Should I stay or should I go? Female brood desertion and male counterstrategy in rock sparrows

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Brood desertion involves a series of interactions between the members of a pair. This process is likely to be based on either member's perception of the other's propensity to desert. We manipulated this perception in males by experimentally increasing female body mass in the rock sparrow (*Petronia petronia*), a species in which females can desert their first brood before the nestlings from the first brood leave the nest. We predicted that the male would either desert the brood first or stay even if this implied the risk of caring for the brood alone. We found that males mated to loaded females did not leave but stayed and significantly increased their courtship rate and mate guarding. Unexpectedly, they also increased their food provisioning to the nestlings, even though loaded females did not reduce their nestling-feeding rate. The increase in male feeding rate may be explained as a way for the male to reduce the female's propensity to switch mate and desert or to increase her propensity to copulate with the male to obtain paternity in her next brood. Altogether, our results demonstrate that the perception of the risk of being deserted by the female does not necessarily induce males to desert first, contrary to what is generally assumed by theoretical models. *Key words:* courtship, fertility cue, mate guarding, parental care, sexual conflict. *[Behav Ecol 16:435–441 (2005)]*

In birds, members of a breeding pair typically face a trade-off between seeking additional mating opportunities and spending time and energy caring for their present offspring (Trivers, 1972). This results in a conflict between the parents over the level of parental care (Clutton-Brock, 1991). Brood desertion by one of the parents can occur in species with biparental care if a single parent is capable of rearing its offspring alone (e.g., Beissinger and Snyder, 1987; Pilastro et al., 2001; Székely et al., 1999; Valera et al., 1997). Theoretical studies of brood desertion have revealed a series of factors that may influence this trade-off (Clutton-Brock, 1991; Maynard Smith, 1977; Székely et al., 1996; Webb et al., 2002). Empirical studies have confirmed that some of these factors, such as offspring quality (Erikstad et al., 1997), brood size (e.g., Armstrong and Robertson, 1988; Beissinger and Snyder, 1987), perceived paternity (see reviews by Arnold and Owens, 2002; Westneat and Sherman, 1993), and body condition of parents (Hörak et al., 1999), affect desertion decisions of the parents. Moreover, Székely et al. (1999) demonstrated that desertion is more likely to occur in one sex when its remating opportunities are high.

Most parental care models assume that each parent decides whether to care for the young or to desert them without any information about its partner's decisions (e.g., Balshine-Earn and Earn, 1997; Grafen and Sibly, 1978; Maynard Smith, 1977; Webb et al., 1999). However, this is unlikely to be the case in nature, and we may expect that even small changes in the behavior of one parent (e.g., nest attendance or feeding rate) may be used by the other parent to estimate the risk of being deserted. We would expect each member of the pair to try to anticipate its mate's decision, leaving the partner with the dilemma of whether to stay and care for the brood or to leave and lose all the offspring. Indeed, recent theoretical models analyzed brood desertion games in which each parent did not decide independently of the other (Barta et al., 2002; McNamara et al., 2002; Webb et al., 2002). For instance, Barta et al. (2002) investigated how the parents' condition should affect their deserting decision and predicted that females may strategically reduce their own energy reserves in order to force their mate to provide care. These decisions are expected to be also influenced by the strategies adopted by other individuals in the population (Barta et al., 2002; McNamara et al., 2002; Webb et al., 2002). Furthermore, desertion is likely to be a process in which each member of the pair tries to obtain information about its partner's physical or emotional state (see McNamara and Houston, 2002). Empirical studies are sparse, to date, on whether desertion decisions are really made on the basis of repeated interactions (and information exchange) between the partners (Valera et al., 1997) or on a "sealed bid" between the parents (Royle et al., 2002; Schwagmeyer et al., 2002).

The objective of our study was to examine how male rock sparrows (*Petronia petronia*) reacted to the perceived risk of being deserted by the female. In this species both sexes may desert the brood, usually from the time when the nestlings are at least 8 days old (Pilastro et al., 2001). Female brood desertion is observed only among double-brooding females, 50% of which desert their first brood to lay a new clutch in the nest of another male. A further 25% of double-brooding females do not desert but switch mate between the first and second brood (Pilastro et al., 2001), and the interval between the first and second clutch is so short that the female becomes fertile before the nestlings from the first brood are fledged. So, it is common to see males courting and copulating with their female while she is feeding the nestlings of their first nest (Pilastro et al., 2001, 2003). This suggests that the male may react to a greater perceived risk of being deserted by staying with and courting his female, instead of deserting first. However, about 20% of the males also desert the brood, and

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they may in principle leave first to stop females from deserting (Griggio, unpublished results).

