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ORIGINAL ARTICLE

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Roles of male residence and relative size in the social behavior of Iberian rock lizards, *Lacerta monticola*

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Abstract Many studies on contest competition used residency asymmetry as a discrete variable. However, the probability of winning an interaction may change as a continuous function of the value of the location where the encounter occurs. We performed a field study to examine the importance of location within a home range and relative body size to the outcomes of agonistic interactions between male lizards, *Lacerta monticola*. The distances to activity centers (the most used locations based on a density function of sightings) and relative size play important roles in agonistic interactions and had interacting effects in natural conditions. On the other hand, previous studies with lizards suggested that inferior competitors are able to avoid agonistic interactions in the field. Thus, we staged encounters in the laboratory to examine the behavioral responses of smaller individuals. The responses of each focal smaller male were measured in its own home cage (resident), in the cage of a larger male (intruder) and in a cage in which no male was previously present (control). The predominant behavioral tactics of smaller males were avoidance when they are the intruders and displaying when they are the residents. Submissive displays by smaller males may help reduce the costs of agonistic encounters.

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Introduction

Factors affecting the outcomes of agonistic contests was studied in many species, especially between males competing for mates, territories or rank (Riechert 1998). Traits correlated with fighting ability, such as body size, are often used to settle contests (Parker 1974; Archer 1987). Prior residency may also influence the outcome of the contests or govern settlement (Maynard-Smith and Parker 1976), as was experimentally demonstrated in fish (Beaugrand et al. 1996), lizards (Cooper and Vitt 1987; López and Martín 2001) and birds (Sandell and Smith 1991; Shutler and Weatherhead 1994). Thus, the outcomes of contests predicted by body size differences may be overridden or modulated by residency (Riechert 1998).

Residency status (i.e., resident vs intruder) is usually treated as a categorical variable (Cooper and Vitt 1987; Hammerstein and Riechert 1988; Olsson 1992; López and Martín 2001). However, the role of territoriality or site defense as a more continuous variable was considered as residence time in birds (Beletsky and Orians 1989; Sandell and Smith 1991; Shutler and Weatherhead 1992), fish (Johnsson and Forser 2002) and juvenile lizards (Stamps and Krishnan 1994). The distance to valuable sites was studied infrequently and only in birds (Melemis and Falls 1982; Simpson 1985; Slotow 1996). However, the balance between costs and benefits of an agonistic interaction might change as a function of distance to the most used part of the home range. The value asymmetry hypothesis proposes that a specific area has greater value to residents than to intruders (Bradbury and Vehrencamp 1998) because of familiarity with the physical and social environment (Stamps and Krishnan 1994; Stamps 1995). Therefore, highly used sites should be more valuable for individuals than other parts of their home ranges. Thus, Cooper and Vitt (1987) pointed out that, in already settled adult lizards, the spatial location of an encounter could be important in determining the structure of social interactions, which was recently shown in field studies with different lizards (Husak and Fox 2003; McMann and Paterson 2003).

On the other hand, body size differences influence not only the outcomes of contests (i.e., higher probability of winning for larger opponents), but also the intensity and probability of fights. Game theoretical models indicate that when the outcome of costly interactions is predictable, inferior competitors should avoid such encounters by fleeing before a fight occurs or by showing their lower status (Parker 1974; Maynard Smith 1982; Enquist and Leimar 1983). Field observations suggest that smaller or subordinate lizards are able to avoid costly interactions (Cooper and Vitt 1987; Olsson 1992; Stamps and Krishnan 1994; Aragón et al. 2004) although the mechanisms underlying these results were not examined directly. Social inhibition (Baird et al. 2003) and/or appeasement behaviors (Martins and Lacy 2004) in subordinate males may help to stabilize social systems by reducing the frequency and intensity of aggressive encounters. Appeasement behavior occurs widely in mammals (e.g., de Waal 1986; Keltner and Potegal 1997; Shanas and Terkel 1997). In lizards it was first suggested 6 decades ago (reviewed by Carpenter and Ferguson 1977), but demonstrated only recently (Martins and Lacy 2004). Although there are many studies on territorial displays (reviewed by Carpenter and Ferguson 1977; McMann 2000; Baird et al. 2003), the effect of residency on visual displays by subordinate lizards was not examined experimentally.

Lacerta monticola is a small diurnal lacertid lizard occupying mainly rocky habitats of some high mountains of the Iberian Peninsula. Lizards are active from May to October, mating in May to June and producing a single clutch in July (Elvira and Vigal 1985). In previous studies, we found that during the mating season, agonistic encounters were frequent and larger males participated in more agonistic interactions (Aragón et al. 2001a, 2004). However, there were no differences in home range and core area size among age or size classes in males (Aragón et al. 2004). Dominant males defended core areas more intensely than other parts of their home ranges (Aragón et al. 2004). This suggests that area defense might change as a function of intensity of space use. On the other hand, areas of subordinate males were less exclusive (Aragón et al. 2004). Therefore, it would be advantageous for smaller males to signal their subordinate status to reduce the frequency of aggressive responses by larger/dominant males.

