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Chemosensory assessment of rival competitive ability and scent-mark function in a lizard, *Podarcis hispanica*

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Recent studies have stressed the role of scent marks as signals potentially mediating competitor assessment. According to this view, receivers may use scent marks to derive information about the costs of exploiting a given area, but few studies have directly addressed this hypothesis. One of its main predictions is that scent marks should reflect a signaller's competitive ability. We simulated the situation faced by an intruding male when entering the scent-marked territories of rival males of varying competitive ability to test predictions about the role of scent marks in a lizard, *Podarcis hispanica*. We report that males were attracted to areas marked by males of similar or higher competitive ability (i.e. larger size), but not to areas scent marked by males of lower competitive ability, and that this preference disappeared towards the end of the breeding season. Our results show that (1) male lizards can assess rival competitive ability (i.e. rival size) on the basis of scent marks alone, (2) scent marks do not function as chemical barriers to deter intruders, and (3) male response to marked areas varies throughout the breeding season, suggesting a shift in the cost-to-benefit balance of entering a scent-marked area. We propose that male assessment of rival competitive ability may function as an indirect assessment mechanism of territory resource quality in this species, and thus that scent marks may convey information not only about costs but also about the benefits of exploiting a scent-marked area.

Keywords: assessment; chemical communication; Iberian wall lizard; *Podarcis hispanica*; resource quality; resource-holding potential; scent marks; seasonal variation; territory marking

Probably amongst the most ubiquitous social signals in terrestrial vertebrates, scent marks are peculiar in that the usually high costs of marking an area cannot be bypassed (Gosling & Roberts 2001). Perhaps because of these unavoidable costs, scent marks have been traditionally considered as 'territorial markers', a part of the signaller's extended phenotype which is functional in keeping out intruders. However, the finding that individuals of several species are not only unhindered by the presence of scent marks, but actively seek and explore scent-marked territories, led researchers to reconsider their function (Gosling 1982). Scent marks are currently viewed as signals that function mainly to mediate competitor assessment by conveying the costs of entering a scent-marked area (Gosling & Roberts 2001). An obvious prediction that arises from this assumption is that, at least in territorial or dominance-based social systems, scent marks should convey information about the signaller's competitive ability (Gosling & Roberts 2001; Hurst & Beynon 2004).

The outcome and escalation level of contests are usually determined by existing asymmetries in competitive ability, and thus the assessment of asymmetries in resource-holding potential is a crucial aspect of animal contests mediated by a wide variety of signals (e.g. Bradbury & Vehrencamp 1998). Among the latter, scent marks are peculiar in allowing the transfer of information in the absence of the signaller. Therefore, males that are capable of using scent marks to assess a rival's competitive ability will have the opportunity to avoid the costs of encountering a resident male. This advantage is likely to hold in any polygynous mating system where males defend females, or resources attractive to females, and male–male

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agonistic encounters are frequent and costly. For example, male mice use scent marks to convey dominance status (Hurst 2005) and male salamanders are able to assess relative size asymmetries on the basis of scent marks left by rival males (Mathis 1990).

However, costs are but one of the factors determining the net cost/benefit balance of intruding into a given area (Gosling & Roberts 2001). Benefits are likely to be as important as costs (Enquist & Leimar 1987), and thus the value of a contested resource should also critically affect a receiver's decision of whether to enter a scent-marked area. For example, the presence of conspecific scent marks may convey resource availability (i.e. conspecific attraction; Stamps 1988) and, at least in those species where a male's competitive ability correlates with the quality of its territory (e.g. Haenel et al. 2003), scent marks deposited by dominant males may indirectly reveal resource quality (Gosling et al. 1996). Therefore, scent marks may provide information not only about the costs, but also about the benefits of entering a marked area. Additionally, both the availability and net value of resources, and the costs of agonistic interactions may vary throughout the breeding season (e.g. Baird Day et al. 2001; Borg et al. 2006). Thus, seasonal reversals in the cost/benefit balance of exploiting a given scent-marked area are theoretically possible and a receiver's response to a scent-marked territory may shift across the breeding season.

