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Sexual conflict over care: antagonistic effects of clutch desertion on reproductive success of male and female penduline tits

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Abstract

A fundamental tenet of sexual conflict theory is that one sex may increase its reproductive success (RS) even if this harms the other sex. Several studies supported this principle by showing that males benefit from reduced paternal care whereas females suffer from it. By investigating penduline tits *Remiz pendulinus* in nature, we show that parental conflict may be symmetric between sexes. In this small passerine a single female (or male) cares for the offspring, whereas about 30% of clutches are deserted by both parents. Deserting parents enhance their RS by obtaining multiple mates, and they reduce the RS of their mates due to increased nest failure. Unlike most other species, however, the antagonistic interests are symmetric in penduline tits, because both sexes enhance their own RS by deserting, whilst harming the RS of their mates. We argue that the strong antagonistic interests of sexes explain the high frequency of biparental desertion.

Introduction

Sexual conflict is a pervasive evolutionary process shaping morphology, behaviour and speciation of animals (Rice, 1996; Gavrillets, 2000; Arnqvist & Rowe, 2002). The fundamental assumption of sexual conflict theory is that one sex increases its own reproductive success (RS) even if this may be harmful for the other sex (Chapman *et al.*, 2003; Arnqvist & Rowe, 2005). For example, repeated or prolonged mating increases male RS, whereas it reduces the survival, receptivity or foraging efficiency of females (Parker, 1979; Rowe *et al.*, 1994). Thus a tug-of-war is expected to emerge between the male and female over the control of mating (reviewed by Parker, 2006).

Sexual conflict, however, does not cease at conception, as in many organisms parental care is essential for the survival of young (Lessells, 1999; Houston *et al.*, 2005).

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As both genetic parents receive the benefit of care (i.e. the offspring), whereas only the caring parent pays the costs of raising young, a conflict of interest emerges in multiple brooding animals: *which parent should provide the care?* game-theoretical models pointed out the antagonistic interests of males and females over care (Maynard-Smith, 1977; Lazarus, 1990; Webb *et al.*, 2002) and empirical evidence from natural populations is also gathering. First, brood desertion by males occurs in several biparental birds (reviewed by Székely *et al.*, 1996), and females are often compelled to compensate for the lost effort of their partner (Osorno & Székely, 2004; Draganoiu *et al.*, 2005). Similarly, mates of polygynous males work harder than females of socially monogamous males in facultatively polygynous birds (Davies, 1992; Lundberg & Alatalo, 1992). Desertion and remating are apparently advantageous for the male, whereas their females pay a cost due to increased parental effort or delayed moult (Davies & Houston, 1986; Hemborg, 1999; Lubjuhn *et al.*, 2000; Poirier *et al.*, 2004). Second, mate-removal experiments and handicapping of one parent (for instance, by attaching small weights or clipping wing feathers) also show that widows and mates of handicapped parents, respectively, typically increase their own work (reviewed by Liker, 1995; Sanz

et al., 2000; Houston *et al.*, 2005; Hinde & Kilner, 2007), which presumably precipitate into higher mortality and/or reduced future RS. Most of these studies, however, are based upon an implicit assumption of sexual conflict theory: males are driving the sexual conflict by courting and pursuing new mating opportunities and reducing care (Smith, 1995), whereas females are presumed to respond by being more resilient and compensating the lost care by their mate, if necessary.

Here, we argue that this view of sexual conflict may suit some organisms better than others. Thus sexual conflict may operate similarly in males and females, especially in those species which have flexible breeding systems. The penduline tit *Remiz pendulinus*, a small Eurasian passerine bird (body mass about 9 g), is one of these species in which either the male or the female deserts the clutch before incubation commences, and parental care is provided by a single parent (female-only care: 50–70% of clutches; male-only care: 5–20% of clutches, Franz & Theiss, 1983; Persson & Öhrström, 1989; Franz, 1991). However, 30–40% of clutches are deserted by both parents and thus doomed to failure. After desertion, males and females may remate up to six times during a breeding season, and produce multiple broods (Persson & Öhrström, 1989). Arnqvist & Rowe (2005) summarized the key features of penduline tits' breeding system, and made an appealing argument how their sexual conflict over care may operate. However, neither Arnqvist & Rowe (2005) nor any previous study of penduline tits showed unequivocally that (i) desertion increases the RS of deserting parents, and (ii) desertion reduces the RS of the parents' mate.

