Incubation feeding in snow buntings: female manipulation or indirect male parental care?

Bruce E. Lyon and Robert D. Montgomerie

Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6

Summary. Male snow buntings regularly feed their mates on the nest during the incubation period. We removed males from 7 females at the start of incubation (Early Widows) and from 7 others when the eggs hatched (Late Widows) to experimentally assess the effects of incubation feeding on the behaviour of females and the reproductive success of both parents. Early Widows spent significantly more time off their nests than Late Widows and Controls. As a consequence, Early Widows had significantly longer incubation periods and a significantly higher proportion of them lost two or more eggs during development. There was no difference between Early and Late Widows in any index of reproductive success measured during the nestling period although significantly earlier brood reduction suggests that Early Widows were in poorer condition than Late Widows. Since both parents benefitted from incubation feeding by increased hatching success and shorter incubation periods, we conclude that this behaviour is an adaptive form of indirect parental care by males and is not the result of female manipulation.

Introduction

Males of many bird species feed their mates on the nest during the incubation period. In hornbills (Bucerotidae) and some raptors (Falconiformes, Strigiformes), for example, males provide all of the female's food during incubation (Lack 1968; Kendeigh 1952). In a variety of other species (see Ricklefs 1974, p 218), the male regularly feeds the incubating female, but the female also leaves the nest to forage on her own.

Various studies have shown a correlation between rate of incubation feeding and the female's incubation behaviour (e.g. von Haartmann (1958), Blagosklonov (1978)), but no study to date has found that incubation feeding enhances fitness. Ricklefs (1974) was also unable to find either ecological or taxonomic correlates of incubation feeding in birds and concluded that, in most groups, it probably occurs too infrequently to be of energetic value to females.

Although Roskaft (1983) found that the rate of incubation feeding in rooks (*Corvus frugilegus*) was positively correlated with fledging success, his experiment was not controlled to ensure that some other factors were not responsible for the enhanced reproductive success. For example, in herring gulls (*Larus argentatus*) there is a correlation between the rate that males feed females before incubation (courtship feeding) and the rate that they later feed offspring (Niebuhr 1980), and this sort of correlation could have confounded Roskaft's (1983) results.

To explore the reproductive consequences of incubation feeding in detail, we studied snow buntings (*Plectrophenax nivalis*) nesting in the Canadian high arctic. In this species, the male regularly feeds the female during incubation (Hussell 1972), but only rarely before this period (Lyon 1984). All incubation is performed by the female but she often leaves the nest to forage on her own. Both sexes feed the young until they become independent.

We designed our study to evaluate 3 possible explanations for the evolution of incubation feeding in this species. First, it may enhance the fitness of both parents. This would obtain if incubation feeding is a male tactic that results in an increase in reproductive success during the concurrent breeding episode. Second, incubation feeding may result in an increase in fitness of the female only. This could occur if females manipulate their mates

to perform incubation feeding. Female songbirds that are fed by their mates during courtship or incubation adopt a begging behaviour that is virtually indistinguishable from that of a nestling (Smith 1980; East 1981). Thus, incubation feeding may enhance a female's fitness by reducing her reproductive effort and by improving the probability that she will survive to future breeding attempts. Third, incubation feeding may have no effect on the reproductive success of either sex. This would be true if incubation feeding were accidental, simply as a hold-over from courtship feeding before incubation begins or as mistaken anticipatory feeding of "nestlings" (Skutch 1953; Nolan 1978).

To test these hypotheses, we removed mates from female snow buntings at different stages during the nesting cycle. We compared females under different experimental treatments to determine whether incubation feeding had any effect on female behaviour and whether there were any immediate fitness consequences for both sexes.

Methods

Animals and study area. We studied 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 common on dry tundra areas and nest at densities up to 12 pairs per km² at our study site (Montgomerie et al. 1983). The birds return in late May and by early June males defend nesting areas and begin singing for mates. Most males in the population are monogamous, but as in other populations (Tinbergen 1939), polygyny occurs occasionally. In spite of the short breeding season, clutch completion is relatively asynchronous among pairs (e.g. 19 June to 3 July 1983) partly due to the timing of nest site availability – many cavities and crevices become filled with ice over the winter and the birds have to wait for this to melt before nesting can begin. Females begin incubation before the last egg in the clutch is laid and this results in asynchronous hatching, which facilitates brood reduction (Lack 1968; Ricklefs 1965). Although buntings are double-brooded in some areas (e.g. Greenland; Tinbergen 1939), the short season at Sarcpa Lake limits them to a single brood.

