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Pedro Aragón
Spanish National Research Council

Jose Martin
Spanish National Research Council

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Familiarity modulates social tolerance between male lizards, *Lacerta monticola*, with size asymmetry

P. Aragón [1], P. López [2] and J. Martín [2]

[1] *Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain*
[2] *Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain*

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Theoretical and field studies suggest that inferior competitors may be able to avoid costly agonistic interactions, although the mechanisms involved are poorly understood in lizards. The "Dear enemy recognition" theory proposes that higher tolerance among familiar than among unfamiliar conspecifics may reduce costly interactions. Male lizards *Lacerta monticola* are able to discriminate between familiar and unfamiliar conspecific males through chemical signals alone. To better understand the implications of this discrimination ability, we performed a laboratory experiment on the role of familiarity in social tolerance estimated as the degree of spatial proximity with no sign of aggressiveness between males with a size asymmetry. In natural conditions the outcome of neighbour-stranger interactions might be the result of asymmetries in residence. Therefore, we staged pairwise encounters between familiar and unfamiliar males in neutral terraria to avoid an interacting effect of residency asymmetry. The latency to the first time in close proximity was significantly longer when small males were faced with unfamiliar males. The time that unfamiliar lizards spent in close proximity was significantly lower than that with familiar males. Our design allowed us to conclude that there was a higher social tolerance among familiar individuals with a size asymmetry that was independent of residency asymmetry.

KEY WORDS: Dear enemy recognition, size asymmetry, residency asymmetry, social interactions, social behaviour, lacertids.

INTRODUCTION

In many situations not only the resource holding potential (individual traits correlated with competitive ability) (Parker 1974) but also other uncorrelated

[1] Author for correspondence: Dr Pedro Aragón (E-mail: paragon@mncn.csic.es).

asymmetries, such as residence asymmetry or familiarity among conspecifics, may play an important role in intraspecific competition (Maynard-Smith & Parker 1976). Asymmetries not only influence the outcome but also the probability or duration of agonistic interactions. Thus, theoretical studies show that when the outcome of potentially costly interactions is predictable, inferior competitors should avoid them (Parker 1974, Maynard Smith 1982, Enquist & Leimar 1983). In fact, field studies suggested that smaller or subordinate lizards are able to avoid costly interactions (Cooper & Vitt 1987; Olsson 1992; Stamps & Krishnan 1994; Aragón et al. 2004, 2006a), although the mechanisms involved are poorly understood. The "Dear enemy recognition" hypothesis proposes a higher tolerance among familiar than among unfamiliar conspecifics (Fisher 1958, Jaeger 1981). Therefore, when there is home range overlap among conspecifics the ability to discriminate between familiar and unfamiliar individuals may help to reduce the frequency and intensity of costly interactions. The discrimination of familiarity has been found in a variety of taxa, including amphibians (Bee & Gerhardt 2001), fish (McGregor & Westby 1992), birds (Lovell & Lein 2004), mammals (Rosell & Bjørkøyli 2002) and reptiles (Husak & Fox 2003, López & Martín 2004). This ability to discriminate is often based on chemical stimuli within lizards, including iguanids (Alberts & Werner 1993, Hanley et al. 1999), scincids (Cooper 1996, Bull et al. 2000), gekkonids (Steele & Cooper 1997) and lacertids (Aragón et al. 2000, 2001a, 2001b, 2003; Font & Desfilis 2002). Furthermore, previous studies demonstrated that rival recognition may affect male contest behaviour in lacertids (Olsson 1994, López & Martín 2001).

