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## Rival recognition affects male contest behavior in sand lizards (*Lacerta agilis*)

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**Abstract** Individual male sand lizards meet repeatedly during mate search and engage in costly interactions. If males can recognize rivals, the number of costly fights with a predictable outcome may be reduced. In staged contests between males, second interactions are on average significantly shorter than first ones, suggesting individual recognition. When aggressive behavior differs substantially between the sexes, the more aggressive sex may be predicted to have more variation in skin traits located on the parts of the body displayed during contests; this would facilitate individual recognition. Male (aggressive) sand lizards are more variable in two of three lateral skin traits displayed during males' contests, while females (non-aggressive) are more variable in one dorsal skin trait; in four other dorsal traits there was no difference in variability between the sexes.

**Key words** Contests · Recognition · Skin trait Variability

### Introduction

Conspicuous colors and complex patterns in plumage or skin have been claimed to be the adaptive response to a number of selection pressures, such as isolation between sympatric species, defense against predators, endurance of "wear and tear" in harsh environments, and reproduction (Butcher and Rohwer 1989). Moreover, distinctive and complex dermal or plumage patterns may also facilitate individual recognition (Collias 1943; Whitfield 1986; Fletcher and Michener 1987), and the

estimation of a rival's fighting ability (Rohwer 1975, 1982; Whitfield 1987; Thompson and Moore 1991; Olsson in press). Complexity and variability in skin traits could thus reduce the number of costly interactions between rivals. The more aggressive sex, suffering more costs from contests, should be under stronger selection for individual recognition. Hence, assuming that variation in skin or plumage traits makes individual recognition easier, the variability of such traits among categories of individuals should covary with level of aggression.

The sand lizard, *Lacerta agilis*, has been studied quite extensively in Europe and western Asia (most of the approximately 150 papers dealing with its biology are cited in Bischoff 1984). Here I will only give a brief summary of its biology relevant for this paper.

Males of the sexually di-chromatic sand lizard are polygynous ground-dwellers that interact during the mating season to defend a female of immediate interest (Olsson 1992a); thus, these males do not defend geographically defined territories, but rather, a non-site related territory around himself and his mate. The contests are ritualized and two males display the dorso-ventrally flattened body at a closing distance. The body sides have a bright green nuptial coloration and a complex skin pattern in black and grey, both traits varying in appearance among males. The display may proceed to a "ringdance" as males circle around each other, and the duration of contests varies with degree of escalation from a few seconds to more than a quarter of an hour. About 25% of the interactions among males in a natural population escalate to physical combat, during which males direct bites against each other's heads, bodies and extremities (Olsson 1992a). The bites may inflict open wounds, exposing underlying tissues and mandibular bones and, hence, appear to be costly (Smith 1964; M. Olsson personal observations).

Female sand lizards are not inter- or intrasexually aggressive in nature, although in captivity they may, seemingly unintentionally, bite each other in struggles over food (personal observations). Females are larger

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than males [e.g., mean snout-vent length of 5-year-old lizards (approximate mean longevity), is  $82.9 \pm 3.3$  mm (SD) for adult females and  $77.0 \pm 3.9$  mm (SD) for males (Olsson 1992b)].

In this study, I test the hypotheses that (i) male sand lizards recognize each other, and thus make strategic decisions in contests based on previous contests with the same rival. This predicts (ii) more variation in male lateral skin traits, traits observable during contests. Moreover, if the green nuptial coloration in males facilitates individual recognition, (iii) green nuptial coloration should vary extensively in appearance among males.

## Materials and methods

### Field studies

I studied a population of sand lizards at Asketunnan, 50 km south of Gothenburg on the Swedish west coast during 1984–1991, although less intensively during 1985–1986 (Olsson 1992b). The study site was visited every day with suitable weather during the mating season, summing to a total of over 5000 h in the field by myself and another 1500 h by a field assistant (Tobbe Helin). The lizards were caught by noosing or by hand whereafter (1) they were marked permanently by toe-clipping, and temporarily by putting an adhesive tape with an individual number on the lizard's back, (2) standard morphological measurements were taken. The whole routine took less than 5 min and the animals were remeasured and remarked every 2–3 weeks.

