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Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal

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Abstract Females often base their mating preferences on male sexual secondary traits that are used to settle contests among males. Such traits are likely to be honest indicators of male quality if they are constantly used during costly male–male agonistic interactions. Carotenoid signals have been shown to work as a handicap because they are costly to produce. However, the role of carotenoids as "honest" signals during male contests is less clear, and it is not known whether a carotenoid-based trait can serve in both male–male competition and female choice. In this study, we studied the dual function of a carotenoid feather ornament in the rock sparrow (*Petronia petronia*), a bird species in which both sexes have a yellow throat patch whose size positively correlates with phenotypic measures. First, we investigated, in a field study, whether the size of a male's yellow patch correlates with his ability to acquire a territory. Second, we tested the signal function of the yellow patch in two male–male interaction in captivity experiments. Finally, we measured female preference for males differing in throat patch size in a mate choice experiment. Our experiments revealed that the size of a male's throat patch positively correlated with the number of nest boxes he was able to defend. Moreover, in controlled conditions, males with relatively large yellow patches had earlier access to food than those with small patches. Also,

in an experiment in which a dummy rock sparrow with an experimentally manipulated yellow patch was positioned near a feeder, latency to feed by focal birds positively correlated with dummy patch size. Lastly, in a dichotomous mate choice experiment, females showed a proximity preference for males whose patch was experimentally enlarged. Taken together, these results suggest that the same carotenoid feather signal may be used in both male–male competition and female choice in this passerine bird.

Keywords Male–male competition · Female choice · Mutual selection · Status signaling · Condition-dependent traits

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In many animal species, females prefer to mate with the most ornamented males (Andersson 1994). When male quality is positively correlated with the expression of these ornamental traits, females can gain direct benefits (e.g., through good territories or male parental care) or indirect (genetic) benefits from their choice of mate (Andersson 1994; but see Holland and Rice 1998 for a review). For an ornament to honestly signal an individual's quality, it must be costly to produce (Zahavi 1975; Grafen 1990). This seems to be the case for ornamental traits based on carotenoids, the pigments often responsible for red and yellow skin, scale, or feather coloration (e.g., Kodric-Brown 1989; Gray 1996; Wedekind et al. 1998). Many studies on male secondary sexual characters have concentrated on these carotenoid-based signals because of their potential link with immune function, parasite resistance, and condition and because these pigments cannot be synthesized de novo but must be obtained from the diet (Hudon 1994; Olson and Owens 1998, 2005; Hill 1999a; Møller et al. 2000). Carotenoids function as antioxidants and immunostimulants (Chew 1996), and a trade-off in carotenoid allocation between

maintenance and ornamentation has therefore been hypothesized (Lozano 1994). The rationale behind this hypothesis is that males in better condition should require fewer carotenoids for maintenance (i.e., immune function) and therefore be able to allocate a larger portion of their limited carotenoid stores to ornamentation (Lozano 1994; Olson and Owens 1998; von Schantz et al. 1999; but see Hartley and Kennedy 2004 for a review). Indeed, several examples of honest signaling in animals are based on carotenoid-based ornaments (e.g., Hill 1991; Burley et al. 1992; Nicoletto 1995; Candolin 2000; Peters et al. 2004).

The function of carotenoid ornaments in female choice has been studied in detail in birds (e.g., Hill 1999b), and it has recently been demonstrated that changes in circulating carotenoid levels generate variation in immune function and sexual attractiveness (e.g., Blount et al. 2003; Faivre et al. 2003). These latter cases focused on male ornaments with variable carotenoid levels (bills), which can therefore respond to changes in males' actual levels. Feather carotenoid ornaments, in contrast, are often formed several months before the breeding season and will therefore reflect a male's condition at the time of molt (Navara and Hill 2003). So, one may argue that the dietary limitation or the trade-off between physiological function and ornament may not be sufficient to maintain the honesty of signals formed some months before.

A general mechanism to account for the maintenance of costly male secondary sexual traits is the armament–ornament model (Berglund et al. 1996; recently reviewed in Wong and Candolin 2005), which predicts that females are expected to "exploit" signals used in male–male contests because the reliability of these traits is constantly put on trial in these contests and cannot be faked without incurring high costs. Several studies have confirmed that the same trait can be selected by both female choice and male–male competition (e.g., crest: Jones and Hunter 1999; courtship behavior: Mateos and Carranza 1999; call: Borgia and Coleman 2000; UV reflectance: Alonso-Alvarez et al. 2004; black mask: Tarof et al. 2005, but see Leitao and Riebel 2003 for a negative result on song). In birds, females often base their sexual preferences on variation in feather carotenoid signals (see Hill 1999b for a review), but evidence that these signals are also important in male–male competition is less abundant (Pryke et al. 2001b; Pryke and Andersson 2003a; Evans and Norris 1996; Etman et al. 2001; Preault et al. 2002; Bright et al. 2004; see Griffith et al. 2006 for a review).

