

Female ornamentation and directional male mate preference in the rock sparrow

Matteo Griggio,^a Alessandro Devigili,^a Herbert Hoi,^a and Andrea Pilastro^b

^aKonrad Lorenz Institute for Ethology, Savoyenstrasse 1/A, A-1160, Vienna, Austria and ^bDipartimento di Biologia, Università di Padova, Via Ugo Bassi 58/B, I-35131 Padova, Italy

Albeit there is growing evidence that males prefer to mate with ornamented females, it has been suggested that the production of costly ornaments may reduce female fecundity, hence favoring males with a preference for females with average ornamentation. In the rock sparrow, *Petronia petronia*, males and females possess a sexually selected patch of yellow feathers on the breast (a carotenoid-based trait). To test whether males prefer females with the largest ornament or average ornamented females, male rock sparrows were simultaneously faced with 3 conspecific females differing in breast patch size and a female house sparrow as a control. We found that the house sparrow and rock sparrow female with the smallest patch were least preferred, and males showed a clear proximity preference for the females with the above average-sized patch. Our results demonstrate that, contrary to theoretical predictions, a directional preference for female ornament was observed. Directional male preference may arise as consequence of a male's sensory bias or may be associated with indirect (genetic) benefits of choosing ornamented females, if ornament size is correlated with female genetic quality. Clearly, more work is necessary to identify the conditions under which directional preference for female ornament arises. *Key words*: condition-dependent trait, mutual sexual selection, ornaments, plumage reflectance. [*Behav Ecol* 20:1072–1078 (2009)]

Although controversial for more than a century, Darwin's idea of the evolution of male ornaments through female preference is now widely accepted (Andersson and Simmons 2006). Female preference usually generates a directional sexual selection on male ornaments (Andersson 1994), although preference for intermediate phenotype generating stabilizing selection has also been reported (e.g., Brooks et al. 2005), particularly in the case of male multiple ornaments (Blows et al. 2003). Female preference for exaggerated male ornaments is sustained by a positive correlation between the expression of the male ornament and the benefits (either genetic or direct) that females obtain from mating (Reynolds and Gross 1992; Andersson 1994; Kirkpatrick 1996; Kotiaho et al. 2001; Kokko et al. 2002). There is ample experimental evidence that females choose their mates on the basis of the size of traits signaling male quality, thus generating a directional sexual selection for exaggerated ornaments (Andersson 1994; Andersson and Simmons 2006). However, these ornaments are only susceptible to the evolutionary process if they are heritable (Fisher 1930). Whereas certainly female choice is widespread, recent studies have demonstrated that, also in species without sex-role reversal, males often do not mate indiscriminately but show a mating preference for ornamented females (Jones and Hunter 1993; Amundsen 2000; LeBas and Marshall 2000; Griggio, Valera, et al. 2005; Servedio and Lande 2006; Kraaijeveld et al. 2007). This suggests that the evolution of female ornamentation may be driven by male preference, although mechanisms other than male choice, such as for example, female–female competition for mates or other resources, may also be involved in the evolution of female ornamentation (LeBas 2006).

The evolution of female ornament through male preference, however, is more complex than is the evolution of male ornaments through female mate choice because the evolution

of male mating preferences is thought to be driven mainly by variation in fecundity among females (Andersson 1994). Males are indeed expected to base their choice on cues that are directly correlated with female fecundity (e.g., body size; Itzkowitz et al. 1998; Kraak and Bakker 1998; Bonduriansky 2001; Byrne and Rice 2006) or on ornamental traits that honestly signal female fecundity (Amundsen and Forsgren 2001; Massironi et al. 2005). The evolution of ornamental traits honestly signaling mate quality to the prospective partners is, however, more complicated in females than in males because, to signal honestly, ornaments need to be costly (Zahavi 1975; Iwasa and Pomiankowski 1991). If there is a trade-off between the resources allocated to the ornament and those allocated to reproduction, as it is expected if the ornament is costly, males should not evolve a preference for females that pay such a high cost of signaling that their fecundity is reduced (Fitzpatrick et al. 1995; see also Kokko 1998). In other words, we do not expect to observe a directional male preference for females with the most exaggerated ornaments. It may be worth noting that, in this context, body size is a “cue,” that is, a trait that can be used to guide mate choice for more fecund females but has not evolved as a mean to transfer information, whereas ornaments are “signals,” that is, traits that have evolved to transfer information (see Maynard Smith and Harper 2005). Once they are exaggerated, signals become costly and are therefore expected to trade-off with the resources allocated to reproduction, making directional male preference unlikely to evolve. In the rest of the paper, we will therefore specifically focus on the evolution of male preference for female ornaments (and not for body size). As proposed by theoretical models (Chenoweth et al. 2006), although male preference can initially promote the evolution of female ornaments, at the equilibrium, males should prefer females with average ornament size, as females with average ornament size should be those with the highest fecundity. Indeed, empirical work on *Drosophila* demonstrated that there is a trade-off between resources allocated to reproduction (number of eggs produced) and sexual signaling (cuticular hydrocarbons, Wicker and Jallon 1995), and males tend to prefer females with average ornament size (Chenoweth et al. 2007).

Address correspondence to M. Griggio. E-mail: m.griggio@klivv.oeaw.ac.it.

Received 4 December 2008; revised 9 June 2009; accepted 16 June 2009.

