



# Sexual conflict over parental care in a species with female and male brood desertion

MATTEO GRIGGIO\*† & ANDREA PILASTRO†

\*Konrad Lorenz Institute for Ethology, Vienna, Austria

†Dipartimento di Biologia, Università di Padova

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Each parent has limited resources to invest in current reproduction, so each parent would benefit if its mate did more of the work, which generates a sexual conflict between parents. Parental care behaviour is an adaptive decision, involving trade-offs between remating (and consequently desertion of the brood) and continuing parental effort. The rock sparrow, *Petronia petronia*, is an unusual species in which brood desertion can occur in both sexes. Consequently, the rock sparrow is a good species to investigate the behavioural response of parents to the desertion by their mates and whether sexual difference in this response exists. We compared parental effort of pair members divided into three groups: pairs that cooperated, females that deserted the brood and males that deserted. During the period of biparental care, females fed offspring more often than males, but there were no differences among the three groups. Following desertion the total amount of care in biparental, female-only and male-only broods differed, because both sexes adjusted their care to the absence of their mates, but females overcompensated the mate's absence while males only partially compensated. Nestling survival rate was positively correlated with feeding rate and the mean survival rate was lower in the male-only broods. We suggest that both parents, in a negotiation process, would benefit from withholding parental investment, as proposed in recent theoretical models on sexual conflict over parental care. Altogether our results show an unexpected plastic response of parents to care during the desertion process.

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The amount of parental investment that the parent should provide to its young is a crucial decision and the great number of reviews focused on this subject (e.g. Gubernick & Klopfer 1981; Clutton-Brock 1991; Baur 1994; Westneat & Sargent 1996; Houston et al. 2005) reveals that the study of parental care is one of the crucial point of behavioural ecology. Birds show highly variable patterns of parental care (reviewed by Clutton-Brock 1991). In some species only the male or the female provides care for the offspring, in others both parents participate in caring (about 90% of bird species, Lack 1968), and some species show multiple patterns of care in a single population during the same breeding season (e.g. Persson & Öhrström 1989; Székely et al. 1996; Pilastro et al. 2003).

Correspondence: M. Griggio, Dipartimento di Biologia, Università di Padova, Via U. Bassi 58/B, I-35131 Padova, Italy (email: [matteo.griggio@unipd.it](mailto:matteo.griggio@unipd.it)).

Since parental care is costly, a sexual conflict between parents over parental investment is expected to arise (Trivers 1972). In species where males and females cooperate to raise the young, one resolution of this conflict is to desert the offspring: one parent stops caring before the independence of the young. By deserting and remating in the same breeding season a parent may increase its reproductive success, or the parent may improve its own survival reducing the cost (in time and energy) of caring for the brood deserted (e.g. Olsson 1997; Székely et al. 1999). On the other hand, helping the mate to raise the young may increase the fitness of its current offspring (reviewed by Székely et al. 1996). Empirical studies have confirmed that several factors, such as offspring quality (Erikstad et al. 1997), perceived paternity (see Arnold & Owens 2002; Westneat & Sherman 1993), remating opportunities (Székely et al. 1999) and body condition of parents (Hörak et al. 1999) affect desertion decisions of the parents. Whatever the factors responsible, after the desertion of

one mate, the deserted parent may decide to desert or to stay. In the latter case, the abandoned parent has different options concerning how much effort it should invest in rearing its offspring. For example, a correlative study on magnificent frigatebirds, *Fregata magnificens*, found that deserted females fully compensated after mate desertion, by doubling their feeding rate (Osorno & Székely 2004). In the greater flamingo, *Phoenicopterus ruber*, in contrast, deserted parents continue to provide care at the same level as before desertion (Cezilly 1993). Removal studies found that males usually compensate incompletely and to a lesser extent than deserted females in the great tit, *Parus major* (Sasvári 1986), and in the kentish plover, *Charadrius alexandrinus*, both sexes partially compensate for the experimental removal of the partner (Székely & Cuthill 1999; Kosztolányi et al. 2003). There are two general alternative strategies for reacting to desertion: (1) to increase parental effort to compensate partially or totally for the loss of help from the mate; and (2) to continue to provide care at the same level as that provided before desertion (reviewed in Osorno & Székely 2004).