We manipulated males' perception of the probability of being deserted by their mate by increasing the body mass of females, to simulate their readiness to lay a new clutch of eggs (Jones, 1986). We predicted that males that perceive an increased risk of being deserted may adopt one of two opposite counterstrategies: (1) leave the brood before the females do so or (2) stay and attempt to obtain as many copulations as possible from the female to increase their paternity in the second brood (see Pilastro et al., 2003). In the first case we expected to observe a decrease in the time spent by the male at the nest. In addition, these males may increase their territorial activity at a second nest site—a behavior that is often observed in paired males when the nestlings are close to fledging (Griggio and Pilastro, unpublished results). In the second case we expected the male to increase his sexual activity toward his female and to reduce the time spent at his second nest site. Males perform mate guarding to protect their paternity before and during laying of the first clutch (Pilastro et al., 2002), but some males appear to guard their mate also during the nestling stage (Pilastro et al., 2003). We therefore also expected, in the second case, the males of treated females to increase their mate-guarding effort.

METHODS

Study species

The rock sparrow is a monomorphic cavity-nesting passerine that breeds in middle latitudes of the Palearctic (Cramp and Perrins, 1994). The north Italian Alpine population (see Study Area and Field Methods) shows a wide array of mating patterns, including monogamy, polygyny, and sequential polyandry (Griggio et al., 2003b; Pilastro et al., 2001). Parents cooperate in feeding the young and defending the nest, but there is high variability in the parental effort of both sexes (Griggio et al., 2003a; Pilastro et al., 2003). Males decrease their food-provisioning rate as the nestlings age to the extent that at the end of the fledgling period most of the provisioning is performed by the female (Pilastro et al., 2003; this study). When males do not feed the young, they often remain at the nest and regularly court and copulate with their mate, probably because double-brooding females become fertile again before the young of the first brood fledge (Pilastro et al., 2003). About 20% of males desert the brood, in which case the females care for the fledglings alone (Griggio, unpublished results).

In this population an average of 32.0% of the chicks are not sired by the social father and 54.8% of the broods (mainly from polygynous males) contain at least one extrapair young (Pilastro et al., 2002). Polygynous males allocate less time to guard their mate during their mate's fertile period compared to monogamous males, so polygynous males are cuckolded more frequently than monogamous ones. These results suggest that, in this population of rock sparrow, there is a trade-off between attracting an additional mate and protecting paternity (Pilastro et al., 2002).

Study area and field methods

A rock sparrow population of about 18–20 breeding pairs in the Western Alps, Italy (1550–1800 m above sea level), has been studied since 1991 using nest-boxes and individual color ringing (Tavecchia et al., 2002). The nest-boxes were checked every 2–3 days during the entire breeding season to identify pair bonds and determine laying date (see Pilastro et al., 2001, for details). Observations for the present experiment were carried out on 31 breeding pairs during four breeding seasons (1998, $n = 10$; 1999, $n = 4$; 2000, $n = 2$; and 2002, $n = 15$), during the first hours of the morning (approximately 0600–1030 h), when the level of activity at the nest is highest. Only first broods of females paired to monogamous males ($n = 23$) or primary females paired to polygynous males ($n = 8$) were included. The proportion of polygynous males did not vary significantly between years (Fisher's Exact test, $p = .49$) and treatment groups (Fisher's Exact test, $p = .62$, see below). One of us (M.G.) performed all behavioral observations at each nest for 2 h per day in the two consecutive days before and after the day in which nestlings were 13 days old (± 1 day), for a total of 8 h of observation per nest. We recorded the time spent at the nest (min/h) by the male and the female, male territorial song (min singing/h), and male courtship rate (hereafter displays/h) in the 4 h of observation before and after treatment. The proportion of arrivals to and departures from the nest in which the female was followed by the male was used as a mate-guarding index (Pilastro et al., 2002). We also recorded the number of nestling-feeding trips per hour 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 and Perrins, 1994) with the length of the prey. Prey items, chiefly grasshoppers and caterpillars (Biddau et al., 1995), were assigned to three size classes: approximately 0.5, 1.0, and 1.5 bill lengths, following protocols commonly used in similar experiments (e.g., Schwagmeyer et al., 2002). Accordingly, we estimated the quantity of food delivered by the parents per hour of observation as the number of preys delivered multiplied by their size. In 2002, we also recorded the males' aggressive interactions with other males at the nest (number of aerial chases per hour) and the time spent by males on a secondary nest-box (min/h).

