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Do female Penduline Tits *Remiz pendulinus* adjust parental decisions to their mates' behaviour?

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In contrast to older models of parental care, recent theoretical models assume that parents do not make their decisions independently of one another, but respond to the behaviour of their mates. Studies involving mate removal have mostly been conducted in biparental species and such experiments in uniparental species are scarce. I studied the Penduline Tit *Remiz pendulinus*, a small passerine bird with uniparental care provided either by a female (45% in the studied population) or a male (17%). During the egg-laying period, one parent (or both; 38% in the studied population) deserts the clutch and starts a new breeding attempt. The aim of this study was to find out whether the parental care decision of female Penduline Tits is affected by their mate's decision to desert or not. In the control group (nests where males were caught, ringed and released), almost 50% of the females deserted the nest. By contrast, most females from the manipulated group did not desert their nests after I had removed their mates. In the following days 12 experimental females (60%) mated with replacement males at their nests; this behaviour was not observed in the control group, and is very rare in the study population (3.7%). These results may suggest that female behaviour is affected by the male decision to desert or stay. However, after attracting a replacement male, some females deserted their nests. As a result, only 11 experimental females (55%) stayed and started incubation, which represents a proportion similar to that found in the control group. This study shows that Penduline Tit females respond in real time to the behaviour of their mates and that their reproductive tactics are flexible.

Key words: female decision, game theory, male removal, offspring desertion, parental care, Penduline Tit, *Remiz pendulinus*

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Offspring desertion occurs in many species of vertebrates including fishes, amphibians, birds, and mammals (Clutton-Brock 1991). As pointed out by Trivers (1972), parent's interests differ and there is a conflict over parental care invested in offspring. The best option for every male or female would be to pass on parental duties to the partner and save reserves for future reproduction (Lessels 1999, Arnqvist & Rowe 2005, Houston *et al.* 2005). The parent's decision of whether to care or desert may depend on many factors such as body reserves, remating opportunities, attractiveness, and the behaviour of a partner (Székely *et al.* 2000, McNamara *et al.* 2002). I studied desertion behaviour in the Penduline Tit *Remiz pendulinus*, a small passerine bird with a complex breeding system. Either the male or female abandons the clutch before incubation

commences and both sexes frequently remate after desertion (Persson & Öhrström 1989). Parental care is provided by only a female (45% in the study population) or a male (17%), and about 30–40% (38% in the study population) of clutches are deserted by both parents (Persson & Öhrström 1989, Czyż 2008, Pogány *et al.* 2008a). Clutch size in female-only cared nests is higher than in male-only cared and biparentally deserted nests (Persson & Öhrström 1989, Szentirmai *et al.* 2007). Desertion occurs during egg-laying, usually when the second, third or fourth egg is laid (Valera *et al.* 1997).

Although most older models of parental care assume that the choices of females and males are independent (Grafen & Sibly 1978, Maynard Smith 1982, Yamamura & Tsuji 1993, Balshine-Earn & Earn 1997,

Webb *et al.* 1999), the patterns of care in Penduline Tits (e.g. lack of biparental care) suggest that this assumption is not met in this species (cf. McNamara *et al.* 2002). Recent theoretical models of parental care allow parents to respond to one another and negotiate parental effort. These models predict responses ranging from partial/full compensation to matching (cf. McNamara *et al.* 1999, McNamara *et al.* 2003, Johnstone & Hinde 2006). Most studies that involved either mate removal or handicapping experiments have been conducted in bird species that exhibit biparental care (e.g. Dunn & Hannon 1989, Duckworth 1992, Freeman-Gallant 1998, Lendvai *et al.* 2009). The results of these experiments are not consistent, as some studies found no change in feeding behaviour by the remaining parent, and others reported partial or full compensation (e.g. Wolf *et al.* 1990, Duckworth 1992, Osorno & Székely 2004, Lendvai *et al.* 2009). A detailed meta-analysis showed that, on average, widowed birds partly compensated for the absence of their partner by increasing their feeding effort (Harrison *et al.* 2009). In some cases, males and females were found to respond differently to reduced parental effort in their mates (Sanz *et al.* 2000, Rauter & Moore 2004, Smiseth *et al.* 2005). This may also be the case in Penduline Tits. In all studied populations, the proportion of males deserting clutches is greater than that of females (Franz & Theiss 1983, Persson & Öhrström 1989, Szentirmai 2005, Czyż 2008), which suggests that costs of desertion are higher for females and/or benefits of desertion are greater for males. Moreover, Persson & Öhrström (1989) observed that at biparentally deserted nests, females always deserted clutches before males, which may indicate that the female's decision may depend on her mate's behaviour, i.e. if the male manages to desert first, the female would stay. A detailed study in Hungary showed a different pattern as to which sex deserts first at biparentally deserted clutches, and instances of males deserting before females were observed as well. There was, however, a large number of clutches (79%) where desertion occurred 'simultaneously', and the exact sequence was in fact unknown at these nests (van Dijk *et al.* 2007).

