Ethology **109,** 659—669 (2003)
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ISSN 0179–1613

Male Rock Sparrow (*Petronia petronia*) Nest Defence Correlates with Female Ornament Size

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Abstract

We investigated the relationship between male nest defence and female breast patch size in an alpine population of rock sparrow (*Petronia petronia*) in northern Italy. We presented a mounted weasel (*Mustela nivalis*), a common nest predator, to 28 pairs breeding in nest boxes, with 12–13-d-old nestlings, and measured the intensity of male and female defence reaction. We measured the frequency of attack flights, intensity of alarm calling and total time spent in view, and then combined these for each individual, in a single defence factor by principal component analysis. All the females arrived to defend the nest while only 21 males arrived, and females defended the nest more intensely than males. We analysed, by stepwise regression, the relationship of male defence factor to female behaviour and phenotype (breast patch size, a measure of quality) and brood properties (size, mass, phenology). Male defence factor was significantly related only to female breast patch size. We argue that male rock sparrows apparently make parental investment decisions according to their mate's quality, and examine possible alternative hypotheses.

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Introduction

Parental care in birds is commonly divided in two types, food provisioning of young and defence of nest (or young) against predators (Clutton-Brock 1991; Webster 1991; Reynolds & Székely 1997; Møller & Thornhill 1998). Nest predation is the most common cause of reproductive failure in birds (Ricklefs 1969), therefore nest defence can be crucial to the parent's fitness, especially in species nesting in open habitats, where there could be fewer chances of concealing the nest (Greig-Smith 1980; Knight & Temple 1986; Matessi & Bogliani 1999). Furthermore, nest defence against predators can seriously endanger future

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reproduction of individuals, possibly more than the costs of provisioning, because of risk of injury and death of the defendant (Curio & Regelmann 1985; Gustafsson & Sutherland 1988; Nur 1990). Some avian studies have shown differences in nest defence between the sexes. Such differences in defence intensity have been attributed to differences in the likelihood of re-mating (e.g. Wiklund 1990), the ability to raise offspring unaided (e.g. Brunton 1990), the uncertainty of parentage (e.g. Weatherhead 1989) and the costs of defence (e.g. Wallin 1987). Other studies seem to indicate that various properties of the brood or the habitat affect the levels of nest defence of the adults (Greig-Smith 1980; Redondo & Carranza 1989; Hakkarainen & Korpimäki 1994; Smith & Sandell 1998; Galeotti et al. 2000; Rytkönen 2002).

Recent developments in theoretical and empirical studies of sexual selection have established that both sexes, within most animal species, have a number of alternative mating options with respect to the number of genetic and social partners and the resources to invest in each reproductive event (Andersson & Iwasa 1996; Gross 1996; Cunningham & Birkhead 1998; Qvarnström 2001). Within the ecological constraints of the populations, the alternatives available generally depend on factors such as the condition of the individuals involved (e.g. the 'constrained female hypothesis', Gowaty 1996), the number of potential partners available (e.g. Burley & Calkins 1999) and an individual's attractiveness, either in terms of Fisherian or of viability traits (Andersson 1994; Webster et al. 1995; Gross 1996).

The impact of attractiveness on investment in current reproduction was formalized by Burley (1986) in the 'Differential Allocation Hypothesis', which states that, in species with biparental care, individuals can enhance their fitness by strategically varying their parental investment in response to their relative mating desirability and that of their mate. The second part of the definition, relating parental investment to the attractiveness of the mate, means that, if mate attractiveness affects offspring fitness (i.e. viability or attractiveness), it will consequently influence the value of the breeding attempt with that mate. Given the unpredictable variation in mates encountered, selection should favour individuals that allocate more resources when they breed with an attractive mate (Burley 1986, 1988). In collared flycatchers (*Ficedula albicollis*), for example, males with enlarged secondary sexual characters provided less food to nestlings, while their females provided more, compared with controls (Qvarnström 1997). Till date, Burley's study remains the only test of male differential allocation according to female attractiveness in birds, as all subsequent experimental investigations have concentrated on female differential allocation relative to male attractiveness (Sheldon 2000).