We present field observations on the effects of both body size and distance to activity centers (calculated as the most used locations based on a density function of sightings) on the outcomes of agonistic interactions between male *L. monticola* lizards. To test whether there is a gradient in the use of space (a continuous variation from the activity center to external areas), we calculated for each male the density of sightings at different distances from his activity center. We predicted that males that won agonistic interactions should be at a shorter distance from their activity centers than losers, and that the distance at which a given male can win or lose an agonistic interaction should be modulated by his relative body size. We also performed a laboratory experiment manipulating residency status to examine the effects of prior residence on behavioral responses of smaller males during encounters with dominant, larger males. According to the value asymmetry hypothesis, residence time enhances the value of an area (Beletsky and Orians 1989; Johnsson and Forser 2002). Thus, the cost of leaving a valuable area to avoid agonistic interactions should be higher for residents than for intruders. Therefore, we predicted that the predominant behavioral tactic of smaller males would be avoidance when they are the intruders and submissive displays when they are the residents.

Materials and methods

General field methodology and activity center determination

We conducted field work at “Alto del Telégrafo” (Guadarrama Mountains, Central Spain) at an elevation of 1,900 m. The subspecies *L. monticola cyreni* appears in the study area where it inhabits a relatively limited area on the mountain tops between 1,750 and 2,350 m elevation.

The field study was conducted in 1997 and 1998 on a 0.3 ha plot (80×40 m) that was divided into 32 quadrats of 10×10 m each to form a grid. This plot size allowed us to differentiate between residents and transients by monitoring the activity of the lizards closely (Rose 1982). Residents were defined as those individuals with more than three sightings on different days and at least two sightings separated by at least 15 days over the duration of the entire study (Aragón et al. 2001a, 2004). Only residents were used to calculate distances (see below). Males were captured by noosing and weighed with a pesola spring scale (1997: n=42, $\overline{X} \pm \mathrm{SE} = 7.8 \pm 0.1$ g , range=5–10 g; 1998: n=58, $\overline{X} \pm \mathrm{SE} = 8.2 \pm 0.2$ g , range=5.7–10.0). Their snout-to-vent length (SVL) was measured with a ruler (1997: 73±1 mm, range=61–79 mm; 1998: 70±1 mm, range=61–79 mm). Lizards were individually marked by toe-clipping and acrylic paint marks on the dorsum. They were released at the capture site after less than 5 min. Natural toe loss was often observed in this species. Toe-clipping has no effect on behavior or fitness (Dodd 1993; Ott and Scott 1999; Aragón unpublished data).

Censuses were performed every day except when rainy or cloudy conditions precluded lizard activity during May and June, from 0800 to 1800 h Greenwich Mean Time (GMT). We used binoculars when necessary to observe lizards. The entire plot was covered several times each day of lizard activity. The interval between the recordings of an individual was at least 1 h. A band of 10 m surrounding the study plot (the border zone) was included in censuses to obtain more information on the space utilization of individuals with part of their home range outside the study plot. This band corresponds to 48.5% of the average male’s range span (maximum diagonal) in this population. To map each individual's localities, we recorded on a map the position of every individual captured or sighted with respect to the grid marks (x–y coordinate within the plot). The average number of sightings per resident male was $\overline{X} \pm \mathrm{SE} = 12 \pm 2$, n=29 males in 1997 and $\overline{X} \pm \mathrm{SE} = 13 \pm 2$, n=28 males in 1998.

Activity centers were determined with the kernel fix estimator (Worton 1989) included in the RANGES V computer program (R. Kenward, Institute of Terrestrial Ecology, Wareham, UK) (Larkin and Halkin 1994). The Kernel method describes the intensity of use of the home range at a specific point based on a probability density estimation approach that uses distances among sightings. Thus, where there is a concentration of sightings, the kernel estimate has higher density and the activity center estimating the point where the density of sightings is maximum. A more detailed description can be found in Worton (1989).

Agonistic interactions in the field

During transects, we recorded agonistic interactions between males (chases and fights) and identified the individuals involved when possible. Chases were defined as interactions in which one individual (winner) rapidly ran while performing aggressive display and the other individual (loser) retreated or ran away without physical contact or after being touched lightly on the flanks by the winner. Only three fights (attacks with physical contact and bites) were recorded.

We observed 49 dyads. In 30.6% of these, both opponents were identified as residents. We calculated distances between the location where the agonistic interaction began and each male's activity center to examine whether these distances differ between winners and losers. Only two dyads between residents, with both males identified, were repeated. For these two dyads the average distances were used in the analyses.

