Males prefer ornamented females: a field experiment of male choice in the rock sparrow

MATTEO GRIGGIO*, FRANCISCO VALERA†, ALEJANDRO CASAS‡ & ANDREA PILASTRO*

*Dipartimento di Biologia, Università di Padova
†Estación Experimental de Zonas Áridas, CSIC
‡Konrad Lorenz Institut für Vergleichende Verhaltenforschung

Recent evidence suggests that female ornaments in birds not only are genetic correlates of selection on males but may also have evolved by selection acting directly on females. However, most evidence comes from studies in captivity and it is therefore still debated whether male choice is important under natural conditions. The rock sparrow, *Petronia petronia*, is a monomorphic passerine in which both sexes show a yellow breast patch, although females have a smaller patch than males. Breast patch in females is positively correlated with body mass and fecundity (number of broods per year). We tested whether males preferentially mate with more ornamented females in this species. We examined male mate choice by reducing the size of the yellow breast patch of free-ranging females during the pair formation period in a colony in southeast Spain. We found that females with an experimentally reduced breast patch were courted less intensely and chased less frequently, than control females were. Furthermore, females with an experimentally reduced ornament were less likely to mate and, when mated, did so at a significantly later date than controls. These results are supported by correlational observations from another rock sparrow population, for which a larger data set was available, showing that pairs mated assortatively with respect to breast patch size. Altogether, these results therefore suggest that female ornamentation may be sexually selected in this species.

Sexual selection arises as a result of variance in reproductive success that is nonrandomly associated with aesthetic traits of individuals of the chosen sex (Darwin 1871). Studies of sexual selection in many species of birds have shown that males with relatively high expression of such traits will be preferred by females, usually the choosy sex, or intimidate their competitors thus obtaining mating advantages (Andersson 1994), or both (Berglund et al. 1996). In monogamous species with biparental care, choosing females would also be important for males if females varied in their quality, because the potential reproductive rates of the two sexes should be similar (Trivers 1972; Parker 1983; Clutton-Brock & Vincent 1991) and males' fitness would also be influenced by the

quality (e.g. parental quality or fecundity) of their mates. Male preference for fecund females has been demonstrated in several fish, amphibian and insect species (Andersson 1994), as well as in a few bird species (Monaghan et al. 1996; Jones et al. 2001).

Although in birds, as in many other taxa, extravagant traits may occur in both sexes, female ornaments have been traditionally considered to be the result of genetic correlation with sexually selected male ornaments (Lande 1980), probably because female ornaments are often a drabber or smaller version of the male ones. More recently, however, this view has been challenged and it has been proposed that female ornaments could also be sexually selected, through female–female competition or male preference (Amundsen 2000). There is growing evidence that female plumage ornaments correlate positively with female phenotypic quality in a number of passerine and nonpasserine species (e.g. Møller 1993; Johnsen et al. 1996; Potti & Merino 1996; Amundsen et al. 1997; Linville et al. 1998; Roulin 1999; Pilastro et al. 2003; Pizzari et al. 2003). The evidence that males prefer ornamented females in passerines comes from aviary

Correspondence: A. Pilastro, Dipartimento di Biologia, Università di Padova, Via U. Bassi 58/B, I-35131 Padova, Italy (email: andrea. pilastro@unipd.it). F. Valera is at the Estación Experimental de Zonas Áridas, CSIC, General Segura, 1, E-04001 Almería, Spain. A. Casas is at the Konrad Lorenz Institut für Vergleichende Verhaltenforschung, Savoyenstrasse 1 a, A-1160, Vienna, Austria.

experiments (e.g. Hill 1993; Amundsen et al. 1997; Hunt et al. 1999, but see Wolf et al. 2004), whereas field studies failed to show evidence of such preference (e.g. Hill 1993; Cuervo et al. 1996; Amundsen 2000). The general importance of male preference as a factor favouring the evolution of female ornaments therefore remains debatable, at least in short-lived, passerine birds.

