Effects of body size, throat color and residency on the outcome of intrasexual encounters in the males of the lacertid *Podarcis milensis*: ecological and evolutionary implications

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Introduction. *Podarcis milensis* is a small (Snout Vent Length= 48-70 mm) lacertid lizard endemic to the Milos Islands group (Aegean Archipelago, Greece). The species presents pronounced sexual dimorphism: males are larger than females and have a characteristic color pattern. Their flanks, throat and sides are black with prominent blue, light green, light yellow or whitish spots of variable size. Females have only a few, well-marked dark blotches on a pale white throat. Field studies (unpubl. data) have shown that population density is high (500- 600 animals/ha) and males actively defend territories against other males.

Methods. We conducted three series of laboratory experiments. The first was designed to test the effect of body size on the outcome of male-male interactions. Selected pairs had either at least 4 mm difference in SVL or were equal, matched in both cases for throat color. In a second series of experiments, selected pairs had identical SVL but the area of black color in the throat was significantly different having been manipulated (black color covering 40% or 80% of the throat). In the third series, animals were tested for the effect of residency. Intruders were brought into a resident's cage that differed (large, small) or was equal in body size. In order to evaluate the result of the encounters we have used male aggressive and subdominant behavior patterns. Observed behaviors ranged from neutral, to retreating, to aggressiveness. For the statistical treatment we have assigned the data to one of the following categories: winning, equivalence, neutral or no response.

Results

Effect of body size

In all contests that resulted in winnings, larger lizards were always the winners (14/14, 100%).

There are significantly more winnings than equivalences (two-tailed binomial test, p=0.005, n=19). When the opponents were equal in size, the number of winnings was much smaller than the number of equivalences (two-tailed binomial test, p=0.001, n=19). Respectively, equivalences, when opponents were size matched, were more than equivalences when opponents were unequal (two-tailed binomial test, p=0.002, n= 19).

Throat color-Residency

In all cases there is no significant tendency in "predicting" the throat color of the winner.

"No response" contests

The overall number of "no-response" contests in cases where opponents were equal in size (both with and without residency), was significantly higher when opponents differed in their throat color (vs. opponents size-matched but with the same throat color, two-tailed binomial test, p=0.009). When opponents had the same throat color but differed in size, the "no-response" outcomes didn't show any significance at the 0.05 level effect (p=0.05).

Effect of throat color

There is a tendency for dark males to win (7/10, 70%), however, this is not significant at the 0.05 level (two-tailed binomial test, p=0.09, n=10).

There are significantly more winnings than equivalences (two-tailed binomial test, p=0.035, n=14). When the dark opponent wins, there is no significant difference in the number of total interactions performed (Mann-Whitney *U*-test, Z=-0.237, p=0.81, n_1=4, n_2=9). Moreover, the male that began the interactions was not necessarily the winner of the contest (two-tailed binomial test, p=0.24, n=10).

Effect of residency

In contests where larger lizards were also the residents, larger lizards were always the winners (12/12, 100%). When smaller lizards were the residents, larger lizards won 66% of the fights that had a winner (4/6) (two-tailed binomial test, p=0.27, n=6).

When the resident was the larger lizard, equivalences were significantly fewer than winnings (two-tailed binomial test, p=0.003, n=15), whereas this is not the case when the resident was the smaller lizard (two-tailed binomial test, p=0.71, n=11). When larger lizards were also the residents, the males that began interactions won in 80% of the cases-in this case the larger ones were always the winners- (two-tailed binomial test, p=0.007, n=12). The same is not true when the small lizards are residents (namely they are not necessarily the winners, two-tailed binomial test, p=0.02, n=6).

Finally, when residents and intruders were size matched, the frequency of equivalences was higher than the frequency observed in contests with unequal sizes: a) statistically significant when the resident was large (two-tailed binomial test, p=0.008, n=12), and b) statistically significant only at the 0.10 level when the resident was small (p=0.07).

Correlations

Non residents: There was a weak but statistically significant correlation between size differences of the opponents and the frequency of "active" interactions (aggressive inter.+approaches/total interactions) regarding separately: a) large contestants (positive correlation, r=0.356, p=0.04, n=33, Fig. 1) and b) small contestants (negative correlation r=-0.377, p=0.03, n=33, Fig. 2).

