

Trade-off between sexual activities and parental care: an experimental test using handicapped mates

M. GRIGGIO ^{1,4}, T. MINGOZZI ², F. BORTOLIN ³ and A. PILASTRO ³

¹ *Konrad Lorenz Institut für Vergleichende Verhaltensforschung, Savoyenstr. 1a, 1160 Wien, Austria*

² *Dipartimento di Ecologia, Università della Calabria, Via P. Bucci, 87036 Rende (Cosenza), Italy*

³ *Dipartimento di Biologia, Università di Padova, Via U. Bassi 58/B, 35131 Padova, Italy*

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Electing to invest in parental care is an adaptive decision thought to involve a trade-off between remating and continuing parental effort. The rock sparrow, *Petronia petronia*, is an unusual species in which parental investment is highly variable and both sexes may desert the brood. Males contemporaneously engage in parental care, mate guarding, and courting their current or new females. In this study we experimentally handicapped male rock sparrows during the nestling period by increasing their body mass in order to study the effects on male behaviour and the female response. Handicapped males exhibited lower sexual activity than control males but handicapped males did not reduce their offspring feeding rates. Females with a handicapped partner significantly increased the number of sexual soliciting postures towards their mates compared to females paired with control males. The females' behaviour is probably a response to the sexual behaviour change of their partners. Our results suggest that with choices involving a trade-off between mating investment and parental investment, handicapped males chose the parental investment option.

KEY WORDS: parental effort, *Petronia petronia*, rock sparrow, sexual selection, soliciting posture.

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⁴ Corresponding author: Matteo Griggio (E-mail: m.griggio@klivv.oeaw.ac.at).

INTRODUCTION

Animals that provide postnatal care to their offspring are likely to need to trade off allocations of time among diverse activities (see CLUTTON-BROCK 1991). In particular, theory suggests that a trade-off exists between male parental effort and mate attraction effort (TRIVERS 1972). It is generally assumed that males would increase their reproductive success by mating with as many females as possible while reducing parental care to a minimum, because male reproductive success is more strongly correlated to mating opportunities than is that of females (BATEMAN 1948). Moreover, while females can be secure in the knowledge that supported offspring are also their biological offspring, males cannot. However, the existence of males of different species that provide care for the young at the cost of further mating opportunities indicates a net benefit for these males (CLUTTON-BROCK 1991). The optimal allocation of resources between sexual activities and parental care is influenced by life history traits, various ecological variables and the probability of finding a new partner (SZÉKELY et al. 1996, SZÉKELY & CUTHILL 2000, SEKI et al. 2007). Moreover, the optimal allocation varies between males because individual quality and age may influence reproductive investment (MCNAMARA & HOUSTON 1996, KOKKO 1997, BLEEKER et al. 2005).

In male birds, courtship behaviour and parental care are generally thought to be mutually exclusive, but male rock sparrows, *Petronia petronia*, simultaneously engage in courtship displays, directed at their partners or other females, and nestling care (PILASTRO et al. 2003; GRIGGIO et al. 2003a, 2005). Indeed, in this species parental care is highly variable among individuals: males may desert the brood, cooperate with the female in food provisioning, try to copulate with their current, or new, mates, or take sole care of the nestlings when the female deserts (GRIGGIO & PILASTRO 2007, GRIGGIO & VENUTO 2007). For this reason, this species is a good subject for considering the parental care allocation strategy adopted by the male. To investigate the trade-off between sexual activities and parental care, we handicapped fathers (attaching to the base of the tail feathers four "split-shot" fishing weights) during the parental-care period.

The optimal level of investment in the brood for each partner has been previously investigated in several handicapping experiments (e.g. small weight addition or feather clipping) (e.g. WHITTINGHAM et al. 1994, SCHWAGMEYER et al. 2002). Generally, the first result emerging from these manipulative studies was that handicapped individuals decreased their parental care. The response of the partners of the handicapped mates was, however, not so unidirectional, and at least three patterns appeared: no compensation, partial compensation and complete compensation (for a review see SANZ et al. 2000).