Experimental design

During the breeding season of 2002, we randomly assigned 15 breeding pairs to two experimental groups: control I and loaded. When the young were 13 ± 1 days old, we captured the females and measured their body mass to the nearest 0.1 g with a Pesola spring balance. Using an established procedure (Schwagmeyer et al., 2002; Witter et al., 1994), we increased the body mass of eight females (loaded group) by attaching to the base of the tail feathers four nontoxic "split-shot" fishing weights, each of which weighed 0.8 g (total load = 3.2 g). This procedure is reversible because the weights will be lost when the test females molt a few weeks later (Cramp and Perrins, 1994; Cuthill, 1991). The load used represented about 10% of the body mass of a rock sparrow female during this phase of the breeding season (mean body mass, 31.98 g $\pm$ 1.11 SD, $n = 10$), and corresponded to the body mass increase observed in rock sparrow females 1 week before egg laying (mean body mass, 34.43 g $\pm$ 1.40 SD, $n = 6$; difference between these two groups of females, Student's t test $t_{14} = 4.00$, $p = .001$). This difference in body mass is likely to be due to maturing eggs, given that a load of 3.2 g corresponds to somewhat more than the weight of one rock sparrow egg, which is on average 2.68 g $\pm$ 0.21 SD (range = 2.2–2.9 g, $n = 12$). In the second group ($n = 7$ pairs, control I) the females were captured and treated as above, the only difference being that we used four plastic beads with the same size and color as the experimental weights, but each weighing only 0.03 g (total load = 0.12 g). To verify whether female capture and manipulation had an effect per se on the behavior of the pair, we compared the behavior of these 15 pairs with that of further 16 pairs from previous years (1998, $n = 9$; 1999, $n = 5$; 2000, $n = 2$). The females of eight of these pairs were captured at the same nestling age as the loaded group, and released without further manipulation (control II), whereas the fourth group consisted of eight females that were

Table 1

Behavior of male and female rock sparrows at their nest before female manipulation according to the treatment group

	Loaded ($n = 8$)	Control I (plastic, $n = 7$)	Control II (captured, $n = 8$)	Control III (unmanipulated, $n = 8$)	Treatment		Year		Male mating status	
					$F_{2,24}$	p	$F_{2,24}$	p	$F_{1,24}$	p
Laying date	176.3 (2.05)	171.6 (3.06)	171.9 (1.97)	168.5 (1.24)	1.77	.19	2.37	.12	0.92	.35
Brood size (nestlings)	4.25 (0.16)	5.00 (0.38)	4.63 (0.46)	5.38 (0.32)	2.05	.15	0.18	.84	0.05	.82
Male at nest (min/h)	13.97 (4.30)	13.32 (5.43)	12.34 (2.71)	14.19 (2.85)	0.07	.93	0.82	.45	0.14	.72
Courtship rate (min/h)[a]	4.34 (2.20)	5.15 (1.35)	3.41 (1.30)	4.88 (1.30)	0.01	.99	0.02	.98	0.67	.42
Mate-guarding index[b]	0.05 (0.01)	0.10 (0.02)	0.10 (0.05)	0.08 (0.04)	0.32	.73	0.54	.59	0.03	.87
Territorial song (min/h)	12.03 (4.14)	10.25 (4.33)	7.81 (2.00)	8.94 (2.04)	0.22	.81	0.86	.44	0.04	.84
Female at nest (min/h)[c]	4.66 (1.09)	3.45 (0.39)	5.20 (1.36)	2.98 (0.57)	0.17	.85	2.80	.08	0.01	.91
Male feeding trips (trips/h)	0.19 (0.09)	0.71 (0.46)	0.13 (0.08)	0.16 (0.16)	1.20	.32	0.04	.96	0.18	.67
Female feeding trips (trips/h)	6.97 (0.51)	6.96 (0.42)	5.41 (0.49)	5.59 (0.37)	0.36	.70	1.13	.34	1.18	.29
Proportion of male feeding trips (%)	2.91 (1.46)	7.75 (5.06)	2.34 (1.64)	2.23 (2.23)	0.20	.82	0.35	.71	0.53	.47