Studies involving removal experiments in species with uniparental care are scarce, but they may help to explain the evolutionary dynamics of mate desertion (Pierce *et al.* 2010). Such experiments in species without a fixed desertion strategy may also explain how individuals decide to desert or not.

In this study, I experimentally investigated whether the decision making of a female Penduline Tit is affected

by her partner's behaviour by removing the male during egg-laying. In light of the above observations, I expected females to respond to male removal by staying at the nest and starting incubation.

METHODS

The study was carried out in 2007 and 2008 at Milicz fish-ponds (51°33'N, 17°21'E), Wrocław Province, Poland. The study area (1200 ha) comprised 28 ponds (each 18–164 ha) and surrounding land. The pond dykes were vegetated with deciduous trees, mostly oaks *Quercus* sp., willows *Salix* sp., birches *Betula pendula* and poplars *Populus* sp. The area is protected as a nature reserve with extensive carp production.

Males were removed at 13 nests in 2007 and at 7 nests in 2008 (5 in April, 8 in May, and 7 in June). During the nest building stage I caught both males and females using a mist net and song playback, and individually marked them with three colour rings and one metal ring. Additionally, I measured the mask width (at the end of the mask) of the males with a digital calliper to the nearest 0.1 mm. Mask size can be used as measure of male attractiveness since females prefer males with larger masks (Pogány & Székely 2007, Kingma *et al.* 2008, Pogány *et al.* 2008b). The male was caught again on the day when the female laid a second (18) or third egg (2), only when I was sure that the female was still present at the nest. Males may desert as soon as the first egg appears in the nest. In Austria, 45% of deserting males abandoned their clutches on the day when the first or second egg was laid (Valera *et al.* 1997). I placed each of the removed males in a cotton sack, and transported the birds by car to be released at another fish-pond system about 20 km from the study area. This distance was sufficient as only two cases of the males returning to the study area were observed, and both did not return to their previous nest but started to build a new one. The nest was visited on the day of the removal of the male, and on the following days to check if the female was still present, until the start of incubation or female desertion. These visits lasted 30 minutes, which is sufficient to record the presence of the female at the nest (van Dijk *et al.* 2007). The female was considered to have deserted if she was absent for two consecutive visits and no new eggs were found in the nest. The control group ($n = 35$) consisted of nests at which the male was caught during the nest building stage, ringed and immediately released near the nest. Each female was used only once in either the manipulated or control group.

A detailed study on offspring desertion in Penduline Tits in Hungary showed that most biparentally deserted nests were abandoned by both parents on the same day and that the second parent had always deserted the nest by the following day (van Dijk *et al.* 2007). Accordingly, I categorized the female ‘primary’ decision as her parental behaviour (remaining at the nest or deserting it) directly after male removal. I considered a nest as deserted by the female if she disappeared on the day the experiment began or one day later. I defined female ‘final decision’ as her decision to start incubation or desert the clutch.

I compared the proportions of deserting and staying females using a chi-square test with Yates’ correction for continuity. I built a logistic regression model of females’ behaviour (desert or stay) from the manipulated group with attractiveness of their males and date of laying the first egg as explanatory variables. Statistical analyses were performed using R (version 2.10.1) software (R Development Core Team 2009) and provided probabilities are two-tailed.

RESULTS

Only two of the 20 females in the manipulated group deserted on the day when I removed their mate (two eggs in the nest), and one female deserted the clutch the following day after laying the next (third) egg. The remaining 17 females stayed and continued egg-laying (2–6 eggs). Five females, after laying eggs and carrying out solitary nest building, started incubation, but the remaining 12 females attracted replacement males to their nests (either on the day of the removal (5) or the following day (7)). The new pairs built the nest together and copulated. In three cases, the new male was a female’s neighbour (building a nest solitarily), two males had just deserted their earlier clutches, while the other males did not have nests within the study area. One of these males started incubation after the female’s desertion when five eggs were in the nest. Six out of these 12 females deserted the nest and six started incubation. In the control group, 18 females started incubation and 17 deserted.

