

Nuptial coloration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability

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Abstract. In the sexually dichromatic sand lizard the area of the nuptial green coloration in males is allometrically related to body mass, and males with higher fighting ability have more saturated nuptial colours. Experiments in the laboratory showed that the extent of the bright nuptial coloration in males affects their contest behaviour; manipulated males with more colour were more likely both to initiate contests and to win. Further, when manipulated males had badges of unequal size the contests were settled more quickly than when the badges were the same size. This predicts that superior fighters with larger badges should have higher mating success; this was confirmed by field studies of a natural population.

Bright colours have evolved in many species and the underlying selective mechanisms have been particularly well studied in birds. In this taxon conspicuous and distinctive pigmentation may function as reinforcements of feathers in extreme environments, defence against predators, threats to conspecifics, a means to attract and distinguish between mates and as isolation mechanisms between sympatric species (Butcher & Rohwer 1989). In this paper I examine the ultimate and proximate function of conspicuous, nuptial coloration in a population of Swedish sand lizards.

Males of the sexually dichromatic sand lizard (for papers dealing with its biology see Bischoff 1984) are ground-dwellers that fight during the mating season to defend a female of immediate interest (Olsson 1993a). The contests are ritualized and the male's lateral green nuptial coloration is displayed towards a rival approaching with the body dorso-ventrally flattened. The green coloration covers the side of the body to some degree in all males, although its total area and pigment saturation vary between males. Contests last from a few seconds to more than 15 min; one in four on average escalates into physical combat (Olsson 1992a).

During the mating season, especially the early part (late April to June) the lateral bright green colour makes the males highly conspicuous in the greyish brown habitat. After the mating season, the green pigmentation gradually disappears, as does male aggression (personal observation).

PREDICTIONS

In male contests, an honest signal of resource-holding potential will benefit both contestants if costly fights with a predictable outcome can be avoided (Parker 1974; Maynard Smith 1982). Especially in populations with frequent interactions plumage variability may perhaps evolve to make a male's fighting ability easily identifiable (the status signalling hypothesis; e.g. Rohwer 1975, 1982; Whitfield 1987). This hypothesis would be equally applicable in sexually and naturally selected contests. In this paper I test predictions of intra-sexual selection (male competition) from an animal-communication viewpoint (Zuk 1991), by asking questions about the structure and function of the male nuptial coloration. Initially, I test the assumption that colour traits may convey information about individual males' fighting abilities. When such cues to fighting ability are energetically cheap to produce, they have been referred to as 'badges' (Dawkins &

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Krebs 1978), a definition that I shall adhere to throughout this paper.

Some game theory models, and in particular the sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984), posit that contesting males assess each other's fighting ability during a sequence of inter-correlated behaviour patterns. Since sand lizard contests can be viewed as a sequential assessment game (Olsson 1992a), I use this model to help generate testable predictions about how manipulated badges should affect the opponent's contest behaviour. If body mass, snout-vent length, age and factors that influence a male's motivation to fight are kept constant (prior copulations and contests, relatedness and previous experience of the fighting arena: Barlow et al. 1986), one may manipulate the size of the badge and study its effect on male contest behaviour. I tested the following predictions. (1) Wallace (1987) pointed out that a 10% increment in mass corresponds to only about a 3% increase in a linear dimension; that is, an increase in body mass may be difficult to perceive. Assuming that the green badge enhances the perception of a rival's size and fighting ability, the pigmented area should scale allometrically to body mass. A function that scales badge area to body mass would be predicted to have an exponent of $3/2$ (Wallace 1987). (2) The saturation of the green pigment should be positively related to body mass, giving a male with high fighting ability a more pronounced signal.

Under the assumption that males have been selected in the wild to consider the green badge as a cue to fighting ability, one may predict the following outcomes in contests. (3) Males with a large badge should initiate threat displays more often than males with a small badge, as the latter should hesitate to threaten a male with higher fighting ability. (4) The sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984) predicts that large sampling errors in the males' estimation of their opponents' fighting ability ('theta', in their model) will make contests last longer. In staged contests, dominance should be established faster when contestants have different badge sizes than when their badges are the same size. (5) Males with a large green badge should win over males with a small green badge. (6) Under the assumption that males with larger badges are superior in contests,

males with larger badges should also have higher mating success.