Experiments. In 1983 we created 2 sets of widows by removing 7 males at the end of laying (Early Widows) and another 7 males at hatch (Late Widows). Both sets of widows were chosen at random from the nests available at the time and Controls were chosen from the remaining 20 nests found that season. Thus, Control and Late Widow females were fed by their mates during incubation, but only Control females received male help during the nestling and fledgling periods. To examine the reproductive consequences during the nestling period that result from the loss of incubation feeding, we compared Early and Late Widows. This controlled for the confounding effects of presence or absence of male parental care during the nestling period. Although we started with 7 Early Widow nests, 1 was preyed on before hatch. Complete data on chick weights were obtained from only 4 of the remaining 6 Early Widow nests because chicks in 2 nests could not be captured

during the latter part of the nestling period. Data on hatching success were collected from 12 Control nests.

If incubation feeding is nutritionally important, females could respond to the loss of their mates by (1) altering their incubation schedules to increase their time spent foraging or (2) maintaining their incubation schedules but suffering a reduction in their general body condition. We therefore investigated components of reproductive success relevant to both the incubation and nestling periods.

Data collection and analysis. Almost all nests were found before clutch completion and were monitored daily throughout the incubation period. Since our schedule of nest visitation allowed us to estimate the timing of hatch of the first egg more accurately than other eggs, we used the interval between the laying of the last egg and the hatching of the first egg as an index of the length of the incubation period. We calculated the maximum and minimum possible incubation period for each nest and used the mean values for analysis. The difference between maximum and minimum estimates ranged from 3 to 48 h, depending on the nest. We determined hatching success by monitoring the fate of all eggs. Unhatched eggs were removed to determine the stage of embryonic development at death.

During the incubation period, we observed each widow and 10 of the Control nests for several 1-h observation periods to document the females' incubation schedules (all nests) and the rates of incubation feeding by the males (Late Widows and Controls). During each observation period we noted the number of foraging trips made by the female, the duration of each trip, and the total number of minutes spent off the eggs each hour. All observations were made between 0800 and 1800 hours at randomly chosen times.

To compare the relative quality of chicks in the different experimental treatments, we weighed chicks throughout the nestling period. Nests were checked every second day and chicks were weighed to the nearest 0.1 g on a Pesola balance. Following Ricklefs (1983), we fitted the data for each chick to the logistic growth model using the NLIN procedure of the SAS statistical package (SAS Institute, 1982). The form of the logistic model used was

$$W = A/(1 + b\,e^{-Kt})$$

where W is the weight (g) of the nestling on day t, A is the asymptotic weight (g), and b is a dimensionless fitting constant. In this version of the logistic, t equals 0 at hatch. K is the relative growth rate (d^{-1}) and measures the rate of approach to asymptotic weight. Since K is sensitive to differences in asymptote, it may not reflect real growth rate (in g/d) when asymptotic weight is variable, as it was in our study. We therefore used the absolute growth rate ($KA/4$ in g/d; see Hussell 1972 for details). For analysis we used the mean of each brood for both absolute growth rate and weight at fledging because values for chicks from the same brood were not independent – an analysis of variance revealed significant brood effects for both of these variables.

Results

All male removals were successful in that no females deserted their nests, and none of the males were replaced by "altruistic" males (see Weatherhead and Robertson 1980). All males in the Late Widow and Control groups fed their females (Fig. 1) but there was considerable variation
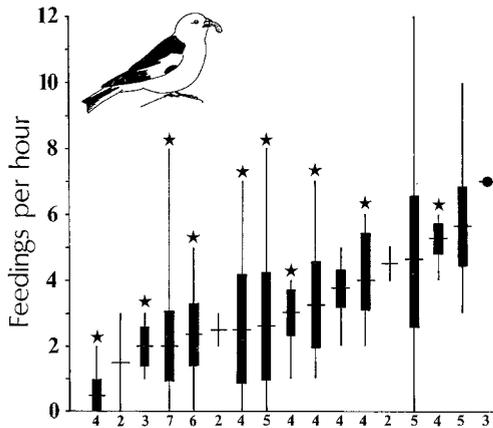
Fig. 1. Mean rate of incubation feeding (±SE, range) for Control (marked with a star) and Late Widow females. The number of 1-h observation periods is shown below the data for each female

Fig. 2. The relation between date of clutch completion and A number of chicks fledged and B mean chick weight at fledging for each brood. The regression line shown ($y = -0.60x + 44.3$) illustrates the predicted reduction in mean fledging weight through the season

among males in the rate of feeding. Some males regularly fed their mates at least 4 times per hour, while others did not feed at all during some of the 1-h observation periods (Fig. 1).

