

Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*)

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Summary. Male sand lizards (*Lacerta agilis*) are polygynous and guard individual females for several hours to days after copulation. Even though the copulation itself only lasts 2–4 min, the total time that a male invests per female is considerably more and may constitute a substantial investment during a mating season. In such situations, when male copulation frequency is constrained, or when variation in female fecundity is high, mate choice by males may be adaptive. Large body size in female sand lizards is correlated with higher fecundity. In choice experiments performed in the laboratory, male sand lizards preferred to court large females rather than small females. In addition, when there was little difference in size between the females in the experiment, the males visited the two females more often before they started to court the preferred female. The results from a field study during 1984 and 1987–1990 showed that females are non-aggressive, have small neighboring home ranges (c. 100 m²) and may share burrows and sites for thermoregulation. This means that females can be found close together and thus gives males the opportunity to choose a mate. Assortative mating with respect to size was observed in a natural population, as well as a limited number of direct choices of females by males. These results support the results of the choice experiment.

Introduction

Females usually exhibit larger parental investment than males, and are therefore expected to be more particular in their choice of mates (Darwin 1871; Trivers 1972). The advantages of mate choice may include genetic as well as immediate material benefits. Houde and Endler (1990) showed that female guppies seem to base their mate choice on male coloration, and this may increase offspring crypsis and survival. Watt et al. (1986) in a series of elegant experiments showed that female sulphur butterflies choose males with high flying ability, which

is genetically related to the phosphoglucose isomerase (PGI) enzyme locus. More immediate, non-genetic, benefits have also been described as a reason for mate preferences, for instance nutrients in prey gifts (Gwynne 1982).

To sum up, female choice has been demonstrated in a number of species with mate preferences based on quite different cues and causes. The analysis of the evolutionary consequences of mate choice by females gives rise to some of the classical problems in evolutionary ecology (e.g., Bradbury and Andersson 1987).

Males, on the other hand, usually make lower parental investment than females, and hence risk less in making an unsuitable mate choice. Generally, they are also able to replenish gametes more quickly than females, and for these reasons choosiness in males should be under less selective pressure than in females. However, male choice may be predicted when there are high costs of mating, as in some species with limited ejaculations, low fertilization rates or strong sperm competition (Dewsbury 1982; Nakatsuru and Kramer 1982; Schwagmeyer and Parker 1990). Male choice would also be adaptive when an appreciable increase in reproductive success can be gained by choosing highly fecund females, for example in species where fecundity and female size is correlated. When males invest time in guarding females with whom they have copulated, this is likely to reduce the risk of sperm competition and increase the probability of paternity. However, it will also constrain males from searching for, and copulating with, more females. If guarding occupies males during a substantial part of the mating season, they should not mate indiscriminantly but, when there is an opportunity, choose females that maximize males' reproductive success. Although less attention has been paid to male mate choice than to female mate choice, it has been empirically demonstrated in insects (e.g., Johnson and Hubbell 1984), salamanders (Verrell 1985) and fish (Sargent et al. 1986).

The reproductive biology of the sand lizard (*Lacerta agilis*) has been described in detail elsewhere (Bischoff 1984). Males are polygynous and compete for females

by aggressive competition (Olsson 1992a) and have widely overlapping home ranges. Females are non-aggressive and have small neighboring home ranges or may share burrows and basking areas (Olsson 1984). After copulation, the male guard individual females for hours or several days, whereafter they resume mate searching (Kitzler 1941; Olsson 1992b). Females reject males outside the female's receptive period. However, females have not been observed to reject and thereby discriminate among males during their period of receptivity; when receptive, a female copulates with males that she rejects outside her period of receptivity (Olsson 1992b). Rejection involves a characteristic head-bobbing behavior (see Kitzler 1941 for a detailed description of courtship and contest displays).

I investigate the hypothesis that males prefer large, fecund females by testing the following predictions. (1) In the laboratory, males in staged choice experiments should (a) prefer large females, and (b) spend more time choosing when females are closely size-matched. (2) In the field, (a) males should choose large females and (b) male choice should lead to assortative mating for body size, as large dominant males may exclude small males from large females. In the sand lizard, females do not choose males (Olsson 1992b) and therefore assortative mating cannot be explained by female rejection of small males.