In contrast with general theoretical predictions, however, in several bird and fish species in which females have sexual ornaments, such as color patches or elongated feathers, males have been shown to prefer the most ornamented females (for a review, see Amundsen 2000). For the reasons stated above, a directional male preference for ornamented females is unexpected, as it should either be lost or should develop into a preference for females with average ornament size (Kokko and Johnstone 2002; Chenoweth et al. 2006; Servedio and Lande 2006). The evolution of directional male preference for costly female ornaments, however, is not theoretically impossible. Models of female choice evolution have demonstrated that when direct (e.g., fecundity) benefits are being sought, if there is sufficient genetic variation in 1 sex, a costly trait can simultaneously function as a signal for both direct and indirect benefits, despite the intrinsic trade-off between the trait and the direct benefit obtained (Price et al. 1993; Kokko 1998). This is because the cost of the signal is condition dependent and expected to decrease with individual quality (Grafen 1990; Iwasa and Pomiankowski 1991; for a review, see Andersson and Iwasa 1996). Although indirect benefits are thought to play a minor role in male choice evolution (Bonduriansky 2001), any kind of mating biases for direct benefits actually leads to the possibility of indirect benefits if the offspring of chosen males inherit the ability to deliver direct benefits (Kokko et al. 2003). When they do, the likely effect is a shift of the male preference toward strongly signaling females (Chenoweth et al. 2006).

Considering the expected negative effect of costly ornaments on female reproductive allocation (Chenoweth et al. 2006), the circumstances under which males would benefit from choosing females are limited to those cases in which mating with 1 female does trade-off with fitness acquired in future matings (e.g., Kokko and Monaghan 2001; Reinhold et al. 2002). This may happen, for example, in socially monogamous species with paternal care and in which females do not show large variation in fecundity. In these cases, the variation in female genetic quality may be comparable with the variation in female fecundity and a costly ornament would function as a simultaneous signal for both direct and indirect benefits, despite the intrinsic trade-off between the trait and the direct benefit obtained (Price et al. 1993; Kokko 1998).

Alternatively, in species in which males provide resources to reproduction, the directional male preference for female ornamentation may be evolutionarily stable if male reproductive allocation is positively correlated with female ornamentation. One such case is represented by the dance fly, *Rhizophomyia tarsata*, in which males prefer ornamented females (with large pinnate scales) and the size of the ornament is correlated with female fecundity, possibly via increased nutrition from male nuptial gifts (LeBas et al. 2003).

Another explanation for this paradox, however, is that the experimental design usually employed for male choice studies may actually fail to reveal nonlinear mating preferences. For example, in commonly used fixed stimulus mate-choice experiments, males are given the choice between 2 groups of females whose ornament size is close either to the largest or the smallest values observed in the species (e.g., Griggio, Valera, et al. 2005). Clearly, this experimental design will fail to detect a nonlinear male preference such as, for example, that for females with average ornament size (Wagner 1998), and it has been suggested that the male preference for females with average ornamentation may have been overlooked (Chenoweth et al. 2006).

In this paper, we investigated the shape of the male preference function for female ornamentation in the rock sparrow, *Petronia petronia*. In this species, a yellow breast patch is present in both sexes and its size is not correlated with age

(Pilastro et al. 2003). Females have, on average, a smaller breast patch than males, but the distribution of ornament size in the 2 sexes largely overlaps (see Study species). Nonbreeding individuals have smaller yellow patches than breeding individuals in both males and females, and breast patch size correlates with female body size in females (Pilastro et al. 2003). Field experiments done in the rock sparrow demonstrated that males prefer females with a large yellow patch over females with a small yellow patch (Pilastro et al. 2003; Griggio, Valera, et al. 2005), possibly suggesting a directional male preference for female ornament. As clutch size does not correlate with the size of the yellow patch in the rock sparrow (Griggio M, Pilastro A, personal observation), an explanation of male preference for ornamented females may be that males seek it for other reasons. The rock sparrow feather ornament is carotenoid based and condition dependent (Serra et al. 2007). As in many other bird species, carotenoid-based traits are costly to produce (Hill and McGraw 2006) and may therefore be an honest indicator of individual genetic quality (Grafen 1990; Iwasa and Pomiankowski 1991). The variation in clutch size is limited in rock sparrows, as in many other bird species, and an important component of a female's reproductive value for males may therefore be represented by her genetic quality, in addition to the resources she will be able to allocate to the offspring. Although a direct demonstration that females with larger ornaments produce offspring of higher quality is lacking in the rock sparrow, it is known that egg size or egg content of carotenoids, immunoglobulins, and hormones can vary greatly among females in other species (Pilz et al. 2003; Williams and Ames 2004; Biard et al. 2005), and it is possible that they covary with female ornament. For example, better quality females may require fewer carotenoids for maintenance and may therefore be able to allocate a larger portion of their carotenoid reserves to ornamentation and egg contents (e.g., Doutrelant et al. 2008; Pizzolon et al. 2008). If the marginal costs of ornament expression are lower for females of high quality, these females should be able to both produce offspring of higher quality and bear a larger ornament than low-quality females, following the same reasoning that has been used to explain the evolution of colorful and exaggerated traits in males (Zahavi 1975; Grafen 1990).

In previous mate-choice experiments in the rock sparrow, however, males were given the choice only between 2 groups of females whose ornament represented the 2 extremes of the size distribution and the shape of the preference function cannot be determined (Pilastro et al. 2003; Griggio, Valera, et al. 2005). The possibility that males actually prefer females with an average ornament size cannot therefore be ruled out. To investigate the mate preference function of male rock sparrows, we presented a group of individual male rock sparrows with a trio of females with small, intermediate, or large breast patch size and estimated their preference from the time spent in front of the 3 females.