In a previous experimental study on rock sparrows, the female's body mass was increased in order to manipulate the male's perception of the female's readiness to lay a second clutch and consequently to desert the brood (GRIGGIO et al. 2005). Males mated to heavier females did not leave the nest but remained, increasing both their sexual activity and their parental care, even though loaded females did not significantly reduce their nestling feeding rate. This unexpected increase in food provisioning was explained as a pos-

sible way for males to signal their paternal ability to the female in order to mate with her in the subsequent breeding attempt, or to use nestling feeding as a courtship strategy (trade food for copulations).

Our paper has two aims: (i) to understand the trade-off between parental investment and mating investment, and (ii) to study the response of females to changes in their partners' investment strategy, i.e., their behaviour. In particular, we want to learn whether handicapped males are capable of contemporaneously maintaining a high level of investment in both sexual activities and parental care. If not, it is likely that handicapped males will decrease their parental investment, maintaining — or even elevating — their sexual activities.

METHODS

Study species

The rock sparrow is a passerine with a variable mating system: in a north Italian Alpine population about 1/3 of the males are polygamous and desertion of the brood by both females and males occurs (GRIGGIO & PILASTRO 2007). Usually, the rock sparrow exhibits a biparental care system in which males decrease their food provisioning rate as the nestlings age (nestlings stay in the nest for about 18 days after hatching, GRIGGIO et al. 2003a), to the extent that during the last few days most of the provisioning is performed by the female. Females take complete care of broods in the face of male abandonment (about 25% of fathers desert the brood, GRIGGIO et al. 2003b). Less frequently, some males may take exclusive care of the nestlings when their females desert and begin to lay a second clutch (about 10% of females that successfully raised their first brood, PILASTRO et al. 2001). In still other cases, males do not feed the young but remain at the nest courting, and trying to copulate with their mate (GRIGGIO et al. 2005). Some males defend a second nest-box and try to attract a second female. When the nestlings are close to fledging these males increase their territorial activity at the second nest site (GRIGGIO et al. 2005).

Experimental design: handicapping males

During the breeding seasons of 2003 ($N = 9$ pairs) and 2004 ($N = 14$ pairs), we randomly assigned 23 pairs to two experimental groups: control ($N = 11$) and loaded ($N = 12$). We conducted the experiment in two neighbouring study areas. The first study area was located between 1550 and 1800 m a.s.l. in the higher Susa valley, Western Italian Alps (Italian population). The population includes about 18-20 breeding pairs per year (GRIGGIO et al. 2005). A part of this experiment ($n = 9$) was carried out in a second study area (French population) near the French-Italian border (for more details see MATESSI et al. 2005). This second population consists of about 30 breeding pairs per year. We recorded pair bonds, laying date, brood size and fledging success (no. young fledged/no. eggs hatched). Nest boxes were designed to also work, when necessary, as trapping devices. Trapped adults were individually colour-ringed and body mass (to the nearest 0.1 g), tarsus and wing length (to the nearest 0.1 mm) were measured (SVENSSON 1992). Only the first broods of monogamous males ($N = 17$) or primary broods of polygynous males ($N = 6$) were included in the study. Using the same procedure as GRIGGIO et al. (2005), when the young were 5 ± 1 days old, we increased the body mass

of males by attaching to the base of the tail feathers four non-toxic “split-shot” fishing weights (total load = 3.2 g). The load used represents about 10% of the body mass of male rock sparrows in the breeding season (GRIGGIO et al. 2005). In the control group, males were captured and treated as above, but in this case we used four plastic beads similar to the experimental weights but weighing in total only 0.12 g.

Behavioural observations

Birds were observed, and their behaviour recorded, for 1 hr the day before males were captured and manipulated. Then, from the day after the capture date, we performed 2 hr of behavioural observations every 2-3 days (until the young fledged). The mean observation time per nest over the whole experiment was 10.65 ± 0.22 hr (± 1 SE; range 9-13.50 hr, $N = 23$), for a total of 245 hr.