The purpose of this work is to relate variation in brood defence by rock sparrows (*Petronia petronia*) to features of parents and offspring that are related to breeding success. The rock sparrow breeds in open habitat, in loose colonies near, or in, human settlements, in the Mediterranean region (Cramp & Perrins 1994; Pilastro et al. 2001; Tavecchia et al. 2002). Females are usually able to complete reproduction on their own or with little contribution from the male, with the exception of cases of female nest desertion (Pilastro et al. 2001). Normally, even if they do not leave the female by the time the young are 10 d old, males spend most of their time singing, courting the female and attempting copulations rather than feeding the young (M. Griggio & G. Matessi, unpubl. data). Both males and females have a yellow breast patch the size of which is related to phenotypic quality and mating status. In particular, non-breeding individuals have smaller breast patches than either breeding males or females, and secondary females of polygynous males have a smaller patch than primary females; breast patch size correlates with body size and double brooding in females, but is not correlated with age (Pilastro et al. 2003). In a parallel experiment of female breast patch size manipulation, males attended the nest and courted females with reduced patches less than control females or females with enlarged patches (Pilastro et al. 2003). Rock sparrows therefore allow us to relate nest defence differences between males and females to brood properties and to their own ornament size and that of their mate, and to discuss what potential benefits each sex, and males in particular, can derive from differential parental investment decisions.

Methods

We tested the intensity of nest defence against a terrestrial predator in 28 pairs of rock sparrow, breeding in nest boxes in a population in the Alta Valle Susa (Italy, 44°56′N 6°48′E). The whole population, breeding in a total of 52 nest boxes, was marked with individual colour plastic rings, and has been the subject of a long-term study for more than 10 yr (Mingozzi et al. 1994; Pilastro et al. 2001). We performed the nest defence tests in the breeding seasons of 1999 and 2000. As most nest boxes were built to function as trapping devices also, unmarked individuals could be captured and ringed any time and such operation did not interfere with nest building or egg laying. We measured the breast patch size of adult individuals by placing a strip of transparent acetate over the breast, holding the bird on its back, with bill and head perpendicular to the body, and drawing the contour of the yellow patch. We then measured the major and minor axes of the outline to the nearest 0.1 mm using callipers. We used the length of the major axis as a measure of overall 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). We traced the patch twice and measured its major axis in a random sample of 20 individuals of each sex to evaluate the repeatability of this measure (males $r = 0.87$, $F_{19,20} = 13.8$, $p < 0.001$; females $r = 0.67$, $F_{19,20} = 5.03$, $p < 0.001$; Lessells & Boag 1987). To minimize disturbance to nests and to avoid endangering the broods, we caught only 18 males and 21 females for breast patch measurement, with a total of 13 nests where both parents were sampled. Average breast patch size was 14.51 ± 0.48 mm (range 11.4–18 mm) for males and 11.65 ± 0.56 mm (range 5.7–16 mm) for females.

Reproduction was monitored during the whole season, with regular 1 h behavioural observation periods and nest content checks every 3–4 d. We therefore had data on male and female behaviour in the days preceding the nest defence tests, in the form of minutes spent at the nest per hour of observation. When the chicks reached the age of 11–15 d, they were ringed and weighed. The nest defence tests were conducted at an average of 12.7 d (range 9–15) of age of the chicks, prior to ringing, on mornings without rain between 6:30 and 8:00 h.

We conducted the tests as follows: one of three, randomly chosen, mounted weasels (*Mustela nivalis*) was placed on top of the nest box, with the head pointing towards the entrance; once the observer (always MG) was in position, 25–30 m away, a 30-min maximum latency interval started; if in this interval at least one of the members of the pair arrived, the experiment was started and the behaviour of the individual(s) was recorded for 30 min, after which the predator was removed and the experiment concluded. In all the experiments the female arrived within 30 min, and therefore the maximum total treatment time (and disturbance to the nest) was < 60 min. We measured, for each individual observed during the experiment, the following variables of defence intensity: number of attacks per minute against the predator (direct flight towards the predator, ending within 2 m of it); time spent performing alarm calls (minutes); time spent in view (minutes). We extracted, by principal component factorial analysis, one 'defence factor' for each parent from the three individual nest defence intensity variables. We tested whether the 'defence factors' were related to individual quality, measured by breast patch size, or to the brood size, average nestling weight in the nest and laying date. We used a forward stepwise regression analysis, because these variables were to some extent correlated (correlation coefficients between −0.25 and 0.49). All variables except male and female defence factors were log-transformed.

