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Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*

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Abstract The establishment of fighting rules and the ability to recognise individual conspecifics and to assess their fighting ability and/or roles may help to reduce costs of fighting. We staged encounters between males of the lizard *Podarcis hispanica* to examine whether lizards used fighting strategies and whether a previous agonistic experience affects the outcome and characteristics of a subsequent encounter. The results showed that simple rules such as body size differences and residence condition were used to determine the outcome of agonistic interactions as quickly as possible. Thus, larger males were dominant in most encounters. However, when size differences between opponents are smaller, they may be more difficult to estimate and, then, residence condition was more important. In addition, the intensity of interactions between males could be explained according to the "sequential assessment game", supporting the idea that *P. hispanica* males acquire information about fighting ability gradually during the progress of a fight. Our results also showed that the second fight of the same pair of males was less aggressive, even when its outcome was the opposite of the first. This result suggests that male *P. hispanica* can recognise individual opponents and that they use this information to reach a contest outcome more quickly, thus reducing unnecessary aggression levels in subsequent interactions. These fighting strategies and assessment mechanisms may help to stabilise the social system of this lizard.

Keywords Agonistic behaviour · Fighting strategies · Individual recognition · Lizards

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Introduction

The ultimate goal of a fight is that the winner may take sole possession of a resource, but since fighting entails costs such as time and energy expenditure and risk of injury, both opponents benefit from settling disputes as cheaply as possible (Huntingford and Turner 1987; Archer 1988). Thus, different fighting strategies and decision rules have evolved for resolving conflicts depending on the balance between costs of fight and expected benefits (Maynard Smith and Price 1973; Maynard Smith 1982).

Asymmetries between contestants are used to settle fights and to decide how much to escalate (Maynard Smith and Parker 1976; Hammerstein and Parker 1982). For example, individual males with larger bodies, and hence greater fighting ability, are usually dominant in contests over smaller ones and, in fights between the owner of a resource and an intruder, a simple convention such as "owner always wins" can be an evolutionarily stable strategy (Maynard Smith 1982). In addition, the model of fighting behaviour called "the sequential assessment game" (Enquist and Leimar 1983) suggests that animals may gradually acquire information about fighting ability during the progress of a fight. This model predicts that in fights where opponents differ only in fighting ability, longer and more escalated fights will occur when the difference between opponents is small because assessment of this asymmetry is more difficult (Enquist and Leimar 1983). Furthermore, in fights with both an asymmetry in fighting ability and a role asymmetry, the most intense fights will occur when the intruder is slightly stronger, and fights will be more intense if won by the intruder than by the owner (Leimar and Enquist 1984).

In dominance hierarchies or territorial systems with extensive overlap between home ranges, assessment of the probable outcome of future encounters is likely the best way to economise on energy and reduce the risk of injury (Barnard and Burk 1979). When two individuals have already fought each other, prior experience may influence their fighting behaviour when they meet again.

This can be achieved only if animals are able to recognise familiar neighbour individuals based on, for example, distinctive dermal or plumage patterns (Whitfield 1987; Olsson 1994) or chemosensory cues (Halpin 1986; Alberts and Werner 1993). This "dear enemy" recognition would be adaptive because it minimises the energy expended on aggressive acts and may prevent escalated contests between neighbours (Jaeger 1981; Glinsky and Krekorian 1985; Qualls and Jaeger 1991).

The Iberian wall lizard, *Podarcis hispanica*, is a small (50–70 mm adult snout-vent length, SVL) diurnal lacertid lizard of the Iberian Peninsula, common in rocky habitats or at artificial walls (Martín-Vallejo et al. 1995). Males are aggressive, and although they are not strictly territorial, a male defends some area around himself and his females (Gil et al. 1988). Population densities are high and individuals aggregate around favourable areas with rock crevices. Overlap between male home ranges is extensive and agonistic encounters are frequent during the mating season (P. López and J. Martín, unpublished data). Individuals with higher agonistic interaction levels may incur greater energetic and survival costs (Marler and Moore 1988, 1989). Therefore, mechanisms of reducing the frequency of aggressive encounters and the levels of aggression would be advantageous. We hypothesised that the establishment of fighting rules and the ability to recognise individual conspecifics and to assess their fighting ability and/or roles may help to reduce these costs.