[a] Once corrected for the time spent by the male at the nest, model, $F_{6,24} = 0.10$, $p = .99$; treatment, $F_{2,24} = 0.20$, $p = .82$; year, $F_{2,24} = 0.02$, $p = .98$; male status, $F_{1,24} = 0.01$, $p = .92$.

[b] ANOVA after arcsine square root transformation.

[c] ANOVA after log transformation.

Means and SE (in parentheses) are given. Statistics refer to ANOVA models in which brood characteristics and parent behavior were the dependent variables, and female treatment group, year, and male mating status were the factors. Interactions were all nonsignificant and removed from the model.

not captured while breeding and for which we carried out observations at the same nestling stages as the other three experimental groups (control III).

Statistical analyses were performed using SPSS 10.1. Data were transformed (log transformation and arcsine square root transformation), when appropriate. The behavior of the male and the females before and after treatment (or at the two correspondent nestling ages for the control III, unmanipulated group) was compared using repeated-measure ANOVA in which the behavior before and after were the dependent variables (within-subject factors) and treatment group (loaded, control I, control II, and control III), year, and male mating status (monogamous or polygynous) were the independent variables (between-subject factors). None of the higher order interaction terms were significant (all $p > .05$), and the final model therefore included only the within-subject and between-subject effects. In none of the analyses year and male mating status were significantly associated with the change of male and female behavior (see Results), and removing these two factors from the analyses gave similar results (results not shown). If not otherwise stated, means ± SE are given. All probabilities are two tailed.

Ethical note

Handling and ringing were performed under appropriate permits. We took care to keep the disturbance to the parents to a minimum. The female manipulation (ringing, where necessary, and lead and plastic application) lasted usually less than 5 min, and we avoided to visit the nest again on the day of capture. Loading apparently did not impair females because their nestling-feeding rate did not differ from that of the control females (see Results). All broods except one, which belonged to control II group and failed at a late stage, successfully fledged their young.

RESULTS

Characteristics of four experimental groups are given in Table 1. The four groups of nests did not differ significantly for any of

the brood traits and the two parents' behavior before female treatment. Female treatment did not affect the time spent by the female at the nest (within-subject effects, $F_{1,24} = 0.0004$, $p = .99$; treatment, $F_{2,24} = 0.22$, $p = .81$; year, $F_{2,24} = 3.16$, $p = .06$; male status, $F_{1,24} = 0.008$, $p = .93$, Table 1). On the other hand, male singing rate (territorial song) and time spent at nest decreased in the loaded group (Figure 1a,b), but the difference was not significant (territorial song: within-subject effects, $F_{1,24} = 0.60$, $p = .45$; treatment, $F_{2,24} = 1.54$, $p = .24$; year, $F_{2,24} = 0.17$, $p = .85$; male status, $F_{1,24} = 0.06$, $p = .81$; time at nest: within-subject effects, $F_{1,24} = 1.75$, $p = .20$; treatment, $F_{2,24} = 0.53$, $p = .60$; year, $F_{2,24} = 0.83$, $p = .45$; male status, $F_{1,24} = 0.07$, $p = .79$).

In contrast, males of the loaded group significantly increased their mate guarding (within-subject effects, $F_{1,24} = 4.06$, $p = .055$; treatment, $F_{2,24} = 10.88$, $p = .0004$; year, $F_{2,24} = 1.25$, $p = .30$; male status, $F_{1,24} = 0.22$, $p = .65$, Figure 1c) and showed an increase in courtship activity, although this difference was only marginally nonsignificant (within-subject effects, $F_{1,24} = 21.35$, $p < .0001$; treatment, $F_{2,24} = 2.80$, $p = .08$; year, $F_{2,24} = 4.79$, $p = .02$; male status, $F_{1,24} = 1.49$, $p = .23$). Once corrected for the time spent at the nest (males of the loaded group spent less time at the nest, although not significantly so), the increase of courtship rate of the loaded females' mates was highly significant (within-subject effects, $F_{1,24} = 7.24$, $p = .013$; treatment, $F_{2,24} = 5.86$, $p = .008$; year, $F_{2,24} = 0.95$, $p = .40$; male status, $F_{1,24} = 0.60$, $p = .46$, Figure 1d).