The rock sparrow, *Petronia petronia*, is a monomorphic species in which both males and females have a yellow patch of feathers on the breast. Yellow coloration in the breast patch is due to lutein and zeaxanthin (R. Stradi, personal communication). The size of this ornament is smaller, on average, in females than in males, does not depend on age, and it is positively correlated with individual phenotypic quality (Pilastro et al. 2003). In particular, the size of the patch correlates with female body mass and double-brooding females have on average a larger ornament than single-brooding females. Polygynous males have a larger badge than monogamous males, although the difference is only marginally significant. Finally, nonbreeding individuals have smaller patches than breeding individuals (Pilastro et al. 2003).

When the size of the yellow breast patch of females was either enlarged or reduced during the nestling stage, the time spent by the males at the nest singing and courting the female was positively correlated with the postmanipulation size of the female ornament (Pilastro et al. 2003). This behaviour was interpreted as a strategy adopted by males to increase their paternity in a potential second brood laid by the female. Since double-brooding females have a large yellow patch, mate switching is frequent between the first and second brood, and females can become fertile again before the nestlings from the first brood leave the nest (Pilastro et al. 2001). There is also correlative evidence that males defend the brood from predators more intensely when their mate has a large yellow patch (Griggio et al. 2003a). Altogether, these results indicate that paired male rock sparrows adjust their courting and parental effort to the size of their mate's breast patch, although it is not clear whether this enhanced male parental effort translates to a greater breeding success for the female or simply in a greater chance for the male to remate with the same female (see discussion in Pilastro et al. 2003). Furthermore, these studies have been carried out when most, if not all, females in the population are breeding and opportunities for males to attract further mates are scarce (Pilastro et al. 2001). It is therefore not clear whether males discriminate between females with regard to the size of their breast patch during the pair formation period. During this period, males invest most of their time in trying to attract a female to their nest and competition for mates is high. Furthermore, early breeding is associated with higher reproductive success and, at the beginning of the breeding season, males may not be selective with respect to female phenotype, as evidenced in other field studies (e.g. Hill 1993; Cuervo et al. 1996; Amundsen 2000).

To verify whether male rock sparrows prefer ornamented females, we manipulated the size of the female's yellow breast patch during the period of pair formation. We did so in a Spanish colony of rock sparrows in which capture and manipulation of the female breast patch were possible during the pair formation stage. We tested whether females whose breast patch size was experimentally reduced were courted less and paired at a later date than control counterparts. We further looked for a positive correlation between male and female breast patch size in rock sparrow pairs in an Italian population, for which a larger data set was available.

METHODS

Study Species

The rock sparrow's social mating system varies from monogamy to polygamy, with both male and female brood desertion (Pilastro et al. 2001; Griggio et al. 2003b). The level of extrapair paternity is high, although it appears to be limited nearly exclusively to the nests of polygynous males (Pilastro et al. 2002). The rock sparrow breeds in colonies varying from a few to hundreds of pairs in particularly favourable conditions (Cramp & Perrins 1994). Inter- and intrasexual interactions usually take place at the breeding site: during the pair formation period, males able to occupy a nest site (usually holes in buildings or small cliffs, but also nestboxes, where available, Pilastro et al. 2001; Tavecchia et al. 2002) spend a long time sitting in front of the hole and singing to attract a female. Females visit several holes before pairing and nest building (personal observations). Males display their yellow breast patch or tail towards the females in courtship bouts lasting 8–12 s. Courtship is sometimes followed by a chase flight in which males closely follow the female and try to copulate with her (Cramp & Perrins 1994; Pilastro et al. 2003; M. Griggio, unpublished data).

Breast Patch Size Manipulation

We carried out breast patch manipulation during March–May 2003 in the Desert of Tabernas, Almería, southeast Spain (37°05′N, 2°21′W), at a rock sparrow colony on a sandy cliff approximately 100 m long and 3–5 m high. The birds of this colony used nest burrows excavated by bee-eaters, *Merops apiaster*, in previous breeding seasons (Casas-Crivillè & Valera 2005). We mapped the nest holes, which were a few centimetres to a few metres apart, at the beginning of the breeding season. Rock sparrows started to bring nest material at the end of April and the first nestlings appeared during the third week of May (personal observations).