MATERIAL AND METHODS

Paired Encounters

From my captive population of about 150 first generation offspring wild sand lizards, I selected males for pair-wise contests by the following criteria: (1) snout-vent lengths must be identical within error of measurement (I tested how accurately I could remeasure the snout-vent lengths of the males and found that 1 mm was the biggest difference between a first and a second measurement, therefore I allowed a 1 mm difference between males in the staged contests); (2) mass must be within the mass of an average faecal pellet (0.5 g), as some males defecate while handled; (3) males must be unrelated, to avoid any bias of kinship; and (4) all males must be in good health. After hibernation the males were separated and kept singly in cages measuring $0.5 \times 0.4 \times 0.5$ m, so that they had no prior experience of either females or other males before the contests in a given mating season. Males started eating 1-3 days after hibernation was interrupted, and developed nuptial coloration within a week to 10 days when skin shedding followed.

The experiment was carried out in a cage measuring $1.8 \times 0.6 \times 0.5$ m, subdivided into three compartments. One male (called Green) had his green area enlarged with water colour to cover his entire body side and the other male (called Brown) had his nuptially coloured area reduced to a third of the body side. These manipulations are all within the range occurring in a natural population, although Green were given a badge that normally the largest males have in the natural population. The rest of the body side was painted with the darker greyish-brown hue that naturally covers the non-green parts of the body sides. The same paint was used for all males. I determined which male was to be Green and Brown by flipping a coin. The males were placed in the two outer compartments of the cage; I determined the choice of compartment for each male by flipping a coin. The lizards were painted about 1 h before they were introduced to the contest cage. During each contest I noted (1) who initiated the fight, and (2) who won it. I used male aggressive dominance behaviour (arching of the back, attack)

and subdominance behaviour (lowering of the chin to the ground, fleeing on attack) to determine who was the aggressor, winner and loser (see Kitzler 1941 for a more detailed description of contest behaviour). A contest was interrupted as soon as a male showed subdominance behaviour. No males were in any way physically harmed in the contests. This routine was used in 1989; in 1990 I repeated the experiment with a new cohort and also timed the contests. A male was used only once in the experiment. The following contests were staged and timed between males of presumably equal fighting ability but with manipulated badges: (1) a male (Green) with a large green badge versus a male (Brown) with a small badge ($N=20$, five of these were timed); and (2) two males with equally large badges ($N=7$, all these were timed).

Field Studies

I studied a wild population of sand lizards during 1984–1991, although less intensively during 1985–1986. The study site was visited every day with suitable weather, summing to over 6500 field hours. The lizards were caught by noosing or by hand after which (1) they were marked permanently by toe-clipping and temporarily by putting an adhesive tape with a number on their backs, and (2) snout–vent length (SVL) and body mass were measured. The lizards were remeasured, and if necessary the tape was renewed, every 2–3 weeks. Toe-clipping was used because no other method of permanent identification was known and because the toe-tips, which were preserved in formalin, enabled the ages of the lizards to be determined by skeleto-chronology (Hemelaar 1985). Two or at most three toe-tips were removed, because lizards often lose toes in the wild, making removal of one toe-tip insufficient for purposes of identification. To reduce suffering the operation was carried out as rapidly as possible; the whole routine, from capture to release, took less than 5 min after which the lizard was released at the place of capture. A clipped toe healed within a few days and on several occasions I saw lizards copulate within minutes of being marked. During 1984–1991 I marked more than 1200 lizards in this way and none of them showed any ill-effects from the treatment. Furthermore, there was no significant difference in the rate of recapture of animals that had two or three toe-tips

removed ($\chi^2=0.16$, $df=1$, $P>0.05$), suggesting that clipping had no effects on survival.

