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ORIGINAL PAPER

Male Iberian rock lizards may reduce the costs of fighting by scent matching of the resource holders

Pilar López · José Martín

Abstract Animals should adopt strategies to minimize the costs of intraspecific aggressive interactions. For example, individuals should be able to identify resource holders in advance and avoid fighting with them because residents are generally more likely than intruders escalate aggression. It has been suggested that scent marks function mainly to allow competitor assessment by conveying the costs of entering a scent-marked area. Individuals may identify territory owners by comparing the scent of substrate marks with the scent of any conspecific they encounter nearby, assessing whether these two scents match or not, a mechanism known as scent matching. Here, we examined the response of male *Iberolacerta cyreni* lizards to areas scent-marked by other males and the potential role of scent matching in agonistic interactions. We designed a laboratory experiment where we allowed a male to explore the scent-marked substrate of another male, and then we immediately staged agonistic encounters in a nearby clean neutral area with either the male that had produced the scent marks (matching treatment) or with a different non-matching individual male. The higher chemosensory exploratory rates of substrate scent marks in comparison to clean substrates suggested that males detected and spent more time exploring scent marks to obtain information on the donor male. Moreover, this information was later used to decide the fighting strategy. Intruding males delayed time until the first agonistic interaction, reduced the intensity of fights and the number of aggressive interactions, and won less interactions with males which scent matched that of scent marks (because they would be considered as the territory owners) than with other non-matching individuals. Our results show that male *I. cyreni* lizards use scent matching as a mechanism to assess the ownership status of other males, which could contribute to modulate intrasexual aggression, reducing costs of agonistic interactions.

Introduction

The goal of intraspecific fights is that the winner takes possession of the resource, such as a territory or a mate (Krebs and Dawkins 1983). However, there are some associated costs to escalated fights such as loss of time and energy and risk of injury (Huntingford and Turner 1987; Marler and Moore 1988, 1989; Marler et al. 1995). For that reason, animals should adopt strategies to avoid or minimize the level of aggressive interactions, thereby reducing the associated costs (Maynard Smith and Parker 1976; Maynard Smith 1982). By assessing in advance their potential opponents, individuals may predict the outcome of a fight and decide whether to initiate aggression or retreat (Maynard Smith 1982; Huntingford and Turner 1987). For example, holders of a territory are generally more likely than intruders to escalate aggression to defend it (e.g., Krebs 1982; Grafen 1987; López and Martín 2001; Aragón et al. 2006). This is because a specific area has greater value to residents than to intruders because of familiarity with the physical and social environment (e.g., Stamps and Krishnan 1994; Stamps 1995). Thus, to reduce costly agonistic encounters with resource holders, individuals should be able to identify them in advance.

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Scent marking to signal occupancy of territories is common among many terrestrial vertebrates (Wyatt 2003; Müller-Schwarze 2006). Scent marks are signals that function mainly to allow competitor assessment by conveying the costs of entering a scent-marked area (Gosling and Roberts 2001). Because chemical signals persist in the environment after being emitted (Alberts 1992), conspecifics can use scent marks to obtain information about the scent donor even in its absence (e.g., Ferkin et al. 1997; Aragón et al. 2001a). Individuals may identify territory owners by directly comparing the scent of substrate marks with the scent of any conspecific they encounter nearby, assessing whether these two scents match or not, a mechanism known as scent matching (Gosling 1982, 1990). A few studies support the existence of scent matching in small rodents (Gosling and McKay 1990; Hurst et al. 1996; Luque-Larena et al. 2001) and in beavers (Sun and Müller-Schwarze 1998), and scent matching has also been suggested to occur in a salamander (Simons et al. 1997) and a lizard (Edsman 2001). In general, males reduce their willingness to fight with a territory owner, but not with other males, after they have matched his odor with that of the scent marks present in the vicinity (Gosling and McKay 1990). For males, recognition of holders of a territory by scent matching might be particularly useful to minimize costly aggressive interactions because the probability of winning a fight with a resident male is low.