However, contrary to this general picture, some authors have presented models in which, under particular circumstances, the deserted parent overcompensates for the loss of help from its mate, by providing greater parental investment per nestling compared to that of both parents. So, young are better off when cared for by a single parent than when cared for by both parents (Parker 1985; McNamara et al. 2003; Houston et al. 2005). In particular, McNamara et al. (2003) focused on the difference between the partial loss of a partner's contribution to parental care and its complete loss in a context of sexual conflict over parental care. This model predicts that when one parent reduces its parental effort, the effort of the other parent should increase, but not up to full compensation to avoid to be exploited. As a result, the two parents continuously 'negotiate' during each breeding event over each one's level of care, because such negotiation reduces the opportunities for one parent to be exploited by the other. In contrast, when one parent deserts, the other parent is expected to increase its parental effort to its best. This may result in uniparentally fed broods receiving more care than offspring cared for by both parents (McNamara et al. 2003). Support for this prediction comes from an aviary experiment on the zebra finch, *Taeniopygia guttata*, in which the level of parental care provided by the two parents was compared with that of single females caring for a half brood. Consistently with predictions, nestlings cared by the female only received 25% more care (per nestling) than those cared by both parents (Royle et al. 2002). However, evidence that overcompensation occurs in natural conditions, where food is limited, is still lacking.

In the rock sparrow, *Petronia petronia*, brood desertion by both sexes occurs during the nestling feeding stage, and either parent is able to provide care on its own (Pilastro et al. 2001; Griggio et al. 2003a). Consequently, this species is a good subject to explore how males and females adjust their parental effort when deserted, and how this potentially impacts their reproductive success. To obtain a clear understanding of the parental effort adjustment during the desertion process we compared the parental

behaviours before and after desertion among three different groups of breeding pairs, in which (1) females deserted the first brood (and renested; for more details see Pilastro et al. 2001), (2) males deserted the brood (stopped feeding the young and were seen at a secondary nest), and (3) males and females collaborated in parental care.

## METHODS

### Study Species

We studied a northwest Italian alpine population of rock sparrow, in the higher Susa valley, as part of a wider long-term study of rock sparrow ecology (Mingozzi et al. 1994; Biddau & Mingozzi 1995; Tavecchia et al. 2002; Griggio et al. 2003b). A mean of 40 nestboxes (range 36–51) were set-up in small villages each year. The population included approximately 20 breeding pairs each year. Nestboxes were also designed to work, when necessary, as traps so that adults could be individually colour-ringed and measured.

We checked the nestboxes every second or third day at the start of the breeding season (late May–early June) each year from 1998 to 2000 and from 2002 to 2004 inclusive. We recorded pair bonds, laying date, clutch size, hatching and fledging dates. More details of the methods are given in Pilastro et al. (2002). A wide array of mating patterns, including monogamy, polygyny and sequential polyandry have been recorded in this population (Pilastro et al. 2001; Griggio et al. 2003b). The rock sparrow shows a highly variable system of biparental care in which some males cooperate with females during the first week after hatching, and then gradually decrease their food provisioning rate as the nestlings age. This can occur to the extent that, some days before nestlings are fledged, most of the provisioning is performed by the female (Griggio et al. 2005). In this study approximately 25% of the males deserted the brood. More rarely, some males cared exclusively for the nestlings when their females deserted and started to lay a second clutch in another nest (ca. 10% of the females that successfully raised their first brood).

### Behavioural Observations

Behaviour of pairs was observed for 1 h every 2–3 days throughout the six breeding seasons to determine pair bonds and study reproductive behaviour (Pilastro et al. 2002). We observed individuals and their nestling feeding trips with 20–60× spotting scopes while sitting in the open, approximately 30–50 m from the nest. Each nest was observed during periods of peak activity (Griggio et al. 2003a) in the morning and late afternoon (0600–1030 and 1530–1900 hours, respectively). Brood desertion was confirmed when one parent was no longer observed at the nest and was seen at a second nest (for more details see Pilastro et al. 2001). Desertion was assumed to have taken place midway between the dates the partner was seen for the last time and the subsequent observation (Székely & Lessells 1993).

After hatching, nestlings remain in the nest for about 18 days (the period of postnatal care). During this rearing period, the mean observation time per nest was

5.32 ± 0.21 h (±1 SE; range 4–8 h). We distinguished three types of breeding pairs according to the pattern of parent desertion. The first group included pairs where males stopped feeding the young, deserted the brood, and started to defend a second nestbox (F-only group,  $N = 16$ ). In the second group females deserted the first brood to breed in a second nest, leaving the male to rear the young (M-only group,  $N = 9$ ). The third group was represented by pairs in which females laid only one clutch during a given breeding season and both parents cooperated in parental activity (biparental group,  $N = 30$ ). In total we carried out 293 h of observations on 55 nests (1998 = 11; 1999 = 10; 2000 = 12; 2002 = 6; 2003 = 7; 2004 = 9). In these 55 nests the frequency of deserting males and females varied among years (from 0 to 50% and from 0 to 30%, respectively).