Once the weasel was positioned, the defending individual(s) arrived performing alarm calls and in general immediately attacked the mount. The defendants kept calling between and during attacks, and the attacks were repeated at short intervals. At the end of an attack, the individual generally returned briefly to a preferred perch. The intensity of the response declined on average after 20 min, both in number of attacks and intensity of calling. The individual(s) were nonetheless vigilant and observed the mount with raised crown feathers. Attacks by the parents were both simultaneous and alternated. Birds only rarely touched the mount during attack flights.

Paternity levels may affect a male's willingness to defend the brood and may be a confounding factor in our tests (e.g. Reyer et al. 1998). We had paternity data for a subset of the nests tested, from previous projects (see Pilastro et al. 2002 for details), which we also compared with levels of nest defence and ornament size. The results are based on too small a sample to be conclusive, but suggest the effect of paternity to be minimal. The proportion of legitimate young in the nest ($\bar{x} \pm$ SE: 0.88 ± 0.074, range 0.17–1.0, $n = 12$) was not related to male or female breast patch size nor to male defence factor for the 12 nests for which data were available, three of which contained extra pair young (Spearman rank coefficient, all $p > 0.4$).

Polygynous males ($n = 7$) and their primary females did not differ significantly from monogamous males ($n = 21$) and their females in breast patch size or any of the brood properties measured (all $F < 1.97$, all $p > 0.17$, one-way ANOVA), and therefore data were pooled in all analyses.

The body mass of chicks in nests that received the experimental treatment were not different from those of other nests in the population in the same years (treatment: $\bar{x} \pm$ SE: 31.1 ± 0.39 g, $n = 28$ nests; no treatment: 29.7 ± 0.6 g, $n = 31$; Mann–Whitney U-test: $Z = -1.52$, $p = 0.13$). There were no differences between years or among mounts in any of the variables, so the experimental data were pooled for all analyses.

We performed all analyses using the SPSS (version 9) statistical package. When data did not meet the assumptions for parametric statistics we either transformed the variables or used corresponding non-parametric tests. All dates mentioned are calculated with 1 Jan. = day 1.

Results

Females attacked the predator more frequently than males (Table 1). Females also stayed longer and performed more alarm calling than males that arrived to defend, although not significantly so (Table 1). Seven of the 28 males never arrived while the predator was present, while all the females arrived to defend the nest ($\chi^2 = 5.88$, df = 1, $p = 0.01$). We had data on presence at the nest in the three days prior to testing for 21 of the 28 males. Males which never arrived spent on average significantly less time at the nest 3 d before the test date (male not arrived: $\bar{x} \pm$ SE: 0.8 ± 0.58 min/h, $n = 5$; male arrived: 9 ± 2.83 min/h, $n = 16$; Mann–Whitney U-test: $Z = -2.291$, $p = 0.021$). We considered this to be an indication that males which did not arrive to defend were no longer attending the nest before the experiment and they were omitted from further analyses.

The principal component analysis on behaviour of 21 males and 28 females extracted a ‘defence factor’, which explained more than 50% of the variance in both sexes (Table 2). We tested whether male defence factor depended on the quality of the female, measured by its breast patch size, on the intensity of its nest defence, or on brood size ($\bar{x} \pm$ SE: 4.5 ± 0.25), average weight and age of nestlings in the nest ($\bar{x} \pm$ SE: 31.1 ± 0.39 g and 12.7 ± 0.3 d, respectively) and laying date ($\bar{x} \pm$ SE: 166.4 ± 1.93). The intensity of the male's defence (defence

Table 1: Comparison of male and female defence intensity variables

Variable	Females	Males	Z	p
Time in view (min)	25.48 ± 1.42	22.62 ± 2.1	−1.042	0.32
Attack flights (min^{-1})	0.41 ± 0.06	0.24 ± 0.05	−3.099	0.001
Alarm calling (min)	7.82 ± 1.44	5.2 ± 1.69	−0.946	0.35

Descriptive statistics ($\bar{x} \pm$ SE) and Wilcoxon pairwise test results are given. Data refer to the nests in which males arrived to defend ($n = 21$).

