

Differential selection according to the degree of cheating in a status signal

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The maintenance of honesty in a badge-of-status system is not fully understood, despite numerous empirical and theoretical studies. Our experiment examined the relationship between a status signal and winter survival, and the long-term costs of cheating, by manipulating badge size in male house sparrows, *Passer domesticus*. The effect of badge-size manipulation on survival was complex owing to the significant interactions between the treatments and original (natural) badge size, and between the treatments and age classes (yearlings and older birds). Nevertheless, in the experimental (badge-enlargement) group, males with originally large badges had increased winter survival, while males with originally small badges had decreased survival. This indicates that differential selection can act on a trait according to the degree of cheating.

Keywords: badges of status; cheating; house sparrows; winter survival

1. INTRODUCTION

Over the last three decades, considerable effort has been put into generating and testing hypotheses to explain the evolution and functions of animal signals (Maynard Smith & Harper 2003; Searcy & Nowicki 2005). Animal signals often convey information on individual phenotypic and/or genetic quality and constitution. Badges of status are one category of such signals that are widespread across the animal kingdom (Whiting *et al.* 2003), especially in avian societies (Senar 2006). Badges of status are thought to be used to settle minor conflicts without wasteful fights, because the size of badge reflects the possessor's fighting ability (Senar 2006).

In a badge-of-status system, an obvious question is why individuals do not use their signal in an inappropriate manner or why cheating does not happen. The maintenance and cost of badges of status have attracted both theoretical and empirical treatments (Senar 2006). The costs associated with badge size can be divided into two categories: intrinsic and extrinsic costs. The intrinsic cost (e.g. production cost) of a badge of status is often explained in the framework of

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the handicap principle (Getty 2006). On the other hand, the social control hypothesis is often considered to be the main explanation for the extrinsic cost of badges of status (Rohwer 1977). This hypothesis assumes that agonistic interactions occur mostly among individuals with similar signals, as shown by Rohwer & Ewald (1981) under some circumstances (also shown theoretically by Ripoll *et al.* 2004). Large-badged cheats are then expected to suffer the cost of contending with honest large-badged signallers, resulting in a reduction in fitness that outweighs the benefit of bearing a large badge. The extrinsic cost might also entail a predation risk, because larger-badged individuals are more conspicuous to predators (Møller 1989; but see Bókony *et al.* 2008).

In this study, we examined the extrinsic cost of a badge of status in house sparrows, *Passer domesticus* (Nakagawa *et al.* 2007a), by manipulating the black throat patch of males. House sparrows experience an annual moult in autumn, and the badge size of the same individuals can differ following each moult (Griffith 2000). Previous studies provide equivocal results for the social control hypothesis. Møller's (1987) badge-size manipulation experiment showed that cheats with enlarged badges were socially punished. By contrast, Gonzalez *et al.* (2002) found that males with enlarged badges achieved higher status, despite their fake badges. The limitations of these studies were not only their use of small, artificial flocks in indoor aviaries, but also the failure to observe the long-term consequences of badge-size manipulation (cf. Veiga 1995; see the electronic supplementary material for the relationship between the present work and Veiga 1995).

Our aims were twofold as follows: (i) to elucidate the role of badge size in winter survival, in which dominance must play an important role (Piper 1997) and (ii) to reveal the long-term consequences of cheating in a wild population.

2. MATERIAL AND METHODS

We conducted our study on Lundy, a small island off the coast of southwest England (51°10' N, 4°40' W). Natural migration of house sparrows to and from Lundy Island is rare owing to their sedentary nature and their flight ability not being suited for a long, continuous distance (Anderson 2006). All breeding birds and almost all fledglings since 2000 were marked with unique colour band combinations, so that the exact ages of most birds were known (see the electronic supplementary material for more details on the study area and population).

Basic morphological measurements were taken according to Svensson (1992). We measured badge size following the method of Griffith *et al.* (1999), which measures the length of the 'hidden badge'. This hidden badge (referred to as 'natural badge size' hereafter) is highly correlated with the visible area of the badge, which increases over the season as the pale tips of the badge feathers wear off (for repeatabilities and correlations of these measurements, see Nakagawa *et al.* 2007b).

