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Mate guarding, intrasexual competition and mating success in males of the non-territorial lizard *Lacerta schreiberi*

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Schreiber's green lizard *Lacerta schreiberi* showed a high degree of overlap in individual home ranges which the males did not actively defend. The number of mates and estimated mating success of males were not related to the size of male home ranges. The population sex ratio was skewed towards males and a promiscuous mating system was detected; individual males mated with 0-4 females. Mating frequency, number of mates, and mating success of males were positively correlated with snout-vent length. Moreover, there was assortative mating by size. Males guarded individual mated females for several hours, keeping in physical contact with them, and attacking approaching males. Male contest success was related to body size, but not to home range size. The winning males mated more often with more females and probably had higher reproductive success. However, males could not guard more than one female simultaneously and they rarely monopolized individual females which were polyandrous.

KEY WORDS: intrasexual competition, *Lacerta schreiberi*, mate guarding, mating success, territorialism.

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INTRODUCTION

In polygynous and non-territorial mating systems, male competition can involve intrasexual selection where males fight amongst themselves to mate with females

(Halliday 1992, Cooper & Vitt 1993, Andersson 1994). For species that exhibit intrasexual selection, success in competition over mates is crucial for the fitness of males and traits that improve success in fights are favoured in the competing sex (Andersson 1994). However, in non-territorial mating systems males that mate with several females have less time to allocate to each one, and inferior competitors can occasionally have access to females by avoiding contests with superior rivals. Males that mate with fewer females may monopolize the matings of their mates, preventing opportunistic mating by other males. In this context, game theory (Enquist & Leimar 1983) suggests a trade-off for males between mate search and mate guarding. Many lacertid lizards show agonistic behaviour among males and male choice (Kramer 1937, Kitzler 1941, Molina Borja 1981, Olsson 1992). However, intrasexual selection and mating systems have been rarely investigated in lacertid lizards.

We studied the mating system and intrasexual competition in a natural population of *Lacerta schreiberi* for 3 years. We document the relationships among number of mates, mating success, contest success, home range size and body size of individual males.

MATERIAL AND METHODS

Lacerta schreiberi is a medium-sized lacertid lizard that inhabits humid areas near rivers and mountain streams in the Northern and Central Iberian Peninsula (Salvador 1984, Marco 1997). Males mature on average one year earlier than females (snout-vent length range for adult males: 72-116 mm; SVL range for adult females: 86-115 mm; Marco 1995), and have longer, wider heads, and brighter colouration on the back and belly. Furthermore, during the mating season males develop a prominent blue colouration on the throat. Females have relatively longer abdomens (Braña 1996). Females are sexually receptive for approximately 3 weeks and they lay only one clutch within a breeding season (Marco et al. 1994).

For 3 years (1990-1992) we studied a *L. schreiberi* population in the Sierra de Béjar (province of Salamanca, Spain, U.T.M. co-ordinates: 30TTK653691), in a humid Holm oak (*Quercus pyrenaica*) forest. The study site has an altitude of 1250 m and a temperate climate characterized by the existence of frequent frosts from October to May and frequent snowfalls between December and March.

Data were gathered on a 0.25 ha (50 × 50 m) experimental plot for three breeding seasons (April through May). At the beginning of the breeding period, all the adult lizards observed inside the plot (108 individuals) were captured, marked by toe-clipping, and painted on the back with two spots on combinations of four body sites (head, neck, midback, and among legs) and five colours. Snout-vent length (SVL), weight, and reproductive state (oviductal or vitellogenetic eggs, copulation marks, and lateral skin folds for females, and blue sexual colouration of throat for males) were recorded for each lizard. Age was determined for some lizards from marked hatchlings. Behaviour was observed during all days when the lizards were active in the breeding season. The study plot was checked several times every day by an observer walking slowly through it, recording each lizard seen. The observer was usually at least at 5 m away from lizards and always used binoculars to identify individuals. We recorded 764 observations of individual lizards including 30 agonistic interactions between known males and 116 matings between known males and females.

To estimate home range sizes, we recorded the X and Y coordinates of a lizard on the plot at every observation with a precision of 0.5 m (the references were stakes on a measured grid). We only recorded home range data when the observation was made at least 1 hr after the previous observation of the same individual. We have estimated 62 adult home ranges during the mating period and home range overlaps with the program Ranges IV (Kenward 1987). The home range was estimated with the convex polygon method using the arithmetic average with the 100% of the observations (AC100) and then excluding the 10% most external ones (AC90) (Schoener 1981). Home range overlap was the percentage of a lizard home range that was overlapped by the home ranges of another lizards.

The sex ratio was calculated for each year by dividing the number of adult males by the number of adult females found on the study plot. Mating frequency was calculated for each year as the quotient between the number of observations corresponding to a mating and the total number of observations for each lizard. The mating success of each male was estimated for each year considering the number of mates, the relative number of each female mating lead by that male and the estimated clutch size of each female involved (Stamps 1983), using the formula

$$MS_j = \sum_{i=1}^{n_j} [(N_{ji}/N_{ti}) * CS_i]$$

where Ms_j = mating success of male “j”; n_j = number of mates of male “j”; N_{ji} = number of matings between female “i” and male “j”; N_{ti} = total number of matings of female “i”; and Cs_i = estimated clutch size of female “i”. Clutch size was estimated using a linear regression obtained from females of an adjacent population during the same years (r = 0.79; F = 53.5; $P < 0.001$; N = 26, SE = 2.152; Marco et al. 1994).