In this paper, we staged encounters between male *P. hispanica* in outdoor terraria to analyse the outcome and detailed behaviours involved in agonistic interactions. We aimed to determine whether lizards used fighting strategies during these encounters and to examine the possibility of rival recognition. We specifically examined: (1) the counteracting effect of body size and residency on fighting strategies; (2) whether lizards fight according to the rules of the sequential assessment model; (3) whether a previous agonistic experience with another male affects the outcome and characteristics of a subsequent encounter, and (4) the interaction of fight strategies, based on body size differences and residency, with the effect of a previous experience.

Methods

Study animals

We captured adult male *P. hispanica* on rocky outcrops in an oak forest near Cercedilla (40°44′ N, 4°02′ W, Madrid province, Spain). We captured lizards in different places over a large area to ensure that individuals had not been in previous contact, which may have affected the outcome of the interactions (Olsson 1994). Lizards were housed individually at "El Ventorrillo" Field Station (5 km from the capture site) in outdoor plastic cages (60×50×50 cm) containing sand substrate and rocks for cover. We provided mealworms dusted with a multivitamin powder as food and water ad libitum. The experiments were carried out during April and May, which coincided with the lizard mating season in their original natural population. All lizards were healthy during the trials and, at the end of the experiment, were released at their capture sites.

Staged agonistic interactions

In the first experiment, we staged encounters (*n*=43) between pairs of males with asymmetries in body size and residence to investigate their independent and counteracting effects in confrontations between unfamiliar conspecifics. We staged all agonistic encounters in the home cage of one of the males, where he had been maintained and fed for at least 10 days prior to staged encounters. Thus, he should have had the initial advantage of being resident and was competing to maintain his status as owner. The other male acted as an intruder. With this design, we tried to mimic the natural field situation where, in almost every encounter, one of the males is resident and finds a conspecific in his home range. First, we conducted encounters in which the larger male was also the resident (*n*=22), while in another set of encounters with different pairs of males (*n*=21), the smaller contestant in a dyad was given the possible advantage of residency, to obtain information on the relative importance of this factor versus size for a male's competitive ability, and to determine which factor would better predict the outcome of the contest. In each test, the two contestant males had never been together before the encounters.

In a second experiment, we tried to assess the effects of prior experience with a conspecific on the outcome and fighting strategies of a subsequent encounter between two individuals. We conducted encounters (*n*=20) between pairs of males where one male was the resident and the other acted as an intruder. The size category (large or small) of the resident and intruder were chosen randomly. The following day, we conducted the reversed encounters changing the residence condition. Thus, the male that was previously the intruder was now the resident and was paired in his own cage with his familiar former partner (*n*=20 encounters) and then with an unfamiliar new partner (*n*=20 encounters). The order of presentation of these two conditions was counterbalanced. Males used as unfamiliars were used as familiars with other males, and were randomly assigned to a new pair. Thus, all males participated in three contests.

To begin an encounter, we took the intruder male lizard from his cage, placed him gently in the middle of the cage of the resident male and, from a blind, we recorded their behaviour. We scored the intensity of the aggressive behavioral response of males on a ranked scale representing increasing levels of escalation: "neutral" (individuals were together but no response or a non-aggressive interaction was observed), "retreat" (a male approached his opponent without aggressive display or contact and the other male ran away), and "aggressive responses". The later includes: "approach" (approaching another male with aggressive display and making the other male retreat but without physical contact; approaching males employed threatening postures, strutted toward an opponent on raised, stiff forelegs with an arched neck arched, the snout pointing slightly down), "touch" (approaching another male with aggressive display and making the other male retreat after physical contact, by touching him on the tail or flanks), "bite" (approaching another male and biting him, specially on the snout or head, and making the other male retreat or adopt submissive behaviour), and "physical combat" (both males simultaneously interlock jaws by reciprocal biting and clasping.). The criterion for establishment of dominance was observed avoidance behaviour in one of the contestants (e.g. rapid retreat and running away, sometimes following submissive behaviour such as flattened body, tail twitches and foot shaking). We calculated an unweighted sum of dominance patterns less subordinate patterns for each male of each pair, and defined the male with the highest positive sum as the dominant individual (Martín and Salvador 1993). Typically, males considered as winners repeatedly dominated their opponents over a series of interactions in an encounter.