Numerous studies have shown that chemical communication is important in lizard social behaviour, allowing lizards to derive complex information regarding species, sex, reproductive status, familiarity, relatedness, fluctuating asymmetry or even size-specific information (e.g. Pianka & Vitt 2003; Shine et al. 2003; Labra 2006). Most lacertid lizards present multiple epidermal glands, termed femoral pores, located ventrally on the posterior edge of the hind legs. These holocrine glands are hypertrophied during the breeding season, are usually much larger in males than in females, and are probably under direct androgenic control (e.g. Mason 1992). Femoral pores produce waxy chemical secretions that can be smeared on surfaces during locomotion, and apparently mediate many of the chemical discrimination abilities found in lizards (e.g. Pianka & Vitt 2003). Furthermore, most lizard species have polygynous mating systems with intense intrasexual competition, and are hence ideal subjects to test hypotheses concerning the role of scent marks (Pianka & Vitt 2003). Our aim in this study was to investigate the function of male scent marks in intrasexual competition in a lacertid lizard, *Podarcis hispanica*. Size strongly determines fighting ability and dominance status in this and other lizard species (e.g. Tokarz 1985; Olsson 1992; López & Martín 2001). Thus, we set up an experimental procedure simulating the situation faced by a male when intruding the scent-marked territories of rival males of different relative sizes during the early and later part of the breeding season to test (1) whether males show differential responses to scent-marked areas according to the size of scent-marking males (i.e. males are able to assess the relative size/competitive ability of a rival male on the basis of scent marks alone), (2) whether males avoid scent-marked areas (i.e. scent marks function as territorial 'keep out' signals), and (3) whether male response to scent-marked areas varies throughout the breeding season.

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 noose from seven different locations around the city of Valencia (Spain). In this area, the breeding season of *P. hispanica* usually begins in February–March and lasts until July (Castilla & Bauwens 2000; E. Font, unpublished data). For the 'early breeding season' experiment we collected 44 adult male lizards [snout–vent length (SVL), $\overline{X} \pm \mathrm{SE} = 53.6 \pm 0.8$ mm] in March 2005, during the first week in which reproductive behaviour was observed in the field. For the 'late breeding season' experiment, 44 adult male lizards were collected by noosing (SVL, $\overline{X} \pm \mathrm{SE} = 55.2 \pm 1.1$ mm) in June 2004, during which time courtship, matings and contests between males could still be observed in the field. Capture locations were far apart to ensure individuals had not been in previous contact. In the laboratory, lizards were individually housed in glass terraria ($40 \times 25 \times 20$ cm) with a gravel substrate, a water dish, and rocks for basking and shelter. Terraria were held in a temperature-controlled room at ambient humidity. Temperature and light–dark cycle were set to mimic average field conditions. A 40-W incandescent bulb suspended over a basking rock provided additional heat and light during the light phase of the photoperiod. Lizards were fed three times weekly, the diet being small *Tenebrio molitor* larvae dusted with vitamins (Nekton MSA, Pforzheim, Germany). Tests began 10–14 days after capture.

Each experimental male was subject to four tests that were conducted in a clean glass terrarium ($50 \times 25 \times 30$ cm) lined with two pieces of filter paper dividing it in two halves (Simons et al. 1994). One half was always covered with unmarked clean filter paper, while the other half, the treated side, was (1) scent marked by a male smaller than the experimental male (-5 ± 1 mm in SVL), (2) scent marked by a male similar in size to the experimental male (± 1 mm in SVL), (3) scent marked by a male larger than the experimental male ($+5 \pm 1$ mm in SVL), or (4) unmarked (i.e. control condition). This last treatment was included so that responses to the three marked substrates could be compared with the response to a control blank substrate. The treated side was randomly assigned in the first test, and alternated thereafter between right and left for each lizard. The order of the four experimental conditions was also systematically changed to balance possible carryover effects. Lizards were tested only once per day with an intertrial interval of 2 days. Substrates were prepared by placing donor males in a terrarium with a substrate consisting of a piece of filter paper measuring 50×30 cm precut in half, and leaving them to mark for 18 h before testing (Font & Desfilis 2002). Immediately preceding trials, one of the pieces of filter paper was transferred to an

