



Male rock sparrows adjust their breeding strategy according to female ornamentation: parental or mating investment?

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We investigated the relations between female quality and ornamentation and between male breeding investment and female ornamentation in the rock sparrow, *Petronia petronia*, a passerine in which both sexes have a yellow breast patch. Breast patch size in females was positively correlated with body mass and breeding status; double-brooding and primary females of polygynous males had a larger patch, and patch size could therefore be an indicator of female phenotypic quality. We conducted a field experiment to test whether males allocate their parental effort in relation to female quality, as predicted by the differential allocation hypothesis. We increased and reduced the ornament sizes of paired females and compared the behaviour of their males before and after manipulation. Frequency of brood feeding by the male was not affected by female ornament manipulation; there was a nonsignificant trend for females with enlarged ornaments, contrary to predictions, to increase their feeding rate. Reducing female ornaments resulted in a decrease in male nest attendance, a measure of passive brood defence, whereas enlarging the ornament had no effect. Males concurrently reduced their territorial (song output) and sexual activity (courtship and copulation). The reduction in sexual activity suggests that males may have changed their nest attendance in response to their mate's re-nesting probability. Whatever the interpretation, these results provide some of the first evidence that not only female, but also male, birds change breeding strategy according to their mate's phenotype in the wild.

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Individuals of species with biparental care can enhance their fitness by strategically varying their mating and parental investment in the current reproductive attempt in response to their own relative mating desirability and that of their mate. This is known as the differential allocation hypothesis (DAH, [Burley 1986](#)). A relation between one's breeding investment and attractiveness of one's mate is possible because, if mate attractiveness contributes to offspring fitness (i.e. viability or attractiveness), it will consequently influence the value of the breeding attempt with that mate. Because the quality of potential mates can vary, selection should favour individuals that allocate more resources when paired with an attractive mate ([Burley 1986, 1988](#); [Sheldon 2000](#)). Since its original formulation, the DAH has been tested and supported in a number of taxa possessing different attractiveness traits and levels of parental care (reviewed in [Sheldon 2000](#)), but the studies have almost exclusively

related female breeding investment to male attractiveness. Differential allocation of parental investment by males according to female attractiveness was tested in [Burley's \(1988\)](#) original experiments with captive zebra finches, *Taeniopygia guttata*. Male zebra finches paired with females manipulated to be more attractive had higher relative parental expenditure than males paired with unattractive females. The manipulated trait was an artificial one, leg ring colour ([Burley 1988](#)).

Mating investment (of which mate choice is a component) by males has been shown to vary in relation to female ornamentation in a number of studies on birds, most of which were either aviary based or nonexperimental ([Amundsen 2000](#) and references therein). An aviary-based test of male choice ([Jones et al. 2001](#)) showed that male zebra finches can detect and show a preference for more fertile females. The results of such experiments, however, can be difficult to generalize to the wild. An example of an experimental field study is [Jones & Hunter's \(1993, 1999\)](#) work on the crested auklet, *Aethia cristatella*. They manipulated crest size in mounts of males and females and found that both sexes displayed more in front of opposite-sex mounts with large crests.

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Nevertheless, as well as mating investment, males of many bird species can be expected to adjust their parental investment when female quality is highly variable and, if the mating system is predominantly monogamous, the quality of both parents is crucial to offspring survival (Amundsen 2000). Field evidence that male birds strategically allocate their parental investment in relation to female phenotype is still lacking (Sheldon 2000).

After the eggs have been laid, parental investment is essentially composed of brood care (incubation, brooding and feeding of offspring) and nest defence, which ranges from simple nest attendance (passive brood defence) to fending off predators and competitors (active brood defence; Clutton-Brock 1991; Webster 1991; Owens & Bennett 1994; Reynolds & Székely 1997; Møller & Thornhill 1998). Both brood care and nest defence are costly for adults (Owens & Bennett 1994). Nest attendance can be costly in terms of lost remating opportunities for polygamous species or species with multiple broods within a season. Therefore, optimal allocation of such resources should be favoured by selection. The DAH predicts that even where these two components of parental care are not equally divided between the sexes (e.g. only females feed the offspring), males should invest in their portion of parental care differentially according to the value of the current brood, measured in terms of mate attractiveness (Burley 1988).

