

Nest size variation and its importance for mate choice in penduline tits, *Remiz pendulinus*

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Persson & Öhrström (1996) state that our evaluation of our data on female mate choice and nest desertion in penduline tits (Hoi et al. 1994) is based on serious misinterpretations which make our conclusions questionable.

They first criticize our statement that initial ring size determines final nest size in this species. In our study area nest size (measured externally using nest height from the nest attachment at the point of suspension to the nest bottom) varies between 12.5 and 25 cm (calculated on the basis of 306 nests). We found a significant correlation between the size of the initial ring base and the final nest size (determined in the first 2 days of incubation). In effect, the bigger the initial ring base, the bigger the final nest (Spearman rank correlation: $r_s = 0.98$, $N = 21$, $P < 0.001$). This suggests that ring size determines nest size.

Persson & Öhrström go on to question the explanation of the different nest categories we distinguished. They proceed on the assumption that we are unaware that nest building continues after egg laying. This is not true and we even referred to this fact indirectly (page 745). Nevertheless, we did assume that nest size does not increase during incubation, although in many of our cases the incubating parent returned from a foraging trip with a piece of nest material which was incorporated into the nest. In 1-h observation periods during incubation (between days 4 and 10) at 22 nests (one observation period for each nest) material was incorporated into the inner part of the nest on 47.5% of occasions when the female returned, and was attached outside on 5% of occasions, while on 47.5% of occasions the female arrived without nest material. Percentages refer to

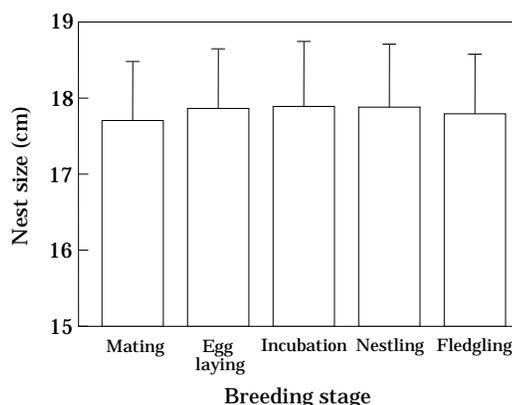


Figure 1. Mean (\pm SE) nest size of eight nests in different breeding stages. Mating period comprises five nests where males were chosen in the advanced 'basket' stage and three nests where males were chosen in the 'pouch' stage (see Schönfeld 1994, for description of nest-building stages).

the number of times females arrived at the nest with/without nest material, that is on average 4.5 (± 0.49 SE, $N = 22$) arrivals in each hour. When material was stolen from the nest, the incubating parent repaired the nest (Schleicher et al. 1993). We should have included data on potential variation in nest size during a breeding cycle in our previous paper and we are grateful to Persson & Öhrström for pointing this out. Therefore, we offer the following additional data to support our assumptions.

First, we measured eight nests, which were chosen by females (1) during nest building prior to female choice, (2) during egg laying, (3) in the middle of incubation (day 7–8), (4) in the middle of the nestling phase (at chick ages of 8–10 days) and (5) after chicks had fledged. The results (Fig. 1) demonstrate that there is almost no change in nest size during the breeding cycle (repeated-measures ANOVA: $F_{4,28} = 0.01$, $P > 0.9$).

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The average maximum variation in nest size for these eight nests was 0.4 cm (± 0.05 SE), which is about 3% of the variation in nest size between different nests ($N=306$). The average increase in nest size from the nest building stage to the fledgling phase is only 0.06 cm (± 0.07 SE). This is 0.5% of the observed variation between nests ($N=306$). Variation in the size of a nest during different breeding phases seems to be mainly due to different environmental conditions. There may be a slight increase in nest size during rainy weather and nests may shrink slightly if it is very hot and dry (personal observation).

Second, Schleicher et al. (in press) show a significant repeatability of nest size in successive nests built by a male during a breeding season ($N=29$ males), whereas nest size varies significantly between males. This might indicate a genetic determinant in male nest-building ability, but it at least supports the assumption that nest size is determined by the male rather than the female.

Finally, we tested whether the weight of the nest plus a parent and nestlings affects nest size. Ten nests collected from the field were filled with a weight of half a kilo to create a pressure of 0.5 kilopond on the bottom of the nest, which equals the weight of about 50 adult penduline tits. Nests were exposed to this heavy load for 5 days. We measured nest size prior to the experiment (mean nest size \pm SE = 16.9 ± 0.4 cm), immediately after adding the weight (mean nest size = 17.3 ± 0.4 cm), and 5 days later (mean nest size = 17.4 ± 0.4 cm). The results demonstrate that nest size did not change (repeated-measures ANOVA: $F_{2,27}=0.6$, $P>0.5$).