experimental terrarium kept at the same temperature and illumination conditions as the holding terraria. Shed skin, faeces and other obvious visual stimuli left by the odour donor were removed by brushing paper substrates prior to trials. Trials began by gently placing the experimental male in the middle of the experimental terrarium (always facing inwards), and lasted 10 min from the male's first movement. Trials were video-recorded and later analysed (blind coded) from video replays using a laptop computer equipped with event-recording software (JWatcher 0.9; Blumstein et al. 2000). We recorded the amount of time lizards spent in each side of the experimental terrarium. The time lizards spent trying to climb up the walls or rubbing their snout against the walls of the experimental terrarium (i.e. 'escape attempts'; Font & Desfilis 2002) was included in the analysis. We also recorded the number of air-licks (i.e. a lizard extrudes its tongue and waves it in the air) and tongue-touches (i.e. a lizard extrudes its tongue and touches the substrate) performed in the treated side of the experimental terrarium. Tongue-touches and air-licks function in squamates to sample chemical stimuli for vomerolfaction, which mediates complex social communication in lizards, and are frequently used as an index of chemosensory exploratory behaviour (e.g. Burghardt 1970; Cooper 1998). All trials were conducted between 1500 hours and 1830 hours (local time) when lizards were fully active. Of the 44 males caught for each experiment, we assigned males as experimental or odour donors so as to maximize the amount of possible independent trials. Odour donors were always from a different site than experimental males. Twelve out of 18 lizards in the 'early breeding season' and 11 out of 19 in the 'late breeding season' participated as donors in two trials. The remaining lizards acted as donors only once. Trials in which lizards failed to explore both sides of the experimental terrarium within the first 2 min of testing were discarded. This was an arbitrarily set criterion to ensure that lizards investigated both sides of the terrarium in the early stages of each test. Only animals that produced valid trials in the four experimental conditions were included in the analysis. We therefore had to eliminate four of the 14 experimental males in the 'early breeding season' experiment ($N = 10$) and six of the 16 experimental males in the 'late breeding season' experiment ($N = 10$). Overall (i.e. pooling for both early and late breeding season experiments) male sizes (SVL, $\overline{X} \pm \mathrm{SE}$) were 'smaller' odour donors $= 48.8 \pm 0.13$ mm, 'equal' odour donors $= 54.4 \pm 0.13$ mm, 'larger' odour donors $= 60 \pm 0.15$ mm, and experimental males $= 55.0 \pm 0.09$ mm.

Ethical Note

Animal care and experimentation were conducted according to guidelines provided by the Association for the Study of Animal Behaviour, the Animal Behavior Society and the American Society of Ichthyologists and Herpetologists. The lizards used in this study were caught under permit GV-Rept-02/91 from the Generalitat Valenciana to E.F. No deaths occurred and lizards were healthy during the experiments and were later released at their capture site after being marked by toe clipping to avoid recapture. Individual marking was necessary because lizards for the early and late breeding season experiments were collected at the same sites to avoid the possible effect of interpopulation differences. Paint markings wear out with skin shedding, and other indirect techniques, such as photo identification, are not reliable in *P. hispanica* lizards (E. Font, personal observation). Toe clipping has been widely used as a permanent marking technique in lizards (e.g. Huey et al. 1990), where natural toe loss is frequent (e.g. Hudson 1996). Although toe clipping can affect clinging performance in pad-bearing arboreal lizards (e.g. Bloch & Irschick 2005), several studies have shown that nonextensive toe clipping does not affect clinging performance or running speed in terrestrial lizards (e.g. Huey et al. 1990; Paulissen & Meyer 2000; Borges-Landáez & Shine 2003). It is difficult to judge the amount of distress inflicted by toe clipping in lizards, but a recent study reported that toe clipping did not induce a significant increase in corticosterone levels, suggesting that it generated relatively little stress (Langkilde & Shine 2006). To mark lizards, we clipped a maximum of two toes by cutting the distal two-thirds with a pair of sharp surgical scissors. We only clipped 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.

