Acta Zoologica Academiae Scientiarum Hungaricae 51 (1), pp. 59–66, 2005

THE INFLUENCE OF NEST SIZE ON HEAT LOSS OF PENDULINE TIT EGGS

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The size and quality of nest influence mate choice and parental behaviour in several birds. Previous works in Penduline Tits showed that females prefer to mate with males that build large nests, and females desert small nests whereas they incubate eggs in large nests. We tested whether female preference may be related to the benefits of having large nests by investigating the influence of nest size (height, volume and thickness) on cooling rates of eggs and terminal egg temperatures in the laboratory using two ambient temperatures (10°C and 25°C), and clutch sizes (3 and 9 dummy eggs). Cooling rate of eggs was slower at 25°C than at 10°C, and 9 eggs cooled slower than 3 eggs. In addition, cooling rates decreased with nest thickness, although they were unrelated to nest height and volume. The influence of nest thickness on egg cooling rates was stronger at 10°C than at 25°C indicating that nest thickness is particularly important to insulate the eggs in relatively cold environment. Our results are thus consistent with a previous field study that showed a stronger female preference for large nests early in the breeding season, when ambient temperatures are low, than late in the season.

Key words: egg heat loss, nest size, mate choice, Penduline Tit, *Remiz pendulinus*

INTRODUCTION

Nest quality influences mate choice and breeding system of many birds (reviewed by COLLIAS & COLLIAS 1984, HANSELL 2000). For example, males benefit from building a sophisticated nest, since these nests increase their mating success (Satin Bowerbird *Ptilonorhynchus violaceus*, BORGIA 1985), or enhance the parental effort of their females (Black Wheatear *Oenanthe leucura*, MORENO *et al.* 1994; Barn Swallow *Hirundo rustica*, SOLER *et al.* 1998*a*; Magpie *Pica pica*, SOLER *et al.* 2001). Nest quality may also signal the males' ability (or their willingness) to care for the offspring, which in turn influences how much effort their female puts into providing care (Rufous Bush Robin *Cercotrichas galactotes*, PALOMINO *et al.* 1998, see also SOLER *et al.* 1998*b*).

Penduline Tits (*Remiz pendulinus*) exhibit ambisexual breeding system in which both males and females may mate with up to four consecutive partners in a single breeding season (PERSSON & ÖHRSTRÖM 1989, FRANZ 1991, SZENTIRMAI & SZÉKELY unpubl. data). Unmated males build elaborate pendulous nests to attract females, and females prefer large nests to small ones (HOI *et al.* 1994). The Penduline Tit is also one of the handful of species in which the offspring are deserted by one (male or female) or both parents. For instance, 48% of clutches are reared only by females, 18% only by males and 34% are deserted by both parents in Sweden (PERSSON & ÖHRSTRÖM 1989). Desertion behaviour is also related to nest size, since nests incubated only by females are larger than nests incubated by males (HOI *et al.* 1994).

Females may gain two sorts of benefits from choosing a male with a large nest. First, nest size may indicate the male's genetic quality, and males that build large nests may sire more viable and/or attractive offspring than males that build small nests (indirect benefits, JENNIONS & PETRIE 2000). Second, large nests may be better insulated than small ones, and thus reduce fluctuations in egg temperature. In turn, stable egg temperature accelerates embryonic and chick development (WEBB 1987, MØLLER 1991), and decreases the energetic costs of incubation (WILLIAMS 1996). In line with these arguments female Penduline Tits spent less time on incubation in large nests than in small ones, and they also fledged more chicks (GRUBBAUER & HOI 1996). The results of the latter study, however, may have been confounded by parental quality: thus females may spend less time incubating large nests since females that chose large nests may be more efficient incubators than females that chose small nest.

Separating the influences of parental quality from nest quality is not straightforward in nature, thus we carried out a study in the laboratory.

