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Beyond ‘nasty neighbours’ and ‘dear enemies’? Individual recognition by scent marks in a lizard (*Podarcis hispanica*)

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True individual recognition (TIR), the ability to recognize conspecific individuals on the basis of identity cues, is required for the evolution of several social traits (e.g. the maintenance of dominance hierarchies). However, knowledge about the distribution and functional significance of TIR is scant in some vertebrate groups, such as reptiles. In this study we used a functional modification of a habituation–dishabituation paradigm to investigate the existence and adaptive significance of TIR in a territorial lizard (*Podarcis hispanica*, Lacertidae). Males discriminated between individual rivals of similar characteristics (e.g. size, weight, familiarity) solely on the basis of their scent marks. Males also remembered the spatial location of scent marks and subsequently behaved more aggressively towards rival males that consistently marked in the core than on the periphery of their experimental terrarium. Together, these results suggest that, in this species, scent marks function to identify the potential threat posed by each individual neighbour, allowing resident males to allocate their aggressive behaviour accordingly. Our findings challenge the simplistic and commonly held view that ‘dear enemy’ phenomena in lizards are exclusively based on familiarity asymmetries, and support an alternative threat level hypothesis in which TIR may be more important than previously acknowledged.

Keywords: dear enemy; Iberian wall lizard; individual recognition; *Podarcis hispanica*; scent mark; territoriality

The ability to recognize conspecific class characteristics such as sex, reproductive status, social rank, kinship, group membership or familiarity, has long been acknowledged as one of the cornerstones of complex animal societies (Bradbury & Vehrencamp 1998; Wyatt 2003). Such recognition mechanisms, which in practice may allow organisms to discriminate between two conspecific individuals, are usually referred to as ‘individual recognition’ mechanisms. However, the recognition of conspecifics as belonging to classes containing more than one individual, termed ‘class categorization’ or ‘social recognition’ (Gheusi et al. 1997; Mateo 2004), is not the same as ‘true’ individual recognition (TIR): the ability to discriminate between two individuals on the basis of individual identity cues (Thom & Hurst 2004; see also Tibbetts et al. 2008 and Steiger & Müller 2008 for a recent discussion). TIR is paramount to many social systems by, for example, allowing pair bonding through the recognition of long-term mating partners (Carter & Roberts 1997), fledgling or chick recognition (Clark et al. 2006; Draganoiu et al. 2006), or mediating certain social phenomena such as pregnancy block (i.e. ‘Bruce effect’) or the ‘Coolidge effect’ in the context of mate choice (Wyatt 2003).

Even though theory predicts the widespread occurrence of TIR in many taxa, the fact is that TIR has proven notoriously elusive to empirical demonstration in most animal groups (Halpin 1986; Wyatt 2003; D’Etorre & Heinze 2005; Brennan & Kendrick 2006). True individual recognition will usually require the assessment of multiple stimuli, and its underlying mechanisms are thus bound to be more complex and sophisticated than those mediating social recognition (Thom & Hurst 2004). Moreover, it is often difficult to distinguish between discrimination based on general class features of the signals or cues involved in a given discrimination task (e.g. differences in familiarity) as opposed to specific identity features (Thom & Hurst

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2004). While TIR has been relatively well studied in birds (Stoddard et al. 1991; Weary & Krebs 1992; McGregor 1993; Aubin et al. 2000), mammals (i.e. mostly rodents: Johnston 2003; Brennan & Kendrick 2006; Brennan & Zufall 2006; primates: Cheney & Seyfarth 1988) and some fish species (Griffiths & Ward 2006), information from reptiles is practically nonexistent (LaDage & Ferkin 2006).

The social and/or mating system often determines the type of recognition mechanism expected in any given species. Lizard studies have traditionally stressed the advantages of rival discrimination (i.e. 'dear enemy' recognition) in those species that actively defend their territories against the repeated intrusions of rival males, whereby both the energetic costs of territory defence and the risks of suffering injuries can be minimized by reducing aggression towards familiar neighbours (e.g. Stamps & Krishnan 1998; Whiting 1999; López & Martín 2001, 2002). Although available evidence strongly hints at the existence of TIR in some lizards (e.g. Whiting 1999; Husak & Fox 2003a), most of the studies that have reported social familiarity recognition (i.e. neighbour–stranger discrimination) have not specifically tested for its existence (e.g. Glinski & Krekorian 1985; Olsson 1994; Whiting 1999; Font & Desfilis 2002; López & Martín 2002).

Moreover, although the assumption that the relative threat posed by a rival is proportional to its degree of familiarity is likely to hold in many species (Temeles 1994), the idea that potential threat and familiarity are related overlooks some instances where this assumption may not hold (e.g. Müller & Manser 2007). For example, the threat posed by different familiar rivals is bound to vary, regardless of familiarity, according to their competitive potential or to the degree of territory overlap with the owner (Switzer et al. 2001). At least in some of these cases, evolution should favour males capable of recognizing individual rivals and hence allocate their efforts against territorial intrusions according to the specific threat posed by each rival.

