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## Why are sand lizard males (*Lacerta agilis*) not equally green?

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**Abstract** Sexual selection theory and game theory posit that cues to mate quality and fighting ability should be costly to be honest. Male sand lizards (*Lacerta agilis*) consider a rival's nuptial coloration when making strategic decisions in contests, and in this paper I examine five mechanisms (both proximate and ultimate ones) that could constrain male nuptial coloration. Three of these mechanisms were rejected as potential constraints on male nuptial coloration: testosterone, predation, and parasites. Two mechanisms could not be rejected as constraints on male pigmentation: differential allocation of energy to reproduction versus somatic growth among males, and social costs due to high aggression from conspecific males.

**Key words** Nuptial coloration · Variability  
Proximate causation · Ultimate causation

### Introduction

Most pigments have generally been considered energetically cheap to produce (Kodric-Brown and Brown 1984); male color ornaments or cues of fighting ability may therefore be open to deception by inferior males (Andersson 1982; Maynard Smith 1982; Stamp-Dawkins and Guilford 1991). Sexual selection theory and game theory posit that cues to mate 'quality' (i.e., heritable fitness related traits) and a rival's fighting ability should be costly to be evolutionarily stable. If factors, proximate or ultimate, such as parasites, growth, and social costs of aggression (Howard and Minchella

1990) constrain the synthesis of pigments, male ornaments could be honest cues to a male's 'quality' or to his resource-holding potential (RHP, *sensu* Maynard Smith 1982).

In this paper I consider five factors that may constrain the magnitude of the green nuptial coloration in male sand lizards (*Lacerta agilis*). My aim is not primarily to identify ongoing selection on male nuptial coloration, as this has been reported elsewhere (Olsson in press). Rather, I look for factors that prevent males from developing equally conspicuous coloration. For three of these factors I present original data: (i) parasites, (ii) social costs, and (iii) differential allocation of energy to activities associated with reproduction among males of different sizes. The two remaining factors, i.e., the effect of testosterone and the cost of predation on male nuptial coloration will be discussed using published data (Olsson 1993; Olsson and Silverin 1992).

During the mating season (late April to June) the bright green males of the sexually di-chromatic sand lizard are highly conspicuous in their grayish brown habitat. The area of the bright green coloration on their body sides is displayed in conflicts over females as the body is dorso-ventrally flattened towards the opponent (Kitzler 1941; Olsson in press). About 25% of the male interactions escalate to physical fights, lasting from a few seconds to more than a quarter of an hour (Olsson 1992a). Males may wound each other during these fights, exposing underlying tissues and mandibular bones (Smith 1964; M. Olsson personal observations). However, the majority of fights only leave superficial scars, which gradually change in color and appearance during the following 2–3 weeks, disappearing thereafter.

The appearance of the green area on the body side varies among males; the area increases allometrically with body size and its pigment saturation is correlated both with body mass and with an index of body condition [ $\text{mass}^{1/3}$  (g) / snout vent length (mm); Olsson in press]. In staged male contests in which body size, prior experience of fighting and mating, kinship and previous experience of fighting arena were controlled, males with

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experimentally enlarged badges initiated and won more contests than males with experimentally reduced badges (Olsson 1992a).

## Reviewed hypotheses and predictions

### *Predation*

Predators of several taxa may feed on sand lizards (Simms 1970; Olsson 1993), e.g., in the kestrel *Falco tinnunculus* sand lizards may constitute 16% of the diet (Kristin 1987). When males have a selective advantage in being conspicuous, e.g., when the conspicuous trait is sexually selected, the selective advantage of a male's conspicuousness is expected to be countered by increased predation; this predicts that conspicuousness will be arrested at an optimal level (Andersson 1982), which has been suggested for example in brightly colored fishes (e.g., Haskins et al. 1961; Endler 1980). If the green nuptial coloration in male sand lizards were limited in expression by predation, male models with green flanks should be more often detected and attacked than models lacking these colors. In a predation experiment with plastic models, models with green flanks were not significantly more attacked than models lacking such distinctive coloration (Olsson 1993); of 51 attacks on the models, 31 (61%) were directed at the models *without* green flanks, contrary to the prediction that conspicuous males are more frequently attacked.

### *Testosterone*

In some iguanid lizards, seasonal development of nuptial coloration may be induced by artificially administered testosterone (Cooper et al. 1987). If nuptial coloration and aggression (an important component of RHP) are both influenced by plasma levels of testosterone, nuptial coloration could be used as a cue to an important component of a rival's fighting ability. However, in a laboratory experiment, Olsson and Silverin (1992) found no dose-response relationship between plasma concentrations of testosterone and the size of the nuptially colored area in male sand lizards.