Staged encounters in the laboratory

This experiment was performed to examine behavioral tactics of smaller males to avoid costly interactions when they are intruders or residents. On May 1999, we captured our subjects by noosing 40 male *L. monticola* close to the study plot. Males were weighed and their SVLs were measured (body mass: $\overline{X} \pm \mathrm{SE} = 14.1 \pm 0.3$ g, range=11–18 g; SVL: $\overline{X} \pm \mathrm{SE} = 69 \pm 1$ mm, range=59–77 mm). Only mature males were captured as estimated from their SVLs (Elvira and Vigal, 1985). Lizards were individually housed at "El Ventorrillo" Field Station (Navacerrada, Madrid Province) 5 km from the capture site in outdoor plastic cages (60×40 cm). Each cage contained a shelter. Food (larval *Tenebrio molitor*) and water were provided ad libitum. Males were held in their home cages for a week before testing to allow them to establish residency and scent-mark their cages (Aragón et al. 2001b). Encounters with opponents did not result in injuries and all lizards were healthy during trials. At the end of the experiment, they were released at their capture points.

We staged encounters between pairs of male lizards in which every focal male was shorter and lighter than his opponent (SVL difference: $\overline{X} \pm \mathrm{SE} = 10.1 \pm 0.2$ mm, range=4.0–13.5 mm; body mass difference: $\overline{X} \pm \mathrm{SE} = 3.0 \pm 0.13$ g, range=0.5–5.5 g). Size difference within pairs in this experiment was significantly greater than in dyads involved in agonistic interactions in the field ($F_{1,31}$=40.45, P<0.0001) to facilitate the study of the tactics smaller lizards use to avoid interactions.

We used a repeated measures design in which each smaller male was tested in three different treatments in random order of presentation. The behavioral response of each smaller lizard was recorded in his own home cage ("resident"), in the home cage of the larger male ("intruder"), and in a clean control cage in which both males were nonresidents ("control"). It was previously demonstrated that these treatments modulate the aggressive response of lizards (Cooper and Vitt 1987; López and Martín 2001).

To standardize the traits of the larger males (e.g., size or weight) among treatments, each larger male was presented to three different smaller males through the three treatments in a random order of presentation. No lizard was tested more than once a day, nor did any lizard face the same contestant more than once. No lizard changed size category (smaller or larger) through the experiment. Intruders and residents were handled in the same way when they were used to initiate trials and when they were returned to their home cages. We conducted 60 trials (20 focal males×3 treatments). The duration of each trial was 10 min, which had been demonstrated to allow individuals of *L. monticola* to obtain information about relative size of conspecifics from their chemical cues (Aragón et al. 2001b). All trials were conducted in outdoor conditions during June 1999 on sunny days between 0900 and 1200 h GMT. Lizards were allowed to bask for at least 2 h before trials to attain normal activity temperature.

To begin a trial the shelter of the experimental cage was removed to ensure visual contact between males. Experiments were recorded on videotape (Hi-8 format, 25 frames/s) using a video camera aligned perpendicularly over the center of the cages. The presence of humans may elicit antipredatory displays in lizards similar to foot-shaking (Cooper et al. 2004). Therefore the experimenters were not present during the filming. From the videotapes we noted (1) the time that the smaller lizard spent moving through the cage (walking or running), (2) the time that the smaller lizard spent attempting to escape (by standing against the wall of the cage and scratching the wall with the forelegs), (3) the number of bouts of foot-shaking behavior (rapid up and down movements of the legs) performed by the smaller male, and (4) the number of agonistic interactions initiated by the larger male (chases and/or single quick bites). The times spent moving and attempting to escape were considered as measures of activity (Aragón et al. 2001b) and avoidance behavior (Aragón et al. 2003), respectively. Foot-shaking had been interpreted as submissive or appeasement behavior in lacertids and agamids (Carpenter and Ferguson 1977).

Data analyses

Field data

A gradient in the intensity of the use of the space from the activity center (the point of highest density) to the border area must exist to justify the use of residence as a continuous variable. For each male we calculated a central area with the 20% of the total sightings nearest to the activity center and successive concentric ring areas with 20% of sightings. To test whether there was a gradient in the intensity of the use of space, we performed a regression analysis (REG Procedure, SAS Institute, 1999) examining the relationship between the densities of sightings at standard intervals and the distance to the activity center. The density of sightings was log-transformed to meet normality assumption of the residuals.

We examined the distances of a given male and its opponent from their activity centers. Since the response of each male should depend not only on its own characteristics and location, but also on those of their opponents (Enquist and Leimar 1983), data within dyads cannot be considered a priori to be independent. Therefore we set the statistical unit at the level of the dyad to test for differences between winners and losers regarding relative size and distance. For this analysis we used a repeated measured design in which the subjects were dyads. For each dyad we had two measurements: (1) the two distances between the location of the agonistic interaction and (2) the activity centers of the winner and the loser. Because within each dyad there was always a winner and a loser, two levels (winner or loser) formed the within-subject factor of our model and the continuous variable was the distance at which the interaction occurred. It was widely demonstrated that relative body size plays an important role in the dominance of lizards (López and Martín 2001; Olsson 1992; Stamps and Krishnan 1994). Therefore we included relative body size in the model because the distance at which a given male won or lost an agonistic encounter can be associated with the relative competitive ability. Relative body size was calculated as the difference between the SVLs of the winner and the loser within each dyad. To analyze these data we used the MIXED procedure (SAS Institute, 1999), which included the interaction between the within-subject effect and relative body size in the backward selection procedure. We started with a model including winning vs losing, year effect and relative size either as main effects or as first order interactions.