Our aim in this study was to investigate the existence and functional significance of TIR via chemical cues in a lizard. *Podarcis hispanica* is a territorial lacertid lizard: males actively defend areas around themselves and nearby females, and agonistic encounters are very frequent during the breeding season (López & Martín 2001; E. Font, unpublished data). Numerous studies have shown that chemical stimuli allow recognition of sex, reproductive status, familiarity, relatedness and even size-specific information in squamates (e.g. Cooper 1998; Pianka & Vitt 2003; Shine et al. 2003; Labra 2006). In particular, chemical stimuli are used by *P. hispanica* males to assess familiarity (Font & Desfilis 2002), female reproductive status (Cooper & Pérez-Mellado 2002), rival competitive potential, and possibly even territory quality (Carazo et al. 2007). We used a functional modification of a typical habituation–dishabituation procedure in which subject males were simultaneously challenged with scent marks from two unfamiliar rival males of similar class characteristics, but we placed individual rivals' scent marks so that, across habituation trials, each rival male always marked either at the periphery or at the core of the owner's experimental terrarium (i.e. different threat levels; Schradin 2004). Following habituation trials, we conducted one dishabituation trial in which we reversed the position of rivals' scent marks. This kind of correct–incorrect boundary paradigm has been previously used to study territorial TIR in several bird species (e.g. Falls 1982; McGregor 1993). We predicted that, if males are capable of TIR on the basis of scent marks and if they are able to associate chemical identity cues with the specific spatial location of scent marks, then subject males' chemosensory exploration rates should increase during dishabituation trials. Finally, we staged agonistic encounters between each resident male and its two scent mark donors to investigate whether the spatial location of scent marks within the resident male's terrarium affects aggression towards donor intruders. Such a result would suggest that, beyond mediating TIR, scent marks function to assess the threat level imposed by different familiar intruding males.

METHODS

The Iberian wall lizard, *P. hispanica* (Squamata: Lacertidae), is a diurnal heliothermic lizard found mainly in rocky habitats throughout the Iberian Peninsula, the Mediterranean coast of France and northern Africa. Subjects were caught by noosing in seven locations around the city of Valencia, Spain. Lizards were collected during the middle of the reproductive season in this area (April–May), during which agonistic interactions are usually intense in the field. However, we surveyed natural lizard populations to ensure that, at the time of capture and during experimentation, courtship, mating and agonistic behaviours were readily observed in the field. We collected adult male lizards (snout–vent length, SVL, $\overline{X} \pm \text{SEM} = 54.7 \pm 0.6$ mm) in early May 2007. In the laboratory, lizards were haphazardly assigned as subject or scent mark donor males and thereafter grouped so that subject males and scent mark donors participating in the same trial were always from locations far apart, to ensure individuals had not been in previous contact. Donor males ($N = 20$) were individually housed in glass terraria (50 × 25 cm and 30 cm high) with a gravel substrate, a water dish, a shelter and a construction brick (11 × 11 cm and 3 cm high) for basking, over which a 40 W incandescent lamp was suspended. All lizards were additionally provided with full spectrum light (Reptistar, Sylvania, Danvers, U.S.A.) for 1.5 h on a daily basis (1200–1330 hours), and during agonistic encounters (see below). Subject males ($N = 10$) were housed in large experimental transparent glass terraria (70 × 30 cm and 40 cm high) that were divided in half by a white opaque sliding plastic partition. All but the front wall of experimental terraria were covered with brown cardboard paper on the outside. The frontal wall was left uncovered to allow filming during agonistic encounters (see below). Subject lizards were confined to one-half of the experimental terraria (i.e. 'core' side), with brown carpeting as a substrate, a water dish, a shelter and a brick (11 × 11 cm and 3 cm high) for basking placed under a 40 W incandescent lamp, and were given access to the other side (i.e. 'periphery' side) only during trials.

Peripheral sides were lined with clean filter paper that was replaced at the end of each trial, also had a brick (11 × 11 cm and 3 cm high) for basking under a 40 W incandescent lamp, and were otherwise visually equivalent to 'core' sides. Terraria were held in a temperature-controlled room at ambient humidity. The temperature and light: dark cycle were set to mimic average field conditions (18 °C at night, 25 °C during the day, 14.5: 9.5 h). Lizards were fed *Tenebrio molitor* larvae dusted with vitamins (Nekton MSA, Pforzheim, Germany) three times weekly. Water was permanently available in water dishes.

Experimental Design

Habituation–dishabituation procedure

Each subject lizard was assigned two size-matched male scent mark donors (± 1 mm) of similar size to the subject male (± 3 mm). Scent marks were collected by gluing (with BluTack) one piece of filter paper (10 × 10 m) to the surface of each male donor's basking brick and leaving it for 20 h before each trial. All trials began 10 days after capture from the field, once lizards had habituated to holding conditions and to the presence of the researcher (i.e. fed normally and did not flee or hide upon detecting the researcher's presence). All trials took place between 1100 and 1500 hours, when lizards are usually active in the field during this time of the year. Immediately before trials, the water dish was removed from the core side and filter paper pieces bearing scent marks from donor males were introduced as described in Fig. 1. Briefly, during habituation trials lizards were presented with three pieces of filter paper bearing scent marks from 'core' donors in the 'core' side (i.e. one piece of filter paper (10 × 5 cm) on their basking brick and one piece (5 × 5 cm) on each of two corners) and with three pieces of filter paper bearing scent marks from 'periphery' donors in the 'periphery' side (i.e. one piece of filter paper (10 × 5 cm) on the basking rock and one piece (5 × 5 cm) on each of two corners); the location of marked papers was reversed during the final dishabituation trial. Once the filter papers were in place, the plastic partition was removed so that subject lizards had access to both sides of the experimental terrarium. All behavioural recording was conducted by the same observer. Trials began once subject lizards had come into contact with the filter papers bearing scent marks from both donors, and lasted for 10 min. After the trials, lizards were allowed an additional hour to explore the terrarium before we removed all the pieces of filter paper and restored the plastic partition to confine subjects to the 'core' side of the experimental terraria. During trials, we used a laptop computer equipped with event-recording software (J. Watcher 0.9 event-recorder; D. T. Blumstein, C. S. Evans & J.C. Daniel, http://www.eeb.ucla.edu/Faculty/Blumstein danpubs.html) to record how long lizards spent in each side of the experimental terrarium, how long they spent in locomotion, and the number of tongue-flicks directed to marked and unmarked substrates in each side, which allowed us to calculate tongue-flick rates. Tongue-flicks function to sample chemical stimuli for vomerolfaction, which mediates complex social communication in lizards, and tongue-flick rates are frequently used as an index of chemosensory exploratory behaviour (Burghardt 1970; Cooper 1998; Font & Desfilis 2002). To ensure that behavioural recording was done following a blind procedure, the day on which the dishabituation was conducted was randomly determined by a researcher different from the one recording behaviours. Thus, the researcher that conducted behavioural recordings was unaware of whether recordings corresponded to a habituation or dishabituation trial. Owing to logistic constraints, we had to divide experimentation into two consecutive replicate blocks of trials ($N = 5$ each). Thus, lizards were randomly divided into two groups so that half the subject males had their dishabituation on day 8 and the other half on day 5. Graphical exploration of data suggested that there were no differences in tongue-flick rates of subject males after day 4, nor in tongue-flick rates to dishabituation trials between animals that had their dishabituation on day 5 versus day 8. However, we included 'block' (i.e. dishabituation day) as a fixed factor in our statistical analyses (see below).