To sum up, predation (ultimate causation) and testosterone (proximate causation) do not seem to explain substantial variation in the nuptial coloration of male sand lizards. At least three other mechanisms may be suggested in order to explain such variation among males: (i) parasites, (ii) social costs of cheating, and (iii) differential allocation of energy and nutrients to reproduction versus somatic growth among males.

### *Parasites*

Hamilton and Zuk (1982) suggested that female passerines (*Aves*) could use the bright color of males as a cue

to heritable parasite resistance of mates (see Endler and Lyles 1989). Less attention has been paid to the effect that parasites may have on signals of fighting ability (Howard and Minchella 1990). In reptiles, ticks are common ectoparasites and have a pathogenic affect on their hosts (Reichenbach-Klinke and Elkan 1965). Thus, assuming that parasites affect male vigor and fighting ability parasite numbers should be negatively correlated with estimates of pigmentation (Hamilton and Zuk 1982; Read 1988; see Endler and Lyle 1989).

### *Social costs*

A cheap signal open to deception by low status individuals may become evolutionarily unstable, and unreliable as a cue of fighting ability (Whitfield 1987). However, this could be controlled socially by unacceptably high costs of cheating from aggressive conspecific males, as shown in house sparrows (Møller 1987) and suggested in fish (Kodric-Brown and Brown 1984). In adders, males with high fighting ability (large males) engage in more interactions than do small ones (Madsen et al. in press). If this is also the case in sand lizards, a cue of high fighting ability may mean frequent interactions for a "cheater", increasing the absolute costs of "cheating", and preventing males from being dishonest.

In the sand lizard, most interactions are rapid and settled by displaying (Olsson 1992a), which reduces the chances of observing interactions between males in the field. An indirect way of estimating social costs in sand lizards could be to count the scars due to interactions in various size classes of males. Such scars are possible to separate temporally as they change in color and appearance over time, similar fading scars can be observed in females after copulations (van Nuland and Strijbosch 1981; Olsson 1992b). Unfortunately this yields a joint estimate of the social costs associated with both male body size and the potential costs of "cheating" by wearing too large a badge; these costs could be teased apart statistically by using partial correlation coefficients and be given estimates independent of each other. This does not yield a testable prediction but, rather, suggests to look for a relationship between scar numbers and the area of nuptial coloration (and the joint effect of body size).

Furthermore, under the hypothesis that social costs constrain males (ultimately) from developing too large a pigmented area (i.e., prevents cheating) we may also make a second prediction: in a plot of area of the male nuptial coloration against a reliable predictor of fighting ability (e.g., body mass, Olsson 1992 a), males with positive residuals should include the "potential cheaters"; thus, the group including potential cheaters would be expected to suffer more costs, e.g., higher mortality, than males with negative residuals, following directly or indirectly from harassment of cheaters by conspecific males.

## Allocation of energy to reproduction versus somatic growth

In the sand lizard, male body size is sexually selected, larger males having higher fighting ability and winning more contests for females; growth is therefore of crucial importance for future reproduction (Olsson 1992b). Both sexes grow throughout life but growth rate drops when they are sexually mature and then gradually declines (M. Olsson, unpublished data); this is a widespread pattern in many reptiles (Andrews 1982). Thus, recently matured males (that are smaller and/or younger) invest more in somatic growth than do larger and/or older males; thus, younger and smaller mature males ought to invest relatively less on average in activities associated with current reproduction. If the production of pigments requires an energy investment, males that still grow at a fast rate would be predicted to have less pronounced pigmentation.

## Methods

A population of sand lizards (*Lacerta agilis*) was studied during 1984–1991 at Asketunnan, 50 km south of Gothenburg on the Swedish west coast, although less intensively during 1985–1986. The study site was visited every day during the mating season when the weather permitted lizard activity, summing to about 6500 field h (including 1500 hours by a field assistant, Tobbe Helin). The lizards were caught by noosing or by hand. Thereafter (1) they were marked permanently by toe-clipping, and temporarily by a tape on the back with an individual number, (2) various morphological measurements were taken, (3) bite marks were counted and aged before released at the place of capture. The whole routine took less than 5 min. The animals were marked and measured again every 2–3 weeks. The clipped toes were preserved in formalin for skeletochronological age-determination (Hemelaar 1985).

