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Female choice on male quantitative traits in lizards – why is it so rare?

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Abstract Female choice on the basis of male traits has been described in an array of taxa but has rarely been demonstrated in reptiles. In the sand lizard (*Lacerta agilis*), and possibly in other non-territorial reptiles, a male's contribution to a female's fitness is restricted to his genes. In order to choose males of high genetic quality, females have to trade the fitness gain against the costs of active choice. In a Swedish population of sand lizards, long-lived males sired offspring with higher embryonic survival compared to offspring sired by short-lived males. In spite of this female sand lizards did not mate selectively with older and/or larger males. There appeared to be no reliable cues to male longevity; age-specific male body size was highly variable. Furthermore, estimates of male nuptial coloration did not covary with ectoparasite load and, hence, females cannot use male coloration as a cue to heritable resistance to pathogenic parasite effects. When cues to male genetic quality are poor, or inaccurate, and males make no parental investment, we predict that female choice will be rare. Sand lizard females mating with many partners lay clutches with higher hatching success. Thus, females may obtain “good genes” for their young by multiple mating, thereby avoiding costs associated with mate choice.

Key words Lizard evolution · Bright colors · “Good genes” · Female choice · Sperm competition

Introduction

Darwin (1871) tentatively suggested that male secondary sex traits could evolve by female choice (intersexual selection). The renewed interest in intersexual selection during the last decade has indeed confirmed that Darwin was correct; female choice is a potent evolutionary force, moulding behavior and morphology of many species of insects, crustaceans, fishes, amphibians, birds and mammals (Andersson 1994). In some less mobile species, like sea elephants, females may choose mates by rejecting unpreferred mates (Cox and Le Boeuf 1977; Parker 1983). In other species, particularly lekking ones, females may visit several males before returning to the selected male for the copulation (e.g., Andersson 1989; Parker 1983).

It is our ambition in this paper to investigate why female choice has so rarely been reported in such a well-studied taxon as lizards (in only one case study, Cooper and Vitt 1993). In few species data is sufficient to admit powerful enough tests to convincingly demonstrate why females do *not* choose males. However, we believe that our data set on sand lizards may admit such tests.

Male and female sand lizards (*Lacerta agilis*) grow throughout life, although at a diminishing rate (Olsson 1992a). Females grow larger than males (Olsson 1992a). The larger body size provides females with a physical ability to reject courting males, usually communicated by a characteristic nodding behavior lasting for less than a minute (Kitzler 1941; Olsson 1992a). During the mating season male sand lizards are neon-green while females are grayish brown. The bright green coloration on a male's body sides is displayed during contests and courtships and varies in appearance among males (Kitzler 1941; Olsson 1994a–c). The area of the green nuptial coloration increases allometrically with body size and in older males nuptial coloration is under intra-sexual selection (Olsson 1994a).

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In this study we test the following predictions:

1. *Male "good genes"*: There is variation in male genetic quality and females could produce more viable offspring by mating with genetically superior males. Specifically we test the assumption that longlived males sire more competitive young.

2. *Cues for female choice*: male size accurately reflects male age.

3. Males heavily infested with ectoparasites have less pronounced nuptial coloration.

4. *Female choice*: Females do not mate with younger or smaller males.

5. Females avoid the risk of becoming infested with parasites by not mating with heavily parasitized males (as observed in for example pheasants, *Chrysolophus colchicus*; Hunter et al. 1993).

6. When there is a choice, females are more attracted to male morphs with extensive nuptial coloration.

In order to test these predictions, we report results from a study on a lizard population conducted in south-west Sweden from 1984 to 1991, and an experiment carried out in the laboratory in 1986–1988, and 1990.