All contests were interrupted after 15 min. We also decided to stop any interaction that involved persistent attacks or desperate attempts to escape. This was, however, not necessary, as interactions usually consisted of threatened displays and short chases and only very rarely escalated to single quick bites that did not cause observable injury. None of individuals suffered physical injuries or showed physical stress during or after the trials, and all of them had maintained or increased their original body mass at the end of the trials. When in a contest males were unresponsive and consistently exhibited non-aggressive interactions, the data were discarded, because the lack of a response could have been induced by the test situation.

Experimental male lizards were weighed (mean±SE=4.60±0.1 g, range=2–6 g) and SVL was measured (mean±SE=64.2±0.5 mm, range=50–69 mm) immediately after termination of a contest. Body mass and SVL were highly significantly correlated (r=0.91, F=187.60, P<0.0001). Relative differences in weight and SVL were calculated as the absolute values of ln(weight A/weight B) and ln(SVL A/SVL B), respectively. Statistical analysis of data were based on procedures in Sokal and Rohlf (1995).

Results

Effects of counteracting asymmetries in body size and residence

In contests where the larger lizards were also the residents, the larger lizards were the winners in 95.5% (21/22) of the fights (two-tailed binomial test, P<0.0001), whereas when the smaller lizards were the residents, the larger lizard won only 38.1% (8/21) of the fights (two-tailed binomial test, P=0.38). Thus, when adding residence asymmetry in favour of the smaller lizards, there was a highly significant effect on the outcome of the fights won by smaller lizards (Fisher exact test, P<0.0001). This suggests that some smaller lizards could offset their lower fighting ability, resulting from a smaller body size, by being the resident. However, when the smaller resident lizards won the fights, the differences in body mass between opponents were significantly smaller (0.35+0.08 g) than when the larger lizard won (0.96±0.23 g; Mann-Whitney U-test, Z=2.43, n_1=13, n_2=8, P=0.015). The differences in SVL were similar but non-significant (smaller lizard won: 3.6±0.7 mm; larger lizard won: 6.1±1.8 mm; Mann-Whitney U-test, Z=1.04, P=0.30).

In addition, as the “sequential assessment game” predicts, the total number of interactions (aggressive and non-aggressive) won by the smaller resident lizard (8.7±1.3) was significantly lower than when the larger intruder lizard won (14.9±3.1; Mann-Whitney U-test, Z=2.11, P=0.035). Similarly, the number of aggressive interactions when the smaller resident lizard won (5.7±0.8) was also significantly lower than when the larger intruder lizard won (11.9±3.2; Z=2.23, P=0.026).

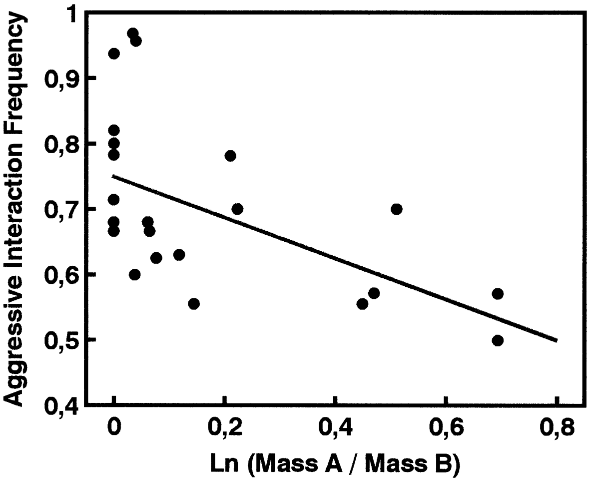

Fig. 1 Relationship between relative body mass differences between pairs of male *Podarcis hispanica* and frequency of aggressive interactions in contests of these pairs of males. The line (interactions=0.76–0.33×mass differences) is the significant linear regression on the frequency of aggressive interactions

In contests with larger males as residents, the frequency of aggressive interactions, relative to the total number interactions, decreased as the size difference between contesting males increased, both considering differences in SVL (r=–0.47, F=5.47, P=0.03) and differences in body mass (r=–0.53, F=7.53, P=0.013) (Fig. 1). There was also a similar decrease in aggressive interactions with physical contact (including interactions with touch, bite and physical combat) when the size differences between contesting males increased, although these reductions were not significant (SVL: r=–0.42, F=4.02, P=0.059; mass: r=–0.35, F=2.58, P=0.12). Conversely, non-aggressive interactions increased as the size difference increased (SVL: r=0.47, F=5.47, P=0.03; mass: r=0.53, F=7.53, P=0.013). These results were similar in contests with smaller males as residents.

