Male rock sparrows differentially allocate nest defence but not food provisioning to offspring

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(Accepted: 13 June 2008)

Summary

Secondary sexual characters may provide information about individual quality to a partner, which may use it during parental care to strategically allocate resources to the current breeding attempt (Differential Allocation Hypothesis). Differential allocation by females has been demonstrated for a number of species, while male differential allocation based on female secondary sexual traits has received less attention. Yet females of many species, among birds in particular, are ornamented. We performed a test of male differential allocation based on a female ornament in the rock sparrow (\textit{Petronia petronia}), a monomorphic species in which both sexes have a yellow breast patch, the size of which correlates with individual reproductive quality. We reduced the breast patch in a sample of females and compared the parental care of their partners (chick feeding and nest defence) with the parental care of males paired to sham-manipulated controls. Nest defence was assessed by placing a dummy predator on the nest box. Males of ornament-reduced females defended the nest less but did not feed the chicks less than males paired to control females. Our results only partially support male differential allocation and are in agreement with previous tests of male differential allocation in rock sparrows.

\textit{Keywords}: differential allocation hypothesis, parental care, male parental investment, female ornaments, nest defence.

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\textbf{DOI:10.1163/156853909X410748}

Also available online - \url{www.brill.nl/beh}
Introduction

Differential allocation theory predicts that individuals will invest in parental care to the offspring of the current reproduction according to their own and their current mate’s quality, possibly measured by own and mate’s degree of ornamentation. This applies to females in most cases, but also to males at least in cases in which remating opportunities are low (e.g., monogamous semelparous species) and female quality is crucial for offspring survival (e.g., species with bi-parental care; Burley, 1986; Sheldon, 2000). Male differential allocation may at least partly explain why females of some species are ornamented (Amundsen, 2000). Female differential allocation has been tested in a number of species, with variable results (e.g., Johnsen et al., 2005; Gilbert et al., 2006; Navara et al., 2006). Despite both sexes being included in the hypothesis and tested in the first experimental investigation of it (Burley, 1988), male differential allocation has rarely been tested. In pied flycatchers (*Ficedula hypoleuca*) egg colour is used by males as a cue for parental allocation decisions (Moreno et al., 2004, 2006). Other female ornaments are also associated with reproductive success in pied flycatchers (Morales et al., 2007). Sheldon (2000) presents a review of the most relevant tests of the differential allocation hypothesis.

A recent test of male differential allocation (Pilastro et al., 2003) showed that male rock sparrows (*Petronia petronia*) attend the nest less and court their females less if females had experimentally reduced yellow breast patches, a trait subject to mutual sexual selection (Griggio et al., 2005a, 2007). Male feeding investment was not affected, but most males stop feeding chicks early and, therefore, the experiment, performed close to chick fledging, was not conclusive in this respect. Further indication of male differential investment in nest defence was also found in rock sparrows, where male defence against a dummy predator placed on the nest box was positively correlated to female ornament size (Griggio et al., 2003a). Yellow breast patches in rock sparrows are produced by carotenoid pigmentation and males have larger patches than females (Griggio et al., 2007a). The size of the breast patch in female rock sparrows seems to correlate with re-nesting probability and breeding success (Pilastro et al., 2002, 2003).

We tested male rock sparrow parental investment in the early stages of chick feeding by manipulating female ornaments and recording male feeding effort first, and then testing male predator defence effort by dummy predator intrusions. If males differentially allocate parental investment according
to their current partner’s ornamentation we predict that: (i) males paired to females with experimentally reduced ornaments will perform fewer feeding trips and bring smaller prey than males paired to control females; and (ii) males paired to reduced females will defend less intensely against a simulated predator than males paired to control females. Males rarely court their females in the early stage of chick feeding, although they resume courtship later on (Pilastro et al., 2003), so we do not expect to find an effect on male mating investment, in contrast to Pilastro and co-workers (2003).