I used snout–vent length and body mass (cube root transformed to make dimensions equal) to calculate a condition index ($\text{mass}^{1/3}/\text{SVL}$). In 1990 I also photographed the males laterally and dorsally at a standard distance. I used a 100 ASA ektachrome slide film for all photographs, projected at a standard distance on white paper. The chroma ('pigment saturation') of each male's nuptial coloration was determined by two assistants, using Munsell colour charts (Zucker 1988). A silhouette of each individual was thereafter drawn on the paper and the green area of the body side was cut out and weighed to estimate its area. The same brand and paper quality was used for all the lizards.

A male guards a recently copulated female by resting his chin or an arm on the female's back for several hours or days after a copulation (Olsson 1993b). I noted the number of copulations and mate guardings for each male to estimate his mating success.

To investigate whether badge size is a sexually selected trait I calculated standardized selection coefficients on badge size (Lande & Arnold 1983). Thus, I first estimated the shift in mean of badge size during selection (the selection differentials, mathematically equivalent to the covariance between mating success and trait values). Second, I performed a multiple regression analysis with the independent variables badge area, body mass, snout–vent length, head length and width, and the first day of observation after hibernation. The dependent variable was my estimate of mating success. Thus, in this way I estimated the badge's contribution to mating success independently of the other variables in the multiple regression model (the selection gradient, estimated by the multiple regression coefficient, β). As normality of badge size cannot be assumed, I used Spearman's rank order correlation coefficients for the tests of the selection differentials, and Spearman's rank order partial correlation coefficients for the tests of the selection gradients. I used square roots of areas and cube roots of mass to make dimensions equal.

As badge attributes and body size change throughout a mature male sand lizard's life, age has to be controlled for in the analyses of selection coefficients (Lande 1981). My sample sizes were too small to do this by looking at each cohort

separately, so I split the adult males into three age groups: 3–4 years old, 5–6 years and more than 7 years old (when growth has almost stopped). Males of different ages within these groups overlapped strongly in size and in the estimates of their badge areas.

RESULTS

Badge Traits

All these results derive from the photographs taken in the field.

Pigmented area

A regression of logarithmically transformed variables showed that the badge area scaled allometrically to body mass by the equation $\log(Y) = 2.71 + 1.21 \log(X)$ ($T = 12.19$, $df = 54$, $P < 0.0001$). The scaling factor in this equation (1.21) was significantly larger than 1 ($T = 5.18$, $df = 53$, $P < 0.0001$), and was also significantly smaller than 1.5 ($T = -7.44$, $df = 53$, $P < 0.001$). Badge area correlated significantly with body mass ($r_s = 0.37$, $N = 47$, $P < 0.01$), but not with age ($r_s = 0.18$, $N = 47$, $P > 0.05$), or snout–vent length ($r_s = 0.28$, $N = 47$, $P = 0.063$). I analysed the partial correlations between these three variables and badge area by using Spearman's partial correlation coefficients, since age and badge size were not normally distributed. Badge area was also significantly correlated with male body condition ($\text{mass}^{1/3}/\text{snout-vent length}$; $r_s = 0.82$, $N = 52$, $P < 0.0001$).

Pigment saturation

The value of 'chroma' in the Munsell colour system (i.e. the saturation of the pigment) was highly significantly correlated with body mass ($r_s = 0.49$, $N = 47$, $P < 0.001$; mean estimate of chroma \pm SD = 8.0 ± 1.96). Moreover, the pigment saturation was significantly correlated with body condition ($\text{mass}^{1/3}/\text{snout-vent length}$; $r_s = 0.35$, $N = 42$, $P < 0.05$).

In conclusion, attributes of the green badge were correlated with factors related to the males' fighting ability.

Paired Contests

The green area was correlated with body mass; this, and the strong control of other potential

components of fighting ability, made the males' badges approximately matched in size before I manipulated them.

In 13 interactions I tried to establish who initiated the threat display. Two encounters were draws (the males started to display simultaneously and I could not separate the initiator); the male with the larger badge started nine of the 11 remaining interactions (binomial test: $P < 0.05$).