Here, we test whether the fundamental prediction of sexual conflict theory, i.e. desertion enhances the RS of deserting parent, but reduces the RS of its mate, may hold for both males and females. We test this prediction separately for males and females using path analysis (Loehlin, 1992). We expected that desertion was beneficial by allowing the deserter to remate and produce a new clutch. However, desertion by one sex should reduce its mate's RS, because the deserted parent either accepts the costs of caring alone, or deserts the clutch too so that the clutch fails. Therefore, desertion by either parent will have an effect on both parents' RS, mediated by the number of mates and offspring. As males and females may have different parental abilities, we also took into account the differences in offspring survival in male-only vs. female-only cared clutches (Székely & Cuthill, 1999).

Materials and methods

Data collection

We studied the penduline tits at Fehértó, southern Hungary (46°19'N, 20°5'E) between 2002 and 2004. Fehértó is an artificial fishpond system (1321 ha), where

approximately 90 males and 50 females bred on the dykes separating the fishpond units each year. Males and females were caught using mist nets and song playback at their first nest, and they were individually colour ringed. We followed the pair bonds of 78 males and 64 females throughout an entire breeding season (April–August) by checking their nests at least every other day. At each nest ($n = 240$) the following variables were recorded: (i) the date of nest initiation, i.e. the date when the male started building his nest. Seventy-four nests were found on the first day of nest building and hence their date of initiation was known. The initiation dates of those nests that were found in more advanced building stages were estimated using equations fitted to the progress of nest building at those nests that were found at initiation (see details in Szentirmai *et al.*, 2005). (ii) Date of pairing, i.e. when the male was first seen copulating and/or building the nest together with a female. (iii) Desertion by the male and/or female, i.e. if one (or both) parent(s) was (were) not seen at the nest for at least two consecutive nest checks (see Szentirmai *et al.*, 2005). (iv) Clutch size was determined between the sixth and ninth day of incubation, or in biparentally deserted nests immediately after desertion. (v) The nest was visited on the expected day of hatching (14 days after the start of incubation, Cramp *et al.*, 1993), and then once or twice until the last chick hatched (2–3 days after the first chick hatched), when the number of hatchlings was recorded. (vi) We counted the number of nestlings when the youngest chick was 10 days old. More detailed methodology is given by Bleeker *et al.* (2005) and Szentirmai *et al.* (2005).

Data processing and statistical analyses

Over an entire breeding season, for each male and female we calculated the total number of mates, the number of their clutches that they (or their mates) deserted, the number of eggs, hatchlings and nestlings. For three males and one female we had data from more than one year; for these individuals we chose one year randomly. In addition, for each clutch we calculated hatching success (proportion of hatched eggs) and nestling survival (proportion of hatchlings that survived until day 10). Clutch size, hatching success, nestling survival and the number of nestlings were compared between female-only cared, male-only cared and biparentally deserted clutches, and we only use those clutches for which all these variables were known ($n = 119$).

Reproductive success was defined as the total number of nestlings produced per individual over a breeding season. The number of nestlings was used instead of the number of fledglings, because the former can be determined more reliably. As only 8% of nestlings die before fledging, our measure of RS is tightly related to number of fledglings (I. Szentirmai, unpublished data).