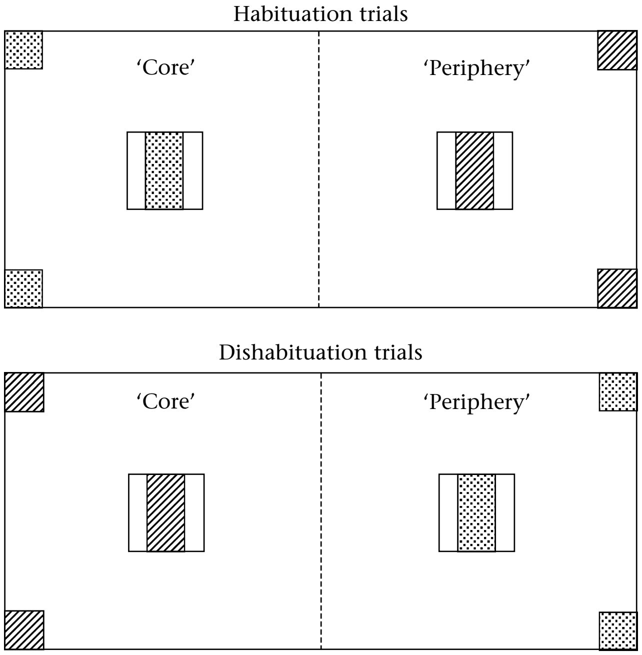

Figure 1. Experimental terrarium. During habituation/dishabituation trials subject lizards were given access to both sides of the experimental terrarium and were presented with filter paper bearing scent marks from 'core' donors (░) at the 'core' of their territory (one 10 × 5 cm piece of filter paper on their basking brick and one 5 × 5 cm piece on each of the corners) and filter paper bearing scent marks from 'periphery' donors (▨) at the 'periphery' of their territory (one 10 × 5 cm piece of filter paper on the basking brick and one 5 × 5 cm piece on each of the corners).

Male–male contests

Contests between resident males and scent mark donors were held on 2 consecutive days following the dishabituation trial. Thus, we held a total of 20 staged contests (i.e. two for each resident male). Immediately before the contests, we removed the plastic partition so that subject males had access to both sides of the experimental terrarium, which had no chemical stimuli other than those left by the resident male. The intruder male was then gently placed on the side opposite to that occupied by the resident male at that moment. The order of presentation of donor males (i.e. ‘core’ versus ‘periphery’ donors) was counterbalanced across lizards. Trials were initiated with the first locomotion bout, which often corresponded to the resident lizard’s approaching the intruding male, and lasted 5 min, during which time they were filmed using a digital video camera (Canon XL1). We established an intervention rule so that contests that drew blood were immediately interrupted, but this did not happen in any of the staged contests. Contests were later played back (following a blind protocol), during which we continuously recorded the behaviours listed in Table 1. Each behaviour was assigned a score (adapted from Whiting 1999) so that, in each contest, we were able to calculate an aggression index as the sum of the aggression scores associated with each contestant’s behaviour. Thus, the aggression index provided a quantitative estimate of the level of aggression of resident and intruder males during staged contests. Although there are no data regarding male territories in this species, home ranges of *P. hispanica* are much larger than our experimental terraria (e.g. Diego-Rasilla & Pérez-Mellado 2003). Working with artificial territories that are smaller than natural territories has the advantage of ensuring active territorial defence by resident males. In fact, preliminary experiments confirmed that, under our experimental conditions, male lizards actively defend their terrarium against intruders within ca. 7 days from being captured and housed in the laboratory.

Ethical Note

Animal care and experimentation were conducted according to guidelines provided by the Association for the Study of Animal Behaviour, the Animal Behaviour Society and the American Society of Ichthyologists and Herpetologists, and was approved by the University of Valencia’s Ethics Committee. The lizards used in this study were caught under permit from the Generalitat Valenciana to E.F. No deaths occurred, and lizards were healthy during habituation/dishabituation experiments and after staged contests. All but three of the 20 staged contests (Table 2) escalated to full-blown aggressive behaviour where bites and bite-holds were very frequent. However, the size of experimental terraria enabled lizards to flee rapidly from attacking rivals, so bite-holds did not last long (i.e. <5 s). Lizards were thoroughly examined after staged contests to confirm the absence of any injuries, and two lizards that had minor bruises (i.e. minor scratches in the skin that did not draw blood) were treated with topical antibiotics (Terramicine) until released back to the field. Before releasing them at their capture sites, we closely monitored lizards in the laboratory for 10 days after the end of experimentation. All lizards basked, drank and ate normally during this period, which also served to ensure that the two individual lizards with minor bruises were completely healed before their release. Prior to being released, lizards were marked by toe clipping to avoid recapture. Details of how and why we conducted toe clipping can be found in Carazo et al. (2007). Briefly, we clipped a maximum of two toes by cutting the distal two-thirds with a pair of sharp surgical scissors. We clipped only one toe per limb and always selected small digits that did not usually draw blood. After clipping, injuries were cleaned with alcohol and treated with Terramicine to avoid future infections. Lizards that presented natural toe loss were not toe clipped.

