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INCUBATION BEHAVIOR OF LONG-TAILED TITS: WHY DO MALES PROVISION INCUBATING FEMALES?¹

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Abstract. The incubation period of Long-tailed Tits *Aegithalos caudatus* is highly variable, ranging from 14 to 21 days. Females alone incubate the eggs, but males provide females with some food during the incubation period, although females must also forage for themselves. Our aim was to investigate whether male provisioning of incubating females influenced female incubation behavior and the length of the incubation period. Provisioning rates varied between males, and female nest attentiveness was negatively related to short-term variation in the rate at which their partner fed them. However, the provisioning rate of individual males also varied significantly through time, and there was no significant effect of male care on female incubation across the whole incubation period. There was no evidence that variation in the behavior

of either males or females influenced the length of the incubation period.

Key words: *Aegithalos caudatus*, *courtship feeding*, *incubation*, *Long-tailed Tit*.

Male birds often provide food for females during the breeding season, behavior known as courtship feeding. Provisioning may occur during pairing or egg-laying, but it also is frequent during the incubation period (Ricklefs 1974). The traditional interpretation of courtship feeding is that it serves a pair-bonding function, helping to cement the relationship between breeding partners (Lack 1940, Kluijver 1950). A second hypothesis proposes that courtship feeding provides information to females about male quality, in particular, his ability to feed nestlings (Nisbet 1973, 1977). Female fitness may depend on the extent of paternal care (Lyon et al. 1987, Yasukawa et al. 1990, Davies and Hatchwell 1992), so such information, and male ad-

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vertisement of it, may be an important cue for mate choice by females (Nisbet 1977).

A third hypothesis proposes that courtship feeding represents a significant nutritional contribution for the female (Royama 1966, Krebs 1970). If feeding of females by males occurs during the pre-laying and laying periods, the food may constitute a major proportion of the resources required by females for egg formation (Royama 1966). Provisioning of females by males may be equally important during incubation; indeed, in hornbills and some raptors, females are wholly dependent on males for food during incubation (Kendeigh 1952, Lack 1968, Kemp 1995). More often males feed incubating females who also spend some time off the nest foraging for themselves, a strategy termed assisted gyneparental incubation (Williams 1996). The most likely benefit of incubation feeding (the term used to describe courtship feeding during incubation) is the reduced need for females to fulfill their energetic demands by foraging for themselves, allowing them to spend more time incubating.

Many open-nesting passerine bird species suffer extremely high rates of nest depredation (Ricklefs 1969, Martin 1995). Decreasing the length of the incubation and/or nestling periods may reduce the period of vulnerability. For example, one of the benefits of biparental nestling care in Willow Warblers *Phylloscopus trochilus* is a reduction in the length of the nestling period (Bjørnstad and Lifjeld 1996). The incubation period also may offer opportunities for parental behavior to reduce the duration of incubation, thereby reducing predation risk (Clark and Wilson 1981, Nilsson and Smith 1988).

Long-tailed Tits *Aegithalos caudatus* build elaborate nests which are extremely vulnerable to predators, particularly during the laying and incubation phases (Gaston 1973, Hatchwell et al. 1999); they also exhibit a variable incubation period. The primary objective of this study was to investigate whether male provisioning of females during incubation in Long-tailed Tits serves an energetic function and permits females to spend more time incubating, thus reducing the length of the incubation period. Our data also allow us to evaluate the evidence for the pair-bonding and quality indicator hypotheses to explain courtship feeding in this species.

METHODS

We studied a color-banded population of 18–35 pairs of Long-tailed Tits from 1994–1997 in the Rivelin Valley, Sheffield, U.K. Long-tailed Tits start each season breeding independently in monogamous pairs. The female alone incubates the clutch, and the pair male feeds the female on the nest. Following failure of a breeding attempt, breeders may become helpers at the nests of their relatives, assisting in the care of their offspring (Lack and Lack 1958, Glen and Perrins 1988). Only very rarely do helpers assist before the nestling period.

The observations of incubation behavior reported in this paper were conducted at 39 nests: 4 in 1994, 18 in 1995, 2 in 1996, and 15 in 1997. We monitored the breeding activity of all pairs in the study area throughout the breeding season (March–June). Most nests

were found during building and, thereafter, were routinely visited every two to three days during the building, laying, incubation, and nestling periods. Long-tailed Tit nests are closed and have a small entrance hole, so the nest contents of accessible nests were checked by touch to determine the start of laying. Eggs are laid daily and the clutch size of accessible nests (33/39 nests, 85%) was determined by removing eggs from nests using a teaspoon once incubation had begun. Females start incubation on the day that the last egg is laid, never earlier (Glen 1985; Hatchwell, pers. observ.). The length of the incubation period of accessible nests that survived to hatching (20/39 nests, 51%) was determined from daily checks by touch for hatched nestlings from day 12 of incubation onwards. Only incubation periods known to within 24 hr are included in analyses. Hatching success was determined from the number of unhatched eggs remaining in the nest when nestlings were banded (day 11 of the nestling period).