Statistical Analyses

To test whether males use scent marks to assess rival size, and whether male response to scent marks varies throughout the reproductive season, we compared male responses to the treated side of experimental terraria across treatments, between both experiments. Because graphical exploration showed that data could not be assumed to be normally distributed, we fitted a partly nested robust analysis of variance (ANOVA) (Quinn & Keough 2002) model using SPSS 11.5 (SPSS Inc., Chicago, IL, U.S.A.). We used a groups by trials repeated measures unbalanced design with individual males nested as random factor within 'time of breeding season' and both 'time of breeding season' and 'odour treatment' as fixed factors. Where significant odour treatment effects were found, we performed planned contrasts between the response to the control condition and the response to the other three treatment conditions. Variables for which significant interactions were detected were tested for simple main effects by conducting simple factor repeated measures robust ANOVA separately for the two experiments. 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 assumed (Quinn & Keough 2002). Wilcoxon's signed-ranks test for paired replicates was used to test whether, in each of the odour treatments (except in the control condition), males spent a significantly different amount of time in the treated

versus untreated side of the experimental terrarium. For this analysis we only included data recorded after the experimental lizard had visited both sides of the terrarium. Except when noted, results reported as significant remained so after applying the sequential Bonferroni method described by Holm (1979), that was used to control experimentwise error rate due to multiple testing. Significance level for the rejection of the null hypothesis was set at $\alpha = 0.05$. All reported probabilities are two tailed. Finally, we checked for seasonal morphological differences in absolute SVL, mass and corpulence of experimental and donor males using nonparametric statistics (Mann–Whitney test; Siegel & Castellan 1989). Corpulence was calculated as the residual values of a reduced major axis (RMA) regression performed on log-transformed measures of mass and SVL (Green 2001). Similarly, we fitted a repeated measures robust ANOVA model to check for seasonal differences between 'early' and 'late breeding season' experiments in relative mass or relative corpulence for any of the experimental treatments.

RESULTS

The results of the ANOVA model are summarized in Table 1. Mauchly's test yielded nonsignificant results for all four variables (time spent in treated side: $W = 0.607$, $P = 0.139$; escape attempt time: $W = 0.591$, $P = 0.118$; tongue-touches: $W = 0.844$, $P = 0.726$; air-licks: $W = 0.865$, $P = 0.789$) so sphericity was assumed to hold and adjustment of univariate F ratios was judged unnecessary (Quinn & Keough 2002). Results show a significant effect of 'treatment condition' and a significant interaction between 'treatment condition' and 'time in the breeding season' on the time males spent in the treated side of experimental terraria (Table 1). Data for the simple main effects tests approached nonsphericity (early breeding season: $W = 0.273$, $P = 0.077$; late breeding season: $W = 0.272$, $P = 0.076$) so corrected univariate F ratios and multivariate statistics were conducted. In the early breeding season, both univariate ($F_{2.154,19.388} = 9.636$, $P = 0.001$) and multivariate ($F_{3,27} = 29.323$, $P < 0.001$) tests show that treatment effects are highly significant. In the late breeding season, multivariate statistics yielded significant treatment effects ($F_{3,27} = 5.377$, $P = 0.031$) but univariate statistics did not ($F_{2.128,19.151} = 1.052$, $P = 0.373$). Planned comparisons and the interaction plot (Fig. 1) show that, in comparison with the control condition, 'early breeding season' males spent significantly more time in areas marked by males similar in size ($F_{1,9} = 36.101$, $P < 0.001$) or larger ($F_{1,9} = 8.528$, $P = 0.017$) than themselves, but not in areas marked by smaller males ($F_{1,9} = 1.299$, $P = 0.284$). In the 'late breeding season', males did not spend significantly more time in areas scent marked by smaller ($F_{1,9} = 5.015$, $P = 0.052$), similar ($F_{1,9} = 0.520$, $P = 0.489$), or larger males ($F_{1,9} = 0.025$, $P = 0.877$). We also found a significant effect of treatment condition, but not of time in the breeding season, on the number of tongue-touches directed to treated substrates (Table 1). Planned comparisons show that males only directed more tongue-touches to areas scent marked by smaller males ($F_{1,9} = 7.898$, $P = 0.012$), and not by similar ($F_{1,9} = 1.488$, $P = 0.238$) or by larger ($F_{1,9} = 1.956$, $P = 0.179$) males, than to the control condition. We found no significant effects of 'treatment condition' or 'time in the breeding season' for air-licks. We reanalysed these results considering tongue-touch and air-lick rates (i.e. number of tongue-flicks per second spent in the treated side of the experimental terrarium) to correct for possible carryover effects of 'time spent in treated side' on tongue-flicking. We also found a significant effect of treatment condition in tongue-touch rate ($F_{3,27} = 2.839$, $P = 0.046$), but not in air-flick rate ($F_{3,27} = 0.893$, $P = 0.451$). However, planned comparisons did not detect any differences between tongue-touch rates scored in any of the three treatment conditions (smaller males: $F_{1,9} = 1.460$, $P = 0.243$; similar males: $F_{1,9} = 1.952$, $P = 0.179$; larger males: $F_{1,9} = 0.173$, $P = 0.682$) and in those scored in the control condition. We found no significant effects of 'treatment condition' or 'time in the breeding season' for time devoted to escape attempts (Table 1), which was low in all treatments and in both experiments ($\overline{X} \pm \mathrm{SE} = 27.51 \pm 7.29$ s).

