

Female mate choice and nest desertion in penduline tits, *Remiz pendulinus*: the importance of nest quality

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Studies of female choice generally determine which cues females use and how these cues correlate with their future benefits. In birds, these cues include characteristics of a territory (e.g. habitat structure; Lenington 1980; Alatalo et al. 1986) or male quality in terms of morphological or behavioural attributes (Borgia 1987; Hill 1990). In some bird species such as the village weaver, *Ploceus cucullatus*, mates are attracted by more or less completed nests (Collias & Victoria 1978) but there is little information on the importance of the nest itself and its role in mate choice. A nest may, for instance, indicate male parental quality, age, experience or genetic quality (Borgia 1985). Females, however, could also benefit directly by choosing a safe nest to reduce predation risk (Martin 1988) or a high quality nest in terms of thermal insulation capacity (White & Kinney 1974) which might reduce their energy demands for incubation (Weathers 1985) and also influence the partitioning of time and energy between supplying heat to their eggs and providing for their own needs for self-maintenance (Nilsson & Smith 1988). In some cases, nest size can also determine clutch size (see Snow 1978).

In penduline tits, males build elaborate pendulous nests (Franz & Theiss 1983) to attract females. In spite of this high initial investment (Schleicher et al. 1993) males are not always able to attract females. During our study, we estimated a turn-down rate of 34%; i.e. nests with which males could not attract a female. Even in those cases where males were chosen, 31% of females deserted their mates after having laid one or two eggs. These deserted nests were not used by males in future breeding attempts since no females accepted a nest already containing eggs. Finally, only 35% of all nests were used by females to rear young. We investigated (1) the influence of nest characteristics on female mate choice and (2)

possible benefits related to the nest directly. Pendulous nests, like that of the penduline tit, are especially exposed to adverse weather such as wind and precipitation. As female penduline tits are very small birds with no food subsidy or help with incubation from their mate (Franz 1991) they are very likely to encounter periods of energy stress during incubation, which may result in decreased reproductive performance (Nilsson & Smith 1988). So one would expect that thermal insulation is important for the quality of this type of nest.

We conducted the study at two sites about 60 km from Vienna (Austria), one at Lake Neusiedl (47°46'N, 16°48'E) and the other along the River March (48°16'N, 16°57'E) during the breeding seasons of 1992 and 1993. Birds were mist-netted and individually colour ringed.

According to the different levels of female choice males were classified as (1) unsuccessful, i.e. not chosen by a female, (2) chosen but deserted after one or two eggs were laid and (3) chosen and their females incubated. Each male and female was used only once in the analyses. For each male, only one nest was included in the analyses although males can build several (up to eight) nests. Since there is no seasonal variation in nest size ($r = -0.12$, $N = 34$, $P = 0.2$) nests were chosen ad libitum. Nest quality was estimated in two ways. (1) Nest size: nest size was measured externally using nest height from the nest attachment at the point of suspension to the nest bottom. Nest construction begins with a ring base. After the ring is finished, the birds build up the walls and then the entrance tube. Therefore, initial ring size determines final nest size. Since females often choose their mates during an early nest building phase (see Franz & Theiss 1983), nest size is probably the only cue they can use for every building stage. We measured only

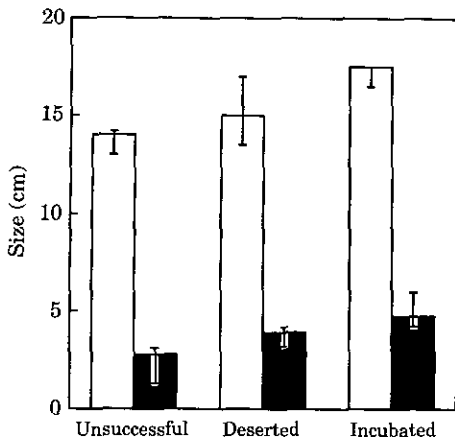


Figure 1. Nest size (□) and thickness of nest bottom (■) of unsuccessful ($N=11$), deserted ($N=9$) and incubated nests ($N=14$). Medians and inter-quartiles are given.

completed nests or nests in advanced building stages. (2) Nest thickness: we measured the thickness of the nest bottom in completed nests by inserting a needle into the centre of the egg-chamber to measure the distance between it and the bottom.