In this study, we examined the dual function of a carotenoid feather ornament in the rock sparrow (*Petronia petronia*). The rock sparrow is a monomorphic cavity-nesting passerine that breeds in the middle latitudes of the Palearctic (Cramp and Perrins 1994). Rock sparrows feed on the ground, eating mainly small weed seeds, but also grain and insects, particularly caterpillars and grubs, on which the young are fed until they fledge. The rock sparrow's social mating system varies from monogamy to polygamy (Pilastro et al. 2001), and it usually breeds in colonies varying from a few to hundreds of pairs. Inter- and intrasexual interactions usually take place at the breeding site (holes in buildings or small cliffs and also nest boxes, where available). Male and female rock sparrows exhibit a small carotenoid-based yellow feather patch (R. Stradi and F. Giomi, personal communication). This (roughly trapezoid-shaped) feather patch is positioned between the throat and the upper breast. Males use these patches during territorial disputes and courtship displays (Cramp and Perrins 1994). During courtship displays, males exhibit their yellow breast patches and white tail spots toward females, combined with wing shivering and vibrating the feathers of the breast. During the antagonistic display, males extend their throats to show off the yellow patch or they assume a "wing-up posture" in which they show the yellow patch and fan-out the tail (for more details, see Cramp and Perrins 1994). However, in this paper, we did not investigate the role of tail white spots of the male as a cue in mate choice or in male–male competition. Rock sparrow males prefer females with a large yellow patch (Griggio et al. 2005). Indirect evidence indicates that females may prefer males with a large yellow patch, as suggested by assortative mating with respect to patch size (Griggio et al. 2005). However, the role of the male's yellow patch in intra- and intersexual contexts has never been investigated experimentally in this species. In this study, we first determined whether, under natural conditions, the size of a male's yellow patch correlates with his competitive ability, as indicated by the number of nest boxes a male is able to defend during the breeding season. We also investigated the function of the yellow patch during male–male contests in aviary experiments. Finally, we measured females' preferences for male yellow patch size using an aviary two-choice test in which females were presented with two males whose yellow patch was experimentally reduced or enlarged. We predicted that (1) the size of the yellow patch would be a signal of dominance, and males with relatively larger yellow patches would have an advantage in intrasexual contests, and (2) that large-patched males would be preferred by females.

Materials and methods

Male polyterritoriality and yellow patch size in natural conditions

The study area was located in the upper Susa Valley, western Alps, where 39 nest boxes were set up every spring

in two neighboring villages (one village was located at 1,550 m and the second at 1,800 m above sea level, Griggio et al. 2003a,b). During 1998, 1999, 2000, and 2002, we trapped territorial males in their nests. Birds were individually marked with a numbered aluminum ring and a unique combination of colored rings. We measured the maximum wing chord length (hereafter: wing length, Svensson 1992) to the nearest 0.5 mm and the tarsus length to the nearest 0.1 mm. Body mass was recorded to the nearest 0.1 g. The width of the yellow patch was measured to the nearest 0.1 mm (more details in "Yellow patch size measurements" subsection below). For the following analyses, males were aged in two groups: 1 year old and older. Age was known on the basis of their age at first capture (most males were first ringed as nestlings). Other individuals were ringed as adults in previous breeding seasons and were included as "older" birds. In late May, males started defending one or more nest boxes by regularly singing on the top of the nest box or in its close vicinity. We collected 1 h behavioral observations every 2–3 days at the nest. If a male defended only one nest box during the first part of the breeding season (the first 3 weeks of June), it was defined "monoterritorial"; males that defended more than one box at the same time for more than three consecutive days were termed "polyterritorial". The data analyzed in this paper include 30 breeding males (4 males in 1998, 9 in 1999, 4 in 2000, and 13 in 2002). Mean observation time per male±SE was 4.53±0.13 h (range: 4–6). Each male was used in this analysis only once.

Maintenance of captive birds

We captured 27 yearling individuals (17 males and 10 females) in the central Apennines (L'Aquila, 42°23′N– 13°18′E) between 6 and 8 August 2003. The birds were captured with mist nets at two different sheep watering places (the distance between the two places was 10 km), where hundreds of rock sparrows converged daily from a wide catchment area. They visited the area singly or in small flocks (two to five individuals) from about 1 h after dawn to sunset. Twenty-two birds were in active primary molt, while five had not yet started. On the basis of primary molt advancement, we estimated that they were approximately 4–8 weeks old (Cramp and Perrins 1994). Each bird was marked with a numbered aluminum ring and a unique combination of three colored rings (excluding yellow, orange, and red to minimize potential effects on visual communication, Burley 1988). On the last day of trapping, the birds were transferred to the Istituto Nazionale Fauna Selvatica (Ozzano Emilia, 44°28′N–11°30′E) and housed individually in cages (58×33×31 cm) that were visually isolated from each other. All birds were housed in the same room (housing room). Each cage was open to light

(artificial and natural through windows) only on the front side (with grating bars), all other sides being of enameled sheet steel. Cages were hung up on opposite sides of a rack, each side hosting 16 cages. Acoustic contact was not prevented. All birds were fed with a mixed diet of commercial bird seed, fruit, and vitamins. 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. The yellow patch size was measured (more details in "Yellow patch size measurements" subsection below).