**Methods**

Female rock sparrows have a patch of yellow feathers on the breast (average width of yellow patch = 12.2 mm, range 6.1–18.6 mm; average height of yellow patch = 5.6 mm, range 3.3–8.8 mm, $N = 114$) analogous to that of rock sparrow males (average width = 13.8 mm, range 6.6–19.5 mm, average height = 6.2 mm, range 3.4–8.9, $N = 99$). Though smaller and less obvious than males’ (width: $t = -5.37$, $p < 0.001$, df = 211; height: adjusted $Z = -5.35$, $p < 0.001$; Student’s $t$-test and Mann–Whitney $U$-test, respectively), the breast patch is visible when females assume the copulation position or stretch their neck (G. Matessi, pers. obs.; Wilson, 1994) and males have been shown to court more intensely females with experimentally enlarged patches compared to controls (Griggio et al., 2005a, 2007). Between 2002 and 2004 we manipulated 20 females from an alpine population living in nest boxes in a loose colony along the French-Italian border. Almost all individuals were colour ringed and individually recognisable (see Griggio et al., 2003a; Pilastro et al., 2003 for field methods). The females were randomly assigned to two groups: for 9 females we cut the lateral yellow breast patch feathers reducing the yellow surface by an average of 26% (reduction range 15–35%; original width range 8.4–13.7 mm; reduced width range 6.6–10.3 mm; reduced group) and for 11 females we cut the brown feathers bordering the yellow patch (average yellow surface change 3%; change range from $-10$ to $+16%$; changed width range from $-1.2$ to $+2.2$ mm; control group). There was no bare patch of skin on females of either group after manipulation since we cut only superficial feathers. We did not modify the height of the yellow area in either group. We manipulated six females per treatment in 2002, three control and two reduced in 2003 and two
control and one reduced in 2004. We manipulated all the females when the chicks were six days old, except for two broods which were eight days old (one for each treatment). The manipulation significantly changed the width of the breast patch of the reduced females (treatment (reduced vs. control): $F_{1,18} = 8.09, p = 0.011$; time (before vs. after) $F_{1,18} = 35.716, p < 0.001$; interaction $F_{1,18} = 26.51, p < 0.001$; repeated measures ANOVA) but did not change significantly the width of the breast patch of control females (control before vs. control after $p = 0.93$, reduced before vs. reduced after $p < 0.001$, reduced before vs. control before $p = 0.79$, reduced after vs. control after $p = 0.03$; Tukey’s HSD post-hoc comparisons).

We tested for potential negative effects of female manipulation on chick condition by comparing the average residuals of the regression of mass (measured to the nearest 0.5 g) on tarsus length (measured to the nearest 0.1 mm) of chicks in the nests of manipulated females with those of chicks in the nests of non-manipulated females breeding on similar dates in the same years. All chicks were measured at the same age of 14 days after hatching.

**Feeding investment observations**

We observed each nest for 1 h from a 50 m distance using a spotting telescope (30× magnification), on two consecutive days before and two consecutive days after the day of treatment, for a total of 4 h of observation per nest. Observation schedules relative to breeding stage were, thus, identical for the two treatment groups. For each individual we measured the number of feeding trips and prey size per nestling. We estimated prey item size (mainly grasshoppers and caterpillars) in three categories by comparing it with adult bill length (0.5 bills, 1 bill, 2 bills or larger). We also recorded courtship display duration (proportion of observation duration), mate guarding index (proportion of arrivals/departures from the nest in which the male followed the female), nest attendance duration (proportion of observation duration) and singing rate (number of songs). There was no correlation between any of the male behaviours and the corresponding female behaviours before manipulation.

**Nest defence tests**

After the last hour of observation we tested the intensity of nest defence against a terrestrial predator in 14 pairs (7 reduced and 7 controls), placing
a mounted weasel (*Mustela nivalis*) on top of the nest box. The nest defence tests were run on mornings without rain between 6:30 and 8:00. We conducted the tests as follows: The mounted weasel was placed on top of the nest box, with the head pointing towards the entrance; once the observer 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 began and the behaviour of the individual(s) was recorded for 30 min, after which the predator was removed and the experiment ended. In all the experiments the female arrived within 30 min and all males arrived before the end of the experiment. Therefore, the maximum total treatment time (and disturbance to the nest) was less than 60 min. We measured for each parent: latency to arrive at the nest; number of attacks per min against the predator (direct flight towards the predator, ending within 2 m of it); time spent performing alarm calls (min); time spent in view (min). We extracted, by principal component analysis, one ‘defence factor’ for each parent from the four response variables (Table 1). We then used the defence factor of each parent as dependent variable in a general linear model with treatment group as categorical predictor and the defence factor of the other parent as continuous predictor.