During 22–29 November 2004, we modified male badges using Nyanzol D. One group of males (experimental group: $n=42$) had the visible badge size enlarged to a fixed size that was at the largest end of the range of the natural variation (a length of 52 mm). The other group (control group: $n=48$) had their badge dyed without any enlargement (for more details on the procedure, see Nakagawa *et al.* 2007b). Owing to the nature of our population, all individuals that were not observed in a subsequent breeding season (April–August 2005) were considered dead (see the electronic supplementary material for more details on resighting/capturing procedures).

We used generalized linear models (GLMs) with binomial error structure (logit link function) in R (v. 2.3.1; R Development Core Team 2006) to analyse the binary response of survival. We constructed a full model with five variables and their second-order

Table 1. Results from the minimal adequate model (GLM with binomial error structure; AIC=102.93, d.f.=84) for survival in relation to the treatment ($n(\text{experiment})=42$; $n(\text{control})=48$), age class ($n(\text{young})=35$; $n(\text{older})=54$) and natural badge size. (Effect size d is calculated as the difference between the experimental and control groups; a negative value of d therefore indicates that the experimental group had a smaller value than the control group.)

response	predictor	likelihood ratio χ^2	p	effect size	95% CI
survival	treatment	$\chi_1^2=0.23$	0.635	$d=-0.100$	-0.514 to 0.314
	age class	$\chi_1^2=3.26$	0.071	$r=0.190$	-0.017 to 0.382
	natural badge size	$\chi_1^2=0.56$	0.454	$r=-0.080$	-0.282 to 0.130
	treatment \times age class	$\chi_1^2=6.11$	0.014	$d=-0.540$	-0.962 to -0.118
	treatment \times natural badge size	$\chi_1^2=8.56$	0.003	$d=0.648$	0.223 to 1.073

interactions, excluding the interactions between the two continuous variables (12 terms) as follows: (i) treatment (control or experiment), (ii) natural badge size, (iii) age class (first year birds, referred to as 'young', or birds older than the first year, referred to as 'older'), (iv) weight, adjusted for the time of capture, and (v) tarsus length. The latter four variables were used in the model not only because we were unable to balance these variables systematically between the two treatment groups but also because they are likely to affect an individual's survival (Johnston & Fleischer 1981). We subsequently obtained a minimal adequate model using the Akaike information criterion (AIC; cf. Nakagawa & Cuthill 2007); we used this model for parameter estimation.

3. RESULTS

The results of the minimal adequate model are shown in table 1; the information on the full model, which showed similar results, is summarized in the electronic supplementary material. There were significant interactions between the natural badge size and 'treatment' and the 'age class' and treatment (table 1). None of the main effects was significant, mostly because these significant interactions cancelled out the main effects, which are depicted in figure 1. Survival probability increased with an increase in the natural badge size in the experimental group (slope = 0.598 ± 0.451 (95% CI), $t_{84}=2.64$, $p=0.008$), whereas it decreased in the control group (slope = -0.405 ± 0.360 (95% CI), $t_{84}=-2.24$, $p=0.025$; figure 1a). By contrast, the survival probability decreased with age in the experimental group (slope = -3.04 ± 2.64 (95% CI), $t_{84}=-2.30$, $p=0.022$), whereas it increased in the control group (slope = 2.63 ± 2.01 (95% CI), $t_{84}=2.60$, $p=0.009$; figure 1b).

4. DISCUSSION

One of the aims of our study was to determine whether winter survival was related directly to badge size. In the present experiment, we failed to show a straightforward relationship between badge size and survival (for relevant observational work, see Griffith 2000; for a nonlinear relationship between survival and badge, see Figuerola & Senar 2007). Our manipulation, however, led to an interesting phenomenon, which resulted in the observed significant interactions between the treatments and the original badge size and also between the treatments and the age classes.