RESULTS

Home range overlap

The sex ratio during the mating period was on average 1.92:1 (males:females). Males overlapped their home ranges on average with 5.9 males (SD = 3.23; range = 0-12). Females overlapped their home ranges on average with 6.6 males (SD = 2.8; range = 2-12). Males overlapped their home ranges on average with 3.1 females (SD = 1.9; range = 0-6), but only mated on average with 0.9 females (SD = 1.1; range = 0-4; N = 71). The number of female home ranges which overlap with a male home range was correlated with his number of mates (Spearman correlation r = 0.36; P = 0.03; N = 43) but was not correlated with male body size (Spearman correlation r = 0.01; $P > 0.05$; N = 43).

Mating success

Males guarded individual mates for several hours after the initial approach, having physical contact with them and attacking approaching males. Of adult females observed during the mating period 76.8% were guarded by an adult male. We never observed one male with more than one female nor more than one male with one female. Males rarely monopolized all the matings of any female. Females mated on average with 2.5 males (range = 1-5; N = 22).

Mating frequency (Pearson correlation r = 0.775; $P < 0.001$; N = 70), average size of mates (Pearson correlation r = 0.536; $P < 0.001$; N = 35), and mating success (Pearson correlation r = 0.721; $P < 0.001$; N = 70; Fig. 1) were positively correlated with male SVL. Male home range size was not related to mating success (Spearman correlation r = 0.25; P = 0.108).

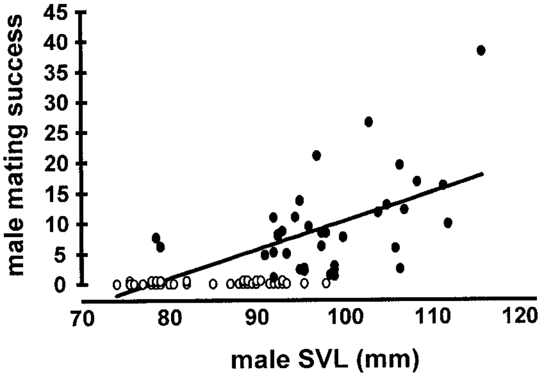

Fig. 1. — Relationship between mating success and SVL of *Lacerta schreiberi* males. The line indicates the linear regression. Open points correspond to lizards that were never observed to mate.

The mating frequency of males with four mates was higher than that of males with fewer mates (one-way ANOVA F = 55.612; $P < 0.001$; df = 4, 55), but post-hoc comparisons showed no difference in average mate frequency among males that had three, two or one mate. On average, males with four mates had the highest mating success (one-way ANOVA F = 63.98; $P < 0.001$; df = 4, 65; Fig. 2). However, post-hoc comparisons showed no difference in average mating success among males that had three, two or one mate. Some individuals with only one mate had higher mating success than some males with two or three mates.

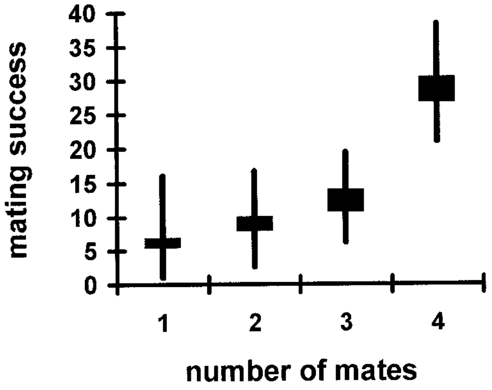

Fig. 2. — Relationship between number of mates and mating success in a population of *Lacerta schreiberi*. Columns indicate mean ± SE and lines indicate range.

Intrasexual competition

Of the adult male observations made during the mating period 9.95% involved agonistic contests. Males performed ritualistic displays that could escalate into physical fights. In many contests, winning males threatened losing lizards with aggressive and fast body movements, without actual physical contact. The losing male usually escaped and was chased for 1-2 m. In 16% of the observed male-male interactions, they usually performed ritualistic displays. In the displays, both males were oriented in opposite directions, with the head of one lizard at the level of the fore limbs of the other. They stood high on their legs, raising the body from the ground and bending the vertebral column to form an vertical arc. Maintaining this posture, they appeared to watch one another for several seconds to several minutes. If neither animal was brought to submission, the ritual could escalate to multiple aggressive bites to the head. These fights result in black marks in the pileus and submaxilary areas.