Table 1. Aggressive behaviours and associated aggressive scores

Score	Behaviour
0	No response
1	Approach
2	Chase
3	Display
4	Lunge
5	Bite
6	Bite-hold

Scores used to construct aggression indexes measuring the level of aggression of resident and intruder males during contests (adapted from Whiting 1999). ‘Display’ includes any single occurrence or combination of any of the aggressive displays shown by *Podarcis hispanica* males during agonistic encounters with other males (i.e. throat extension, trunk compression, back arching and gape; Verbeek 1972). Lunges occurred when a male hit a rival with its mouth closed and could occur in conjunction with ‘display’. In ‘bite-hold’, a male bit a rival but held his grip for at least 2 s, as opposed to ordinary bites of much shorter duration (i.e. < 1 s).

Statistical Analyses

To test for habituation, dishabituation and possible differences in chemosensory exploration in ‘core’ and ‘periphery’ sides, we compared tongue-flick rates of lizards in both sides of the experimental terrarium between the first three habituation trials, the last habituation trial, and the dishabituation trial (Gheusi et al. 1997; Johnston & Bullock 2001; Johnston 2003; Mateo 2006). Graphical exploration showed that data could not be assumed to be normally distributed. We therefore rank-transformed data and fitted a partly nested three-factor repeated measures robust ANOVA model (Quinn & Keough 2002) using SPSS 11.5 (SPSS Inc., Chicago, IL, U.S.A.) with ‘block’ (i.e. lizards that had their dishabituation day on day 5 versus day 8; see above), ‘side’ (i.e. ‘core’ versus ‘periphery’) and ‘treatment day’ (i.e. day 1, day 2, day 3, last habituation trial and dishabituation trial) as fixed factors. We used the same analysis to test for ‘block’, ‘treatment day’ and/or ‘side’ effects on both the total time subjects spent on each side of the experimental terrarium and time spent in locomotion while in each side. We used Mauchly’s test to test the sphericity assumption and adjusted univariate *F* ratios (Greenhouse–Geisser) and provide multivariate ANOVA statistics (Pillai trace) when sphericity could not be safely assumed (Quinn & Keough 2002). Where significant treatment effects were found, we performed planned contrasts between tongue-flick rates shown during habituation versus the dishabituation trials. To control

Table 2. Latency to first aggressive behaviour and aggression indexes

Resident	Intruder	Latency (s)	Approaches	Displays	Lunges	Bites	Bite-holds	Resident's index	Intruder's index
1	'Core' donor	128	12–0	3–0	21–0	16–0	4–1	165	5
	'Periphery' donor	160	6–0	4–0	14–0	19–1	6–1	162	9
2	'Core' donor	64	3–1	5–1	5–0	3–0	0–0	40	3
	'Periphery' donor	90	7–0	12–2	15–1	7–4	5–3	129	38
3	'Core' donor	7	4–0	4–0	23–0	7–0	1–1	114	5
	'Periphery' donor	6	4–0	3–0	16–0	4–0	0–0	74	0
4	'Core' donor	30	14–0	5–0	18–0	12–1	2–0	136	4
	'Periphery' donor	3	7–0	3–0	12–0	9–0	0–0	85	0
5	'Core' donor	41	2–0	1–0	4–1	0–3	4–0	36	15
	'Periphery' donor	288	2–0	0–1	1–0	1–1	1–0	14	6
6	'Core' donor	23	1–1	3–6	1–14	1–8	0–0	14	87
	'Periphery' donor	240	1–1	1–1	0–0	0–0	0–0	3	3
7	'Core' donor	38	3–1	2–0	13–0	10–0	0–0	86	1
	'Periphery' donor	–	0–0	0–0	0–0	0–0	0–0	0	0
8	'Core' donor	15	11–0	13–1	7–0	7–0	1–0	91	2
	'Periphery' donor	170	3–0	6–2	7–2	4–0	1–0	57	10
9	'Core' donor	60	20–1	25–2	30–2	12–6	8–0	248	35
	'Periphery' donor	43	12–0	17–4	29–4	10–3	11–1	228	37
10	'Core' donor	25	0–2	2–2	4–18	2–6	0–1	24	89
	'Periphery' donor	–	0–1	0–2	0–2	0–0	0–0	0	11

Raw data for latency to first aggressive behaviour, total frequency of each aggressive behaviour recorded during contests (see Table 1) and total aggression scores for resident and intruder males. Note that data for the frequency of aggressive behaviours are provided for both residents (first) and intruders (second) in the same column.

for the possible existence of differences between 'core' and 'periphery' scent mark donors in variables that have been previously related to competitive potential in this and other lizard species (Tokarz 1985; Olsson 1992; López & Martín 2001), we checked for both average (i.e. overall) and paired differences (i.e. differences between 'core' and 'periphery' scent mark donors taking part in the same trial) in SVL, head width and weight. Graphical exploration of the data suggested that the data were not normally distributed, so we used nonparametric statistics. We used Mann–Whitney tests to evaluate the existence of average differences and the Wilcoxon signed-ranks test to evaluate the existence of paired differences (Siegel & Castellan 1989). We used a sign test (Siegel & Castellan 1989) on the latency to first aggressive behaviour (i.e. any of those included in Table 1) and aggression index data from staged contests to assess whether subject males escalated first and/or were more aggressive to 'core' donors than to 'periphery' donors (Whiting 1999). To evaluate the possible effect of intruder behaviour on resident aggressive behaviour during contests, we also used a sign test to test for differences in the aggressive behaviour (i.e. aggressive indexes) shown towards resident males by 'core' and 'periphery' intruders. We further performed a Spearman rank correlation to test for the existence of a significant correlation between the aggressive behaviour of resident and intruder males taking part in the same staged encounter. All results reported are two tailed.