Material and methods

Field studies

In 1984 and 1987–1991 the senior author plus field assistants visited the study site (Asketunnan, 50 km south of Göteborg on the Swedish west coast) every day during the mating season (April–July) when the weather permitted lizard activity in all about 6500 h. In 1985–1986 field work was less intense. Lizards were caught by hand or by noosing, snout-to-vent length (SVL) and total length were measured to the nearest millimeter, lizards were weighed to the nearest 0.1 g, and ectoparasites (Bauwens et al. 1983; Svahn 1974) were counted. Lizards were marked individually by toe clipping and by painting a number on an adhesive tape placed on the lizard's back (average number of marked lizards per year = 124 ± 23 , SD, sex ratio 1:1, Olsson 1992a). During the mating seasons we monitored lizard reproductive behaviors by observing male visits to site-tenacious females (Olsson 1992a), and noted the males with which they were associated. This conforms approximately to the focal animal sampling technique (Altmann 1974; Olsson 1992a). Fights, copulations and the mate guardings that characteristically follow the copulations were continuously monitored (see details in Olsson 1992a, 1993a).

Females were brought to the laboratory about a week prior to oviposition, and kept in separate cages ($0.4 \times 0.5 \times 0.5$ m). After egg laying, eggs were transferred to plastic containers with vermiculite mixed with water (10:1 ml). All eggs were incubated at an ambient temperature of 25°C ($\pm 1^\circ\text{C}$) and they hatched after about 40 days. Mean hatching success was 77% (Olsson et al. 1994a). Unhatched eggs were dissected in order to determine if they were fertile (Olsson et al. 1994a, b).

Lizard age was determined by skeletochronology (bone age determination, Hemelaar 1985). We estimated longevity (in months) as the time elapsing from a lizard's approximate hatching date (1 September) to the last date it was observed. Sand lizards are highly site tenacious (Yablokov et al. 1980; Olsson 1992a, 1993a), so the year after the last observation they were recorded as dead

(and the latest observation date the previous year was considered to be the date of death). Furthermore, every year 0–600 m circumference around the study area was searched for marked lizards, to check that missing lizards had not simply moved. The searched distance should be more than adequate considering these animals' maximum home range size (Olsson 1986); the searched circumference varies depending on the distance to water surrounding the peninsula on which the study area was situated.

During 1990 we also photographed all males laterally, using Kodak Ektachrome 100 ASA slide film. The photographs were taken about 1 week after moult against blue sky at a standard distance of 0.45 m; hence, we took every precaution in the field to standardize the light conditions at which the photographs were taken. Slides were projected at a standard distance on white paper. Using Munsell color charts (Zucker 1988), we determined the pigment saturation ("chroma") of the males' green nuptial coloration. 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. This mass was used as an estimate of the size of the nuptial coloration. The same brand and quality of paper was used for all lizards.

During the mating seasons 1987–1991, 27 out of 85 monitored females were observed with only one partner. This made it possible to correlate traits (age and snout-vent length, SVL) of individual males with the survival of their embryos (hatching success). When males mated with more than one single-partner female in 1987–1991, the years in which females were brought to the laboratory, or were observed doing so in more than 1 year, we used the average hatching success of a male's sired clutches. Six males were observed with single-partner females in more than 1 year (males 189, 191, 193, 228, 592 and 893). We used the data for these males in an analysis of covariance to look for a change in the hatching success of clutches sired by individual male's with age.

We also considered the alternative hypothesis that offspring viability was determined by the females; males could sire viable offspring simply because they mated with females that produced viable young. Our data did not allow a nested analysis of variance of the hatching success of clutches sired by individual males within that of females. Instead, we looked for a correlation between a female's longevity and her mean hatching success, and controlled for female longevity in a Pearson's partial correlation analysis between male longevity and mean hatching success.

Since we pooled data from 5 years, using averages when more than one observation was made per individual, we also looked for differences in hatching success among years. If both adult survival and hatching success were particularly good in some years, this could have given rise to spurious positive correlations between these variables.

