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White tail markings are an indicator of quality and affect mate preference in rock sparrows

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Abstract In birds, colourful and elaborate feathers are important traits in mate choice. Distinct tail white patches are present in many species of birds, but they remain little studied. Tail markings may indeed have a signal function because in many species males spread the tail offering a good view of these markings to females during courtship behaviour. Here, we investigated whether white tail spots in male rock sparrow, *Petronia petronia*, play a role in mate choice. In a free-living population of rock sparrows, we found a reduction in white tail spots size as the breeding season progressed due to abrasion, which was expected if tail spots act as a reliable quality indicator (i.e. a handicap). The same reduction was found under captive conditions, and males in worse condition (individuals that lost more weight) abraded a bigger part of white. This suggests that white tail markings are an indicator of male quality. In captivity, we measured female preference for males differing in white patch size in a mate choice experiment.

The experimental reduction of the size of the males' white spots resulted in a lower sexual interest by females. During courtship display, male rock sparrow shows a yellow breast patch (a carotenoid-based, sexually selected ornament) together with the white spots in the tail. The sizes of these two traits are positively correlated, but only the abraded white area in the tail correlates with a surrogate of individual quality (lost of weight). In conclusion, we can assert that the size of the white spots is preferred by female rock sparrows and it is a part of a multiple signal system.

Keywords Carotenoids · Condition-dependent trait · Honest signalling · Mate choice · Melanins · Ornaments · Multiple signals · Plumage condition · Sexual selection

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Intersexual selection works by favouring ornaments or other traits of one sex that are preferred by the other sex (Darwin 1871). In birds, ornamented tails have become an example of sexual selection theory and have been frequently shown as indicators of individual phenotypic quality (e.g. Andersson 1982; Møller 1988). Tail length has been the most frequently studied tail characteristic so far (see Barbosa and Møller 1999) and references therein) and shown to be important in female choice (Andersson 1982; Møller et al. 1998; Pryke and Andersson 2002; Romero-Pujante et al. 2002). Furthermore, tail length has been shown to be reflected in several fitness traits such as breeding performance (Møller et al. 1998; Regosin and Pruett-Jones 2001) or survival (Møller and Nielsen 1997). On a database of 520 bird species, Fitzpatrick (1998) found that nearly 80% of them displayed their tails. Among these, significantly more species with marked (colour spots) than unmarked tails had tail displays. Despite this fact, the question whether tail ornamentations, like white markings, have a signal function has received less attention (Höglund et al. 1990; Fitzpatrick 1998; Alvarez 2004).

In quality handicaps, sexual selection for more elaborate expressions is restrained by the costs to the bearer of development and maintenance of the elaborate trait (Zahavi 1975; Grafen 1990; Andersson 1994; Johnstone 1995). White plumage patches are special signals used as ornaments by birds (Gustafsson et al. 1995; Török et al. 2003; Galvan 2008; Olea et al. 2010), because contrary to other feather ornaments, like melanin- and carotenoid-based colourations, require neither pigment nor specialized feather structures (McGlothlin et al. 2007). Indeed white results from the scattering of light in all directions by unpigmented feather keratin (e.g. lack of melanin from feathers) (Prum et al. 1999). Therefore, production costs for these patches should be almost non-existent and then their importance as honesty signals has been questioned (Török et al. 2003). However, it was also suggested that the production of white plumage ornaments is not so inexpensive as usually assumed (Gustafsson et al. 1995). Recently, McGlothlin and colleagues (2007) found that in dark-eyed juncos, *Junco hyemalis*, individuals that received a high-protein diet grew their feathers more quickly and grew larger and brighter white patches. Other costs such as predation costs (Dale and Slagsvold 1996), parasite costs (Kose et al. 1999), breakage (Kose and Møller 1999) or social costs (Qvarnström 1997) have been reported for white ornaments in the plumage. Moreover, the relationship with body condition (Török et al. 2003), mate choice (Höglund et al. 1990) breeding success (Alvarez 2004) and immune defence (Hanssen et al. 2009) supports the hypothesis that white patches could be reliable signals of individual quality (Fitzpatrick and Price 1997; but see Lehikoinen et al. 2010).

