Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*

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During the mating season, male sand lizards perform ritualistic displays that may escalate into physical combat. A displaying male raises itself up on all four limbs and turns its green body side, extended dorso-ventrally, against the opponent. A contest may be settled at this stage but may also escalate into a 'ring-dance' and, further, into a 'fight' that comprises biting and locking of jaws. This can be analysed from the perspective of game theory models in which two contestants assess asymmetries in relative fighting ability during the interaction. This was first discussed by Parker (1974), and later developed by Enquist & Leimar (1983) into the concept and model of the sequential assessment game. The model posits that each behaviour pattern in a repertoire has a corresponding asymmetry that can be estimated, with some uncertainty, and that the asymmetries of these behaviour patterns are inter-correlated. Leimar (1988) gave the example of rates of roaring in red deer, *Cervus elaphus*, stags which are compared during the initial stages of a contest and which seem to correlate with ability in antler fighting (Clutton Brock & Albon 1979). The behaviour sequence during a contest between male sand lizards seems to parallel this.

During the mating seasons in 1984–1990, observations were made every day on which weather permitted lizard activity, at a study site on the Swedish west coast, summing to over 4500 h by myself and an additional 1500 by a field assistant. Males have widely overlapping home ranges but typically defend a non-site-related territory around themselves and around the female of immediate interest (Olsson 1986). We observed 24 interactions between 34 different marked males of known size. Intruding males crossed into resident males' territories, which resulted in contests, allowing males to be classified as residents or intruders. The animals were caught by noosing or by hand, weighed to the nearest 0·1 g and measured snout to vent and total

length to the nearest mm. An individual may be represented in more than one interaction with different contestants in the analysis below, assuming that a contest between A and B will not affect the outcome of a contest between A and C. I also assume that enough time has passed between contests, minimum 24 h, to make effects on motivation negligible. The mean ($\pm$ SE) number of contests per male was $1·44 \pm 0·02$. Six contests were timed and the duration of non-timed contests rarely exceeded a few seconds, ending at the display phase or a rapid chase. Six of the 24 interactions led to physical fighting, with bites mainly directed towards head and extremities. Deep cuts into jaw muscles and underlying tissues exposing mandibular bone were observed in several males and missing phalanges were common. This suggests that escalated fights can be costly.

The data can be divided into two groups to test predictions generated by Enquist & Leimar's models: one in which a measureable difference in size can be shown between contestants and another in which males are regarded as matched in size. To classify two contestants as being of the same size they had to fulfil two requirements; snout–vent length had to be within the error of measurement (± 1 mm) and the differences in mass had to be less than the mass of an average fecal pellet (0·5 g). Considering both characters seems relevant since lateral body area appears to be a cue to resource-holding power during the display phase and body mass is most important during the fighting phase.

The two groups were then used to test the following predictions generated by the sequential assessment game.

(1) Large males will win over small males, and the ratio in resource-holding power, here measured by body mass, will be negatively correlated with fighting duration. Because of decreasing certainty in
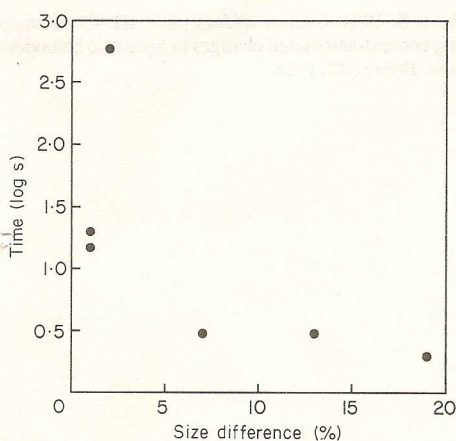
Figure 1. Duration of contests plotted against percentage mass difference between contesting males.

assessment of relative fighting ability, fighting time increases as the difference in resource-holding power gets smaller ('Θ' in Enquist & Leimar's 1983 model).

(2) The frequency of physical combat will be higher in combatants of equal size than between those of different size. This is also predicted by a higher degree of uncertainty in assessing asymmetries.

(3) Residents will win over intruders when no size difference prevails.

(4) The longest fights should be expected between an intruder and a slightly smaller resident male.

Predictions (3) and (4) follow from the facts that (1) the resource value (sired young) is potentially higher for the male who has already mated than for the intruder and (2) the resource value seems high relative to the contest cost (Leimar & Enquist 1984).

The test of the predictions gave the following results.

(1) Large males won over small males (12/2; binomial test: $N = 14$, $P < 0.006$) and fighting time was negatively correlated with the ratio of mass between the contestants (Fig. 1, $r_S = -0.986$, $N = 6$, $P < 0.003$). This correlation coefficient is higher than that predicted by game theory ($r = 0.3 - 0.6$). However, it is based on a subsample (the six timed interactions) of the 24 interactions; it may therefore be inflated owing to the small sample size and it may not be entirely representative.

(2) Physical combat was significantly more frequent in the group of males of equal size (4/5, $N = 9$) than in the males with a measurable size difference (1/13, $N = 14$; Fisher's exact test, $P = 0.004$).

(3) Although not significant, residents won six out of nine fights with males of equal size (Fisher's exact test $N = 9$, $P = 0.367$).

(4) An anecdotal observation supports prediction (4). Five of the fights were timed to between 2 and 30 s. The sixth fight comprised the two males with the smallest mass difference (2%) with the resident male the lightest. The fight lasted 12 min, which makes it 24 times longer than the next longest fight.

In conclusion, my results on ritualized contests in male sand lizards agree with those expected from the sequential assessment game (Enquist & Leimar 1983). Males matched in size fought longer and more often than males of different size, possibly as a higher degree of uncertainty in assessing relative fighting ability requires more and longer sampling. Resident males did not win significantly more often than did intruders, although they won two-thirds of observed fights and the sample size was small. In a territorial lizard, *Podarcis muralis*, the impact of residency has been shown to influence the outcome of contests (Edsman, in press), and web area influenced the contest behaviour of owners but not intruders in spiders, *Agelenopsis aperta* (Riechert 1984).

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