Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher

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SUMMARY

Experimental enlargement of sexually selected traits that are energetically cheap to produce is expected to reveal costs resulting from increased risk of predation or social competition. Given a trade-off between sexually selected traits and life history traits such costs may be expected to affect not only the males themselves but also their offspring. In this study I manipulated the size of the forehead patch, a sexually selected trait that functions as a badge of status in male collared flycatchers (*Ficedula albicollis*). First, I found that a male's likelihood to establish a breeding territory with respect to his original badge size was affected by the treatment such that old males (older than or equal to two years) with relatively small original badges enjoyed an increased likelihood of establishing a breeding territory while young males (yearlings) suffered a reduced likelihood of establishment when their badges were enlarged as compared to unchanged. Second, young males with enlarged badges that were able to establish a territory fed their nestlings less in relation to their females compared to the control males. However, the females adjusted their parental effort to such an extent that no significant differences were observed in total feeding rate nor in reproductive success between the two groups of males. These results suggest that experimentally enlarged badge size in the collared flycatcher may result in increased male competition and that males have to trade their effort spent in male contest against their parental effort.

1. INTRODUCTION

An important theory in sexual selection states that display traits may be used to assess the quality of potential mates and/or opponents (Andersson 1994). Males with relatively high expression of such traits will therefore be preferred by females and/or intimidate their rivals and, as a result, will gain mating advantages. A central question then becomes how the honesty of such signals can be maintained: why should males in bad condition honestly signal their sorry state?

Dishonest strategies may be prevented if producing, maintaining or merely 'possessing' display traits will impose a cost on their bearer (Zahavi 1975), such that the cost of cheating surpasses the potential gain (Maynard Smith & Harper 1988; Grafen 1990). Often, however, it is not possible to detect such costs by examining natural relationships between variation in the level of investment in display traits and in other fitness components, as uncontrolled variation in condition and overall health may affect several fitness components in the same direction (Partridge & Harvey 1985; Clutton-Brock 1988; Partridge 1989). Experimental manipulations of male display traits may also fail to reveal fitness costs related to the level of ornamentation, since they obviously do not reflect developmental costs (Partridge 1994). This problem

can be overcome when the main cost of the trait is to maintain or possess it rather than producing it, as was shown in an experiment with barn swallows (*Hirundo rustica*, Møller 1989). Male swallows with experimentally elongated tail enjoyed a mating advantage compared to males with shortened tail, but they also foraged less successfully resulting in worse physical condition, which in turn caused reduced tail length and reduced mating success in the following year. Many colour badges (i.e. signals of social status used to settle disputes minimizing escalation) in birds are at least presumably energetically cheap to produce (Rohwer 1982; Butcher & Rohwer 1989). Manipulations of such traits may therefore be expected to reveal costs resulting from increased risk of predation (Andersson 1994), but empirical evidence is lacking (see also Götmark 1994) or social competition (Rohwer 1975, 1982; Møller 1987; Andersson 1994). However, whether competitive costs are sufficient to maintain the honesty of status signals has recently been questioned (Owens & Hartley 1991; Johnstone & Norris 1993).

In the migratory collared flycatcher (*Ficedula albicollis*) the characteristic male white forehead patch is used in male contests, where individuals with relatively large patches enjoy a competitive advantage in disputes over nest boxes (Pärt & Qvarnström 1997).

Winners in these disputes acquired females more quickly than did losers. In addition, males with relatively large forehead patches were found to be more likely to become polygynous (Gustafsson *et al.* 1995) and to have a smaller proportion of extra-pair young within the nest they attend (Sheldon *et al.* 1997). The size of the forehead patch, which is determined during a partial winter moult, thus predicts male mating success. Furthermore, recent evidence shows that the size of the forehead patch is sensitive to a male's nestling environment and to past reproductive effort (Gustafsson *et al.* 1995) suggesting that current physiological condition may influence the forehead patch size of males. Similarly, badge size was shown to be determined by nutritional status at moulting in another passerine bird species, namely the house sparrow (*Passer domesticus*) (Veiga & Puerta 1996). However, the fact that these badges of status have been shown to be condition dependent must not be taken as conclusive evidence of a cost of producing the badges. In the collared flycatcher there is probably neither a direct energetic cost of changing the size of this white unpigmented area by a few mm², nor an increased risk of predation (Pärt & Qvarnström 1997). Therefore, the reliability of the signal is most likely socially enforced.