The rock sparrow, *Petronia petronia*, is a passerine with a slight sexual dimorphism. This species undergoes a complete post-nuptial moult that ends in December (Serra et al. 2010). Both males and females have a yellow breast patch, a carotenoid-based trait, which seems to be slightly wider in males (Griggio et al. 2003a). There is evidence that the yellow breast patch is a signal of phenotypic quality of individuals: (1) non-breeders have smaller patches than breeding males or females (Pilastro et al. 2003); (2) its size is positively correlated with the ability to acquire a territory (Griggio et al. 2007) and (3) males with large yellow patches access to food earlier than males with small patches (Griggio et al. 2007). Both sexes also have conspicuous markings in the tail: all rectrices have white terminal tips and interindividual variation in size is large. Both the breast patch and the tail are displayed in heterosexual and agonistic behaviours but while the breast patch has been shown to have a functional meaning in mate choice (Griggio et al. 2005, 2007, 2009a), no study has addressed this issue for tail markings in this species. Rock sparrows forage on the ground and usually breed in holes and

crevices in cliffs and rock faces. They usually use their tails as a fulcrum while entering their holes or staying at the cliff so that the inner parts of the extreme of the rectrices (and thus the white tips) are subjected to wearing. Thus, we hypothesise that tail white spots in the rock sparrows are reliable indicators of quality that may play an important role in sexual selection processes.

In this paper, we first investigate in a free-living population if there are sexual differences in this trait which would support it as a target for sexual selection. Secondly, we test whether tail markings are quality handicap indicators signals. For this we explore whether white tail spots involve costs in terms of tail feathers abrasion. If so, individuals displaying large white spots would advertise the quality of their feathers (being more resistant to abrasion). Thirdly, we test by means of experimental manipulation whether females use tail white spots of males as a signal in mate preference process. We then predict that females should prefer males with enlarged white spots while keeping other ornaments constant. Finally, considering the presence of the yellow breast patch in the rock sparrow and its function in mate choice (Griggio et al. 2007), we study the relationships between both signals in the context of multiple sexual signals.

Methods

Study species and study area

The rock sparrow is a secondary cavity nester that breeds in colonies whose size can vary from a few sparse pairs to hundreds of pairs in particularly favourable conditions (Cramp and Perrins 1993). In our study site, located at the Desert of Tabernas (Almería, south-east Spain, 37°05′ N 2° 21′ W), rock sparrows used nest holes built by bee-eaters (*Merops apiaster*) in previous breeding seasons along a sandy cliff approximately 100 m long and 3–5 m high (see Casas-Criville and Valera 2005 for more details). Rock sparrows in this region are seriously limited by the scarce nest site availability and competed for nesting sites. Nests vary in several basic features like depth, distance to neighbouring occupied holes or inclination, some of them being completely vertical; whereas, others had platforms in front of the entrance that were used by sparrows for displaying. Rock sparrows are characterised by a social mating system varying from monogamy to polygamy, with both male and female brood desertion (Griggio et al. 2003b; Griggio and Pilastro 2007). The level of extrapair paternity is high, although it appears to be limited exclusively to the nests of polygynous males (Pilastro et al. 2002). Inter- and intrasexual interactions usually take place at the breeding site during the pair formation period and males able to

occupy a nesting site spend a long time sitting in front of the hole and singing to attract a female. Females usually visit several holes before pairing and starting to build the nest. Males courtship displays consist of the exhibition of the breast patch and/or the fanned tail towards the females and each courtship bout lasts usually 10 s (Griggio et al. 2005). Female courtship is sometimes followed by a chase flight in which males follow the female and try to copulate with her (Cramp and Perrins 1993; Griggio et al. 2005).

Field methods

Starting at mid-April (in 2001) and mid-March (in 2002) until the first week of July, adult birds were mist-netted at the colony and individually colour ringed. Body mass (to the nearest 0.1 g), bill length (exposed culmen), maximum wing, tarsus, and tail length (Svensson 1992) were measured. While holding the bird to expose its ventral side, with its bill and head perpendicular to the body, we measured the width (major axis) and height (minor axis) of the yellow breast patch. We also measured the major and minor axis of the oval white spots of the outermost right and left rectrices and, for a subsample of birds, the major and minor axis of the white spots in all the rectrices. The area of each white spot was calculated assimilating them to an ellipse and using the corresponding formula (major semiaxis×minor semiaxis×π). All linear measurements were taken with a dial calliper (to the nearest 0.1 mm).

