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Patterns of intraspecific behavioral interactions in *Podarcis bocagei* and *Cnemidophorus velox*

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Interactions between lizards may differ depending on whether they encounter conspecifics or different species, and agonistic behavior and tolerance have been the subject of many studies (BRATTSTROM 1982, CARPENTER 1960, CREWS & FITZGERALD 1980, GRASSMAN & CREWS 1987, MILSTEAD 1957, STAMPS & TANAKA 1981). *Podarcis bocagei* (Lacertilia: Lacertidae) is a common arboreal/saxicolous lizard in north central Portugal. Males and females are sexually dimorphic. *Cnemidophorus velox* (Teiidae) is a terrestrial, all-female, triploid, parthenogenetic lizard found in deserts at relatively high altitudes in New Mexico, USA. Both species are widely foraging insectivores, however, *P. bocagei* is territorial and has extended foraging times both daily and seasonally (GIL et al. 1988) whereas *C. velox* is not territorial and is active briefly during the day in the summer (BOWKER et al. 1986). Both species frequently encounter conspecifics in nature. Here we examine social interactions occurring when conspecific individuals meet under laboratory conditions designed to encourage social interactions. The overall goals are to determine if a dominance hierarchy exists, to determine the intensity of intraspecific interactions, and finally to establish correlates with dominance and aggressive/submissive behavior.

Material and methods

Groups of *P. bocagei* were noosed near Cantanhede and Coimbra, Portugal during May-July 1990 and *C. velox* near Los Alamos, Los Alamos County, New Mexico, USA (elev. 1650 to 1950 m) during June 1983 and used experimentally within one week of capture. An experiment consisted of pairing each animal with every member of its group. Group composition ranged from all males to various combinations of the sexes in *P. bocagei.* Two animals were placed in a glass terrarium (42×23×22 cm) with a 50 Watt heat lamp. All lizards attempted to "sun" under the lamp. However, the area under the lamp was restricted by barriers to create a "core area" (DRICKAMER & VESSEY 1982) thus increasing encounter frequency by reducing the favorable habitat. Trials lasted 15 minutes for *P. bocagei* and 20 minutes for *C. velox*, after a 5 minute adjustment period. The number of aggressive, submissive and neutral behaviors were counted for each animal. The animal with the most aggressive behaviors and the most time in the core area was termed the "winner"; the most submissive animal was the "loser". When interactions were neutral or nonexistent, the trial was termed a "tie".

Results and discussion

Behaviors exhibited during the experiments were similar to field observations and gave us some confidence in the experimental design. However, we are cautious about extrapolating from laboratory experiments to field behaviors. An obvious winner and loser could be determined in 91.1% of the pairings for *P. bocagei* (82/90 trials) and for 89.3% of the *C. velox* trials (25/28). Furthermore, since trials were conducted between every group member (6-8 lizards), a group dominance hierarchy could be established with the dominant animal winning most often and the subordinate winning the least.

Podarcis bocagei males generally dominated females, and juveniles usually were submissive, although there was some ambiguity in the results. All *C. velox* were females, and the smaller animal of the pairing tended to be the most aggressive and hence win the encounter.

For all *P. bocagei* (winners and losers combined), animal mass was positively correlated with number of aggressions ($r= 0.517$) and negatively correlated for all *C. velox* ($r= -0.381$) (Fig. 1). The average number of aggressive behaviors between winners and losers and among sexes (males, females and juveniles) for *P. bocagei* were compared using a two way ANOVA. Winners and losers differed significantly in average number of aggressive behaviors ($F= 41.24$, $df= 1, 152$, $p< 0.0001$). Although aggressions among sexes (male-female-juvenile) were not statistically different, male *P. bocagei* tended to be the most aggressive.