Taking into account the results on the differences between winners and losers (see Results), we performed another analysis to examine the effects of relative distance, relative size, and the interaction on the probability of winning an encounter. For this analysis we used a maximum likelihood approach (GENMOD procedure; SAS Institute, 1999), using a binomial distribution categorized by winner or loser and a logit link term. To ensure independence of data, we selected at random only one member of each dyad, counterbalancing winners and losers. Relative distance was calculated as the difference between the distances of the focal male and the opponent from their activity centers.

Laboratory data

We tested for differences in the response variables (% time attempting to escape, % time walking through the cage, foot-shaking and agonistic interactions) among treatments (within-subjects factor). Because the within-subjects factor had three levels, we performed the univariate repeated measures analyses using the MIXED procedure (SAS Institute, 1999), which allowed us to search for the appropriate within-subjects variance–covariance structure matrix (Wolfinger 1993; Quinn and Keough 2002). We used the Akaike Information Criterion to select the covariance structure (Littell et al. 1996). The covariance structure selected was the Huynh–Feldt structure (sphericity) for the percent of time attempting to escape and foot-shaking bouts, whereas in the percent of time walking the covariance structure selected was compound symmetry. The SVL of focal smaller males and the interaction with treatment were included in the model to control for size. In addition, the MIXED procedure computed least-square means that were averaged across repeated measures. Pairwise comparisons of least-square means were performed using Tukey–Kramer's tests.

To examine the role of foot-shaking response as a submissive behavior, we used a Wilcoxon matched-pairs test (NPAR1WAY procedure; SAS Institute, 1999) comparing this response between the smaller and the larger male within pairs. For the comparison among treatments, foot-shaking data were log-transformed to meet the normality assumption (Quinn and Keough 2002).

To verify whether our experimental design produced asymmetries in residency, we compared the level of agonistic interactions (chases and/or single quick bites) initiated by the larger male within each pair. We used a Wilcoxon matched-pairs test to compare only the resident and intruder treatments because no aggressive response, and therefore no variance, was scored in the control treatment. Taking into account results from field studies (Stamps and Krishnan 1994; this study) and laboratory experiments (Cooper and Vitt 1987; López and Martín 2001) on the effect of residence in lizards, we predicted that the aggressive response by larger males should be stronger when smaller males were intruders. For this analysis significance was set at a one-tailed critical region because there was a clear a priori prediction (Quinn and Keough 2002).

Unadjusted probabilities for each set of tests are reported, but significance was verified using the sequential Bonferroni adjustment of Rice (1989).

Results

Agonistic interactions in the field

There was a strong significant negative correlation between the density of sightings and the distance to the activity center ($r=-0.74$, $F_{1,158}=188.89$, $P<0.0001$). Thus, the farther from the activity center the lower the density, indicating that there is a gradient in the intensity of space use. Therefore, under the assumption that highly used zones are the most valuable, residence can be modeled as a continuous variable in this species.

The distance from the location of the interaction to the activity center was shorter in winners than in losers (MIXED procedure; winners: $\overline{X} \pm \mathrm{SE} = 4.2 \pm 0.7$ m, losers: $\overline{X} \pm \mathrm{SE} = 6.7 \pm 1.2$ m; $F_{1,11}=15.76$, $P=0.002$). The effect of the relative body size was significant as a main effect ($F_{1,11}=8.74$, $P=0.013$). However, the interaction of body size difference with encounter outcome (winning vs losing) was significant ($F_{1,11}=20.30$, $P=0.0009$; Fig. 1). Thus, the distance at which a given male won or lost an agonistic interaction was correlated with the difference in body sizes (winners' SVL–losers' SVL). There was a positive relationship between the distance and the relative size in the case of winners, whereas the opposite was true for losers. In other words, larger lizards were able to win at longer distances from their activity centers than smaller lizards. For losers, distance from activity center was longer when they were larger in relation to the winner size. There were no significant effects of year as a main effect or in interaction with the other effects ($P>0.63$ in all cases).

The probability of winning an encounter was significantly higher when males were larger (GENMOD procedure; $n=13$, $X^2_1=11.59$, $P=0.0007$). There was a significant interaction between relative distance and relative size ($X^2_1=12.66$, $P=0.0004$). Thus, the probability of winning an interaction was higher when males were larger and closer to their activity center in relation to their opponent.

Staged encounters in the laboratory

All lizards were active in all conditions. The percentage of time that the smaller (focal) lizards spent attempting to escape in the presence of their larger partners differed significantly among conditions (MIXED procedure; $F_{2,38}=37.24$, $P<0.0001$; Fig. 2). The percentage of time attempting to escape was significantly higher when the smaller males were intruders than in the other two treatments (Tukey's tests: $P<0.0001$ in both cases). The control and the resident condition did not differ significantly ($P=0.76$). There were no significant effects of SVL as a main effect or in interaction with treatment ($P>0.88$ in both cases).

The difference among treatments in percentage of time spent walking was not significant ($F_{2,38}=2.45$, $P=0.099$). There were no significant effects of SVL as a main effect or in interaction with treatment ($P>0.70$ in both cases).