Aviary experiment: size of white tail spots and female preference

The experiment, designed to evaluate the preference of females for large- and small-tail spotted males, was carried out during May 2005 (eight trials), 2006 (five trials) and 2008 (eight trials) at the Konrad Lorenz Institute for Ethology of the Austrian Academy of Sciences in Vienna. Forty-two males and 21 females (24 individuals from Italy, 11 from Spain, and 24 born in captivity) were kept in single-sex flocks aviaries until they entered in the experimental phase. Males and females did not see each other during acclimatisation. Aviaries were provided with perches and shelters and bathing water, and birds were fed daily with a mixed diet of commercial seeds and fruits and water.

The dimensions of the white tail spots were measured by drawing the contour of the white area of all rectrices on a strip of transparent acetate placed on the flattened rectrices. Drawings were scanned and areas calculated with UTHSCSA Image Tool software (http://ddsdx.uthscsa.edu/dig/download.html). A total area of white spots was then calculated by summing all the areas.

Forty-two stimulus males were randomly divided in two groups: with reduced white spots and with enlarged white spots (hereafter reduced and enlarged males, respectively). Manipulation of the size of the white spots was done on the left and right outermost feathers both because of the difficulties in manipulating all tail feathers and because the white area of the outermost left and right rectrices is highly correlated with the white area of the whole tail feathers both for birds in the wild (Pearson's correlations, for males—$r=0.80$, $P<0.001$, $N=23$; for females—$R=0.78$, $P<0.001$, $N=20$, field data from Spain) and for males used in the experiment ($r=0.42$, $P=0.006$, $N=42$). To manipulate the size of the white spots we use moulted, external rectrices collected during the previous autumn (24 feathers). A set of rectrices ($N=12$ feathers) was prepared for the reduction treatment by painting with a black marker on the white margins of the spots so that we did not modify the shape of the spot but its size that remained within the natural range. For the enlargement treatment, we chose several external rectrices ($N=12$ feathers) with natural large white spots. As a control for the use of black marks, we painted the black periphery of the spots with a black marker so that neither size nor shape of the white spots was modified but the likely reflectance effect that the marking pen could have caused was thus balanced. Rectrices with the manipulated spots were stapled (two staples per feather) on the basis of the original left and right outermost rectrices of the experimental males (covering the original outermost rectrices). This procedure did not affect foraging ability or any other behaviour or survival. Staples were easily removed shortly after the experiment by opening one extreme of the staple with a forceps.

In total, we produced 12 pairs of outermost feathers, six small and six large pairs (reduced, $X\pm SE=61.69\pm 0.13$ mm^2; enlarged, $X\pm SE=129.81\pm0.81$ mm^2) so that the manipulated area (both in the reduction and enlargement treatment) was within the natural range ($X\pm SE= 95.7\pm2.6$ mm^2; range, 61.1–129.7 mm^2; $n=42$ males). The pair of feathers to be used for the small and large spotted pair of males in a given trial was chosen at random. There was no difference in the white area of the outermost feathers or the total white area of the tail between the two groups of males before the experimental manipulation of the tail markings (Table 2). After manipulation, the white area of the outermost feathers and the total white area of the reduced males were significantly smaller than the white area of the outermost feathers and the total white area of the enlarged group (see Table 2).

It could be argued that this manipulation may increase the variance among all feathers and that this change in variance may be different in the two groups that could affect signal assessment by females. However, the variance

between tail feathers (outermost and inner feathers) was similar in the two groups and it was within the natural range ($P>0.11$).