We used path analysis to investigate RS in relation to desertion. Path analysis is a multivariate multiple

regression method, in which partial regression parameters are estimated using iterative estimation procedures (Wright, 1968; Li, 1975; Loehlin, 1992). Partial regression parameters (paths coefficients) vary between -1 and 1 , and are estimated for the relationships specified by the modeller. We used path analysis because we expected that desertion will have an indirect effect on the deserting individual's RS mediated by a number of variables. The relationships given in Fig. 1 are assumed *a priori*, and are based upon previous studies of penduline tits (Franz & Theiss, 1983; Persson & Öhrström, 1989; Franz, 1991; Hoi *et al.*, 1994; Valera *et al.*, 1997). We expected that RS will increase with desertion by enhancing the number of mates, which in turn increase the number of eggs and hatchlings (Fig. 1). Conversely, desertion is expected to reduce the RS of mate via reduced clutch size or offspring survival (see Results; Persson & Öhrström, 1989). Therefore we specified the paths between desertion and the number of eggs, and desertion and the number of nestlings (Fig. 1). The relationship between male desertion and clutch size was

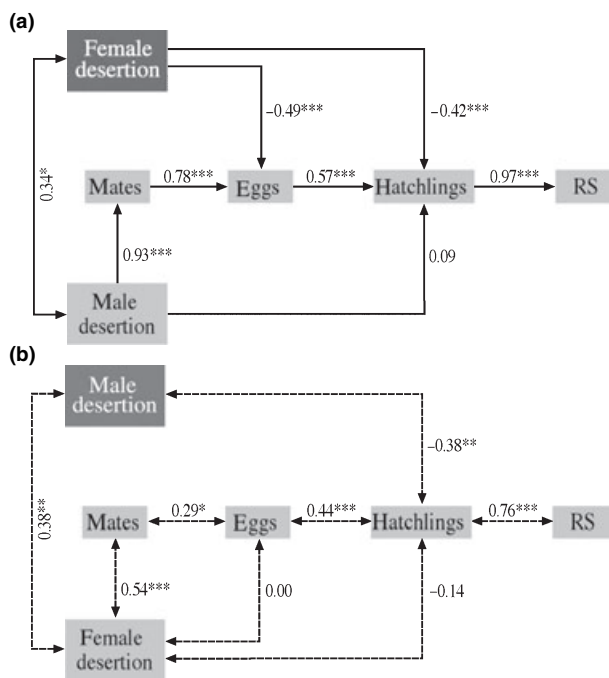


Fig. 1 Clutch desertion in relationship to reproductive success (RS) of (a) male and (b) female penduline tits. (a) Path diagram of male RS. Arrows indicate direct linear relationships between explanatory and response variables, and standardized path coefficients are shown next to the paths. (b) Correlations between female RS, male desertion and female desertion. Double headed arrows with dashed lines indicate correlations between variables, and Spearman rank correlation coefficients are shown next to the arrows. In both diagrams variables of the focal sex (a: male; b: female) are shown in light grey boxes and desertion of their mate in dark grey boxes. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

not taken into account, because male cared and male deserted clutches were not significantly different in size (see Results). We took into account the time each individual spend on the study site by correcting all variables in the path model for the number of days they spent at Fehértó. For males, the number of days spent at the study site was defined as the number of days between the initiation of their first nest and the last day when they were observed on the study site. For females, we calculated the number of days between their first mating and the last day when they were observed on the study site. None of the time-corrected variables differed between years in males (Kruskal–Wallis tests: all $P > 0.120$) or in females (all $P > 0.140$), therefore year was not considered as a confounding variable in the analyses.

We used SPSS 11 (SPSS Inc., Chicago, IL, USA) for statistical analyses, except path analysis which was carried out using LISREL 8.72 (Scientific Software International Inc., Chicago, IL, USA). As several variables in the model were not normally distributed, we used robust maximum likelihood estimation to calculate path coefficients, and tested model fit by Satorra–Bentler corrected chi-square test (Satorra & Bentler, 1994; Boomsma & Hoogland, 2001). Although both path models (male and female) had a good fit to the data (males: $\chi^2_7 = 2.519$, $P = 0.926$, $n = 78$; females: $\chi^2_7 = 0.267$, $P = 0.999$, $n = 64$), in the female model some path coefficients fell out of the -1 and 1 range, indicating multicollinearity between model components and unreliable path coefficients (Jöreskog *et al.*, 2000). For females, we therefore used Spearman correlations to explore the relationships between analogous components to the path model of males. We used partial rank correlations to control for indirect relationships in the model (Daniel, 1990); for instance we controlled for number of mates when tested the relationship between female desertion and eggs (see Fig. 1b). We provide mean \pm SE, two-tailed probabilities and rejected the null hypothesis at $P < 0.05$.