The rate of foot-shaking differed significantly among treatments ($F_{2,38}=25.30$, $P<0.0001$; Fig. 3). The main effect of SVL was not significant ($F_{1,18}=3.49$, $P=0.062$); nor was its interaction with treatment ($F_{2,36}=0.06$, $P=0.94$). The rate of foot-shaking events in the control treatment (neutral cage) was significantly lower than in the other two treatments (Tukey's tests: $P<0.0005$ in both cases). It is interesting to note that the rate of foot-shaking events performed by the smaller males was significantly higher when they were residents than when they were intruders (Tukey's tests: $P=0.018$).

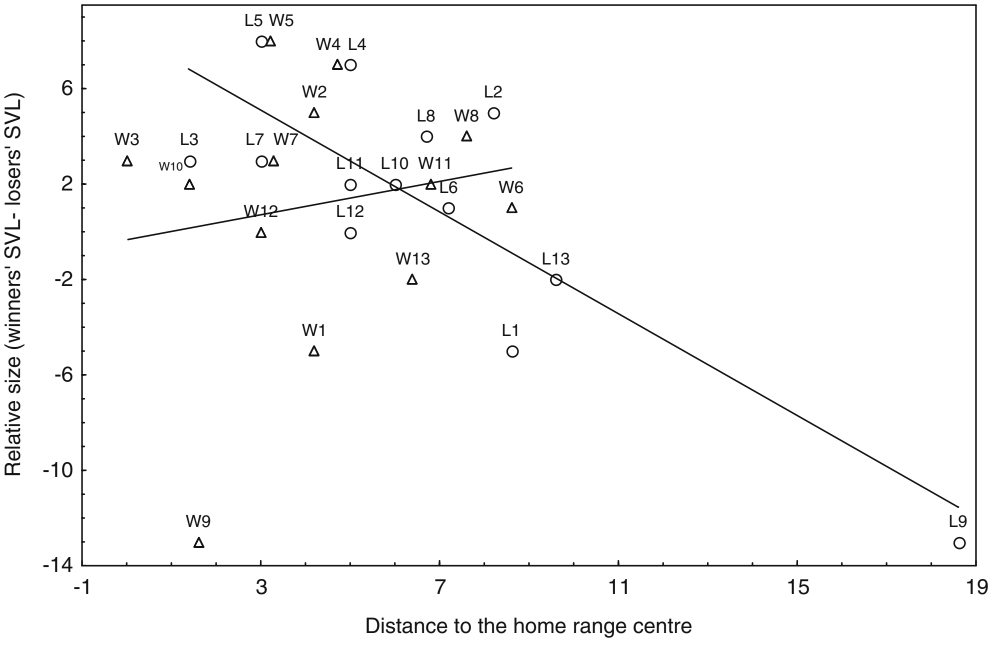

Fig. 1 Relationships between the distance of the male *Lacerta monticola* from the site of an agonistic interaction to the activity center, and the relative body size (winners' SVL–losers' SVL) within dyads observed in the field, for winners (positive correlation) and losers (negative correlation). Numbers in the scatterplots refer to the winner (*W*) and loser (*L*) within each dyad, ($n=13$)

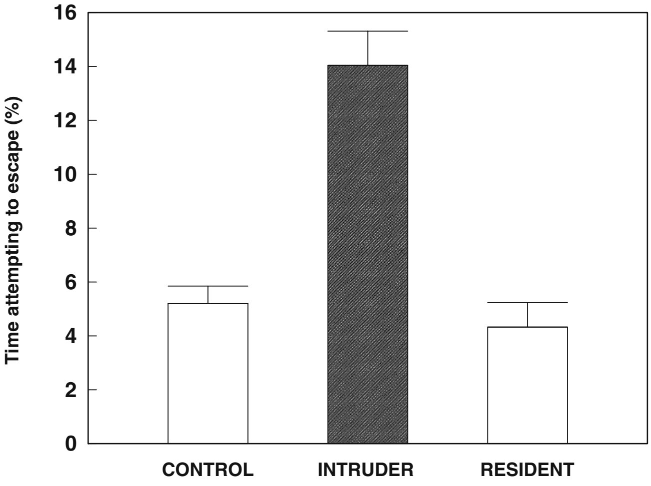

Fig. 2 Time (%) ($\bar{X} \pm 1$ SE, n=20) spent attempting to escape during a period of 10 min by the focal smaller male *Lacerta monticola* within each pair in a neutral clean cage (*control*), in the home cage of the focal male (*resident*), and in the cage of the larger male (*intruder*)

The rate of foot-shaking events performed by smaller lizards was higher than that of their larger partners in all treatments (Wilcoxon matched-pairs test, n=20; intruder condition, Z=2.86, P=0.004; smaller: $\bar{X} \pm \mathrm{SE} = 0.29 \pm 0.07$ events/min, larger: $\bar{X} \pm \mathrm{SE} = 0.03 \pm 0.02$ events/min; resident condition, Z=3.41, P=0.0006; smaller: $\bar{X} \pm \mathrm{SE} = 0.54 \pm 0.11$ events/min, larger: $\bar{X} \pm \mathrm{SE} = 0.02 \pm 0.01$ events/min). In the control treatment larger males did not perform any foot-shakes (n=20, smaller: $\bar{X} \pm \mathrm{SE} = 0.03 \pm 0.01$ events/min).