Males with equal badge size had an average contest duration of 103 ± 44 s (\pm SD), which was significantly longer than the 36 ± 28 s (\pm SD) observed when contestants had unequal badge sizes (Mann-Whitney U -tests: $U = 3$, $N_1 = 5$, $N_2 = 7$, $P < 0.01$). Two of five interactions (40%) between males with equal badge sizes escalated to physical contact, while one of seven interactions (14%) escalated between males with unequal badge sizes; although there was a trend in the predicted direction, this difference was not statistically significant ($P > 0.05$).

Males with a large badge won over males with a small badge in 16 out of 20 interactions (binomial test: $P < 0.01$).

Field Data

In 1987–1991 21% of 3–4-year-old males mated ($N = 119$), 32% of 5–6-year-old males ($N = 111$), and 76% of males older than 7 years ($N = 68$); the minimum number of matings per male was zero in each age group and the maximum number of matings per male was three (one male) in the youngest males, four in the second age group and six in the oldest males.

The selection differential for the green badge (in 1990) was 0.08 ($N = 22$, $P > 0.05$) in the youngest males, 0.64 ($N = 18$, $P < 0.01$) in the next age group and 0.914 ($N = 16$, $P < 0.01$) in the oldest males. The selection gradients were non-significant in the two youngest age groups ($\beta = -0.15$, $N = 22$, $P > 0.10$, and $\beta = 1.15$, $N = 18$, $P > 0.10$), but significant in the oldest males ($\beta = 1.75$, $N = 16$, $P < 0.05$, $r^2 = 0.89$, $P < 0.01$). The correlation coefficients between the green badge and the other variables in the model ranged between 0.57 and 0.61. Thus, in the oldest males, the green badge was under significant sexual selection.

DISCUSSION

Three alternative hypotheses, often associated with the evolution of coloration (Butcher &

Rohwer 1989), are unlikely to explain the evolutionary origin, adaptation and variation in male sand lizard nuptial coloration. (1) Thermoregulation, as a proximate function of the green coloration, would predict males to have the darker olive-brown colour at low ambient temperature early in the season, while the opposite is true. (2) Crypsis is unlikely to explain the evolution of male nuptial coloration in sand lizards because (a) the dominant predators on sand lizards are birds (Simms 1970), hence, if cryptic, the pattern ought to be dorsal, and (b) male coloration is green predominantly when the background is dull and greyish brown. It fades to olive-brown at the peak of the vegetation period. The reversed pattern would be predicted if green coloration was important as camouflage (Olsson 1993c). (3) Aposematism predicts that males should be distasteful or poisonous and not eaten by predators. In captivity, snakes readily eat sand lizards (personal observation) as do birds in the field (Kristin 1987). Thus, aposematism does not seem to be the proximate function of male green coloration.

The exponent of the power function relating badge size to body size (1.21) was significantly higher than 1 but significantly lower than 1.5, predicted theoretically by Wallace (1987). Most fights occur between large males (Olsson 1992b). If the minimum badge size observed in the population is related to male snout-vent length by the exponent 1.5, rather than the observed 1.21, a medium-sized animal would have a badge that ranks among the largest in the population, covering its body side. If so, badge size could then no longer convey information about fighting ability in larger males among which interactions are most frequent. Thus, as male body size constrains badge size, perhaps this also constrains badge size to scale to snout-vent length with a smaller exponent than the theoretically predicted 1.5.

Rohwer (1975, 1982) predicted that status signalling should evolve predominantly in (1) non-territorial birds with frequent interactions that (2) live in 'moderately' unstable flocks (my quotation marks). Two things could relax these requisites: high costs of fighting and low costs of conspicuous signalling. In sand lizards, fighting males may inflict open wounds on each other, exposing underlying mandibular bones (Smith 1964; Olsson 1992b). The risk for such wounds ought to be correlated with the duration and the intensity of interactions. Males with manipulated equal badge

sizes had significantly longer contests, suggesting that neither individual experienced himself as inferior, and did not show submissive behaviour early to end the interaction. In dark-eyed juncos, *Junco hyemalis* (Balph et al. 1979) and house sparrows, *Passer domesticus* (Møller 1987), birds with badges of similar size were more likely to fight each other. Although not statistically significant, this was also suggested in the sand lizard.

