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EFFECT OF HEATING NEST BOXES ON EGG LAYING IN THE BLUE TIT (*PARUS CAERULEUS*)

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ABSTRACT.—Nest boxes of Blue Tits (*Parus caeruleus*) were heated from the time that nests were completed and lined (a few days before the first egg appeared) until several days after the completion of the clutch. Night-light candles placed underneath the box increased the temperature of the air in the nest box by an average of 6°C. The calculated energy savings for an average Blue Tit roosting one night in a heated nest was 0.768 Kcal, which is estimated to be equivalent to 35% of the cost of producing an egg. The percentage of nests that showed an interruption in the laying sequence was significantly lower in heated nests than in control nests. Minimum ambient temperature four and five days before these interruptions occurred was a significant factor in explaining their frequency, indicating that this is a critical period in egg production. In addition, five of six interruptions in heated nests occurred after a night when the candle was extinguished by wind, suggesting that unpredicted low temperatures on the night before laying also may affect egg laying. *Received 6 January 1992, accepted 29 July 1992.*

VARIOUS BREEDING parameters of birds are known to be affected by ambient temperature, which could influence them by changing the availability of food, or by affecting the quantity of food required for daily maintenance (Perrins 1970). Females form their eggs out of the energy surplus available to them after their maintenance needs have been met, but low spring temperatures increase maintenance costs, thus making it difficult for them to form eggs as early as they would in a warmer year (O'Connor and Morgan 1982). Thus, ambient temperature could influence laying date (Perrins 1970) and egg mass (Jones 1973). Inclement weather early in the breeding season does result in a delay of gonadal maturation (Wingfield 1984), and severe weather conditions during the egg-laying period could cause interruptions in the normal laying sequence (Dhondt et al. 1983, Ojanen 1983a, b, Schmidt and Hamann 1983 [and references therein]). Even small differences in ambient temperature might affect the laying date—tits breeding in warmer nest boxes lay a day or two earlier than those nesting in cooler boxes (O'Connor 1978, Dhondt and Eyckerman 1979). Physiological studies also indicate that ambient temperature has considerable effect on the energy needs of birds (Haftorn and Reinertsen 1985).

In this study we investigated the effect of heating nest boxes on egg laying in Blue Tits (*Parus caeruleus*). We expected that heating would cause one or more of the following in the experimental nests: early laying; larger clutches; heavier eggs and continuous laying of the eggs (i.e. laying an egg a day, without interruption).

MATERIALS AND METHODS

This study was conducted in Wytham Wood, Oxfordshire, where Blue Tits breed in nest boxes made from cement and sawdust. We followed the population from nest building onwards during the breeding season in 1991. Each nest was checked daily until one week after clutch completion. Eggs were individually weighed when the clutch was complete.

A soon as nests were identified as those lined by Blue Tits (rather than by Great Tits, *P. major*), the nests were randomly allocated to either the experimental (heated) or control (unheated) groups. An empty aluminum soft-drink can, which was painted uniformly brown, was attached to the bottom of all the nests. An opening was cut at the bottom of each can and several smaller holes made at its top to enable air flow. Heating was provided by a small night-light candle, which was lit every evening about 2 to 3 h before sunset. The candle flame sat roughly 8 cm below the bottom of the nest box. Preliminary experiments indicated that these candles increase the temperature of the nest cavity (above the lining) by an average of 6°C, and burn for an average period of 10 h. However, since females entered their boxes at about dusk, they probably only roosted in the heated boxes for an average of 7 h per night.

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TABLE 1. Length of interruptions in laying sequence in control and heated Blue Tits nests (including those heated nests where candles blew out).

	Interruption length (days)						
	1	2	3	4	5	6	Total
Control	7	3	0	0	1	1	12
Heated	4	1	1	0	0	0	6

TABLE 2. Number of interruptions in laying sequences in control and heated nests. For a subset of nests where no candles blew out, $X^2 = 13.3$ ($P < 0.001$). When all nests included, $X^2 = 6.2$ ($P < 0.013$).

	Subset		All nests	
	Control	Heated	Control	Heated
Uninterrupted	9	5	9	5
Interrupted	1	12	6	12

There were 16 control nests (14 of which had eggs laid in them by end of experiment) and 20 heated nests (16 of which had eggs laid in them). In two control nests, there were only two eggs laid in each, and these were not included in the analyses because it is unlikely that these were the result of normally breeding pairs. In eight nests, heating was only started on the day following the appearance of the first egg and in the eight others it was started several days before. Although the candles were lit every evening, many were extinguished by the wind, which tilted the nest boxes and the attached cans with their candles, causing the liquid paraffin of the candle to flood the wick. Each nest was heated for an average of 7.0 ± SD of 4.5 nights (range 2–16), of which 1.9 ± 2.4 nights (range 0–8) occurred before laying started and 5.1 ± 2.7 nights (range 1–12) occurred during laying itself. Weather records used in the analysis were for Oxford, about 3 km from the study site, as recorded at the Radcliff Meterology Station at the School of Geography, Oxford. For ease of analysis and statistical conservatism, all data were reduced to single-parameter estimates per nest for use in chi-square tests, while estimates per day across all nests were used in regression analyses against ambient temperature values.