### Table 1. Male and female behaviour towards a dummy predator on the nest box.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Reduced</td>
<td>Control</td>
</tr>
<tr>
<td>Latency (min)</td>
<td>9.43 ± 2.41</td>
<td>2.94 ± 1.35</td>
</tr>
<tr>
<td>Time in view (min)</td>
<td>8.29 ± 3.05</td>
<td>14.86 ± 5.24</td>
</tr>
<tr>
<td>Attack rate (No./min)</td>
<td>2.93 ± 2.03</td>
<td>3.49 ± 2.18</td>
</tr>
<tr>
<td>Alarm call rate (No./min)</td>
<td>12.14 ± 3.74</td>
<td>24.79 ± 1.72</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>2.63</td>
<td>65.8</td>
</tr>
<tr>
<td>Explained variance (%)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For each variable we report mean ± SE for the two female ornament treatment groups, as well as the factor loading, Eigenvalue and explained variance (%) from the principal component analysis.
**Statistics**

We performed all analyses with Statistica v. 7.0, except for the stepwise model selection analysis of the nest defence data, performed with GenStat v. 7.0. All variables were checked for normality and homogeneity of variances and transformed where required. We applied an ANCOVA using the change in value of each of the parental provisioning behaviours (after minus before) as dependent variable, treatment (reduced vs. control) as categorical predictor and the value before treatment as continuous covariate. We first tested for homogeneity of slopes and then applied a standard main effects analysis or a separate slopes analysis as required. We applied a generalized linear model (GLM) procedure with a backward stepwise removal analysis based on a best fit model selection to the nest defence behaviour. We calculated effect sizes and their 95% confidence intervals (CIs) for all variables as unbiased Cohen’s $d$ coefficients, calculated from the corresponding $t$ values obtained from the ANCOVA and general linear model analyses, and as Pearson’s $r$ for correlations (Nakagawa & Cuthill, 2007). Effect sizes are conventionally considered medium if Cohen’s $d > 0.5$ and large if $d > 0.8$.

**Results**

**Chick feeding and sexual behaviour**

We found no significant effects of treatment on the change in number of male feeding trips, prey size or nest attendance, but we found a significant negative relationship between change in feeding trips and number of feeding trips before treatment (Table 2). The whole model for this variable was also strongly significant (Table 2), and a best subsets analysis indicated that the best minimum model included both treatment and covariate as predictors (Mallows $C_p = 3.0$, $R^2_{adj} = 0.36$). The direction and strength of the treatment and time effects for the above variables are illustrated in Figures 1a–c.