If conspicuous signalling is costly from a predation viewpoint, Green lizard models should be attacked by predators more than Brown models. In a predation experiment with model sand lizards (Olsson 1993c), no increase in predation could be detected by adding green badges to lizard models (rather there was a trend towards higher predation on brown models); that is, the cost of conspicuousness appeared to be low in this sand lizard population (the same study population as the present study).

Larger males with higher fighting ability allocate less resources to growth (Andrews 1982) and more resources to reproduction. This could, if pigments are at all costly, constrain smaller males from developing larger badges and to some extent prevent 'cheating'.

In conclusion, there may be (1) high costs of long contests, (2) low costs of signalling from a viewpoint of predation, and (3) costs of producing pigments that prevent smaller males from developing large badges, highly saturated with pigments. However, a more detailed analysis of the interplay between factors that makes this signalling system evolutionarily stable, and what costs prevent 'cheating', is outside the scope of this paper.

Sand lizards may live for over 10 years (Olsson 1992b), and breed every year from 2-3 years of age onwards. Hence, the lack of correlation between age and badge traits suggests that traits such as fighting skill, acquired over time, are not communicated by the badge. In the laboratory experiments, males with larger badges initiated threat displays more often. This followed after the male with the smaller badge had shown submissive behaviour, or was reluctant to display; he was apparently intimidated by the opponent's larger badge. So, what intimidates the loser, or rather, what does the badge communicate: aggression or 'brute strength'?

Assuming that badges play a part in repeated sampling of a rival's fighting ability (Enquist &

Leimar 1983; Leimar & Enquist 1984), presumably during its non-escalated early phase, badges can honestly reflect only relatively static components of fighting ability; badges do not vary in appearance within a relevant time frame, such as a mating season (or within moults in birds). Some major components of fighting ability are temporally variable, most often aggression which is correlated with overall motivation to fight. Motivation to fight is dependent on previous experience of contests (Jackson 1991) and copulations (Olsson 1993a). Therefore 'intrinsic aggression' as a component of fighting ability has to be estimated independently of motivation. This may make it difficult to interpret the results of studies that link badge traits to estimates of aggression without considering the confounding effect of motivation. Provided that aggression is affected by testosterone or some other rapidly changing hormone (Wingfield & Marler 1988; Wingfield & Wada 1989), the badge would be more likely to aid in the perception of some less fluctuating component of fighting ability, such as body size or body condition. Thus, badges are unlikely to reflect temporally variable components of fighting ability such as aggression or overall motivation to fight. In the sand lizard, this is supported by the lack of a 'dose-response' relationship between plasma testosterone levels and the size of the badge (Olsson 1992b). (However, there is evidence that castration of males in peak coloration prevents them from developing nuptial coloration in the following season: Regamy 1935.)

The influence on the outcome of contests by temporally versus static components of fighting ability, and how these correlate with badge attributes, ought to determine to what extent animals should take notice of badges in conflicts.

In conclusion, when good predictors of fighting ability do not change much within a relevant time frame, such as size or age during a limited mating season, these could be reflected in, and be made more easy to perceive by, a 'badge'. Intuitively, it seems more likely that aggression and motivation to fight, traits that may change rapidly, would be more commonly communicated by traits that vary in appearance over time, such as behaviour. Nevertheless, temporally variable 'badges' do exist, such as the brightly coloured heads in some agamid lizards (Madsen & Loman 1987); these may provide interesting systems for manipulation studies.

As predicted, sand lizard males with larger badges had higher mating success, when other male traits were kept constant. This applied only to larger, older males, however. This result would be predicted if younger mature males invoke a less conspicuous strategy and, hence, their mating success is affected more by other behaviour such as sneaking. Similar observations have been made in birds (Lyon & Montgomerie 1986).

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