In 1990 I photographed the males laterally at their peak of nuptial coloration, about 1 week after the first skin shedding. The photographs were taken at a distance of 0.45 m, using the sky as background and, hence, all photographs were taken in a standardized manner. A 100 ASA Kodak Ektachrome slide film was used for all photographs, which were projected at a standard distance on white paper. The "chroma", i.e., the saturation of pigments of a male's color, was determined by two assistants, using Munsell color charts (Zucker 1988). A silhouette of each individual was drawn on the paper and the green area was cut out and weighed as an estimate of its area. The same brand and paper quality were used for all lizards.

Growth rates were estimated by dividing the log-transformed snout-vent length of a male in 1990 with the log-transformed snout-vent length of the male recorded in 1989 (the first observation in a given year was used). This estimate was regressed on the snout-vent length in the 2nd year, and the residual values were used as estimates of size specific relative growth rate. Thus, I refrained from using standard growth equations as I regarded the number of remeasurements per lizard inadequate (three or less for most lizards).

Similarly, the log-transformed square root of the area of the male's nuptial coloration was regressed on log-transformed snout-vent length and the residuals were used as size-specific estimates of the pigmented area.

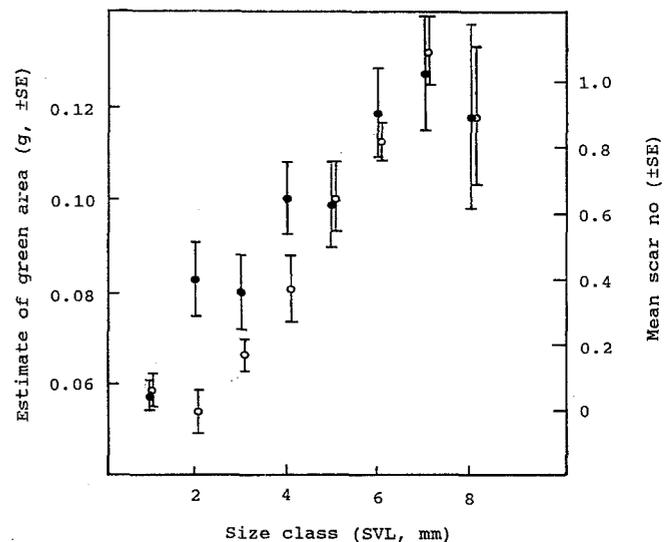
## Results

### Parasites

Ticks (*Ixodes ricinus*) infest sand lizards with on average 15.0 ticks per male (min = 1, max = 48). Their abundance is significantly correlated with male mass ( $r_s = 0.31$ ,  $P = 0.0001$ ,  $n = 367$ , Spearman's rank-order correlation test). This may be explained by earlier appearance of larger males after hibernation (Olsson 1984), so that larger males have a longer exposure time to parasites than smaller ones. There was no significant correlation between the size of the green area and the number of ticks when controlling for body size ( $r_s = 0.16$ ,  $P = 0.25$ ,  $n = 36$ , Spearman's partial rank-order correlation test, holding male body mass constant). Moreover, number of ticks was not significantly correlated with pigment saturation ("chroma" in the Munsell color system,  $r_s = -0.04$ ,  $P = 0.81$ ,  $n = 36$ ).

### Social control

The number of fighting scars does increase with the area of nuptial coloration, but also with male body size (Fig. 1). An attempt was made to tease these estimates apart statistically by using Spearman's partial correlation coefficient (available in SAS). However, when body mass was held constant, the partial correlation coefficient between the number of scars and the area of the nuptial coloration was not significant ( $r_s = 0.03$ ,  $P = 0.86$ ,  $n = 51$ ). Also, when the area of nuptial coloration was held constant, the partial correlation be-



**Fig. 1** Descriptive data of mean estimates of areas (○, ±SE) of nuptial coloration, and scar numbers (●, ±SE) in eight size classes of males (≥ 65 mm, 2-mm interval). The estimates are based on the following sample sizes, the first for color and the second for scars:  $n_1 = 7, 21$ ;  $n_2 = 12, 31$ ;  $n_3 = 8, 36$ ;  $n_4 = 15, 62$ ;  $n_5 = 14, 56$ ;  $n_6 = 18, 62$ ;  $n_7 = 15, 44$ ;  $n_8 = 5, 18$

tween body mass and the number of scars turned out not to be significant ( $r_s = 0.08$ ,  $P = 0.59$ ,  $n = 51$ ).