We also measured the size of the breast patch of experimental birds by holding the bird to expose its ventral side, with its bill and head perpendicular to the body, by placing a strip of transparent acetate over the throat and drawing the contour of the yellow area and by measuring with a calliper the width of the patch (see Pilastro et al. 2003; Griggio et al. 2003a, b, 2005, 2009a for a detailed description of this method). Before the experiments commenced, we standardized the size (i.e. width) of the breast patches of all males ($N=42$) by cutting the distal feathers on the sides of the patch (for more details, see Griggio et al. 2005, 2007). The mean breast patch size of the two groups of males before manipulation of this trait was similar (Table 2). There was no difference between the two groups of males in breast patch width after reduction (Table 2). Since this experiment aims to highlight the role of white patches in mate choice criteria of rock sparrows and given that breast patch is a signal of phenotypic quality of individuals used in mate choice by females and males (Griggio et al. 2005, 2007, 2009a), we preferred to minimize the role of this trait by reducing its size (but keeping it within the natural range, see Tables 1 and 2) and the variability among individuals. Whereas this approach may introduce a mismatch between different components of male signals used by females in mate choice, it allows a clear assessment of the importance of white patches for mate choice.

The trials were run in a two-choice indoor cage ($1\times1.1\times0.5$ m) in which the female, placed in a central cage, was allowed to choose between two stimulus males (i.e. a reduced and enlarged male), each one placed in adjacent cages. Opaque dividers were erected on the two sides of the central enclosure so that they avoided visual interaction between the two males and prevented females from simultaneously observing the two males. Perches were provided so that both males and the female could keep visual contact but also stay out of sight (for similar

experimental apparatus see Griggio and Hoi 2006; or Griggio et al. 2007). As a measure of preference, we measured the time spent by a female on the perch in front of either male's compartment (choice time) (Griggio et al. 2007). When females perched in the zone where visual access into both male compartments was obscured (i.e. the neutral zone), we recorded no preference with respect to either male (neutral time). Males and females were allowed to acclimatise to their compartments for at least 2 h (on average 3 h) before the experiment started. Following acclimatisation, the position of the female was recorded every 15 s for 1 h (i.e. 240 records per trial). Males with increased and decreased white spots were alternated with respect to left and right compartments among consecutive trials. In total, 21 trials in which females visited both stimulus males were obtained. The mate choice trials were performed between 0800 and 1000 h. All behavioural observations were carried out from a hide placed approximately 4 m from the choice apparatus. No female and no stimulus male were used more than once. After the experiment (end of May), all the birds were released in outdoor aviaries where most of them bred.

Estimation of the rate of feather abrasion in captivity

In February and May 2008, we measured body mass, maximum wing length, tarsus and tail length as well as the total white area of tail spots and the size of the yellow breast patch from 38 individuals (23 males and 15 females) of a captive population held at the Konrad Lorenz Institute. The dimensions of the white tail spots and yellow breast patches were measured as described above (see "Aviary experiment: size of white tail spots and female preference"). Birds were kept in a big outdoor aviary ($10\times6\times4$ m) equipped with vegetation, rocks, several perches and nest boxes. Commercial food for granivorous passerines, fruits, vegetables and water were provided ad libitum. We calculated the abraded area (%) in the tail and breast patch as the difference between the two measurements divided by the area measured the first time.

Table 1 Sex-related differences in body size parameters, breast patch and area of white spots in the tail of male and female rock sparrows from Spain

Mean and SE and ANOVA test are offered

	Males	Females	F (df)	P
Tarsus length (mm)	18.2±0.15 (39)	18.3±0.12 (36)	0.50 (1, 73)	0.47
Bill length (mm)	14.4±0.09 (39)	14.8±0.11 (36)	7.98 (1, 73)	0.006
Wing length (mm)	97.3±0.32 (38)	94.4±0.34 (37)	36.06 (1, 73)	<0.001
Tail length (mm)	58.0±0.5 (39)	55.8±0.55 (36)	9.49 (1, 73)	0.003
Body mass (g)	31.3±0.27 (39)	32.2±0.33 (31)	4.10 (1, 68)	0.046
Yellow patch width (mm)	5.7±0.20 (39)	4.6±0.19 (36)	15.21 (1, 73)	0.0002
White area outermost feathers (mm^2)	109.2±4.4 (26)	88.9±3.4 (20)	12.23 (1, 44)	0.001
White area in tail (mm^2)	417.2±15.6 (23)	342.0±12.3 (20)	13.76 (1, 41)	0.0006

Table 2 Morphological data of the two groups of males used in female mate choice experiment