Many lizards have well-developed chemosensory systems that can be used to detect chemical cues of conspecifics (Mason 1992; Mason and Parker 2010; Martín and López 2011). Some lizards scent mark their territories using feces or chemical secretions from specialized glands that are deposited on substrates as lizards move (Mason and Parker 2010; Martín and López 2011). These scent marks may provide information to conspecifics on the characteristics and individuality of the male that has scent marked an area (Carazo et al. 2007, 2008). True rival or familiarity recognition in lizards has received little attention (LaDage and Ferkin 2006; Carazo et al. 2008), although discrimination by lizards between the scent of familiar and unfamiliar conspecifics has been found in several iguanid (Glinski and Krekorian 1985; Alberts and Werner 1993) and lacertid lizards (Aragón et al. 2001a, b, 2003; Font and Desfilis 2002; López and Martín 2002). Individual or rival recognition, often based on chemical cues, may be used during agonistic interactions to decide the level of aggressiveness (Whiting 1999; López and Martín 2002; Osborne 2005). However, although it is probable that male lizards can obtain information from conspecific males based on territorial scent marks, we know little about how this information may affect subsequent social and agonistic behavior (but see Edsman 2001; Carazo et al. 2008).

The rock lizard *Iberolacerta cyreni* (formerly *Lacerta monticola cyreni*) is a small diurnal lacertid lizard found mainly in rocky habitats of some high mountains of the Iberian Peninsula (Martín and Salvador 1997; Pérez-Mellado 1998). Males of this species defend territories against other males, but overlapping between home ranges is extensive and agonistic encounters are frequent during the mating season (Martín and Salvador 1993; López et al. 1998; Aragón et al. 2001a, 2004, 2006). The males scent mark rock substrates with feces and femoral gland secretions (López et al. 1998; Aragón et al. 2001a). Males are able to detect and discriminate their own scent from those of other males and to discriminate between familiar and unfamiliar individual males based solely on chemical cues in feces or scent marks (López et al. 1998; Aragón et al. 2000, 2001a, b). Moreover, the behavior of a male going into a previously unknown area is affected by the presence of scent marks or fecal pellets of another male (López et al. 1998; Aragón et al. 2000, 2001a, c). Also, chemical characteristics of male scent may signal fighting ability and affect the outcome of agonistic encounters (López et al. 2006; Martín and López 2007). However, it is not known how information from scent marks can be integrated in the subsequent fighting decisions of male rock lizards.

Here, we specifically examined the response of male *I. cyreni* lizards to areas occupied (i.e., scent-marked) by other males and the potential role of scent matching in male–male agonistic interactions. We hypothesized that males could use the scent-matching mechanism to recognize resident males, which might be useful to decide their subsequent aggressive response in an eventual agonistic encounter, thus reducing the costs of fighting. We designed a laboratory experiment where we allowed a male to explore the substrate scent marks of another male, and then we immediately staged agonistic encounters in a nearby clean neutral area with either the male that had produced the scent marks or with a different individual male. We predicted that immediately after exploring a scent-marked area, intruding males should delay time until the first agonistic interaction and be less aggressive towards males found in the proximity of scent marks and which scent matched that of scent marks explored immediately before (because they would be considered the potential owners of that territory even if in the experimental situation they actually were not) than to other non-matching individuals. As a consequence, we expected that responding males would win fewer interactions with matching males than with non-matching males,

Materials and methods

Study animals

We captured by noosing 34 adult male *I. cyreni* of similar body size (snout-to-vent length, SVL : $\overline{X} \pm SE = 75 \pm 1$ mm;

range=73–77 mm) in June, at 'Alto del Telégrafo' (Guadarrama Mountains, Central Spain), at an elevation of 1,900 m. In this area, *I. cyreni* is found between 1,750 and 2,350 m elevation. Mature individuals are approximately between 61–90 mm (SVL). Lizards are active from May to October, mating in May to June, and producing a single clutch in July (Salvador et al. 2008). We captured lizards in different places over a large area to ensure that individuals had not been in previous contact, which may affect the outcome of the experiments (Olsson 1994; López and Martín 2001, 2002).