We observed the nest entrance with 20-60 × spotting scopes while sitting in the open, 30–50 m from the nest. Each nest was observed during the morning and late afternoon (between 0600-1030 and between 1530-1900 hr), when the level of activity at the nest is highest (GRIGGIO et al. 2005). We recorded the number of feeding trips to the nest per hour by both parents (feeding trips/hr). The dimensions of the prey were also recorded. Prey items were assigned to three size classes: approximately 0.5, 1.0 and 1.5 (or more) times the bill length, following the protocol used in GRIGGIO et al. (2005). We calculated the quantity of food delivered by the parents per hour of observation by multiplying the number of prey delivered by their size (quantity of food/hr). Moreover, we recorded the faeces removal trips per hour. We also recorded the time spent at the nest (min/hr) by the male and female; male courtship rate, measured as the time spent performing courtship displays (males display their yellow breast patch and/or tail towards females with ruffled plumage), hereafter displays/hr; the number of copulations per hour; and compiled a mate guarding index (the proportion of arrivals to, and departures from, the nest in which the female was followed by the mate). We recorded the number of times in which females assumed the soliciting posture (a horizontal posture with plumage ruffled and wings shivering, see also CRAMP & PERRINS 1994) showing their readiness to copulate (hereafter soliciting/hr). Lastly, for the Italian population we recorded the time spent by males on a secondary nest-box (min/hr).

Statistical procedures

The effects of manipulation on provisioning rate (feeding trips, amount of food), faeces removal trips, mate guarding, and presence at the nest of both parents were analysed using a repeated-measures ANOVA in which the behaviour before and after manipulation were the dependent variables (within-subject factors) and treatment group, year and site (Italian or French population) were the independent variables. No copulations, female soliciting postures or male courtship displays were observed before the treatment, so ANOVA models were used, in which these behaviours were the dependent variables and treatment group, year, and site were the independent variables. All statistical analyses were performed by using SPSS 13 (NORUSIS 1993). All probabilities were two tailed and all means are reported \pm SE.

Ethical note

Handling and ringing were performed with the appropriate permits and we took care to keep the disturbance to the parents and nestlings to a minimum. Manipulation

of the males (ringing, where necessary, and lead and plastic application) usually lasted 5 min and we avoided visiting the nest again on the day of capture. Loading did not have any apparent adverse effects on either the nestlings themselves or on their provisioning (see results below).

RESULTS

We did not detect any differences between the two groups of males in weight, wing or tarsus length (Student *t*-test, all $P > 0.42$). There were no significant differences in brood traits between the two groups of nests, nor in the (parental) behaviour of males and females, before the treatments (Table 1, 2). The treatment did not significantly affect the time spent by the male or by the female at the nest (Table 2). After the treatment, we did not detect any differences between the two groups in terms of maternal effort in either the number of feeding trips or in the quantity of food delivered by the females to the nestlings (Table 2). After the treatment, loaded males performed a comparable number of feeding trips to those of the control group males (Table 2). The quantity of food delivered by the males to the nestlings after the treatment also did not differ significantly between groups (Table 2). Loaded males courted their mates significantly less than did control males (Table 1). Moreover, females paired with loaded males assumed a significantly higher number of soliciting postures compared to females paired with control males (Table

Table 1.

Brood traits and sexual behaviour of male and female rock sparrows at their nest after male manipulation according to the treatment group.