We found no significant differences between the treatments in mate guarding, but a significant effect of mate guarding before treatment (Table 2). Changes in male courtship and singing activity were not normally distributed, but the corresponding variables before and after were, so we applied a repeated measures ANOVA instead of the ANCOVA. We found no significant difference between the groups or between before and after treatment.
Table 2. Male and female parental care and mate guarding in response to female breast patch manipulation.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$F_{1,17}$</th>
<th>$p$</th>
<th>ES ($d$)</th>
<th>CI lower</th>
<th>CI upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male feeding trips — whole model</td>
<td>6.305*</td>
<td>0.009*</td>
<td>$R_{adj}^2 = 0.358$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>3.529</td>
<td>0.08</td>
<td>0.88</td>
<td>-0.04</td>
<td>1.8</td>
</tr>
<tr>
<td>Trips before</td>
<td>7.375*</td>
<td>0.01*</td>
<td>1.27</td>
<td>0.3</td>
<td>2.23</td>
</tr>
<tr>
<td>Male prey size — whole model</td>
<td>2.421</td>
<td>0.12</td>
<td>$R_{adj}^2 = 0.222$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>0.037</td>
<td>0.8</td>
<td>0.09</td>
<td>-0.79</td>
<td>0.97</td>
</tr>
<tr>
<td>Prey size before</td>
<td>4.235</td>
<td>0.06</td>
<td>0.96</td>
<td>0.03</td>
<td>1.89</td>
</tr>
<tr>
<td>Male nest attendance — whole model</td>
<td>1.681</td>
<td>0.2</td>
<td>$R_{adj}^2 = 0.067$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>2.887</td>
<td>0.11</td>
<td>0.79</td>
<td>-0.12</td>
<td>1.7</td>
</tr>
<tr>
<td>Attendance before</td>
<td>0.418</td>
<td>0.5</td>
<td>0.3</td>
<td>-0.58</td>
<td>1.19</td>
</tr>
<tr>
<td>Mate guarding — whole model</td>
<td>2.532</td>
<td>0.11</td>
<td>$R_{adj}^2 = 0.139$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>0.311</td>
<td>0.6</td>
<td>0.26</td>
<td>-0.62</td>
<td>1.14</td>
</tr>
<tr>
<td>Mate guarding before</td>
<td>4.824*</td>
<td>0.04*</td>
<td>1.03</td>
<td>0.09</td>
<td>1.96</td>
</tr>
<tr>
<td>Female feeding trips — whole modela</td>
<td>5.369*</td>
<td>0.009*</td>
<td>$R_{adj}^2 = 0.408$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>4.76*</td>
<td>0.04*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment × trips before</td>
<td>7.389*</td>
<td>0.005*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trips before (control)</td>
<td></td>
<td></td>
<td>0.88</td>
<td>-0.04</td>
<td>1.81</td>
</tr>
<tr>
<td>Trips before (reduced)</td>
<td></td>
<td></td>
<td>1.56</td>
<td>0.56</td>
<td>2.57</td>
</tr>
<tr>
<td>Female prey size — whole model</td>
<td>3.156</td>
<td>0.07</td>
<td>$R_{adj}^2 = 0.185$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>0.313</td>
<td>0.6</td>
<td>0.26</td>
<td>-0.62</td>
<td>1.15</td>
</tr>
<tr>
<td>Prey size before</td>
<td>5.951*</td>
<td>0.03*</td>
<td>1.14</td>
<td>0.19</td>
<td>2.09</td>
</tr>
<tr>
<td>Female nest attendance — whole model</td>
<td>9.049*</td>
<td>0.002*</td>
<td>$R_{adj}^2 = 0.459$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>0.523</td>
<td>0.5</td>
<td>0.34</td>
<td>-0.55</td>
<td>1.22</td>
</tr>
<tr>
<td>Attendance before</td>
<td>18.009*</td>
<td>0.0005*</td>
<td>1.98</td>
<td>0.91</td>
<td>3.06</td>
</tr>
</tbody>
</table>

We applied an ANCOVA with change in behaviour (after minus before) as dependent variable, treatment (reduced vs. control) as categorical predictor and behaviour before manipulation as continuous covariate. We report ANCOVA statistics for the whole model (df = 2, 17), each independent variable, effect sizes (Cohen’s $d$ calculated from the corresponding estimated $t$ values, see Nakagawa & Cuthill, 2007) and their 95% confidence intervals.

a A separate slopes analysis was applied due to significant interaction term, no effect size calculated for the treatment factor.

* Significant effects at $\alpha = 0.05$.

in male courtship behaviour (all $F_{1,18} < 2.144$, all $p > 0.16$) nor in male territorial song (all $F_{1,18} < 0.687$, all $p > 0.42$).

We found a significant effect of treatment on change in number of female feeding trips (Table 2). Females in the control group reduced feeding
effort on average, while females in the reduced group slightly increased effort on average (Figure 2a). We also found a significant negative effect of the interaction term on change in female feeding trips, which means that the number of female feeding trips before treatment has a stronger negative effect on the change in behaviour of the reduced females than on that of the control females (Table 2). Treatment had no effect on the other two female parental investment variables (prey size and nest attendance; Table 2 and Figure 2b,c), but in both cases the behaviour before treatment had a significant negative effect on the change in behaviour (Table 2). We found that females in general spent less time at the nest after the treat-
Figure 2. Effects of manipulation on female parental behaviour. (a) Comparison of the effects of the number of feeding trips per chick performed before breast patch manipulation on the change in number of feeding trips, according to the type of manipulation received (control or reduced) based on a separate slopes ANCOVA procedure. Means and standard errors of change in (b) size of prey per chick and (c) nest attendance (proportion of observation time) in response to manipulation of female breast patch size corrected for the corresponding variables before manipulation of the female (open bars = reduced patch size, solid bars = control sham manipulation).

ment than before the treatment, independently of the type of treatment received (Figure 2; $t_{19} = 2.35$, $p = 0.03$, $d = 0.88$, CI = 0.02–1.75; paired Student’s $t$-test). We tested whether the effects of treatment on females affected chick condition. Average chick condition was not significantly different among nests of non-manipulated ($N = 21$), control and reduced females ($F_{2,35} = 0.568$, $p = 0.6$; one-way ANOVA), nor between non-manipulated nests and the manipulated nests pooled ($F_{1,35} = 1.121$, $p = 0.3$).
Nest defence