Starting at the end of March, adult birds were clapnetted at the colony and individually colour ringed; we measured body mass (± 0.1 g) and tarsus length (± 0.1 mm; Svensson 1992). We also measured the size of the patch of individuals by placing a strip of transparent acetate on the breast and drawing the contour of the yellow area. We then measured the major axis (width) of the outline (for more details on the method and the measure repeatability see Pilastro et al. 2002). Birds were sexed according to the shape of the cloacal protuberance (Svensson 1992). Sex determination was successively

validated through behavioural observations and recapture later in the breeding season, when females develop a brood patch.

Four sessions of bird capture (2–3 days) were alternated with sessions of behavioural observations (5 consecutive days; capture sessions: 8–27 April). Captured females were randomly assigned to two experimental groups. In the first group (Reduced, $N = 10$), we reduced the width of the breast patch by cutting the distal half of some yellow feathers on the two sides of the patch. In the second group (Control, $N = 10$), we cut approximately the same number of feathers (five or six), chosen among the contour feathers bordering the two sides of the yellow patch, as for the reduced group. Capture date (and therefore the timing of subsequent observations, see below) did not differ significantly between the two experimental groups (days from 1 January; reduced group: $\overline{X} \pm SD = 102.1 \pm 6.77$; control group: 102.7 ± 3.02; two-tailed Mann–Whitney test: $U = 33$, $P = 0.22$).

We did not use an enlarged group because a previous study showed that males respond to female ornament enlargement less than to its reduction (Pilastro et al. 2003). We released the female immediately after manipulation (which lasted about 20 min). The mean size of the breast patch of females before manipulation $\pm$ SD was 13.7 ± 1.90 mm ($N = 10$) in the reduced group, and 12.9 ± 3.16 mm ($N = 10$) in the control group (Student's t test: $t_{18} = 0.71$, $P = 0.486$). In the reduced group, mean patch size after manipulation $\pm$ SD was 8.1 ± 1.07 mm (range 6.6–10.5, mean reduction -40.23%). There was no difference between the two groups of females in tarsus length (reduced: $\overline{X} \pm SD = 18.30 \pm 0.84$ mm, range 17.0–19.9, $N = 10$; controls: 18.54 ± 0.39 mm, range 18.0–19.1, $N = 10$; Student's t test: $t_{18} = 0.79$, $P = 0.43$) and in body mass (reduced: $\overline{X} \pm SD = 31.34 \pm 1.27$ g, range 29.6–33.4, $N = 10$; controls: 32.17 ± 1.11 g, range 30.1–33.5, $N = 10$; Student's t test: $t_{18} = 1.57$, $P = 0.13$).

One of us (M.G.) carried out all the behavioural observations at a distance, using a spotting telescope ($30 \times$ magnification). Behavioural daily observations at the colony were carried out from 10 April to 9 May, during the morning (0700–1100 hours), when the activity at the colony was highest. Since it was impossible to keep the entire colony under observation at the same time, we divided the colony into six parts of the same length (about 18 m), and each part was observed every 2 days for 1 h (total time of observation for each part of the colony: $\overline{X} \pm SD = 10.33 \pm 1.21$ h, range 9–12). Using a stopwatch, we recorded the time spent by the experimental females at the colony per hour of observation (female attendance time). In order to have comparable observation periods, we considered for each female the observations collected during the first 5 days after the day of female manipulation. A courtship rate index (hereafter courtship rate) was estimated as the proportion of time in which an experimental female was courted by males during her presence at the colony. Male behaviour was recorded at 15-s intervals over each 1-h observation period, using a metronome, and translated into s or min/h according to the analyses. When two or more males counted the same female, we used the mean courtship time calculated as the total courtship time divided by the number of courting males. We further recorded the proportion of a female's arrivals to and departures from the colony in which she was followed by one or more males (sexual chase index, Pilastro et al. 2002). We also recorded the number of males present at the colony per hour of observation at any given sector under observation and the mean time spent singing by territorial males per hour of observation (min/h). Finally, female pairing date was determined as the first day in which she was observed transporting nest material into a male's burrow.

Assortative Mating

Data of breast patch size of breeding pairs were collected, over four breeding seasons (1997, 1998, 1999 and 2002), in a population breeding in nestboxes on the western Alps, Italy. More details on this population are given in Pilastro et al. (2001, 2003). We monitored reproduction during the whole season (from May to July), by observing each of the 40 nestboxes for 1 h twice a week. Breeding birds were colour ringed and the breast patch size was measured as above. We included in the analysis only the monogamous pairs and the pairs formed by the polygynous males and their primary female (i.e. the first female to start laying).