	Reduced (N=21)	Enlarged (N=21)	F	P
Tarsus length (mm)	18.6±0.14	18.6±0.14	0.01	0.96
Tail length (mm)	55.6±0.37	56.1±0.43	0.84	0.36
Body mass (g)	31.0±0.25	31.4±0.98	1.72	0.2
Yellow patch size (mm)	16.9±0.41	16.21±0.33	1.72	0.2
Yellow patch size after manipulation (mm)	10.4±0.12	10.1±0.09	2.05	0.16
White area outermost feathers (mm^2)	94.3±4.07	97.0±3.33	1.96	0.17
White area outermost feathers after manipulation (mm^2)	71.37±5.27	118.98±5.26	6.39	< 0.001
White area in tail (mm^2)	527.3±21.97	554.1±26.1	0.79	0.43
White area in tail after manipulation (mm^2)	497.2±20.35	588.6±26.6	2.72	0.010

Statistic refers to ANOVA test. Mean and SE are offered

Molecular sexing

Blood samples were taken from birds from both the field and captivity by draining 50–100 µl from the brachial vein using disposable heparinised capillaries and used for molecular sexing. The sex of individuals was determined by using the W chromosome linked avian CHD gene (Ellegren et al. 1996). Throughout polymerase chain reaction amplification of two homologous genes (CHD1W and CHD1Z), using the primers P2 and P8, we identified females as showing two gene copies (CHD1W plus CHD1Z) whereas males displayed a single copy (CHD1Z), as described in Griffiths et al. (1998).

Statistical analyses

For the field data, sexual differences in body size were tested with a multivariate analysis of covariance (MANCOVA), with gender and year as independent variables and body mass, tarsus, bill, wing and tail length as dependent variables and capture date as a covariant. Sex-related differences in breast patch dimensions were tested with a MANCOVA with gender and year as independent variables, patch width and height as dependent variables and capture date as a covariant. Sexual differences in white area in the tail were tested with an analysis of covariance (ANCOVA), with gender and year as independent variables, total white area in the tail as the dependent variable and tail length and capture date as covariates.

Forward stepwise multiple regression analyses were run to explore the relationship between the size of white spots (measured as the sum of the white area of the left and right outermost feathers as well as the sum of the white area of all the tail feathers) and morphological variables (wing, tarsus, bill and tail length, breast patch width and height and body mass). Since tail spots get abraded as the season progresses (see "Results") and we want to study the relationship between original size of tail spots and patch size, we restrict our data to the first 2 months of the breeding season (19 March to 19 May).

Outcomes from all female preference experiments were analysed with a generalized linear model (GLM), in which female preference (proportion of time spent in front of a particular male) was the dependent variable. The following males' variables were entered in the model as covariates: year of the experiment, natural (original) and manipulated yellow breast patch size, natural (original) and manipulated white spots area (for the whole tail), tail and tarsus length, body mass and the origin of birds used in the experiment (Italy, Spain or born in captivity).

All data were checked for normality, and appropriate transformations were used when necessary. Proportions were arcsine square root transformed before the analyses (Sokal and Rohlf 1995). All probabilities are two-tailed and, unless otherwise stated, means±SE are given.

Results

Ornaments in males and in females

Male and female rock sparrows show sexual dimorphism in body size (MANCOVA—gender, $F_{5, 60}$=10.5, P<0.001; capture date, $F_{5, 60}$=3.2, P=0.013; year and the interaction year×gender, P>0.05) so that males have longer wings and tails (Scheffé post hoc comparisons, P<0.01 for both variables) (see also Table 1).

Dimensions of the breast patch also differ between males and females (MANCOVA—gender, $F_{2, 69}$=6.4, P=0.003; capture date, $F_{2, 69}$=5.7, P=0.0048), the former having a wider patch (univariate test, P<0.01) and a higher patch, though not significantly (P=0.06). We found a significant effect of year (MANCOVA, $F_{2, 69}$=14.1, P<0.001), but the interaction between year and gender was not significant ($F_{2, 69}$=0.03, P=0.9).