Yellow patch size measurements

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. 2003a; Griggio et al. 2005). We traced the patch twice and measured its major axis on 27 individuals maintained in captivity to evaluate the repeatability of this measure. The mean difference between the two measures ±SE was 4.46±1.0%. A detailed description of measuring the yellow patch of the rock sparrow can be found in the studies of Pilastro et al. (2002, 2003).

We did not quantify patch color in this study. However, in a parallel, spectrometric study, we found that patch color is much less variable among individuals (coefficients of variation in brightness in red and yellow part of the spectrum=4.9 and 5.0%, respectively. Red brightness= summed reflectance between 625 and 700 nm; yellow brightness=summed reflectance between 550 and 625 nm) than patch width (CV=20.4%, authors' unpublished results). Furthermore, patch brightness and width were positively correlated (red: $r=0.48$, $P=0.014$; yellow: $r=0.50$, $P=0.01$, $n=25$, authors' unpublished results). Thus, although patch color is likely to be important, patch width captures a large part of the interindividual variation in signal quality.

Yellow patch size and male–male competitions in captivity

We conducted 22 male–male interaction trials from 11 to 27 February 2004. Experiments were carried out in the morning between 0800 and 1100 hours in a cage of the same size and shape (58×33×31 cm) as the housing cages. Before the experiment, the birds had been housed visually (but not acoustically) isolated from all other birds. We used

six males with large yellow patches (average width: 19.8 mm±1.07 SD, range: 18.5–21.1 mm) and six males with small yellow patches (average width: 15.9 mm±0.86 SD, range: 15.0–16.9 mm). Yellow patch widths were in the natural range of male patch sizes in the alpine population (average width: 15.7 mm±3.12 SD, range: 8.1–22.4 mm, n=72; authors' unpublished results). Each trial was comprised of two males, one with a large yellow patch and one with a small yellow patch, which were unfamiliar to each other. The same male individual was used in two to six different trials (mean=3.67±1.44 SD) but never more than once against the same opponent. The number of replicates per male varied because in six cases, neither of the two males went to the feeder, and these tests were excluded from the analysis. The experiment cage contained perches on either side of a central feeder in which only one bird could feed at a time. The outcome of such conflicts may be influenced by the hunger of the contestants (Andersson and Ahlund 1991). For this reason, we removed all food from the aviary feeders at 1800 hours the evening before. Each bird was placed on one side of the experiment cage, which was divided by a central, removable opaque divider. After 10 min, the divider was removed, and the time spent (seconds) by each male at the feeder was recorded for 30 min. Dominance within each dyad was expressed as the difference in time spent feeding (Etman et al. 2001; Pryke and Andersson 2003b). All behavioral observations were carried out by a single observer (AM) from a hide situated approximately 4 m from the male–male interaction aviary. All trials were video-recorded. To increase the precision of our observations, we later scored the video recordings to compare them with the feeding time already recorded by the observer. As each male was used more than once, we statistically controlled for nonindependence of the data using Mantel tests (see "Statistical analyses" subsection below).

Males' response to dummy stimuli with manipulated yellow patches

We conducted a second experiment on dominance (February 2005) using one of the two stuffed males mounted in the same posture on an identical support. Two yellow patches, one artificially enlarged (made by adding yellow feathers taken from a male rock sparrow; yellow patch width=20.6 mm) and the other reduced (using brown feathers placed on the margins of the original yellow patch; yellow patch width=8.3 mm), could be attached to either dummy. The use of dummy stimuli (e.g., Liker and Székely 1997; Preault et al. 2002) avoids the problems associated with manipulating live animals, which may inadvertently affect their behavior (Jones and Hunter 1993, 1999). The artificial patches were within the natural size range for this

species (see above and Pilastro et al. 2003 for reviews) and were constructed using a small piece of adhesive tape, to which feathers were attached, and a thin, transparent monofilament line which enabled us to apply the artificial patch to (and remove it from) the stuffed males. The central part of natural patch of dummy was visible when the artificial small patch was applied. In this experiment, we used similar methods to those described for the male–male interactions experiment except that the dummy was positioned in the same compartment as the focal male at a distance of about 20 cm from the feeder. The model was connected to a thin, transparent fishing line that was operated remotely by an observer from a hide placed approximately 4 m from the cage. Once the dummy was positioned near the feeder, the male was placed in the cage, and after some minutes, the observer gently turned the dummy male approximately 10° from its original orientation in each direction for 1 min to simulate a live bird (see Pryke et al. 2001b for a similar experimental design). Following the movement of the dummy bird, we recorded the time (seconds) taken for the focal male to feed (latency) over a 35-min trial period. Experiments were carried out in the morning between 0800 and 1100 hours. We used 15 males, each of which was tested twice in the same morning: once with each dummy type. Dummies and artificial patches were randomly assigned to each trial. To do this, we flipped a coin to decide which of the two dummies would be used first. In the second trial, with the same male, we again randomly selected the dummy as above, which was then mounted with the other artificial throat patch. The position of the dummy in relation to the central feeder (left or right of the feeder) was also assigned at random.

