Fit and fat from enlarged badges: a field experiment on male sand lizards

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To investigate the impact of nuptial coloration (the badge) on male fitness in the Swedish sand lizard (*Lacerta agilis*), we conducted a manipulation experiment in a natural population. Males in one group had their badges enlarged by being painted as cheaters and were compared to a control group with respect to mate acquisition, body condition and survival. Badge enlargement did not affect survival, but elevated mate acquisition by almost 400%, and body condition in small males. This increase in condition is likely to stem from greater access to female-associated sites with high food availability.

Keywords: status; signalling; badge manipulation; reproductive success; condition

1. INTRODUCTION

In spite of the wisdom that colours are an integral part of lizard communication and reproductive biology (Hover 1985; Cooper & Vitt 1988; Thompson & Moore 1991; Martín & Forsman 1999), there is only a single published report where colour has been manipulated in a natural population and the concomitant effects on components of fitness monitored (Olsson 2001). The present study is, to our knowledge, the first such experiment to be performed on a sexually dichromatic species (the Swedish sand lizard, *Lacerta agilis*) in a natural population.

In sand lizards, females are greyish brown, whereas males develop bright green nuptial coloration on their body sides (the badge). Previous studies have demonstrated that females mate with males regardless of the extent of their coloration (Olsson & Madsen 1995), and that males make tactical decisions in contests depending on rival badges (being more reluctant to attack more colourful males). They have prolonged contests when rivals are more equally coloured, and lose more often to more colourful males (Olsson 1994; Olsson & Madsen 1998). These results not only hold true in experimentally controlled contests (i.e. where male coloration is manipulated), but are also supported by a confirmed link between male colour and fitness in a selection analysis on a natural population (Olsson 1994). However, it remains to be demonstrated that experimental manipulation of male nuptial coloration influences male acquisition of prey and partners in a natural population. That is the aim of the present work.

2. MATERIAL AND METHODS

The Swedish sand lizard (*L. agilis*) is a sexually dichromatic, small (up to 20 g, 90 mm long snout to vent), ground-dwelling lizard species. General biology, evolutionary ecology and molecular population genetics of the population used in the present study have been described elsewhere, with most publications referenced in Olsson & Madsen (2001).

At the Asketunnan study site, 50 km south of Gothenburg on the Swedish west coast, male sand lizards were caught by noose or by hand in the first week of May 2002. Standard morphological measurements were taken: snout–vent length (SVL) to the nearest millimetre, and mass to the nearest 0.01 g. The lizards were marked dorsally with an oval piece of fabric tape (TESA tape, Germany; *ca.* 10 mm × 20 mm) labelled with an individual number.

Males were then assigned at random to one of two treatment categories ('badge-enlarged' versus 'controls'). The colour treatment consisted of painting the body sides of every second male with biologically inert, green human tattoo colour. Three different tattoo colours were mixed to match (by eye) a reflectance spectrogram of an adult male sand lizard in the upper quartile of the size and age distribution (Spuck Baulding, New York, colour nos 9046 'emperor green', 9029 'parrot green' and 9028 'radiant green'). To expose all males to the same handling procedure, every second male was painted with water and dried. Although this means that control males do not carry the thin permeable paint layer of badge-enlarged males, this treatment retains the complex background colour pattern with white ocelli on a grey and black background. Furthermore, subsequent to painting, all males were sprayed on their body sides with moisture-vapour-permeable spray dressing (Smith & Nephew, Hull, UK). This fixed the tattoo paint and increased its durability in the wild during the approximately three-week-long mating season. Thus, although badge-enlarged males showed no signs of discomfort from the treatment, if such effects were at all present, the fitness benefits from the badge enlargement should be underestimated compared to control males (that lacked the paint layer). Unpublished spectrophotometry data show that sand lizard males lack reflectance in the ultraviolet (UV) spectrum (M. Olsson and S. Andersson, unpublished data). We also confirmed that our paint did not reflect in the UV spectrum and, hence, that UV signalling does not compromise interpretation of the experimental data. After this procedure, the lizards were released at their sites of capture and monitored by four field workers on all days when the weather permitted lizard activities throughout the mating season. At the end of the mating season (the last week in May), males were recaptured (our proxy of survival), re-measured and reweighed.

Reproductive success was estimated by monitoring the number of females mate guarded by a male. Considering that copulation takes only 2–4 min and, hence, often goes undetected in the wild, the number of females a male is observed mate guarding for several hours, for up to more than 10 days, is more likely to accurately estimate mate acquisition than the number of observed copulations. Furthermore, mate guarding has been confirmed with molecular genetics techniques (micro- and minisatellites) to accurately reflect paternity (Gullberg *et al.* 1997). No molecular data on paternity were collected to assess paint treatment effects on mate acquisition (number of partners), partly because such estimates may be biased by cryptic female choice on male relatedness, not badge size (Olsson *et al.* 1996), and by the effects of sperm competition.