RESULTS

Laying started on 14 April 1991. A spell of cold weather, with low ambient temperatures and high winds occurred between 17 and 22 April. Average minimum temperatures were 0.9 ± 1.2°C during the cold spell, and 6.7 ± 2.0°C during the 10 days preceding it. Several isolated cold days also occurred later in the laying period.

Clutch size declined during the laying season at a rate of 0.12 eggs/day, exactly the same rate of decline recorded by Lack (1966). There were no differences in mean mass of eggs or clutch size between groups.

There were 18 interruptions in laying sequences in 14 nests, which lasted from one to six days with 67% of the interruptions occurring in control nests (Table 1). Most interrupted nests had only one interruption event, but in three control nests there was more than one interruption per nest: three one-day interruptions in one; two one-day interruptions in another; and one one-day and one two-day interruption in a third nest. Nearly all of the interruptions in heated nests (i.e. five of six) occurred after a night when the candle was extinguished by the wind, although these boxes were not always heated on every previous night. In only one nest was laying interrupted while heating was provided and, in this case, the laying sequence was interrupted for three days.

Comparison of the number of nests with laying interruptions in control and heated groups showed that the difference between the two groups is highly significant, whether all the nests were included in the analysis ($X^2 = 6.2$, $P = 0.013$; Table 2), or the nests where the candles blew out were excluded ($X^2 = 13.3$, $P < 0.001$; Table 2). This shows that females breeding in control nests were significantly more likely than those with heated boxes to have their laying interrupted.

The effect of heating nest boxes might lead us to expect some effect of natural variation in minimum temperature on the variation in the number of laying interruptions on different days. For the 22 days during the laying period, the minimum ambient temperature on the night before egg laying was regressed against the percentage of nests (both heated and control) in which there were interruptions in the laying sequence. Although there was no significant effect of the minimum temperature the night before ($R^2 = 0.016$, $P = 0.570$), there was a significant effect of the minimum temperature at night five days before (Fig. 1; $R^2 = 0.227$, $P = 0.025$). Figure 2 shows the R^2 values of the effect on the percentage of interruptions of the minimum temperatures one to eight days before egg laying. Clearly, only the minimum temperatures four and five days before eggs were laid had an effect on the percentage of nests with interruptions in their laying sequence.

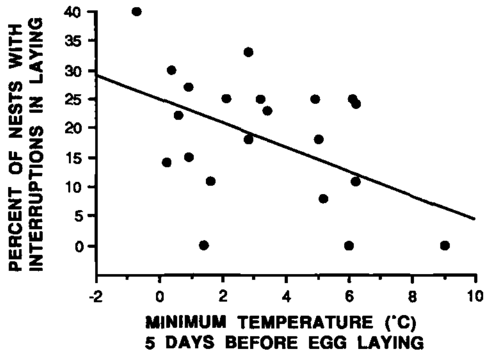

Fig. 1. Effect of minimum ambient temperature five days before laying on percentage of nests with interruptions in their laying sequence ($Y = 24.95-2.0875X$, $R^2 = 0.227$, $P = 0.025$). Regression run on arcsine transformation of the percentages. Total number of nests with laying females varied from 7 to 17 ($\bar{x} = 16.3$).

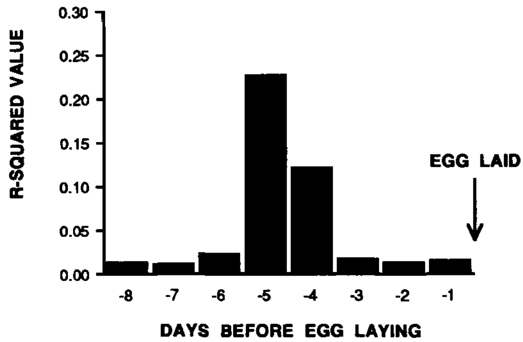

Fig. 2. R-squared values for regressions of minimum ambient temperature, one to eight days before laying, on percentage of nests with interruptions in their laying sequence ($n = 22$ for each regression).

Discussion

Gaps in the laying sequences lasting a number of days could be considered as long interruptions in laying, or as desertions followed by a repeat clutches. However, all but two of the interruptions in our study were less than four days in length, suggesting that we were recording interruptions and not repeat clutches. Dhondt et al. (1983) have shown that the incidence of laying interruption in Blue Tits in Belgium fluctuates between 1.9 to 17.9%, and suggested that these rates are probably underestimates. Schmidt and Hamann (1983) reported that in Blue Tits in Germany the average interruption rate is 37% after spells of cold weather. We found that the rate of laying interruption could be as high as 40% when minimum ambient temperatures four or five days before the interruption fell to about 0°C. However, no interruptions in control nests occurred when these temperatures remained above 6°C.