Methods

Field study. Data on female clutch size and morphometrics were gathered during 1984 and 1987–1990 at a field site 50 km south of Gothenburg on the west coast of Sweden. Clutch size was determined by bringing females into the laboratory 3–7 days prior to oviposition; the females' snout-vent lengths were recorded and the lizards were released at the place of capture. The Spearman rank order correlation coefficient was used to describe the relationship between female body length and fecundity.

The duration of the mating season was estimated as the time elapsing between the dates of the first and last ovipositions. Though offset by approximately 2 weeks, this should correspond with the duration of receptivity in the field. The duration of guarding time was estimated by revisiting in the mornings and evenings females that had copulated and noting when the pairs split up. Length of mate guarding was then divided into guarding sessions longer or shorter than 24 h, to determine the frequency of long, and presumably costly, mate guardings. Mate guarding sessions had to meet the following two criteria to be included in the analysis: firstly, no sessions interrupted by observed female rejection behavior were included ($n=11$); secondly, if the first male left the female within 24 h, the first male's visit would be counted as a 'short guarding session' (these females were revisited by a second male and were still receptive; thus, the first male decided to leave the still receptive female after maximum 24 h).

To investigate potential size-assortative mating, the snout-vent lengths of guarding males and their females were analyzed by Spearman rank order correlation coefficient.

Laboratory experiment. The animals used in the laboratory mate choice experiment were first-generation offspring of wild sand lizards, reared together under semi-natural conditions in outdoor terraria. The lizards were fed crickets and mealworms *ad libitum*, and reached adult size and matured in less than 1 year. After 7 weeks of hibernation, males and females were allowed 10 days to enter reproductive condition, shed skin and, in males, adopt

breeding coloration. After hibernation the animals were kept in separate cages. Before the experiment, females were tested for receptivity by introducing them to a courting male not used in the choice experiment. Only females confirmed as receptive, because they did not reject courtship and lifted their tails, were used in the experiment. The 12 females used had a mean snout-vent length of $85 \text{ mm} \pm 4.1$ (SD) and a mean weight of $17.7 \text{ g} \pm 3.4$ (SD). The ten males used to test male choice averaged $72.7 \text{ mm} \pm 4.0$ (SD) snout to vent, and weighed on average $11.3 \text{ g} \pm 1.5$ (SD). These measures reflect the sexual dimorphism in snout-vent length in the natural population (Olsson, pers. obs.).

A test cage with three chambers was used for the experiment, with each chamber arranged in a standard fashion to resemble the housing cages, and with a spotlight to allow thermoregulation. Before each trial, the two participating females were assigned to either of the peripheral cages by tossing a coin, and were left alone until thermoregulation was resumed, which generally occurred within minutes. The male was placed in the center compartment. Trials were started by raising the walls separating the chambers, 1 h after the animals were introduced to the experimental cage; all three animals had resumed thermoregulation by then. The animals could now move freely between the compartments, to make male olfactory confirmation of female receptivity possible (Simon 1983).

Once the walls separating the three chambers were raised (slowly, as not to startle the lizards) the following behavior was noted: (1) the number of male visits and active investigations of either or both females, (alternating visits of the females involving tongue flicks, henceforth 'sampling'), and (2) male choice, i.e., which female the male eventually courted. A courted receptive female begins a 'mating march' ('*Paarungsmarsch*', Kitzler 1941), while the courting male follows her, biting her tail and flanks. Copulation usually follows within minutes. In this study, once a male attempted to copulate he was regarded as having made his choice and the trial was ended.

Individual males were receptive for longer than females (as in the wild), therefore males could be used in more than one trial to enable a comparison of male behavior among different combinations of large and small females.

Results

Clutch size correlates highly with female snout-vent length ($r_s=0.631$, $P<0.0001$, $n=128$), within-year as well as for pooled data for all years (Fig. 1).