To observe incubation behavior, we sat 20–40 m from nests and recorded the times at which females entered and left the nest and all visits by males to feed the female on the nest. The length of observation periods varied because a fixed period would bias observations towards short incubation and foraging bouts. We collected a few observations opportunistically during nest checks, but the great majority were collected during systematic watches in which we observed nests until a pre-determined number of incubation bouts (either three or four) had been observed. Our aim was to observe incubation behavior at each nest on at least three occasions spread through the incubation period, but the high rate of nest predation resulted in many nests failing during incubation (Hatchwell et al. 1999). Therefore, in analyses using nests as independent data, we used only those nests where a minimum of five incubation bouts was recorded (mean [\pm SD] observation time per nest = 366 \pm 188 min; n = 32 nests). In analyses using observation periods as independent samples, we used only those periods in which a minimum of three consecutive incubation bouts were observed. A total of 79 such observation periods with a mean duration of 135 \pm 37 min were recorded at 37 nests.

We also observed nests during the nestling period to determine the rate at which parents and helpers fed chicks. Provisioning rates were recorded for 18 of the 32 nests that we had watched for a minimum of five incubation bouts; most of the remainder were depredated before eggs hatched. Nests were observed at two day intervals until fledging or nest failure (mean observation time = 611 \pm 356 min, n = 18 nests). Provisioning rates increased with nestling age, so we used residuals from the regression of feeding rate against nestling age to control for this effect (see Hatchwell and Russell 1996 for details). Weather data were recorded 3 km from the study site and were obtained from Sheffield City Museums Department. Means are given \pm SD and two-tailed tests are used throughout with a significance level of $P < 0.05$.

RESULTS

The mean length of incubation bouts was 24.2 \pm 4.9 min (n = 32 nests with at least five bouts observed),

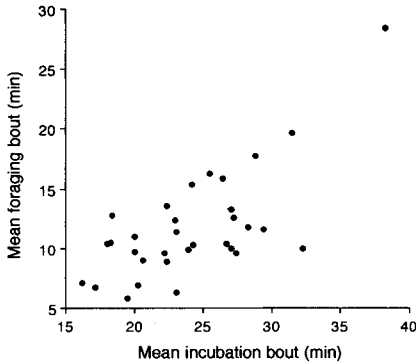


FIGURE 1. The relationship between the mean duration of foraging bouts and the mean duration of incubation bouts in female Long-tailed Tits ($r_s = 0.51$, $n = 32$, $P < 0.01$; $n = 32$ females).

and the mean length of foraging bouts was 11.7 ± 4.5 min ($n = 32$). Incubation and foraging bout lengths were positively correlated (Fig. 1), but the proportion of total time that females spent incubating, termed "nest attentiveness," varied among nests ($68.0 \pm 5.6\%$, $n = 32$, range = 57–79%). The duration of the incubation period also was variable, ranging from 14–18 days (16.0 ± 1.2 days, $n = 20$) in the sample of observed nests, and up to 21 days in a larger sample of nests not included in this study. The clutch size in observed nests ranged from 8 to 12 eggs (9.9 ± 0.9 eggs, $n = 33$), but there was no significant relationship between clutch size and incubation period ($r_s = -0.32$, $n = 18$, $P > 0.10$) or incubation behavior (mean incubation bout $r_s = -0.11$, $n = 18$, $P > 0.50$; mean foraging bout $r_s = -0.04$, $n = 18$, $P > 0.50$; nest attentiveness $r_s = 0.06$, $n = 18$, $P > 0.50$). Therefore, we have not controlled for clutch size in subsequent analyses.

DOES INCUBATION FEEDING INDICATE MALE QUALITY?