We investigated the relation between male breeding strategy and a female ornament, a yellow breast patch, in a passerine species, the rock sparrow, *Petronia petronia*. We manipulated the size of the yellow patch of breeding females in the wild and measured their male's response in terms of two forms of parental investment, offspring feeding and nest attendance, and of two forms of mating investment, territorial and courtship behaviour. We predicted from the DAH that males paired with females of increased apparent quality should increase at least one of the two types of investment.

METHODS

Study Species

The rock sparrow is a monomorphic species. It breeds in middle latitudes of the Palaearctic in warm temperate Mediterranean, steppe and desert climates, but in some regions favours alpine meadows, grassy or shrubby riversides and human settlements. It usually breeds in small, loose colonies. The north Italian alpine population, in the higher Susa valley, is the subject of a long-term ecology and conservation study (Mingozzi et al. 1994; Biddau & Mingozzi 1995; Tavecchia et al. 2002). This population presents a wide array of mating patterns, including monogamy, polygyny and sequential polyandry; males and females can cooperate in parental care or can desert the brood (Mingozzi et al. 1994; Pilastro et al. 2001). Males and females cooperate in feeding the young during the first week after hatching but male behaviour subsequently varies. The male can stay and feed the young (usually at a lower rate than the female), attend the nest without feeding the young, or can desert the nest

altogether and look for a new mate (A. Pilastro & M. Griggio, unpublished data). Females can also desert the first brood and lay a new clutch in the nest of another male (Pilastro et al. 2001). Males and females have a yellow patch on the upper breast, which is used in courtship displays and is variable in size in both sexes (Wilson 1994). The patch has a roughly trapezoid shape, with the base slightly larger than the upper side.

General Field Methods

The study area was between 1550 and 1800 m above sea level in the higher Susa valley, western Italian Alps. A total of 39 nestboxes (11 × 12 cm and 50 cm long) were set up in two small villages. The distance between the two villages was about 2 km. Nestboxes were also designed to work, when necessary, as trapping devices, and adults trapped within the nestboxes were colour ringed. The population included about 20 breeding pairs. From 1990, we censused all the nestboxes every second day from the onset of the breeding season (late May–early June). We recorded pair bonds, laying date, clutch size, hatching and fledging dates. More details of the methods are given in Pilastro et al. (2001, 2002). We measured the size of the breast patch of adults by placing a strip of transparent acetate over the breast, holding the bird on its back, with bill and head perpendicular to the body, and drawing the contour of the yellow area. We then measured the major and minor axes of the outline, with dial callipers (± 0.1 mm). This method produces repeatable measures of patch size (Pilastro et al. 2002). From preliminary observations we found that the breast patch varied mostly in the major axis (width). We therefore used width as an index of patch size. We investigated patch size variation and its relation to female phenotypic quality in 90 birds captured in 1997–1999. For these birds, we evaluated the relation between patch size and age, body mass, breeding status (nonbreeder, monogamous, primary or secondary female of polygynous male) and success (one or two successful broods). Because some individuals were recaptured in different years, the sample sizes differ according to the analysis. This sample did not include the individuals involved in the patch size manipulation experiment (see below).

Experimental Design

We manipulated patch sizes during two breeding seasons, 1999 and 2000. We grouped 24 nesting pairs into eight trios with young of similar age (± 2 days) and, within a trio, randomly assigned each female to one of three groups: control (female captured and released), reduced (patch width decreased) and enlarged (patch width increased). When young were 12–14 days old and concurrently with their ringing, we captured the female in the nestbox and measured the patch. We then enlarged the patch in eight females by dyeing the feathers on either side of the patch with an alcoholic 1% solution of picric acid. We added picric acid until the breast feathers matched, to the human eye, the colour of the feathers of