Statistical Procedures

Data were analysed with parametric tests when assumptions of the tests (normality of the distribution and homogeneity of the variance) were met. When these assumptions were violated even after appropriate transformation, the correspondent nonparametric test was used (Zar 1974). Proportions were arcsine square-root transformed when used in parametric tests (Sokal & Rohlf 1995). Statistical tests were performed using SPSS 11.5 (Norušis 1993). We used two-tailed tests throughout.

Ethical Note

Care was taken to minimize handling of birds, which were captured by expert ringers with permits from the Istituto Nazionale per la Fauna Selvatica (Bologna), the Ministerio de Medio Ambiente and Junta de Andalucia. Manipulations were done with permission of the Dirección General de Gistión del Medio Ambiente (Consejería de Medio Ambiente, Junta de Andalucia). No short-term negative effect was observed for the handled birds and all captured birds were observed at the colony in the days after ringing.

RESULTS

In the 5 days after manipulation, control and reduced females did not differ significantly in the number of 1-h observation sessions during which they were at the colony (reduced: $\overline{X} \pm SD = 5.80 \pm 1.54$ h, range 4–8, $N = 10$; control: 6.7 ± 1.49 h, range 5–9, $N = 10$;

Student's t test: $t_{18} = 1.32$, $P = 0.20$) nor in the mean female attendance time (reduced: $\overline{X} \pm SD = 48.02 \pm 11.14$ s/h, range 33.8–75.0 $N = 10$; control: 49.99 ± 19.98 s/h, range 34.3–102.5 $N = 10$; Student's t test: $t_{18} = 0.27$, $P = 0.79$). There were no differences between the two groups of females in the number of males present at the respective colony sector during female visits (reduced: $\overline{X} \pm SD = 3.06 \pm 0.52$, range 1–5, $N = 10$; control: 2.87 ± 0.38, range 1–5, $N = 10$; Student's t test: $t_{18} = 0.941$, $P = 0.36$), nor in their singing rate (reduced: $\overline{X} \pm SD = 35.8 \pm 3.31$ min/h, range 28.8–42, $N = 10$; control: 34.8 ± 2.89 min/h, range 29–38.8, $N = 10$; Student's t test: $t_{18} = 0.78$, $P = 0.45$).

Male courtship rate directed towards control females was significantly higher than that directed towards females with the experimentally reduced breast patch (reduced: $\overline{X} \pm SD = 0.51 \pm 0.20$, range 0.07–0.82, $N = 10$; control: 0.80 ± 0.14, range 0.57–0.97, $N = 10$; $t_{18} = 3.73$, $P = 0.002$, after arcsine square-root angular transformation; Fig. 1a). The frequency of sexual chases by the males of the colony was higher for control females than for those with a reduced breast patch (reduced: $\overline{X} \pm SD = 0.23 \pm 0.14$, range 0–0.41, $N = 10$; control: 0.48 ± 0.20, range 0.21–0.82, $N = 10$; $t_{18} = 3.13$, $P = 0.006$, after arcsine square-root angular transformation; Fig. 1b). The intensity of male sexual chases was significantly associated with the size of the female breast patch after manipulation, once the differences between the two groups were statistically accounted for (ANCOVA: female group: $F_{1,17} = 0.11$, $P = 0.74$; covariate: $F_{1,17} = 9.64$, $P = 0.006$), whereas the intensity of male courtship rate was not (female group: $F_{1,17} = 4.42$, $P = 0.05$; covariate: $F_{1,17} = 0.30$, $P = 0.59$; Fig. 2). The interactions between female breast patch width and female group were not significant (interaction: sexual chases: $F_{1,17} = 1.06$, $P = 0.32$; courtship rate: $F_{1,17} = 0.93$, $P = 0.35$) and were removed from the ANCOVA model. Finally, we found a positive correlation between courtship rate and the intensity of sexual chases (Spearman rank correlation: $r_S = 0.55$, $N = 20$, $P = 0.01$). Capture date was not significantly correlated with male courtship rate and sexual chases after statistically controlling for treatment group (all $P > 0.13$).

