

## Contest success and mate guarding in male sand lizards, *Lacerta agilis*

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*(Received 30 September 1992; initial acceptance 5 November 1992; final acceptance 21 January 1993; MS. number: sc-807)*

Female sand lizards mate multiply with one or several males (Olsson 1992). After copulation the male stays temporarily with the mated female and vigorously attacks approaching males, whereafter he resumes mate search (Olsson 1992). Such agonistic behaviour by male lizards during the mating season is not novel (Carpenter 1977; Stamps 1983). However, in the majority of studies it has been investigated in territorial species, where resource defence polygyny may be the ultimate reason for aggression (Deslippe & M'Closky 1991). Thus, the male may be defending a particular area, and the presence of the recently mated female may be irrelevant to his agonistic behaviour. To my knowledge, the hypothesis that males specifically defend recently copulated females has never been explicitly tested in squamate reptiles, although it has been reported in other taxa such as insects (Simmons 1990; Sakalus 1991), birds (reviewed in Birkhead & Møller 1992) and mammals (Oglesby et al. 1981; Sherman 1989; Birkhead & Hunter 1990).

My aim in this study was to investigate whether a copulation, and the presence of the newly mated female during male contests, increased the mated male's probability of defeating rivals. In a laboratory experiment, I controlled the ecological resources that may influence male behaviour, and therefore any differences in male behaviour must have resulted from the presence of the female. This could explain the guarding behaviour previously reported in a natural population of sand lizards (Olsson 1992).

From a captive population of first-generation offspring from wild sand lizards, I tried to select pairs ( $N=11$ ) of males that were within the error of measurement in size (1 mm in snout–vent length was the maximum difference in repeat measurements of the males; 0.5 g difference in body mass was allowed between contesting males as some males defecate while handled, 0.5 g being the approximate mass of a fecal pellet). The average ( $\pm$ SD) snout–vent length of the contesting males was  $73.0 \pm 3.8$  mm and body mass was  $12.2 \pm 1.9$  g

( $N=22$ ). This approximately reflects the average male size in a natural population of sand lizards (personal observation). In two male pairs, the differences in male size fell just outside the estimates of the error of measurement. Therefore, the female was presented to the smaller male, to make the test conservative. The selected males were kept in separate cages before the trials. Thirty minutes before the contests, I placed the males in a cage with a floor area of  $2 \times 1$  m; a wall in the middle of the cage separated it into two compartments. A receptive female to court and mate was presented to one of the males, determined by flipping a coin. After the mating the male stayed near the female, generally resting his chin and a forelimb on top of her. This behaviour is commonly observed under natural conditions (Olsson 1992). Thirty minutes later, I slowly raised the wall separating the males and noted the behaviour of the lizards.

Of the 11 staged contests, one was a 'draw'; I could not determine who won as both males withdrew after a first quick burst of activity. Nevertheless, the mated male stayed with the female after the interaction. In the remaining 10 interactions, the mated male attacked the intruder almost immediately and won in all 10 interactions (binomial test, two-tailed,  $N=10$ ,  $P=0.004$ ). The intruding male responded at first with agonistic behaviour, i.e. arching his back in a threat display, and both males exchanged bites which resulted in jaw-locking and wrestling. I determined who was the winner and who was the loser by the subordinate behaviour shown by the defeated male, i.e. lowering of the head to the ground or running away (see Kitzler 1941, for a detailed description of sand lizard display behaviour). Once the subordinate male showed submissive behaviour, I stopped the trial immediately. No physical injury such as open wounds was identified in any of the lizards. The females remained passive in all 11 contests.

The males spent the same time (30 min) in the test cage prior to the contest, so, except for the female, there was no difference in male access to resources

that could have elicited the agonistic behaviour. The result seems to leave little room for alternative interpretations; mating motivates a male to defend the newly mated female.

This experiment mimics the situation in which mate guarding can be observed in the wild (Olsson 1992). Nevertheless, the exact mechanism that causes the aggressive behaviour cannot be addressed with this experimental design. The copulation might cause a testosterone surge that may boost male aggression; the mere presence of the female could similarly influence male aggressiveness, and both mechanisms could work in concert. My aim, however, was not to clarify the exact physiological mechanism that elicits mate defence but to determine whether the apparent mate-guarding behaviour of male sand lizards was a direct response to the female's presence, or simply an indirect consequence of male territorial behaviour. My results show that these male lizards do indeed guard their mates after copulation, irrespective of other potential resources (Olsson 1992).

I am indebted to Thomas Madsen and Rick Shine who criticized early drafts of the manuscript.

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