Treatment group was the only significant predictor of male defence behaviour (treatment $F_{1,11} = 5.457$, $p = 0.04$, $d = 1.31$, CI = 0.15–2.46; female defence factor $F_{1,11} = 3.271$, $p = 0.098$, $d = 1.01$, CI from −0.1 to +2.13; whole model $F_{2,11} = 3.84$, $p = 0.05$; GLM). The backward stepwise removal analysis, based on a best fit model selection procedure using either Mallows’ Cp or $R^2_{\text{adj}}$ criteria showed that the best model included both predictor variables (Mallows’ Cp = 3.0, $R^2_{\text{adj}} = 0.304$) and did not include the interaction term. Males paired to females with a reduced breast patch defended less intensively than males paired to females of the control group (Figure 1d). The difference is probably due to males of the reduced group arriving later, alarm calling less and spending less time in view of the predator (Table 1). Male and female defence factors were positively but not significantly correlated ($r = 0.35$, $p = 0.2$, CI from −0.23 to +0.95).

Discussion

We tested male rock sparrow differential allocation of parental investment by experimentally manipulating female ornamentation (yellow breast patch) and assessing male provisioning and nest defence. If males allocated parental investment according to current female ornamentation, we would predict a change in provisioning and defence for males paired to females with reduced ornaments. We found a significant effect of ornament reduction on male nest defence, but not on food provisioning to the nestlings. Males paired to females with reduced breast patches defended the nest less intensively against a dummy predator on the nest box. We found no effect on male sexual behaviour, as predicted. Females of both treatment groups reduced their nest attendance, and we found a significant effect of type of manipulation on number of female feeding trips.

The difference we found in male nest defence is in agreement with the results of a descriptive study using the same approach (simulated predator) but without female manipulation, in which male nest defence was positively correlated with female breast patch size (Griggio et al., 2003a). Our results, on the other hand, do not agree with the original results on zebra finches, in which male nest and nestling care, but not nest defence, were affected by female ornamentation (Burley, 1988). Zebra finches were raised and observed...
in captivity, which may have reduced the relevance of differential investment in nest defence (Burley, 1988). Furthermore, most of the behaviours considered as nest defence in Burley (1988) were actually different types of vigilance, while in our tests the simulated threat directly affected perception of risk to both parents and offspring. One of the most frequent causes of clutch loss in our population of rock sparrows was predation by the garden dormouse (*Eliomys quercinus*), which preyed upon at least 20 nests with either eggs or chicks, and even killed one adult female, until 2006, the year in which we adopted effective nest protection (G. Matessi, unpubl. data). Male and female defence behaviours are positively but not significantly correlated so it is unlikely that the effect of female breast patch manipulation on male defence is due to female behaviour. Rock sparrow males do not invest differently in nestling provisioning, contrary to the prediction of the differential allocation hypothesis and contrary to zebra finches (Burley, 1986, 1988; Sheldon, 2000). Even though the whole model for number of male feeding trips was significant (Table 2) and both predictors were retained in the model, we only found a near-significant effect of treatment on change in feeding trips and a moderate but not significant effect on change in nest attendance. The effect sizes of both variables were moderate to large, but their confidence intervals were wide. We would, therefore, conclude that the size of a female’s breast patch at best only weakly affects a male’s feeding effort and with an effect which is possibly too small to be detected as significant by the limited sample size in this study. It is possible that some of the information on female quality is encoded in the colour properties of the yellow breast patch more than in its size (e.g., Hegyi et al., 2007), but we had no access to field colour spectrometry equipment and female breast patches are too small to allow us to remove enough feathers for laboratory analysis (Quesada & Senar, 2006). However, this seems unlikely as it has been shown that yellow patch size and colour saturation are positively correlated (Serra et al., 2007), and colour saturation is less variable than patch size (Griggio et al., 2007). Given the incidence of nest predation in our rock sparrow population, male contribution to nest defence is possibly more crucial to offspring survival than male provisioning, although we have no information on the effectiveness of nest defence (Griggio et al., 2003b; Pilastro et al., 2003). Alternatively, as in other species, male contribution to provisioning may be more relevant or modulated in the post-fledging phase (e.g., Johnson et al., 2007), and females may still succeed in fledging young without male contribution (Griggio et al., 2003b).
rock sparrows do feed newly fledged young, but collecting systematic data on male feeding effort is complicated because of unpredictability of movement patterns of the brood once fledged. The negative relationship between feeding effort and change in feeding effort after manipulation of the female and other variables may be due to the intrinsic nature of such variables and may, therefore, not reflect any specific parental investment strategy (Kelly & Price, 2005).