Lizards were individually housed at 'El Ventorrillo' Field Station (Navacerrada, Madrid Province) 5 km from the capture area in outdoor plastic cages (60×50×60 cm) with a substrate of absorbent paper to collect lizards' scent and a rock that was used as shelter. We provided food (mealworm larvae dusted with multivitamin powder) and water ad libitum. Lizards were held in captivity at least 10 days before testing to ensure acclimation to captivity conditions and to the presence of the experimenter. This period was also considered long enough to ensure the scent marking of the substrate papers with the male scents (feces and femoral pores secretion). All males were healthy during the trials and were released at their exact capture site at the end of the trials, 1 month after their capture date.

General experimental procedure

To test whether male lizards used the mechanism of scent matching during agonistic interactions, we designed an outdoor experiment. We first left a responding male to explore scent marks of a conspecific male and immediately after we staged, an agonistic encounter of this responding male with an opponent male of similar body size in a nearby clean neutral arena (without lizards' scent marks). We compared the fighting behavior of male lizards in two different treatments: a responding male fought with (1) an opponent male which scent marks had been previously explored by the responding male ('matching treatment') and with (2) an opponent male which scent did not match with the substrate scent marks previously explored by the responding male ('non-matching treatment'). Responding males ($N=17$) were tested in the two treatments with different individual opponent males in a random order with an elapsed period between trials of 1 week. Opponent males ($N=17$), which were used to obtain the scent marks, also participated in the two treatments with different individual responding males. Thus, every male fought just once with a given individual male to prevent previous outcomes of a fight from affecting subsequent fights (Olsson 1994; López and Martín 2001, 2002). The treatment and the pairing of males were randomly assigned. We used a blind protocol such that the experimenter that performed observations of chemosensory and fighting behavior did not know the assigned treatments.

Chemosensory exploration of conspecific scent marks

Previous to the staged encounters, we allowed the responding males to explore the scent marks of other male. This was carried out in cages identical to the home cages (60×50×60 cm) that were empty but with a substrate of an absorbent paper divided into two halves and fixed to the bottom of the cage with an adhesive film at the back. One half of the cage was covered with an absorbent clean paper (without any previous contact with any lizard). The other half of the cage was covered with an absorbent paper previously scent marked by another conspecific male (the donor of the scent). Scent-marked papers were those placed at the beginning of the experiment in the home cages of donor lizards. We divided the terraria into two halves to compare responses of the same lizard in areas scent marked and in clean areas (see below). The cages were washed between trials with clean water and left to dry in the open for at least 1 day without using them to avoid odor contamination from previous trials. We conducted all the manipulation of cages, papers, and lizards using plastic gloves to avoid odor contamination.

We conducted trials in outdoor conditions between June and July, and between 1000–1600 hours GMT, when lizards were fully active. Each responding male was allowed to bask in his home cage for at least 2 hours before trials to achieve an optimal body temperature. Thereafter, we took one responding male from his cage and placed him gently in the middle of the experimental cage with a clean paper and a paper scent marked by another male. We left the responding male for 15 min in the cage to allow him to explore the scent marks of the other male. To ensure that the two males that participated in the fights were exposed to the same manipulation before the agonistic contest, we immediately took the other opponent male selected for the trial and placed him for 15 min in another identical cage but with clean absorbent papers without conspecific odors.

Previous studies have shown that *I. cyreni* is able to detect and discriminate between scents of familiar and unfamiliar males (Aragón et al. 2001a, b). Differences in tongue-flicking rates presumably indicate chemosensory recognition in lizards (Cooper and Burghardt 1990). We recorded from a blind total tongue flicks emitted by the responding male in each half of the terraria (papers with or without scent marks) during the exploratory periods to know whether males detected the conspecific scent. We considered that responding males explored and detected the scent marks because when they were in the cage over the marked substrate, they increased tongue-flick rates (see 'Results').

Staged agonistic interactions

We staged encounters (34 encounters where each of 17 experimental lizards was tested in two conditions) between

pairs of males immediately after each exploration trial. The encounters were staged in a neutral clean cage identical to the home cages (60×50×60 cm) and to the cage where the experimental male had explored the scent marks, but with a substrate of clean absorbent paper fixed to the bottom of the cage with an adhesive film at the back. This cage was placed adjacent to the previous experimental cage where the male was allowed to explore the scent marks. With this design, we avoided the effects of residence, which may affect the outcome of contests (Olsson 1992; López and Martín 2001). Thus, we avoided that opponent males could consider themselves as residents and behave differentially if the scent of the substrate during interactions matched their own scent, which may be a problem of previous experimental designs (Edsman 2001). We cleaned experimental cages after each trial thoroughly with clean water and changed the substrate papers to avoid odor contamination in successive trials.