In a plot of green area against body size, males with positive residuals (among them the potential "cheaters") were tested against males with negative residuals for equal recapture rate during the following year. Although not statistically significant ( $P = 0.16$ , Fisher exact test,  $n = 51$ ), there may be a trend for lower survival of males with positive residuals, i.e., those males with body-size-specific badge sizes larger than average.

#### Allocation of energy to reproduction versus somatic growth

The size specific estimate of growth rate is correlated negatively with the area of the pigmented area ( $r_s = -0.62$ ,  $P = 0.03$ ,  $n = 12$ ). This suggests that males that grow more quickly (younger and, or, smaller males) invest less in activities associated with reproduction, such as producing pigments and engaging in costly interactions (Fig. 1).

### Discussion

Male nuptial coloration does not seem to be affected by the density of ticks. Moreover, these ectoparasites may also act as vectors for endoparasites, e.g., coccidians in sand lizards (Svahn 1972, 1974) and possibly also piroplasmids (Svahn 1976), both being blood parasites. High incidence of coccidians (*Karyolysus*) yields clear pathological effects, such as leucocytosis and anaemia in laboratory kept sand lizards (Svahn 1974), and Svahn concludes that there was possibly a relationship between high densities of blood parasites and sudden death in sand lizards. Assuming a correlation between tick numbers and blood parasite numbers (as predicted by Svahn's data), two parasite taxa may have been reflected in my parasite estimates: ticks and hemoparasites, both pathogenic. Thus, possibly neither ticks nor blood parasites affect the magnitude of nuptial coloration, at least not at the abundances found in the wild.

No statistically significant difference in mortality could be found between males with positive versus males with negative residuals in the plot of green area against body size ( $P = 0.16$ , Fisher's exact test). However, this estimate of costs of cheating may be too simplistic; e.g., aggression from conspecific males may result in other fitness related costs, such as lower probability of obtaining matings for "cheaters". Moreover, the majority of males in the group with potential cheaters are males within the natural variation of the trait, making a cost for cheaters difficult to pick up, if there is one. Thus, the null result in the cost analysis should be treated with caution.

The frequency of interactions increased in upper male size classes in the natural population. Assuming that males signalling for "large size" are realized as such

by conspecific males, these males ought to be involved in more social conflicts than males with less apparent coloration; this would make cheating increasingly costly the more a male cheats. The probability of having a false trait checked also increases progressively, and this could function as a social control against deception. A critical test would be to count scars from escalated contests on males with manipulated badges. However, the practicality of doing this over a long enough time in the field is limited; water color will wear off and larger areas of skin cannot be covered by enamel paint as it is harmful.

Mature sand lizard males with high growth rates, generally younger and smaller males, overall seem to invest less in activities associated with reproduction, specifically, they are engaged in fewer interactions and have less pigmentation. This suggests that in fact pigments may be costly, their synthesis needing nutrients and energy. In birds, melanin is incorporated less into growing feathers during the night (Grubb 1989). Apparently, energy and nutrients need to be readily available for successful production of melanin; during the nightly "shortage" of energy and nutrients somatic maintenance or other factors more strongly correlated with survival are under priority. Among bird breeders, it is common knowledge that pigmentation can be artificially induced, for example canaries produce red feathers after the administration of paprika (carotenoids) (Ralph 1969) and, hence, pigment production may require foraging and is not necessarily cheap. Although in birds green pigmentation may be caused by turacoverdin (Ralph 1969), the pigments causing green coloration in sand lizards have never been investigated at the level of structural chemistry. Therefore, it is not possible to explain the physiological interplay between these pigments and growth.

To sum up, five alternative mechanisms (both ultimate and proximate ones) were discussed that may limit the magnitude of male nuptial coloration in sand lizards. Three of these were rejected as important for explaining variation in coloration among males. Testosterone and predation appear to have no influence on the variation of developed male coloration and a male's number of parasites does not influence size specific nuptial coloration (at least at the abundances of parasites normally seen in the field).

Two mechanisms could not be confirmed to be irrelevant for explaining variation in male green pigmentation, namely social control and differential allocation of energy and nutrients to somatic growth and reproduction among males. Interaction frequencies increase both with male size and area of green pigmentation, and some males' higher investment into growth (generally smaller and, or, younger males) seems to act as a constraint on pigment production; these two mechanisms could work in concert to make nuptial coloration an honest signal of fighting ability. Size-specific allocation of resources to growth and to future reproduction (residual reproductive value) in this lizard may prevent

smaller, fast-growing males with less fighting ability from developing dishonest signals.