In this study I manipulated the size of the forehead patch of male collared flycatchers upon their arrival to the breeding grounds, and investigated the effect of the manipulation on their subsequent territory establishment, mating success, parental effort and reproductive success. In this species male interactions are most frequent during territory establishment (Pärt & Qvarnström 1997). I therefore expected that males with an experimentally enlarged badge should incur additional costs resulting from increased social competition when trying to establish a territory as compared to control males. This may be reflected by a change in probability of establishment and reduced physical condition and/or parental abilities.

2. METHODS

(a) General methods

The study was performed in 1995 and 1996 in a 21 ha nest box area on the southern part of the island of Gotland (57°10' N, 18°20' E), Sweden. Each day, from early May to early June, the plot was thoroughly searched by three people for newly arrived males and females, established unpaired males and established breeding pairs. The data were collected mainly between 04.00 and 12.00 (Swedish summer time) but additional observations were regularly made during three hours in the afternoon as well. Males were caught on their first day of observation, which was assumed to be their date of arrival. In cases where the male had already established a pair bond with a female before he was observed (i.e. he was not singing and was seen in company with a female) he was not captured. All males were ringed and measured using standard procedures (see Gustafsson 1989; Pärt & Gustafsson 1989) and assigned randomly to one of two experimental groups. The first group (*enlarged*) had their forehead patch enlarged by 4 mm Tipp-Ex correction fluid (GmbH

Figure 1. The effect of the experimental treatment on the relationship between original badge size and male probability to establish a breeding territory, predicted from the regression models for (a) old males and (b) young males. Note that this figure shows midpoint intervals of badge sizes but raw data were used in the statistical analysis.

and Co.KG) being added to the height of the patch. The second group of males (*control*) were painted with 4 mm Tipp-Ex on their white patch without changing its original size. The use of Tipp-Ex for artificial colouring of birds has been criticized (Bennett *et al.* 1994) because of selective reflection in ultraviolet wavelengths (Coemans & Vos 1992). However, in my study this is not a problem since white feathers of flycatchers have been shown to decline in reflectance in the UV part of the spectrum and the maximum contrast between white and black feathers are found within our visual spectrum (Götmark & Hohlfalt 1995), as also is the case for Tipp-Ex and black feathers. Since the forehead patch of the male collared flycatcher mainly functions as a badge of fighting ability before males have established site dominance (Pärt & Qvarnström 1997), most males (85%) were removed from their territories for 24 h before they were released in the same plot in order to break any such site dominance. During detention they were kept outdoors in cages and fed *ad libitum* with meal worms. Combinations of colour rings were randomly assigned for individual identification of all manipulated males in the field.

Breeding males and females were caught again when feeding seven-day-old nestlings. All birds were weighed (nearest 0.5 g) and measured. Nestlings were measured and weighed when 12 days old and their condition was calculated as the residual from a linear regression of body

Table 1. *The effect of treatment, original badge size (OBS) and age category on change in condition between arrival and the seventh day of feeding young among male collared flycatchers*

(Treatment refers to males with experimentally enlarged forehead patches or control birds, and age refers to old (older than or equal to two years) and young (yearling) males. Interaction terms with $p > 0.10$ were deleted from the final model. m.s., mean square.)

source	d.f.	m.s.	<i>F</i>	<i>p</i>
treatment	1	0.152	0.310	0.5809
OBS	1	6.785	13.808	0.0007
age	1	0.245	0.500	0.4841
residual	37	18.183	0.419	—

weight on tarsus length. Feeding rate, i.e. number of visits to the nest, of males from the two experimental groups and their females, were measured for two 1 h periods on two consecutive mornings when nestlings were 8–10 days old. Observers were placed 30–35 m from the nest and were unaware of male treatment. Total feeding rate was defined as the sum of the male and female feeding rate, and male share was calculated by dividing male feeding rate with total feeding rate. Pairing speed was estimated as number of days passing between the release of a male until the onset of nest building corrected for date of release. Data on reproductive performance of all breeding pairs were collected using standard procedures (see Pärt & Gustafsson 1989).