At first, just after male removal, females in the manipulated group were more prone to stay than those in the control group ($\chi^2_1 = 4.83$, $P = 0.03$; Fig. 1). However, the final behaviour of females in the two groups did not differ: the proportion of females that stayed and started incubation was similar ($\chi^2_1 = 0.01$, $P = 0.97$; Fig. 1). The behaviour of females in the manipulated group was not affected by date of egg-

laying or first male attractiveness as measured by mask width (Table 1). The mask width of first and replacement males was similar (paired Wilcoxon signed rank test: $W = 16.5$, $P = 0.73$, $n = 8$ pairs).

The clutch size of nests deserted by females from the manipulated group ($n = 9$) tended to be larger compared to the nests naturally deserted by females in the study population ($n = 46$) (Mann–Whitney test: $U = 135.5$, $P = 0.09$; Fig. 2), which indicates that the females from the manipulated group stayed longer at the nest before they deserted.

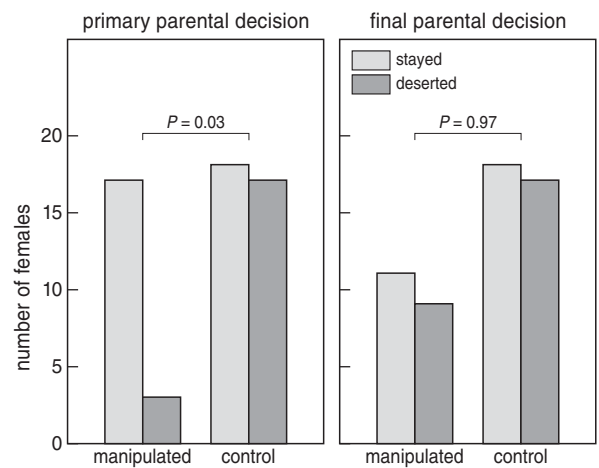


Figure 1. Female Penduline Tit behaviour after male removal in manipulated and control nests.

Table 1. Logistic regression models of female primary and final decisions as dependent on date of laying the first egg and male mask width (manipulated nests only).

Decision	Variable	Coefficient	SE	P
Primary ^a	Intercept	3.278	5.978	0.583
	Date of first egg	0.008	0.028	0.790
	Male mask width	-0.210	0.597	0.724
Final ^b	Intercept	5.572	4.603	0.226
	Date of first egg	-0.007	0.021	0.737
	Male mask width	-0.547	0.457	0.231

^aResidual deviance = 16.7 (17 df), null deviance = 16.9 (19 df).

^bResidual deviance = 25.9 (17 df), null deviance = 27.5 (19 df).

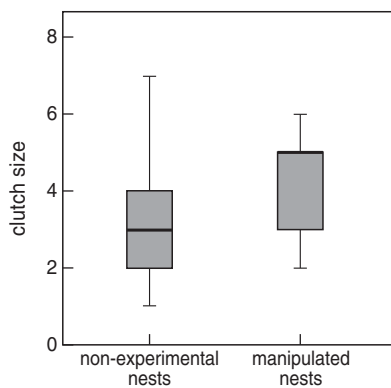


Figure 2. The clutch size of manipulated ($n = 9$) and non-experimental ($n = 46$) nests deserted by female Penduline Tits. Nests were manipulated by removing the male during egg-laying. Box plots with range, median and interquartile range are shown.

DISCUSSION

The results obtained in this study suggest that the parental behaviour of female Penduline Tits (her decision to stay or desert) is determined by the male's decision. This indicates that females generally stay at the nest if males manage to desert first, and some of them try to compensate for the male's absence by attracting a new mate. During four years of studying Penduline Tits (187 nests), I recorded only seven cases of females attracting a second male to natural nests (3.7%). It is possible that some of the females intended to desert the clutch, but when their mates were removed in the experiment, tried to pass the parental duties to the new males. In natural conditions, such females may have more time to desert before males, since the experiment was carried out one day before most of the natural desertions take place (Valera *et al.* 1997). Females may benefit from attracting a new mate in several different ways. First, females gain male help during nest building. Male help is important because females build mostly when sitting inside the nest while their mates are bringing nest material (Bleeker *et al.* 2005). Female Penduline Tits start laying eggs into incomplete nests (Schönfeld 1994) and need time to accumulate reserves for egg production. Also, females may benefit from copulation with several males, comparable to females engaged in extra-pair copulations (EPC), e.g. to gain extra male parental care and insurance against male infertility, genetically diverse offspring, or acquire higher genetic quality of offspring (Birkhead & Møller 1992, Kempenaers & Dhondt 1993). The frequency of