In 1990 I also photographed the lizards laterally and dorsally at 0.45 m against the sky; thus, I took every precaution under field conditions to minimize the variation in light conditions between each male's photograph (sand lizards are only active in relatively sunny weather). A 100 ASA Kodak Ektachrome slide film was used for all photographs, which were projected at a standard distance on white paper. Hue ("shade of color"), value ("lightness"), and chroma ("pigment saturation") of each male's nuptial coloration were determined by two assistants using Munsell color charts (Zucker 1988). A silhouette of each individual was thereafter drawn on the paper, and the green area was cut out and weighed to the nearest 0.00001 g to estimate its area. The same brand and quality of paper was used for all lizards.

Aside from the male's green coloration, the skin pattern in the male and female sand lizard is very similar (see plates in Yablokov et al. 1980; Bischoff 1984). I estimated the variability in eight distinct skin traits in a sample of 20 males and 20 females by using a slightly modified description of the traits reported by Yablokov et al. (1980). The estimates of the following eight traits were included in the analyses: (A) *lateral*: (i) dark lateral patches with one ocelli ('eye spot'), (ii) dark lateral patches with more than one ocelli, and (iii) dark patches located ventrally of the ocelli. (B) *dorsal*: (i) white spots interrupting the dorsal lines, (ii) white stripes interrupting the dorsal lines, (iii) brown spots interrupting the median line, (iv) white spots interrupting the median line, and (v) white stripes interrupting the median line.

The difference between males and females in the variance of these traits was tested with Kruskal-Wallis non-parametric analysis of variance (SAS 1987).

### Laboratory studies

From my captive population of first generation offspring from wild sand lizards, males were randomly paired for the coming contests (in all 16 males and, hence, 8 pairs). All males in the staged trials were in good condition. After a 6-week period of

artificial hibernation, the males were held in separate tanks in order to avoid prior experience with other males or females.

Thirty minutes before a contest, I put the two males in a cage with a floor area of  $0.5 \times 1.2$  m; a wall in the middle of the cage separated it into two compartments. The experimental tank was new to both males, but each compartment was set up as the lizards' home cages; it contained a basking rock and a spotlight for thermoregulation. A male's compartment was decided by flipping a coin. Thirty minutes later, the wall separating the compartments was slowly raised, which did not appear to startle the basking lizards. The winner (identified by repeated attacks while arching his back) and the loser (identified by fleeing and by lowering his chin to the ground) was determined, and the contest duration was timed. The contest was regarded as settled when the inferior male showed submissive behavior (lowering the chin to the ground), which eventually happened in all interactions (see Kitzler 1941 for a more detailed description of reproductive behavior in the sand lizard).

Five hours after the first contest between two males, I staged a second contest under identical conditions between the same two males. All interactions took place in the same cage. The 5 h separation of the trials was motivated by observations of male contests in the natural population; a defeated male may need time to regain motivation to take on a new rival (Olsson 1992a,b). This experimental design seems critical as (i) the contests must occur close enough for a male to remember his rival, and (ii) losers must have had time to regain motivation after being defeated. The second contests were also timed and the winner was noted.

The difference in time between the first and the second male-male contest was analyzed by the Wilcoxon signed-rank test.

## Results

### Recognition of opponents

All second interactions commenced the same way as first interactions, both males threat displayed by arching their backs and showing their rival their flattened body sides. In the second interactions the males did not show any signs of having altered their initial lateral display behavior, and all interactions were eventually interrupted by me. Rather, the difference between first and second interactions was the duration of the contests after the initial threat displays; the second contests between two males were significantly shorter than the first ones. First interactions lasted on average  $178 \pm 267$  s (SD) while second ones lasted only  $7 \pm 63$  s (SD) ( $P = 0.041$ ,  $n = 8$ , Wilcoxon signed-rank test). Submissiveness by the inferior male was shown at a distance of about 30 cm. In one contest, the loser from the first interaction came out winner in the second, and therefore dominance was probably not established after the first fight. The first contest between these males lasted for 13.2 s, while the second contest lasted for 73 s. The contests escalated to physical fighting in five out of eight (62%) first interactions, and in three of the eight second ones (38%), which is not a statistically significant difference (Fisher exact test,  $P = 0.24$ ).