Lacerta monticola is a small diurnal lacertid lizard found mainly in rocky habitats of some high mountains of the Iberian Peninsula. Lizards are active from May-October, mating in May-June and producing a single clutch in July (Elvira & Vigal 1985). During the mating season, agonistic encounters between males are frequent (Aragón et al. 2001c). Although there is home range overlap among males, home range areas of dominant males are more exclusive than those of subordinate males. Moreover, the core areas of larger males are more exclusive than their total home ranges, which is not true in smaller although mature males. Also, larger males participate in more agonistic interactions (Aragón et al. 2004). Therefore, for inferior competitors, mechanisms to reduce the frequency of potentially costly interactions, such as a higher tolerance among familiar males when there is a marked asymmetry in competitive ability, would be advantageous. In fact, it has been previously demonstrated that male *L. monticola* are able to discriminate between familiar and unfamiliar conspecifics through chemical cues in the absence of the signallers. In these previous studies, familiarity between males was either estimated from the degree of home range overlap in the field (Aragón et al. 2000, 2001a, 2003), or, in laboratory conditions, by keeping pairs of males together in the same cage (Aragón et al. 2001b). Therefore the ability to differentiate between familiar and unfamiliar males on the basis of scent should play an important role in the social behaviour of this species. The potential savings in time and energy may be particularly important in this species because individuals have to mate and store reserves to survive in the winter during a short period of annual activity that often is intermittent due to the adverse climate.

We present here a laboratory experiment on the role of familiarity in social tolerance between male *L. monticola* with a marked asymmetry in size. We staged pairwise encounters where we maintained constant the resource quality and body size asymmetry, but manipulated the familiarity between individuals (familiar vs unfamiliar). To examine how inferior competitors might avoid potentially costly interactions, size asymmetry within pairs in this experiment was greater than the average observed in male dyads in the field (ARAGÓN et al. 2004). We predicted that tolerance between males should be higher between familiar than between unfamiliar males even when a marked size asymmetry within pairs existed.

METHODS

During June 1999, we captured by noosing 38 adult mature male *L. monticola* at "Alto del Telégrafo" (Guadarrama mountains, Central Spain) at an elevation of 1990 m. Males were weighed ($\bar{x} \pm$ SE = 14.0 ± 0.3 g, range = 11-18 g) and their snout-to-vent length (SVL) was measured ($\bar{x} \pm$ SE = 68.8 ± 0.9 mm, range = 59.5-77 mm). The sexual maturity of the lizards was estimated from their SVL (see ELVIRA & VIGAL 1985) and only mature males were captured. Lizards were housed in pairs at "El Ventorrillo" Field Station (Navacerrada, Madrid Province) 5 km from the capture site in outdoor plastic cages (60 × 40 cm) containing rocks for cover. Food, in the form of mealworms (*Tenebrio molitor*), and water were provided ad libitum. To establish familiar pairs, males were held together for 2 weeks before testing began (ARAGÓN et al. 2001b). To ensure a marked size asymmetry each focal male was clearly smaller than his cage mate (see below). To ensure that the lizards had not been in previous contact, the distances between the capture sites of each pair of males were at least 500 m, which corresponds to 2427% of the average male range span (maximum distance within home ranges) in this population (ARAGÓN et al. 2004). On this basis, we considered males that were housed in different cages to be unfamiliar. All the lizards were healthy during the period of testing. At the end of the experiment, the lizards were released at their original capture points.

Staged encounters involved pairs of male lizards in which every focal male was smaller in size and body mass than his partner (SVL difference: $\bar{x} \pm$ SE = 10.5 ± 0.2 mm, range = 7-14.5 mm; body mass difference: $\bar{x} \pm$ SE = 3.0 ± 0.1 g, range = 1-5 g). Thus, we fixed a marked asymmetry in body size within the pairs but experimentally manipulated familiarity between pairs in the staged encounters. This protocol was designed to examine the tolerance between pairs in which one individual was at a clear disadvantage regarding his competitive ability. Staged encounters were performed in neutral clean cages where both males of each pair were non-residents to avoid a potential interacting effect of residence asymmetry (LÓPEZ & MARTÍN 2001). The duration of each trial was 10 min, which has been demonstrated to be sufficient time for individuals of *L. monticola* to discriminate among familiar and unfamiliar conspecifics through chemical cues (ARAGÓN et al. 2001a). All trials were conducted in outdoor conditions during June on sunny days between 09:00-12:00 hr GTM. Lizards were allowed to bask for at least 2 hr before trials in their home cages to standardize thermoregulatory requirements.