the patch. We reduced the patch, in the other eight females, by painting the left and right sides of the patch with waterproof brown acrylic tempera (UniPOSCA PC-5M B, Mitsubishi Pencil Ltd, Tokyo, Japan), which matched the colour of the breast feathers and hid the yellow of the patch. Before manipulation, average patch width \pm SD was 13.1 ± 2.5 mm ($N=8$), 12.9 ± 2.5 mm ($N=7$) and 12.1 ± 1.9 mm ($N=8$), for the enlarged, reduced and control females, respectively (ANOVA: $F_{2,20}=0.42$, $P=0.67$). In one female from the reduced group the patch was not measured before manipulation, giving unbalanced sample sizes for this test. In the reduced group, patch width after manipulation was 6.4 ± 3.4 mm (range 3–10, mean reduction -51.3%). In the enlarged group, patch width after manipulation was 14.7 ± 2.1 mm (range 13–17, mean increase $+21.2\%$). The extent of patch manipulation was reasonable given the mean and natural range of female patch sizes (12.3 ± 2.76 mm, range 5.7–19.2). We used only first broods of females paired with monogamous males or primary females paired with polygynous males.

One of us (M.G.) carried out all the behavioural observations and was blind to the treatment to which each female had been assigned. Each nest was observed for 2 h from a distance of about 50 m, using a spotting telescope ($30\times$ magnification), on 2 consecutive days before and 2 after the day of treatment (in total 8 h of observation/nest). Observations were done in the morning, when the activity at the nest is highest (0600–1030 hours). We recorded the time spent by both the male and the female at the nest or within 10 m from it (nest attendance), the number of songs given by the male (song rate) the number of the male's courtship displays (display rate) and the number of times he attempted or succeeded in copulating (number of copulations). We calculated a mate-guarding index as the proportion of arrivals to and departures from the nest in which the male followed the female. We also recorded the number of feeding trips to the nest by the two parents. Although number of feeding trips is not an optimal measure of feeding investment, other more accurate measures are more invasive and would have required frequent chick manipulations, which we wanted to avoid. In the analysis, we pooled the 2 observation days before and after manipulation, and all behaviours are expressed as mean/h. We calculated the change in male and female behaviour after the treatment by subtracting the measure of their behaviour before treatment from that after treatment.

Statistical analyses were performed with SPSS 9.0 (Norušis 1993). All probabilities are two tailed. Data were checked for normality and homogeneity of variances, where necessary. Where these assumptions were not met even after transformation, we used nonparametric statistics (Zar 1974). In the latter case, exact probabilities are given (SPSS '/Method/Exact' procedure, Norušis 1993).

Ethical Note

All handling, ringing and plumage manipulations were 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 manipulated individuals and their offspring did not suffer any detectable reduction in welfare and survival. All offspring fledged normally and the adults were seen on the study site repeatedly after the experiment.

RESULTS

Patch Size and Female Quality

Breast patch width differed between the sexes: males had larger yellow patches than females, although with largely overlapping distributions (males: $\bar{X} \pm SE=13.9 \pm 2.38$ mm, range 8.1–19.2, $N=43$; females: 12.3 ± 2.76 mm, range 5.7–19.2, $N=47$; Student's t test: $t_{88}=3.03$, $P=0.003$). Within the sexes, patch size did not differ between first-year and older birds (females: first year: 11.5 ± 1.23 mm, $N=7$; second or older: 12.4 ± 0.49 mm, $N=40$; $t_{30}=0.44$, $P=0.39$; males: first year: 14.3 ± 0.78 mm, $N=9$; second or older: 13.9 ± 0.44 mm, $N=34$; $t_{36}=0.81$, $P=0.42$). Patch size did not increase with age within individuals (mean change: $+5.8 \pm 4.4\%$; one-sample t test: $t_{18}=1.30$, $P=0.21$). Non-breeding individuals had smaller patches (9.4 ± 0.55 mm, $N=10$) than both breeding males and females (Scheffé post hoc comparisons: $F_{2,97}=14.23$, $P<0.001$). Among females paired with polygynous males, primary females had a larger patch ($\bar{X} \pm SD=12.4 \pm 1.69$ mm) than secondary females (10.9 ± 1.18 mm; paired t test: $t_{10}=2.55$, $P=0.029$). Finally, patch size was positively correlated with body mass in females (Spearman rank correlation: $r_s=0.32$, $N=39$, $P=0.04$) and double-brooding females had a larger patch than single-brooding females (single-brooding: $\bar{X} \pm SE=11.6 \pm 1.90$ mm, $N=31$; double-brooding: 12.7 ± 1.87 mm, $N=13$; Mann-Whitney U test: $U=122$, $P=0.04$). We performed a sequential Bonferroni test (Rice 1989) on all the P values obtained ($k=8$), resulting in all $P<0.029$ remaining significant at the $\alpha=0.05$ level.