Choice experiment

At the onset of each trial, all three animals were basking under the spotlight, one in each compartment. Females generally remained basking when the walls were slowly raised, while the male almost invariably approached a female immediately. Only one trial per male, and for each combination where the same females were paired, was drawn at random for the binomial test. However, for male number 3 experiment 4 happened to include females 3 and 8 which were also drawn in experiment 17 for male 9. To avoid the risk of pseudoreplication I therefore deliberately included experiment 3 (instead of 4) in the statistical test, including two females (number 2 and 10) that were not used in any other experiment. This does not affect the result (male 3 choose the largest female in both his trials) but it avoids any risk of pseudoreplication and it increases the number of females in-

volved in the experiment. By doing so, I controlled for (1) individual differences in male choosiness and (2) 'uncontrolled attractiveness' by individual females that could have interfered with the results. Trials 1, 2, 3, 7, 8, 13, 17 and 19 were represented in the statistical

analysis (Table 1, in which all trials are shown). In 7 of these 8 trials the largest female was chosen by the males ($P < 0.035$). In all, males chose the largest female in 16 out of 19 trials.

Consistency in individual male choice was tested in

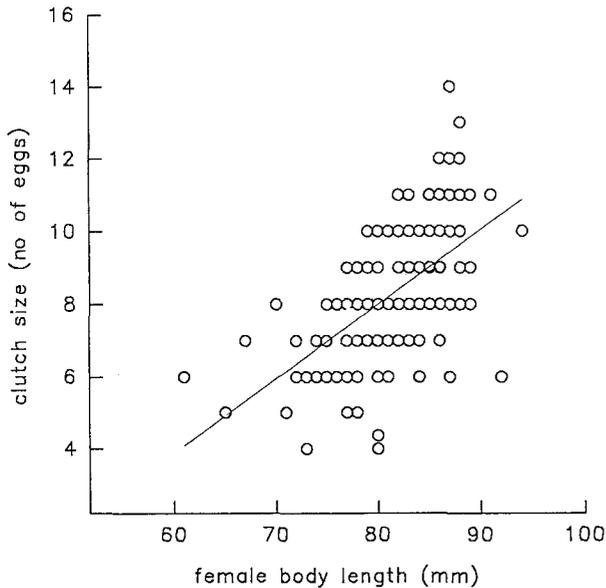


Fig. 1. The relationship between clutch size (number of eggs) and female body size in the sand lizard, *Lacerta agilis* ($r_s = 0.631$, $P < 0.0001$, $n = 128$)

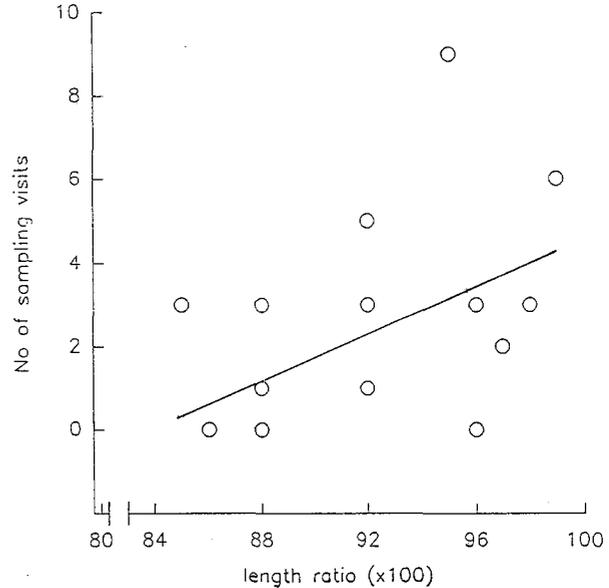


Fig. 2. The relationship between female size difference and the number of male sampling visits ($y = -0.19 + 0.24x$, $P = 0.05$, $n = 19$)