Nine of the 40 individual males and eight of the 42 females considered in this study were present in more than one breeding season, although the combination of each breeding pair always differed among years (i.e. each male was paired to a different female in each breeding year and vice versa). Among the nine males that participated in more than one breeding event in our sample, five took part in two, two in three and two in four breeding events. The nine females that were represented more than once in our sample took part in two (five females) and three (four females) breeding events. We therefore selected a fully independent, reduced data set ( $N = 35$ , 14 biparental, 13 F-only, and 8 M-only), in which individual males and females appeared only once. Our criterion for selection was to maximize the sample size of our samples, but was random with respect to year (to avoid bias towards younger or older individuals by selecting the first or the last breeding attempt). Analyses of male and female parental behaviour (see below) were then conducted on both full and reduced (fully independent) data set.

We recorded the number of nestling feeding trips/h by the two parents. Prey size was estimated by comparing the length of the exposed bill culmen of adults (range 13.1–14.8 mm, Cramp & Perrins 1994) with the length of the prey. Prey items, chiefly grasshoppers and caterpillars, were assigned to three size classes: approximately 0.5, 1.0 and 1.5 (or more) bill lengths, following protocols commonly used in similar studies (e.g. Schwagmeyer et al. 2002; Griggio et al. 2005). Accordingly, we estimated the quantity of food delivered by the parents to the brood per hour of observation as the number of prey items delivered multiplied by their size. We compared the behaviour of rock sparrow parents before and after the date of desertion among the three groups. Day 9 after hatching was considered to be the 'date of desertion' in biparental group (i.e. the limit to split the observations between early and late parental care in biparental group). This time represents the average male's and female's dates of desertion (see below).

## Statistical Analyses

Statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, IL, U.S.A.) (Norušis 1993). Proportions were arcsine square-root transformed, and log

transformation was used where appropriate. Where normality and homogeneity of variances were not met even after transformation, we used nonparametric statistics (Zar 1999). Unless otherwise stated, mean ± SE are given, and all probabilities are two tailed. We first compared the behaviour of male and female rock sparrows using a Generalized Linear Model, in which parental behaviour was the dependent variable, year, sex, and time (before or after desertion) were entered as fixed factors, the date on which the female started to lay as a covariate, and individual and nest identity (nested within group) as random factors, to control for repeated measures. We then compared the parental effort (feeding rate/h and total food delivered/h) of the deserted parent (male or female according to the group) with the total parental effort of biparental pairs, before and after desertion. Independent factors in the GLMs were time and group (fixed factors), and nest identity (random factor, nested within group). The effect of parental effort on the proportion of nestlings that survived in a brood (number of surviving nestlings over initial number of nestlings) was modelled using a logistic regression (i.e. a generalized linear model with binomial distribution and logit link function). Nonsignificant terms were backward dropped using a stepwise elimination procedure. All tests of fixed effects are two tailed with a significance level set to  $\alpha = 0.05$ .

## Ethical Note

All handling and ringing was performed by expert ringers provided with the appropriate ringing permits issued by the Istituto Nazionale Fauna Selvatica (Ozzano Emilia, Italy). The long-term nature of the study allowed us to confirm that handled birds and their offspring did not suffer any detectable reduction in welfare and survival.

## RESULTS

### Desertion Timing Pattern

In our sample, timing of desertion was significantly different according to whether the deserting sex was the male or the female. In particular, males deserted their brood earlier (age of nestlings at desertion:  $6.93 \pm 0.52$  days, range 4–11 days,  $N = 16$ ) than females ( $11.77 \pm 1.70$  days, range 12–15 days,  $N = 9$ ; Mann–Whitney  $U$  test:  $U = 35.00$ ,  $P = 0.033$ ).

