

Sexual conflict over parental care in Penduline Tits *Remiz pendulinus*: the process of clutch desertion

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Do the two parents at a nest make simultaneous decisions whether to care for their offspring or to desert? If a single parent is sufficient for rearing young, one parent (typically, the male) may desert and reproduce with a new mate within the same breeding season, leaving the other parent with the brunt of care. As each parent is expected to maximize its own reproductive success, the interests of the two parents do not necessarily coincide, and a sexual conflict over care may emerge. Here we investigate the process of clutch desertion in a small passerine bird, the Penduline Tit *Remiz pendulinus*. Among birds, this species has a remarkably variable breeding system, because a single parent (either the male or the female) may provide the full care of the young, whereas about 30% of clutches are abandoned by both parents. First, we show that biparental desertion occurs within a single day in 73.7% of the clutches ($n = 14$), whereas desertion decisions are sequential in 26.3% of the clutches ($n = 5$) (male first: 10.5% ($n = 2$); female first: 15.8% ($n = 3$); $n = 19$ clutches in total). Secondly, we observed the behaviour of both parents before desertion, and investigated whether desertion can be predicted from their behaviour. However, neither singing nor nest-building behaviour predicted whether the male or the female would desert. We therefore suggest that biparental desertion may be simultaneous by male and female in our population of Penduline Tits. Furthermore, the parents do not appear to signal their intention to desert their mate. We argue that the parents' interest may be actually to disguise their intention to desert.

How do parents decide which of them should provide care? To understand parental behaviour, we need to know the costs and benefits of caring and deserting (Clutton-Brock 1991, Székely *et al.* 1996), and the process of interactions between the parents (Houston & McNamara 1999). Although data on the costs and benefits of caring are gradually accumulating from several avian species (reviewed by Bart & Tornes 1989, Liker 1995, Houston *et al.* 2005), our understanding of parental interactions has lagged behind. Most models of parental care (e.g. Maynard Smith 1977, Houston & Davies 1985) assume that the parents make a single and simultaneous decision independent of their mate ('sealed bid'; Royle *et al.*

2002). Theoretical analyses show that, when the decisions are not simultaneous, i.e. the male or the female decides before its mate, this has profound implications for the predicted pattern of care (Barta *et al.* 2002, McNamara *et al.* 2002). Although these arguments have firm theoretical foundations, the behavioural interactions that lead to desertion are rarely investigated in nature (but see Beissinger 1987, Valera *et al.* 1997).

We investigated parental interactions in a small passerine bird, the Penduline Tit *Remiz pendulinus* (body mass 9–10 g), which exhibits an unusually variable breeding system (Persson & Öhrström 1989, Szentirmai 2005). Unmated males start building sophisticated nests and sing to attract a female. Male and female finish the building of their nest together. Shortly thereafter, once the female has started egg-laying, either the male or the female or both desert the nest during the egg-laying period. A single parent (the male or the female) always incubates the eggs

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and rears the young (Persson & Öhrström 1989, Valera *et al.* 1997). The main benefit of desertion is re-mating and reproducing with a new mate: deserting parents may re-mate up to five or six times within a single breeding season (I. Szentirmai, unpubl. data). Approximately 30% of clutches are abandoned by both parents before incubation commences, presumably as a cost of the intense race for new mates (Persson & Öhrström 1989, Valera *et al.* 1997, Arnqvist & Rowe 2005). Biparentally deserted clutches are doomed to failure. By deserting the clutch, the parent offloads care to its mate, whereas he (or she) may increase his (or her) own reproductive success by abandoning the clutch, and mating with a new partner.

We had two objectives in this study. First, we measured whether desertion was simultaneous or sequential in biparentally deserted clutches. In taxa with internal fertilization, such as birds, the male releases sperm before the female lays the eggs. Thus, while the female is forming the egg, the male can abandon her (Dawkins & Carlisle 1976), and this suggests that desertion first by the male might be expected. On the other hand, Valera *et al.* (1997) argued that female Penduline Tits can desert first, because they are able to manipulate the males by concealing the information on the progress of egg-laying by covering the eggs and expelling the male from the nest chamber. Secondly, if a parent prepares to desert first, he/she may reveal this intention. For instance, Beissinger (1987) noted that in Snail Kites *Rostrhamus sociabilis*, in which either the male or the female can desert during brood rearing, provisioning of nestlings was significantly lower in the deserting parent. Thus, the would-be deserter appears to save energy by reducing its parental contribution. In this study, we tested whether either vocal or nest-building behaviour of parent Penduline Tits predicted later desertion.

METHODS

We studied the Penduline Tits between April and August in four consecutive years (2002–2005) in southern Hungary (46°19'N, 20°5'E) at an extensive fishpond (Fehértó, 1321 ha) where approximately 60–90 males and 45–50 females bred each year on the dykes separating fishpond units. The number of nests per year varied from a minimum of 158 in 2005 to a maximum of 214 in 2002. Penduline Tits were ringed with a unique combination of colour rings and a numbered metal ring (see Bleeker *et al.* 2005). Returning rates of individuals across years are very low: of 248 colour-ringed males, only 15 were

re-sighted in our area in the next year between 2002 and 2005. For females, of 125 colour-ringed females, only nine were seen in more than one year (R.E. van Dijk unpubl. data).