We used a repeated measures design in which each focal smaller male faced two different treatments in a random order of presentation. Thus, each smaller male was presented in the experimental neutral cages to a larger familiar male (his partner in the home cage) and to a larger unfamiliar male (previously unknown). We performed 38 trials (19 focal males × 2 treatments). No lizard was tested more than once per day, and no pairing of lizards was repeated.

Experiments were recorded on videotape (Hi-8 format, 25 frames/sec) using a video camera aligned perpendicularly over the centre of the terraria. The experimenter was not present during filming. From, the videotapes we noted the following variables: (1) the latency to the first time that the males stayed in close proximity (at a distance of less than 1 cm) with no sign of aggressiveness (threat displays, persecutions and/or bites), (2) the number of times that the males spent in close proximity with no sign of aggressiveness, and (3) the total time that males spent in close proximity with no sign of aggressiveness. We considered that two males stayed in close proximity when the two lizards approached to within 1 cm of each other up to the point when they moved further than 5 cm apart. Time spent in close proximity has been used in previous experiments as an indicator of social tolerance in lacertids (DOWNES & BAUWENS 2004, ARAGÓN et al. 2006b).

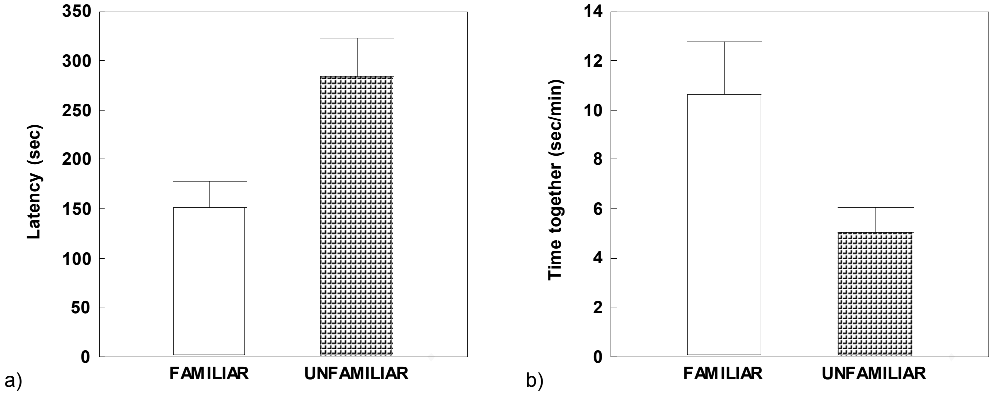

Fig. 1. — (a) Latency (sec) ($\bar{x}$ ± 1 SE) to the first time in close proximity (at a distance of less than 1 cm) and (b) time (sec/min) ($\bar{x}$ ± 1 SE) in close proximity with familiar and unfamiliar conspecific *L. monticola* males of greater size. The staged encounters lasted 10 min.

To test that size differences within pairs were similar between treatment conditions we used one-way ANOVAs. To examine differences in the dependent variables between treatment conditions, we used repeated measures ANOVAs (Sokal & Rohlf 1995) with treatment as the within-subjects factor. Normality of raw data and residuals was checked for each variable using the Kolmogorov-Smirnov test (Sokal & Rohlf 1995). The number of times spent together was log-transformed. Sphericity was not checked because all the within-subjects factors had only two levels and therefore each variance-covariance matrix was a vector (Quinn & Keough 2002). All average data are showed as untransformed means ± SE.

RESULTS

Asymmetries in body size and body mass within pairs were similar between treatment conditions (one-way ANOVA, SVL difference: $F_{1,36}$ = 0.11, P = 0.73; body mass difference: $F_{1,36}$ = 0.2, P = 0.88).

All lizards were active during the trials. The latency to the first time in close proximity was significantly longer when small males were faced with unfamiliar males (repeated measures ANOVA: $F_{1,16}$ = 10.36, P = 0.005; Fig. 1a). The number of times that pairs of males spent in close proximity was significantly lower when males were unfamiliar (Familiar: $\bar{x}$ ± SE = 0.51 ± 0.07 events/min, Unfamiliar: $\bar{x}$ ± SE = 0.32 ± 0.06 events/min; $F_{1,18}$ = 4.42, P = 0.049). The time that unfamiliar lizards spent in close proximity was significantly lower than that spent with familiar males ($F_{1,18}$ = 5.31, P = 0.033; Fig. 1b). There was no sign of aggressiveness in any trial.