### Male and Female Feeding Rate in Biparental Pairs

Neither laying date nor brood size (either before or after desertion) differed significantly among years (all  $F_{5,48} < 0.8$ ,  $P > 0.57$ ) and therefore the data from the different years were pooled. In biparental group, males contributed less to feeding the nestlings both during the early and the late stage of nestling rearing (GLM, dependent: number of feeding trips/h; fixed factors: time:  $F_{1,58} = 12.72$ ,  $P < 0.001$ ; sex:  $F_{1,58} = 366.77$ ,  $P < 0.001$ ; sex\*time interaction:  $F_{1,58} = 49.64$ ,  $P < 0.001$ ; random factors: nest identity:  $F_{13,58} = 0.86$ ,  $P = 0.59$ , individual

identity:  $F_{29,58} = 0.73$ ,  $P = 0.83$ , Table 1; dependent: food delivered/h; fixed factors: time:  $F_{1,58} = 18.36$ ,  $P < 0.001$ ; sex:  $F_{1,58} = 245.95$ ,  $P < 0.001$ ; sex\*time interaction:  $F_{1,58} = 32.65$ ,  $P < 0.001$ ; random factors: nest identity:  $F_{13,58} = 0.59$ ,  $P = 0.85$ , individual identity:  $F_{29,58} = 0.80$ ,  $P = 0.74$ ). The same results were obtained using the reduced data set (number of feeding trips/h; fixed factors: time:  $F_{1,26} = 4.81$ ,  $P = 0.038$ ; sex:  $F_{1,26} = 220.76$ ,  $P < 0.001$ ; sex\*time interaction:  $F_{1,26} = 21.52$ ,  $P < 0.001$ ; random factors: nest identity:  $F_{13,26} = 1.23$ ,  $P = 0.36$ , individual identity:  $F_{13,26} = 0.70$ ,  $P = 0.74$ ; dependent: food delivered/h; fixed factors: time:  $F_{1,26} = 8.90$ ,  $P = 0.006$ ; sex:  $F_{1,26} = 172.59$ ,  $P < 0.001$ ; sex\*time interaction:  $F_{1,26} = 16.08$ ,  $P < 0.001$ ; random factors: nest identity:  $F_{13,26} = 0.50$ ,  $P = 0.89$ , individual identity:  $F_{13,26} = 0.53$ ,  $P = 0.88$ ). The significant interaction between time and sex showed that females increased their feeding effort with time, whereas males decreased their feeding effort. Neither year nor laying date nor their interaction was significant predictors of parents' feeding rate.

### Male and Female Feeding Effort after Mate Desertion

Before desertion males and females from the three groups did not differ in their feeding effort (total feeding trips/h and total food delivered/h by male and female, all  $F_{2,52} < 0.99$ ,  $P > 0.38$ ). Similar results were obtained comparing only male and female feeding behaviour before desertion in F-only and M-only groups (all  $P > 0.21$ ). After being deserted by their mate, males and females differed in their feeding effort. When compared to the parental effort (total feeding trips/h and total food delivered/h by both parents in biparental group), males did not fully compensate for the lack of female care, in contrast to deserted females, whose feeding effort was greater than that of both parents in biparental group (Table 1; Fig. 1). The results were similar when considering the full data set (GLM, dependent: number of feeding trips/h; fixed factors: time:  $F_{1,52} = 11.12$ ,  $P = 0.002$ ; group:  $F_{1,52} = 8.60$ ,  $P = 0.001$ ; group\*time interaction:  $F_{1,52} = 5.23$ ,  $P = 0.007$ ; random factor: nest identity (group):  $F_{52,52} = 1.00$ ,  $P = 0.50$ ; dependent: food delivered/h, time:  $F_{1,52} = 22.36$ ,  $P < 0.001$ ; group:  $F_{1,52} = 5.24$ ,  $P = 0.008$ ; group\*time interaction:

$F_{1,52} = 2.84$ ,  $P = 0.067$ ; random factor: nest identity:  $F_{52,52} = 1.23$ ,  $P = 0.23$ ) and the reduced data set (GLM, dependent: number of feeding trips/h; fixed factors: time:  $F_{1,32} = 10.05$ ,  $P = 0.003$ ; group:  $F_{1,32} = 6.95$ ,  $P = 0.003$ ; group\*time interaction:  $F_{1,32} = 5.38$ ,  $P = 0.01$ ; random factor: nest identity:  $F_{32,32} = 1.38$ ,  $P = 0.18$ ; dependent: food delivered/h, time:  $F_{1,32} = 19.04$ ,  $P < 0.001$ ; group:  $F_{1,32} = 4.09$ ,  $P = 0.026$ ; group\*time interaction:  $F_{1,32} = 2.63$ ,  $P = 0.088$ ; random factor: nest identity:  $F_{32,32} = 1.56$ ,  $P = 0.11$ ).