The average size of males that were involved in agonistic interactions, but did not perform ritualistic displays, was 93.37 mm (SE = 1.681). This average was higher than the average SVL of adult males that were never observed in an agonistic interaction (88.49 mm; SE = 1.637) and lower than the average SVL of males that performed ritualistic fights (101.68 mm; SE = 1.912) (one-way ANOVA F = 7.96; $P < 0.001$; df = 2, 68). Males that performed ritualistic fights were 5 or more years old. The number of victories was positively related to the body size of males (Pearson correlation r = 0.45; F = 17.49; $P < 0.001$; N = 70). The average SVL of winning males (99.24 mm; SD = 7.57) was significantly higher than average SVL of losing males (91.35 mm; SD = 8.52) (Student t-test t = 4.19; $P < 0.001$). The SVL difference between winning and losing males of each contest was in average 7.86 mm (SD = 11.798) and ranged between – 12.5 to 37.5 mm. These contests occurred throughout the entire mating period and males continuously defended their individual mates. We detected several fights between the same males with different results. There was a positive relationship between the number of victories in contests and the number of mates (Spearman correlation r = 0.814; $P < 0.005$) and also between the number of victories in contests and mating success (Spearman correlation r = 0.821; $P < 0.005$; Fig. 3).

Fig. 3. — Mating success (mean ± SE) of *Lacerta schreiberi* males that won a different number of male-male contests.

DISCUSSION

Larger males had more mates, larger mates, higher mating success, and probably greater reproductive success. To improve male mating success in a non-territorial species with female multiple matings, there is a trade-off for males among mating with larger females, increasing the number of mates and increasing the time allocated to each one (ENQUIST & LEIMAR 1983). Large *L. schreiberi* females lay more eggs per clutch than small females (MARCO et al. 1994). Thus, males can get a potential advantage if they mate with larger females. If males prefer larger females as mates, intrasexual competition among males to mate with large females would be high and, consequently, the costs of mating with large females would also be higher than mating with small ones. On the other hand, if males mate with several females, they would have less time to allocate to each one and the probability of paternity in the progeny of each mated female would be lower than if males mate with fewer females. In our study, mating success of the most successful males (highest MS = 38.2) was higher than those of a hypothetical monogamous male [maximum clutch size recorded = 24 eggs (MARCO et al. 1994)]. Thus, the polygamic strategy of large males could be advantageous in this non-territorial species if the mating success reflects the probability of paternity. OLSSON et al. (1994) pointed out that neither order nor time between multiple female copulations had an impact on the reproductive success of first or last males in *L. agilis*. Furthermore, sand lizard females mating with many partners lay clutches both sired by different males and with higher hatching success (OLSSON & MADSEN 1995). We believe that the spatial concentration of large females in small areas of high habitat quality could explain why in our lizard population there was assortative mating by size and also that larger males mated with more females than small males. However, a more successful strategy for medium size males could be to guarantee high paternity of the clutch of one mate rather than trying to mate with as many mates as possible. In our study, some males with only one partner had higher mating success and probably higher reproductive success than males with two or three mates. This situation may be common in suboptimal areas where female density is low and the cost for males of mating with several females may be high.

In the *L. schreiberi* population studied, there was no relationship between male home range size and male reproductive success. However, male-female home range overlap rate was correlated with male mating success. An increase in male home range size could increase the number of mates but the male would allocate less time to each one, and thus, the probability of paternity could be lower (STAMPS 1983). In spite of this, the strategy of large adult males to increase their reproductive success could be related to the home range site selection in the mating season. An increase in the adult female density or the proximity among them would permit an increase in the reproductive success of males. Females of *L. schreiberi* have smaller home ranges than males and select specific areas with a high availability of refuges and basking sites on open and stony areas (MARCO 1996). At these sites, there is a high density of adult females (MARCO 1996) which favours the polygamic behaviour of the large males. Males may have a high home range overlap with females at the selected areas. Large non-territorial males select areas with a high density of females. This trend has also been shown in territorial lizards by SCHOENER & SCHOENER (1982) in species of *Anolis*, and by PÉREZ-MELLADO et al. (1988) in *Lacerta monticola*.

Intrasexual competition was observed and some males controlled the access of others to individual mates, by physical herding of the mate and physical exclusion of males. Usually larger males won contests. When males were matched in size, they usually performed ritualistic displays which could culminate in aggressive bites to their heads. The stereotyped fights between males were similar to behaviour recorded for sand lizards (Olsson 1992) and other lizard families (Carpenter & Ferguson 1977). Contests were observed throughout the mating season without the establishment of dominance hierarchies. Winning males had more mates, more matings with them and higher mating success.

Males mature 1 year earlier than females, and at a smaller body size. Young males (3 year old) overlapped their home ranges with both large males and females but they had low mating success. In contests, the young lizards usually lost and escaped. This early maturity acquisition (Marco 1995) could be related to the existence of opportunities for a relatively high mating success for young males. In situations with high male mortality rates or low males density, the opportunistic strategy of young males could be advantageous. Moreover, given that polygamic males cannot monopolize the access of other males to their individual mates, inferior competitors may occasionally mate with solitary females. The costs in growth derived from the early maturity in young males could be compensated in non-territorial mating systems by the possibility of mating with temporarily solitary females and by the low risk of physical damage in contests with competitors (Andersson 1994).

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