Male Strategy and Female Patch Size

The breast patch size of males did not differ significantly between groups (reduced: $\bar{X} \pm SE=14.9 \pm 3.0$ mm; enlarged: 15.5 ± 1.9 mm; control: 14.7 ± 1.3 mm; $F_{2,14}=0.27$, NS). Before the manipulation, males of the three groups attended the nest, courted the female, fed the young and produced territorial song at the same rate (Kruskal-Wallis ANOVAs: all $P>0.1$, Table 1).

The change in male parental behaviour (after minus before patch manipulation; Fig. 1) differed significantly between treatments for male nest attendance (Kruskal-Wallis ANOVA: $\chi^2_{2,23}=9.95$, $P=0.003$), but not for male feeding rate (trips/h; $\chi^2_{2,23}=1.73$, $P=0.44$). There was no significant variation in female nest attendance ($\chi^2_{2,23}=2.9$, $P=0.24$). Females of the reduced group slightly decreased, and females of the enlarged group slightly increased, their feeding rate, although this difference was not significant ($\chi^2_{2,23}=5.79$, $P=0.054$; Fig. 1). Male feeding trips did not

Table 1. Behaviour of male rock sparrows from the three treatment groups before and after female ornament manipulation

	Reduced	Control	Enlarged	χ^2	<i>P</i>
Time at nest (min/h)					
Before	8.97±3.22	11.02±2.76	9.88±3.10	0.91	0.65
After	4.60±1.74	22.16±4.41	24.98±6.89	10.03	0.003
Feeding trips/h					
Before	0.59±0.31	0.13±0.08	0.88±0.35	0.03	0.22
After	0.38±0.37	0.06±0.06	0.63±0.39	1.93	0.48
Song (min/h)					
Before	8.91±4.23	7.81±2.00	9.74±3.67	0.44	0.81
After	4.33±1.63	14.84±2.31	19.78±4.61	9.98	0.003
Displays/h					
Before	0.63±0.27	0.92±0.18	0.66±0.27	1.42	0.51
After	0.31±0.13	2.85±0.61	2.75±0.37	13.17	0.0001
Copulations/h					
Before	0.06±0.04	0.31±0.16	0.03±0.03	2.01	0.31
After	0.06±0.06	1.16±0.49	1.17±0.34	6.37	0.06

Means are given \pm SE. *N*=8 for each group. *P* values are for differences in behaviour between groups before and after female patch manipulation (Kruskal–Wallis one-way ANOVA). Significant χ^2 and *P* values remained significant after a sequential Bonferroni test with *k*=10.

differ significantly between groups in terms of relative contribution to total feeding (male feeding trips/total feeding trips: $\chi^2_{2,23}=1.12$, *P*=0.57). We observed only five of 24 males (one reduced, one control and three enlarged) feeding the young after female patch manipulation ($G_{\text{adj } 2}=1.8$, NS). Similar results were obtained from the same analyses comparing male and female behaviour only after the manipulation (Tables 1 and 2, respectively). The exception is female nest attendance, with females from the enlarged group attending significantly less (Table 2).

The change in male sexual behaviour (after minus before manipulation; Fig. 2) differed significantly between treatments for song rate ($\chi^2_{2,23}=10.69$, *P*=0.002), display rate ($\chi^2_{2,23}=10.22$, *P*=0.003) and number of copulations ($\chi^2_{2,23}=7.85$, *P*=0.014). There was no significant difference in the change in mate-guarding index ($\chi^2_{2,23}=2.657$, *P*=0.27). The ordered heterogeneity test (Rice & Gaines 1994) confirmed that males from the reduced group spent less time at the nest, solicited the female less frequently and copulated less frequently than those from the control or the enlarged groups (H_0 : reduced=control=enlarged; H_A : reduced<control<enlarged; *P*<0.002 for all variables; Fig. 2). Similar results were obtained from the same analyses comparing male behaviour only after the manipulation (Table 1).