Size of the yellow throat patch and female choice

In this experiment, we measured the proximity preference of ten females that were given a choice of a large- or a small-patched male (3 and 6 June 2004) in a dichotomous choice chamber (Fig. 1). We experimentally enlarged the yellow patch of seven males by dyeing the feathers on either side of the patch with an alcoholic 1% solution of picric acid (for more details, see Pilastro et al. 2003). We reduced the size of the yellow patches on a further eight males by cutting the distal feathers on the sides of the patch (for more details, see Griggio et al. 2005). The mean patch size of the two groups of males before manipulation was 16.3 mm±1.9 SD (n=8, reduced group), and 15.8 mm±1.2 SD (n=7, enlarged group; Student's t test: t_{13}=0.50 P=0.62). In the reduced group, the mean patch size after manipulation was 10 mm±1.1 SD (range: 8.0−11.7 mm, mean reduction: −38.1%). Mean patch size after enlargement was 19.7 mm±0.9 SD (range: 18.3−20.9 mm, mean enlarge-

Fig. 1 Plain view of the mate choice apparatus. The *dashed lines* in the scheme indicate the position of the perches. The *gray* area represents the neutral zone
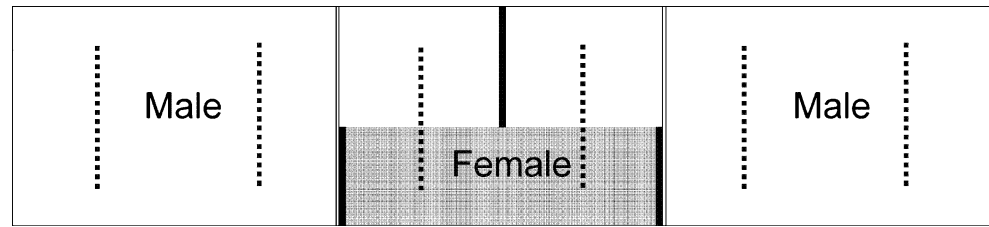
ment: +24.8%), so there was no overlap in sizes of experimentally enlarged and reduced patches.

Ten of the stimulus males were used only once, while the five males that were used in two trials were paired with a different female in each trial to minimize pseudoreplication. The trials were run in a two-choice indoor apparatus in which the female, placed in a central aviary (see below), was allowed to choose between enlarged and reduced yellow-patched males placed individually in two adjacent aviaries. Opaque dividers were erected on the two sides of the central aviary to avoid visual interaction between the two males. The dividers also prevented the females from simultaneously observing the two males. Two perches were positioned so that the female could perch in the left or in the right side of her aviary. Perches had a line traced in the middle of their length, which corresponded to the edge of the separators. This line marked the part of the perch from which a female could observe the male in the nearby compartment. As a measure of proximity preference, we measured the time spent by a female on the perch in front of either male's compartment (choice time). 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). We defined the preferred male as the male with whom the female spent most of the time.

The experimental room was similar to the room in which birds were normally housed. During the experiments, the birds were in vocal contact with the rest of the group placed in the adjacent housing room. Males and females were allowed to acclimatize to their compartments for at least 15 min (on average 25 min) before observations started. After acclimatization, the position of the female was recorded every 15 s for 1 h (for a total of 240 records). Males with increased and decreased patches were alternated with respect to left and right compartments among consecutive trials. The mate choice trials were performed between 0800 and 1200 hours. Two of us (MG and DL) carried out all behavioral observations from a hide placed approximately 4 m from the choice apparatus. All trials were video-recorded. We later scored the tape to compare the location of the female with that already recorded by the observer so as to increase the precision of our observations.

Statistical analyses

Some of the 27 individual rock sparrows were used in more than one experiment. Twelve males were used in the male–male interaction experiment (February 2004), and fifteen males were used in the male–male dominance experiment with dummies 1 year later (February 2005). Between the two dominance experiments, males were also used as stimulus in the female choice test (June 2004). During the female choice tests, the stimulus males interacted only with the female, and therefore it seems reasonable to assume that the results of the three experiments were not influenced by having used the same birds. All the rock sparrows used in these three experiments were captured as juveniles and maintained in individual cages (in acoustic but not in visual contact) until the experiments were performed. Thus, males and females were probably socially naïve (see "Maintenance of captive birds" subsection) before being used in the three experiments in which they were tested in three different contexts. These were more controlled experimental conditions than are usually achieved when adult birds captured in the wild are used or in most field experiments. Of course, we recognize that the experimental design adopted is a compromise between a fully independent design, in which different individual birds (both as stimulus and test birds) are used in each experiment, which would require about 90 individuals in total, and a design that minimizes the number of birds captured in the wild and detained in captivity.

In the male–male interaction experiment, in which the same males were used in different trials, we tested the significance of the correlation between the difference in feeding time (a dominance index) and the difference in phenotype by using a permutation test (Mantel 1967; Manly 1991). Basically, a correlation coefficient ($r_{S\ obs}$) between two matrices (in our case, the difference in feeding time vs the difference in a phenotypic trait) is calculated, and its value is compared with the distribution of 10,000 correlation coefficients obtained by randomly permuting one of the two matrices and calculating a randomized correlation coefficient ($r_{S\ rand}$) at each permutation. The P value is then expressed as the proportion of cases in which $r_{S\ rand} \geq r_{S\ obs}$.