Before treatment, 3.68% ± 1.38 SE of the overall feeding trips to the nest were done by the male ($n = 31$). After the treatment, we observed a sharp increase in the proportion of feeding trips by the males of the loaded group compared to those of the three control groups (within-subject effects, $F_{1,24} = 0.01$, $p = .92$; treatment, $F_{2,24} = 6.14$, $p = .007$; year, $F_{2,24} = 0.002$, $p = .99$; male status, $F_{1,24} = 0.07$, $p = .80$, arcsine square root transformation, Figure 2a). This change was due to an increase in the absolute number of feeding trips done by the males of the loaded group (within-subject effects, $F_{1,24} = 0.01$, $p = .99$; treatment, $F_{2,24} = 4.82$, $p = .017$; year, $F_{2,24} = 0.02$, $p = .98$; male status, $F_{1,24} = 0.45$, $p = .51$, Figure 2b) because the number of feeding trips done by the females increased with
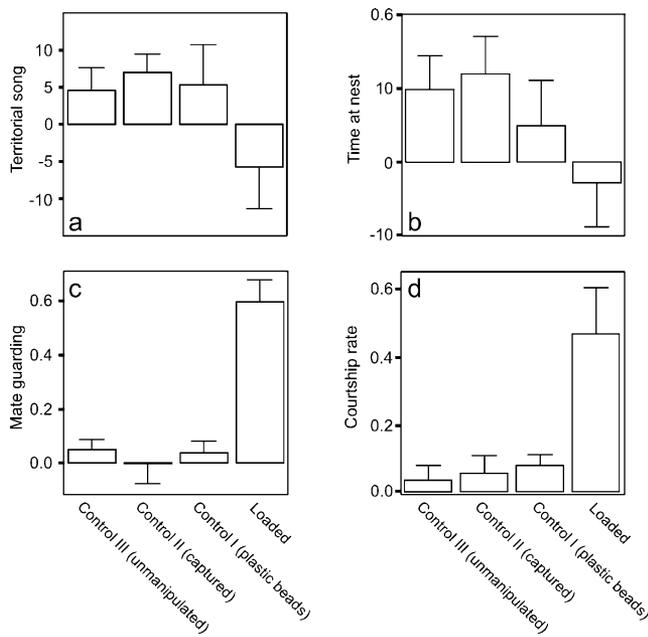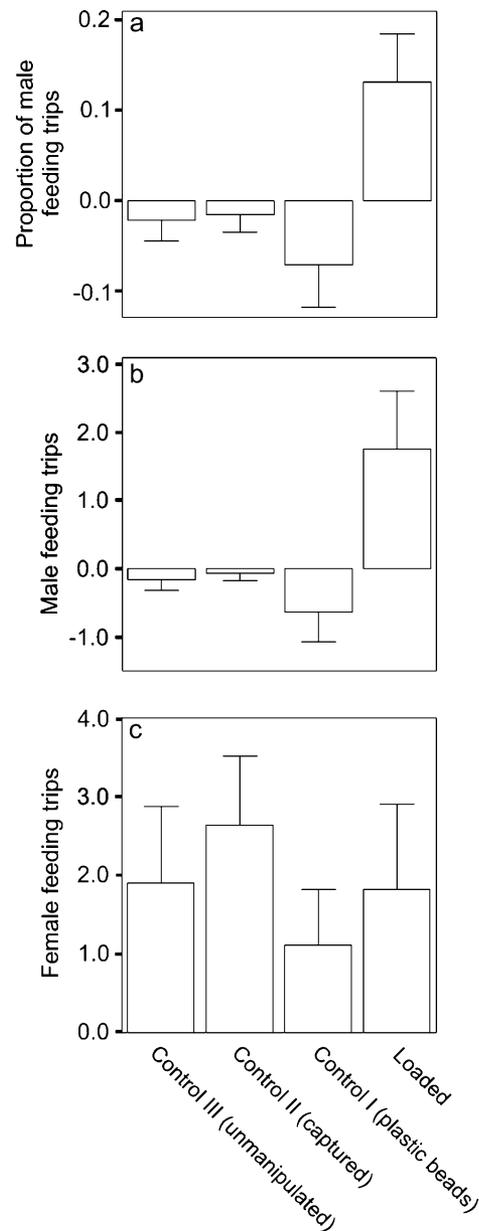
Figure 1
Changes in male behavior (after − before female manipulation, mean ± SE) according to female treatment group (loaded, $n = 8$; control I, $n = 7$; control II, $n = 8$; and control III, $n = 8$). (a) Territorial song (min singing/h), (b) time spent at the nest by the male (min/h), (c) mate-guarding index (proportion of the female departures from and arrivals to the nest in which she was followed by her mate), and (d) male courtship rate (number of courtship displays per minute spent by the male at the nest).