RESULTS

We found no significant differences between 'core' and 'periphery' scent mark donors in average SVL ('core' donors: $\overline{X} \pm \text{SEM} = 54.4 \pm 0.70$ mm; 'periphery' donors: 54.8 ± 0.95 mm; Mann–Whitney U test: $U = 49.5$, $N_1 = 5$, $N_2 = 5$, $P = 0.970$), weight ('core' donors: $\overline{X} \pm \text{SEM} = 3.95 \pm 0.20$ g; 'periphery' donors: 3.73 ± 0.20 g; $U = 33.5$, $N_1 = 5$, $N_2 = 5$, $P = 0.356$) or head width ('core' donors: $\overline{X} \pm \text{SEM} = 9.25 \pm 0.16$ mm; 'periphery' donors: 9.11 ± 0.17 mm; $U = 27$, $N_1 = 5$, $N_2 = 5$, $P = 0.141$). Similarly, we found no significant differences in SVL (Wilcoxon signed-rank test: $T^+ = 20.5$, $N = 10$, $P > 0.5$), weight ($T^+ = 39$, $N = 10$, $P = 0.275$) or head width ($T^+ = 37$, $N = 10$, $P = 0.375$) between 'core' and 'periphery' pairs of lizards acting as scent mark donors in the same trial.

ANOVA analysis revealed habituation of tongue-flick rates over the first few days of testing, followed by a rebound to rates similar to those observed on day 2, when the location of scent marks from the two donors was reversed (Fig. 2). Habituation/dishabituation rates were not significantly different in the 'core' versus 'periphery' side of the experimental terrarium or between blocks of lizards. Our analysis of total tongue-flick rates yielded a significant effect of 'treatment day' ($F_{4,32} = 40.984$, $P < 0.001$) but not of 'side' ($F_{1,32} = 0.043$, $P = 0.841$) nor of 'block' ($F_{1,8} = 5.122$, $P = 0.053$). Planned comparisons showed that total tongue-flick rates during the dishabituation trial were (1) significantly lower than in the first trial ($F_{1,8} = 79.195$, $P < 0.001$), (2) not different from those in the second ($F_{1,8} = 3.220$, $P = 0.110$) or in the third trial ($F_{1,8} = 4.002$, $P = 0.080$) and (3) significantly higher than tongue-flick rates during the last habituation trial ($F_{1,8} = 28.391$, $P = 0.001$).

Breaking up this analysis into tongue-flick rates while directly in contact with marked versus unmarked substrates did not modify the results obtained (Fig. 3). The analysis of tongue-flick rates at marked sites showed a significant effect of 'treatment day' ($F_{4,32} = 9.996$, $P < 0.001$) but not of 'side' ($F_{1,32} = 0.002$, $P = 0.968$). In this analysis, we obtained a significant 'block' effect ($F_{1,8} = 11.359$, $P = 0.010$). Planned

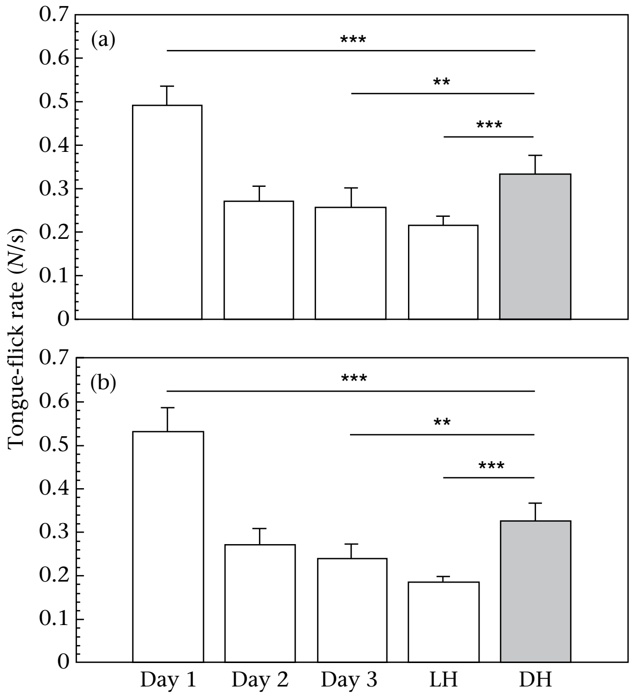

Figure 2. Tongue-flick rates across trials in (a) the 'core' side of the experimental terrarium and (b) the 'periphery' side of the experimental terrarium. Note that the last habituation day (LH) and the dishabituation day (DH) were different for each of the two blocks of lizards (see Methods for details). Bar plots show data before rank transformation for the robust ANOVA. Asterisks indicate statistically significant planned contrasts (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Error bar = 1 SEM.