We tested whether nest size (height, volume and thickness) influences egg cooling rates, using two ambient temperatures and clutch sizes each. First, we expected that large nests insulate the eggs better from the ambient environment than small nests. This hypothesis predicts that the eggs should cool down slower in large and thick nests, than in small and thin ones. Second, we expected that ambient temperature and clutch size would influence heat loss of eggs. Specifically, we predicted that eggs would cool faster at low ambient temperature and small clutch size.

MATERIALS AND METHODS

Laboratory experiment

Twenty Penduline Tit nests were collected at Hortobágy Halastó, eastern Hungary (47°38'N, 21°05'E) on 11 and 12 August 2000. All nests appeared to be complete, and were not used by

Penduline Tits at the time of collection. Penduline Tits use each nest only for one breeding attempt, and nest-building usually terminates in July (FRANZ & THEISS 1983).

The experiment was carried out in November and December 2001 at the Department of Colloid Chemistry, Eötvös University, Hungary. We placed artificial eggs in each nest and investigated their heat loss at two ambient temperatures (10°C and 25°C; natural range during the breeding season: 8–36°C, SZENTIRMAI unpubl. data), and two clutch sizes (3 and 9, natural range: 2–9 eggs, SZENTIRMAI unpubl. data). Eggs were made from plasticine, and their weight, length and breadth matched real Penduline Tit eggs. One egg was embedded with a thermistor which was connected to an automatic datalogger (LogitLab, DCP Microdevelopments Ltd). The embedded egg was positioned in the centre of the clutch.

First, the eggs were placed inside the nest, and the nest was placed in a thermostat (U10 Ultra-thermostat, Prüfgeräte-Werk Medingen GmbH, Germany), which was set to 25±1°C ('ambient temperature'). Ambient temperature remained constant during each trial. Second, when the internal egg temperature reached the ambient temperature, a light bulb (25 W) was inserted into the nest above the eggs, and eggs were heated to 35°C. When egg temperature reached 35°C, the light bulb was removed from the nest, and egg temperatures were logged at every 30 second for 15 minutes. We choose 35°C as initial temperature because this egg temperature was recorded in a closely related species, the Blue Tit (*Parus caeruleus*), during incubation (HAFTORN & REINERTSEN 1985), that has a body size similar to the Penduline Tit.

Two trials were carried out for each nest at both 25°C and 10°C: one trial with 3 eggs, and one trial with 9 eggs. Thus, each nest was used in four treatments in the following sequence: 25°C and 9 eggs, 25°C and 3 eggs, 10°C and 9 eggs, 10°C and 3 eggs. The four treatments were repeated twice on each nest and the mean of the two measured temperatures was used in later analyses.

Nest measurements

After the trials were completed, we measured the height of each nest, the thickness of nest and chamber volume. Nest height was measured as the maximum length of nest (accuracy: ±0.5 cm) between the nest top and the bottom. We measured both the right and the left side of the nest, and the mean of these measurements was used in the analyses. Chamber volume was measured by filling the nest with plastic beads (diameter ca. 4 mm), and then pouring the beads in a 500 cm^3 graduated cylinder (accuracy: ±1 cm^3). Finally, the nests were cut in half vertically, and nest thickness was measured on both sides by a sliding calliper (accuracy: ±1 mm) at the bottom of the nest and at the side of the nest just beneath the funnel. The mean of these four measurements was used in the analyses.

Nests size was highly variable (N = 20 nests): nest height was 179.9±2.5 mm (mean±SE, range 155–210 mm), chamber volume was 314.0±17.0 cm^3 (range: 180–470 cm^3), and nest thickness was 22.7±1.3 mm (range: 15.0–34.8 mm). Nest size variables were unrelated to each other (Pearson correlations, height and thickness: $r_p = 0.341$, P = 0.142, N = 20; height and volume: $r_p = 0.382$, P = 0.097, N = 20; volume and thickness: $r_p = -0.404$, P = 0.078, N = 20).

Statistical analyses

We fitted an exponential function (egg temperature = $B \times \exp(-C \times \text{time (in seconds)})$) to the cooling curves of eggs (mean $R^2 = 0.986$), where B and C were fitted constants. The exponential cooling coefficient (C) was used as a measure of cooling rate. This function has the advantage over the traditional Newton's cooling function (egg temperature = ambient temperature + [initial egg temperature – ambient temperature) × exp (–C × time)]) that it allowed us to compare cooling rates between different ambient temperatures.