Results

Success of male-only and female-only cared clutches

Female-only cared clutches were larger than male-only cared ones (Mann–Whitney U -test, $Z = 5.517$, $P < 0.001$; Table 1). Biparentally deserted clutches (2.7 ± 0.2 eggs, $n = 49$ clutches, range: 1–6) were smaller than female-only cared ones, whereas they were not significantly different from male-only cared ones (Mann–Whitney U -tests, female-only vs. biparentally deserted: $Z = 8.133$, $P < 0.001$; male-only vs. biparentally deserted: $Z = 1.841$, $P = 0.066$). In contrast, both hatching success and nestling survival were lower in female-only cared clutches than in male-only cared ones (Table 1). Nevertheless, female-only clutches produced more nestlings than male-only cared

	Female-only cared (<i>n</i> = 53 clutches)		Male-only cared (<i>n</i> = 17 clutches)		<i>P</i> *
	Mean ± SE	Range	Mean ± SE	Range	
Number of eggs	5.91 ± 0.16	3–8	3.24 ± 0.24	2–5	< 0.001
Hatching success†	0.76 ± 0.03	0.2–1	0.91 ± 0.04	0.33–1	0.001
Nestling survival‡	0.81 ± 0.05	0.4–1	0.92 ± 0.05	0.25–1	0.004
Number of nestlings	3.62 ± 0.19	1–6	2.65 ± 0.24	1–4	0.006

*Mann–Whitney *U*-tests between female-only cared and male-only cared clutches.

†Proportion of eggs hatched.

‡Proportion of hatchlings survived until day 10.

ones (Mann–Whitney *U*-test, $Z = 2.737$, $P = 0.006$; Table 1).

Desertion and reproductive success

Male RS increased with male desertion (total path coefficient = 0.262, i.e. the sum of direct and indirect paths from male desertion to RS), and this effect was mediated by positive relationships between male desertion and the number of its mates, the number of its eggs, and the number of hatchlings it sired, and finally, between the number of hatchlings and the male's RS over a breeding season (Fig. 1a). Female desertion however, had a negative effect on male RS (total path coefficient = -0.542). The latter negative effect was due to negative relationships between female desertion and the total number of eggs in nests of the male, and female desertion and number of hatchlings fathered by the focal male (Fig. 1a).

The analyses of female RS showed striking similarities to that of the males (Fig. 1b); note that for females we used rank correlations (see Materials and methods). Desertion by the female increased the number of its mates (Fig. 1b), which in turn increased the total number of its eggs, the number of its hatchlings, and ultimately, its RS over the breeding season (Fig. 1b). However, desertion by the male reduced the number of female's hatchlings (Fig. 1b), and overall, decreased its RS over the breeding season.

Discussion

Our study showed that clutch desertions have antagonistic effects on RS of males and females. Somewhat unusually among most animals that have been studied to date, the effects were parallel between males and females. To our knowledge, the penduline tit is the first natural system in which both males and females may increase their own RS by deserting, and by doing so they reduce their mate's RS. This conflict of interest is reminiscent of the dunnock *Prunella modularis* (Davies, 1992), although in the dunnock sexual conflict appears to be over mating: by strategically allocating copulations, the female attempts to recruit several males to increase its

Table 1 Reproductive success of female-only cared and male-only cared clutches in penduline tits.

RS. Conversely, males compete with other males to fertilize females, and the outcome of their competition impacts upon male RS (Davies & Houston, 1986).

Male penduline tits enhance their RS through desertion as they often remate and obtain multiple broods. The more often a male deserted, the more mates, and eventually more offspring, it had by the end of the breeding season. Although Persson & Öhrström (1989) argued that RS should increase with the number of mates in penduline tits, their data did not provide statistical support for this argument. Our results are in line with avian studies showing that males benefit from polygyny due to multiple broods (e.g. Davies & Houston, 1986; Lubjuhn *et al.*, 2000; Poirier *et al.*, 2004). Male desertion however, had a negative effect on female RS through reduced hatching success (Fig. 1b). This negative effect may be due to an increased chance of clutch failure. Therefore, if a male deserts the clutch, the clutch has about 50% chance to fail as, on average, females also desert half of their clutches – assuming independent decision of males and females (Franz & Theiss, 1983; Persson & Öhrström, 1989; Franz, 1991). However, females may adjust their decision about desertion to the males' decision (McNamara *et al.*, 2002), so that the observed frequency of female desertion is lower after male desertion than predicted by independent decisions.