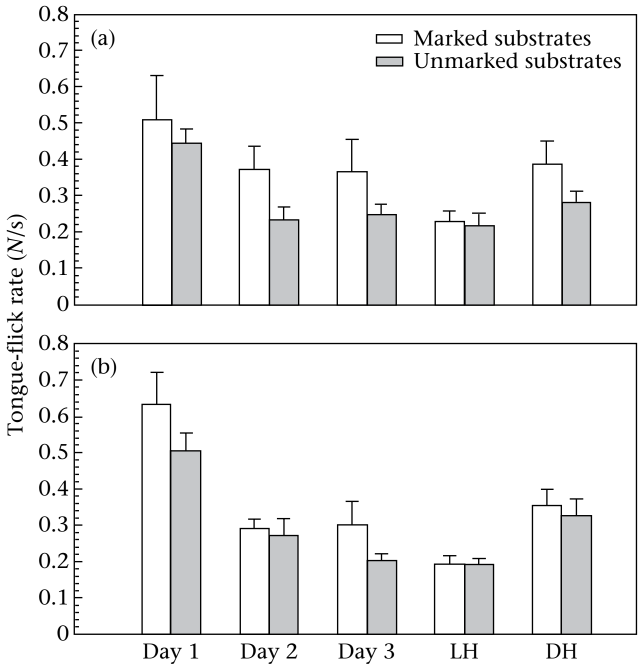

Figure 3. Tongue-flick rates across trials while at marked (i.e. filter paper squares bearing scent marks from 'donor' males) versus unmarked (i.e. the remaining surfaces of the experimental terrarium) substrates in (a) the 'core' side of the experimental terrarium and (b) the 'periphery' side of the experimental terrarium. Bar plots show data before rank transformation for the robust ANOVA. Error bar = 1 SEM. LH: last habituation day; DH: dishabituation day.

comparisons showed that, in marked substrates, tongue-flick rates during the dishabituation trial were: (1) significantly lower than in the first trial ($F_{1,8} = 7.917$, $P = 0.023$), (2) not different from those in the second ($F_{1,8} = 1.067$, $P = 0.332$) or in the third trial ($F_{1,8} = 4.549$, $P = 0.066$) and (3) significantly higher than tongue-flick rates during the last habituation trial ($F_{1,8} = 26.558$, $P = 0.001$). Similarly, the analysis of tongue-flick rates at unmarked sites revealed a significant effect of 'treatment day' ($F_{4,32} = 22.982$, $P < 0.001$) and a significant 'block' effect ($F_{1,8} = 8.270$, $P = 0.021$), but no 'side' effects ($F_{1,32} = 0.006$, $P = 0.940$). Planned comparisons showed that tongue-flick rates in unmarked substrates during the dishabituation trial were: (1) significantly lower than in the first trial ($F_{1,8} = 49.038$, $P < 0.001$), (2) not different from those in the second ($F_{1,8} = 1.711$, $P = 0.227$) or in the third trial ($F_{1,8} = 1.230$, $P = 0.300$) and (3) significantly higher than tongue-flick rates during the last habituation trial ($F_{1,8} = 10.814$, $P = 0.011$).

Our ANOVA analysis revealed that subjects spent significantly more time and showed more locomotion in the 'periphery' side than in the 'core' side of the experimental terrarium (Fig. 4). The analysis of 'total time' and 'locomotion' both revealed a significant effect of 'side' (time: $F_{1,32} = 11.247$, $P = 0.010$; locomotion: Greenhouse–Geisser: $F_{1,32} = 12.562$, $P = 0.008$; Pillai's trace: $F_{1,32} = 12.562$, $P = 0.008$), but not of 'treatment day' (time: $F_{1,32} = 1.230$, $P = 0.318$; locomotion: Greenhouse–Geisser: $F_{1,32} = 2.104$, $P = 0.142$; Pillai's trace: $F_{1,32} = 4.015$, $P = 0.080$). We found a significant block effect in 'total time' ($F_{1,32} = 11.799$, $P = 0.009$); but not in 'locomotion' ($F_{1,32} = 1.504$, $P = 0.255$).

Of 20 staged contests, 19 escalated to aggressive interactions between contestants; the mean aggression index ± SEM was 85.2 ± 23.6 (Table 2). The mean difference between the resident lizard's aggression indexes against 'core' versus 'periphery' scent mark donors ± SEM was 20.5 ± 14.2. The sign test for paired replicates did not yield significant differences between the latency to first aggressive behaviour towards 'core' versus 'periphery' scent mark donors ($k = 4$, $N = 8$, $P > 0.5$) but showed that subject males were significantly more aggressive towards 'core' donors than towards 'periphery' donors ($k = 9$, $N = 10$, $P = 0.022$). However, we did not find significant differences in the levels of aggression directed towards resident males by 'core' and 'periphery' intruders ($k = 4$, $N = 10$, $P > 0.5$). Furthermore, we did not find a significant correlation between residents' and intruders' aggressive indexes across trials (Spearman rank correlation: $r_S = 0.11$, $N = 20$, $P = 0.644$).

DISCUSSION

True Individual Recognition in Lizards

Although social categorical recognition has been well studied in reptiles (e.g. Glinsky & Krekorian 1985; Bull et al. 1994, 2001; Olsson 1994; Olsson & Shine 1998;

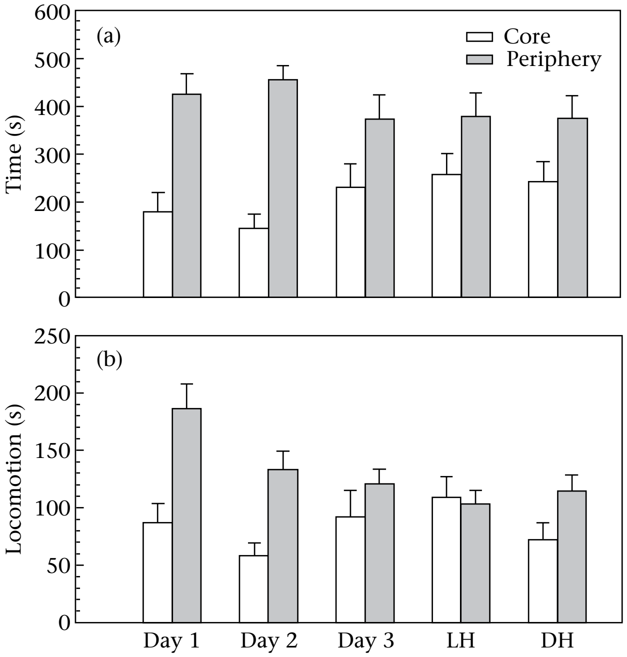

Figure 4. (a) Total time and (b) time spent in locomotion across trials by males while in the 'core' versus the 'periphery' sides of the experimental terrarium. Bar plots show data before rank transformation for the robust ANOVA. Error bar = 1 SEM. LH: last habituation day; DH: dishabituation day.