MATERIALS AND METHODS

Study species

The rock sparrow is a slightly sexually dimorphic species. Biometrical data (collected from 2005 to 2008) on 42 males and 26 females from our captive population (see below) revealed that males had longer wings and tails than females (males: 97.57 ± 0.26 mm, females: 95.54 ± 0.45 mm, Student's *t*-test: $t_{66} = 4.16$, $P < 0.001$; males: 55.83 ± 0.28 mm, females: 52.08 ± 0.40 mm, Student's *t*-test: $t_{66} = 7.84$, $P < 0.001$, respectively). Body mass and tarsus length, in contrast, did not differ between the sexes (males: 30.82 ± 0.16 g, females: 30.16 ± 0.37 g, Student's *t*-test: $t_{66} = 1.87$, $P = 0.065$; males: 18.59 ± 0.1 mm,

females: 18.7 ± 0.23 mm, Student's t -test: $t_{66} = -0.85$, $P = 0.4$, respectively). Yellow breast patch was wider in males than in females (males: 16.56 ± 0.27 mm, females: 15.0 ± 0.37 mm, Student's t -test: $t_{66} = 3.41$, $P = 0.001$). After controlling for sexual body size dimorphism (wing and tail length), the size difference for this ornament remained statistically significant (analysis of covariance test: wing length as a covariate, sex: $F_{1,65} = 5.98$, $P = 0.017$, tail length as a covariate, sex: $F_{1,65} = 11.78$, $P = 0.001$).

Maintenance of birds and morphological measurements

We used 41 rock sparrows (25 males and 16 females). Twenty individuals were caught in central Italy (for more details, see Griggio et al. 2007), 10 individuals were caught in southeast Spain (Almería, $37^{\circ}05'N$, $2^{\circ}21'W$), and 11 were born in captivity at the Konrad Lorenz Institute (Vienna, Austria, $48^{\circ}13'N$, $16^{\circ}17'E$).

All birds were housed in cages ($100 \times 50 \times 50$ cm) in the same room (housing room) under a natural light regime, and each cage was inhabited by 2 or 3 birds of the same sex. All birds were fed with a mixed diet of commercial bird seeds, fruits, and vegetables. We took standard measurements of wing length to the nearest 0.5 mm and tarsus length to the nearest 0.1 mm. Body mass was recorded to the nearest 0.1 g. While holding the bird to expose its ventral side, with its bill and head perpendicular to the body, we measured the size of the yellow patch by placing a strip of transparent acetate over the throat and drawing the contour of the yellow area. We measured the major axis (width, the major axis of a roughly trapezoid-shaped patch) with a dial caliper (to the nearest 0.1 mm). We used the major axis as an index of yellow patch size as it has been shown in other studies to correlate with other phenotypic traits and to be used by males in assessing females (Pilastro et al. 2003; Griggio et al. 2003; Griggio, Valera, et al. 2005). A detailed description of measuring the yellow patch of the rock sparrow can be found in the studies of Pilastro et al. (2003); Griggio et al. (2003); and Griggio, Valera, et al. (2005). Captivity birds present yellow breast patch sizes in the natural range of the species (Pilastro et al. 2003; Griggio, Valera, et al. 2005), with males more ornamented than females (males: 16.6 ± 0.5 mm standard error [SE], range: 11–22.1 mm, $n = 25$; females: 14.8 ± 0.4 mm SE, range: 11.3–18.3 mm, $n = 16$; Student's t -test: $t_{39} = 2.45$, $P = 0.02$), as previously reported (Pilastro et al. 2003). Among these females, in accordance with the objectives of our study, 3 groups were formed according to the yellow breast patch size (small female group, SF: 13.1 ± 0.5 mm SE, $n = 5$; intermediate female group, IF: 14.8 ± 0.1 mm SE, $n = 5$; large female group, LF: 16.3 ± 0.5 mm SE, $n = 6$; see Table 1).

The yellow breast patch reflectance in the 300–700 nm range was measured with an Ocean Optics, Inc. (Eerbeek, The Netherlands) USB 2000 spectrometer and a deuterium–halogen source (DH-2000). The light source illuminated the feathers through an optical fiber and was reflected through a plastic window cut at 90° . A software package (Spectrawin 4.2, Ocean Optics) computed reflectance spectra relative to a white reference tile (SW-2). For each individual, 5 measurements (each spectrum was averaged from 5 scans) were taken, the probe being removed between each measurement. We then averaged the 5 measurements for each individual. We quantified color using 5 standard parameters of reflectance spectra: the hue ($\lambda_{[R_{max}]}$), brightness ($R_{300-700}$), chroma ($[R_{max} - R_{min}]/R_{average}$), yellow chroma ($R_{550-625}/R_{300-700}$), and UV chroma ($R_{300-400}/R_{300-700}$) of each individual. These parameters have been used in previous studies on birds (Hunt et al. 1999; Sheldon et al. 1999; Griggio and Hoi 2006).