When the larger lizards were also the residents, the males that began the interactions were not always the winners at the end of the contest (45.5% of 22 contests; binomial test, P=0.83). However, the males who won the first aggressive interaction in the contest dominated their opponents repeatedly and the results were consistent throughout the entire contest (81.8% of 22; binomial test, P=0.0043). When the smaller lizards were the residents, both the males that began the interactions (80.9% of 21 contests; binomial test, P=0.0072), and the males that won the first interaction (76.2% of 21; binomial test, P=0.027) dominated their opponents repeatedly and the results were consistent throughout the entire contest.

Effects of prior experience with a conspecific

In 14 out of 20 pairs of males, one of the males of the pair consistently won both contests, independent of residence condition. However, in the other 6 contests, males won when they were residents, but they lost the contests when they were intruders. These differences between individuals could be explained by the magnitude of the differences in body size between the opponents. Thus, when the larger male always won, differences in size were larger (SVL: 7.8±1.6 mm; mass: 1.26±0.20 g) than when residence status determined whether a male won or not (SVL: 0.7±1.3 mm; mass: 0.17±0.06 g; Mann-Whitney U-tests, SVL: Z=1.70, n_1=14, n_2=6, P=0.08; mass: Z=2.91, P=0.004).

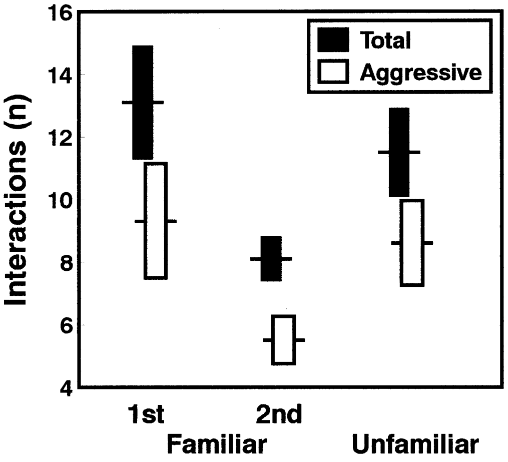

Fig. 2 Mean (±SE) number of total and aggressive interactions in the first contest of a pair of males, in the second contest of the same familiar pair of males, and in the first contest of one of the males tested and an unfamiliar new male. The order of presentation of the last two conditions was counterbalanced

The total number of interactions and the number of aggressive interactions decreased significantly from the first to the second contest of the same pair of familiar males, but the values for both were higher when one of the experimental males encountered an unfamiliar new partner (Friedman two-way ANOVA, total: $\chi^2=10.64$, $P=0.005$; aggressive: $\chi^2=6.86$, $P=0.03$; Fig. 2). The number of interactions (total and aggressive) of the first contests of any pair of males were not significantly different (non-parametric multiple comparisons a posteriori, $P>0.20$ in all cases), whereas the number of interactions in the second contest of the same pair of males was significantly lower than in their first contest ($P<0.05$ in all cases).

Discussion

The results from our experiment show that simple rules such as body size differences and residence condition are used by *P. hispanica* to determine as quickly as possible the outcome of agonistic interactions, thus reducing possible costs of fighting. Our results also suggest that rival recognition, and the previous assessment of his fighting ability or resource-holding potential, is one of the most important means used to reduce unnecessary aggression levels in subsequent interactions. In addition, lizards should balance the costs and benefits of fighting in each particular encounter, which may explain why the result of an encounter between the same pair of males may change when the residence conditions change.

Body size is an important determinant of dominance in numerous lizard species (Tokarz 1985; Carpenter 1995), and individual males with larger body size are usually dominant in contests over smaller ones (Cooper and Vitt 1987; Olsson 1992; Molina-Borja et al. 1998). Larger male *P. hispanica* were also dominant in the majority of encounters. Estimation of body size is probably the easiest way to assess the fighting potential in lizards, even at long range. Thus, lizards may decide whether to avoid a possible agonistic interaction with the opponent, thus evading unnecessary costs of fighting. Differences in body mass, rather than in body length, seemed to be more important in deciding the outcome of a fight, probably because weight is more closely related to muscle mass which should be more relevant to actual fighting ability.

