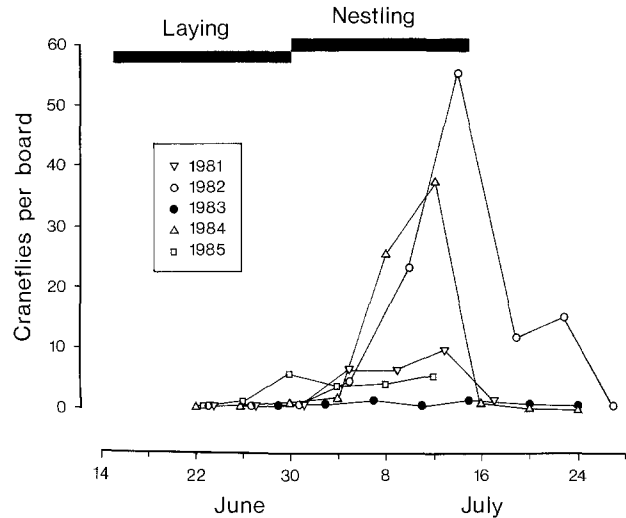


Fig. 2. Seasonal abundance of craneflies on the study area for 5 consecutive years. Plotted are the mean number of craneflies captured per sticky board during the previous 4-day period. Eight boards were sampled in 1981 and 20 boards were sampled in the other 4 years. The egg-laying and nestling periods of 63 nests found over the 5 years of this study are indicated — one outlying nest was removed from each end of this distribution

(Fig. 2). The difference between 1982 and 1983 in availability of food for nestlings is reflected in both the total (male plus female) feeding visit and food delivery rates of pairs (Table 1). Both total feeding visit rate (15.1 vs 9.2 feeds/h; 1982 vs 1983) and total food delivery rate (30.1 vs 21.3 food units/h; 1982 vs 1983) were significantly higher in 1982 ( $P<0.05$ , Mann-Whitney  $U$ -tests), the year of more abundant food.

Despite this year-to-year variation in the food supply, there was no correlation between the average annual clutch size and the index of cranefly availability in the same year (Spearman rank  $r_s=0.100$ ,  $n=5$ ,  $P=0.63$ ). We conclude, therefore, that females do not appear to be able to adjust clutch size to the availability of food for nestlings.

## Discussion

### Importance of male parental care

It is clear from our results that male snow buntings are *useful* in that they enhance female reproductive success but they are not *essential* for the rearing of at least some offspring, even in a year of poor food availability. Widows were able to fledge only about 60% of the number of young raised by pairs (Fig. 1) and these young had, on average, a significantly lower mass at fledging (Table 2), suggesting that they were in poorer condition. The average

mass of entire broods raised by Widows was only slightly more than half of that fledged by Control pairs. If we use brood mass as an index of both the quality and quantity of offspring produced, then male parental care effectively doubled the reproductive success realized from a brood.

It is interesting that widowed females were able to compensate somewhat for the loss of their mates, especially since they suffered no decline in body condition as a result of their increase in feeding visit rates (Table 2). This suggests that when both members of the pair were present, females (and probably males, too) did not work at their maximum capacity. The ability of widows to increase their food delivery rate is particularly surprising in a year of poor food availability and indicates that pairs are capable of raising more offspring than they do. It is unlikely that the compensation was achieved at the expense of brooding, since the chicks are normally only brooded for the first two to three days.

Moreover, clutch sizes at our study area were not correlated with overall nestling food supply and may instead have been determined by food conditions at or before the time of egg laying. Thus, in many years the number of eggs laid in a clutch may be somewhat lower than the maximum number of nestlings that the parents could successfully raise. Hussell (1972), for example, found that snow bunting pairs could successfully raise broods experimentally enlarged to 7 or 8 chicks.