Laboratory experiments

In all cages and, or, compartments, each individual had access to a 40-W spot light for thermoregulation, to ensure that female behavior was not altered by an inappropriate thermal environment. Thus, all animals in these experiments were allowed to maintain their preferred body temperature.

Experiment 1

In the first laboratory experiment we addressed female choice by rejection of individual males. A group of 30 females and 16 males was used. The size range of the males reflected that of a natural population. Lizards were hibernated at 4°C in a climate chamber for 6 weeks. After hibernation females were kept in separate cages ($0.5 \times 0.4 \times 0.5$ m) and males were presented to females one at a time while we monitored female rejection or acceptance (lifting of tail, or no rejection).

Experiment 2

In the second laboratory experiment, designed to investigate female choice based on area of nuptial coloration, we controlled for individual differences in male morphology and behavior by using replicas of a male sand lizard. The models were made by injecting epoxy into a mould, made by allowing silicone to set around a dead, frozen male sand lizard; thus, the models were morphologically identical. The models were painted by a professional wildlife artist, and elicited display behavior in males when used in a field experiment (Olsson 1993b).

An experiment cage, $1.5 \times 0.6 \times 0.4$ m, was divided into three compartments of equal size by two sliding walls; this probably makes the distance between two males somewhat smaller than in the wild, but had the advantage of making sure that females could see both models simultaneously. Before a trial a female ($n=10$) in oestrus (confirmed by female acceptance behavior towards a courting male, Olsson 1993a) was placed in the center compartment. A male model was placed in each peripheral compartment; on one model the complete body sides were painted green, a trait only exhibited by the oldest males in the natural population (Olsson 1992a, 1994a–c). On the other model only one-third of the body sides were painted green, a trait exhibited by younger males in the natural population (Olsson 1992a, 1994a–c). The compartment of each model was determined by flipping a coin. Thirty minutes after the female was introduced to the experiment cage, we raised the walls and noted (1) how females approached the models (directly, or coincidentally while investigating the cage), (2) which model the female first visited, and (3) whether she visited both males and, if so, whether she did that repeatedly. If a female seemed disinterested the trial was terminated after 10 minutes.

Results

Field data

Effects of parental longevity on hatching success

Long-lived males sired a larger proportion of viable offspring than short-lived males (Fig. 1, correlation between male longevity and average hatching success $r=0.58$, $P=0.004$, $n=23$, number of clutches averaged per male = 1.5 ± 1.1 ; means are quoted \pm SD). Of the 23 males in the sample, 10 were still alive in 1991 (last field season) and, hence, the longevity of these males were underestimated. The mean longevity of the dead males was 65.6 months (± 22.1 , $n=13$), and the mean age of the still alive males was 76.7 months (± 23.4 , $n=10$).

Male snout-vent length (SVL) was correlated with age ($r=0.65$, $P=0.0009$, $n=23$, mean SVL = 77.8 ± 3.8 mm, $n=23$). However, the variation in age-specific size between males was extensive (Fig. 2).

Male SVL was not correlated with hatching success when longevity was held constant (Pearson's partial correlation analysis, $r=-0.003$, $P=0.99$, $n=23$). Longevity, however, was still correlated with hatching success when SVL was held constant (Pearson's partial correlation analysis, $r=0.48$, $P=0.02$, $n=23$).

The analysis of covariance demonstrated that male age (within male number) was not significantly associated with hatching success ($P=0.66$, $df_{\text{model}}=6$, $df_{\text{error}}=8$, $F_{\text{male age}}=1.0$, $df=1$, $P=0.35$, mean number of observations per male = 2.5 ± 0.8 range = 2–4). Thus, a male does not become increasingly better at siring viable offspring during his life.