The rate of agonistic interactions initiated by larger males was significantly higher when the smaller male was the intruder than when smaller males were the residents (Wilcoxon matched-pairs test, n=20, Z=2.17, P=0.014, one-tailed test; resident condition: $\bar{X} \pm \mathrm{SE} = 0.005 \pm 0.01$ interactions/min, intruder condition: $\bar{X} \pm \mathrm{SE} = 0.24 \pm 0.12$ interactions/min). No smaller lizard initiated an agonistic interaction. No persistent attacks or injuries occurred.

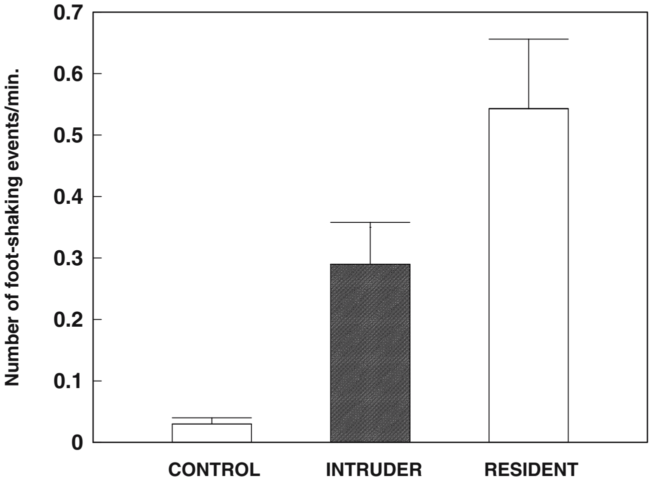

Fig. 3 Number ($\bar{X} \pm 1$ SE, n=20) of foot-shaking events in staged encounters between the male *Lacerta monticola* during a period of 10 min. The responding males were the smaller males within each dyad in a neutral clean cage (*control*), in the home cage of the focal male (*resident*), and in the cage of the larger male (*intruder*)

Discussion

Evolutionary game theory explains animal contests in terms of costs and benefits (Riechert 1998). In reptiles, highly used zones within a home range should be valuable due to familiarity (Stamps and Krishnan 1994) or because there are more females there to guard. For example, site familiarity modulates the antipredator behavior of the amphisbaenian *Blanus cinereus* (López et al. 2000). Moreover, in *L. monticola*, both males and females are promiscuous (Moreia and Birkhead 2004) and larger males guard females more often than smaller males (López et al. 2003). Thus, site familiarity may reduce the costs of trade-offs between avoiding predators and mate guarding that often occur in lizards (Cooper 2003; Martín et al. 2003).

Our results suggest that differences in body size and distance from activity centers may have counteracting effects when these differences have opposite effects on an individual's advantage (i.e., closer to the activity center but smaller in size and vice versa). Thus, the larger males were in relation to their opponents, the longer were the distances from the activity centers where they were able to win (Fig. 1). The additive effect that should result from relative size and distance differences acting in the same direction is less evident. We did not observe any losers of smaller size at a longer distance than 8.2 m (i.e., doubly disadvantaged individuals). This suggests that smaller males might avoid costly interactions far from areas valuable to them. This hypothesis agrees with empirical (Stamps and Krishnan 1994) and theoretical (Parker 1974; Maynard Smith 1982; Enquist and Leimar 1983) studies showing that when the outcome of contests is clearly predictable, costly interactions are unnecessary. Inferior competitors could avoid costly interactions by several nonexclusive mechanisms. In addition to escaping, smaller males perform less conspicuous activities than dominant male *L. monticola* (Aragón et al. 2004) and *Crotaphytus collaris* (Baird et al. 2003). That smaller males exhibited foot-shaking more frequently than their opponents strongly suggests that this response is a submissive display (Carpenter and Ferguson 1977). In the iguanid *Cyclura carinata*, smaller individuals perform headbob displays in the presence of larger ones, reducing the aggressiveness of larger individuals (Martins and Lacy 2004).

The time spent attempting to escape was interpreted as an indication of the degree of area avoidance in this species (Aragón et al. 2003) and in *L. vivipara* (de Fraipont et al. 2000). That smaller males spent significantly more time attempting to escape when they were intruders than when they were residents and in the control treatment indicates avoidance of areas where smaller males are intruders. Thus, lizards are able to assess residence status in the experimental conditions, which agrees with our field results and with those for other lizard species (Cooper and Vitt 1987; López and Martín 2001). Scent-matching, widely reported in mammals (Gosling and Mckay 1990; Luque-Larena et al. 2001) and documented in lacertids (Edsman 2001), is among the potential mechanisms underlying ability to discriminate between being a resident or intruder at a given site. According to the scent-matching hypothesis, individuals can assess residence status by comparing scents of a conspecific with those found on the substrate. This mechanism can be seen as a response to familiarity with their own scents. Although other nonexclusive mechanisms may be involved in natural conditions, such as familiarity with the habitat, in our experiment the habitat did not vary among treatments.