#### *Monogamy in snow buntings*

Wittenberger and Tilson (1980) suggested that, even when males are not essential for the raising of some offspring, male parental care may still favour monogamy when a female that mates with an unmated male realizes a higher reproductive success than she would have if she had mated with an already-mated male. In snow buntings, bigamy is too rare to permit a comparison of bigamous and monogamous pairs but we can use the results of our removal experiments to assess the consequences of polygyny for female reproductive success. If we assume that males and females each contributed 50% of the effort required to raise a brood (Table 1), and were working at their maximum capacity, then a secondary female would realize, at best, only about 75% of the reproductive success of a monogamous female (assuming that the male divides his time equally between the 2 broods). Thus, to achieve the same reproductive success as a monogamous female, a secondary fe-

male would have to contribute about 75% of the effort required to raise a brood. Even when working at their presumed maximum capacity, widows were able to bring their nestlings only about 62% of the food delivered by monogamous pairs. We conclude, therefore, that females, on average, benefitted from monogamy in the year of our experiments.

#### *Monogamy in variable environments*

Despite the theoretical importance of male parental care to the evolution and maintenance of monogamy (Wittenberger and Tilson 1980), few experimental studies of altricial birds have assessed the ability of females to raise young alone after male removal. Even in these few studies the apparent importance of male parental care has varied. For example, two different studies of European tits (*Parus* spp.) found that widows raised significantly fewer and lighter chicks than monogamous pairs (Bjorklund and Westman 1986; Sasvari 1986). In experimental studies of both song sparrows (*Melospiza melodia*; Smith et al. 1982) and savannah sparrows (*Passerculus sandwichensis*; Weatherhead 1979), on the other hand, lone females raised only 46% and 82%, respectively, of the number of offspring raised by females that had male help, but neither of these differences was significant. Gowaty (1983) found that widowed bluebird (*Sialia sialis*) females actually raised more fledglings than did pairs, although this difference, too, was not significant.

There are 3 possible reasons for the inconsistency of results among these various experimental studies. First, there may simply be variation among species in the importance of male parental care and thus monogamy may be favoured for some other reason (see Wittenberger and Tilson 1980). Second, even though the results of Weatherhead (1979) and Smith et al. (1982) were suggestive, large variances in fledging success coupled with small absolute differences between their control and experimental groups may have obscured potentially significant effects. Thus, male parental care may often be important in monogamous birds but just difficult to document with relatively small samples. Third, the importance of male parental care may vary from year-to-year but, because of unpredictability of food supplies, monogamy may be the best long-term strategy that maximizes lifetime fitness. This explanation has not previously been proposed but it has important implications for the conclusions that can be drawn from short-

term studies on the adaptive significance of male parental care and its influence on mating systems.

Five of these six studies (including ours) were done in a single year and the other study (Sasvari 1986) was done in 4 different years but the data were all pooled for analysis. Thus, it is impossible to assess the effects of year-to-year variation in food supply on the role of male parents. Our experiments, however, were done in a year when nestling food supply was extremely low (Fig. 2). It is therefore not surprising that our removals revealed that males were very important to female reproductive success. Given the small year-to-year variation in clutch size, it is possible that, in years of abundant food, females alone could easily provide enough food for their offspring and polygyny would not be disadvantageous to them. Why, then, are snow buntings almost always monogamous even when food supply is apparently abundant?

In a variable environment like this, we might also expect females to maximize clutch size with respect to nestling food supply such that full male parental care would always be useful. In our study, however, year-to-year variation in snow bunting clutch size did not track the variation in food supply, suggesting that the food availability during the nestling period was not predictable at the time of laying.

Since nestling food supply does not appear to be predictable at the time of pair formation in mid-June (see Fig. 2), we suggest that monogamy is largely a bet-hedging strategy due to the potential importance of male parental care. Such a strategy may also explain the failure of some short-term studies of monogamous birds (e.g. Gowaty 1983) to find any apparent value to male parental care. Thus short-term studies cannot be used to reject the hypothesis that male parental care sometimes enhances female reproductive success. In an unpredictable and fluctuating environment, selection will favour the mating system that yields the highest lifetime fitness, even when that mating system does not seem to be adaptive in some years. As a result, the real influence of male parental care on the evolution of monogamy can only be assessed by examining the adaptive value of monogamy during the entire lifetime of individuals.

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