Submissive behavior rates decreased significantly with increasing mass in *P. bocagei* (Fig. 2). Average rates of submissive behaviors between winners and losers and among sexes (males, females and juveniles) for *P. bocagei* was also compared using a two way ANOVA. Winners were significantly less submissive than losers (averages= 3.1 vs. 27.0; $F= 69.346$, $df= 1, 152$, $p< 0.0001$). Sexes differed significantly in number of submissive behaviors (males-females-juveniles; $F= 3.872$, $df= 2, 152$; $p< 0.02$). Among winners, males had the fewest submissive behaviors and juveniles had the most; within losers, juveniles were the most submissive.

The trends in Figs 1 and 2 are interesting. For *P. bocagei*, big animals were both more aggressive and less submissive than small animals. The rates of aggressive and submissive behaviors for P. *bocagei* were therefore largely determined by individual characteristics of sex and size. Conversely, *C. velox* individuals responded strongly to behaviors received. Rather than a size-class of individuals having intrinsic rates of behaviors, rates of aggression were determined by the actions of other member of the pair (Fig. 3). Aggression by the winner was strongly correlated with aggression by the loser for *C. velox* ($r= 0.627$, $p< 0.0008$), and very weakly correlated for *P. bocagei* ($r= 0.25$, $p< 0.02$). The steep slope ($m= 0.51$) for *C. velox* indicated that aggression by one individual elicited a strong response from the other.

Characteristics of the winners and the losers: Both species

Winners of both species displayed similar rates of aggressive behaviors ($t = 0.452$, $df = 105$, ns). *Podarcis bocagei* winners averaged 11.6 aggressive behaviors per hour ($SD = 9.3$, $n = 82$) and *C. velox* averaged 10.7 aggressions per hour ($SD = 4.9$, $n = 25$). However, *P. bocagei* losers were much less aggressive (0.7 aggressions/hr, $SD = 2.7$) than *C. velox* losers (5.0 aggressions/hour, $SD = 4.0$). Thus while the winners for both species were similar, the loser characteristics were quite different.

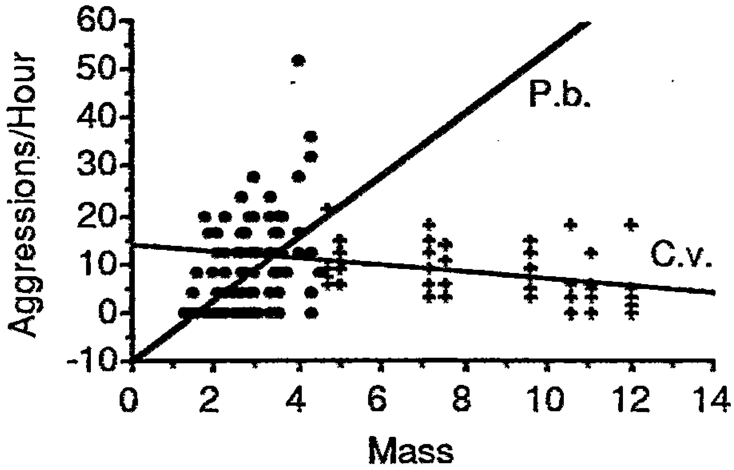

Fig. 1. Relationship between aggression rate and mass for *P. bocagei* (•, $r^2 = 0.268$, $p < 0.0001$) and *C. velox* (+, $r^2 = 0.145$, $p < 0.01$)

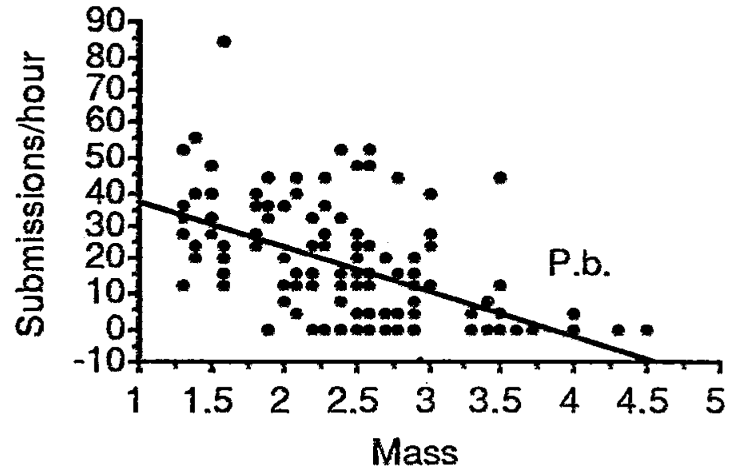

Fig. 2. The relationship between the rate of submissive behaviors and mass for all *P. bocagei* ($r^2 = 0.341$, $p < 0.0001$)