Table 2: Correlation matrix of the components from a factorial analysis of male and female defence intensity variables (n = 21 and n = 28, respectively)

Defence intensity variable	Male defence factor	Female defence factor
Attack flights (min^{-1})	0.69	0.79
Alarm calling (min)	0.71	0.81
Time in view (min)	0.84	0.5
Eigenvalue	1.67	1.53
Percentage explained variance	55.8	51

Table 3: Results of a stepwise regression analysis of male defence factor vs. female quality, female defence factor and nesting phenology (n = 16)

Variables	Coefficient	t	p
Included[a]			
Constant	−10.948	−2.493	0.026
Female breast patch size[b,c]	5.411	2.529	0.024
Excluded[a]			
Female defence factor	0.227	0.926	0.37
Laying date[c]	0.146	0.631	0.54
Brood size[c]	−0.129	−0.549	0.59
Nestling age[c]	0.347	1.55	0.14
Nestling mean weight[c]	−0.208	−0.935	0.37

[a] Criterion for inclusion: $p < 0.05$; criterion for exclusion: $p > 0.1$.
[b] Female breast patch size: corrected $R^2 = 0.27$.
[c] Log-transformed values.

factor) was related positively to female patch size, but not to any of the other variables entered in the model (Table 3, Fig. 1). Female defence intensity did not relate to any of the variables entered in the model ($p > 0.2$ for all independent variables). Male and female patch sizes were not significantly correlated (Pearson correlation coefficient $r = -0.24$, $p = 0.42$, $n = 13$). Defence factor and patch size within each sex were not significantly correlated (females: $r = 0.33$, $p = 0.15$, $n = 21$; males: $r = 0.24$, $p = 0.38$, $n = 15$).

Discussion

Male rock sparrows defend their brood from predators with an intensity directly proportional to the size of the ornament of their mate, and independent of the value of the brood measured by its size or phenology. This is in accordance with the differential allocation hypothesis, which predicts that individuals paired to attractive mates allocate more resources to the current reproduction (Burley 1986, 1988). This test of the differential allocation hypothesis is not experimental, as the presentation of a model predator is

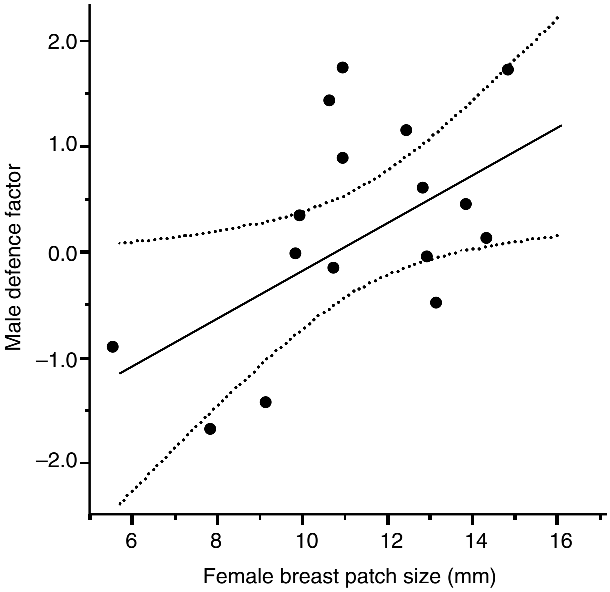

Fig. 1: Relationship between male nest defence, measured by the factor extracted from a principal component analysis of three defence variables, and female quality, measured as breast patch size. The 95% confidence intervals for the regression line are given (dotted curves and solid line, respectively)

mainly an aid in the collection of data, but it forms a strong basis to test the hypothesis with more crucial manipulative experiments. One of the predictions of the differential allocation hypothesis which was not met in our experiments is that attractive individuals, in turn, should invest less. Therefore females with large ornaments should have defended relatively less intensely than females with smaller ornaments (Burley 1986, 1988). Contrary to the prediction, the correlation between female breast patch size and defence factor was positive, although not significant. This indicates that rock sparrow males appear to practice 'incomplete investment compensation' (Burley 1988, p. 612). Females with larger ornaments did not withdraw any investment and the effect of female ornament size on male defence represents a further addition to the overall investment in the brood. Offspring of attractive females will benefit from more than average total investment. An alternative explanation of the results, e.g. that more aggressive males can mate with females with a larger breast patch, cannot be ruled out without manipulating female ornament size, but the lack of a correlation in ornament size between the sexes and between male aggressiveness to the predator and breast patch size seems to point against it. The present results are in partial agreement with an experimental test of the relationship between female ornaments and male investment, where male rock sparrows adjusted the time they spent at the nest but not their food provisioning to the brood following female breast patch manipulation (Pilastro et al. 2003), although in that case, active nest defence was not measured.