Terminal temperature was defined as egg temperature at the end of the trials. Terminal temperature, the volume of the nest chamber and nest thickness were log (x + 1) transformed for parametric tests. The effects of ambient temperature and clutch size on cooling rate and terminal temperature were investigated by two-way repeated-measures ANOVAs. In these models the response variable was either cooling rate (Model 1), or terminal temperature (Model 2). General-linear models were used to test the effect of nest size and quality on cooling rates (Model 3) and terminal temperature (Model 4). In Models 3 and 4 nest height, nest volume and nest thickness were covariates. All two-way interactions were tested in these models, and their results are provided when significant. We used SPSS 9.0 for statistical analyses, and provide two-tailed probabilities. Results are given as mean±SE.

RESULTS

The effects of ambient temperature and clutch size

Cooling rate was 1.33±0.03 × 10^{-2} min^{-1} at 25°C with 9 eggs treatment, 1.55±0.02 × 10^{-2} min^{-1} at 25°C with 3 eggs, 3.71±0.13 × 10^{-2} min^{-1} at 10°C with 9 eggs, and 4.82±0.09 × 10^{-2} min^{-1} at 10°C with 3 eggs. Cooling rates were influenced by both ambient temperature and clutch size (Model 1, ambient temperature: $F_{1,19} = 1110.911$, $P < 0.0001$; clutch size: $F_{1,19} = 102.811$, $P < 0.0001$; Fig. 1). A significant interaction between ambient temperature and clutch size ($F_{1,19} = 30.350$, $P < 0.0001$) showed that clutch size had a greater effect on cooling rate at 10°C than 25°C (Fig. 1).

Terminal temperatures were higher at 25°C than at 10°C (Model 2, $F_{1,19} = 1333.596$, $P < 0.0001$), and they were higher with 9 eggs than 3 eggs ($F_{1,19} = 92.735$, $P < 0.0001$, Fig. 1). A significant interaction between ambient temperature and clutch size ($F_{1,19} = 44.999$, $P < 0.0001$) indicated that clutch size had a greater effect on terminal temperature at 10°C than 25°C (Fig. 1).

The effects of nest size

Cooling rates decreased with nest thickness (Model 3, $F_{1,16} = 8.431$, $P = 0.010$). In addition, the effect of nest thickness was stronger on cooling rate at 10°C than at 25°C (thickness × ambient temperature: $F_{1,16} = 8.193$, $P = 0.011$).

Terminal temperature increased with nest thickness (Model 4, $F_{1,16} = 7.627$, $P = 0.014$), and the influence of nest thickness was stronger at 10°C than at 25°C (thickness × ambient temperature: $F_{1,16} = 7.790$, $P = 0.009$, Fig. 2).

Neither nest height (Model 3, $F_{1,16} = 1.135$, $P = 0.303$), nor chamber volume (Model 3, $F_{1,16} = 1.148$, $P = 0.300$) influenced cooling rates. Similarly, terminal temperatures were unaffected by nest height (Model 4, $F_{1,16} = 0.568$, $P = 0.462$) and chamber volume (Model 4, $F_{1,16} = 0.811$, $P = 0.381$).

DISCUSSION

Our study provided three key results. First, we showed that nest size influenced the heat loss of eggs. However, only nest thickness had a significant effect: cooling rates decreased and terminal temperature increased with nest thickness. In contrast, neither nest height, nor volume of the nest chamber influenced cooling rates and terminal temperatures. Second, the effect of nest thickness on egg heat loss was stronger at low ambient temperature than at high ambient temperature. Third, we found no interaction between nest thickness and clutch size (Model 3 & 4, $P > 0.05$), indicating that nest thickness has similar effects on insulation for nests with both small and large clutches.