The results did not change substantially after a sequential Bonferroni test (Rice 1989; *k*=8 and *k*=2 for tests on males and females, respectively). Only the change in male copulation behaviour became nonsignificant after correction.

Experimental manipulation did not affect survival to fledging of the young: none of the nests failed, and the three groups did not differ significantly in the number of young fledged ($\chi^2_{2,23}=2.16$, *P*=0.35).

DISCUSSION

The size of the female rock sparrows' ornament was correlated with indicators of reproductive quality. Breast patch size was correlated with body mass, and double-brooding females and primary females of polygynous males had larger patches (this study) and higher breeding success (Pilastro et al. 2002) than single-brooding and secondary females, respectively. Males responded to the reduction of their female's ornament by reducing their parental investment in nest attendance, as predicted by the DAH, but not by modifying their feeding rate to the brood. Instead, the patch manipulation decreased the male's territorial, courtship and copulation behaviours. We found an effect of the reduction but not of the enlargement treatment, which might have been caused by an imbalance in the extent of the manipulations or by picric acid not mimicking breast patch colour closely enough to a bird's eye. Alternatively, individuals may be better at avoiding very bad mates than at distinguishing between normal and better mates.

Our manipulations of the female ornament did not necessarily affect the properties of the trait in the way we intended, given that we do not know how the birds perceived the picric acid and the brown pigment, and that we did not take spectrographic measurements of the treated feathers. This problem is common to many manipulations of visual signals. None the less, reduction of the female breast patch produced an effect on the behaviour of rock sparrow males in the expected direction and the overall trend of the treatments was as expected. We therefore feel confident in interpreting the results as a positive correlation between female ornamentation and male breeding investment.

Males paired with females whose breast patch was enlarged did not increase the number of feeding trips to

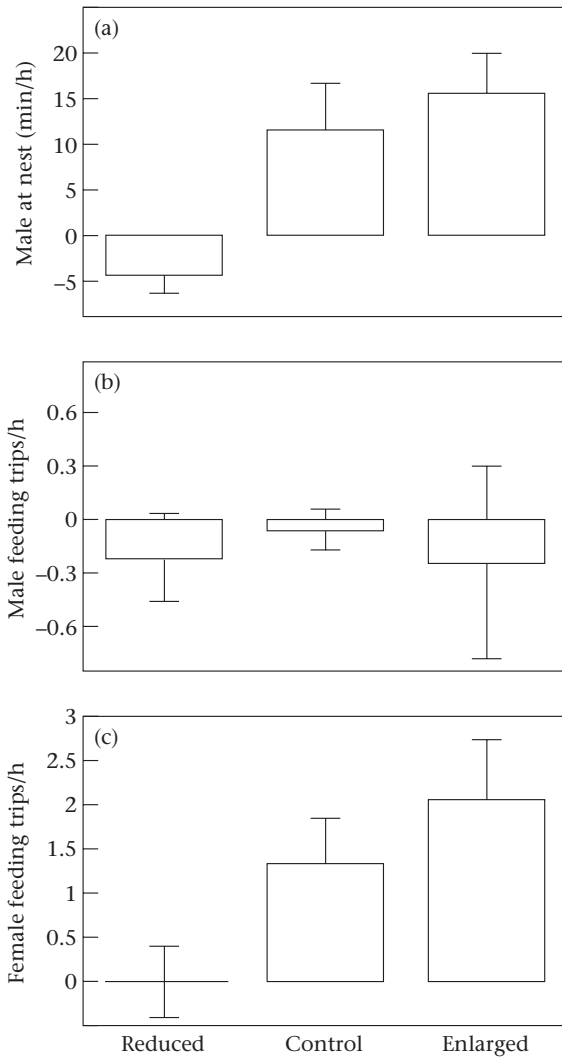


Figure 1. Effect of female ornament manipulation on parental behaviour of males and females. Change (after minus before) in (a) time spent at the nest by the male (min/h); (b) number of male feeding trips/h; (c) number of female feeding trips/h. Means are given \pm SE ($N=8$ for each group).