Experimental design

We conducted a male mate-choice test using a 4-choice apparatus ($2 \times 2 \times 0.5$ m, Figure 1) that was positioned in a room similar to the housing room. The apparatus consisted of 4-choice chambers, separated by opaque dividers, at the 4 sides of the central choice chamber. An opaque divider was also set up in each of the 4 sides of the central chamber to avoid visual interaction between the 4 stimulus females (see Figure 1). The dividers also prevented the males from simultaneously observing 2 or more females. In 1 corner of the 4 dividers, an opening (14×14 cm) covered by a metal web allowed the male to observe the females in the side chambers. During the experiment, the males could see the females through these holes, but they could not physically interact. A perch was positioned in front of each of the 4 chambers. Perches had a line traced, which corresponded to the limit from which a male could observe the female in the nearby compartment (Figure 1). In accordance with the objectives of the study, males had a choice between 3 conspecific females with small, intermediate, and large yellow breast patches (SF, IF, and LF groups, respectively). In every experimental trial, one of us randomly chose a female from each group. To control for position effects, chambers were randomly assigned to the stimulus females. As a control, the fourth chamber contained a non-conspecific female, namely, a female house sparrow, *Passer domesticus* (CF group, $n = 10$) to ensure that males were sexually motivated and did not move randomly among compartments.

The experiment consisted of 25 mate-choice trials, each with a different male as the respondent. To present a new set of different females for each trial, we should have captured and

Table 1
Phenotypic and spectrometric differences between the 3 groups of rock sparrow females used for the experiment

Female trait/index	Small ornament	Intermediate ornament	Large ornament	<i>F</i>	<i>P</i>
Breast patch size (mm)	13.12 ± 1.07	14.80 ± 0.30	16.34 ± 1.14	16.080**	<0.001
Wing length (mm)	91.50 ± 2.09	92.90 ± 2.77	95.91 ± 2.63	4.445*	0.034
Body mass (g)	29.0 ± 1.97	28.50 ± 1.60	30.53 ± 1.16	2.518	0.119
Tail length (mm)	51.80 ± 2.36	52.30 ± 1.79	53.91 ± 2.11	1.553	0.248
Tarsus length (mm)	18.92 ± 1.74	19.32 ± 0.67	19.11 ± 0.62	0.162	0.852
Breast patch brightness	32.35 ± 5.61	44.31 ± 5.61	44.33 ± 1.47	2.424	0.127
Breast patch chroma	1.43 ± 0.12	1.36 ± 0.09	1.25 ± 0.06	0.954	0.411
Breast patch yellow chroma	0.29 ± 0.01	0.29 ± 0.01	0.27 ± 0.01	1.861	0.195
Breast patch UV chroma	0.15 ± 0.01	0.17 ± 0.01	0.18 ± 0.01	1.524	0.254
Breast patch hue	637.80 ± 24.15	619.30 ± 18.52	646.84 ± 21.26	0.428	0.660

Analysis of variance test. All degrees of freedom = 2, mean \pm SE are given.

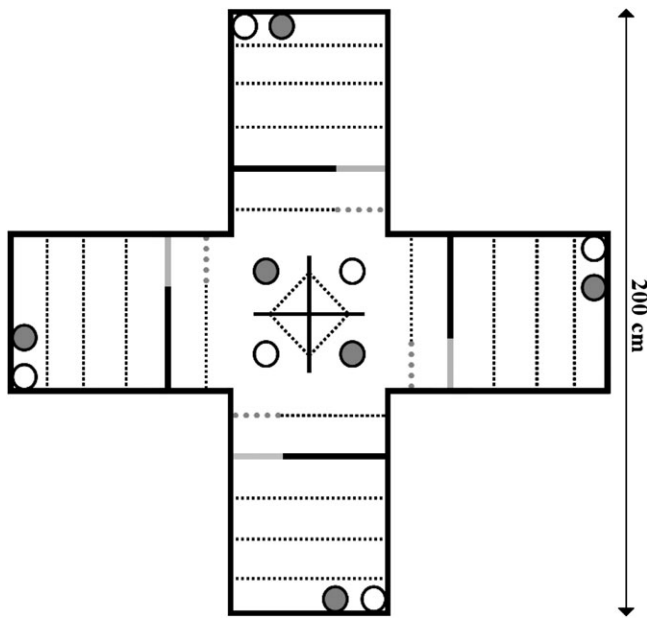


Figure 1
Schematic overview of the experimental apparatus. Solid black lines: opaque dividers. Dashed lines: perches. Solid gray line: metal web. Dashed gray lines: part of the perches considered as choice location. Gray and white circles: food and water.

maintained in captivity 75 individual rock sparrow females. To minimize the number of females kept in captivity, we used in total 16 females, which were used on average 4.6 ± 2.0 times each. Once a trial ended, the stimulus females were returned to the housing cages, and a standardized housing setting for all stimulus females was maintained throughout the experiment. Water and food were provided ad libitum during the experiments.

At the beginning of a trial, test male and stimulus females were placed in their experimental chambers and allowed at least 30 min to acclimatize before the trial began. After that period, the opaque separators were removed and the position of the male was recorded every 1 s for 2 h (all trials were video recorded and then analyzed). For an estimator of proximity preference, we measured the time spent by a male on the part of the perch in front of a female's compartment (choice time). Preference was expressed as the proportion of time in front of each female over the total time in the choice area (e.g., Hill et al. 1999; Brooks 2000; Aguilar et al. 2008; Hoi and Griggio 2008). Moreover, a courtship rate index (seconds spent courting per hour) was estimated as the time a female was courted by the male. During courtship behavior, males display their yellow breast patch and/or white tail spots toward the female (Griggio, Valera, et al. 2005).

Statistical analyses were performed with SPSS 15.0 (Norušis 1993). All the results are presented as mean \pm SE. All tests are 2 tailed. Analyses were checked to ensure that they met the assumptions of parametric statistics.