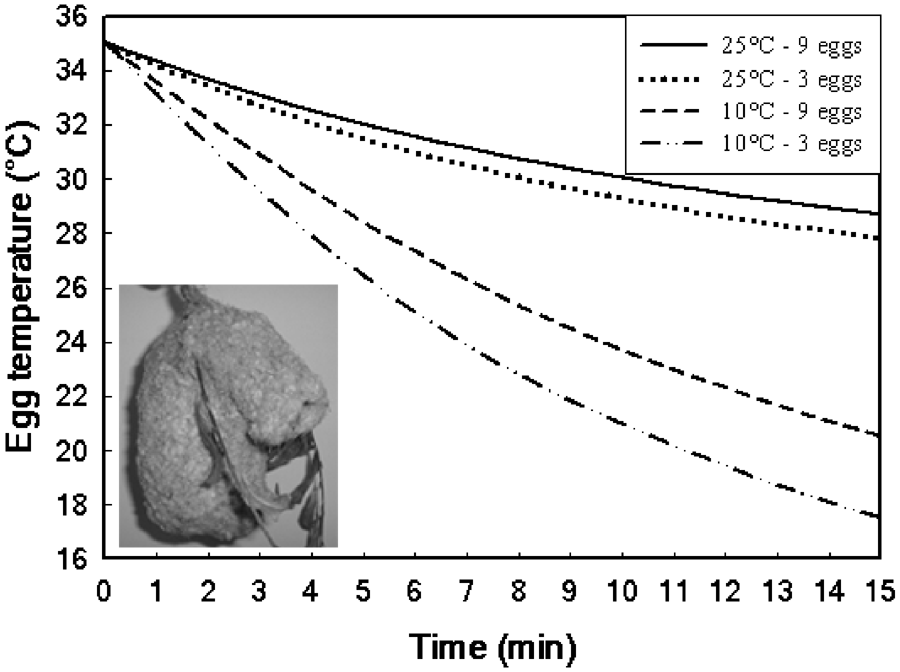

Fig. 1. Changes in internal egg temperatures (mean °C) during trials with Penduline Tit nests (treatments: ambient temperature – clutch size)

These results support the hypothesis that nest characteristics significantly influence the insulation properties of Penduline Tit nests, and females may preserve energy during incubation by choosing nests with the best insulation properties (GRUBBAUER & HOI 1996, REID *et al.* 2000). Males, if they decide to care, may also benefit from a large nest. Furthermore, the benefits that sexes gain from caring for clutches in large nests appear to be unrelated to clutch size. The latter result is important, since the average clutch size of male-incubated nests (3.4±1.4 eggs, mean±SD) is less than the average clutch size of female-incubated nests (5.1±1.5 eggs, PERSSON & ÖHRSTRÖM 1989). Our results also suggest that nest thickness may be the best predictor of the nest's insulation properties, whereas nest height and chamber volume appear to provide less information, at least in some populations, than showed by earlier studies (HOI *et al.* 1994).

Our results are different from a previous investigation that found reduced heat loss in large Penduline Tit nests (HOI *et al.* 1994). We suggest that the discrep-