The reduction in time spent at the nest by females of both treatment groups may be due to a combination of increased demands by the growing offspring and wariness towards observer presence after having been captured. In order to be certain of trapping the right individual at least two of us had to be present and were probably visible during capture operations. However, a previous experiment comparing the time spent at the nest by captured and non-captured females failed to find any effect of capture itself (Griggio et al., 2005b). There was indeed an effect of treatment on the number of female feeding trips, but it was due to a reduction by control females, which is difficult to interpret. The interpretation of this result is further complicated by the significant interaction of treatment and covariate effects. The negative relationship between original feeding effort and change in effort is stronger and steeper in the reduced females (Figure 2a). In any case, all female parental effort variables showed a significant negative relationship between the change in behaviour and the behaviour before the treatment which, like the corresponding results on males is likely to be a statistical artefact (Kelly & Price, 2005). The reduced time at the nest and the change in feeding trips in this study did not in any case reflect negatively on chick condition.

The scenario suggested by our current results, combined to other available information on rock sparrow breeding investment, is that female breast patch size is used by males to choose a mate during pair formation (Griggio et al., 2005a), to allocate investment in a potential remating with the current female (Pilastro et al., 2003), and to decide investment in nest defence in the early nestling phase (this study) and around the time of fledging of the young (Griggio et al., 2003a). In contrast, male nestling provisioning is not influenced by female attractiveness (this study; Pilastro et al., 2003). Theoretically, defending against a predator implies more risk and, therefore, higher potential survival costs compared to chick provisioning (e.g., Lambrechts et al., 2000 and references therein). It is, therefore, surprising that rock sparrow males differentially invest in the most costly behaviours and not in less...
costly ones. However, a male may not need to trade-off the nest defence behaviours which seem most responsible for our present results (Table 1) with mate guarding and remating opportunities, while nestling provisioning is less compatible with mate guarding, courtship and mating. Therefore, males may increase offspring survival without paying additional costs in remating opportunities. We have no estimates of the survival costs of the specific nest defence behaviours adopted by rock sparrows, but at least some of them (e.g., alarm calling and nest attendance) may indeed be a relatively cheap way of showing off to one’s own female, as part of a strategy to increase the chances of mating with her in her next breeding attempt, or at least to gain paternity in her next brood (Pilastro et al., 2003; Griggio et al., 2003a).

The behaviour of rock sparrow males shows support of the differential allocation hypothesis only for one component of parental investment, nest defence. The signal value of female breast patches may be more important in a competition context where, as in males, it is used to establish dominance ranks, possibly at feeding grounds (Griggio et al., 2007), when competing for nesting sites (Matessi et al., 2007) or for mates (Pilastro et al., 2001, 2003; Griggio et al., 2005a). It could be interesting to investigate further the fitness consequences of nest defence, its effectiveness and its use by females as a source of information for mate choice compared to nestling provisioning. More information on the degree of flexibility of nestling provisioning by males and on the use of ornaments in female-female competition would also make a useful contribution to understanding the breeding strategies of rock sparrows and other species.

Acknowledgements

We thank Roger Garcin for his logistic support, help with ringing and permits and contacts to local authorities. Domenico Rosselli of the Parco Naturale Regionale della Val Toncea provided the mounted weasels for the predation experiments, together with valuable general support. Toni Mingozzi has provided constant support by way of discussion of ideas and exchange of information. Francesca Bortolin, Leandro Drago, Carlo Matessi, Chiara Morosinotto and Valeria Zanollo provided help in the field at various stages of the experiments. We are grateful to the direction and the personnel at the Centre ELAN of Val des Pres for providing accommodation during the study. We are grateful to two anonymous referees for significantly improving a previous version of the manuscript, especially by suggesting fruitful alternative statistical analyses. The research was supported in part by a post-doctoral fellowship by the University of Padova and part by a European Union Marie Curie Individual Fellowship (HPMF-CT-2001-01474), both granted to G.M., and by a MIUR COFIN2003 Grant and Research grants from the University of Padova (2000-4 ex60% grants) to A.P.
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