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 statistical tests were done using SPSS (version 13, Norušis 1993), with the exception of the Mantel test and the logistic regressions which were done using GenStat (version 7, Payne and Arnold 2003). All probabilities were two-tailed, and, if not otherwise stated, means±SD are given.

Results

Male polyterritoriality and yellow patch size in natural conditions

Morphological measurements of 30 territorial males were available from the nest box population. Among these males, 14 defended one nest box (monoterritorial males), and 16 males defended two or more nest boxes (polyterritorial males). We checked for differences among years and found that neither yellow patch size nor male status (monoterritoriality or polyterritoriality) differed significantly among years (all $P>0.59$). The size of the yellow patch differed significantly between the males defending one nest (average patch size=12.47±2.08 mm, range 9.6−16.1 mm, n=14) and polyterritorial males (average patch size=14.24±1.59 mm, range 11.0−16.8 mm, n=16; Student's t test: t_{28}=2.63, P=0.014; Fig. 2). In contrast, the males of the two groups did not differ in body mass, wing length, body condition (all t<0.46, all P>0.65, n=30), or age (χ^2=0.48, P=0.37, df=1). To test for the effect of all these factors simultaneously, we performed a multiple logistic regression. The logistic regression is analogous to a linear regression in which the dependent variable has a binomial distribution. In the starting model, polyterritoriality (i.e., whether or not a male was polyterritorial) was the dependent variable, and yellow patch size, wing length, body condition, and male age were the independent variables. The probability for a male to be polyterritorial was positively correlated with throat patch size (b=0.53±0.26 SE, t_{25}=2.08, P=0.048) but not with wing length (b=0.18±0.26 SE, t_{25}=0.69, P=0.50), body condition (residual body mass on tarsus length, b=−0.02±0.32 SE, t_{25}=0.05, P=0.96), or with male age (yearling or older, b=0.23±0.93 SE, t_{25}=0.25, P=0.81, logistic regression model, dependent variable: polyterritoriality; deviance ratio=1.28, P=0.30, dispersion parameter estimation based on Pearson's χ^2, Payne and Arnold 2003). Nearly identical results were obtained using body mass as the dependent variable (yellow patch size, b=0.54±0.26 SE, t_{25}=2.08, P=0.047; body mass, b=−0.03± 0.30 SE, t_{25}=0.09, P=0.93; deviance ratio=1.28, P=0.30). A backward stepwise proce-
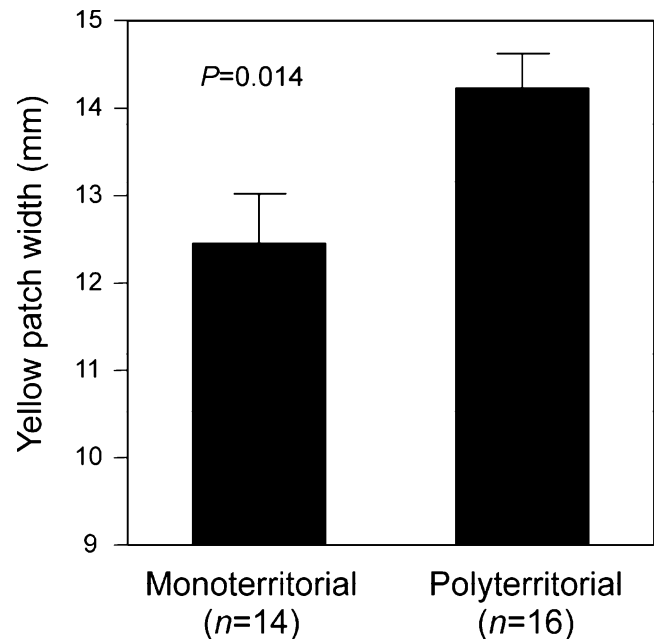

Fig. 2 Mean (±SE) size of the yellow patch (width, millimeters) of male rock sparrows according to the number of nest boxes defended during the pair-formation period (1–21 June). Monoterritorial=one nest box defended (n=14), polyterritorial=two or more nest boxes defended (n=16)

dure in which one nonsignificant independent variable, starting from the least significant one, was removed at each step selected the yellow patch size as the only significant predictor of male polyterritoriality (b=0.51±0.23 SE, t_{28}=2.22, P=0.035; deviance ratio=5.03, P=0.033). The overall fitting of the final model was greater than that of the full model (deviance ratio=5.03 vs 1.28), confirming that the other male traits considered in this analysis did not contribute to predicting polyterritoriality in our sample.