Table 1. Male choice between a large and a small female

Trial no	Male no	Large female no	Small female no	Ratios in female		Female chosen	No. of visits with	
				Body length	Clutch size		♀ large	small
1 ^a	1(67)	4(87)	8(77)	0.88	0.67	4	1	0
2 ^a	2(69)	1(92)	6(85)	0.92	0.82	1	2	1
3 ^a	3(75)	10(82)	2(81)	0.99	1.0	10	3	3
4	3(75)	3(89)	8(77)	0.86	0.50	3	2	0
5	4(77)	1(92)	6(85)	0.92	0.82	1	2	1
6	5(70)	1(92)	2(81)	0.88	0.82	1	2	0
7 ^a	5(70)	3(89)	11(82)	0.92	0.92	3	2	0
8 ^a	6(78)	1(92)	2(81)	0.88	0.82	1	1	0
9	6(78)	5(89)	7(86)	0.97	—	5	1	1
10	6(78)	3(89)	4(87)	0.98	0.50	3	2	1
11	7(79)	1(92)	6(85)	0.92	0.82	1	2	1
12	8(70)	1(92)	2(81)	0.88	0.82	1	2	1
13 ^a	8(70)	3(89)	4(87)	0.98	0.50	3	3	1
14	8(70)	5(89)	6(85)	0.96	—	5	1	0
15	9(76)	6(85)	2(86)	0.95	1.0	6	5	4
16	9(76)	9(83)	7(86)	0.96	0.73	7	1	2
17 ^a	9(76)	3(89)	8(77)	0.86	0.50	3	2	1
18	10(70)	1(92)	6(85)	0.92	0.82	6	2	3
19 ^a	10(70)	12(86)	11(82)	0.95	1.57	11	2	3

The snout-vent lengths of males and females are given within parentheses after the individual's number. The snout-vent length measurement of the smaller female, and her clutch size (— indicates missing value), has been divided by that of the larger female and the quotients are given. The number of male visits per individual female in each trial are also given. ^a Indicates trials randomly drawn for the binomial test of male preference for large vs. small females

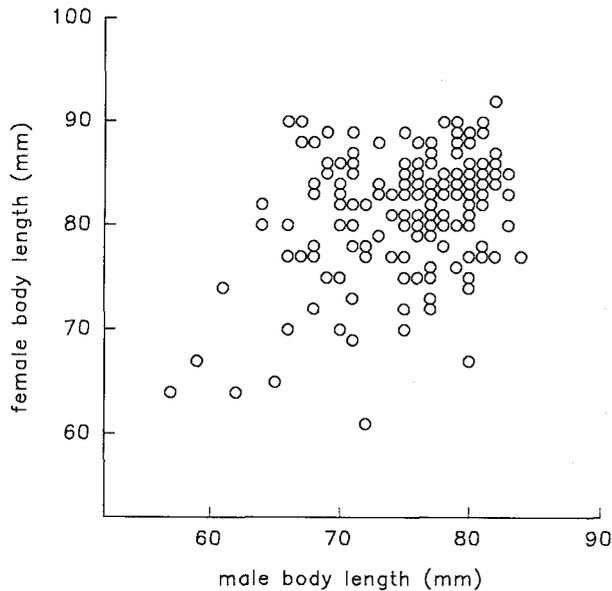


Fig. 3. Assortative mating for pairs found in the field in the sand lizard, plotted as female body length against male body length ($r_s = 0.37$, $P < 0.0001$, $n = 214$)

six males by repeating the choice experiment two or three times for as long as I had receptive females available, each time with a new set of females. Male 9 chose the small female in one trial but the large in the other two. Male 10 chose the shortest female both times. Alternating visits between females ('sampling') occurred in 13 of the 19 trials by seven of the ten males (Table 1). In trials 4 and 6, the male discontinued courtship, thermo-regulated and then resumed courtship, so two visits were paid to the same female with no visit of the other female in between (Table 1). There was a significant relationship (see figure legends) between the number of visits a male paid to the two females and the similarity in size between them (Fig. 2). The same relationship, although not independent of female size, was observed between the relative difference in clutch size and the number of visits paid to each female (arcsine-transformed data, number of visits = $-3.3 + 5.7$ (clutch ratio), $n = 16$, $P < 0.014$). Thus, the smaller the size difference between two females, and/or the smaller the difference in clutch size, the more sampling visits seem necessary before a male courts and mate with one of the females.