Whiting 1999; Bee & Gerhardt 2002; Font & Desfilis 2002; Husak & Fox 2003a; López & Martín 2004; Van Dyk & Evans 2007), supportive evidence of TIR is scant. LaDage & Ferkin (2006) recently reported that male leopard geckos, *Eublepharis macularius*, are able to discriminate between two equally familiar females, but the nature of the stimuli involved was not studied. In the present study, we found that male *P. hispanica* lizards rapidly habituated to scent marks placed at specific locations in their experimental terrarium (i.e. 'core' versus 'periphery') by two different rival males with similar class characteristics (i.e. size, weight, familiarity). More importantly, we found that exchanging the position of the scent marks of rival males produced a dishabituation response, as evidenced by significantly higher tongue-flick rates during dishabituation trials. Territorial TIR has often been studied using correct–incorrect boundary paradigms in which residents are shown to increase their response towards signals from displaced familiar neighbours (Falls 1982; McGregor 1993). This kind of evidence has traditionally been considered a litmus test of TIR. However, some authors have questioned the validity of location dependence studies because, in most cases, the response of territorial residents towards displaced neighbours does not differ from their response towards strange males (but see e.g. Falls & Brooks 1975), which could indicate that a neighbour's signals in a novel location are simply perceived as pertaining to an unfamiliar male (Bee & Gerhardt 2002). In our experiment, males behaved more aggressively towards donors that consistently marked in the 'core' than towards males that marked in the 'periphery' of their terrarium, which argues against this possibility. Furthermore, our results indicate that these differences were not due to differences in the aggressive behaviour of donor males. In short, our results strongly suggest the existence of TIR on the basis of scent marks in a lizard.

We did not find differences in the resident's latency to first aggressive behaviour according to whether intruding males were 'core' or 'periphery' scent mark donors, but this result is hardly surprising because, in our experiment, most residents first sampled intruders' scent marks during escalation (i.e. following the first physical contact between the interacting lizards). As lizards had not had previous visual contact with each other, our experimental design precluded the possibility that resident males could visually recognize intruding lizards prior to escalation. Furthermore, the similar latencies to first aggression in contests with 'core' and 'periphery' scent mark donors suggest that resident males were not basing their strategic decision of whether to allocate more or less aggression on visual stimuli that might provide information regarding the competitive potential of intruding lizards.

Unlike tongue-flick rate, the time lizards spent in each side of the experimental terrarium or the amount of locomotion while in each side did not vary in a consistent way during the process of habituation–dishabituation to scent marks. Both these variables can be related to a number of factors, such as exploration or overall activity levels, which need not be directly associated with territorial behaviour. In fact, previous studies have found that, in this species, habituation to scent marks results in a decrease in tongue-flick rates, but not in locomotion or in time spent in marked substrates (Gómez et al. 1993). Furthermore, both of these variables have been shown not to correlate with chemical exploration in territorial contexts (e.g. Carazo et. al. 2007). Alternatively, habituation of patrolling behaviour, including locomotion and time spent in each side, may take longer than habituation of chemoreceptive responses, which seems to be relatively rapid in this species (see Results; Gómez et al. 1993). We also found that lizards spent more time and showed more locomotion while in the 'periphery' side of the experimental terrarium. While it may be tempting to read these results as suggesting that lizards spend more time patrolling the periphery of their territory (i.e. where more encounters with rival males may be expected; Gosling & Roberts 2001), a more likely interpretation is that *P. hispanica* lizards spend more time and invest more time in locomotion in areas with which they are less familiar (Gómez et al. 1993).

Spatial Memory and Learning in Lizards

Our experimental design provides some insight into the nature of the information that *P. hispanica* males may associate with individual identity namely, the spatial location of scent marks. With few exceptions (e.g. food-storing birds; Shettleworth 1998), the type of spatial problems that animals face in their natural habitats are essentially very similar across vertebrates (Holtzman 1998). However, studies of spatial learning and memory have focused on birds and mammals (e.g. Bingman et al. 1990; Healy 1992; Sherry et al. 1992). The available evidence suggests that snakes and lizards are capable of learning the spatial location of food items or shelters inside their home range (Burghardt 1977; Holtzman 1998; Day et al. 1999, 2003; Schall 2000; Zuri & Bull 2000; Punzo & Madragon 2002; E. Font & E. Desfilis, unpublished data), but there seems to be a consensus that reptiles require many training trials to learn simple spatial tasks under laboratory conditions (Burghardt 1977; Holtzman 1998; Schall 2000). In this study, lizards learned the spatial location of scent marks in only four to seven trials, which argues against this commonly held assumption. The former view is probably an artefact of inadequate non-naturalistic experimental designs that require, for example, excessive handling of subjects or the use of learning paradigms that have been designed for other vertebrate groups (e.g. mammals), and could thus be inappropriate for reptiles (Burghardt 1977; Holtzman 1998). As a corollary, our experimental set-up imposed intertrial intervals of 23 h, and subject males responded to the consistent location of scent marks, and not just to the last location in which they were found (see below). This strongly suggests that the spatial memory underlying this learning task in *P. hispanica* may be 'long-term' memory (Healy 1992; Shettleworth 1998; see also Punzo 2002; Labra et al. 2004).