nestlings' age but did not change between groups (within-subject effects, $F_{1,24} = 9.17$, $p = .006$; treatment, $F_{2,24} = 0.23$, $p = .79$; year, $F_{2,24} = 2.62$, $p = .09$; male status, $F_{1,24} = 0.09$, $p = .77$, Figure 2c). As a result, the total number of nestling-feeding trips done by the two parents increased in the loaded group (change in the total number of feeding trips, after − before: control I, $+0.46 \pm 0.37$; control II, $+2.57 \pm 0.89$; control III, $+1.74 \pm 0.87$; loaded, $+3.56 \pm 1.23$; within-subject effects, $F_{1,24} = 9.72$, $p = .005$; treatment, $F_{2,24} = 2.83$, $p = .08$; year, $F_{2,24} = 2.54$, $p = .10$; male status, $F_{1,24} = 0.49$, $p = .49$). This difference became significant when the three control groups were pooled together (change in the total number of feeding trips, after − before: controls, $+1.64 \pm 0.46$; loaded, $+3.56 \pm 1.23$; within-subject effects, $F_{1,25} = 13.54$, $p = .001$; treatment [loaded versus controls], $F_{1,25} = 5.68$, $p = .02$; year, $F_{2,25} = 2.38$, $p = .09$; male status, $F_{1,25} = 0.01$, $p = .97$).

Similar results were obtained when we considered the quantity of food delivered by the parents to the nestlings: males of the loaded group also increased the quantity of food delivered (change in food delivered, after − before: control I, -0.95 ± 0.62; control II, -0.81 ± 0.50; control III, -0.41 ± 0.41; loaded, $+3.05 \pm 0.65$; within-subject effects, $F_{1,24} = 0.82$, $p = .38$; treatment, $F_{2,24} = 4.52$, $p = .022$; year, $F_{2,24} = 0.91$, $p = .42$; male status, $F_{1,24} = 0.45$, $p = .51$), whereas no difference was observed among females with respect to the experimental group (change in food delivered, after − before: control I, $+3.64 \pm 1.80$; control II, $+5.88 \pm 1.10$; control III, $+1.47 \pm 1.32$; loaded, $+4.81 \pm 1.62$; within-subject effects, $F_{1,24} = 27.88$, $p < .0001$; treatment, $F_{2,24} = 0.42$, $p = .67$; year, $F_{2,24} = 2.36$, $p = .12$; male status, $F_{1,24} = 2.98$, $p = .10$, after log transformation). Also when considering the total quantity of food delivered to the nestlings by the parents, the offspring of the loaded females received significantly more food than the

Figure 2
Changes in nestling-feeding rate (after − before female manipulation, mean ± SE) of male and female according to female treatment group (loaded, $n = 8$; control I, $n = 7$; control II, $n = 8$; and control III, $n = 8$). (a) Change in the proportion of feeding trips done by the male over the total number of feeding trips done by the two parents, (b) change in the number of feeding trips (trips/h) done by the male, and (c) change in the number of feeding trips (trips/h) done by the female.

controls (within-subject effects, $F_{1,25} = 23.99$, $p < .0001$; treatment [loaded versus controls], $F_{1,25} = 5.81$, $p = .024$; year, $F_{2,25} = 1.66$, $p = .20$; male status, $F_{1,25} = 2.49$, $p = .13$, data not shown).