Early Widows spent significantly more time off their eggs than Late Widow and Control females (Table 1) and 2 of the 7 Early Widows spent more time off the nest than any of the 17 other females. This increased time off was the result of an increase in the duration of each trip, rather than number of trips (Table 1). As a consequence, the incubation period of Early Widows was significantly longer than that of Late Widows and Controls (Table 1).

Since the breeding season at Sarcpa Lake is so brief, a longer incubation period may result in overshooting peak food abundance and fledging fewer or lower quality chicks. We examined this indirectly by investigating the relation between timing of breeding and the number or quality of chicks fledged by Control females. There was no relation between date of nest initiation and the number of chicks fledged (Fig. 2A), but there was a substantial decrease in chick weight at fledging
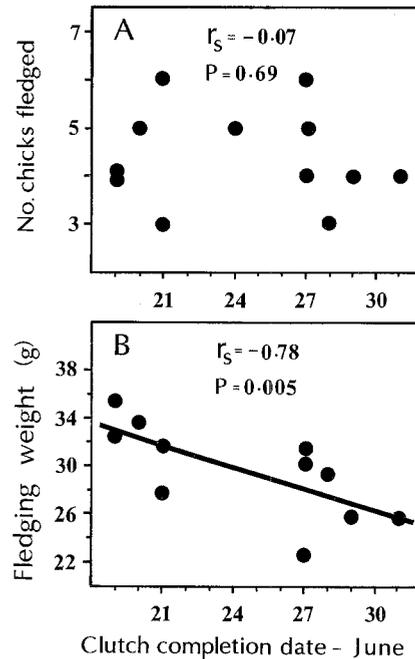
as the season progressed (Fig. 2B). This result is particularly important because the decrease in mean fledging weight occurred during a period of only 2 weeks and resulted in an average decrease of 0.6 g per day.

The most striking difference in reproductive success between females with (Early Widows) and without (Late Widows and Controls) incubation feeding was the occurrence of 2 or 3 unhatched eggs in 2 Early Widow nests ($n=6$). Among females that were fed during incubation, we found only 1 unhatched egg in 1 nest in the Late Widow and Control groups ($n=19$) and 1 in a nest studied in 1982 ($n=17$), and there was no sign of embryonic development in either of these eggs. The 5 un-

Table 1. Incubation behaviour of females with (Late Widows and Controls) and without (Early Widows) incubation feeding

	Early Widows			Late Widows and controls			Comparison[a]	
	Mean	Range	n	Mean	Range	n	U	P
Mean time off/h (min)	29.1	14.7–47.8	7	19.4	9.7–31.5	17	28	<0.025
Trip length (min)	7.5	4.2–10.3	7	5.5	2.8–12.8	17	25	<0.025
Number of trips/h	2.7	1.8–4.0	7	3.2	2.0–5.5	17	44	>0.10
Incubation period (d)	13.4	11.3–17.1	6	12.0	10.0–13.9	14	19	<0.05

[a] Mann-Whitney U-test

Table 2. Indices of reproductive success and female condition measured during the nestling period for Early and Late Widows. Growth rates and weights at fledging are calculated from mean values per nest

	Early Widows			Late Widows			Comparison[a]	
	Mean	Range	n	Mean	Range	n	U	P
Chicks fledged/nest	2.3	0–4	6	2.9	2–5	7	12	0.12
Growth rate (g/d)	4.2	2.7–5.9	4	3.8	2.4–5.3	7	11	0.32
Fledging weight (g)	24.9	20.8–29.0	4	24.8	21.5–29.7	7	14	0.54
Nestling deaths/nest	1.8	0–4	6	2.3	0–4	7	16.5	0.29
Timing of brood reduction (days after hatch)								
First chick	4.5	1–10	5	5.0	1–9	6	12	0.33
Second chick	3.3	1–5	3	7.6	5–12	6	0.5	0.02

[a] Mann-Whitney U-Test

hatched eggs in Early Widow nests all contained small embryos that had died sometime during the first week of development. We have never found 2 or more unhatched eggs in a snow bunting nest except those of Early Widows. Thus, a significantly higher proportion of Early Widows lost more than 1 egg during incubation than Controls and Late Widows combined ($P=0.05$, Fisher Exact Test). As a result, the probability that an egg would hatch in an Early Widow nest (84.8%, $n=33$ eggs) was lower than that in Late Widow and Control nests (99.0%, $n=101$ eggs).

The loss of incubation feeding had no effect on any of our measures of post-hatch reproductive success (Table 2). However, in those nests in which 2 or more nestlings died, the second chick died significantly earlier in Early Widow than in Late Widow nests (Table 2). This difference in the timing of brood reduction suggests that the loss of incubation feeding may have reduced the condition of females and consequently affected their ability to provide parental care to their nestlings.