Yellow patch size and male–male competition in captivity

We performed 22 male–male interaction trials to which 12 individual males participated (on average, each male took part in 3.66±1.44 trials, range 2–6 trials). During the experiments, males usually exhibited their yellow patches by extending their throats. Less frequently, they also showed white tail spots. No physical contacts were observed during male–male interaction trials. In each trial, we calculated the difference in feeding time (seconds at the feeder) and the difference in yellow patch size and body size (body mass, wing length, and body condition) between the two males involved. We constructed one similarity matrix of feeding time and male morphology for each morphological trait measured in this study (i.e., yellow patch size; body size, expressed as wing length; tarsus length; body mass) by calculating

the difference in feeding time and the difference in each morphological trait between each pair of males used in each dominance trial. The correlations between the difference in the feeding time and the difference in male morphology (for each morphological trait) were assessed using the Mantel test, which estimated the statistical association between two similarity matrices using a permutation test (Mantel 1967; Manly 1991). To do this, the rows/columns of one matrix are permuted at random while the other is kept constant; and the association between the randomized matrix and the other matrix is recalculated for each permutation. As a metric of association, we used the Spearman's rank correlation coefficient (r_S), although nearly identical results were obtained using Pearson's r or sums of squares. The significance of the association corresponds to the proportion of 10,000 permutations in which the metric is greater than or equal to the metric of the original association (Payne and Arnold 2003). Tarsus and wing lengths were not significant predictors of feeding time ($r_S=0.243$, $P=0.15$ and $r_S=-0.114$, $P=0.68$, respectively). Instead, feeding time was positively and significantly correlated with body mass, body condition, and yellow patch size, although the correlation with patch size was strongest (body mass: $r_S=0.597$, $P=0.005$; body condition: $r_S=0.551$, $P=0.009$; patch size: $r_S=0.786$, $P<0.0001$, Fig. 3). We therefore reran the Mantel tests between feeding time and body mass, after statistically controlling for yellow patch size (i.e., using the residuals of the regression of body mass on patch size), and between feeding time and patch size, statistically controlling for body mass (i.e., using the residuals of the regression of patch size on body mass). The association between body mass and feeding time was no longer significant after statistically controlling for patch size ($r_S=0.342$, $P=0.082$), whereas the correlation between feeding time and yellow patch size remained significant after controlling for body mass ($r_S=0.634$, $P<0.0001$), suggesting that yellow patch size was, at the least, more important than body mass in predicting the outcome of the interaction trials. Nearly identical results were obtained using body condition instead of body mass (body condition: $r_S=0.339$, $P=0.091$; patch size: $r_S=0.653$, $P<0.0001$).

In principle, males may also have been influenced by their previous experience in the test cage. In particular, males may have increased their feeding time as they became more familiar with the experimental conditions. Absolute feeding time of a male, however, was not affected by the order in which he was tested (i.e., feeding time did not increase or decrease as the number of times an individual bird was tested increased), suggesting that this carry-over effect is unlikely to have influenced our results (see Fig. 3).
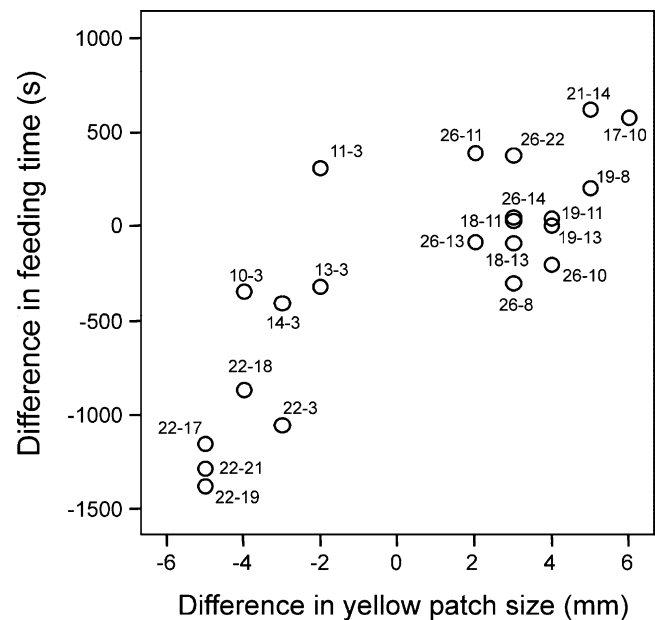

Fig. 3 Relationship between the difference in yellow patch size (width, millimeters) and the difference in feeding time (seconds) among pairs of male rock sparrows that were allowed to feed from the same feeder. *Point labels* indicate the identity of the males forming each pair. Feeding time was not affected by males' previous experience in the test cage (GLS, dependent variable: feeding time; random factors: male identity, $F_{11,22}=9.39$, $P=0.001$; test number, $F_{21,22}=1.09$, $P=0.464$; covariate: testing order, $F_{1,22}=2.89$, $P=0.12$)

Males' response to dummy stimuli with manipulated yellow patches

Twelve of the 15 trials were in the expected direction (i.e., the male started to feed earlier when the dummy had a small yellow patch, sign test with binomial distribution, $P=0.035$). The latency to feed was significantly greater when a dummy bird with a large yellow patch was presented (median 17.67, range 0.11–33) vs a small-patched one (median 12.0, range 0.11–26.7; $z=2.05$, $P=0.041$, $n=15$, Wilcoxon paired test). The side of the feeder on which the dummy was presented had no effect (Fig. 4). During the experiment, males postured to show off the yellow throat patch in front of the dummy (antagonistic display) similar to male–male interactions observed in the wild and in the previous experiment (see above).