The relationship found here between the incidence of laying interruptions and minimum temperatures four and five days before interruptions occurred suggests that this is a critical period in egg formation. If the cost of a cold night directly reduced nocturnal energetic investment in the egg by the female at this stage, then a large part of the yolk must have been laid down at this time as suggested by Kluyver (1951, 1952). However, direct evidence from the measurement of egg sizes during the different stages of development in the House Sparrow (*Passer domesticus*; Schifferli 1976) and in the Great Tit (C. M. Perrins unpubl. data) has shown a gradual build up of yolk over the five days before laying. Therefore, only a minimal amount of energy was invested in the initial stage of egg formation, four or five days prior to laying, but somehow low temperatures at this time caused a cessation of egg production. Once this initial stage was passed, egg formation carried on regardless of low temperatures, despite substantial energetic investments in the yolk each day until laying. Thus, the influence of low temperatures on laying interruptions does not appear to be a purely physiological effect, operating through energy reserves in the female's body, and some other mechanism is required to explain this sensitivity in the early stages of egg formation.

Cold temperatures cause high metabolic demands for body maintenance, thus reducing the energy available for egg production. The significantly fewer interruptions in heated boxes were probably the result of the energy saved from being in a warmer box on cold nights. The energy savings for a Blue Tit roosting for one night in a heated nest box can be calculated using Haftorn and Reinertsen's (1985) data on the energetic costs of free-living roosting Blue Tits. The relationship between air temperature (X, °C) and standard metabolic rate (Y, ml O_2/[g·h]) in this species is described by Haftorn and Reinertsen in the equation: $Y = 9.85 - 0.29X$. The average mass of a British Blue Tit during laying is 13.3 g (Perrins 1979) and, in a heated nest box at sunset, a bird of this size would have experienced an average elevation in air temperature inside the box of 6°C for 7 h. The savings amount to 162 ml O_2 for the bird and, using a conversion factor of 4.74 cal/ml O_2 (Vleck 1981), this is equivalent to 0.768 Kcal. The cost of producing an egg was estimated by Ricklefs (1974) to be 40% of daily basal metabolic rate (BMR) of the female. Given the calculated BMR of a 13.3-g Blue Tit is 5.42 Kcal (Lasiewski and Dawson 1967), the cost of producing an egg is 2.17 Kcal. The energy savings of 0.768 Kcal for a bird in a heated box, therefore, was equivalent of 35% of the cost of an egg. Kluyver (1951) estimated that 53% of the energy in eggs is in the yolk alone, and the yolk has recently been measured at 62% of the energy in a Great Tit egg by J. C. Yoo (unpubl. data). Roosting in a heated nest box for one night during the critical period of yolk formation four or five days before laying, therefore, could have saved females at least one-half the amount of energy that is contained in a whole yolk. The calculation above does not include any error terms in the various figures used. However, these estimates do show that the experimental manipulation of heating boxes could have energetic consequences of the same order of magnitude as that required in egg production.

The energetic savings were large enough to allow tits roosting in heated nest boxes to lay continuously even after very cold nights and, thus, complete the laying of their clutch by an average of 2.1 days before control birds. Since early hatchlings have higher chances of survival in comparison to late ones (Perrins and McCleery 1989), the heating of the nest boxes probably benefited the birds breeding there.

Five of six interruptions in heated nests occurred after a night that the candle was extinguished by wind, suggesting that cold temperatures also could affect the final stages of egg formation. Egg shell is much less costly than yolk (i.e. 16% of an egg; Kluyver 1951), but it could still be a critical energetic cost on cold nights (0.35 Kcal), and the calculated energy savings of heating the nest (0.768 Kcal) provided more than double this amount. Schifferli (1976) has shown that shell formation in the House Sparrow starts about 17 h before laying, but at 12 h before laying (i.e. the time at which candles were lit each evening) only 32% of the shell was formed. Hence, the heating provided by the candle could have enabled the bird to complete shell formation even in a cold night. However, in Blue Tits the eggs can appear to be fully formed, including pigment, 1 h after dusk, although Blue Tits are known to wait until dawn to lay (Perrins 1979). The frequency of interruptions also was unaffected by natural variation in the minimum temperature on the night before laying. Therefore, although suggestive, with five of six interruptions in the laying associated with candles blowing out in heated boxes, it remains to be tested whether shell formation is affected by low temperatures on the night before laying.

This experiment should be considered as preliminary. Future experiments of this kind should use a more reliable source of heat or insulation, which will produce energy at a constant rate without being disturbed by ambient conditions. We believe that such experiments will influence not only the rate of laying interruption but also laying date, and possibly clutch size as predicted by Yom-Tov and Hilborn (1981).

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