The mean male provisioning rate of incubating females across the whole incubation period was 2.34 ± 2.34 feeds hr^{-1} of incubation ($n = 32$ nests; range 0–12 feeds hr^{-1}). There was significant variation among males in their provisioning rate (Kruskal-Wallis ANOVA, $H_{29} = 81.4$, $P < 0.001$; data from 27 males in 30 breeding attempts; two nests where males were assisted by helpers are omitted). Three males were observed in two different breeding attempts when paired to different females in different years. In one case a male fed the two females at significantly different rates (Mann-Whitney U -test, $U = 20.5$, $n_1 = 9$, $n_2 = 12$, $P < 0.02$), and in the other two cases there was no significant difference in feeding rates ($U = 22.5$, $n_1 = 7$, $n_2 = 8$, $P > 0.50$; $U = 22$, $n_1 = 7$, $n_2 = 8$, $P > 0.40$).

The pair-bonding hypothesis predicts that females are more likely to divorce males who provide relatively little food during incubation. Divorce sometimes occurred between breeding attempts within a season following early nest failure (Hatchwell, unpubl. data), but there was no significant difference in the provisioning

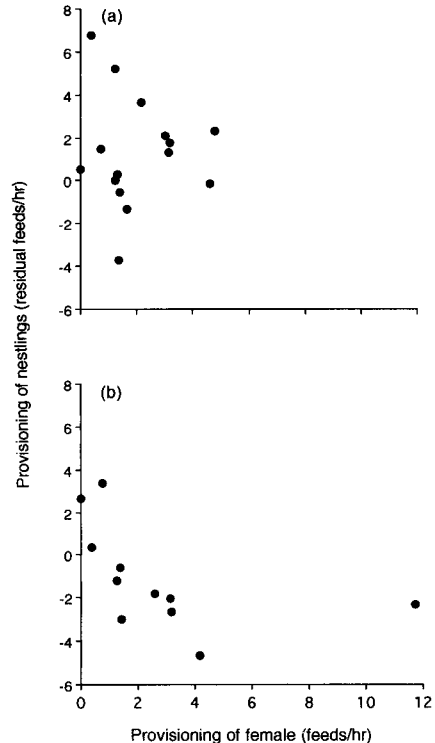


FIGURE 2. The relationship between the rate at which male Long-tailed Tits provisioned nestlings and incubating females: (a) nests without helpers ($r_s = -0.03$, $n = 15$, $P > 0.50$), (b) nests with helpers ($r_s = -0.84$, $n = 11$, $P < 0.01$).

rate of males who divorced and those who remained paired (divorced, 2.70 ± 3.18 feeds hr^{-1} of incubation, $n = 3$; paired, 2.04 ± 1.44 feeds hr^{-1} , $n = 8$; Mann-Whitney U -test, $U = 10.5$, $P > 0.50$), although the sample size for this analysis was very small. Thus, there was no evidence that incubation feeding plays a role in the maintenance of pair-bonds within a season.

If incubation feeding indicates a male's ability or willingness to invest parental care, a positive relationship would be predicted between provisioning rates during the incubation and nestling phases. There was no significant correlation between male provisioning of nestlings and females when a pair had no helpers (Fig. 2a), but when helpers were present at a nest there was a significant negative correlation (Fig. 2b). Thus, males who fed females frequently during incubation fed nestlings less frequently, but only when helpers assisted in brood care. Female provisioning of nestlings, with or without helpers, was not significantly correlated with either female incubation behavior or male provisioning rate (Spearman correlations, all $P > 0.20$).

DOES INCUBATION FEEDING HAVE AN ENERGETIC FUNCTION?

Male provisioning might allow females to spend more time incubating by reducing the duration of foraging

bouts and/or increasing the duration of incubation bouts. However, female incubation behavior was not significantly correlated with their partner's mean provisioning rate across the incubation period (mean incubation bout $r_s = 0.14$, $n = 32$, $P > 0.40$; mean foraging bout $r_s = -0.15$, $n = 32$, $P > 0.40$; nest attentiveness $r_s = 0.13$, $n = 32$, $P > 0.40$).

The provisioning rates of males observed at the same nest on more than one occasion were variable: in 6 out of 26 nests where statistically valid comparisons could be made, there was significant variation in male provisioning among observation periods, despite small sample sizes (Kruskal-Wallis tests on provisioning rates in separate watches with three or more incubation bouts observed). Given this variation, adjustment of incubation behavior by females in response to male provisioning rates may occur over a short time period rather than over the entire incubation period. Therefore, instead of using nests as independent data, we investigated incubation behavior using observation periods as independent samples. The number of watches conducted on each nest varied (2.14 ± 0.86 watches, range 1–4, $n = 37$ nests), so to avoid the problem of pseudoreplication by inclusion of multiple watches of some nests, a series of 30 conservative analyses were performed in which each nest was represented only once in a random selection of observation periods ($n = 37$ nests). In 10 out of the 30 randomly assembled data sets there was a significant positive correlation (Spearman correlations: $P < 0.05$) between nest attentiveness and male provisioning rate, significantly more than expected by chance ($G_1 = 8.53$, $P < 0.01$). This result indicates that male provisioning influenced nest attentiveness in the short-term.