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## References

- Andersson M (1982) Sexual selection, natural selection and quality advertisement. *Biol J Linn Soc* 17:375–393
- Andrews RM (1982) Patterns of growth in reptiles. In: Gans C, Pough FH (eds) *Biology of the reptilia*, vol 13, Physiology D, Physiological Ecology. Academic Press, London, pp 273–335
- Cooper W Jr, Mendoca MT, Vitt LJ (1987) Induction of orange head coloration and aggression by testosterone in the male broad-headed skink *Eumeces laticeps*. *J Herpetol* 21:96–101
- Endler JA (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34:76–91
- Endler J, Lyles AM (1989). Bright ideas about parasites. *Trends Ecol Evol* 4:246–248
- Grubb TC Jr (1989) Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* 106:314–320
- Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387
- Haskins CP, EF Haskins, McLaughlin JJ, Hewitt RE (1961) Polymorphism and population structure in *Lebistes reticulatus*, an ecological study. In: Blair WF (ed) *Vertebrate speciation*. University of Texas Press, Austin, Texas, pp 31–51
- Hemelaar A (1985) An improved method to estimate the number of growth year rings resorbed in phalanges of *Bufo bufo* (L) and its application to populations from different latitudes and altitudes. *Amphibia-Reptilia* 6:323–341
- Howard RD, Minchella DJ (1990) Parasitism and mate competition. *Oikos* 58:120–122
- Kitzler G (1941) Die Paarungsbiologie einiger Eidechsen. *Z Tierpsychol* 4:335–402
- Kodric-Brown A, Brown JH (1984) Truth in advertising: the kinds of traits favored by sexual selection. *Am Nat* 124:309–323
- Kristin A (1987) Überlappung trophischer Ansprüche der Nestlinge *Asio otus* und *Falco tinnunculus* in den Windbrechern. *Biologia Bratislava* 42:625–632
- Madsen T, Shine R, Loman J, Håkansson T (in press). Determinants of reproductive success in male adders *Vipera berus*. *Anim Behav* 45:491–499
- Maynard Smith J (1982) *Evolution and the theory of games*. Cambridge University Press, Cambridge
- Moller A-P (1987) Social control of deception among status signalling house sparrows *Passer domesticus*. *Behav Ecol Sociobiol* 20:307–311
- Nuland GJ van, Strijbosch H (1981) Annual rhythmicity of *Lacerta vivipara* Jacquin and *Lacerta agilis* L. (Sauria, Lacertidae). *Amphibia-Reptilia* 2:83–95
- Olsson M (1984) Spatial patterns and social system in the sand lizard, *Lacerta agilis*. Honors thesis, University of Göteborg
- 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*. Ph D 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*
- Olsson M (1993) Nuptial coloration and predation risk in model sand lizards, *Lacerta agilis*. *Anim Behav* 46:410–412
- Olsson M, Silverin B (1992) A green badge in the male sand lizard *Lacerta agilis*: what component of fighting ability does it reflect? In: Olsson M, Sexual selection and reproductive strategies in the sand lizard *Lacerta agilis*. Ph D thesis, University of Göteborg
- Ralph CL (1969) The control of color in birds. *Am Zool* 9:521–530
- Read AF (1988) Sexual selection and the role of parasites. *Trends Ecol Evol* 3:97–102
- Reichenbach-Klinke H, Elkan E (1965) *Diseases of reptiles*. TFH Hong Kong, pp 474–495
- Simms C (1970) *Lives of British lizards*. Goose, London
- Smith M (1964) *The British amphibians and reptiles*. Collins, London, pp 183–192
- Stamp-Dawkins M, Guilford T (1991) The corruption of honest signalling. *Anim Behav* 41:865–873
- Svahn K (1972) Coccidian blood parasites in lacertids. Ph D thesis, Lund
- Svahn K (1974) Incidence of blood parasites of the genus *Karyolysus* (Coccidia) in Scandinavian lizards. *Oikos* 25:43–53
- Svahn K (1976) A new piroplasm *Sauroplasma boreale* sp. n. (Haemosporidia, Theileriidae) from the sand lizard *Lacerta agilis*. *Norw J Zool* 24:1–16
- Whitfield DP (1987) Plumage variation, status signalling and individual recognition in avian flocks. *Trends Ecol Evol* 2:13–18
- Zucker N (1988) A method for rapid and precise documentation of lizard coloration. *Herpetol Rev* 19:13–16