Size of the yellow throat patch and female choice

There was no difference between the two groups of males in tarsus length (reduced: $X\pm SD=18.5\pm0.6$ mm, range 18.1–19.8 mm, $n=8$; enlarged: $X\pm SD=18.3\pm0.2$ mm, range 18.1–18.7 mm, $n=7$, Student's t test: $t_{13}=0.850$, $P=0.411$), tail length (reduced: $X\pm SD=55.2\pm1.3$ mm, range 54.0–57.0 mm, $n=8$; enlarged: $X\pm SD=55.0\pm1.3$ mm, range 53.0–57.0 mm, $n=7$, Student's t test: $t_{13}=0.376$, $P=0.713$), or body mass
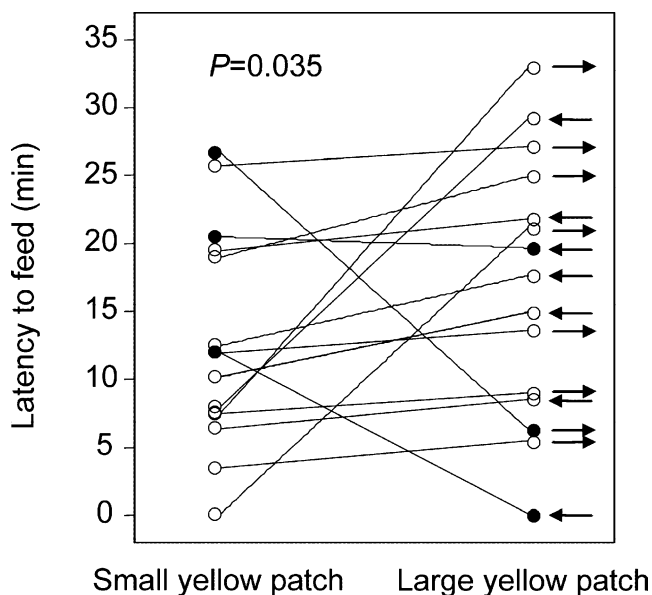
Fig. 4 Latency to feed (minutes) by aviary subject in relation to the size of the yellow patch (width, millimeters) of a rock sparrow dummy close to the feeder. We used 15 males, and each bird was tested twice: once with a small-patched dummy and once with a large-patched dummy. *Arrows* indicate the position of the dummy in relation to the central feeder (*left* is ←, *right* is →). *Black circles* highlight males that showed a shorter latency time with the large-patched dummy than with the small-patched dummy. Twelve of the 15 males started to feed earlier when the dummy had a small yellow patch (sign test with binomial distribution)

(reduced: $X \pm SD = 28.39 \pm 0.8$ g, range 26.7−29.3 g, $n=8$; enlarged: $X \pm SD = 29.6 \pm 2.6$ g, range 27.0−34.8 g, $n=7$; Student's t test: $t_{13}=1.230$, $P=0.241$). During the observation period, females moved back and forth between the males several times extending their necks to show off the yellow patch to the males. Males often performed sexual displays in front of the female. In all the trials, the female visited both the left and right sides of the response area and spent more time in front of the male with the larger yellow patch (sign test with binomial distribution, $P=0.002$). Females spent on average $40.6 \pm 27.4\%$ (range 1.3−83.3%) of their time within the neutral area, $51.8 \pm 24.3\%$ (range 16.3−93.8%) near the enlarged-patch male, and $7.6 \pm 9.2\%$ (range 0.4−30%) near the reduced-patch male (Fig. 5). Comparing the time spent in the two response sectors, females spent significantly more time ($88.9 \pm 11.4\%$, range 60.4−98.3%) in front of the enlarged-patch male than in front of the reduced-patch male (Wilcoxon paired test: $W=0$, $z=2.81$, $P=0.002$). When only the trials in which the female spent >40% of her time in the response sectors were considered (mean time in neutral area=$30.3 \pm 18.8\%$, near the large-patched male=$60.5 \pm 18.0\%$, near the small-patched male=$9.3 \pm 9.6\%$), the strength of the female preference for large-patched males was unchanged ($87.3 \pm 12.2\%$; Wilcoxon paired test: $W=0$, $z=2.52$, $P=0.008$, $n=8$).

Discussions

Taken together, the results from field observations in this and in previously published studies (see below) and aviary experiments suggest that the size of the yellow patch may be used both in male–male competition and in female choice in rock sparrows, probably as a signal of male quality. In rock sparrows, the yellow patch size varies from one individual to another and does not correlate with age (Pilastro et al. 2003; this study). Early breeders (males and females) have larger yellow patches than late breeders, but the yellow patch size of males is not associated with extra pair paternity (Pilastro et al. 2002). In particular, polygynous males have larger yellow patches than monogamous males, although the difference is only marginally significant. Polygynous males are cuckolded more frequently than monogamous males because polygynous males invest less time in mate guarding (there is a trade-off between attracting an additional female and protecting paternity; Pilastro et al. 2002). In turn, polygynous males may be more likely to sire young in other polygynous males' nests than in monogamous nests. So, an inclusion paternity study is needed to improve our estimate of male reproductive success in relation to a male's phenotype.