Immediately after the exploration trial (see above), we gently moved each male from the cages where males explored scent marks to one corner of the adjacent experimental arena. This cage was divided into two halves by opaque perspex. We allowed males 5 min to acclimation to the experimental arena. Then, we slowly approached to the cage, removed gently the division, and the trial began.

During 15 min, we recorded from a blind all the interactions between both males. In agonistic contests, 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, the snout pointing slightly down), 'touch' (approaching another male with an aggressive display and making the other male retreat after physical contact by touching him on the tail or flanks), and 'bite' (approaching another male and biting him, notably on the snout or head, and making the other male retreat or adopt submissive behavior). The criterion for establishment of dominance was an observed avoidance behavior in one of the contestants (e.g., rapid retreat and running away, sometimes following submissive behavior such as flattened body, tail twitches, and foot shaking). We calculated for each staged encounter an unweighted sum of dominance patterns less subordinate patterns for each male of the pair, and defined the male with the highest positive sum as the 'winner' individual of that encounter (Martín and Salvador 1993). Typically, males

considered as winners repeatedly dominated their opponents over a series of interactions in an encounter. We calculated an 'aggressiveness index' for each encounter as the sum of the number of interactions weighted according to their aggressiveness level: neutral (1), retreat (2), approach (3), touch (4), and bite (5). We also recorded time to the first agonistic interaction (any type of interaction but a neutral one) and to the first aggressive interaction, and noted the individual male that started and won these first interactions.

A trial was terminated after 15 min. We decided to stop any interaction that involved persistent attacks or desperate attempts to escape. This was, however, not necessary as most interactions consisted of threat displays and short chases, and only very rarely escalated to single quick bites, which did not cause an observable injury. No individual suffered physical injuries or showed physical stress during or after the trials, and all animals had maintained or increased their original body mass at the end of the trials.

We used Wilcoxon signed-ranks tests to examine differences of means in dependent variables between treatments (matching vs non-matching) (Siegel and Castellan 1988). To compare whether the responding males began or won more times the first interaction or fights than expected by chance within a given treatment, we used binomial tests assuming that the probability of beginning or winning the first interaction or the fight was equal for any of the two males.

Results

Chemosensory exploration of conspecific scent marks

When responding males were introduced in the experimental cages with papers scent marked by other males on one half and clean papers on the other half, all males moved exploring with tongue flicks both halves of the terraria, but males spent significantly more time on the substrates scent marked by other males $(\overline{X} \pm SE = 10.9 \pm 0.4\,min)$ than on clean substrates $(\overline{X} \pm SE = 3.6 \pm 0.3\,min;$ Wilcoxon signed rank-matched pair test, $Z=3.62$, $P<0.001$). Males repeatedly tongue flicked all the substrates, but explored significantly more intensively (i.e., a higher tongue-flick rate) the scent-marked substrates $(\overline{X} \pm SE = 2.4 \pm 0.3\,TF/\,min)$ than the clean substrates $(\overline{X} \pm SE = 0.8 \pm 0.1\,TF/\,min;$ Wilcoxon signed rank-matched pair test, $Z=3.62$, $P<0.001$).

Staged agonistic interactions

Fighting was observed in all the trials, and males interacted and fought repeatedly through the encounters. However, agonistic interactions mostly consisted of threat displays

and short chases, and biting, the most aggressive interaction, occurred only once in all trials (Table 1). There were significant differences between the characteristics of the fights depending on whether the scents of the opponent males matched or did not match with the substrate scent marks that had been previously explored by the responding male (Table 1). As predicted by the assessment hypothesis, there was a significantly greater delay before the first agonistic interaction or the first aggressive interaction when the opponent male was the donor of the scent marks previously explored by the responding male (matching treatment) than when the opponent was another male different from the donor of the scent (non-matching treatment) (Table 1).