Persson & Öhrström (1996) found a significant correlation between the number of pair-days and the number of eggs laid and suggest that this may explain why large nests contain larger clutches, and as a consequence more young fledge from these nests. Hence they argue that if males stay longer they can go on building for longer which should affect nest size, and as a result the number of fledglings. Our data do not support this view. First, we found no change in nest size after a female had chosen a mate (Fig. 1); rather if the male stayed, he completed the nest and enlarged the tunnel (personal observations). Second, we found no relation between nest size and clutch size (Hoi et al. 1994, page 745; see also Grubbauer 1995), but we did find a positive relation between

nest size and number of young fledged (page 745) and more specifically, a relation between nest size and hatching success even when controlling for clutch size, ambient temperature and female quality (Grubbauer 1995). Persson & Öhrström's correlation between number of pair-days and number of eggs laid is likely to be an outcome of the battle of the sexes. We found that male penduline tits desert as soon as they recognize the first egg in the nest (personal observations). However, females very often bury one or more eggs in the soft material of the nest base (see Schönfeld 1994). So, the time a male stays with the female at the nest depends on whether she can hide the eggs (e.g. on the thickness of the nest bottom or the experience of a male in detecting buried eggs). The more eggs a female buries the higher the number of pair-days and the bigger the final clutch size.

Finally, Persson & Öhrström state a discrepancy between our 1994 data and the data of other studies regarding the percentage, as well as the average size, of deserted clutches. They report an average size for deserted clutches of 3.8 eggs and say that only 15% of the clutches were as small as one or two eggs. This is also true for our study area, where we found that 22 out of 131 (16.9%) clutches were deserted with one or two eggs. This value includes clutches attended by males and females. However, in our 1994 paper we say that 31% of females desert after laying one or two eggs. This apparent discrepancy in the values is due to the fact that we excluded clutches attended by males in the 1994 paper, where we were mainly interested in female desertion and nest quality. The mean number of eggs for deserted clutches is 2.8 ± 0.14 SE ($N=54$ nests).

Persson & Öhrström summarize that there is little support for our conclusions and go on to say that female desertion is mainly the result of a female trying to become polyandrous, a conclusion with which we agree. However, a male will almost never attend a clutch with one or two eggs. In our study 44 out of 223 (19.7%) clutches were attended by the male (mean clutch size was 4.1 ± 0.21 SE, $N=30$), but in only one out of 30 nests was the clutch as small as two eggs. So, it seems to be very unlikely that females desert a nest with one or two eggs to become polyandrous. We therefore used nests deserted with this low clutch size (one or two eggs) to study the effect of other factors on desertion behaviour, in this case nest quality.

In conclusion, we assume that nest size as a determinant of quality is important in female choice and might also be responsible for desertion. There is a slight increase in size from the initial ring to final nest size, but the high correlation between ring size and final nest size suggests that females could use nest size even from the very beginning of building as a measure for nest quality, although pair formation is very rare at such an early stage (for example only four out of 41 (9.7%) females chose their mates in the 'ring' stage and only one (2.4%) female in the 'swing' stage).

Since there is nearly no variation in nest size in the subsequent building and breeding stages (Fig. 1) it seems unimportant when the measurements are taken. In our study we took off the nests after desertion or after completion of the brood to measure them. However, there is one case where it is impossible to measure nest size, that is when other penduline tits destroy the base by stealing nest material (Schleicher et al. 1993).

The hypothesis that in penduline tits female choice is based on nest size (Hoi et al. 1994) is supported by an experimental study. In a choice experiment, Grubbauer (1995) showed that female choice is based on nest size even when controlling for male quality and nest site (habitat) quality. That nest site quality seems to be unimportant for mate choice is further supported by the fact that male mating success is not affected by habitat quality surrounding the nest site (see Schleicher 1993). However, Schleicher et al. (in press) showed that the importance of nest size for female choice varies seasonally, decreasing across the season and with increasing ambient temperatures, while characteristics related to the male itself become more important.

Consequently, there is every reason to assume that nest quality is also important for nest desertion, particularly for those nests deserted with one or two eggs. Of course, there might be other factors leading to desertion of small clutches. For instance, ectoparasite load is significantly higher

for nests deserted with one or two eggs than nests attended by the female (unpublished data). Second, paternity analyses revealed that egg dumping occurs in penduline tits (unpublished data) which could also be a reason for a female to desert a nest (Petrie & Møller, 1991). Finally, the probability of having a 'better option' partner (see Hoi et al. 1994) seems to be important. This factor is likely to vary widely between populations.

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