Males that at the time of treatment were defending a second territory and were paired with loaded females reduced significantly the time spent on the second territory after the treatment (minutes per hour at the secondary nest after manipulation), compared to the control I group (loaded, $n = 5$: before manipulation, 9.70 ± 2.73 SE, after manipulation, 2.20 ± 1.29 SE; control I, $n = 6$: before manipulation,

10.75 ± 2.34 SE, after manipulation, 9.83 ± 2.34 SE; within-subject effects, $F_{1,12} = 10.22$, $p < .013$; treatment, $F_{1,12} = 7.15$, $p = .028$; male status, $F_{1,24} = 0.79$, $p = .40$, after log transformation; observations were available only for 2002). Furthermore, we observed an increase in aggressions by other males toward the males of the loaded group at their primary nest-box compared to the control I group (attacks/h, loaded, $n = 8$: before manipulation, 0.03 ± 0.03 SE, after manipulation, 1.00 ± 0.25 SE; control I, $n = 7$: before manipulation, 0.29 ± 0.29 SE, after manipulation, 0.29 ± 0.21 SE; within-subject effects, $F_{1,12} = 8.68$, $p < .012$; treatment, $F_{1,12} = 6.67$, $p = .024$; male status, $F_{1,24} = 2.13$, $p = .17$, after log transformation).

DISCUSSION

Our results clearly indicate that male rock sparrows perceived the change in body mass of their mates as an indication of their readiness to lay a second clutch and consequently to desert the offspring. We did not measure flight performance of females before and after loading, but similar experiments demonstrated that loading reduces a bird's flight performance, in particular its ascent rate (Jones, 1986; Witter et al., 1994). Males probably use this, and possibly other, flight cues to detect fertile females (Jones, 1986). Indeed, we observed an abrupt change in male mate-guarding intensity in the loaded group (in 64.7% ± 7.8 SE of their arrivals to and departures from the nest the loaded females were followed by their mate), which reached a value similar to those observed during the prelaying and laying phase (Pilastro et al., 2002), whereas in the three control groups the mate-guarding index remained very low (12.1% ± 2.5 SE, $n = 23$). Furthermore, males of the loaded group courted the female more frequently after female manipulation, a behavior that males are expected to adopt when their mate is fertile. In contrast, males did not differ among control groups for any of the behaviors measured, indicating that change in female body mass itself, and not the manipulation (i.e., capture and application of plastic beads on female), affected male behavior.

Theoretical models of parental conflict give increasing attention to the possibility that members of a pair do not behave independently (utilizing state-dependent or behavioral information). Dynamic models show that the decision of brood desertion may involve a series of interactions between pair members. These models assume that the male decides first and the female subsequently makes her choice on the basis of her partner's decision (Barta et al., 2002; McNamara and Houston, 2002; McNamara et al., 2002). To date, however, little information is available on whether desertion decisions are really made on the basis of repeated interactions (and information exchange) between the partners. One example comes from the penduline tit (*Remiz pendulinus*, Valera et al., 1997). In this species there is uniparental care, and the sex of the parent that deserts the nest depends on male detection of eggs during the laying period. Females bury the first eggs laid in nest material to avoid their detection. They are also aggressive toward their mates and prevent them from entering the nest during the laying period (Valera et al., 1997). If the female succeeds in concealing the clutch from the male, she deserts the clutch as soon as it is completed. Otherwise, males desert the nest as soon as the female starts to lay eggs (Valera et al., 1997). In rock sparrows, male response to the perceived possibility of being deserted by their mate was not to desert first. On the contrary, males remained and tried to obtain paternity in the second clutch potentially laid by their female by courting and closely guarding her, even if this would allow females to desert first and leave males to take complete care of the first brood. Consistently, males of the loaded group also reduced the time spent on a second nest-box. In our rock

sparrow population, about 75% of the double-brooding females switch mates between the first and second clutch and some of them (about 50% of double-brooding females) start to lay their second clutch when the nestlings from the first brood are still in the nest (Pilastro et al., 2001). If a female is close to laying a new clutch 4–6 days before the nestlings fledge (i.e., at the nestling age when we loaded the females), the risk for the male of being deserted is high.