Within the period in which the colony was kept under daily observation, the time elapsed from the manipulation date to the latest date in which an experimental female was observed at the colony did not differ for the two groups (reduced: $\overline{X} \pm SE = 27.0 \pm 2.06$ days, range 12–31 days; control: 26.3 ± 0.96 days, range 24–31 days; Mann–Whitney test: $U = 33$, $N_1 = N_2 = 10$, $P = 0.22$). At the end of the daily observation period (9 May, when most females were building the nest or incubating the eggs, personal observation) all 10 control females were paired, whereas only four of 10 reduced females were paired (Fisher's exact test: $P = 0.011$). These latter females paired, on average, at a later date than the control group, both considering the absolute date and the number of days after patch manipulation (absolute date, reduced: median = 117.5, range 116–119; control: median = 112, range 110–155; Mann–Whitney test: $U = 0$, $N_1 = 10$, $N_2 = 4$, $P = 0.001$; days after manipulation, reduced:
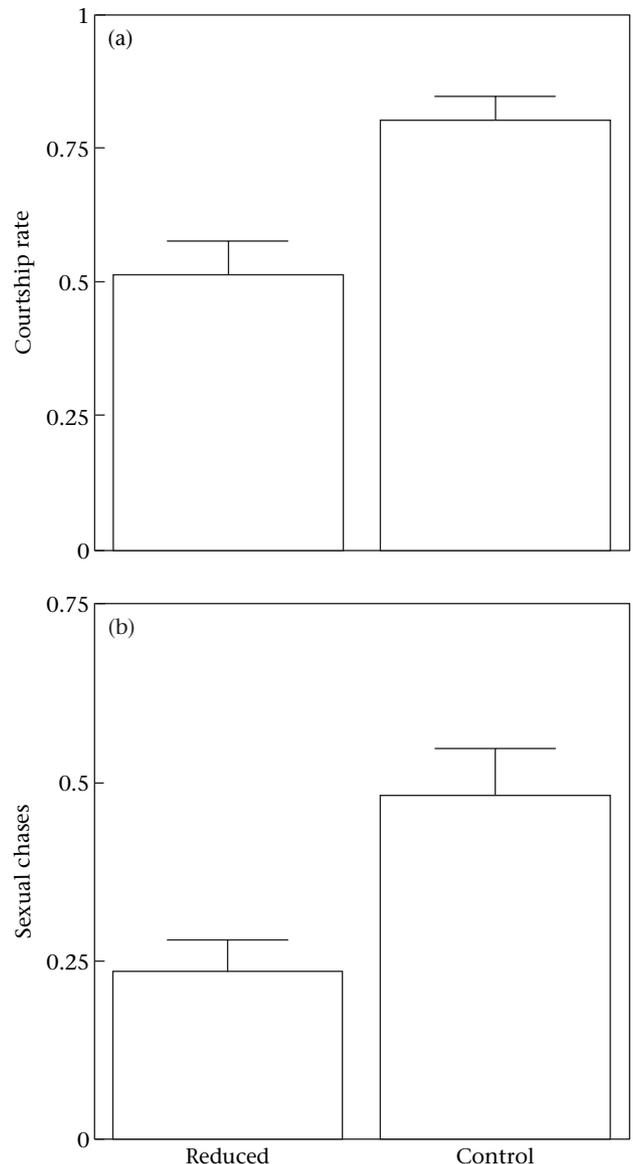

Figure 1. Effect of the manipulation of the size of the female ornament on male sexual behaviour: (a) courtship rate (proportion of time in which a female was courted during her presence at the colony sector); (b) sexual chases (proportion of arrivals to and departures from the colony in which the female was chased by males). Bars represent means + SE ($N = 10$ for reduced group, $N = 10$ for control group).

median = 18.5, range 18–21; control: median = 9.5, range 5–14; Mann–Whitney test: $U = 0$, $N_1 = 10$, $N_2 = 4$, $P = 0.002$; Fig. 3). Furthermore, pairing date and size of female breast patch were negatively correlated ($r_S = -0.62$, $N = 14$, $P = 0.019$).