Male *P. hispanica* did not spend more time in the unmarked than in the marked side of terraria in any of the three treatment conditions tested, in either of the two experiments. Rather, males spent more time in the marked side when it had been marked by similar and larger males in the 'early breeding season' experiment (smaller: $T = 39$, $P = 0.28$; similar: $T = 55$, $P = 0.002$; larger: $T = 49$, $P = 0.028$; this last value becomes marginally nonsignificant at $P = 0.056$ when conducting Bonferroni correction) and when it had been marked by smaller males in the 'late

Table 1. Analysis of variance table for time spent in treated side, tongue-touches directed to treated substrate, and air-licks performed in the treated side of the experimental terrarium (after rank transformation)

		Time spent		Tongue-touches		Air-licks		Escape attempt time	
Source of variation	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between subjects									
Time in breeding season	1	2.34	0.143	2.67	0.120	0.52	0.479	2.17	0.158
Within subjects									
Odour treatment									
Sphericity assumed	3	3.91	0.013	3.46	0.022	1.96	0.131	1.590	0.202
Treatment*season									
Sphericity assumed	3	3.98	0.012	0.65	0.588	2.49	0.070	0.654	0.584

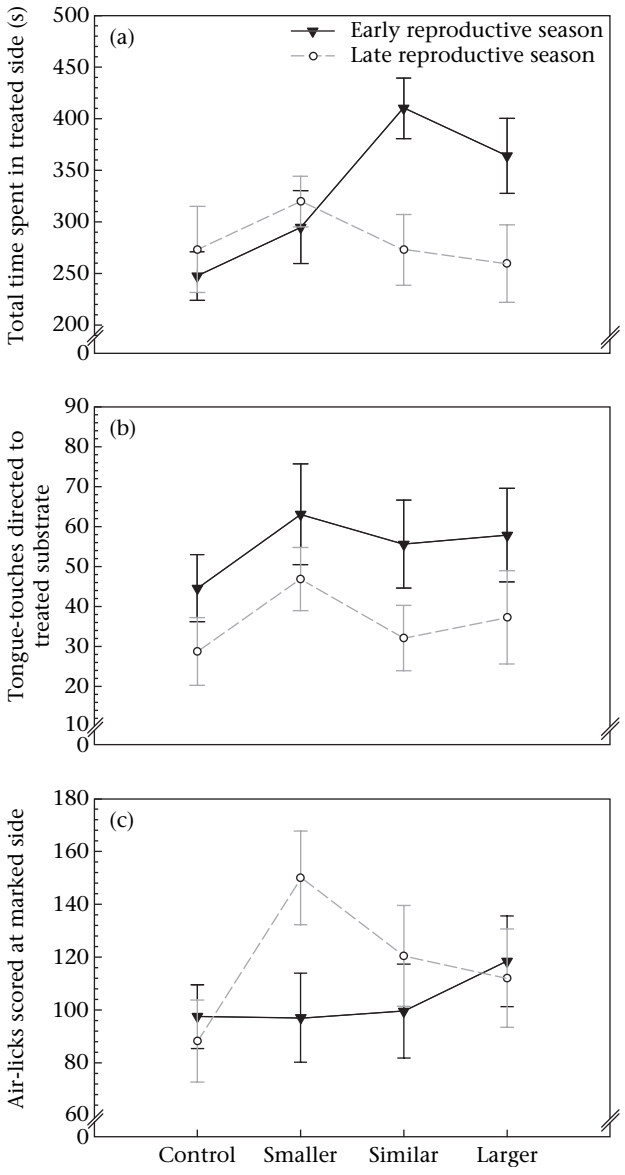

Figure 1. Interaction plot of cell means and standard errors (Quinn & Keough 2002) for data on effects of treatment condition (i.e. unmarked control substrate, substrate marked by smaller males, substrate marked by similar males or substrate marked by larger males) and time in the breeding season (i.e. early versus late in the breeding season) on (a) time spent in treated area, (b) number of tongue-touches directed to treated substrate and (c) number of air-licks scored at treated substrate.

breeding season' experiment (smaller: $T = 53$, $P = 0.006$; similar: $T = 26$, $P > 0.5$; larger: $T = 25$, $P > 0.5$).