Previous work has shown that the size of a female's yellow patch is subject to sexual selection rather than simply due to a genetic correlation between the sexes (Pilastro et al. 2003; Griggio et al. 2005). In a study in which the size of the yellow patch of free-ranging females was experimentally reduced, it was found that males
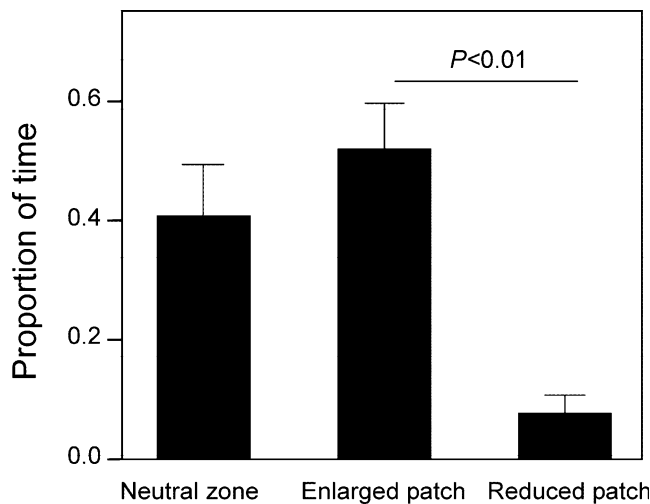

Fig. 5 Female proximity preference in relation to the yellow breast patch of the male. *Neutral zone* The space from which the female could not see either male. *Enlarged patch* Male's yellow patch was enlarged by dyeing the feathers on either side of the patch with picric acid ($n=7$). *Reduced patch* Male's patch was reduced by cutting the distal half of the yellow feathers ($n=8$). Mean time (seconds) ±SE are given

directed less courtship toward females with smaller yellow patches than toward control females, possibly resulting in assortative mating with respect to the yellow patch size (Griggio et al. 2005). The results of the two male dominance experiments combined suggest that the size of the yellow throat patch predicts the outcome of male–male competition for food. Although male body mass was positively correlated with patch size in the experiment in which dyads of males interacted, patch size remained a significant predictor of dominance after statistically controlling for body mass. Along with the results obtained in the experiment with dummies, this suggests that the size of the yellow throat patch is probably used by male rock sparrows to assess the quality of competitors. Rock sparrows also possess other feather marks such as a brown crown, eye stripes, and distal white spots on the tail. The possibility that these other feather marks may have a role in male–male contests is suggested by the exhibition of tail spots during aggressive interactions (Cramp and Perrins 1994; authors' personal observation). A possible role of head markings in such contests may, thus, be worth investigating.

Carotenoid-based ornaments are correlated with individual quality in many species (Olson and Owens 1998; Hill 1999b; Hill and Farmer 2005). These signals are generally considered to be honest indicators of male quality because carotenoids cannot be synthesized de novo but must be obtained from the diet. The question arises, however, on how the honesty of this trait is maintained when it is used in female choice many months after its formation (as is often the case for feather signals). Our results suggest that the use of such signals during male–male interactions reinforces the honesty of the plumage trait. Of course, dual function and carotenoid limitation are not mutually exclusive mechanisms linking the size of the signal to the quality of the bearer. Further experiments are needed to test the effect of carotenoid limitation (or other factors) on the size of this signal.

Whereas numerous studies have revealed that females prefer males with large carotenoid-based ornaments (reviewed in Hill 1999b), the support for their role in male–male competition is more controversial (e.g., Brown and Brown 1988; Belthoff et al. 1994; McGraw and Hill 2000 for negative evidence; and Pryke et al. 2001b; Pryke and Andersson 2003a,b for positive evidence). The dual function of carotenoid feather ornaments has been examined in very few species and with contrasting results. In the house finch (Carpodacus mexicanus), the males' red coloration is favored by female choice (Hill 1994; Hill et al. 1999) but is not associated with male social status (McGraw and Hill 2000, but see Brown and Brown 1988 and Belthoff et al. 1994 for reviews). By contrast, in the red-collared widowbird (Euplectes ardens), the males' red

collar has a role in male agonistic interactions, while females base their mate choice on tail length and not on the size of the red collar (Pryke et al. 2001a). Female siskins (Carduelis spinus) choose mates on the basis of variation in the yellow wing stripe (a carotenoid-based trait), while the size of black bib (a melanin-based trait) has been shown to be a badge of status and does not correlate with the wing stripe or influence female choice (Senar and Camerino 1998; Senar and Escobar 2002; Senar et al. 2005). Lastly, common yellowthroat (Geothlypis trichas) males display a carotenoid-based yellow bib, with the size of which was unrelated to success in male–male competition or to female choice in captivity experiments. On the contrary, the black facial mask is the best predictor of both male–male competition and female choice in the common yellowthroat (Tarof et al. 2005).

To our knowledge, our study of rock sparrows is the first to suggest the possibility of the dual action of carotenoid-based plumage signals in both female mate choice and male–male competition. It is interesting to note that males also base their mate preference on the size of female yellow patch (Griggio et al. 2005), suggesting that this carotenoid-based ornament is mutually sexually selected (Amundsen 2000; MacDougall and Montgomerie 2003). Altogether, our results are in agreement with the hypothesis that secondary sexual characters both function in male–male competition and as cues for female choice (Berglund et al. 1996) and, in particular, reinforce the view that carotenoid signals can be selected in both contexts (Griffith et al. 2006).

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