The white area in tail feathers differed between sexes (ANCOVA—gender, $F_{1, 37}=6.8$, $P=0.012$; capture date, $F_{1, 37}=3.6$, $P=0.064$; no significant effect of year, tail length or the interaction between year and gender) so that males had larger white spots than females (Table 1). This is also the case if we consider only the area of the outermost right and left tail feathers (gender, $F_{1, 40}=9.0$, $P=0.004$; capture date, $F_{1, 40}=5.1$, $P=0.03$, the remaining factors being non-significant).

Relationship between tail markings and breast patch size

A forward stepwise multiple regression analysis with field data from both study years shows that the only phenotypic variable associated with the total white area in males' tail feathers is the width of breast patch ($F_{4, 14}=3.9$, $P=0.024$, $R^2=0.53$; Beta=0.64, $P=0.005$). When using the white area of the outermost feathers as dependent variable, the factors entering the model ($F_{3, 16}=4.55$, $P=0.017$, $R^2=0.46$) are patch height (Beta=−0.55, $P=0.014$) and patch width, though not statistically significant (Beta=0.37, $P=0.061$).

White tail markings and abrasion

Tail spots of captive birds (all feathers) abraded on average $12\pm2\%$, after 3 months in the aviaries. The percentage of area reduction of white spots was significantly larger than the one recorded for the yellow breast patch in the same period ($6\pm2\%$; Student's t test, $t_{74}=2.04$, $P=0.045$). Abrasion of the white spots was more intense in males than in females, though differences are not statistically significant (percentage or area reduction—male, $15\pm3\%$; range, 1–45%, $N=23$; female, $7\pm3\%$, range, 0–42%, $N=15$; Student's t test, $t_{36}=1.95$, $P=0.059$). We found no significant correlation between the percent of area reduction in white spots for the whole tail and any of the phenotypic variables considered measured in February, either for males or females (Pearson's correlations, all $P>0.15$ and all $r<0.311$ for 23 males and 15 females). The percentage of reduction of white spots was not correlated with the initial area of the same white spots (male—Pearson's correlation, $r=-0.096$, $P=0.66$, $N=23$; female—Pearson's correlation, $r=0.026$, $P=0.93$, $N=15$). However, in males there was a negative correlation between the body weight after 3 months and the amount of white abraded for the whole tail (Pearson's correlation, $r=-0.541$, $P=0.008$, $N=23$), but this was not the case for females (Pearson's correlation, $r=-0.300$, $P=0.28$, $N=15$). Similar results were obtained using the difference in body weight between the two measurements (data not shown). Lastly, there was no significant correlation between body weight after 3 months and yellow patch abrasion for both males and females (male—Pearson's correlation, $r=-0.323$, $P=0.13$, $N=23$; female—Pearson's correlation, $r=0.434$, $P=0.16$, $N=15$).

White spots abrasion was also evident under natural conditions. The white area of males' outermost tail feathers decreased as the season progressed (Pearson correlation's, $r=-0.50$, $P=0.009$, $N=26$, data from both years). This is also the case for the white area in the whole tail for 2001 ($r=-0.65$, $P=0.008$, $N=15$) but not for 2002 ($r=0.16$, $P=0.71$, $N=8$), even though this result can be affected by the low sample size.

Female mate preference and white tail markings

Experimental and control males exposed to choosing females did not differ in any morphological feature except the size of the white spots after manipulation (Table 2). During the experiments, females moved back and forth between the males several times extending their necks to show off the breast patch to the males. In all 21 trials, the female visited both the left and right side of the response area. However, females spent significantly more time in front of the male with the enlarged white spots than in front of the reduced male (Paired t test, $t_{20}=2.71$, $P=0.014$) (Fig. 1).

Lastly, there were no significant differences in female preferences based on male original ornaments sizes (yellow breast patch size and white spots area), morphology (tail, tarsus and weight), provenience of the birds, and the yellow patch size after manipulation, year of the experiment (GLM analysis, all $F_{1, 41}<2.79$, $P>0.1$). In the GLM model, only the manipulated white spots total area had an effect on female preference ($F_{1, 41}=6.07$, $P=0.02$).
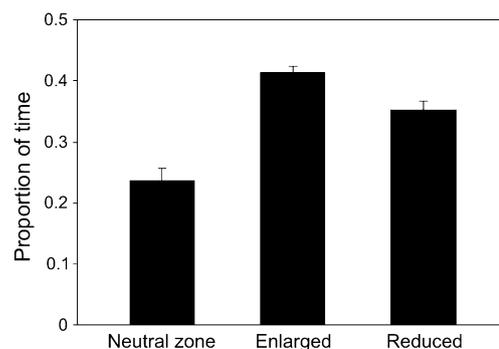