That smaller males performed more foot-shaking displays when they were residents is consistent with findings about the effects of residency on visual displays. In seminatural conditions 1-day residents and new arrivals of *Anolis sagrei* performed visual displays differently (McMann 2000). In desert grassland spiders, *Agelenopsis aperta*, residents smaller than intruders perform a visual display instead of escalating or withdrawing (Hammerstein and Riechert 1988). Although smaller lizards are clearly at a disadvantage, the balance between cost and benefits depends on whether they are residents or intruders. Despite obvious costs of interaction with a larger male, home cages should be more valuable than other cages. Thus, even with a marked difference in size, smaller resident males should display their lower status, rather than leave the area, when an encounter occurs. When smaller males are intruders they should leave because the benefit of staying and displaying is less because the area is less valuable.

Residency in laboratory conditions provided an advantage during agonistic interactions in *L. monticola*, as in the lacertid *Podarcis hispanica* (López and Martín 2001) and the skink *Eumeces laticeps* (Cooper and Vitt 1987). However, the average size asymmetry found in the field agonistic interactions was smaller. The majority of aggressive responses by larger males should occur when smaller males were intruders because smaller males did not have the opportunity to leave the cage.

Size and residency or site familiarity can play important roles in determining the outcomes of contests in lizards (Cooper and Vitt 1987; López and Martín 2001; Stamps and Krishnan 1994). Our findings show that the location of the encounter and the relative sizes of contestants have interacting effects in natural conditions. The results from the experiment show that smaller males use different behavioral tactics depending on the direction of their residence status. Both our field and laboratory results are compatible with the value asymmetry hypothesis. Submissive displays of smaller males may help reduce the intensity and frequency of agonistic encounters, and thus the costs of agonistic behavior.

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References

Aragón P, López P, Martín J (2001a) Seasonal changes in activity and spatial and social relationships of the Iberian rock lizard, *Lacerta monticola*. Can J Zool 79:1965–1971

Aragón P, López P, Martín J (2001b) Chemosensory discrimination of familiar and unfamiliar conspecifics by lizards: implications of field spatial relationships between males. Behav Ecol Sociobiol 50:128–133

Aragón P, López P, Martín J (2003) Differential avoidance responses to chemical cues from familiar and unfamiliar conspecifics by male Iberian rock lizards (*Lacerta monticola*). J Herpetol 37:583–585

Aragón P, López P, Martín J (2004) The ontogeny of spatio-temporal tactics and social relationships of adult male Iberian rock lizards, *Lacerta monticola*. Ethology 110:1001–1019

Archer J (1987) The behavioural biology of aggression. Cambridge University Press, Cambridge

Baird TA, Timanus DK, Sloan CL (2003) Intra- and intersexual variation in social behavior. In: Fox SF, McCoy JK, Baird TA (eds) Lizard social behavior. Johns Hopkins University Press, Baltimore, pp 7–46

Beaugrand JP, Payette D, Goulet C (1996) Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience, and prior residency. Behaviour 133:303–319

Beletsky LD, Orians GH (1989) Territoriality among male red-winged blackbirds III. Testing hypotheses of territorial dominance. Behav Ecol Sociobiol 24:333–339

Bradbury WJ, Vehrencamp L (1998) Principles of animal communication. Sinauer, Sunderland, Mass, pp 771–782

Carpenter CC, Ferguson GW (1977) Variation and evolution of stereotyped behaviour in reptiles. In: Gans C, Tinkle DW (eds) Biology of the reptilia, Ecology and behaviour A, vol 7. Academic, London, pp 335–554

Cooper WE (2003) Social behavior and antipredatory defense in lizards. In: Fox SF, McCoy JK, Baird TA (eds) Lizard social behavior. Johns Hopkins University Press, Baltimore, pp 107–141

Cooper WE, Vitt LJ (1987) Deferred agonistic behavior in a long-lived sicincid lizard *Eumeces laticeps*. Oecologia 72:321–326

Cooper WE, Pérez-Mellado V, Baird TA, Caldwell JP, Vitt LJ (2004) Pursuit deterrent signalling by the bonaire whiptail lizard *Cnemidophorus murinus*. Behaviour 141:297–311

Dodd CK (1993) The effects of toe-clipping on sprint performance of the lizard *Cnemidophorus sexlineatus*. J Herpetol 27:209–213

Edsman L (2001) Odours and ownership-scent matching in the territorial wall lizard. In: Vicente L, Crespo EG (eds) Mediterranean Basin lacertid lizards. A biological approach. Proceedings of the 2nd international symposium on the lacertids of the Mediterranean Basin. Instituto da Conservaçao da Naturaleza, Lisboa, Portugal, pp 133

Elvira B, Vigal CR (1985) Further data on the reproduction of *Lacerta monticola* cyreni (Sauria, Lacertidae) in Central Spain. Amphibia-Reptilia 6:173–179