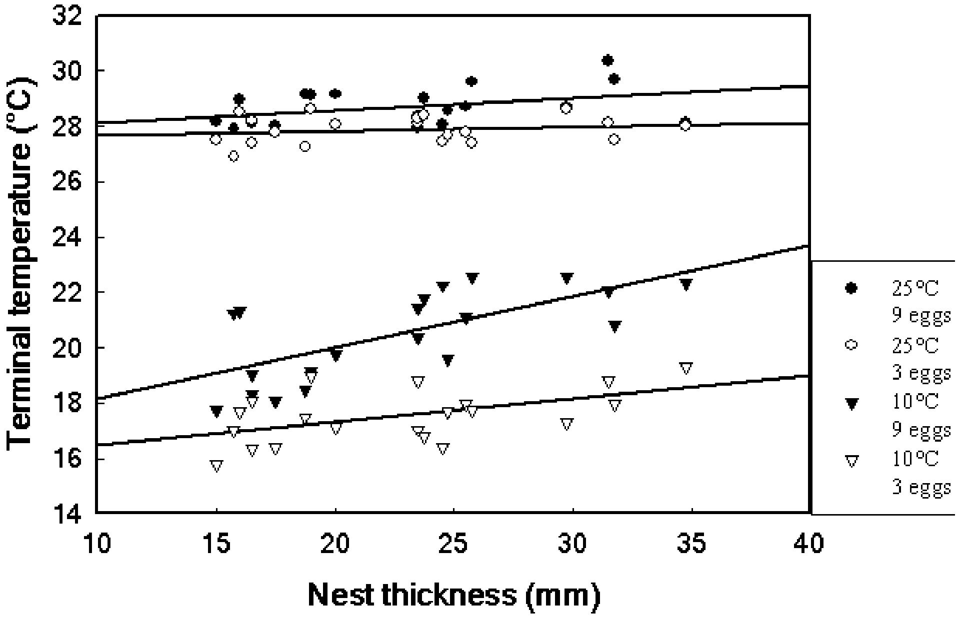

Fig. 2. Effects of nest thickness on terminal temperatures in relation to ambient temperature and clutch size. Each symbol represents one nest (N= 20 nests, all nests were measured in all treatments). We used least-squares regression to estimate the best fit to each pair of treatments separately (regression equations, 25°C & 9 eggs: terminal temperature = 27.64 + 0.05 × nest thickness; 25°C & 3 eggs: terminal temperature = 27.56 + 0.01 × nest thickness; 10°C & 9 eggs: terminal temperature = 16.29 + 0.19 × nest thickness; 10°C & 3 eggs: terminal temperature = 15.66 + 0.08 × nest thickness)

ancy may be due to two reasons. First, in our sample of nests there was no positive correlation between nest height and nest thickness, whereas in HOI *et al.*'s study these traits may covary. Second, in the study of HOI *et al.* the entire nest was heated up whereas we only heated up the eggs inside the nest (for about 2 minutes). We do not think that one or the other method is 'superior', although we note that large nests with better thermal capacities may maintain their temperature for longer than small nests. Our results thus indicate that nest height may not be a general indicator of the nest's insulative capacity. We conjecture that in our population of Penduline Tits female choice and parental care decisions should be driven by nest thickness, and not height. Currently we are testing this proposition in the field.

Eggs cooled faster at 10°C than at 25°C. This result is consistent with field experiments, when the eggs cooled slower in heated nests than in non-heated ones (REID *et al.* 1999, 2000). Furthermore, nest thickness reduced cooling rates to a larger extent at low ambient temperature than at high temperature. In cold ambient environments parent birds may protect their eggs from chilling by increasing their incubation effort and/or by building well-insulated nests (HAFTORN & REINERTSEN 1990, MØLLER 1984). Our results thus indicate that thick nests appear to maintain stable egg temperatures in cold environment of the Penduline Tits, since eggs in the thickest nest lose 4°C less heat over 15 minutes than in the thinnest one. The latter result is also consistent with the observation that female Penduline Tits exhibit stronger preference for large nests early in the season when ambient temperature is low than at later in the season (SCHLEICHER *et al.* 1996).

In conclusion, we found that thickness of Penduline Tit nests influenced egg-cooling rates, and that this effect was particularly strong at low ambient temperature. We found no evidence, however, that nest height, and chamber volume explained the cooling rate of eggs. Taken together, our results are consistent with the hypothesis that females choose thick nests to lower the energetic costs of incubation.

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Acknowledgements – We thank ÁDÁM LENDVAI for his help in the fieldwork, and the Department of Colloid Chemistry, ELTE (Hungary) for providing the laboratory space for the study. The project was founded by OTKA grants to TS (T031706, T43390) and a Royal Society Joint Project Grant (15056). AL was supported by a GYÖRGY BÉKÉSY Postdoctoral Fellowship. The licences were provided by the Hortobágy National Park, Hungary (1405–2/2000).

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Received 4th March, 2004, accepted 14th February, 2005, published 31th March, 2005