We found significant differences in nest size between the three male categories (Kruskal-Wallis test, $H=16.2$, $df=2$, $P<0.001$). A multiple comparison test between the single categories as an extension of Zar (1984) showed that nests with an incubating female were significantly larger than those that were deserted ($z=3.52$, $df=14,9$, $P<0.001$) or that contained no egg at all ($z=3.25$, $df=14,11$, $P<0.001$; Fig. 1). Non-chosen and deserted nests did not differ in size ($z=0.46$, $df=11,9$, $P<0.64$). The thickness of the nest bottom also differed significantly between the three male categories (Kruskal-Wallis test, $H=16.9$, $df=2$, $P<0.001$). The comparison between single categories revealed that the difference was mainly due to nests with incubating females having significantly thicker bottom layers than deserted ($z=2.46$, $df=14,9$, $P=0.01$; Fig. 1) and non-chosen nests ($z=4.1$, $df=14,11$, $P<0.001$). However, there was also a significant difference in the bottom layer of non-chosen and deserted nests ($z=2.3$, $df=11,9$, $P=0.026$; Fig. 1). Moreover, the size of the nest was positively correlated with the thickness of the bottom ($r=0.55$, $N=36$, $P<0.001$). So the final appearance of a nest should largely depend on its size.

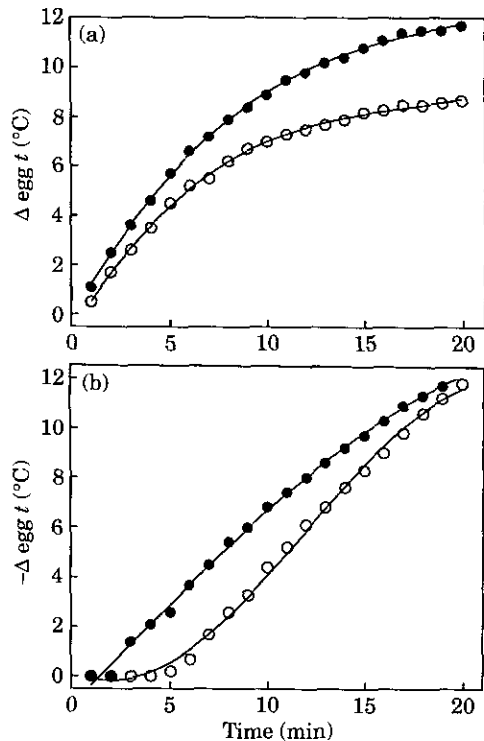


Figure 2. (a) Increase and (b) drop in egg temperature in small (●) and large (○) nests during 20 min. Mean values of the three smallest and largest nests are given. Curve fit was achieved by a third-order regression.

To determine if there is any direct advantage to choosing a larger and thicker nest, we measured the thermal insulation property of nests in the laboratory. A thermistor probe inserted into a wax-filled penduline tit egg was monitored in different nests while a second probe measured the environmental temperature. Each nest was heated up to 40°C in an incubator, with a starting temperature of 20°C . Both the increase and the drop in egg temperature were recorded in 10-s intervals for 20 min. Nests were ranked according to the size and thickness of their bottoms. The three largest and the three smallest nests were used for these measurements. For the statistical comparison a t -test was applied for parallelism of the slope (Kleinbaum & Kupper 1978). For linearity of the data, time was log transformed and temperature differences (Δt) were square-root transformed.