### Variability in skin traits other than nuptial coloration

The skin pattern of sand lizards, except for the male nuptial coloration, is present at hatching. Of the three

lateral characters observable in displaying males, two were significantly more variable in males than in females. For the trait 'dark patches with one ocellus', the standard deviations for males and females were 3.98 and 1.29 respectively ( $P < 0.0002$ , Kruskal-Wallis test,  $\chi^2$  approximation,  $\chi^2 = 14.15$ ,  $n = 20$ ), and for the character 'dark patches ventrally of ocelli', the standard deviations were 2.84 for males and 1.79 for females ( $P < 0.0001$ , Kruskal-Wallis analysis of variance,  $\chi^2$  approximation,  $\chi^2 = 26.80$ ,  $n = 20$ ). Of the five dorsal traits, only one was significantly different between males and females. The trait "white stripes interrupting dorsal lines" was more variable in females, than in males (SD = 7.53 for females, and SD = 5.25 for males,  $P = 0.002$ , Kruskal-Wallis analysis of variance).

### Variability in the green badge

As described above, the area and the saturation of pigments change with male size but appear to be constant during the peak of a mating season. From 124 combinations of hue, value and chroma on the appropriate green Munsell color charts, a unique combination could theoretically have been picked for each male (59 males, 124 combinations). However, the 59 males were grouped into 22 combinations, which means that on average 2.7 males had the same color index.

To sum up, (i) the second interaction between two males was significantly shorter than the first one, (ii) two out of three lateral characters were significantly more variable in males (the aggressive sex), while females were more variable in a dorsal trait (not displayed in male contests), and (iii) 2.7 males on average had the same color index of their nuptial coloration.

### Discussion

If scent had been of primary importance for the recognition of rivals, tongue flicking at a close distance would have been expected. However, submissive behavior was shown at a distance suggesting that males primarily seem to rely on vision for the identification of an individual rival, and for the judgement of his fighting ability. Moreover, it is unlikely that odor from the first contest affected male behavior in the second contest. All contests were staged in the same experimental cage; it seems improbable that the submissive behavior of all inferior males in second interactions was caused by the identification of their rival's scent among that of 15 other males' that may have been left behind during the previous 5 h. Furthermore, sand lizards that are well matched in size may fight fiercely for more than 15 min (Olsson 1992a). Therefore there is no risk that a second fight occurring 5 h after the first one (the first fights lasting on average 2 min 58 s), can be caused by fatigue. A third explanation for short second interactions, other than individual recognition, could be that the animals for

some reason were more stressed in the second interactions. However, conditions were identical in both contests, and stress would have been more likely to upset the lizards the first time that they were introduced to the unfamiliar cage. Male motivation was also controlled for in the experimental design, no male had previous experience of males or females after hibernation, and all males had equal time to regain motivation after the first interaction.

Instead, the statistically significant difference in contest duration, the second contest lasting on average less than 4% of the first one, appears to be caused by individual recognition. Inferior males adjust their fighting behavior after a first interaction with a dominant male and, hence, avoid a second escalated contest with a male superior in a previous interaction. The average duration of contests in this experiment was slightly longer than that observed in a natural population (Olsson 1992a). This is likely to be explained by my predetermined criterion for finishing the contest; I did not interrupt the interaction the first time a male fled, which is likely to settle a contest in the wild, but waited for the inferior male to show submissiveness. This may have prolonged the interactions to some extent, although not in a biased way as the same routine was used in both interactions. In a study of iguanid lizards, *Dipsosaurus dorsalis* (Glinksy and Kreckorian 1985), staged contests between neighboring territorial males were significantly shorter than contests between males with territories more distant from each other. Male sand lizards are not territorial, as males have widely overlapping home ranges (Olsson 1992b). However, since males do meet repeatedly within a mating season during mate search (Olsson 1992b), recognition of individual rivals therefore still ought to be advantageous.