The duration of mate guarding for each male was estimated and compared between the two groups. A male was considered to mate guard a female if he was observed within 50 cm of her on any particular day (males closer than *ca.* 1 m are rejected by non-receptive females; Olsson & Madsen 2001). Body condition was estimated by taking residual scores from a mass–SVL regression before and after the mating season, letting shifts in residuals represent the relative change in body condition.

Variables used in parametric statistics were tested for normality using Wilk's lambda tests (Proc Univariate; SAS Institute 1987). Variables that did not meet the requirements of normality were either successfully normalized (*W*:normal, Pr < *W*, larger than 0.05 in all cases) by transformation (log or exponential transformation following Sokal & Rohlf 1981); alternatively, non-parametric tests were used.

3. RESULTS

(a) *Description of experimental categories of males*

There was no difference in mean scores between badge-enlarged and control males in body mass, SVL, body condition or number of observations per male (table 1). Unless otherwise stated, sample sizes (*n*) were 39 painted and 34 control males.

Table 1. Descriptive data of differences between treatment groups.
(The measurements represent trait differences at the onset of the mating season, except for number of observations. Body conditions are residual scores from a mass–SVL regression.)

feature	mean score ± s.e. (*n*) controls	mean score ± s.e. (*n*) badge-enlarged	test statistics
body mass (g)	9.1 ± 0.53 (33)	8.8 ± 0.40 (39)	$t = 0.46$, d.f. = 0,70, $p = 0.64$
snout–vent length (mm)	69.8 ± 1.25 (34)	69.9 ± 1.03 (39)	$t = 0.04$, d.f. = 71, $p = 0.97$
body condition (residuals)	0.11 ± 0.14 (33)	−0.09 ± 0.15 (39)	$t = 0.96$, $p = 0.34$
number of ectoparasites	20.8 ± 3.18 (33)	19.9 ± 2.6 (38)	$t = 0.22$, d.f. = 0,69, $p = 0.83$
number of observations	6.8 ± 0.88 (33)	7.8 ± 0.74 (38)	$t = 0.88$, d.f. = 71, $p = 0.38$

(b) *Treatment effects*

(i) *Survival and reproductive success*

There was no difference in survival between badge-enlarged and control males (12 out of 39 badge-enlarged males survived, whereas 16 out of 34 control males survived; χ^2-test, $\chi^2 = 2.0$, $p = 0.15$). In both categories of males, mass was correlated with success in mate acquisition (Spearman's rank-order correlation analysis; $r_s = 0.33$, $p = 0.038$, $n = 39$, and $r_s = 0.45$, $p = 0.009$, $n = 33$, for badge-enlarged versus control males, respectively). A homogeneity of slopes test confirmed that mating success increased differently with mass in the two groups (mass × treatment interaction, $F = 7.44$, $R^2 = 0.18$, $p = 0.0012$), with a steeper increase in badge-enlarged males ($\beta = 0.16 \pm 0.039$, $t = 4.01$, $p = 0.0002$) than in control males ($\beta = 0.14 \pm 0.037$, $t = 3.67$, $p = 0.0005$). Most of this effect arose from a difference in mate acquisition in smaller males, being close to zero in control males while increasing sharply with body mass in painted males.

Previous studies have shown that male coloration is linked to male fighting ability, which is strongly dependent on male body size. Thus, since all males were painted to mimic males in the upper tail of the badge size frequency distribution, the treatment would be predicted to be strongest in small males, that is, with the naturally smallest badges being replaced with a relatively larger badge than in large males. This relationship was supported by separate analyses of males larger and smaller than the mean SVL (dataset truncated at mean SVL). In larger males, there was no significant effect of badge enlargement on male reproductive success (Wilcoxon two-sample test with 0.5 continuity correction, $Z = 0.29$, $p = 0.77$; 20 versus 19 painted and control males, respectively). In smaller males, however, the effect of badge enlargement on mate acquisition was highly significant, with badge-enlarged males having a mating success nearly four times as high as controls (figure 1; Wilcoxon two-sample test with 0.5 continuity correction, $Z = 2.6$, $p = 0.0078$, $n = 19$ and $n = 15$, respectively).

(ii) *Mate guarding*

Male mate-guarding duration increased with male body mass ($r_s = 0.35$, $p = 0.023$, $n = 42$). There was, however, no significant difference in mate-guarding duration between treatment categories ($F = 2.69$, $p = 0.08$, $R^2 = 0.12$; $\beta_{\text{badge-enlarged}} = 0.85 \pm 0.51$, $t = 1.66$, $p = 0.10$; $\beta_{\text{control}} = 0.98 \pm 0.48$, $t = 2.9$, $p = 0.049$, d.f. = 2).