Fig. 1 Female preference in relation to the size of white tail spots of experimental males (expressed as the proportion of time spent in front of each male and of a neutral zone). The neutral zone represents the space from which the female could not see any male. Enlarged group refers to males carrying two outermost rectrices with large white spots ($n=21$). Reduced group refers to males carrying two outermost rectrices with decreased white spots ($n=21$) (see "Methods"). Mean proportion of time (seconds)±SE are given

Discussion

Our results show first that white tail spots differ between sexes suggesting that this trait could be the target of sexual selection. Secondly, we found evidence that tail white markings entail some costs. More specifically, we recorded that both under natural and artificial conditions tail feathers get abraded so that the white spots get a noteworthy reduction in a short time. In particular, males in worse conditions (body weight lost after 3 months) lost a bigger portion of white, suggesting that white tail markings are an indicator of male quality. Field data suggest that feather abrasion increases along the breeding season. Thirdly, our results show that the experimental reduction of the size of the males' white spots resulted in a decreased sexual interest by females in captivity when another signal such as the breast patch is kept constant. These results support our hypothesis that tail white spots in rock sparrows are reliable indicators of quality that may play an important role in sexual selection processes. This agrees with recent results supporting that white patches are reliable signals of male quality in spite of the presumed low costs of production (Török et al. 2003; McGlothlin et al. 2007; Hegyi et al. 2008).

Indicators of phenotypic quality should be costly to produce and/or to maintain (Zahavi 1975; Grafen 1990; Iwasa et al. 1991). White ornaments involve the lack of melanin in the feathers. Thus, their production costs should be low (Serra et al. 2007, Griggio et al. 2009b; but see McGlothlin et al. 2007). Accordingly, there should be a major role for costs of wearing the trait, such as predation costs, parasite costs and social costs (Dale and Slagsvold 1996; Qvarnström 1997; Kose et al. 1999). White spots on the tail may indicate feather quality due to the absence of melanin that weakens keratin and makes it more prone to abrasion in poor-quality individuals (Fitzpatrick 1998; Barbosa et al. 2003) being therefore likely to indicate phenotypic quality. Experimental studies have demonstrated that melanin-free feathers, as in the case of the white spots, are more likely to break than melanised feathers (Burtt 1986; Bonser 1995; Kose and Møller 1999; Kose et al. 1999). Our field data provide scarce cases of broken tail feathers, but the ones observed confirm that breakage frequently occurs in the white area (authors' personal observation). Moreover, captivity data suggest that abrasion acts on the white spots reducing its size regardless of the original white spot size as the time progresses. This means that birds with an initial large white spot will probably keep a proportionally larger spot along the season than birds with a smaller spot. Abrasion can also affect individuals differently. We found a stronger abrasion in males than in females that could be explained by the higher rate of tail display of males or by a higher rate of nest defence at the cliff by males than by females. Moreover, interindividual differences can be exacerbated by differences in competitive abilities to gain access to good quality nesting sites. Rock sparrows nest in crevices and holes, frequently in steep locations, and use their tails as a fulcrum to enter the nest and stay at the rock faces and cliffs. Differences in nest site suitability can probably result in different abrasion rates of the tail feathers and, consequently, in differences in the size of the white spots. Thus, aviary data on abrasion of tail spots provide evidence that the size of the rock sparrows' tail spots act as a handicap signal (Fitzpatrick 1998).

An additional cost of wearing white tail spots is related to parasitism. There is evidence that feather lice prefer eating feathers that lack melanin (Kose and Møller 1999; Kose et al. 1999). A single species of feather lice has been recorded parasitizing the rock sparrow and data from two breeding seasons reveal that lice do not inhabit tail feathers and thus do not affect the size of the white tail markings (authors' personal observation).