Residents: In contests with larger lizards as residents, the frequency of "active" interactions of small intruders, relative to the total number of interactions, decreased as the size difference between the contesting males increased (r=-0.49, p=0.02, n=20) (Fig. 3). When the smaller lizards were residents, there was a significant negative correlation between the size difference of the opponents and the frequency of "active" interactions performed by the large intruders (r=-0.709, p=0.003, n=15, Fig. 4).

Figure 1

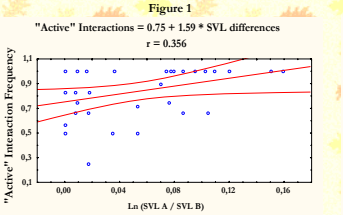


Figure 2

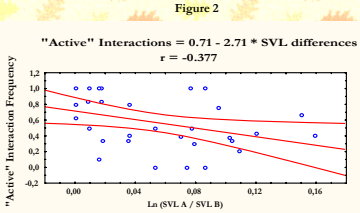


Figure 3

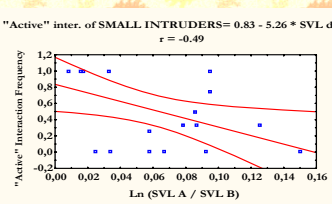
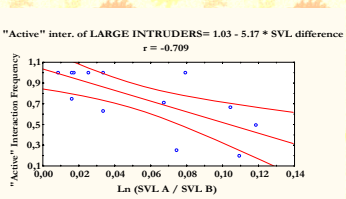


Figure 4



Discussion

Size is what matters !

The results show that body size is the most important determinant of a contest outcome in this population of *P. milensis*, as also shown for numerous other lizard species [1,2,3]. Larger males were dominant in all the staged encounters (with a winning result), suggesting that estimation of body size is probably the easiest way to assess the fighting potential of the opponent (at least in a close range). In simple staged encounters, large males need only to be active towards small ones in order to quickly assert their dominance. In a similar way, small males do not waste their energy in active behaviour when they face a large lizard. However, residency condition does play a role: smaller lizards could offset their lower fighting ability (due to their smaller body size) by being the resident (winning 33% of the fights) (see also Refs [4,5]). Also, residents, regardless of size, behave in a similar way regardless of the size of the opponent, while intruders, regardless of size, do not waste their energy in active behaviour when they face a resident.

Do color traits convey information about an individual male`s fighting ability?

The results do not confirm a strong correlation between throat color and fighting ability or social status between males. The extent of black coloration does play a role, albeit not as significant as the body size difference. However, the observed high frequency of "no response" contests when opponents were size-matched, differing only in throat color (vs. opponents size-matched but with the same throat color) could imply a different kind of involvement of black coloration in status signaling. The darkness of the throat could be a quite valuable badge for long-distance communication. This population inhabits an open area of bare sand with clumped food resources. Males are territorial, exhibiting site defense (pers. observ. & tetherings) and having 2, 3 or more females in their territory. The use of a long distance signal such as the black badge may serve to discourage potential intruders from entering the area.

The "P. milensis system"

Variation in mating and social behavior among islands and/or populations is well documented in lizards (for example, Refs [6,7]). Habitat quality and geometry plausibly affect the opportunity for males to control access to females; with counter selection processes (such as predation pressure) retarding the evolution of coloration [8]. For *P. milensis* females, a basic life history constraint is their clutch size limitation to three eggs – usually 1-2 [9]. Female reproductive success depends on the duration of the breeding season and the frequency of egg laying. Temporally, females lay up to 4 clutches during a very long breeding season (mating starts in January and ends in August depending on weather conditions and female age), and spatially they are found in small overlapping home ranges. It is presumable that male fitness increases by attempting to mate with multiple females who furthermore, are closely spaced. Males use territorial behavior to exclude other males from as many females as possible, which over the long breeding season can result in an endurance rivalry. In such situations an honest signal would benefit both contestants if costly fights with a predictable outcome could be avoided. *P. milensis* males could "use" throat color as a long distance signal for status recognition and body size as a short distance communication. This throat badge and the distinctive coloration of males are not present in other Aegean populations of the genus *Podarcis* as far as we know. This may happen because *P. milensis* has probably been isolated much longer than any other Aegean *Podarcis* species, allowing it to develop its own distinctive sexual characters. Hence, environmental potential for polygyny and sexual selection might be the best predictor of social behavior in this case.

References.

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