	Loaded (<i>N</i> = 12)	Control (<i>N</i> = 11)	Treatment		Year		Site	
			F	<i>P</i>	F	<i>P</i>	F	<i>P</i>
Laying date	161.9 (1.66)	163.9 (2.04)	0.48	.49	0.03	.86	0.92	.35
Brood size (no. nestlings)	5.17 (0.30)	5.09 (0.25)	0.08	.78	1.86	.19	0.03	.87
Copulation rate*	0.34 (0.16)	0.04 (0.03)	3.82	.07	2.13	.16	2.57	.13
Female soliciting rate*	0.16 (0.06)	0.009 (0.005)	6.74	.02	3.11	.09	3.09	.09
Male courtship rate*	0.03 (0.007)	0.08 (0.01)	10.44	.004	0.04	.84	0.56	.47

Details are given in the methods. Means and (SE) are given. Statistics refer to ANOVA models in which brood characteristics and sexual behaviour were the dependent variables, and male treatment group, year and site were the between subject factors. Interactions were all nonsignificant.

*Corrected for the time spent by the male and the female at the nest.

Table 2.

Male and female behaviour at their nests, before and after male manipulation. Data is presented according to treatment group. Details are given in the methods. Means and (SE) are given. Statistics refer to a repeated-measure ANOVA in which the behaviour before and after were the dependent variables, and male treatment group, year and site were the between subject factors.

	Loaded (N = 12)		Control (N = 11)		Within- subject effects		Treatment		Year		Site	
	Before	After	Before	After	F	P	F	P	F	P	F	P
Male at nest (min/ hr)	5.17 (1.23)	8.92 (1.03)	4.91 (1.08)	11.75 (2.22)	5.41	.03	0.31	.59	3.91	.06	2.64	.12
Female at nest (min/hr)	11.44 (3.38)	6.29 (0.80)	6.82 (2.54)	6.25 (0.57)	6.42	.02	0.69	.42	2.76	.12	2.28	.15
Mate guarding index*	0.02 (0.02)	0.05 (0.04)	0.02 (0.01)	0.07 (0.05)	4.05	.06	0.76	.39	3.78	.07	1.69	.21
Male feeding trips (trips/hr)	3.04 (0.50)	1.24 (0.53)	3.54 (0.51)	0.99 (0.25)	31.95	.001	1.11	.31	5.44	.03	5.45	.03
Female feeding trips (trips/hr)	4.37 (0.59)	5.47 (0.45)	3.27 (0.60)	5.81 (0.65)	11.29	.004	3.01	.10	0.13	.73	0.006	.94
Male quantity of food /hr	3.62 (0.59)	1.89 (0.96)	3.64 (1.07)	1.26 (0.34)	12.63	.003	1.98	.18	6.25	.02	7.34	.02
Female quantity of food /hr	5.02 (0.67)	8.66 (0.66)	4.22 (0.74)	9.72 (0.69)	57.44	.001	4.37	.06	0.001	.99	0.13	.73
Male faeces removal (trips/hr)	0.25 (0.13)	0.39 (0.25)	0.27 (0.14)	0.1 (0.19)	0.09	.76	3.64	.08	0.76	.39	.06	.80
Female faeces removal (trips/hr)	1.92 (0.47)	2.83 (0.30)	1.46 (0.41)	3.07 (0.26)	8.41	.01	0.67	.43	9.26	.008	1.72	.21

* Proportion of all flights, arrivals to and departures from the nest-box, initiated by the female, that were followed by the pair male.

1). The number of copulations was higher in the loaded group, but the difference was not significant (Table 1). Lastly, the manipulated males in the Italian population that at the time of treatment were defending a second nest significantly reduced the time spent at the second nest after their manipulation ($N = 5$, before manipulation: 3.90 ± 1.25 min; after manipulation: 0.55 ± 0.76 min), while the control males did not ($N = 6$, before manipulation: 7.08 ± 2.68 min

; after manipulation: 10.71 ± 4.96 min; within-subject effects: $F_{1,9} = 0.031$, $P = 0.86$; treatment: $F_{1,9} = 5.99$, $P = 0.037$; year: $F_{1,9} = 0.028$, $P = 0.87$).