Surprisingly, there was no significant correlation between a female's longevity (our estimate of genetic quality) and mean hatching success of her eggs ($r=0.36$, $P=0.07$, $n=26$, average number of observations per female = 1.27 ± 0.53). Of the 26 females in the sample, 15 died during the study (mean longevity = 57.4 months ± 13.8), while 11 of the females were still alive during our last field season (mean age = 84.8 ± 24.6). Thus, females that were still alive during the last field

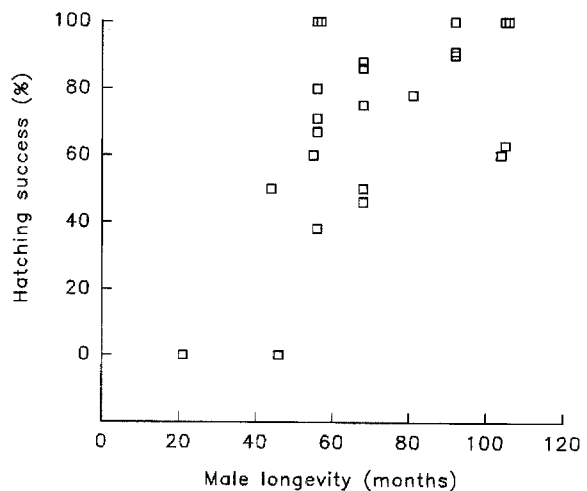


Fig. 1 Average hatching success (%) as a function of male longevity (months)

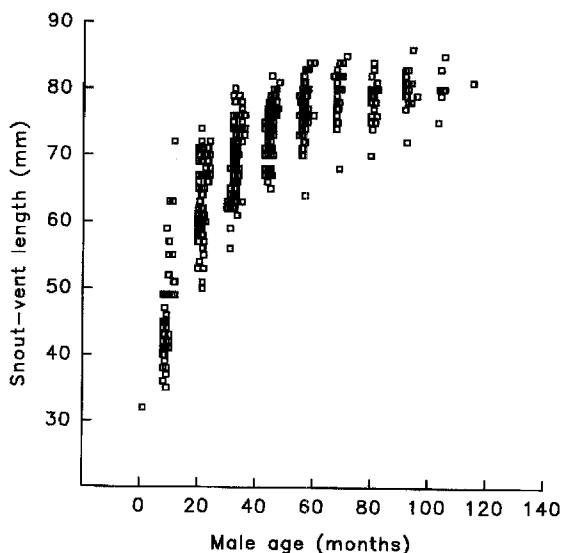


Fig. 2 Age-specific male snout-vent length (mm) in Swedish sand lizards. As this is a descriptive plot only, a male may be represented more than once at different ages ($n=210$)

season were significantly older than females that died during the study period (t -test, $df=24.0$, $t=3.6$, $P=0.001$). However, the (older) females that were still alive did not lay clutches with higher hatching success compared to the short-lived females (t -test, $df=26.0$, $t=1.46$, $P=0.16$).

The tendency ($P=0.07$) for a correlation between a female's longevity and the mean hatching success of her eggs may suggest a relationship between these variables, although weaker than in males. Therefore, we also performed a Pearson's partial correlation analysis between male longevity and hatching success, while holding female longevity constant at its mean. The partial correlation analysis demonstrated that male longevity and hatching success were still correlated also when we controlled for the effect of female longevity on hatching success ($r=0.50$, $P=0.02$, $n=21$).

Hatching success in the population did not vary among years (ANOVA, year as class variable, $df_{\text{model}}=4$, $df_{\text{error}}=145$, $F=0.58$, $P_{\text{model}}=0.6$. Since females grow throughout life, and clutch size covaries with female body size, a female may have been used more than once in the analysis of differences between years). Thus, nothing in our data suggests that the correlation between male longevity and hatching success was a spurious correlation caused by the pooling of data.