Breast patch sizes of males and females of 44 rock sparrow pairs from the Italian population were positively correlated (Fig. 4), suggesting the occurrence of assortative mating with respect to breast patch size (Pearson correlation: $r_{42} = 0.42$, $P = 0.004$). The positive association between male and female ornament size remained significant after controlling for possible differences between
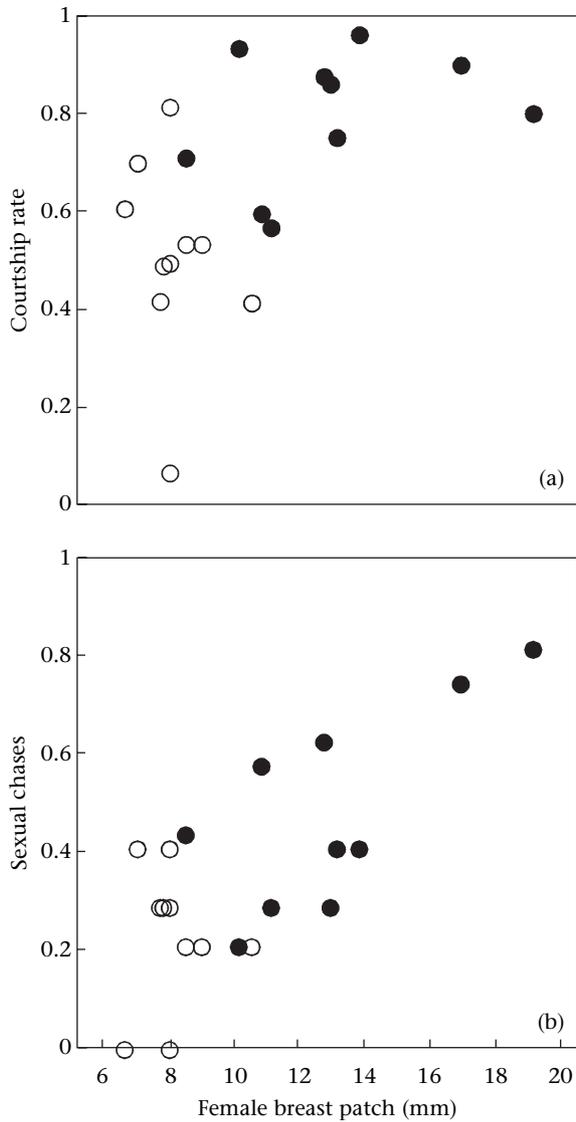
Figure 2. Relation between the width of the female breast patch after manipulation (○: reduced group; ●: control group) and male sexual behaviour: (a) courtship rate (proportion of time in which a female was courted during her presence at the colony sector) and (b) sexual chases (proportion of arrivals to and departures from the colony in which the female was chased by males).

years (ANCOVA: $F_{4,39} = 3.07$, $P = 0.027$; factor (year): $F_{3,39} = 1.05$, $P = 0.38$; covariate (female breast patch size): $F_{1,39} = 9.17$, $P = 0.004$).

DISCUSSION

Our results provide evidence that male rock sparrows have a mating preference for females with larger breast patches, an ornament that is positively correlated with individual female quality (Pilastro et al. 2003). The experimental reduction of the size of the female's breast patch resulted in a decreased sexual interest by the territorial males at the colony. In particular, the females whose yellow breast patch was reduced were courted less intensely and chased
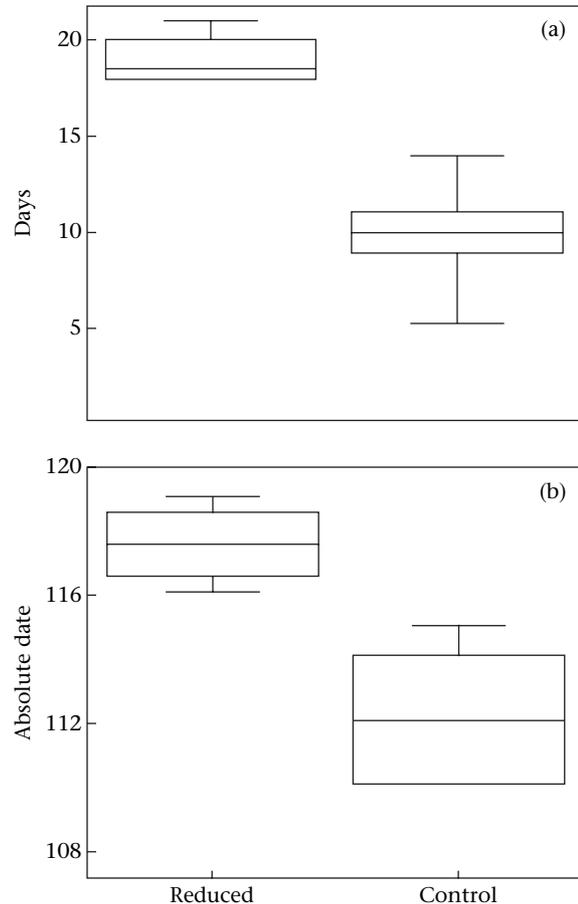