(b) Data analysis

To test whether a male's probability of establishing a territory was associated with his original badge size, age and treatment group I used logistic regression (SAS Institute Inc. 1988). To assess the significance of the independent variables I calculated the difference in deviance for a model with and a model without the variable of interest. The resulting difference in deviance between the two models (G) follows a chi-square distribution with one degree of freedom (Hosmer & Lemeshow 1989). Age was included to adjust for differences in site fidelity between the two age classes since site fidelity is much higher among old than among young males in this population (Pärt 1994).

The effect of the experiment on mating success, parental investment and reproductive performance was examined by using ANCOVAs (Super ANOVA, Abacus Concepts Inc. 1989–1990). Age was included in all analyses and all proportions were angular transformed.

3. RESULTS

(a) Territory establishment

Competition for nest sites was intense, and 55% (of a total of 110 individuals) of the treated males were not found breeding in the plot and probably had moved elsewhere. Treatment, original badge size and age jointly determined a male's probability to establish a territory as revealed by a significant three-way interaction ($G = 8.98$, d.f. = 1, $p < 0.005$). Separate

Table 2. *The effect of treatment, original badge size (OBS) and age category on male share of feeds (number of male feedings/number of male and female feedings) in the collared flycatcher*

(Treat. refers to males with experimentally enlarged forehead patches or control birds, and age category which refers to old (older than or equal to two years) and young (yearlings). Interaction terms with $p > 0.10$ were deleted from the final model.)

source	d.f.	m.s.	<i>F</i>	<i>p</i>
treat. (A)	1	0.085	4.608	0.0376
OBS (B)	1	0.037	2.019	0.1627
age (C)	1	0.001	0.058	0.8106
AC	1	0.066	3.585	0.0652
residual	42	0.778	0.019	—

analyses of the two age categories (one year old and older than or equal to two years old) revealed that the effect of treatment on a male's likelihood to establish a territory depended upon original badge size in both old males ($G = 4.12$, d.f. = 1, $p < 0.05$) and young males ($G = 5.16$, d.f. = 1, $p < 0.05$). Territory establishment increased with increasing original badge size in old control males ($\beta = 0.0778$, s.e. = 0.0392, $G = 3.94$, $p = 0.047$), but was independent of original badge size in the enlarged group ($\beta = -0.00446$, s.e. = 0.02204, $G = 0.04$, $p = 0.84$). Among young males, in contrast, the probability of establishing a territory was not associated with the original badge size in control individuals ($\beta = 0.0207$, s.e. = 0.0336, $G = 0.38$, $p = 0.54$) but it increased significantly with increasing original badge size among males with enlarged badges ($\beta = 0.19$, s.e. = 0.0903, $G = 4.60$, $p = 0.032$). Thus, the experimental enlargement of the forehead patch affected male probability of establishing a territory such that old males with relatively small original badge size enjoyed an increased likelihood to establish a territory while young males with relatively small original badge size suffered reduced likelihood of establishment after enlargement (figure 1).

(b) Change in body condition

I used male change in body condition (weight corrected for body size) between the day of arrival and the seventh day of feeding young as an estimate of his total reproductive expenditure (i.e. the combined expenditure of male contest competition, female attraction and feeding of young). There was a strong significant relationship between original patch size and male change in condition between the two capture events (table 1): males with large forehead patches lost more weight during the breeding season than did males with originally small forehead patches. This result is mainly explained by males with large original badge size, when taking age into account, having arrived in better condition than those with smaller

badges (ANCOVA: $F_{1,97} = 7.48$, $p = 0.01$) since final condition (at seventh day of feeding young) was unrelated to original badge size (ANCOVA: $F_{1,42} = 2.83$, $p = 0.10$) and the experimental enlargement of the badge size did not have a statistically significant effect on male change in body condition (table 1).