Temperatures ranged from 4.4–21.0°C on observation days, and could potentially have influenced incubation behavior. However, using the randomly assembled data sets described above, there was no indication of a strong association between temperature and either nest attentiveness (4/30 Spearman correlations significant at $P < 0.05$) or male provisioning rate (2/30 significant at $P < 0.05$).

DOES BEHAVIOR INFLUENCE INCUBATION PERIOD AND HATCHING SUCCESS?

For the sample of 20 observed nests for which the length of the incubation period was known to within 24 hr, the incubation period was not significantly correlated with either foraging or incubation times (foraging bouts $r_s = 0.18$, $n = 20$, $P > 0.40$; incubation bouts $r_s = 0.16$, $n = 20$, $P > 0.50$; nest attentiveness $r_s = 0.02$, $n = 20$, $P > 0.50$), nor with male provisioning rate ($r_s = -0.21$, $n = 20$, $P > 0.30$).

Ten of the 32 closely observed nests were depredated before hatching. Male provisioning rates did not differ significantly at successful (0.042 ± 0.041 feeds hr^{-1} , $n = 22$) and depredated nests (0.034 ± 0.034 feeds hr^{-1} , $n = 10$; Mann-Whitney U -test, $z = 0.69$, $P = 0.50$). The proportion of eggs that hatched was known in 17 of the 22 successful nests ($89 \pm 20\%$, range 33–100%) and there was no relationship between hatching success and any measure of male or female behavior (foraging bouts $r_s = -0.25$, $n = 17$, $P > 0.30$; incubation bouts $r_s = -0.38$, $n = 17$, $P >$

0.10; nest attentiveness $r_s = 0.03$, $n = 17$, $P > 0.50$; provisioning rate $r_s = -0.20$, $n = 17$, $P > 0.40$).

DISCUSSION

The rate at which males fed incubating females varied significantly among males and had a short-term effect on female nest attentiveness. However, male provisioning rates also varied significantly among watches at the same nest, and there was no significant effect on female incubation behavior across the whole period of incubation. The variable incubation period of Long-tailed Tits was not significantly related to any of the measured behavioral parameters.

There was no support for two of the hypotheses that might explain male provisioning of incubating females in this species: (1) that it strengthens the pair-bond between breeding partners, and (2) that it indicates male parental effort and thus provides a cue for mate choice. Male provisioning of females was seen only during incubation, when birds were already paired; courtship feeding has not been recorded during the pairing period (Cramp and Perrins 1993; Hatchwell, pers. observ.). Therefore, courtship feeding could not be used by females as a basis for initial mate choice, although it might still fulfill either function if used as a basis for female-initiated divorce. However, there was no difference in the provisioning rates of pairs who did and did not divorce between breeding attempts, although the sample size for this comparison was small. Second, incubation feeding did not indicate future levels of paternal investment because male provisioning rates of females and nestlings were not positively correlated; in fact, they were negatively correlated when helpers were present during the nestling period. It is interesting that males who had worked hard during incubation worked less hard in provisioning nestlings when helpers were present (Fig. 2b). Hatchwell and Russell (1996) showed experimentally that during the nestling period parents with helpers significantly reduced their own provisioning effort. The fact that there was no relationship between male provisioning of females and nestlings in the absence of helpers (Fig. 2a) suggests that one of the benefits of helpers for male breeders is the opportunity to recoup some of the costs of relatively high investment earlier in the breeding cycle. By contrast, there was no evidence that female provisioning of nestlings was related to any measure of incubation behavior. This is consistent with the observation that the reduction in female parental effort when helped during the nestling period was less pronounced than that of males (Hatchwell and Russell 1996).

The third hypothesis for the function of incubation feeding is that the food represents a significant nutritional contribution to females. This hypothesis predicts that female Long-tailed Tits would maintain better body condition and/or provide better incubation if provisioned by males at a high rate. We have no information on female condition during incubation, but incubation feeding did influence female incubation behavior. Female attentiveness increased as male provisioning increased, thus supporting this hypothesis for the function of incubation feeding. However, this relationship held only in the short-term, i.e., in analyses

of individual watches, rather than for mean values per nest. Such short-term effects might be expected if environmental factors such as food availability vary from day to day.