Larger nests could maintain egg temperature for about 5 min longer than smaller ones (Fig. 2). The increase and drop in egg temperature was

about 0.3–0.4°C per min faster in smaller nests than in larger ones (Fig. 2, for the increase: $t=3.08$, $P<0.01$; for the drop: $t=1.9$, $P<0.01$ of the egg temperature).

To estimate the importance of nest size in terms of insulation quality for breeding success we used only nests incubated by females that were not predated. Correcting for the seasonal decline in clutch size ($r = -0.24$, $N=34$, $P=0.169$) we found no relation between clutch size and nest size ($r_{\text{part}}=0.03$, $N=34$, $P=0.89$) and a positive relation between clutch size and the thickness of the bottom layer ($r_{\text{part}}=0.596$, $N=34$, $P=0.001$). Correcting for the seasonal decline in breeding success (number of young fledged; $r = -0.706$, $N=34$, $P=0.001$) we found a positive relation between breeding success and both nest size ($r_{\text{part}}=0.538$, $N=34$, $P=0.002$) and bottom thickness ($r_{\text{part}}=0.504$, $N=34$, $P=0.005$).

The nest of penduline tits thus seems to play a major role in female mate choice. Nest size seems to be a cue for nest quality and females benefit by choosing a large nest because of its improved thermal insulation. Fledging success was positively related to nest size as well as to the thickness of the bottom layer.

As small birds have high mass-specific metabolic rates, relatively large clutch masses and low energy reserves, female penduline tits should frequently leave their nest to forage. Well-insulated nests may therefore increase the time for which a female can leave eggs or chicks unattended while searching for food (White & Kinney 1974). Our results show that in larger nests a female could stay about 5 min longer outside (see Fig. 2) which is about a third of the time they usually spend off the nest during incubation. This in turn reduces the number of nest visits and therefore the probability of detection by predators is reduced (Skutch 1962). A better insulated nest may also decrease the energy required to rewarm the eggs after each recess (Biebach 1986). Additionally, it is known that avian embryos develop best in a relatively warm and stable nest microclimate (White & Kinney 1974).

Females run into a problem, however, if they use nest size as a criterion for brood success. They can clearly assess nest quality (e.g. insulation capacity) if nests are small or large. However, some nests are of average size. Deserted nests are neither large nor small (Fig. 1). This suggests that females are unable to evaluate nest quality at the

time of choice. Females build the inner part of the nest (bottom layer) which explains why non-chosen nests have significantly thinner bottom layers than nests deserted after the start of egg laying or nests incubated by females. However, the significant difference in bottom thickness between deserted and incubated nests and the correlation between bottom thickness and nest size suggests that building a thick insulating layer is constrained by nest size. So females seem to assess absolute nest quality after building the bottom layer and laying one or two eggs.

In summary, the nest itself has important implications for the mating system of this species: it offers an explanation for the high desertion rate (see Franz 1991). Moreover, the generally warm and stable nest microclimate of this nest type may have influenced the evolution of single parent incubation which allows the second adult to pursue additional breeding attempts.

Provided that females behave selectively when choosing a nest, female selection of the best nest available has important implications for competitive behaviour between males. Thus, mating and breeding success are probably regulated by means of nest quality, which may account for the high rate of polygyny in penduline tits; nest quality variation may also explain cases of polyandry in this species (Persson & Öhrström 1985; Franz 1991). For instance, if a female has the opportunity to mate with a neighbouring male displaying a 'better' nest, she may desert the first nest with an incomplete clutch. This 'better option' hypothesis might also explain the high desertion rate. It is not based on the assumption that females are unable to assess the quality of medium-sized nests at the time of choice. It seems a less likely explanation for the high desertion rate, however, since we would not expect females to expend extra energy to lay eggs before they decide to desert. Moreover, the two explanations for the high desertion rate (nest size and the better-option hypothesis) are not mutually exclusive. To clarify these questions, further experiments would be necessary.

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