Enquist M, Leimar O (1983) Evolution of fighting behaviour: decision rules and assessment of relative strength. J Theor Biol 102:387–410

de Fraipont M, Clobert J, John-Alder H, Meylan S (2000) Increase pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. J Anim Ecol 69:404–413

Gosling LM, McKay HV (1990) Competitor assessment by scent matching: an experimental test. Behav Ecol Sociobiol 26:415–420

Hammerstein P, Riechert SE (1988) Payoff and strategies in territorial contests: ESS analyses of two ecotypes in the spider, *Agelenopsis aperta*. Evol Ecol 2:115–138

Husak JF, Fox SF (2003) Adult male collared lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours. Anim Behav 65:391–396

Johnsson JI, Forser A (2002) Residence duration influences the outcome of territorial conflicts in brown trout (*Salmo trutta*). Behav Ecol Sociobiol 51:282–286

Keltner D, Potegal M (1997) Appeasement and reconciliation: introduction to an aggressive behavior special issue. Aggr Behav 23:309–314

Larkin RP, Halkin D (1994) A review of software packages for estimating animal home ranges. Wildl Soc Bull 22:274–287

Littell RC, Millinken GA, Stroup WW, Wolfinger RD (1996) SAS systems for mixed models SAS Institute. Cary, North Carolina

López P, Martín J (2001) Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. Behav Ecol Sociobiol 49:111–116

López P, Martín J, Barbosa A (2000) Site familiarity affects antipredatory behavior of the amphisbaenian *Blanus cinereus*. Can J Zool 78:2142–2146

López P, Aragón P, Martín J (2003) Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflect their mating preference for older males. Behav Ecol Sociobiol 55:73–79

Luque-Larena JJ, López P, Gosalvez J (2001) Scent matching modulates space use and agonistic behaviour between male snow voles *Chionomys nivalis*. Anim Behav 62:1089–1095

Martín J, López P, Cooper WE, Jr (2003) Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola.* Behav Ecol Sociobiol 54:505–510

Martins EP, Lacy KE (2004) Complex behavior and ecology of rock iguanas. I. Evidence for an appeasement display. In: Alberts A, Carter R, Hayes W, Martins E (eds) Iguanas: biology and conservation. University of California Press, pp 101–108

Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge

Maynard-Smith J, Parker GA (1976) The logic of asymmetrical contests. Anim Behav 32:564–578

McMann S (2000) Effects of residence time on displays during territory establishment in a lizard. Anim Behav 59:513–522

McMann S, Paterson AV (2003) The relationship between location and displays in a territorial lizard. J Herpetol 37:414–416

Melemis SM, Falls JB (1982) The defense function: a measure of territorial behavior. Can J Zool 60:495–501

Moreia PL, Birkhead TR (2004) Copulatory plug displacement and prolonged copulation in the Iberian rock-lizard (*Lacerta monticola*). Behav Ecol Sociobiol 56:290–297

Olsson M (1992) Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. Anim Behav 44:386–388

Ott JA, Scott DE (1999) The effects of toe clipping and PIT-tagging on growth and survival in metamorphic *Ambystoma opacum*. J Herpetol 33:344–348

Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223–243

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Rice WR (1989) Analysing tables of statistical test. Evolution 43:223–225

Riechert SE (1998) Game theory and animal contests. In: Dugatkin LA, Reeve HK (eds) Game theory and animal behavior. Oxford University Press, Oxford, pp 64–93

Rose B (1982) Lizard home ranges: methodology and function. J Herpetol 16:253–269

Sandell M, Smith HG (1991) Dominance, prior occupancy, and winter residency in the great tit (*Parus major*). Behav Ecol Sociobiol 29:147–152

SAS Institute (1999) SAS/STAT user's guide version 8. SAS Institute, Cary, NC

Shanas U, Terkel J (1997) Mole-rat harderian gland secretions inhibit aggression. Anim Behav 54:1255–1263

Shutler D, Weatherhead PJ (1992) Surplus territory contenders in male red-winged blackbirds: where are the desperados? Behav Ecol Sociobiol 31:97–106

Shutler D, Weatherhead PJ (1994) Movement patterns and territory acquisition by male red-winged blackbirds. Can J Zool 72:712–720

Simpson BS (1985) Effects of location in territory and distance from neighbours on the use of song repertories by Carolina wrens. Anim Behav 33:793–804

Slotow R (1996) Aggression in white-crowned sparrows: effects of distance from cover and group size. Condor 98:245–252

Stamps JA (1995) Motor learning and the value of familiar space. Am Nat 146:41–58

Stamps JA, Krishnan VV (1994) Territory acquisition in lizards: I. First encounters. Anim Behav 47:1375–1385

de Waal FBM (1986) The integration of dominance and social bonding in primates. Q Rev Biol 61:459–479

Wolfinger RD (1993) Covariance structure selection in general mixed models. Commun Stat-Simul C 22:1079–1106

Worton BJ (1989) Kernel methods for estimating the utilisation distribution in home range studies. Ecology 70:164–168