Discussion

Our experimental manipulations revealed that incubation feeding in snow buntings affects their reproductive success during the concurrent breeding episode. These findings support the idea that incubation feeding is an adaptive male tactic that enhances the reproductive success of both members of the pair, and is not the result of female manipulation. While well-developed role specialization by parents in some species strongly suggests that this behaviour is adaptive (e.g. birds of prey (Newton 1979), hornbills (Lack 1968), rooks (Roskaft 1983)), this study is the first to clearly demonstrate that it can enhance reproductive success.

It could be argued that the effects we found were due not to the loss of incubation feeding but

to some other aspect of the male's behaviour that is important during the incubation period. Our observations suggest that this is unlikely. During the incubation period, male buntings do not appear to assist females except by incubation feeding. While nest defence by males may be useful, it occurs only rarely, and the loss of nest defence should have little influence on female incubation behaviour. It is also possible that females may learn the location of high quality foraging sites by following males after they are fed at the nest. Female buntings often leave the nest to forage soon after being fed by the male, but on most of these occasions they do not follow the male. While we do not rule out the possibility that females may occasionally learn the location of high quality foraging sites by following males, the loss of this information cannot account for the pronounced changes in the incubation schedules of widowed females. Thus, we conclude that the reproductive consequences documented here are attributable to the loss of incubation feeding, and not the loss of some other aspect of male parental care during the incubation period.

Our experiments show that female snow buntings change their incubation schedules when they lose their mates. Females that were fed by their mates spent an average of 32% of the time off their eggs, while widowed females spent an average of 49% of ther time away (Table 1). Clearly one of the proximate functions of incubation feeding is to permit females to spend more time on their nests.

The longer periods that Early Widow females spent away from their nests resulted in 2 costs: a longer incubation period and a lower hatching success. Seasonal changes in food availability may penalize individuals with longer incubation periods if they miss the peak of food abundance. This should be particularly important in the arctic

where the breeding season is short. Individual snow buntings whose breeding season is lengthened by even a small increase in the incubation period may therefore raise young of lower quality, since chick weight at fledging is correlated with survivorship in some birds (e.g. Perrins 1965). At Sarcpa Lake in 1983 each extra day of incubation resulted in an average reduction of 0.6 g in chick weight at fledging (Fig. 2b). While the longer incubation periods of Early Widows (1.45 d) would decrease chick weight at fledging by only 0.9 g, even small negative effects on chick survivorship should favor incubation feeding by males. Longer developmental periods (i.e. during incubation or chick growth) also result in a higher probability nest predation (Lack 1968; Ricklefs 1969), but the actual fitness cost of slower development depends on the predation rate.

The other cost of longer absences from the nest − reduced hatching success − was probably due to inadequate incubation during periods of cold weather. Since mean mid-day temperatures during the last 2 weeks of June 1983 were low ($\bar{x} = 4.2°$ C, range 1.4–8.4° C), it is likely that the eggs of Early Widows were frequently exposed to potentially lethal temperatures (Lundy 1969; Romanoff and Romanoff 1972).

The lower hatching success of eggs in Early Widow nests (85% compared to 99% for the control group) represents an immediate and direct reduction of reproductive success. However, since some females were fed 10 times as often as others, the removal of males did not result in a constant reduction of male help from each female. Thus, incubation feeding by males may be much more important to some females than others and it is not surprising that only one third of the Early Widow suffered a reduction in hatching success.

Although all groups of females lost similar numbers of chicks during the nestling period, some chicks in Early Widow nests died significantly earlier than those of Late Widows (Table 2). This difference in the timing of brood reduction did not apparently affect their overall reproductive success but it does suggest that Early Widows were in poorer shape than other females and were less able to carry out their parental duties. Further work will be needed to determine whether such effects on female condition have any longer term reproductive consequences such as reduced longevity.

Many factors affect the costs and benefits of incubation feeding and thus ultimately determine whether or not it evolves. On Greenland, for example, male snow buntings apparently do not feed their mates during incubation (Tinbergen 1939)

and it would be instructive to assess the ecological factors that might account for this difference. For males, the most important cost of incubation feeding is the loss of mating opportunities (e.g. attracting a second mate or cuckolding neighbours) and such opportunities depend on the operational sex ratio (Emlen and Oring 1977), the synchrony female receptivity within the population (Knowlton 1979), and the extent of mate guarding (Birkhead 1979). Given the large number of factors that affect the balance between costs and benefits, and the likelihood that benefits may differ among habitats and species, it is not surprising that ecological correlates of this behaviour have been so difficult to find (Ricklefs 1974).

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