Why should males mated to attractive females defend more intensely (and therefore take higher risks)? The simplest and most general explanation given by the differential allocation hypothesis is that nestlings of attractive females may have higher fitness, because of either their 'aesthetic' or genetic quality (Burley 1986, 1988; Sheldon 2000). Female rock sparrows with a larger breast patch seem to be of higher phenotypic quality, as they have a higher probability of re-nesting successfully and are more often primary females of polygynous males (Pilastro et al. 2003). Therefore, their offspring could also be of better quality, either through direct, genetic or maternal effects. We had insufficient data on female age or breeding experience in our sample, but these could also influence male investment decisions and potentially be indicated by ornament size. Support for a relationship between ornament size and age or experience is weak (Pilastro et al. 2003). In the rock sparrow, males can leave the female to complete the raising of the brood on its own, and search for another mate, or they can cooperate with the female and attempt to obtain paternity in its next brood. Thus, there could be an additional advantage for males to invest more in the brood if mated to females with larger patches, because re-nesting probability increases with female patch size (Pilastro et al. 2001). Males that stay and defend may be able to gain more copulations with the female and possibly obtain paternity in the female's next brood, even if it switches mates. To be paired with a female with a large ornament may therefore increase the fitness gains of staying relative to leaving.

In rock sparrows, females defended the nest more intensely than males. This is contrary to what has been found in a study on great tits (*Parus major*), in which males risk more than females (Regelmann & Curio 1986). This scenario seems to fit the feedback hypothesis (McLean & Rhodes 1992; Pavel & Bureš 2001) which predicts that, in species with unequal share of parental activities, the sex that has the highest proportion of interactions with the nest should defend it more intensely. Normally, as the nestlings develop, growth demands increasing feeding activity by both parents, but the proportion of interactions with the nest increases less for the female than for the male, because the female built the nest and incubated the eggs. Therefore males should defend proportionately more as the chicks grow. However, in this population, female rock sparrows had the highest proportion of interactions with the brood, as male brood feeding activity is lower than the female's. Males frequently reduce or stop feeding the young when they are about 10 d of age (M. Griggio & G. Matessi, unpubl. data). Females therefore defend more, as predicted by the feedback hypothesis. First broods have a high reproductive value for females, as only 20% of the females are able to produce a second brood after a successful first one and second broods have a low fledging success (Pilastro et al. 2001). Annual survival probability of females is < 50% and lower than for males (Tavecchia et al. 2002). The female's ability to complete reproduction alone, combined to the pattern of male behaviour in the late nesting phase and the reproductive value of broods for females could explain the differences in male and female defence responses (Table 1) and the arrival of all the females and only some of the males. The intensity of nest defence of the parents usually depends on the value of the brood (Greig-Smith 1980; Wallin

1987; Redondo & Carranza 1989; Smith & Sandell 1998; Galeotti et al. 2000; Pavel & Bureš 2001), but this does not seem to be the case in this study. Neither male nor female defence intensity were significantly correlated with laying date, brood size, nestling age or weight, although our sample may be too small to draw any final conclusions.

In conclusion, albeit only correlative, our results may represent a case of male differential allocation in relation to female attractiveness. To our knowledge, this is among the few field studies to suggest that males may adjust their breeding strategy according to female quality in birds. These results encourage a more thorough exploration of the relation between male breeding strategy and female ornamentation, for example by a combination of female ornament manipulation and predator presentation (Sheldon 2000).

Acknowledgements

We warmly thank Toni Mingozzi for his continuous practical, logistic, moral and intellectual support. Giacomo Tavecchia, Ester Taverniti, Giampalmo Venuto and Claudia Callegarin gave invaluable help in the field. We thank Mauro Bon, of the Natural History Museum in Venezia, and Domenico Rosselli of the Val Troncea Natural Park Museum for lending us the weasel mounts. We are grateful to the two anonymous referees whose comments significantly improved the manuscript. The research was funded by a grant of the University of Padova (Fondi di Ricerca di Ateneo – 1999/2000) and a grant of the Italian Ministry for Research (Cofin2001) to AP.

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Received: December 9, 2002

Initial acceptance: April 25, 2003

Final acceptance: May 3, 2003 (B. Kempenaers)