DISCUSSION

Our results showed that even when there is a marked asymmetry in competitive ability males responded differently to familiar and unfamiliar conspecifics.

Previous studies demonstrated that males of *L. monticola* use chemical signals to discriminate between familiar and unfamiliar conspecific males in the absence of the signallers (ARAGÓN et al. 2000, 2001a, 2001b). In addition, males seem to show avoidance of scent marks from unfamiliar conspecifics (ARAGÓN et al. 2003). Furthermore, the results of the present study showed that males use their ability to make this discrimination in order to decide whether or not to avoid conspecific males depending on familiarity with the partner in staged encounters. Thus, the degree of avoidance was higher between unfamiliar than between familiar males. Our findings are compatible with the "Dear enemy recognition" theory (JAEGER 1981, QUALLS & JAEGER 1991), suggesting that this ability may help to reduce the frequency and intensity of costly interactions when other factors such as residency asymmetry might induce aggressive interactions in the field. Levels of aggression inversely related to degree of familiarity has been reported in several lizard species, including *Dipsosaurus dorsalis* (GLINSKI & KREKORIAN 1985), *Crotaphytus collaris* (FOX & BAIRD 1992), *Platysaurus broadleyi* (WHITING 1999) and *Liolaemus tenuis* (TRIGOSSO-VENARIO et al. 2002).

In the present experiment, we held fixed a marked size asymmetry within pairs to examine how inferior competitors might avoid potentially costly interactions since previous studies suggest that subordinate individuals of this and other lizard species are able to avoid agonistic interactions in the field (COOPER & VITT 1987; OLSSON 1992; STAMPS & KRISHNAN 1994; ARAGÓN et al. 2004, 2006a). In the field the percentage of overlap with the home ranges of smaller males by other males is higher than the overlap with those of dominant males (ARAGÓN et al. 2004). This previous finding, together with the fact that participation in agonistic interactions by smaller males is lower, strongly suggests that familiarity with neighbours (those whose home range overlaps theirs) may allow inferior competitors to reduce the frequency and intensity of interactions. In fact, males of this species are able to discriminate among males with overlapping and non-overlapping home ranges (ARAGÓN et al. 2001a).

On the other hand, in natural conditions, in encounters between neighbours both males act as residents whereas in encounters between non-neighbours at least one male acts as an intruder. Furthermore, it has been showed that the behavioural responses of lizards may depend on whether the trials are performed in their own captivity cage or not, resembling therefore a residence asymmetry situation (COOPER & VITT 1987, LÓPEZ & MARTÍN 2001, ARAGÓN et al. 2006a). In addition, in lacertids the direction of the differential chemosensory exploration to familiar and unfamiliar conspecifics seems to be dependent on the direction of the residency asymmetry in laboratory conditions (i.e., own cage vs cage scent marked by a conspecific male) (ARAGÓN et al. 2000, 2001a, 2001b; FONT & DESFILIS 2002). However, since this current experiment was performed in neutral terraria (i.e., both males were nonresidents in unlabelled experimental cages), our design allows us to disentangle the potential interacting effects of familiarity and residency asymmetry. Thus, this study shows the first evidence in lacertids of an effect of familiarity with conspecifics independently of any residency asymmetry.

A previous laboratory study in which residency asymmetry was manipulated showed that there was no aggressive response when trials were performed in neutral terraria (ARAGÓN et al. 2006a). In addition, it has been showed that smaller males are able to avoid aggressive interactions in the field (ARAGÓN et al. 2004, 2006a). In the present experiment we selected pairs with greater size asymmetry than that of those dyads involved in aggressive interactions in the field. Taken together, this is in concordance with the non-aggressive response found in the present study.

To conclude, we showed a differential response to familiar and unfamiliar conspecifics independently of residency asymmetry. Our findings showed a higher social tolerance among familiar individuals even when there is a marked asymmetry in competitive ability, which may allow inferior competitors to avoid costly interactions.

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