With respect to the aggressiveness levels of the encounters, when the scent of the opponent male matched with the previously explored scent marks (matching treatment), the fights were significantly less aggressive than when the opponent was another male (Table 1). Thus, in the matching treatment, the total number of interactions was significantly lower and the interactions were less aggressive. There were only significant differences in the number of the more aggressive interactions; there were significantly more 'approach' and 'touch' interactions in the non-matching treatment. Moreover, the only 'bite' interaction occurred in the non-matching treatment (Table 1). Finally, the comparison of the aggressiveness indexes showed that the encounters were significantly less aggressive overall in the matching treatment (Table 1).

With respect to the outcome of the interactions, when the opponent male was the donor of the previous explored scent marks (matching treatment) the responding male began and won significantly less times the first agonistic

interaction or the first aggressive interaction than the opponent male (first agonistic interaction: 4 vs 13, respectively, binomial test, P=0.049 in both cases; first aggressive interaction, begin, 3 vs 14, P=0.013; win, 1 vs 16, P=0.0003). In contrast, when the opponent was a different non-matching unfamiliar male, there were no significant differences in who was the beginner and the winner of the first agonistic interaction (8 vs 9, binomial test, P=0.99 in both cases) or of the first aggressive interaction (7 vs 10, P=0.63 in both cases).

Finally, only one responding male was the final winner of the trial in the matching treatment (1 vs 16, binomial test, P=0.0003), whereas there were no significant differences in who was the final winner when the scent of the contestant did not match with the previous explored substrate scent marks (8 vs 9, P=0.99).

Discussion

Our results show that male _I. cyreni_ lizards use scent matching of territorial substrate scent marks with the scent of conspecific males found nearby and immediately before the encounter as a mechanism to assess the ownership or residential status of these males. Moreover, this estimation is later used to decide the fighting strategy. By avoiding fights with a male that presumably is the owner of a territory, an intruding male may reduce costs of aggressive interactions (Marler and Moore 1988, 1989; Marler et al. 1995). This is because a territory owner will have more costs if he loses the territory and will be prone to escalate fights to a higher degree (Maynard Smith 1982). Therefore, when fighting potential is similar (e.g., both males are of

Table 1 Mean (±1SE) time (in seconds) to the first agonistic interaction (any but a neutral one) and to the first aggressive interaction, number of total interactions, number of each type of interactions, and 'aggressiveness index' of the agonistic encounters between the responding males and other conspecific male in fights in the matching and non-matching treatments

	Matching (_N_=17)	Non-matching (_N_=17)	Z	P
Time to (s)				
First agonistic interaction	120±19	45±11	2.79	0.006
First aggressive	150±24	63±15	2.29	0.02
Total number of interactions	8.8±1.1	11.2±0.8	2.04	0.04
Non-aggressive interactions				
Neutral	2.8±0.3	3.0±0.4	0.15	0.88
Retreat	4.7±0.7	4.4±0.3	0.17	0.86
Aggressive interactions				
Approach	1.0±0.2	2.1±0.4	1.96	0.05
Touch	0.2±0.2	1.6±0.3	3.06	0.002
Bite	0	0.1±0.1	–	–
Aggressiveness index	7.4±1.4	13.6±1.1	3.05	0.002

Results (Z, two-tailed _P_) of Wilcoxon signed rank tests are shown

similar body size), the probability that an intruding male wins a fight to a territory owner would be low, and intruding males should avoid these fights. By being able to identify the territory owners in advance, intruding males would avoid unnecessary costs of fights.

The higher chemosensory exploratory rates of substrates scent marked by conspecific males in comparison to clean substrates suggested that males clearly detected these scent marks and spent more time exploring them to obtain information of the donor male. This result confirms the previous findings that this lizard, as many other species do, detects and discriminates at least between scents of different classes of individuals (i.e., familiar vs unfamiliar, resident vs non-resident) (Aragón et al. 2001a, b), perhaps even at the individual level as other related lizards do (Carazo et al. 2008). Chemical compounds in scent marks may also provide information on characteristics of donor males such as body size or social status (López et al. 2006; Martín and López 2007). Furthermore, this experiment suggests that scent marks may provide information on the ownership status of a male. When an intruding male is moving on an unknown area, scent marks may be used to know, and remember, the scent of the territory owner, even in the absence of this male. Scent marks do not cover all the territory, and, for this reason, the scent marks and the male that has produced them are not necessarily encountered simultaneously. However, if a male is found in the proximity of these scent marks, his scent may be compared with that of substrate marks explored in the immediate past to assess the resident status of that male.