Figure 3. Pairing date of rock sparrow females according to breast patch size manipulation (control, $N = 10$, reduced, $N = 4$). (a) Days after patch manipulation; (b) absolute date (1 = 1 January). Horizontal line = median; box = 50% of the data; bars = range.
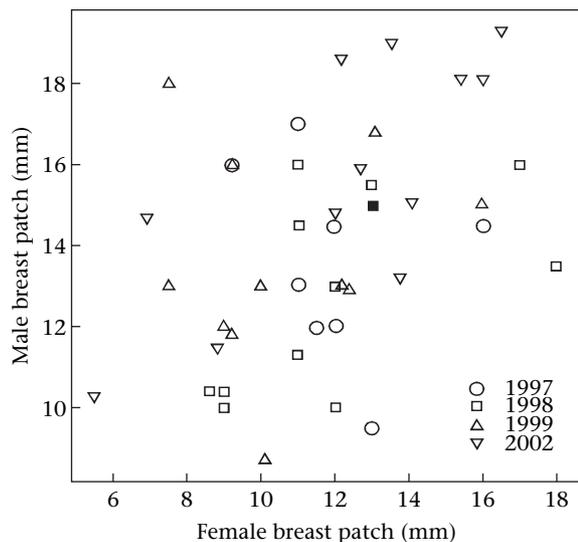

Figure 4. Relation between male and female breast patch size (width, mm) in 44 breeding pairs from an Italian population breeding on the western Alps. The solid square represents two data points. $P = 0.004$, Pearson correlation.

less frequently than control females were. The ANCOVA analysis in which male behaviour was the dependent variable, treatment group the factor and female breast patch after manipulation the covariate showed that the frequency of sexual chases was positively associated with the size of the female breast patch after manipulation, whereas this association was not significant when courtship rate was considered. However, the variance in breast patch size in the reduced group was very small (Fig. 2), and we were therefore unlikely to detect a significant correlation within groups.

Females with a reduced breast patch were not actively rejected by males and we never observed males attacking females, either in the control group or in the reduced group. Sexual chases and courtship rate were positively and significantly correlated suggesting that sexual chases may be part of the male's courtship behaviour, or may be used by males to obtain copulations (e.g. Hoi 1997), or to assess a female's reproductive status (e.g. Jones 1986). The decreased sexual interest that males showed towards the females with the experimentally reduced breast patch was associated in this group of females with a reduced likelihood of pairing compared with their control counterparts. Indeed, within about a month of patch manipulation, less than half of the females in the reduced group were paired, whereas all control females were paired. Furthermore, the four reduced-group females that obtained partners did so at a significantly later date than controls.

Since the size of the breast patch correlates positively with phenotypic quality in the rock sparrow, males paired with the reduced-group females should have, on average, smaller patches than those paired with the control females. We do not have information on the phenotypic quality of the males paired with the two groups of females, since most of them were not ringed. However, the analysis of the breast patch sizes of rock sparrow pairs from another population suggests that males and females mate assortatively with respect to the size of their ornament. Altogether, these results indicate that females with a large badge size may have a two-fold advantage: they mate earlier (breeding success declines as the season advances, Pilastro et al. 2001) and mate with more ornamented males.