Why do not all males desert the brood when the nestlings are old enough to be cared for by a single parent, which occurs at an age of approximately 8 days? One possible answer is that first broods are synchronized in this population (Matessi et al., unpublished results), the proportion of double-brooding females is only 20%, (Pilastro et al., 2001), and the remating opportunities for a male may therefore be low. Males may gain more from staying and copulating with their female, even if she may leave and lay her second clutch in the nest of another male. The question, in turn, becomes why females do not always desert their brood, leaving their mate with the duty of food provisioning, even when they do not lay a second brood (Pilastro et al., 2001). One possibility is that males, when caring alone, do not provide as much food as females. Indeed, females invest more in each brood (Griggio et al., 2003a) and have a lower annual survival rate than males (Tavecchia et al., 2002), a possible consequence of the females' greater parental effort. An additional reason why females desert only to lay a second clutch may be that extra-pair paternity is high in this population (Pilastro et al., 2002), and cuckolded males may not be ready to allocate much parental effort to unrelated nestlings. Whatever the reasons behind male and female brood desertion strategies, our experiments provide evidence that the decision process of brood desertion does involve interactions between the individuals of a pair (e.g., Barta et al., 2002; McNamara et al., 2002; Webb et al., 1999, 2002). More importantly, our results suggest that the outcome of these interactions is difficult to predict, and it is not necessarily true that one parent should desert first when perceiving the risk of being deserted by its mate. Our results suggest that even the sex that usually invests less in parental care (males) may respond to the risk of being deserted by staying and increasing its parental effort instead of leaving.

Our experiment also produced an unexpected result: males paired to the loaded females increased the rate of feeding trips to the nest and the quantity of food delivered to the nestlings. This increased parental effort by the males of the loaded group was not to compensate for the reduced effort of loaded females, as has been reported in other handicapping experiments (reviewed by Sanz et al., 2000). In contrast, loaded rock sparrow females actually increased their feeding rate, even if not significantly so, resulting in a significant increase of the total rate of food provisioning by the two parents. Why then should male rock sparrows increase their feeding rate even if loaded females did not decrease theirs? One possible explanation is that males increase their feeding rate to the nestlings as a reliable indication of their parental quality, to influence their female's decision on whether to remate with them for their next breeding attempt. Males may also trade food provisioning to the nestlings of the first brood with copulations, to obtain some paternity in the female's next brood, should she desert the current one. The extent of male parental care delivered to first-brood offspring may be used by the female to decide her subsequent mating fidelity, as suggested for the Savannah sparrow (*Passerculus sandwichensis*, Freeman-Gallant, 1996), and males may strategically adjust their parental effort according to the probability of remating with the same female (see Pampoulie et al., 2004, for a fish example). House sparrow (*Passer domesticus*) parents

show a pattern of response to female loading similar to that we found in the rock sparrow (Schwagmeyer et al., 2002) and consistent with this interpretation. Males mated to handicapped females significantly increased their food delivery rates compared to control males, despite no significant reduction in their mates' efforts; furthermore, these males did not reduce their contributions as their mates recovered from weighting. In the house sparrow, as in the rock sparrow, the interclutch time of double-brooding females can be very short (Summers-Smith, 1990). It may be therefore possible that male house sparrows also perceive female loading at the nestling stage as a cue of female readiness to lay a second clutch, and the reaction of males whose partners were handicapped may be related to female fertility. This would explain why the results of the house sparrows study are inconsistent with current models of negotiation between parents over the level of parental care (see Sanz et al., 2000).

An association between copulation and courtship feeding has been found in several birds (e.g., Lack, 1940; Velando, 2004; Wiggins and Morris, 1986), whereas in others the females trade extrapair copulations for food (e.g., Catry and Furness, 1997) or for nest material (e.g., Hunter and Davis, 1998). Experimental evidence that males may use nestling feeding as a courtship strategy, however, is still lacking. An experiment in which the level of parental care provided by the male is manipulated is warranted to test whether male nestling-feeding rate affects copulation rate in rock sparrows.

In conclusion, our experiments provide evidence that the decision process of brood desertion of one partner is influenced by the probability of being deserted by the other member of the pair, as suggested by recent models (e.g., Barta et al., 2002; McNamara et al., 2002; Webb et al., 2002) and empirical studies (e.g., Valera et al., 1997). In the rock sparrow, however, males facing the risk of being deserted stay, instead of leaving, and increase their parental effort even before the female deserts the brood, possibly because paternal care is a sexually selected trait in this species. Our results indicate that dynamics and outcomes of the conflict over parental care are more complex than generally assumed and therefore difficult to predict.

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