RESULTS

Males spent on average $42.5 \pm 15.15\%$ standard deviation (range = 17.2–67.6%) of their time in the choice area, and in all trials, males spent at least some time in front of the chamber of each of the stimulus females. As expected, males spent the smallest proportion of their time in front of the house sparrow chamber ($4.5 \pm 6.48\%$). Males spent significantly more time in front of the female with the largest yellow patch (Figure 2; Table 2). The generalized linear model (GLM) analysis con-

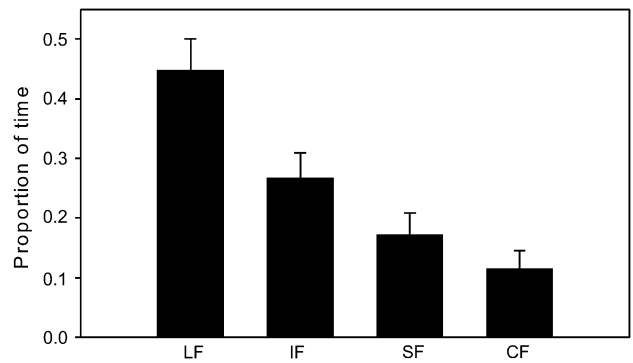


Figure 2
Percentage of time spent by males near the window to the females' cages. CF: control females (house sparrow); SF: females with small ornament; IF: females with intermediate ornament; LF: females with large ornament. Mean time (seconds) \pm SEs are given.

firms that female's group had strong positive effect on the male choice time ($F = 10.17, P < 0.001, n = 25$), and post hoc tests reveal that males spent significantly more time in front of the LF group (Table 2). Including the control female in the analysis did not change the results substantially. Similar results were obtained with the actual size of the yellow breast patch as covariate ($F_{1,49} = 18.78, P < 0.001$). Results do not substantially change when using the area of the yellow patch obtained from the digital photos of the contour drawn on transparent acetate (we measured the area of the yellow patch using UTHSCSA Image Tool; <http://ddsdx.uthscsa.edu/dig/download.html>) instead of patch width (major axis, $F = 8.90, P = 0.004$). In 16 cases, the most preferred female was the one with the largest breast patch, in 6 cases the female with the intermediate breast patch, and in 3 cases the female with the smallest breast patch (chi square = 11.12, degrees of freedom [df] = 1, $P = 0.003$). Similar results were obtained when considering courtship rate: 14 of 25 males courted the females and all of them courted more the female with the largest breast patch (GLM analysis: $F_{2,13} = 11.58, P < 0.001$). Male breast patch size was correlated neither with the time spent near the preferred female (Pearson correlation $r = -0.122, P = 0.56, n = 25$) nor the variance in male preference ($r = 0.147, P = 0.48, n = 25$), suggesting that male mate choice did not vary with the size of a male's ornament. Lastly, there were no significant differences in male preferences based on female plumage colorimetrics (hue, brightness, chroma, yellow chroma, and UV chroma, they were used as covariates in GLM analysis: all $F < 0.95, P > 0.33$).

Table 2
GLM post hoc test (Tukey honestly significant difference test) and contrast analysis result (K matrix) for the choice time, considering the control group as reference

Test	Female groups	Difference	P
Post hoc	LF versus	Control	1026.12* <0.001
		SF	898.52* <0.001
		IF	576.56* 0.029
	IF versus	Control	449.56 0.129
		SF	321.96 0.393
	SF versus	Control	127.60 0.923
Contrast analysis	SF	-273.22 0.031	
	IF	48.74 0.696	
	LF	625.30 <0.001	

DISCUSSION

Our results show that male rock sparrows have a directional preference for the yellow breast patch size of the females, as clearly males preferred the females with the largest ornament. This result contrasts with theoretical models of male mating preference, which suggest that when males seek direct fecundity benefits they should discriminate among females on the basis of traits indicating the number of eggs produced (Fitzpatrick et al. 1995; Servedio and Lande 2006). Consistently, directional male preference for LF body size, a trait that is often correlated with fecundity, has been found in several species (Bonduriansky 2001; Jones et al. 2001; Byrne and Rice 2006, but see Chenoweth et al. 2007). More problematic, however, is the evolution of female costly ornamentation (Chenoweth et al. 2007; Cornwallis and Birkhead 2007). Although a positive correlation between female ornamentation and fecundity has been reported in several species (LeBas et al. 2003; Doutrelant et al. 2008; Wright et al. 2008), it has also been suggested that the evolution of male preference for ornamented females should be inhibited once the costs of producing exaggerated ornaments reduce female fecundity. This in turn should lead to a male preference for females with average ornament size (Chenoweth et al. 2006). Although evidence of male preference for ornamented females is growing (for a review, see Amundsen 2000), establishing whether male preference is directional requires exploring male preference function across the natural range of variation of ornament size. The reconstruction of male preference function has been done rarely, and we are aware of studies on only 2 insect species that, interestingly, obtained contrasting results. LeBas et al. (2003) demonstrated that in the dance fly *R. tarsata*, there is directional male preference for ornamented females (area of pinnate scales). In another insect species, *Drosophila serrata*, Chenoweth et al. (2007) found instead evidence for stabilizing sexual selection in candidate female signal traits, suggesting that females may trade off resources allocated to reproduction and sexual signaling. Despite the convex male preference found in *D. serrata* (Chenoweth and Blows 2005), it is worth noting that there exist differences in the strength of convex and directional selection components among populations (Rundle et al. 2008).