Male lizards that found a male that matched the scent of the nearby substrate marks probably used this match to consider this male as the owner of a territory. Our experimental manipulation suggests that scent matching of the encountered male was relatively more important than other possible mechanisms of rival assessment, such as the behavior of that male, to determine the resource holding power or the territory ownership status of an opponent male. Otherwise, responding males would have not considered as a resident to a male who scent match scent marks, but that in the experimental situation was not really the owner of that territory, and that very likely did not behave as a resident male. In addition, our experimental staged encounters occurred in terraria with clean substrates ensuring that opponent males could not consider themselves as residents and behave differentially. Something that might occur in the scent of the substrate during interactions matched their own scent, which may be a problem of previous experiments (Edsman 2001). Nevertheless, it might be possible that the focal male assesses that a male who scent match the previously found scent marks is a territory owner with a higher resource holding power, but not necessarily the owner of the space in which they are currently interacting.

In the field, scent matching may be a strategy to avoid cheating of males signaling a 'false' ownership with behavioral displays alone. Scent marking a territory, and maintaining these marks through successive days, is costly in terms of time and energy (Gosling and Roberts 2001; Martins et al. 2006). The amount of deposition may convey information about intensity of scent marking that supplements and confers reliability to the chemical signal (Martins et al. 2006). So, scent marks may provide an honest signal on the ownership status of a given male in a territory.

Because the probability of winning to a territorial owner is low, male lizards that found a male presumably identified by scent matching as an owner with a high resource holding power should modify their fighting strategies. In the matching treatment, male lizards delayed time to the first agonistic interactions, which in the field, where space is not as restricted as in a terrarium, may result in males escaping to avoid aggressive interactions. Previous studies with lizards suggested that inferior competitors are able to avoid agonistic interactions in the field (Stamps and Krishnan 1994; Aragón et al. 2004, 2006). In the matching treatment, males also reduced the intensity of fights and the number of aggressive interactions, consisting most interactions in ritualized displays without physical contact. This was not a consequence of the contestant male not being really the owner of that territory because in the non-matching treatment males escalated their fights to a higher degree.

The final outcome of staged encounters was also dependent on the experimental treatment. In the matching treatment, responding males only won one fight suggesting that these males avoided fights and let the presumed owner to win the contest and hold the territory. This resembled a natural situation where one of the two males had a clear residence advantage (e.g., Olsson 1992; López and Martín 2001). In contrast, in the non-matching treatment, responding males won half of encounters, which was expected from a situation with two unfamiliar males, which had similar body size and no residence advantage.

A similar mechanism of scent matching in agonistic interactions was first described for some mammals (Gosling and McKay 1990; Hurst et al. 1996; Sun and Müller-Schwarze 1998; Luque-Larena et al. 2001). It seems that scent matching could be equally used by species with mutually exclusive territories (Gosling and McKay 1990; Hurst et al. 1996) and species with overlapping home ranges (Luque-larena et al. 2001). This latter situation is similar to that found in *I. cyreni* rock lizards (Aragón et al. 2004). However, within areas of overlap use of space by competing individuals may generally differ, each male individually exploiting different locations to a greater extent than other males (Aragón et al. 2006). In fact, the distances to activity centers (i.e., the most used locations based on a density function of sightings) play an important

role in the level of agonistic interactions of rock lizards (Aragón et al. 2006) and other lizard species (Stamps and Krishnan 1994; Husak and Fox 2003). In these cases, it might pay to recognize the holders of particular locations to minimize costly agonistic encounters. In fact, given the spatial overlap between individuals, the chance of invading occupied locations may be even higher than in a strict territorial system. Therefore, we conclude that scent matching could contribute to modulate intrasexual aggression among male rock lizard even if they have nonexclusive home ranges, reducing costs of agonistic interactions.

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