However, small size differences between opponents may be more difficult to estimate and, then, other factors such as residence condition become more important. Our results show that even for the same pair of individual males with previous experience, the change in residence status may decide the outcome of a fight. Male lizard behaviour depended on whether they were residents or intruders (i.e. they assumed different roles). Thus, lizards are probably able to assess the role of the opponent by observing his behaviour (e.g. challenge displays of residents or submissive “foot-shaking” displays of intruders). Lizards might also use scent matching between chemical marks left in the substrate by resident males and the individual scents (Gosling and McKay 1990). These assessment mechanisms are an important function in the behaviour of fighting animals that may greatly contribute to decreasing the costs of fighting.

The intensity of interactions between male *P. hispanica* could be explained according to the “sequential assessment game” (Enquist and Leimar 1983), which would suggest that this species acquires information about fighting ability gradually during the progress of a fight. Even if competitors had some initial indication about the opponent’s strength (i.e. by visually assessing body size), they likely gained most information about their relative fighting ability during the fight. In our experiment, fights were more intense when size differences were smaller and, thus, presumably more difficult to assess by contestants. Additionally, when size was similar, fights were more intense when won by the intruder than by the owner (Leimar and Enquist 1984). Thus, when the resident/intruder roles were not considered, costs of fighting increased.

The second fight of the same pair of males had a lower aggression level, even when the outcome of this second fight was different. This result suggests that male *P. hispanica* are able to recognise individual opponents and that they use this information to determine the outcome of a contest more quickly. Similarly, the duration of contests was shorter when the same pair of male *Lacerta agilis* had a previous agonistic experience (Olsson 1994). Other studies showed that territorial male desert iguanas, *Dipsosaurus dorsalis*, quickly reacted with aggression towards unfamiliar males, whereas neighbours were ignored, and as distance increased between two males, the likelihood of mutual challenge displays increased and the latency to mutual challenge display decreased (Glinsky and Krekorian 1985). Similarly, resident male *Platysaurus broadleyi* were less aggressive towards neighbours than non-neighbours (Whiting 1999). Individual recognition can be combined with the ability to learn the status of individual conspecifics through repeated encounters (Gosling 1982) and, thus, it would help to stabilise the social systems by reducing the frequency and intensity of aggressive encounters (Glinski and Krekorian 1985).

The mechanisms that might be used for individual recognition by *P. hispanica* remain unknown. Chemical cues are known to play an important role in the intraspecific communication of lizards. Several studies have shown pheromonal detection in different species (Mason 1992) and individual recognition through chemosensory cues has been suggested in some species (e.g. Alberts and Werner 1993; Cooper 1996). The presence and relative concentration of pheromone components vary not only between sexes but also among individuals, which may convey information about individual identity and serve a variety of other functions (Alberts 1992). Therefore, in lizards, discriminations based on pheromone components may be more reliable and also may provide more detailed information about conspecific than might be obtained from colour patterns alone. The diversity of colour patterns is rather limited in *P. hispanica*, whereas chemosensory abilities are well-developed. Thus, *P. hispanica* can discriminate between prey- and non-prey-odour-impregnated cotton swabs (Cooper 1990), between conspecifics and heterospecifics (Gómez et al. 1993) and between sexes (López et al., in press) by chemical cues alone. Moreover, the aggressive response of male *P. hispanica* to intruding males is dependent on pheromone-mediated sex recognition (López et al., in press). Our findings suggest the need for further studies of individual recognition during agonistic encounters examining the different roles and the relative importance of colour and chemical cues.

In species with high population densities, agonistic encounters between males can be very frequent, and males with higher agonistic interaction levels may incur greater energetic and survival costs (Marler and Moore 1988, 1989). However, in the lizard *P. hispanica*, agonistic interactions mostly comprised threatened displays and short chases and only very rarely escalated to single quick bites. We conclude that the establishment of fighting rules and the ability to recognise individual conspecifics and to assess their fighting ability and/or roles may help to speed up the outcome of conflicts. Assessment and recognition mechanisms during fighting contribute to reducing the intensity and costs of agonistic encounters in *P. hispanica* and may play an important role in their social system.

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