Our results, in contrast with this latter study, are congruent with a directional male preference for female ornamentation. Although female ornamentation was categorized in 3 groups, the actual variation in ornament size across the experimental (stimulus) females encompassed the variation observed in natural populations. Our results evidenced a significant male preference for females with the largest ornament. Interestingly, in the rock sparrow, female ornament is not correlated with fecundity as estimated from clutch size, although double-brooding females have a larger patch than single-brooding females (Pilastro et al. 2003 but see below). Why then do male rock sparrows prefer to mate with highly ornamented females? Different scenarios could explain why male rock sparrows show a directional preference for the female ornament size. First, it is possible that in female rock sparrows, the cost of ornamentation does not restrict resources allocated to reproduction by the female, and hence, male benefits of mating with females with the largest ornaments (Fitzpatrick et al. 1995). Reproduction and ornament development (including carotenoid demand during feather growth) in female rock sparrows are temporally well separated, as the yellow breast patch is formed at least 7 months before reproduction. Thus, females in good condition, or early moulting females (Serra et al. 2007), may be able to first develop a large ornament and then to make a large investment in reproduction. Double-brooding females have, on average, a larger yellow patch than single-brooding

females, which, in turn, have a larger yellow patch than females that do not reproduce (Pilastro et al. 2003). This may suggest that, even if female ornament does not correlate with clutch size, the total number of eggs produced within a season do. Thus, males paired to females with a large ornament may fertilize a larger number of eggs. It has to be noted, however, that the divorce rate between the first and the second brood is around 75% (Pilastro et al. 2001; Griggio, Matessi, et al. 2005) and that the hatching success of the second brood is on average very low.

A second, not mutually exclusive, explanation is that females vary in the quality of the offspring they are able to produce rather than in their number or in the quantity of resources they are able to allocate to offspring (e.g., the level of parental care). Maximum clutch size is expected to be constrained in birds due to the difficulty of brooding large clutches, and variation in fecundity is therefore expected to be smaller than in insects or in fishes. In birds, females may therefore vary mainly in the resources allocated to each offspring. Clearly, for a female ornament to evolve, it is necessary that the cost of expressing the mating preference paid by the males and the cost of producing the ornament paid by the females are outweighed by the benefit of choosing and of being chosen, respectively. Furthermore, both male preference and female ornament need to be heritable to some extent. For the reasons stated above, directional male preference seems more likely to occur in monogamous species and in those species in which males contribute to reproduction with parental care, as in the case of most birds, in some fishes (e.g., Pizzolon et al. 2008), and in those insects in which males provide females with nuptial gifts (LeBas et al. 2003).

Another possible explanation for the observed directional male preference for ornament size in the rock sparrow is that females are exploiting a sensory bias of the males, for example, a male preference for yellow. Preexisting bias models propose that mating preferences are by-products of natural selection on sensory systems, and the preferences for particular signals are not expected to be adaptive (Ryan 1990; Endler and Basolo 1998). Such preferences are shaped by natural selection (e.g., in a foraging context) and may be "exploited" by 1 sex to drive a sexual preference of the other sex (e.g., Madden and Tanner 2003). Carotenoids represent an important component of animal diet, and rock sparrows may be selected to preferentially feed on food items with yellow coloration conferring a high carotenoid content as has been shown in other species (Grether et al. 2005). Specific experiments, for example, on food color preferences, would be needed to test this hypothesis. Although the role of preexisting sensory biases in the evolution of mate preferences is probably more important than previously thought (Arnqvist 2006), such exploitation should bring about costs to the exploited sex, eventually leading to the evolution of resistance (Kokko et al. 2002) or to the exaggeration of the ornament which will eventually become honest (García and Ramirez 2005).

In summary, we found that, contrary to theoretical predictions, male rock sparrows exhibit a directional mate preference for female ornament. This result confirms previous evidence (LeBas et al. 2003) that directional sexual preference is not limited to females but that it can arise also in males. Whether this applies to other vertebrate species with male mate choice for ornamented females (Amundsen 2000), however, still needs to be investigated. There are several causes for the presence of male preferences for female ornaments that remain to be clarified. For example, whether male directional preference has any fitness consequence for the females has not been determined in those vertebrate species for which a male preference for ornamented females has been demonstrated. We therefore do not know whether directional male

preference results into effective directional selection on female ornament. Second, whether or not male preference is adaptive in the rock sparrow remains to be demonstrated, as clutch size does not correlate with female ornament, but there is an indication that the total number of eggs produced in a breeding season may increase with her ornament (Pilastro et al. 2003). Thus, the possibility that the male directional preference is resulting from a preexisting sensory bias exploited by the females should not be discounted. Clearly, determining the nature (direct or indirect) of any fitness advantages associated with male mate choice and the heritability of the traits involved would help cast light on the evolution of male preference and the evolution of female ornaments. The 2 species in which directional male preference has been demonstrated (LeBas et al. 2003, this study) are characterized by substantial male contribution to reproduction. More empirical studies are necessary to determine the frequency of directional male preference for female ornamentation, as compared with preference for females with average ornamentation, and which conditions promote its evolution.

FUNDING

Istituto Veneto di Scienze Lettere ed Arti (Andrea Marconato Award); Fondazione Trentino Università (to A.D.); University of Padova (CPDR069979 and 60A06-9110 to A.P.).

We thank the Konrad Lorenz Institute staff, in particular C. Grabmayer and W. Pegler, for assistance during the experiment. We are very grateful to V. Zanollo for practical helping. We thank Hans Hofmann and 2 anonymous reviewers for their constructive and helpful comments on previous versions of the manuscript. All the manipulations of birds performed during this study comply with the current laws of the country in which the experiments have been carried out.