Size was an important determinant of outcome for *P. bocagei* and unimportant for *C. velox*. *Podarcis bocagei* winners were larger than losers in mass ($MASS_w$= 3.0g, SD= 0.66; $MASS_l$= 2.2g, SD= 0.56) and snout vent length (SV_w= 5.4 cm, SD= 0.34; SV_l= 5.0 cm, SD= 0.33). Both mass and SV differed at the $p< 0.0001$ level ($t= 8.359$ and $t= 6.928$ respectively). Conversely, *C. velox*. winners tended to be slightly, but not significantly, smaller than losers ($MASS_w$= 8.0 gr, SD= 2.44; $MASS_l$= 8.8 gr, SD= 2.8; $t= -0.994$, ns).

Podarcis bocagei winners were also significantly more investigative (more tongue flicks per hour, $TONGUEFLICKS_w$= 13.0, SD= 9.0; $TONGUEFLICKS_l$= 6.8, SD= 6.7) than the losers ($t= 4.879$, $p< 0.0001$).

Male-male interactions: *Podarcis bocagei*

Twenty two experiments involved only interactions between males. Winners were statistically larger than the losers in both mass ($p< 0.0002$; $t= 4132$, $df= 42$) and SV length ($p< 0.005$; $t= 3$; $df= 42$). In only 2 out of 22 experiments did the loser weigh more than the winner; winners displayed significantly more aggressive behaviors than losers (14.2 vs 0.5, $p< 0.001$) and significantly fewer submissive behaviors (2 vs 28, $p< 0.001$). Following the same pattern as for all-lizards, the number of aggressive behaviors of the male winners correlated positively with winner mass ($r= 0.343$) and the number of submissive behaviors correlated negatively with winner mass ($r= -0.395$). Thus, big male winners were both more aggressive and less submissive than their smaller male counterparts, an obvious advantages for a territorial species.

Female-female interactions: Both species

Unlike the males, female winners and losers did not differ statistically in size. However, size was related to the number of aggressive behavior the female loser received (Fig. 4) and aggressive behaviors of the winners were negatively correlated with losers mass for both species (*P. bocagei*, $r= -0.546$; *C. velox*, $r= -0.447$).

Consequently, big female losers received fewer aggressive behaviors than small losers. In general, the females seemed to follow different behavioral rules than males, although determining correlates of female dominance is difficult.

Male-female interactions: *Podarcis bocagei*

When males and females interact, the patterns change. The females showed no aggressive behaviors towards males whatsoever, and males showed very few submissive behaviors toward females. Of the 16 males-female encounters, the males won every time. Males averaged 9.5 aggressive behaviors/hour (SD= 6.5) toward females and no aggressive behaviors by females toward males were observed. None of the size and aggressive relationships demonstrated for male-male pairings were apparent. However, the number of tongue flicks by males (average= 16.3, SD=

11.6) increased dramatically and differed statistically (t= 3.888, $p< 0.0005$) from the number exhibited by the females (average= 4.0, SD= 4.8). This indicates considerable interest by males in females. These experiments were conducted during times when lizards in the field exhibited sexual behaviors. The number of tongue flicks of the winners (males) is positively correlated with the winner mass ($r= 0.637$, $p< 0.008$).

In sexually reproducing species, the fitness of the sex with the lowest parental investment (males) can be greatly enhanced by dominating other members of the same sex, and hence gaining greater access to females and other limited resources.