DISCUSSION

Handicapped males decreased their sexual activity compared to control males somewhat, while their feeding rates were maintained at the same level. Females with a handicapped partner significantly increased their number of soliciting postures relative to females paired with control males. The females' behaviour is probably a response to the sexual behaviour change of their partners. Moreover, Italian loaded males that at the time of treatment were defending a second nest significantly reduced the time spent on the second territory after the treatment compared to control males. Thus, our results seem to suggest that with choices involving a trade-off between sexual behaviour and parental investment, handicapped males chose the parental investment option.

A previous study on rock sparrows experimentally increased female body mass (GRIGGIO et al. 2005). In that study it was observed that males mated to loaded females significantly increased their courtship rate and mate guarding but, unexpectedly, also increased their food provisioning to the nestlings, even though the manipulation did not significantly affect the female's behaviour. The sexual interest of males paired with loaded females clearly indicated that male rock sparrows perceived the change in body mass of their mates as an indication of their readiness to lay a second clutch. Moreover, it was proposed that the increase in male provisioning rate may be a way for the male to reduce the female's inclination to desert him or to increase her propensity to copulate with him and thus to obtain paternity in her next brood (GRIGGIO et al. 2005).

The results presented here, together with the previous study (GRIGGIO et al. 2005), differ from other studies because the reactions of individuals whose partner was handicapped were apparently paradoxical: they increased sexual behaviours. One can argue that the males' reaction is a counterstrategy to the perception of the risk of being deserted by the female (see above). But why did females paired with handicapped males show an increase in their number of copulation solicitations? One possible answer is that females increased their copulatory propensity to maintain elevated sexual interactions to strengthen the pair bond. In other words, it seems that females paired with handicapped males tried to increase the sexual interest of their apparently unmotivated partners; probably to influence their male's decision on whether or not to stay with them. Males may respond to the copulatory propensity of their females by staying and helping females with parental care. In turn, males may exchange parental care of the nestlings of the first brood with copulations, to obtain some paternity in the females' next brood (see also GRIGGIO et al. 2005). This interesting hypothesis calls for further experiments directed specifically to this question.

Another question arises from our studies on the rock sparrow (here, and GRIGGIO et al. 2005): is the prestige of male rock sparrows increased (and thereby their direct fitness) by exhibiting good parental skills? Females can use various cues to assess the quality of potential mates (SUNDBERG & LARSSON

1994, PENTERIANI et al. 2002, for a review see ANDERSSON & SIMMONS 2006). As are other behaviours, such as singing or nest building, parental performance could also be under sexual selection pressure (LOTEM et al. 1999, DANCHIN et al. 2004). If parental care is an element of mate selection, we can expect that, at least in some circumstances, the signal of care quality will evolve: the investment in current reproduction could function as a cue in mate choice for the next breeding attempt (e.g. ZAHAVI 1975, WAGNER et al. 1996, LOTEM et al. 1999). Recently, in a laboratory experiment, it was found that a fish, the male sand goby, *Pomatoschistus minutus*, fanned longer and did more nest construction in the presence of females, than did males without the visual stimulus of a female. These results suggest that males change their parental care behaviour in response to perceived mating opportunities (PAMPOULIE et al. 2004). It is clear that male parental care has a sexually selected signalling component, at least in this fish, but this hypothesis could also explain the parental performance of handicapped rock sparrows. Female rock sparrows have better chances to breed than do males: the number of available unmated territorial males is always higher than that of unmated females (PILASTRO et al. 2002, GRIGGIO et al. 2003b). Thus, the males' need to signal their quality in order to attract or maintain a mate, should be greater than that of females, as seems to be the case in our population.

In summary, our results suggest that with choices involving the trade-off between female attraction and parental investment, handicapped males chose the paternal investment option. However, evidence from rock sparrows, reported here and previously (GRIGGIO et al. 2005), seems to support the hypothesis that male parental care should be under sexual selection and so the trade-off may be smaller than it initially appears, although other studies are necessary to clarify our understanding of the possible signalling component of male parental care.

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