Older and larger males had more ticks (*Ixodes ricinus*, Spearman's rank order correlation coefficient, $r_s=0.31$, $P<0.0001$, $n=367$, range=1–48), possibly because they emerge from hibernation earlier than smaller males and thus have a longer exposure time to parasites (Olsson 1992a). No significant correlation between size of nuptial coloration and number of ectoparasites was found when we controlled for male SVL (Spearman's partial rank order correlation coefficient, $r_s=0.16$, $P=0.25$, $n=36$, SAS 1988). Neither was number of ticks significantly correlated with our estimate of pigment saturation ("chroma" in the Munsell color system, Spearman's rank order correlation coefficient, $r_s=-0.04$, $P=0.81$, $n=36$).

Rejections of partners in the wild

During the field study 244 pair formations were observed, involving courtships, matings and mate guardings between 86 males and 85 females. In 11 of these male-female interactions (4.5%) we observed determined rejections, lasting about 20 s or less, of the males by the females. In 3 of these cases the female mildly rejected the male and copulations followed. Of the remaining 8 rejections, 3 occurred immediately following hibernation, before the onset of the females' period of receptivity. Five females exhibited rejection behavior towards males that they had previously been recorded mating with. These rejections occurred at the end of the mating season.

Larger and older males had higher mating success than younger males (see Olsson 1992a for a more detailed analysis of male mating success); only 21% ($n=119$) of the 3 to 4-year-old males mated, while mating occurred in 32% ($n=111$) of 5 to 6-year-old males, and in 76% ($n=68$) of the ≥ 7 -year-old males. However, there was no indication that this was not due to larger males' ability to expel rivals and guard their mates, rather than female choice (Olsson 1992a, b, 1993a, c).

We made no attempt to separate the effects of a male's SVL and number of ectoparasites on a female's "willingness" to copulate. However, large males had a higher ectoparasite load and mating success than smaller and younger males. Hence, females did not reject males on the basis of their parasite load.

Laboratory experiments

Experiment 1

In the first laboratory experiment, addressing female choice by rejection of males, we recorded 72 copulation attempts of which 48 involved rejections. As recorded in the field study, all rejections (duration < 20 s) occurred at the beginning and, or, at the end of the females' receptive period. Females ($n=30$) rejected all males ($n=16$) at least once, independent of size and coloration, and a change of male never made a female receptive. Correspondingly, receptive females allowed all males to copulate. Unequivocally, this suggests that rejection behavior is employed by female sand lizards to expel all males outside a female's period of receptivity, *not* to mate selectively with individual males.

Experiment 2

In our choice experiment, seven of the ten females approached the models, three visited the model with the larger green area, and four visited the model with the smaller green area. No female visited both models. Three females showed no interest in the models, investigated the cage, but returned to the center spotlight without approaching either model. Thus, we could not confirm that females preferred male models with more nuptial coloration.

Discussion

Although we were unable to demonstrate any form of mate choice in female sand lizards, null results should be interpreted with caution. For instance, even though wild male sand lizards exhibited threat display towards our male replicas (Olsson in 1993b), females are often more choosy than males and might not have identified our models as live male sand lizards. However, all of

our different sources of information are consistent, as females did not mate selectively in spite of the existing variation in male traits and paternal genetic quality.

Sand lizards do not exhibit lek behavior (Olsson 1992a) and, hence, if female sand lizards sample males, female movements during the mating season should be extensive. However, during the period of this study females had small home ranges (c. 100 m²) and were highly sedentary (Olsson 1986), not supporting the hypothesis of female choice by sampling.

Can females obtain “good genes” without mate choice?

Madsen et al. (1992) reported that adder females mating with many partners sired more viable offspring and advocated that this was because genetically superior males must have more competitive sperm and sire most of the offspring. Wildt et al. (1987) lent some qualitative support to this assumption: in an inbred population of lions (*Panthera leo*) the incidence of malformed sperm was remarkably high and, hence, inbred genotypes had a strong tendency to produce low quality sperm.