Beyond 'Nasty Neighbours' and 'Dear Enemies'

Many territorial species, including most territorial lizards for which information is available (Glinsky & Krekorian 1985; Qualls & Jaeger 1991; Fox & Baird 1992; Whiting 1999; but see Husak & Fox 2003b), show 'dear enemy' phenomena: competing neighbours fight to establish their territories and then settle a truce in which residents are typically less aggressive towards familiar neighbours than towards nonresident male strangers. Two hypotheses have been put forward to explain 'dear enemy' phenomena. The familiarity degree hypothesis (Ydenberg et al. 1988) states that the escalation level of territorial interactions will depend on the degree of familiarity between contestants, which in turn has been used by some authors to suggest that animals may fight to learn about each other (Getty 1989). However, recent findings show that reduced aggression towards neighbours may disappear when resources are limited (i.e. females; Leiser 2003) and, most importantly, that males of some species are consistently more aggressive towards neighbours than towards strangers ('nasty neighbours', e.g. Ferkin 1988; Temeles 1994; Müller & Manser 2007). Alternative to the familiarity hypothesis, the threat level hypothesis states that neighbours and strangers may reflect different threat levels (e.g. if they compete for different resources) that may differ in either direction (Temeles 1994). Hence, although resident territory owners generally stand to lose more against strangers (e.g. floaters) than against neighbours, this situation may reverse (i.e. Leiser 2003) so that neighbours are met with greater aggression than unfamiliar males (Ferkin 1988; Temeles 1994; Müller & Manser 2007). In either of these scenarios, residents that are able to distinguish between familiar and unfamiliar males will benefit from being able to allocate their aggressive behaviour according to which type of rival poses a greater threat (i.e. 'dear enemies' versus 'nasty neighbours'). This view, that territorial behaviour is mediated by social recognition of familiar versus unfamiliar rivals, is widespread in lizard studies (e.g. Glinsky & Krekorian 1985; Font & Desfilis 2002; Van Dyk & Evans 2007; but see Husak & Fox 2003a).

Although the latter hypothesis probably holds true for many species, asymmetries in threat levels need not always covary with existing asymmetries in familiarity. For example, male striped mice, *Rhabdomys pumilio*, are more aggressive towards male strangers met near the nest than at territory boundaries (Schradin 2004). Resident fiddler crabs, *Uca pugilator*, are more aggressive towards close neighbours of similar size, which are likely to pose a greater threat than smaller familiar rivals or neighbours further away from their burrow (Pratt & McLain 2006). Male red-winged blackbirds, *Agelaius phoeniceus*, increase their vigilance and aggression towards neighbours that have recently intruded into their territory or are more likely to achieve extrapair fertilizations (Olendorf et al. 2004). Similarly, it has long been known that 'dear enemy' phenomena usually disappear if neighbours are experimentally displaced from their usual boundary and placed at a new boundary, thus reflecting a potentially greater threat (e.g. Falls 1982; McGregor 1993). Theoretical and empirical data hence predict that an optimum allocation of territorial defence (e.g. aggressive behaviour) may depend on the ability to determine the relative threat posed by each rival male in each specific context. A correct and precise evaluation in this sense will crucially depend on TIR in those instances where social recognition mechanisms (e.g. neighbour/stranger discrimination) are insufficient to track the specific and potentially changing threat imposed by each rival (e.g. Olendorf et al. 2004).

We have provided strong evidence that this may be the case in *P. hispanica*. Scent marks, usually perceived by the receiver in the absence of the signaller, are currently viewed as signals that mediate territorial behaviour by allowing competitor assessment, and are probably among the most common social signals in terrestrial vertebrates (Gosling & Roberts 2001). In mammals, territorial marking and countermarking by scent marks represents an excellent functional assay providing invaluable insight into the mechanisms and functional significance of various recognition systems, including TIR (Hurst & Beynon 2004; Thom & Hurst 2004; Brennan & Kendrick 2006). Scent marks are equally ubiquitous in lizards, where many species have multiple epidermal glands (i.e. femoral or precloacal pores) that produce waxy chemical secretions that can be smeared on surfaces during locomotion, and that are apparently responsible for many of their chemical social discrimination abilities. For example, recent evidence suggests that scent marks allow assessment of the competitive potential of rivals and even territory quality in some species (Labra 2006; Martins et al. 2006; Carazo et al. 2007), suggesting they may play an important role in territorial behaviour.

In our study, subjects remembered the position of individual scent marks in their terrarium and were significantly more aggressive towards donor males that had consistently marked at the 'core' than donor males that had consistently marked at the 'periphery' of their territory. This happened even though scent mark position was reversed in the last (i.e. dishabituation) trial before any agonistic encounters, which suggests that subject males did not attend to this temporal change in location. Most previous studies of territorial TIR have focused on temporal changes in the location of radiated signals (i.e. acoustic, electrical or seismic), where the location of the sender is inferred on the basis of intrinsic properties of the broadcast signal through a process known as 'ranging' (McGregor 1993; Bradbury & Vehrencamp 1998). In contrast, scent marks inform of the exact position of the signal, but provide no information about the location of the sender when the signal is received. Hence, scent marks will convey useful information about the approximate location of neighbours (e.g. territory size, location of boundaries, degree of territory overlap) to the extent that they are repeatedly encountered at the same sites, and receivers can be expected to base their behaviour on the consistent location of scent marks. Therefore, intruders that consistently mark at the core of a resident male's territory are likely to represent a greater threat than males that usually mark at the periphery (e.g. Schradin 2004; Pratt & McLain 2006). In summary, we suggest that lizards use a combination of scent marks' intrinsic (i.e. chemical identity cues allowing TIR) and extrinsic properties (i.e. spatial location within their territory) to assess the relative threat posed by each neighbouring male, and allocate their aggressive behaviour accordingly. Our results support the notion that territorial defence in lizards may best be explained by a general threat level hypothesis that points to TIR as an underlying mechanism that may be more widespread and important than previously suspected.

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