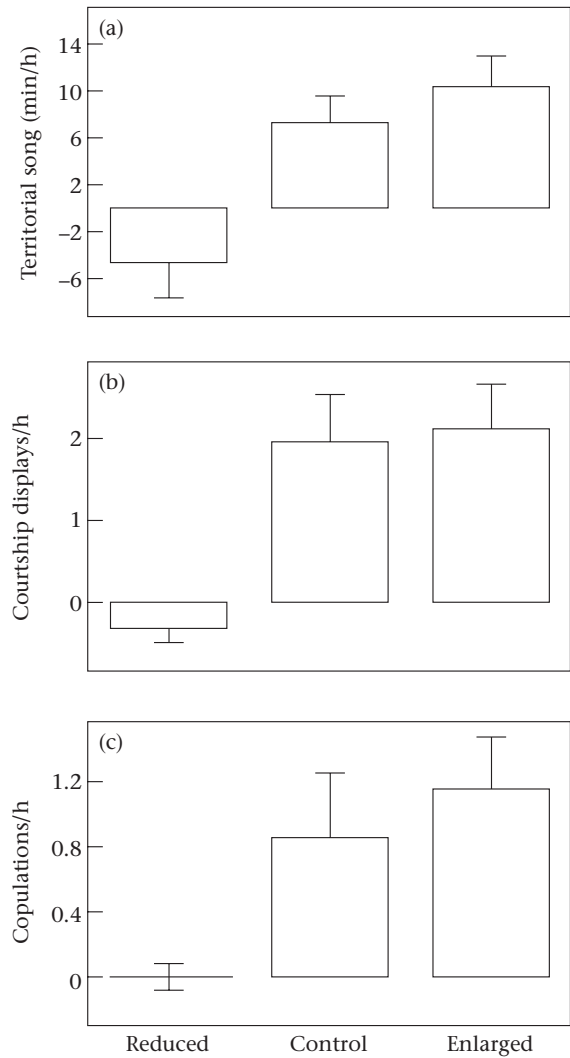


Figure 2. Effect of female ornament manipulation on sexual and territorial behaviour of males. Change (after minus before) in (a) territorial song rate (min/h); (b) number of male courtship displays/h; (c) copulations/h. Means are given \pm SE ($N=8$ for each group).

the nest. Most of the feeding is done by the female at the nestling stage, that is, when we did the manipulation (Wilson 1994; unpublished data; see also Schwagmeyer et al. 2002 and references therein for house sparrows,

Passer domesticus). Male rock sparrows decrease their food provisioning rate as the nestlings age (e.g. Table 1), but males vary markedly and can even take exclusive care of the nestlings (Pilastro et al. 2001). The high variance in

Table 2. Behaviour of female rock sparrows from the three treatment groups before and after female ornament manipulation

	Reduced	Control	Enlarged	χ^2_2	P
Time at nest (min/h)					
Before	2.36 \pm 0.38	3.87 \pm 1.36	1.70 \pm 0.43	2.83	0.25
After	2.67 \pm 0.89	2.03 \pm 0.66	0.61 \pm 0.15	7.98	0.013
Feeding trips/h					
Before	4.63 \pm 0.44	5.41 \pm 0.49	3.88 \pm 0.60	3.59	0.18
After	4.63 \pm 0.55	6.73 \pm 0.63	5.91 \pm 0.52	4.50	0.10

Means are given \pm SE. $N=8$ for each group. P values are for differences in behaviour between groups before and after female patch manipulation (Kruskal–Wallis one-way ANOVA). Significant χ^2 and P values became nonsignificant after a sequential Bonferroni test ($k=4$, $\alpha_{corr}=0.013$).

male feeding behaviour suggested to us that allocation decisions at the late nestling stage may be important, and guided our choices in terms of experimental timing. Male feeding may be crucial under exceptional, severe environmental conditions (e.g. [Kopachena & Falls 1991](#)), which did not occur during our experiments, or at the postfledging stage (e.g. [Kopachena & Falls 1993](#); [Rivera et al. 2000](#)), possibly explaining why males did not change chick-feeding rate in response to female patch manipulation. Alternatively, there may be a trade-off for males between chick feeding and sexual behaviour (see below), and males may try to optimize both parental and mating investments.