Similarly to males, females also enhanced their RS through desertion and remating. The more often a female deserted its clutches, the more mates it had, and all correlations along the path between female desertion and RS were positive and significant (see Fig. 1b). Female desertion, however, reduced male RS in two ways. First, clutches deserted by females were approximately half the size of those cared by females (Table 1). Second, female desertion increased the chance of clutch failure due to biparental desertion (see above). Female deserted clutches may be smaller than female cared ones either because females try to control parental conflict by deserting before the male notices that the clutch is complete (Valera *et al.*, 1997; Arnqvist & Rowe, 2005), or to minimize the potential loss by biparental desertion and clutch failure. These results of female RS however, should be treated with some caution, as we could not use path analysis for females, and used Spearman rank

correlations and partial rank correlations. This is less powerful than path analysis, as the fit of the model, i.e. the structure of the relationships in our hypothetical model (the path diagram), cannot be tested against the observed covariances between the model components (Loehlin, 1992). This means that we cannot statistically justify that female desertion influences female RS along the pathways we assumed in our analysis. Biological sense and previous studies however, suggest that females enhance their RS by desertion through enhancing their number of broods (Persson & Öhrström, 1989).

Our results thus reveal an intensive conflict between males and females over care. Both males and females enhance their RS by desertion, whereas desertion by their mates reduces their RS. This accelerated sexual conflict may explain the extremely high frequency of biparental desertion in penduline tits in all populations that have been studied to date (30–40%, e.g. Franz & Theiss, 1983; Persson & Öhrström, 1989; Franz, 1991). If the benefits of desertion are high relative to its costs for both sexes as in penduline tits, then parents can risk that their partners will also desert. Intensive sexual conflict may also explain the frequent aggressive interactions between the parents during egg-laying. Valera *et al.* (1997) suggested that aggression arises as part of a game between the parents in which females try to conceal their eggs from males, so that females can desert before the male notices the commence of egg-laying. By removing nest material from the eggs in some of the nests, researchers were able to promote male desertion (Valera *et al.*, 1997). However, if males are able to determine the stage of the clutch they may desert before the female, so that the male leaves the female in a 'cruel bind' (Trivers, 1972; Valera *et al.*, 1997).

Our study has three potential limitations. First, the amount of extra-pair young may differ between male-only cared and female-only cared clutches, and this might confound the relationship between male desertion and male RS. This effect is, however, not likely because extra-pair paternity appears to be uncommon in penduline tits (Schleicher *et al.*, 1997). Currently we are genotyping offspring to test paternity in our population. Second, we had no information on lifetime reproductive success (LRS) of adults, and therefore survival consequences of desertion were not accounted for in our analyses. However, penduline tits are short-lived therefore for most individuals the annual RS is expected to be equal to LRS. The low returning rates (< 5%) of adult penduline tits to our study area is also consistent with the latter argument. Third, correlation does not necessarily imply causation, and some uncounted variable may confound our results. Although path analysis allowed us to quantify *a priori* relationships, other unmeasured variables may be important in determining the RS of individuals (Loehlin, 1992). For example, deserting and caring individuals may differ in some traits that influence RS independently from their caring/

deserting behaviour. Experimental studies manipulating parental decisions are necessary to quantify the effect of clutch desertion on RS.

In conclusion, our results are consistent with sexual conflict theory, specifically in the context of parental care. Male penduline tits enhance their RS by desertion, whereas this behaviour reduces female RS. Conversely, female desertion is beneficial for the female, but harmful for its mates. These conflicting interests are likely to generate antagonistic coevolution between males and females. An important, yet untested, implication is that the high frequency of biparentally deserted clutches emerges as an outcome of intense sexual conflict over care.

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