Female sand lizards also mate multiply with several males, resulting in broods with multiple paternity both in laboratory experiments and in the wild (Olsson et al. 1994a,b). In our study population the genetic diversity is low (Olsson et al. 1994b). Moreover, a female's number of partners is positively correlated with hatching success, and with juvenile survival during the 1st year, and negatively correlated with the proportion of malformed young in broods (Olsson et al. 1994b). This strongly suggests that multiply mating sand lizard females are at a selective advantage, and may promote sperm competition by mating repeatedly. Similar suggestions have been proposed on both theoretical (Curtsinger 1991) and empirical grounds (Smith 1984; Bellis and Baker 1990; Madsen et al. 1992).

Why is female choice rare in lizards?

The most detailed studies of sexual selection and evolutionary ecology in lizards have been performed on iguanids (Iguanidae) (e.g., Ruby 1981; Burghardt and Rand 1982; Dugan 1982; Huey et al. 1983; Sigmund 1983; Stamps 1983; Andrews 1985; Hews 1990), of which most species are territorial (Stamps 1983). Thus, in order to unequivocally demonstrate female choice on male traits, territory quality must be controlled for. Only Hews (1990) has aimed to do so, and she found no influence of female choice on male mating success in *Uta palmeri*. In *Anolis carolinensis* (Sigmund 1983) female mate choice is based on male coloration. However, Sigmund's study was not designed to investigate female choice based on within-species variation in a male trait (e.g., pigment saturation), but as a cue

for mate or species recognition. Hence it remains unknown to what extent intersexual selection has affected intraspecific variation in male coloration in this species. To the best of our knowledge, only Cooper and Vitt (1993) have convincingly demonstrated female choice on a male quantitative trait in lizards, females of the non-territorial broad-headed skinks (*Eumeces laticeps*) preferring to mate with large males.

In contrast to, for example, birds (Blackburn and Evans 1986), a group in which female choice has been frequently reported (Andersson 1994), paternal care has never been demonstrated in lizards (Shine 1988). Thus, in non-territorial reptiles such as sand lizards, “good genes” is the only resource available to the female. Parker (1992) raised the question that if the partners genome is crucial for the viability of a female adder's offspring, why does not mate choice evolve? We asked ourselves the same question for sand lizards in particular, and lizards in general. A key observation when attempting to answer that question may be that when “good genes” is the single resource available, female choice can only evolve if male genetic quality covaries with male phenotypic traits.

We suggest two hypotheses (not mutually exclusive) that may explain the apparent lack of mate choice in female sand lizards (and possibly in other non-territorial reptiles):

1. Unreliability of male phenotypic traits as cues to heritable fitness for choosy females (i. e., risk of choosing the wrong male, Parker 1983). Male nuptial coloration cannot function as a cue to a possible heritable parasite resistance (*sensu* Hamilton and Zuk 1992), as there was no relationship between these two variables. Compared to short-lived males, long-lived males sired a larger proportion of viable young. However, the high variance in age-specific male size make male body size an inaccurate cue to male age (Fig. 2). Thus, female sand lizards choosing larger males would not increase offspring viability.

2. Risks associated with mate choice (e.g., time waste, energetic expenditure, increased predation, Magnhagen 1991). Female choice might delay matings and thus oviposition. In Sweden sand lizards are at the northern border of their distribution and delayed oviposition may spoil reproduction entirely (Olsson 1992a; Sven-Åke Beglind personal communication). However, this hypothesis would be less probable in the southern part of this species distribution range, assuming that female choice is absent also there.

Increased mobility of females associated with sampling of mates could further increase risk of predation (Madsen and Shine 1992). In a predation experiment (Olsson 1993b), female sand lizard models received 61% of the attacks of birds of prey. Thus, although female sand lizards have a cryptic coloration, predators still pay them considerable attention.

We suggest that multiple matings in female sand lizards may open up an alternative evolutionary pathway to female choice of “good genes”. By mating multiply, females may promote sperm competition and indirectly (by sperm competition) “sieve” good genes for their young.

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