Nest attendance by the male, also definable as passive brood defence ([Burley 1988](#), page 615), is a costly component of parental care ([Owens & Bennett 1994](#)), because it reduces opportunities for the male to forage and remate. In our population, the cost of nest attendance may be high in terms of reduction or loss of remating opportunities, given the differences in breeding success between one and two broods per season ([Pilastro et al. 2001](#)). According to the DAH, and as we found in our study, male nest attendance is expected to vary according to female ornamentation if the latter is positively correlated with her quality and therefore with the quality of her brood ([Burley 1986, 1988](#); [Sheldon 2000](#)). This prediction is also supported by evidence from an experiment, simulating a predator attack on the nest, in which male rock sparrows attacked the predator model with an intensity directly proportional to their female's breast patch size ([Griggio et al., in press](#)). Our result is in contrast to [Burley's \(1988\)](#) experiment where zebra finch males did not attend the nest more when paired with an attractive female. One reason for these different results could be that our experiment was conducted in the wild, where nest defence may be crucial to offspring survival ([Ricklefs 1969](#)). Even though our population breeds in nestboxes, in 3 years (1998–2000) we observed two cases of predation by garden dormice, *Eliomys quercinus*, and two cases of nestling mortality caused by competition for nestboxes with house sparrows (T. Mingozi, G. Matessi & M. Griggio, unpublished data).

Alternatively, the association of increased time spent at the nest with the observed change in courtship and copulation activity may suggest that males may be strategically adjusting their mating investment. Courtship and copulation are regularly observed in rock sparrow pairs with nestlings in the nest, independently of female trait manipulation ([Table 1](#)). Brood-deserting females, and probably most double-breeding females, become fertile again before the young of the first brood leave the nest ([Pilastro et al. 2001](#)). Males may therefore be investing in a future brood instead of the current brood if females with a larger breast patch have a higher probability of deserting (e.g. double-brooding females have a larger patch than single-brooding females). In particular, males may attempt to gain paternity in the potential second brood of their female if they perceive that she is more likely to lay a second clutch, even if she may eventually renege with another male ([Oring et al. 1992](#)), as happens in 75% of double-brooding females in this population

([Pilastro et al. 2001](#)). However, nest attendance as a male investment in brood defence may not necessarily be an alternative to investment in remating opportunities (copulations), since males attending the nest to defend their current brood could, at the same time, court and copulate with the feeding female without additional fitness costs. This possible double function of nest attendance is also suggested by the observation that males did not change their mate-guarding efforts with female breast patch manipulation. Mate guarding and nest attendance are not strictly equivalent because males stay at the nestbox and do not follow females in their foraging trips, as suggested also by the contrasting results of male and female nest attendance ([Tables 1 and 2](#), respectively). Males instead actively guard their mates during the prelaying and laying stages ([Pilastro et al. 2002](#)).

In conclusion, male rock sparrows modified their breeding behaviour as a consequence of a reduction in female ornamentation. Whether males changed only their mating strategy or also their parental investment remains to be clarified. More experiments are necessary to tease apart the reasons underlying such changes in behaviour. Do males invest in the current brood (defending valuable offspring), in a potential future brood (staying around to copulate) or both? Possible tests would be to manipulate female ornaments at the stage at which females are usually not fertile (e.g. within the first week after hatching), or to simulate, other than by ornament manipulation, an increase in probability of female nest desertion. Whatever the ultimate explanation for the observed changes in male behaviour, our experiment is, to our knowledge, among the few examples of evidence in the wild of male breeding strategy varying in relation to female phenotype.

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References

- [Amundsen, T. 2000.](#) Why are female birds ornamented? *Trends in Ecology and Evolution*, **15**, 149–155.
- [Biddau, L. & Mingozi, T. 1995.](#) Solitary and colonial breeding strategy in the rock sparrow *Petronia petronia*: an experimental case study. *Avocetta*, **19**, 38.
- [Burley, N. T. 1986.](#) Sexual selection for aesthetic traits in species with biparental care. *American Naturalist*, **127**, 415–445.
- [Burley, N. T. 1988.](#) The differential-allocation hypothesis: an experimental test. *American Naturalist*, **132**, 611–628.