Previous studies also have found that nest attentiveness was influenced by food availability. For example, in both Wheatears *Oenanthe oenanthe* (Moreno 1989) and Song Sparrows *Melospiza melodia* (Arcese and Smith 1988) supplementary feeding increased female nest attentiveness by reducing the length of foraging bouts. Across species, the duration of incubation bouts is related to body mass (Kendeigh 1952, Williams 1991), and in the absence of male help during the incubation period, female Long-tailed Tits (mass = 7.8 g) would be expected to have an attentive period of just 13 min (Williams 1991), approximately half the observed bouts of 24 min. It is possible that male provisioning of females on the nest enables them to incubate for such relatively long bouts, although the elaborate and well-insulated nest structure of Long-tailed Tits also is likely to be important in this context.

The failure of Long-tailed Tit nests is very frequent during the incubation period: 47% of nests in which a full clutch is laid are destroyed by predators before hatching (Hatchwell et al. 1999). Thus, strong selection for a reduction in the length of the incubation period would be expected. However, there was no evidence that male or female behavior during incubation had any significant effect on time to hatching or hatching success. One explanation for these results is that our observation periods were too short to reliably measure incubation behavior; the variation observed among watches on the same males could reflect inadequate sampling. Alternatively, it may be an accurate indication of highly variable male provisioning rates. For example, provisioning rates might be sensitive to environmental factors, although there was no evidence that the behavior of either sex was influenced by temperature.

In conclusion, incubation feeding by male Long-tailed Tits does influence female energy budgets in the short-term, enabling them to spend more time incubating. However, males provision females at a variable rate, so there was no evidence that male or female behavior influenced the duration of the incubation period. The cause of the observed variation in incubation period in this species therefore remains unexplained.

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SONG VERSATILITY AND SOCIAL CONTEXT IN THE BOBOLINK¹

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Abstract. We contextually analyzed the song of the Bobolink (*Dolichonyx oryzivorus*) to examine the role of sexual selection on song versatility. Recordings were obtained as territorial males were randomly presented with a caged male (a conspecific intruder), a caged female (a potential breeding partner), and an empty control cage. Sound spectrograms created from the recordings were analyzed and an index of versatility was calculated for each male in each manipulation so that individual song variation could be compared among behavioral contexts. These analyses suggest that more complex or versatile song production is being selected intersexually, whereas short repetitive song is intrasexually selected.

Key words: *Bobolink, Dolichonyx oryzivorus, mate choice, repertoire, sexual selection, song versatility.*

Song repertoires function intersexually in stimulating females to court and copulate and intrasexually in territorial defense (Catchpole and Slater 1995). One way to test which of these functions is more important is to determine whether males emphasize their repertoires more when courting females or when acting aggressively with other males. Using this method, Searcy and Yasukawa (1990) showed that male Red-winged Blackbirds (*Agelaius phoeniceus*) increase their rate of song switching when courting females, and decrease switching rate when confronting conspecific intruders. In this paper, we take a similar approach to examine repertoire function in Bobolinks (*Dolichonyx oryzivorus*).

Bobolinks are usually regarded as having only two

song types per male (Avery and Oring 1977, Wittenberger 1983). These two song types, termed “alpha” and “beta,” are distinguishable within a given population by their unique sequences of introductory notes as well as by overall length. Because male Bobolinks often sing variations of their primary songs that include complete, fragmented, and compound configurations of varying length, we chose to classify each unique vocalization as a distinct song variant. Trainer and Peltz (1996) reassessed the repertoire of the Bobolink, originally proposed by Wittenberger (1983), and suggested that each variant can be considered as a separate song type. Defining song in this way, and using an index of versatility from information theory, Trainer and Peltz (1996) concluded that individual male Bobolinks differ in the versatility of their song.

In this study, we adopt the Trainer and Peltz (1996) approach of viewing each song variant as a song type in the Bobolink, and utilize a versatility index to examine the role of sexual selection on song versatility. We then compare song versatility of territorial male Bobolinks in both male-male and male-female contexts to test whether song pattern versatility functions in intersexual or intrasexual communication in this species.

METHODS

The data analyzed in this study were collected from 20 May–25 June 1987 and from 14 May–28 May 1988 near the University of Pittsburgh’s Pymatuning Laboratory of Ecology in northwestern Pennsylvania. Playback of conspecific song and mist netting were employed to capture territorial males. These males were then color banded for future identification. Some test males were not captured because they displayed plumage features that made them easily recognizable. Several nonterritorial, unpaired males and a few females

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