### Feeding Rate and Nestling Survival

The mean number of nestlings at the nest did not differ among groups before desertion ( $F_{2,54} = 0.95$ ,  $P = 0.39$ ), or after desertion ( $F_{2,54} = 0.45$ ,  $P = 0.64$ ; Table 1), although mean survival rate (proportion of fledged nestlings on hatched eggs) was lower in the M-only group compared with the other two groups (biparental: 0.92; F-only: 0.95; M-only: 0.78; logistic regression model with logit link function: binomial total = no. of nestlings before desertion, or within day 9 of nestlings' life, in the case of biparental group; response variable = no. of nestlings fledged: deviance ratio = 3.24,  $t_{53} = 1.89$ ,  $P = 0.058$ ). Nestlings survival rate was largely dependent on feeding rate (independent variable = feeding trips/h after desertion, or during late nestling stage: deviance ratio = 26.80,  $t_{53} = 4.74$ ,  $P < 0.001$ ).

### DISCUSSION

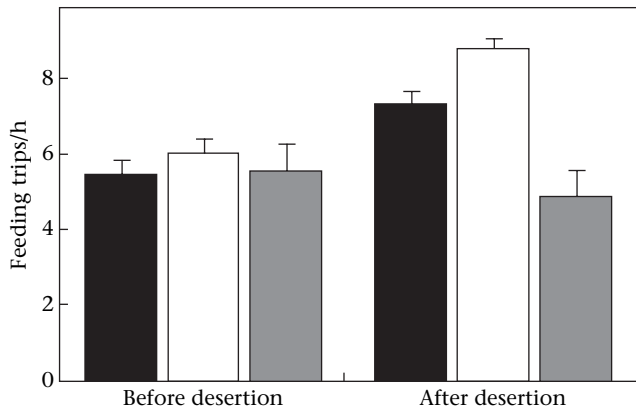
Our results showed that, in rock sparrows (1) males deserted earlier than females, (2) both males and females compensated when deserted by their mate by increasing their feeding effort as compared to that showed in biparental pairs; however, (3) only females overcompensated for the desertion of their mates by increasing their feeding effort above the total level observed in biparental broods. In contrast, males, who decreased their parental effort during the late rearing period in biparental broods, did not fully compensate after desertion by their mate. Finally, (4) the lower parental effort of single males resulted in higher offspring mortality at the nest compared to female-only and biparental reared broods.

**Table 1.** Feeding trips of male and female rock sparrows, number of nestlings and their survival rate during desertion process

	Period	Biparental* (N=30)	F-only (N=16)	M-only (N=9)
Male feeding trips/h	Before desertion	1.45 (0.18)	1.77 (0.18)	1.86 (0.36)
	After desertion	0.56 (0.07)		4.87 (0.68)
Female feeding trips/h	Before desertion	4.01 (0.27)	4.25 (0.25)	3.69 (0.48)
	After desertion	6.72 (0.35)	8.78 (0.24)	
Total feeding rate/h (feeding trips×food item size)	Before desertion	8.02 (0.61)	8.94 (0.93)	7.59 (1.38)
	After desertion	12.55 (0.78)	15.34 (1.32)	8.52 (1.49)
Number of nestlings	Before desertion	5.03 (0.16)	4.62 (0.36)	5.11 (0.20)
	After desertion	4.60 (0.22)	4.37 (0.36)	4.11 (0.63)
Mean survival rate (fledged nestlings/hatched eggs)		0.92 (0.03)	0.95 (0.03)	0.78 (0.11)

Details are given in the **Methods**. Mean and SE are given.

\*The day 9 after hatching was considered the 'date of desertion' in biparental pairs.



**Figure 1.** Total feeding trips of males and females in biparental group before and after day 9 after hatching (■;  $N = 30$ ), the feeding trips in F-only group (□;  $N = 16$ ) and feeding trips in M-only group (■;  $N = 9$ ) before and after the desertion of their mates.