(c) Male feeding share

If males with enlarged badge size incurred a higher cost of competition at territory establishment than control males, this may result in a reduction in their parental investment such as estimated by feeding rate. Feeding rate is affected by several factors such as, for example, number of young and weather conditions. I therefore used male share (male feeding rate/total feeding rate) as an estimate of male feeding effort. As predicted, the experimental treatment had a significant effect on male feeding effort when taking age and original badge size into account (table 2, figure 2). However, total feeding rate did not differ between the two treatment groups when taking age and original badge size into account (ANCOVA: $F_{1,47} = 0.13$, $p = 0.72$), nor did time to pairing (ANCOVA: $F_{1,41} = 1.31$, $p = 0.26$) and reproductive performance estimated as laying date (ANCOVA: $F_{1,45} = 0.05$, $p = 0.83$), clutch size (ANCOVA: $F_{1,45} = 0.01$, $p = 0.91$) brood size (ANCOVA: $F_{1,45} = 0.03$, $p = 0.857$) and total weight of the brood at an age of 12 days (ANCOVA: $F_{1,43} = 0.01$, $p = 0.96$). There was no differences in age between females mated to males with enlarged badges as compared to females mated to control males when taking male age and original badge size into account (ANCOVA: $F_{1,20} = 0.28$, $p = 0.60$).

4. DISCUSSION

(a) *Do males that signal too high a status enjoy an advantage during territory establishment?*

The effect of an experimental enlargement of a colour badge must be considered in relation to the male's fighting ability as demonstrated by his original badge size. This is because the two main predictions are: first, males with relatively low fighting ability, as demonstrated by small original badge size, will intimidate a relatively larger proportion of their potential competitors after the experimental enlargement; second, the cost of cheating should be proportional to the discordance between the obtained badge and the original badge size, i.e. the level of aggression from superior competitors should increase. Thus, both potential benefits and costs from signalling too high a status will depend on original badge size. In the collared flycatcher the balance between benefits and costs from signalling too high a status seems to differ between young and old males since the experimental enlargement of the white forehead patch affected a male's likelihood of establishing a territory differently in the two age categories. Old males with relatively small original badge size enjoyed an increased likelihood to establish a territory while young males

Figure 2. Comparison of parental effort estimated as male share of feeds (number of male feedings/number of male and female feedings, corrected for original badge size) between males from the two treatment groups: filled bars, old males; striped bars, young males.

with relatively small original badge size suffered reduced likelihood of establishment after an experimental enlargement of the badge size. There are several possible ecological and physiological differences between young and old males that may explain the difference in response to the treatment. One such explanation is, for example, that because young males arrive later, i.e. when fewer territories are vacant, the intensity of male competition may be higher for young than for old males. Although there was no significant age difference in establishment probability among my control males (45% versus 56% for young and old males, respectively), there seem to exist a general age difference in establishment probability as judged from a large-scale translocation experiment (Pärt 1995). Therefore, young males may have suffered a relatively higher increase in male competition when trying to establish a territory after the experimental enlargement than did old males. Another explanation is that young males may not be physiologically able to respond with a rise in testosterone levels.

These results thus suggest that the experimental enlargement of the forehead patch in the collared flycatchers resulted in increased male competition. Young males with poor fighting ability, as demonstrated by a relatively small original badge size, suffered in terms of reduced probability to establish a territory. Since the collared flycatcher is a short-lived species, the fitness cost imposed on males that were unable to establish a territory is high since number of breeding occasions explains a high proportion of lifetime reproductive success (Gustafsson 1989). Even if some of them may have bred outside the study area, they would have become considerably delayed, which is a severe disadvantage since the time of breeding is important for fledgling success (Wiggins *et al.* 1994). Thus, young males in bad condition probably even from the very start do best by honestly signalling

their sorry state while some old males seem to be successful as cheaters (see also below).

(b) Do costs from increased competition become detectable later in the season?

Males with enlarged badge size that were able to establish a territory may also have suffered additional costs from increased competition compared to control males. This may be reflected by worse physical condition later in the season leading to reduced survival chances and/or badge size in the following year (Møller 1989; Gustafsson *et al.* 1995). Males with originally large forehead patches had a higher reproductive expenditure, as estimated by the change in their body condition between arrival and the seventh day of feeding young, than males with small forehead patches. However, the experimental enlargement of the badge size was not reflected in a change in male body condition.