REFERENCES

- Aguilar TM, Maia R, Santos ESA, Macedo RH. 2008. Parasite levels in blue-black grassquits correlate with male display but not female mate preference. *Behav Ecol*. 19:292–301.
- Amundsen T. 2000. Why are female birds ornamented? *Trends Ecol Evol*. 15:149–155.
- Amundsen T, Forsgren E. 2001. Male mate choice selects for female coloration in a fish. *Proc Natl Acad Sci USA*. 98:13155–13160.
- Andersson M. 1994. *Sexual selection*. Princeton (NJ): Princeton University Press.
- Andersson M, Iwasa Y. 1996. *Sexual selection*. *Trends Ecol Evol*. 11: 53–58.
- Andersson M, Simmons LW. 2006. Sexual selection and mate choice. *Trends Ecol Evol*. 21:296–302.
- Arnqvist G. 2006. Sensory exploitation and sexual conflict. *Philos Trans R Soc Lond B*. 361:375–386.
- Biard C, Surai PF, Møller AP. 2005. Effects of carotenoid availability during laying on reproduction in the blue tit. *Oecologia*. 144:32–44.
- Blows MW, Brooks R, Kraft PG. 2003. Exploring complex fitness surfaces: multiple ornamentation and polymorphism in male guppies. *Evolution*. 57:1622–1630.
- Bonduriansky R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol Rev Camb Philos Soc*. 76:305–339.
- Brooks R. 2000. Negative genetic correlation between male sexual attractiveness and survival. *Nature*. 406:67–70.
- Brooks R, Hunt J, Blows MW, Smith MJ, Bussiere LF, Jennions MD. 2005. Experimental evidence for multivariate stabilizing sexual selection. *Evolution*. 59:871–880.
- Byrne PG, Rice WR. 2006. Evidence for adaptive male mate choice in the fruit fly *Drosophila melanogaster*. *Proc R Soc Lond B Biol Sci*. 273:917–922.
- Chenoweth SF, Blows MW. 2005. Contrasting mutual sexual selection on homologous signal traits in *Drosophila serrata*. *Am Nat*. 165: 281–289.
- Chenoweth SF, Doughty P, Kokko H. 2006. Can non-directional male mating preferences facilitate honest female ornamentation? *Ecol Lett*. 9:179–184.
- Chenoweth SF, Petfield D, Doughty P, Blows MW. 2007. Male choice generates stabilizing sexual selection on a female fecundity correlate. *J Evol Biol*. 20:1745–1750.
- Cornwallis CK, Birkhead TR. 2007. Experimental evidence that female ornamentation increases the acquisition of sperm and signals fecundity. *Proc R Soc Lond B Biol Sci*. 274:583–590.
- Doutrelant C, Gregoire A, Grnac N, Gomez D, Lambrechts MM, Perret P. 2008. Female coloration indicates female reproductive capacity in blue tits. *J Evol Biol*. 21:226–233.
- Endler JA, Basolo AL. 1998. Sensory ecology, receiver biases and sexual selection. *Trends Ecol Evol*. 13:415–420.
- Fisher RA. 1930. *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Fitzpatrick S, Berghlund A, Rosenqvist G. 1995. Ornaments or offspring—costs to reproductive success restrict sexual selection processes. *Biol J Linn Soc*. 55:251–260.
- Garcia CM, Ramirez E. 2005. Evidence that sensory traps can evolve into honest signals. *Nature*. 434:501–505.
- Grafen A. 1990. Sexual selection unhandicapped by the Fisher process. *J Theor Biol*. 144:473–516.
- Grether GF, Kolluru GR, Rodd FH, de la Cerda J, Shimazaki K. 2005. Carotenoid availability affects the development of a colour-based mate preference and the sensory bias to which it is genetically linked. *Proc R Soc Lond B Biol Sci*. 272:2181–2188.
- Griggio M, Hoi H. 2006. Is preening behaviour sexually selected? An experimental approach. *Ethology*. 112:1145–1151.
- Griggio M, Matessi G, Pilastro A. 2003. Male rock sparrow (*Petronia petronia*) nest defence correlates with female ornament size. *Ethology*. 109:659–669.
- Griggio M, Matessi G, Pilastro A. 2005. Should I stay or should I go? Female brood desertion and male counterstrategy in rock sparrows. *Behav Ecol*. 16:435–441.
- Griggio M, Serra L, Licheri D, Monti A, Pilastro A. 2007. Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. *Behav Ecol Sociobiol*. 61:423–433.
- Griggio M, Valera F, Casas A, Pilastro A. 2005. Males prefer ornamented females: a field experiment of male choice in the rock sparrow. *Anim Behav*. 69:1243–1250.
- Hill GE, McGraw KJ. 2006. *Bird coloration*, vol. II. Function and evolution. Cambridge (MA): Harvard University Press.
- Hill JA, Enstrom DA, Ketterson ED, Nolan V Jr, Ziegenfus C. 1999. Mate choice based on static versus dynamic secondary sexual traits in the dark-eyed junco. *Behav Ecol*. 10:91–96.
- Hoi H, Griggio M. 2008. Dual utility of a melanin-based ornament in bearded tits. *Ethology*. 114:1094–1100.
- Hunt S, Cuthill IC, Bennett AT, Griffiths R. 1999. Preferences for ultraviolet partners in the blue tit. *Anim Behav*. 58:809–815.
- Izkowitz M, Draud M, Barnes J, Haley M. 1998. Does it matter that male beaugregory damselfish have a mate preference? *Behav Ecol Sociobiol*. 42:149–155.
- Iwasa Y, Pomiankowski A. 1991. The evolution of costly mate preferences II. The ‘handicap’ principle. *Evolution*. 45:1431–1442.
- Jones IL, Hunter FM. 1993. Mutual sexual selection in a monogamous seabird. *Nature*. 362:238–239.
- Jones KM, Monaghan P, Nager RG. 2001. Male mate choice and female fecundity in zebra finches. *Anim Behav*. 62:1021–1026.
- Kirkpatrick M. 1996. Good genes and direct selection in evolution of mating preferences. *Evolution*. 50:2125–2140.
- Kokko H. 1998. Should advertising parental care be honest? *Proc R Soc Lond B Biol Sci*. 265:1871–1878.
- Kokko H, Brooks R, Jennions MD, Morley J. 2003. The evolution of mate choice and mating biases. *Proc R Soc Lond B Biol Sci*. 270:653–664.
- Kokko H, Brooks R, McNamara JM, Houston AI. 2002. The sexual selection continuum. *Proc R Soc Lond B Biol Sci*. 269:1331–1340.
- Kokko H, Johnstone RA. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philos Trans R Soc Lond B Biol Sci*. 357:319–330.
- Kokko H, Monaghan P. 2001. Predicting the direction of sexual selection. *Ecol Lett*. 4:159–165.
- Kotiaho JS, Simmons LW, Tomkins JL. 2001. Towards a resolution of the lek paradox. *Nature*. 41:684–686.