The different timing in brood desertion observed between males and females may have several explanations, most of which are not mutually exclusive. First, only females incubate and brood the chicks. Males may thus have earlier opportunities to abandon their broods to establish a second territory and find a second mate (Dawkins & Carlisle 1976, but see Székely et al. 1996). A removal experiment would be necessary to determine the benefit, in terms of remating opportunities, of desertion in the two sexes, as correlative evidence suggests that, at least in females, desertion opportunities seem to be limited by the number of available mates of the opposite sex (Pilastro et al. 2001). A second reason is that the reproductive effort of females before desertion is likely to be greater than that of males, considering that females produce and incubate the eggs. A second breeding attempt may consequently be more demanding for females than for males. A third possibility may be that the costs of desertion are higher for females than for males. Deserted males did not fully compensate for the absence of their mates so that female desertion resulted in a higher mortality rate of nestlings at male-only nests. Reducing the period of male-only parental care may increase the survival rate of the nestlings, thereby reducing the costs of deserting for the female. Furthermore, nestlings are usually brooded only by the female, so that early female desertion may have adverse effects on nestling survival if there are periods of low ambient temperatures, which are not unusual in the study area. The factors influencing desertion timing of the two sexes are likely to vary between species (and even populations) and this is probably the reason for the observed interspecific variation in the timing of desertion in relation to the sex of the parent (reviewed in Székely et al. 1996).

The quantity of food delivered by both males and females increased following desertion of their mates. This suggests that both males and females did not feed the nestlings at their maximum level before their mates deserted, possibly to force their partners to allocate more care to the offspring (Osorno & Székely 2004). Each parent has limited resources to invest in current reproduction so it is in their interests to reduce current investment to save

for future breeding opportunities, and to try to force its mate to invest more, resulting in a sexual conflict over parental investment (Parker 1979, 1985; Barta et al. 2002; McNamara et al. 2003). As a result of this conflict, in some circumstances one parent is expected to provide more care than two parents, in particular when the parental care costs of the two parents are different (McNamara et al. 2003). Our results are in partial agreement with these predictions. Indeed, deserted females provided a greater total amount of food than both parents together in biparental pairs and this is the first evidence that overcompensation occurs in nature (although an experimental desertion would be necessary to confirm this result).

Interestingly, deserted males did not fully compensate. One explanation of the different behaviour in the two sexes may be that initial asymmetries in costs and benefits of desertion and parental care lead to different compensation strategies. In particular, costs of reproduction are likely to be higher in females than males: nest building, egg production, egg and nestling incubation are performed by females, and males' contribution, until brood hatching, consists only in defending the nest site. Furthermore, egg laying and incubation have been suggested to be more energy demanding than rearing the nestlings (Nilsson & Raberg 2001). Consistently, females have been found to have a lower survival probability than males (Tavecchia et al. 2002). Indeed, the females' overcompensation could be the consequence to lower survival prospect in comparison with males. Thus, the observed difference in the parental resources allocated by males and females after mate's desertion could derive from different reproductive investment before desertion and to its consequences to survival prospects and to remating opportunities (Pilastro et al. 2001; Tavecchia et al. 2002).

Certainty of paternity could also explain the differences between the sexes in the compensation strategy. Extrapair paternity is common among birds (Garamszegi et al. 2005; Pitcher et al. 2005) and males are expected to provide less care when the certainty of paternity is low (Whittingham et al. 1992; Xia 1992; Lifjeld et al. 1998; Sheldon & Ellegren 1998; Neff & Gross 2001; but see Wagner et al. 1996; Kempenaers et al. 1998; Dickinson 2003; Bouwman et al. 2005). Extrapair paternity is rather high in this population (32% of the nestlings were not sired by the social father), although most of the extrapair nestlings were found in broods of polygynous males, whereas the present analysis was limited to monogamous males, for which extrapair paternity is much lower (50.5% in polygynous nests, 6.6% of extrapair young in monogamous nests; Pilastro et al. 2002). We also showed that there is a positive correlation between parents' provisioning rate to the nestlings and their survival rate, so that females pay a greater cost, in terms of reduced nestling survival, from desertion than males. In contrast, we did not observe an increased survival rate in female-only broods, as would have been expected given the higher-than-average feeding rate of deserted females. Mortality rate of nestlings in biparental and female-only broods, however, was very low and it is therefore possible that the benefits to the offspring of a high feeding rate include faster growth and/or postfledging survival, which have not been measured in this study.

In conclusion, our results support predictions of theoretical models of parental investment in which sexual conflict is accounted for (Parker 1985; McNamara et al. 2003), although males and females differed in their compensation strategy. A removal experiment would be necessary to exclude that males and females in the three groups differed intrinsically in terms of parental (or mating) quality, although the observation that the same individuals adopted different breeding strategies in different years seems to refute the hypothesis that some individuals tend to invest more in parental care (and are more often deserted by the mate), whereas others invest more in mate attraction (and desert the mate more often).

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