We visited nest-building males nearly every other day (1.8 ± 0.8 days (mean \pm sd), $n = 59$ nests), and watched them for at least 15 min and checked whether the male was mated and, for mated pairs, which of them attended the nest. Fifteen minutes was sufficient to record the presence of parents (if they were still at the nest), as males and females were spotted at the nest within $3 \text{ min } 41 \text{ s} \pm 5 \text{ min } 11 \text{ s}$ (sd) and $6 \text{ min } 48 \text{ s} \pm 7 \text{ min } 31 \text{ s}$, respectively ($n = 46$ nests where detailed behavioural observations were carried out). We considered a male to be mated when the pair copulated near the nest, or when the male and female built the nest together. A parent was considered to have deserted the clutch if it was not seen at the nest for at least two consecutive visits. None of the birds classified as 'deserted' returned to their nest afterwards. Desertion always took place during egg-laying and never before egg-laying or during incubation. Pair-bonds were short and lasted for 4.7 ± 2.6 days ($n = 315$ nests). Nests with female-only care contained a clutch of 5.8 ± 1.3 eggs ($n = 140$ nests), whereas nests cared for by males contained 3.5 ± 1.4 eggs ($n = 35$ nests). One hundred and nine nests were deserted by both parents. The clutch size was known for 82 biparentally deserted nests; these had 3.0 ± 1.3 eggs. Nineteen biparentally deserted nests out of 109 were checked daily, whereas the remaining nests were checked approximately every other day. We tested whether one sex deserts before the other in biparentally deserted nests using a binomial distribution with $P = 0.5$. In this test more than one nest of a given individual in a given breeding season may have been included (out of 98 colour-ringed males in the 109 biparentally deserted nests $n = 22$ males; out of 29 colour-ringed females in the 109 biparentally deserted nests $n = 6$ females). However, the constitution of pairs was always different.

We observed the behaviour of newly mated pairs in 2003, 2004 and 2005. The observations were carried out from a hide at a distance of 10–15 m from the nest, using binoculars. We observed each pair for about 2 h each day (124 ± 50 min, mean \pm sd). Observations were alternated for pairs between morning (05:50 to 12:40 h, CET) and afternoon (11:30 to 19:50 h), thereby controlling for possible effects of time of day. Behavioural observations were collected until one or both of the parents deserted

the clutch. Every 20 s the following behaviours were recorded separately for the male and the female within a radius of 10 m around the nest: nest building, calling and, for males only, singing. The percentage of each behavioural score was calculated for each record assuming that these behaviours only take place around the nest. Twenty-five nests were observed: six were cared for by the male, 12 by the female, and seven were deserted by both parents. At 19 nests both the male and the female were individually colour-ringed, whereas at six nests only the male was ringed. Of six unringed females, three bred at the same time, so we are certain that these were different individuals. For the remaining three females we cannot exclude the possibility that we observed the same individual more than once, although this is unlikely given the size of the study population. One observer collected all behavioural records at 24 nests, whereas one nest was studied by two observers. We found no significant effect of season (i.e. date of desertion), observer or year on the behaviour of male or female (MANOVA; all $P > 0.524$).

We used multinomial logistic regression models to predict parental care (male-only care, female-only care, biparental desertion) in response to the prior behaviour of the male (model (a) in Table 1) or the female (model (b) in Table 1) separately as covariates. Both the model for the male behaviour and the model for the female behaviour predicting parental care fitted the data (Pearson's goodness-of-fit; male: $\chi^2 = 45.476$, $df = 42$, $P = 0.329$; female: $\chi^2 = 50.980$, $df = 44$, $P = 0.218$). Statistical analyses were performed using SPSS 11.5.0 and SPSS 12.0.0 for Windows.

RESULTS

All nests included in this study were deserted by one or both of the parents during egg-laying. The pattern of parental care at nests in our population was similar to that reported by others (e.g. Franz & Theiss 1983, Persson & Öhrström 1989): about 11% had male-only care, 49% had female-only care and 40% suffered desertion by both parents (Szentirmai 2005). Of the 19 biparentally deserted nests that we checked daily, 73.7% ($n = 14$) were deserted by both parents on the same day, 10.5% ($n = 2$) were deserted first by the male and 15.8% ($n = 3$) were deserted first by the female (Fig. 1). At those biparentally deserted clutches where one parent deserted first, the other parent always deserted by the next day ($n = 5$). These results are consistent with the