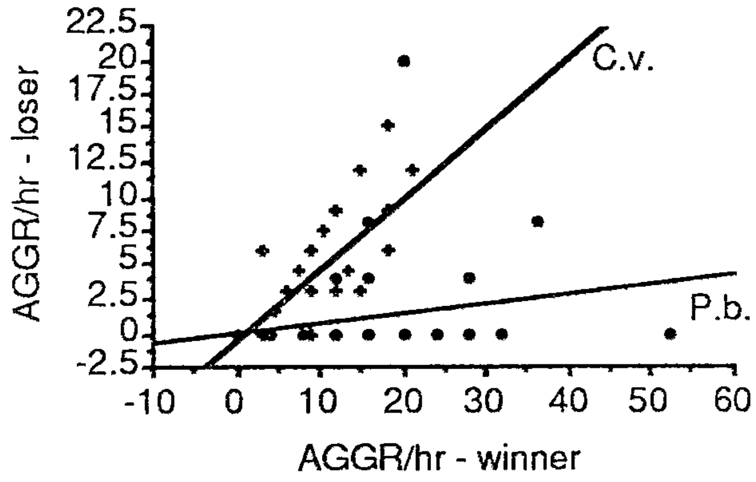

Fig. 3. The relationship between the rates of winner and loser aggressive behaviors for all *P. bocagei* (• , $r^2= 0.062$, $p< 0.02$) and *C. velox* (+, $r^2= 0.394$, $p< 0.0008$)

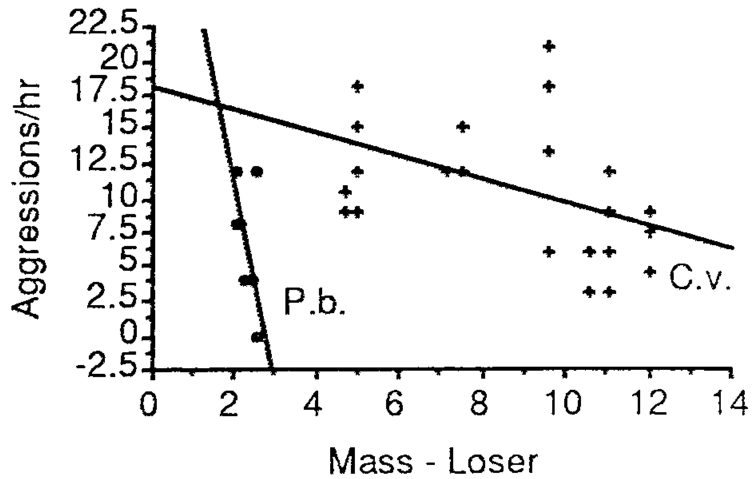

Fig. 4. The relationship between the rate of winner aggressive behaviors and loser mass for female *P. bocagei* (• , $r^2= 0.298$, ns) and female *C. velox* (+, $r^2= 0.227$, $p< 0.02$)

This concept of dominance theory seems to fit well with the social structure of *Podarcis bocagei*. However, for the asexual and non-territorial *C. velox*, the relationships are less clear. Smaller animals most frequently win the encounters and are the most aggressive. They also have the greatest expectation of future offspring and hence the most to gain. MILSTEAD (1957) reported few field observations of overt intraspecific aggressions (and fewer interspecific aggressions) for the genus *Cnemidophorus*; this is consistent with our field observations as well. In contrast, BARBAULT & MAURY (1981) report "frequent aggressive interspecific contacts" between *C. tigris* and *C. scalaris*. In other *Cnemidophorus* species, conspecific tolerance seems to be more common among parthenogenetic than bisexual species; increased aggression between bisexuals may reflect their greater genetic diversity (ECHTERNACHT 1967, LEUCK 1982). Our experiments were designed to encourage animals to interact, whereas in nature they may avoid these encounters by increasing spacing. Aggressiveness should increase individual spacing, thereby decreasing density, reducing competition and ultimately reducing the frequency of aggression. Nonetheless these species display a tendency for aggressive interaction and, in our experiments, both *C. velox* and *P. bocagei* invested considerable time, and presumably energy, in aggressive encounters with conspecifics.

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