Experimentally increasing the brood size of collared flycatcher pairs revealed the operation of a trade-off between a male's parental effort in one year and the size of his forehead patch in the following year (Gustafsson *et al.* 1995). A male investing heavily in current reproduction thus will have to pay a cost in terms of reduced future competitive ability and/or sexual attractiveness with consequences for future reproduction. Similarly, experimentally increased costs of male competition (this paper) or mate attraction (Smith 1995) may be expected to reduce male parental effort. Indeed, male parental investment in relation to original badge size was affected by the experimental treatment such that males with an experimentally enlarged badge size fed their nestlings less in proportion to their females as compared to control males. One may argue that the effect of the treatment on male parental effort is weak. However, it is important to keep in mind that those males with enlarged badges that suffered most severely from an increased competition were in fact unable to establish a territory and therefore are not included in the sample of males that were feeding nestlings. Furthermore, the results indicate that the manipulation had a much stronger effect on male parental effort in young birds supporting the suggestion that young males suffered relatively higher increase in male competition. Old male collared flycatchers therefore seem to be successful cheaters in terms of territory acquisition without detectable reduction in condition nor in parental care. However, this does not mean that the experimental change in badge size did not affect unmeasured components of old males fitness such as survival and/or subsequent reproductive success.

(c) Does reduced parental effort lead to fitness costs?

Among males that were able to establish a territory I found no significant difference in reproductive success. Does that mean that the fitness cost assumed to be imposed on a cheating male at least partly was

counterbalanced by an adjustment of parental effort by his female?

Females have been shown to compensate partially when the feeding ability of their mates has been experimentally reduced (Wright & Cuthill 1989; see also Pärt *et al.* 1992). There probably exists a conflict between the sexes over the division of work, since both parents potentially could increase their future reproductive output if they could 'force' the other bird to work harder. An increase in feeding effort by one partner in most cases should result in a decreased effort by the other (Winkler 1987), and therefore females are not expected to compensate fully because that would allow males to further decrease their parental effort. On the other hand, since badge size in the collared flycatcher predicts paternal genetic effects on nestling fledgling condition, a character related to fitness (Sheldon *et al.* 1997), female collared flycatchers may have been deceived by the false signalling of high quality by males with enlarged badges. Given such deception, two additional explanations to the reduced male share of feeds in the experimental pairs could be that males with increased badge size may be mated to females of relatively high quality (Darwin 1871; Fisher 1958) and/or to females that may be willing to invest relatively more in their offspring as postulated in the differential allocation hypothesis (Burley (1986), for empirical evidence see Burley (1988), de Lope & Møller (1993) and Møller (1994)). However, I found no differences in aspects of quality such as age, lay date or clutch size between females mated to males from the two treatment groups. Furthermore, the differential allocation hypothesis only considers the differential allocation of reproductive effort by females mated to preferred as compared to unpreferred males and males with experimentally enlarged badge size were not preferred by females, as judged from data on 'time to pairing'. In addition female collared flycatchers seem to display only a weak preference for male traits, while paying more attention to territory characteristics (Pärt 1994, see also Alatalo *et al.* 1986). However, female differential allocation may be considered a post-mating strategy in response to the phenotypic quality of their mate. Post-mating strategies have previously been shown to occur in the collared flycatcher, in which females adjust both their participation in extra-pair copulations (Sheldon *et al.* 1997) and the sex ratio of their offspring (Ellegren *et al.* 1996) in relation to the size of the forehead patch of their social mate. The observed effect of treatment on parental care cannot only be explained by female differential allocation since the relatively stronger effect on parental ability of young males with enlarged badges compared to old experimental males is more consistent with a trade-off between competition and parental care.

5. CONCLUSIONS

In the present study young males with experimentally enlarged badge size seemed to be forced to spend more effort in male contest competition in

comparison to control males, and as a result were unable to provide a full amount of parental effort. In light of life history theory the link between forehead patch size and parental effort may be interpreted as a trade-off between number and quality of offspring: a male has to trade the effort spent in male contest competition, which determines how many offspring he will sire, against his parental effort, which affects offspring phenotypic quality. Since males are expected to balance this trade-off in a way that will, on average, maximize their fitness, some males may do so by investing relatively more effort in competitive ability and mate attraction to the expense of their parental duties. In species with biparental care this would then result in a direct cost in terms of increased parental effort by females mated to highly ornamented males.

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