- Clutton-Brock, T. H.** 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.
- Griggio, M., Matessi, G. & Pilastro, A.** In press. Male rock sparrow (*Petronia petronia*) nest defence correlates with female ornament size. *Ethology*.
- Jones, I. L. & Hunter, F. M.** 1993. Mutual sexual selection in a monogamous seabird. *Nature*, **362**, 238–239.
- Jones, I. L. & Hunter, F. M.** 1999. Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. *Animal Behaviour*, **57**, 521–528.
- Jones, K. M., Monaghan, P. & Nager, R. G.** 2001. Male mate choice and female fecundity in zebra finches. *Animal Behaviour*, **62**, 1021–1026.
- Kopachena, J. G. & Falls, J. B.** 1991. An experimental study of brood division in white-throated sparrows. *Animal Behaviour*, **42**, 395–402.
- Kopachena, J. G. & Falls, J. B.** 1993. Postfledging parental care in the white-throated sparrow (*Zonotrichia albicollis*). *Canadian Journal of Zoology*, **71**, 227–232.
- Mingozzi, T., Biddau, L., Rinaldi, F. & Rosselli, D.** 1994. The rock sparrow *Petronia petronia* in the Western Alps: a multidisciplinary research programme. *Proceedings of the 6th Italian Ornithological Congress, Torino*, 363–374.
- Møller, A. P. & Thornhill, R.** 1998. Male parental care, differential parental investment by females and sexual selection. *Animal Behaviour*, **55**, 1507–1515.
- Norušis, M. J.** 1993. *SPSS for Windows Base System User's Guide Release 6.0*. Chicago: SPSS.
- Owens, I. P. F. & Bennett, P. M.** 1994. Mortality costs of parental care and sexual dimorphism in birds. *Proceedings of the Royal Society of London, Series B*, **257**, 1–8.
- Oring, L. W., Fleischer, R. C., Reed, J. M. & Marsden, K. E.** 1992. Cuckoldry through stored sperm in the sequentially polyandrous spotted sandpiper. *Nature*, **359**, 631–633.
- Pilastro, A., Biddau, L., Marin, G. & Mingozzi, T.** 2001. Female brood desertion increases with the number of available mates in the rock sparrow. *Journal of Avian Biology*, **32**, 68–72.
- Pilastro, A., Griggio, M., Biddau, L. & Mingozzi, T.** 2002. Extrapair paternity as a cost of polygyny in the rock sparrow: behavioural and genetic evidence of the 'trade-off' hypothesis. *Animal Behaviour*, **63**, 967–974.
- Reynolds, J. D. & Székely, T.** 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. *Behavioral Ecology*, **8**, 126–134.
- Rice, W. R.** 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Rice, W. R. & Gaines, S. D.** 1994. Extending nondirectional heterogeneity tests to evaluate simply ordered alternative hypotheses. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 225–226.
- Ricklefs, R.** 1969. An analysis of nestling mortality in birds. *Smithsonian Contributions to Zoology*, **9**, 1–48.
- Rivera, J. H. V., Haas, C. A., Rappole, J. H. & McShea, W. J.** 2000. Parental care of fledgling wood thrushes. *Wilson Bulletin*, **112**, 233–237.
- Schwegmeyer, P. L., Mock, D. W. & Parker, G. A.** 2002. Biparental care in house sparrows: negotiation or sealed bid? *Behavioral Ecology*, **13**, 713–721.
- Sheldon, B. C.** 2000. Differential allocation: tests, mechanisms and implications. *Trends in Ecology and Evolution*, **15**, 397–402.
- Tavecchia, G., Pradel, R., Lebreton, J.-D., Biddau, L. & Mingozzi, T.** 2002. Sex-biased survival and breeding dispersal probability in a patchy rock sparrow *Petronia petronia* population. *Ibis*, **144**, E79–E87 (on-line).
- Webster, M. S.** 1991. Male parental care and polygyny in birds. *American Naturalist*, **137**, 274–280.
- Wilson, M. G.** 1994. Rock sparrow *Petronia petronia*: social pattern and behaviour. In: *Birds of the Western Palearctic* (Ed. by S. Cramp & C. M. Perrins), pp. 374–378. Oxford: Oxford University Press.
- Zar, J. H.** 1974. *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice Hall.