Tail markings could also entail social costs (e.g. intra-sexual competition). We found that the size of tail spots is correlated with the size of the breast patch, a phenotypic quality indicator that is sexually selected (Griggio et al. 2005, 2007, 2009a). Previous studies on the breast patch, a carotenoid-based feather signal, demonstrated that the same trait is involved in both mutual sexual selection and male–male competition (Griggio et al. 2007). Moreover, it seems that the yellow breast patch is also involved in female–female competition (Griggio et al. 2010). Thus, it would not be surprising that tail markings also play a role in intrasexual competition. Even though the costs of tail markings associated with predation remain to be evaluated, we do not have evidence that this could play a major role. Male rock sparrows display the tail in short bouts during courtship. Thus, increased predation risk would occur, at most, in brief, specific periods.

Previous studies demonstrated that the yellow breast patch is involved in the mutual sexual selection (Griggio et al. 2003a, 2007). It is possible that tail markings could also evolve as signals of female quality and thus subject to sexual selection. Future studies should therefore take into account the importance of female white spots as sexual signals.

Our results show that male rock sparrows do not only possess larger white spots than females but also that have longer wings and tails. It could thus be conceivable that white spots at the end of the tail feathers could act as amplifiers of tail length. However, we did not find any significant relationship between white spots area and tail length, which indicates that white spots do not facilitate the perception of tail length as expected from an amplifier (Fitzpatrick 1998; Hasson 1991, 1997). Given that inter-sexual differences in tail length, though significant, are small and that tail length in rock sparrows does not seem to

be a crucial trait in sexual selection (in contrast to other species like the barn swallow, *Hirundo rustica*, Møller et al. 1998), we presume that white spots do not act as magnifiers.

As stated before, one main aim of our study was to highlight the role of white patches in mate preference criteria of rock sparrows. For that, we minimized the expression of the breast badge, a sexually selected ornament in this species (Griggio et al. 2005, 2007, 2009a). Thus, choosing females may have been faced with a mismatch between different components of male signals used by females in mate choice that could obscure the assessment of the importance of white patches for mate choice. In contrast, we found a clear pattern: females preferred males with larger white spots. During courtship, male rock sparrows display the breast patch and spread the tail. We also found that the size of white tail spots is correlated with the size of the breast patch. These results together with the ones reported here about the role of white tail spots indicate that female rock sparrows base their choice on different signals components rather than on a single one, probably using a system of multiple sexual signals.

According to the multiple message hypothesis, different signals might convey information on different properties of male quality (Møller and Pomiankowski 1993; Johnstone 1996; Loyau et al. 2005). In particular, carotenoid-based feather ornaments are correlated with individual quality (immune system, parasite resistance and condition) in many species (for a review see Olson and Owens 2005) and also in the rock sparrow (e.g. Pilastro et al. 2003; Serra et al. 2007). These signals are generally considered to be honest because carotenoids cannot be synthesized de novo but must be obtained from the diet (Møller et al. 2000), usually several months before the breeding season. Carotenoid feather traits may be long-term signals that advertise male quality during the production of the trait (moult). On the contrary white tail spots may reflect the capacity to maintain in good condition a trait more susceptible to abrasion, ectoparasite or soiling. Indeed the abrasion of the white spots was correlated with the male's body weight while abrasion of the yellow patch was not. Thus, different feather traits may reflect individual quality over different time scales as proposed by the multiple message hypothesis (Johnstone 1996). Indeed, a recent experiment on moult duration in the rock sparrow revealed that fast-moulting males showed a decrease in size and colour parameters of the breast patch, whereas the effect of moult duration on the size of white spots was very weak (Serra et al. 2007).

Interestingly, white tail spots can only be assessed by females when males spread the tail that can depend on the male motivational level and sexual interest as other sexual behaviours (Hauser 1996). In a recent paper, Loyau et al.

(2005) show a similar scenario for the peacock, finding that the interaction of behavioural (display) and morphological traits improves the discrimination of male quality. Moreover, they suggest that each trait (morphological and behavioural) amplified the message conveyed by the other trait, thereby enhancing information reliability. Although we have no data on the relationship between the magnitude of tail display and the quality of the males, it is a plausible scenario that can be added to the above stated functions.

In conclusion, our results provide evidence that the white tail spots and specifically their size may be used by female rock sparrows for mate preference, probably as a signal of male quality.

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