Field observations

Mate guarding. Females mated for approximately 2 weeks; before and after this period they rejected courting males. Males that were rejected by a female outside her period of receptivity mated with the same female when she was receptive. Courtship may last for only a few seconds before copulation takes place. Females were not reluctant to copulate with unknown or sub-dominant males, as may occur in territorial species (Stamps 1983). To sum, females did not seem to discriminate among

males. The maximum duration of mate guarding observed was 3 days, and of 164 guarding sessions observed 32 (20%) lasted for 2 days or more.

Large males associated with large females (Fig. 3, $r_s = 0.37$, $P < 0.0001$, $n = 214$).

On three occasions I observed males to discriminate between females in the wild. One observation involved a male (number 193) who found two receptive females basking side by side (i.e., the females did not show any characteristic rejection behavior; Kitzler 1941), and within seconds started to court the largest female. The other observations were of two males (212 and 158) each of which abandoned the receptive female it was courting in favour of an approaching female. In the first case the new female was longer, while in the second situation female snout-vent lengths were within measuring error, but the new, preferred female was 13% heavier than the first.

Breeding sex ratios and duration of the mating season

The breeding sex ratio did not deviate significantly from 1 (χ^2 goodness-of-fit test, $0 < \chi^2 < 0.42$, $df = 1$, $0.70 < P < 0.99$). The duration of the mating season was 27 days on average (min = 17, max = 34).

Discussion

Female sand lizards are sedentary and have neighboring home ranges that are less than 100 m² on average (Olsson 1984), and they sometimes share the same rock for shelter and thermoregulation. This makes females predictable and easy to observe for males, facilitating males choice of which females to court, copulate and guard.

The plot of assortative matings (Fig. 3) shows that there is considerable variation in male-female size-matching, suggesting two things. Firstly, even though males prefer large females they do not avoid mating opportunities with smaller females. Secondly, no characteristic size ratio necessary for successful copulation could be identified. Such a size ratio has been demonstrated in amphibians (Davies and Halliday 1977), although in reptiles, which have internal fertilization, such a relationship might not be intuitively predicted. However, in the laboratory experiment the smallest male picked the smaller female in both trials he participated in. He had trouble gripping the female with his jaws during copulation, so male size, and in particular jaw size, could be a constraint on male ability to express mate choice.

In a year with a mating season lasting only 17 days (1989), a single 3-day mate guarding session occupies 18% of the total duration of the mating season; this seems a significant time investment. Six matings with different females were the most that any male obtained, and the clutch size ranged from 5 eggs in a small female to 15 eggs in a large one. In this case, the choice of a large rather than a small female could have a major

effect on male reproductive success, and seems to provide a straightforward argument for males to consider female size in a choice situation. However, the respective sex ratios indicate that males have a limited number of females from which to choose, and, as there is contest competition for females in this species (Olsson 1992a), possibly only larger males will be able to express mate preferences. Small males are probably relegated to smaller females, and this could account for the size-assortative mating observed in this study.

To sum up, the experiment showed (1) that male sand lizards are selective in their choice of mate, and (2) that assessment of female size is more carefully performed when the size difference between the females is small. The field study (1) gave anecdotal support to the idea that males actively choose large females, and (2) that male choice, and possibly the male-male contest competition reported elsewhere (Olsson 1992b), are the likely causes for the observed size-assortative mating.

As far as I know, the only published example of male choice of females in reptiles is in garter snakes (Aleksiuk and Gregory 1974). Gartska et al. (1982) suggested that the mechanism used by males to assess clutch mass in females was a pheromone related to vitellogenin, the precursor of yolk. In the red-spotted newt, Verrell (1985) demonstrated that both olfactorial and visual cues will, independently of each other, result in male choice of large females.

In conclusion, field data lend support to the laboratory results and suggest that males can and do discriminate between females. This would probably be a selected strategy for increasing a male's reproductive success. The mechanism for male assessment of female fecundity in the sand lizard is not known but could include either visual or olfactory cues, or both. Females probably receive enough sperm to fertilize an entire clutch in this polygynous species, with a sex ratio close to 1. Therefore, female size alone explains most of the variation in female reproductive success. Male choosiness therefore seems unlikely to cause strong sexual selection on female body size. It is clear that male mate choice will have a larger effect on male fitness than female fitness in this species.

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