- Kraaijeveld K, Kraaijeveld-Smit FJL, Komdeur J. 2007. The evolution of mutual ornamentation. *Anim Behav.* 74:657–677.
- Kraak SBM, Bakker TCM. 1998. Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Anim Behav.* 56:859–866.
- LeBas NR. 2006. Female finery is not for males. *Trends Ecol Evol.* 21:170–173.
- LeBas NR, Hockham LR, Ritchie MG. 2003. Nonlinear and correlational sexual selection on 'honest' female ornamentation. *Proc R Soc Lond B Biol Sci.* 270:2159–2165.
- LeBas NR, Marshall NJ. 2000. The role of colour signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proc R Soc Lond B Biol Sci.* 267:445–452.
- Madden JR, Tanner K. 2003. Preferences for coloured bower decorations can be explained in a nonsexual context. *Anim Behav.* 65:1077–1083.
- Massironi M, Rasotto MB, Mazzoldi C. 2005. A reliable indicator of female fecundity: the case of the yellow belly in *Knipowitschia panizzae* (Teleostei: gobiidae). *Mar Biol.* 147:71–76.
- Maynard Smith J, Harper D. 2005. *Animal signals*. New York: Oxford University Press.
- Norušis MJ. 1993. *SPSS for windows: base system user's guide*, release 6.0. Chicago: SPSS Inc.
- Pilastro A, Biddau L, Marin G, Mingozzi T. 2001. Female brood desertion increases with number of available mates in the Rock Sparrow. *J Avian Biol.* 32:68–72.
- Pilastro A, Griggio M, Matessi G. 2003. Male rock sparrows adjust their breeding strategy according to female ornamentation: parental or mating investment? *Anim Behav.* 66:265–271.
- Pilz KM, Smith HG, Sandell MI, Schwabl H. 2003. Interfemale variation in egg yolk androgen allocation in the European starling: do high-quality females invest more? *Anim Behav.* 65:841–850.
- Pizzolon M, Rasotto MB, Mazzoldi C. 2008. Male lagoon gobies, *Knipowitschia panizzae*, prefer more ornamented to larger females. *Behav Ecol Sociobiol.* 62:521–528.
- Price T, Schluter D, Heckman NE. 1993. Sexual selection when the female directly benefits. *Biol J Linn Soc.* 48:187–211.
- Reinhold K, Kurtz J, Engqvist L. 2002. Cryptic male choice: sperm allocation strategies when female quality varies. *J Evol Biol.* 15:201–209.
- Reynolds JD, Gross MR. 1992. Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. *Proc R Soc Lond B Biol Sci.* 250:57–62.
- Rundle HD, Chenoweth SF, Blows MW. 2008. Comparing complex fitness surfaces: among-population variation in mutual sexual selection in *Drosophila serrata*. *Am Nat.* 171:443–454.
- Ryan MJ. 1990. Sexual selection, sensory systems and sensory exploitation. *Oxf Surv Evol Biol.* 7:157–195.
- Serra L, Griggio M, Licheri D, Pilastro A. 2007. Moulting speed constrains the expression of a carotenoid-based sexual ornament. *J Evol Biol.* 20:2028–2034.
- Servedio MR, Lande R. 2006. Population genetic models of male and mutual mate choice. *Evolution.* 60:674–685.
- Sheldon BC, Andersson S, Griffith SC, Ornborg J, Sendecka J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature.* 402:874–877.
- Wagner WE. 1998. Measuring female mating preferences. *Anim Behav.* 55:1029–1042.
- Wicker C, Jallon JM. 1995. Influence of ovary and ecdysteroids on pheromone biosynthesis in *Drosophila melanogaster* (Diptera, Drosophilidae). *Eur J Entomol.* 92:197–202.
- Williams TD, Ames CE. 2004. Top-down regression of the avian oviduct during late oviposition in a small passerine bird. *J Exp Biol.* 207:263–268.
- Wright D, Kerje S, Brandstrom H, Schutz K, Kindmark A, Andersson L, Jensen P, Pizzari T. 2008. The genetic architecture of a female sexual ornament. *Evolution.* 62:86–98.
- Zahavi A. 1975. Mate selection—a selection for a handicap. *J Theor Biol.* 53:205–214.