In our experimental treatment, where the badge size of all individuals was increased to a fixed size, males with an originally large badge size had higher than average survival, whereas males with an originally small badge size had reduced survival. This finding suggests that differential selection can act on a trait according to the degree of cheating. In other

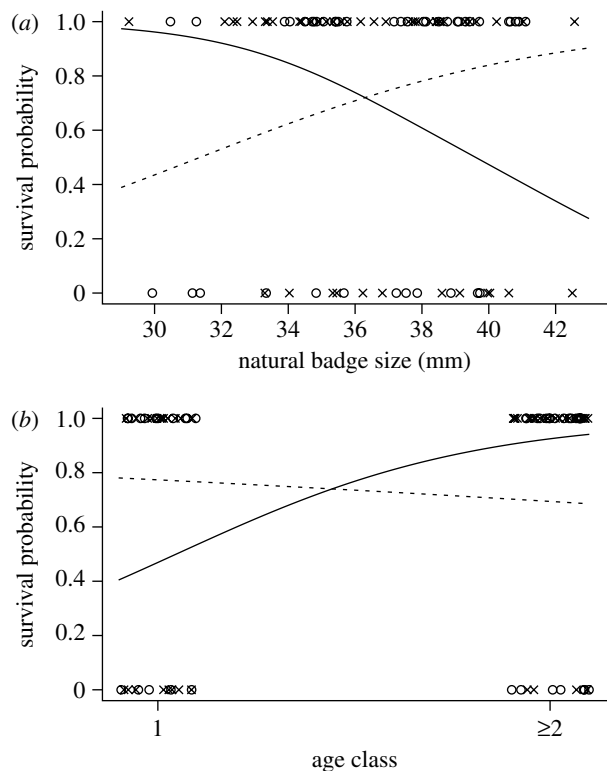


Figure 1. The probabilities of winter survival of the male house sparrows in the two treatment groups, experimental (circle, dashed line) and control (cross, solid line), in relation to (a) the natural badge size and (b) two age classes (arbitrary fractions were added to make data points visible).

words, a small amount of cheating was actually beneficial, while the birds incurred an extrinsic cost when cheating to a larger degree, most probably from social punishment (see the electronic supplementary material for more discussion). However, to draw such conclusions, we would have needed to have two treatments in which individuals with the same badge sizes received either a large or small enlargement of badge. Nevertheless, our results concur to some degree in each case with the contradictory results of Møller (1987), which supported the social control hypothesis, and Gonzalez *et al.* (2002), which provided little support to the social control hypothesis. Our results are comparable to a study of North Island robins (*Petroica longipes*) whose juvenile males have delayed plumage maturation, in which dyed juveniles that resembled mature males suffered higher winter mortality than control juveniles without the dye (Berggren *et al.* 2004). Such a mortality pattern was

owing to dyed juveniles being excluded from suitable habitats during winter, presumably by mature adults.

In the control treatment, the probability of survival decreased with increase in the natural badge size. This unexpected decline with an increase in badge size is difficult to explain, especially considering that in the experimental group the males with large badges had a high probability of survival, which indicates an advantage of having a large badge when the signal is more or less honest (although there are some advantages to being subordinates; see Rohwer & Ewald 1981). A possible explanation for this observation may lie in the very large increase in the number of the males of large badge size owing to our experimental manipulation. If aggression between males with similar badge sizes were more common than for other dyads (Rohwer 1977; Rohwer & Ewald 1981), there would have been an increased number of agonistic interactions for the males with large badge size. Therefore, the manipulation may have had a negative effect on the males with large badges in the control group, although this does not explain why the effect was evident only in the control group.

The significant interaction between the treatments and age class is also difficult to explain. As is often the case in other bird species, house sparrows experiencing their first winter are known to suffer more mortality than older birds (Anderson 2006; see also the electronic supplementary material). However, the fact that the results were opposite to this expectation in the experimental group suggests that the badge enlargement somehow adjusted the pattern of winter survival away from that expected for the age classes, although it is hard to envisage an appropriate mechanism.

To conclude, our work suggests that a large degree of cheating did have a long-term cost, whereas a small degree of cheating seemed beneficial. This finding calls for further investigation, including experimental work to elucidate the true relationship between status signals and survival.

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