(iii) *Body condition*

Badge-enlarged males increased in body condition index by 0.26 residual units (±0.21, $n = 19$), whereas control
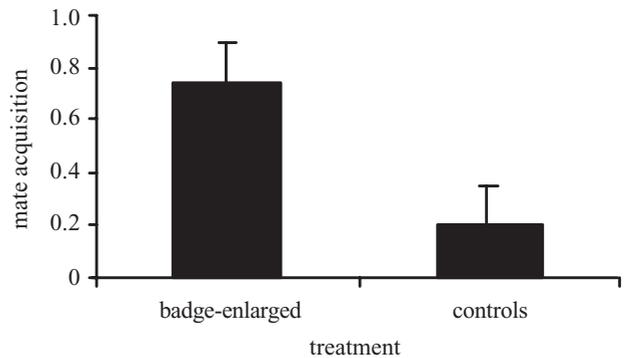

Figure 1. Difference in mate acquisition (mean number of females ± s.e.) between small badge-enlarged and control males.
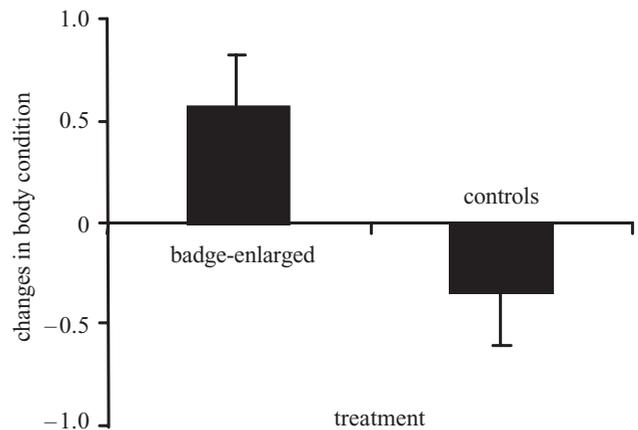

Figure 2. Difference in relative change in body condition between small badge-enlarged and control males (mean residual scores from a mass–SVL regression ± s.e.).

males in fact decreased in condition by 0.36 (±0.15; $t = 2.3$, d.f. = 33, $p = 0.028$). A comparison of body condition revealed a greater increase in body condition for small badge-enlarged males (0.56 ± 0.27) than controls (−0.36 ± 0.25; Wilcoxon two-sample test with 0.5 continuity correction, $Z = -2.06$, $p = 0.039$, d.f. = 1; figure 2; dataset truncated at mean SVL). This treatment effect could, however, not be verified in males with an SVL larger than average, in which both painted and control males decreased in body condition (−0.15 ± 0.32 and −0.35 ± 0.19, $Z = 0.67$, $p = 0.505$, d.f. = 1).

4. DISCUSSION

Our field experiment revealed a significant effect of badge enlargement on two components of male fitness, mate acquisition and body condition. The lack of female mate choice on coloration (Olsson & Madsen 1995), with mate acquisition being an outcome of male–male intraspecific contests, strongly suggests that our results support the assertion that badges function as a cue to male fighting ability. Thus, our manipulation allowed relatively small-badged males to appreciate greater success in mate acquisition through cheating by appearing as males with relatively higher fighting ability.

The results also indicate that badge-enlarged males increased in body condition with control males decreasing in condition, suggesting that males with large badges are better at prey acquisition than controls. This is consistent with the idea that females in several species of lizards are not distributed in relation to males, but in relation to food resources (Hews 1993). Although we only have circumstantial evidence for this, it appears like males, by gaining access to females, also increase their encounter rate with potential prey, and their food intake.

A gain in fitness from possession of large badges leads to an opportunity for cheating, i.e. to develop a larger badge in relation to what is set by convention, in order to enjoy higher fitness. Theory predicts that badge development is constrained (kept honest), for example, by social costs. If this is applied to sand lizards, small painted males should suffer from more frequent challenges by conspecific males than control males. Unfortunately, we do not have the information to test this prediction. The discrepancy between our results and the study on Harris sparrows (Rohwer & Rohwer 1978), in which badge manipulation needed to be supported by a testosterone treatment to take effect, could be related to taxonomy. Rohwers' study was performed on birds, and perhaps the costs for testing another bird's badge are relatively small compared with lizards, where approaching rivals is time consuming and energetically costly, especially if the badge is usually honest. Thus, what may be important is the relative cost and benefit of keeping a signalling system that is approximately correct from both a sender's and receiver's perspective. That some cheating is evolutionarily stable in such a system has been theoretically confirmed (Johnstone 1997).

In summary, the present field experiment demonstrates the positive effects of increased badge size on the components of male fitness. Not only do badge-enlarged males gain more access to females, they also increase in body condition, probably because of a higher encounter rate of food on female home ranges.

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