In a number of bird species, aviary experiments suggest that males may prefer ornamented females (but see Wolf et al. 2004). For example, male bluethroats, Luscinia svecica, presented with dyads of females differing in the size of their blue breast patch performed more sexual displays in front of the more colourful female (Amundsen et al. 1997). Another example is the blue tit, Parus caeruleus, in which males prefer ultraviolet females (Hunt et al. 1999). On the other hand, most studies carried under natural conditions have failed to find evidence of male mate choice (reviewed in Amundsen 2000), thus questioning the importance of male choice in the evolution of female ornaments in birds. For example, in the house finch, Carpodacus mexicanus, a species in which female preference for brightly coloured males is well demonstrated (Hill 1991), aviary experiments showed that males prefer the most brightly plumaged females (Hill 1993). In contrast, field observations demonstrated that female age is the primary criterion of male choice, suggesting that

female coloration may be, at best, a secondary choice criterion (Hill 1993). In the barn swallow, Hirundo rustica, the length of the outermost rectrices (a sexually selected trait in males, Møller 1988) of the females is positively correlated with the number of fledglings and the frequency of second clutches (Møller 1993). However, a field experiment failed to find evidence of any male preference for ornamented females in this species (Cuervo et al. 1996). Similar results have been reported for other bird species (e.g. Muma & Weatherhead 1989; Tella et al. 1997). Firm evidence, to date, that males prefer more ornamented females under natural conditions comes only from nonpasserines. One case is the crested auklet, Aethia cristatella, in which both sexes displayed more in front of mounts with a large crest (Jones & Hunter 1993, 1999). Indirect evidence comes from the barn owl, Tyto alba, in which males preferentially pair with females with large black spots (Roulin 1999). Mate discrimination, in terms of strategic sperm allocation in relation to female phenotypic quality, has also been documented in the fowl, Gallus gallus domesticus (Pizzari et al. 2003). As far as we are aware, the rock sparrow is the only short-lived bird species (Tavecchia et al. 2002) in which evidence for male preference has been found in the wild.

Male rock sparrows may obtain a fecundity advantage by choosing females with a large breast patch, which are more likely to lay two broods per year (Pilastro et al. 2003). The benefit of male choice may be further increased if ornamented females are also better parents and their phenotypic quality has a heritable component that may provide indirect benefits through higher-quality offspring (for instance, more fecund female and more competitive male offspring). There is no information about the heritability of these traits in the rock sparrow. In other passerine birds, carotenoid-based plumage coloration has been shown to have a heritable component (Fitze et al. 2003; but see Johnsen et al. 2003). Furthermore, both female fecundity (e.g. Merila & Sheldon 2000; Sheldon et al. 2003) and other feather ornaments (e.g. Møller 1993) have been shown to be heritable and it is therefore possible that males also obtain indirect benefits by pairing with high-quality females.

Alternative explanations for our results seem unlikely. In theory, the reduced sexual interest of males for females with an experimentally reduced breast patch may be caused by a problem of species recognition. However, the postmanipulation size of the breast patch in the reduced group is within the range observed in this (F. Valera & A. Casas, unpublished data) and in an Italian population (Pilastro et al. 2003). It is therefore very unlikely that our manipulation of the female breast patch resulted in males not recognizing badge-reduced females as conspecifics. A second possibility is that the yellow breast patch may serve for individual recognition (e.g. Whitfield 1986). If so, the manipulation of the breast patch would render females unfamiliar to the males of the colony. This explanation seems unlikely for two reasons. The first is that males should prefer unfamiliar females (Dewsbury 1981), whereas females with an experimentally reduced breast patch were courted less frequently than controls. The second reason is that a previous experiment in which female breast patch was either enlarged or

reduced (Pilastro et al. 2003) produced, as expected, opposite male responses in the two groups in which the female's breast patch was manipulated (see above), whereas the individual recognition hypothesis would have predicted a concordant result in both enlarged and reduced groups compared with controls.

As far as we are aware, male choice in birds has been found in the field only in long-lived species. The rock sparrow provides the first evidence that, under natural conditions, male choice can favour the evolution of a female ornament in a short-lived bird. It remains to be tested whether the female's yellow breast patch also has a role in female–female competition or in social contests outside the breeding season.

Acknowledgments

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