extra-pair paternity (EPP) reported in different populations of Penduline Tits varies from 6.9% to 23.5% of offspring, occurring in 17.3% to 52.7% of nests (Schleicher *et al.* 1997, van Dijk *et al.* 2010). In the studied population, at least one extra-pair young (EPY) was found in 40% of nests, and 18% of nestlings were sired by an extra-pair male (BC, pers. obs.). Although no indirect benefits from EPY were found in Penduline Tits (van Dijk *et al.* 2010), the situation may differ between populations, as reported in Reed Buntings *Emberiza schoeniclus* (Kleven & Lifjeld 2004, Suter *et al.* 2007). Such benefits may be hard to confirm, since the occurrence of EPY in the nest of Penduline Tits does not have to be the result of females seeking EPCs. Some females lay subsequent eggs in nests of two or more males (BC, pers. obs.), thus the first eggs in some nests may be sired by a previous mate of the female.

An alternative explanation of my results follows from the fact that the removal was carried out before most of the natural desertions take place (see Valera *et al.* 1997). If there is a time window for desertion (e.g. individuals have to be in a certain hormonal state to desert), females from the manipulated group might not have taken the disappearance of their mates as desertion but as an unusual event (e.g. his death), and searched for a replacement male. This could explain the large proportion of females in the manipulated group that attracted replacement males compared to the control group. However, males and females quite often desert as soon as the first or second egg appears in the nest (Valera *et al.* 1997; BC, pers. obs.) and the manipulation thus overlaps with the distribution of natural desertions. It seems unlikely that this small and overlapping time difference coincides with an important change in the females' hormonal state.

As pointed out earlier, most removal experiments conducted so far involved bird species that exhibit biparental care and such experiments in uniparental species are scarce. Pierce *et al.* (2010) studied Purple Sandpipers *Calidris maritima*, in which females almost always desert at hatching and all broods are attended by a single parent (most often the male). The authors were able to change female behaviour by manipulating the decision of their mates. Almost all females stayed at the nest after the males were removed. This showed that females of this species do not have a fixed desertion strategy, and their behaviour may be changed. Likewise, Penduline Tit females seem to adjust their desertion behaviour to new circumstances. These findings may give a hint for understanding the process of desertion in the studied species. It is well documented that the breeding system in Penduline Tits is driven by

sexual conflict, since both males and females gain from desertion (Szentirmai *et al.* 2007). In birds, due to internal fertilization, males have opportunity to desert before females, leaving them in a 'cruel bind' (Trivers 1972, Dawkins & Carlisle 1996). Nonetheless, female Penduline Tits try to conceal the start of egg-laying by burying the eggs in the bottom of the nest and preventing males from entering the nest after the first eggs are laid (Valera *et al.* 1997). This behaviour probably gives the female the opportunity to leave before her partner. Deserting females distribute 'normal' clutches (6–7 eggs) to nests of two or more males (BC, pers. obs.), but even such deserting females usually take care of one clutch (larger than those deserted) later in the season (Persson & Öhrström 1989). If, however, the male manages to leave before the female, she seems to be more prone to continue egg-laying at the current nest (as was observed at manipulated nests), instead of leaving the existing eggs, which are then doomed to failure. The situation is more complicated, because there are usually unmated males in the population that are potential replacement males. These findings show that reproductive tactics of female Penduline Tits are flexible and individuals may change their behaviour depending on new circumstances. To fully understand the desertion process in Penduline Tit, additional studies using cameras to continuously record birds during egg-laying are needed.

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SAMENVATTING

Het grootbrengen van jongen is een tijd- en energierovende bezigheid. Dit leidt tot een conflict tussen de ouders: beide zijn er immers bij gebaat als de ander harder werkt. Dan kunnen ze zelf energie besparen voor overleving of zelfs een ander broedsel beginnen. Bij Buidelmezen *Remiz pendulinus* kunnen zowel mannetjes als vrouwtjes in hun eentje een nest jongen grootbrengen. Zodra de eerste eieren in het nest zijn gelegd, gaat een van de ouders er vaak vandoor om elders opnieuw te beginnen. In de onderhavige studie is gekeken of de beslissing van het vrouwtje om wel of niet te blijven, afhangt van wat het mannetje doet. Bij twintig nesten werd het mannetje gevangen en overgebracht naar een gebied 20 km verderop. Dit moest simuleren dat het mannetje het nest verlaten had. Meer dan de helft van de beroofde vrouwtjes had binnen een of twee dagen een nieuwe partner, iets dat in de natuurlijke situatie erg zeldzaam is. Zes van die vrouwtjes gingen er alsnog zelf vandoor. Uiteindelijk ging iets meer dan de helft van de vrouwtjes in de experimentele groep op haar eieren broeden, wat niet afweek van het percentage in de controle groep waar de mannen niet waren verwijderd. (KK)

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