Whitfield (1986) rejected the idea that plumage patterns have evolved to reflect differences in status among breeding turnstones, *Arenaria interpres* (Aves). Rather, he concludes that differences in plumage appearance facilitate individual recognition of aggressive neighbors, although he does not claim that this explains the evolutionary origin of plumage variability.

If male sand lizards recognize each other, on what traits do they rely for recognition? Males were more variable than females in two out of three lateral skin characters, while there was less difference in dorsal characters between the sexes; the only trait with a significant difference in variability between males and females was more variable in females. Stamps and Gon (1983), interestingly enough, pointed out higher variability in female than in male dorsal traits in a wide variety of taxa (including lizards), suggesting that this has been selected for by predation. Thus, my observation seems to adhere to the same pattern.

The variation in (i) nuptial coloration, and (ii) other dermal traits were not measured in the same way, therefore the variance estimates of the two groups of traits are not directly comparable. Thus, the design of this study does not make it possible to separate which skin

trait that is most important for individual recognition, it only allows me to conclude that dermal traits other than nuptial coloration have strong potential for facilitating individual recognition. The low variance in characteristics of nuptial coloration (2.7 males on average had the same index combination) could be due to the coarseness of the Munsell color codes. It seems that, at least, the sexually dimorphic complex skin traits may facilitate individual recognition and reduce the number of costly interactions with a predictable outcome in male sand lizards.

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## References

- Bischoff W (1984) *Lacerta agilis* 1758 – Zauneidechse. In: Böhme W (ed) Handbuch der Reptilien und Amphibien Europas, Band 2/I. Echsen (Sauria) II. AVLA, Wiesbaden, 23–68.
- Butcher GS, Rohwer S (1989) The evolution of conspicuous and distinctive coloration for communication in birds. In: Power DM (ed) Current ornithology: 51–108
- Collias NE (1943) Statistical analysis of factors which make for success in initial encounters in hens. *Am Nat* 77:519–538
- Fletcher DJC, Michener CD (eds) (1987) Kin recognition in animals. Wiley Anchor Brandon, Colchester
- Glinski TH, Krekorian O (1985) Individual recognition in free-living adult male desert iguanas, *Dipsosaurus dorsalis*. *J Herpetol* 19:544–546
- Kitzler G (1941) Die Paarungsbiologie einiger Eidechsen. *Z Tierpsychol* 4:335–402
- Olsson M (1992a) Contest success in relation to size and residency in male sand lizards *Lacerta agilis*. *Anim Behav* 44:386–388
- Olsson M (1992b) Sexual selection and reproductive strategies in the sand lizard *Lacerta agilis*. PhD thesis, University of Göteborg
- Olsson M (in press) Nuptial coloration in the sand lizard (*Lacerta agilis*): an intrasexually selected cue to fighting ability. *Anim Behav*
- Rohwer S (1975) The social significance of avian winter plumage variability. *Evolution* 29:593–610
- Rohwer S (1982) The evolution of reliable and unreliable badges of fighting ability. *Am Zool* 22:531–546
- SAS (1987) SAS/STAT guide for personal computers, version 6 edn. SAS Institute, Cary
- Smith M (1964) The British amphibians and reptiles.
- Stamps JA, Gon SM III (1983) Sex-biased pattern variation in the prey of birds. *Annu Rev Ecol Syst* 14:231–253
- Thompson CW, Moore M (1991) Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. *Anim Behav* 42:745–753
- Whitfield DP (1986) Plumage variability and territoriality in breeding turnstone *Arenaria interpres*: status signalling or individual recognition? *Anim Behav* 34:1471–1482
- Whitfield DP (1987) Plumage variability, status signalling and individual recognition in avian flocks. *Trends Ecol Evol* 2:13–18
- Yablokov AV, Baranov AS, Rozanov AS (1980). Population structure, geographic variation, and microphylogenesis of the sand lizard (*Lacerta agilis*). *Evol Biol* 12:91–127
- Zucker N (1988) A method for rapid and precise documentation of lizard coloration. *Herpetol Rev* 19:13–16