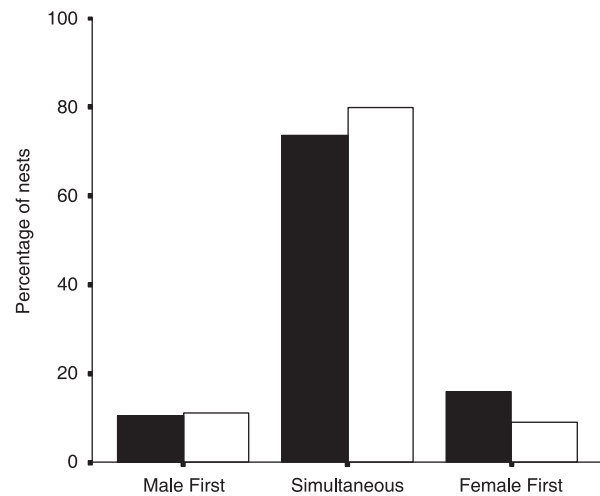


Figure 1. Percentage of Penduline Tit nests deserted by the male first, female first and by both parents simultaneously using nests that were checked daily (filled; $n = 19$ nests), or less regularly (open; $n = 109$ nests).

total sample of biparentally deserted nests, including those that were checked approximately every other day: 78.9% ($n = 86$), 11.0% ($n = 12$) and 10.1% ($n = 11$), respectively (Fig. 1). Thus, the majority of biparentally deserted clutches are deserted by both parents on the same day. The frequencies of nests deserted first by the male and those deserted first by the female were not different from binomial distribution ($n = 23$, $P = 1.000$). When we took only one nest randomly per individually identified male and female, the pattern remains consistent with our previous results (both parents on the same day: 71.4%, $n = 10$; male first: 7.1%, $n = 1$; female first: 21.4%, $n = 3$).

The behaviour of neither male nor female predicted which of the parents, male or female or both, would desert the clutch (Table 1).

DISCUSSION

Biparental desertion is a rapid process in the Penduline Tit, as most biparentally deserted nests were deserted by both parents on the same day. In our population of Penduline Tits, neither sex consistently initiated desertion. This result is different from Persson and Öhrström's (1989) observation of a Swedish population, which suggested that in the biparentally deserted nests it was always the female that deserted first, as they never observed a female at a nest after the male had deserted. Interestingly,

Table 1. Multinomial logistic regression models of parental care strategy in response to (a) male behaviour and (b) female behaviour ($n = 25$ nests, $df = 1$). Separate models were constructed for (a) and (b). The reference category is biparental desertion. Predicted effect sizes and standard errors are given.

Care strategy		Model effect estimate (\pm se)	Wald	<i>P</i>
(a)				
Male-only care	Building	-0.162 ± 0.114	2.003	0.157
	Calling	-0.309 ± 0.519	0.354	0.552
	Singing	0.113 ± 0.476	0.056	0.812
Female-only care	Building	-0.097 ± 0.103	0.901	0.342
	Calling	-0.399 ± 0.460	0.751	0.386
	Singing	0.553 ± 0.406	1.857	0.173
(b)				
Male-only care	Building	0.046 ± 0.061	0.553	0.457
	Calling	-0.589 ± 1.215	0.235	0.628
Female-only care	Building	-0.049 ± 0.063	0.621	0.431
	Calling	-1.582 ± 1.292	1.500	0.221

Valera *et al.* (1997) reported a different pattern in an Austrian population of Penduline Tits (see their table 1, p. 24): males deserted earlier (1.6 ± 0.1 days after the start of egg-laying) than females (2.3 ± 0.1 , Mann–Whitney *U*-test, $Z = \pm 3.403$, $P < 0.001$). Note that Valera *et al.*'s data appear to include both uniparentally and biparentally deserted nests, so they are not directly comparable with our data (see Fig. 1). Nevertheless, the comparison between these three detailed studies suggests that there are differences between populations in the process of desertion.

Although we found no consistent pattern within the Hungarian population, some individuals may consistently desert earlier than others. For instance, attractive males (i.e. males with a larger mask that have a significantly higher chance of attracting a female and need a shorter time to attract a female than males with smaller masks (Szentirmai 2005)) may desert their mate sooner than unattractive ones. Recently, Bleeker *et al.* (2005) showed that parent Penduline Tits in good body condition are more likely to desert than those in poor condition. Thus, parental care strategy (desert or care) is at least partially state-dependent.

One may expect an arms race for desertion between male and female Penduline Tits, as each parent may desert first as a pre-emptive strike, in order to oblige its mate to stay and care for the offspring. Such pre-emptive actions have been analysed in game-theoretic models (Lazarus 1990, Barta *et al.* 2002), although the relevance of these theoretical models in natural populations needs further scrutiny. Furthermore, desertion can be viewed as an interactive

process in which the parents negotiate over care provisioning (McNamara *et al.* 2002). In such an arms race it may be a good strategy to disguise the intention to desert. Indeed, from our behavioural observations, it seems that Penduline Tit parents do not signal or reveal any intention to desert in their behaviour close to the nest.

In conclusion, we showed that clutch desertion is a rapid process in Penduline Tits, given that the decision (care/desert) is made within 1 day, or at most within 2 days, at biparentally deserted nests. We need further studies to establish whether desertion strategies are consistent for a given individual, and to evaluate how state-dependency influences parental strategies. Future work with an increased resolution, e.g. using an interval recording camera to record the behaviour of parents at their nest over a full day, will be important to reveal the subtle interactions between males and females during the critical days of pair-formation and egg-laying.

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