We found no significant statistical differences in SVL (Mann–Whitney test: experimental males: $N_1 = 10$, $N_2 = 10$, Wx = 88, $P = 0.220$; smaller donors: $N_1 = 7$, $N_2 = 7$, Wx = 45, $P = 0.382$; similar donors: $N_1 = 6$, $N_2 = 9$, Wx = 39, $P = 0.328$; larger donors: $N_1 = 6$, $N_2 = 7$, Wx = 32, $P = 0.186$), mass (experimental males: $N_1 = 10$, $N_2 = 10$, Wx = 97, $P = 0.580$; smaller donors: $N_1 = 7$, $N_2 = 7$, Wx = 50, $P = 0.804$; similar donors: $N_1 = 6$, $N_2 = 9$, Wx = 37, $P = 0.224$; larger donors: $N_1 = 6$, $N_2 = 7$, Wx = 31, $P = 0.140$), or corpulence (experimental males: $N_1 = 10$, $N_2 = 10$, Wx = 96, $P = 0.528$; smaller donors: $N_1 = 7$, $N_2 = 7$, Wx = 50, $P = 0.804$; similar donors: $N_1 = 6$, $N_2 = 9$, Wx = 35, $P = 0.104$; larger donors: $N_1 = 6$, $N_2 = 7$, Wx = 46, $P = 0.733$) between males used in the 'early' and 'late breeding season' experiments. Similarly, we found no significant seasonal differences in relative mass (ANOVA: $F_{1,18} = 0.402$, $P = 0.534$) or relative corpulence ($F_{1,18} = 0.199$, $P = 0.661$).

DISCUSSION

Chemosensory Assessment of Rival Competitive Ability

Previous studies have reported the existence of chemical assessment of size-correlated traits or size-specific information in several reptile species. For example, male garter snakes, *Thamnophis sirtalis parietalis*, assess female body size by chemosensory exploration (Shine et al. 2003), iguanid *Liolaemus monticola* lizards are seemingly able to chemically derive size information from other males (Labra 2006), and a recent study suggests that the amount of femoral pore deposits of *Sceloporus graciousus* lizards may correlate with the physiological condition of marking males (Martins et al. 2006). In some lacertid lizards, females may use scent marks to assess male traits such as age, fluctuating asymmetry or condition (Martín & López 2000; López et al. 2003; López & Martín 2005). Previous studies have also suggested that male chemical cues may convey size-specific information to other males in the lacertid *Lacerta monticola* (Aragón et al. 2001a, b). Unfortunately, the latter are correlational studies based on associations between resource-holding potential differences (i.e. usually size differences) and other behavioural measures (e.g. tongue-flick rates or site selection), and thus are not conclusive as their results may be explained by changes in the size of the experimental male (i.e. 'own resource holding potential effects'; Taylor & Elwood 2003). To specifically test if male chemical cues convey size-specific information, studies must use experimental designs where resource-holding potential differences do not correlate with the resource-holding potential of the experimental subject (Taylor & Elwood 2003), for example by using experimental males of approximately the same size or fixing size differences, as in the present study. Our joint analysis of both early and late breeding season experiments revealed significant differences in the time males spent in scent-marked areas according to whether they had been labelled by smaller, similar or larger males (Fig. 1). These results strongly suggest that male *P. hispanica* lizards are able to obtain information on the size of a rival male, an honest measure of dominance status and/or fighting ability in *P. hispanica* (López & Martín 2001), on the basis of intrinsic properties of scent marks deposited on the substrate.

Interestingly, male discrimination of areas marked by similar and larger males was not accompanied by differential tongue-flicking between treatments. The absence of different tongue-flick rates between treatments has been traditionally interpreted as a failure to discriminate

between the chemical stimuli involved. However, recent evidence suggests that male garter snakes assess female body size with just a few flicks of their tongue (Shine et al. 2003), and subsequent tongue-flicking may have to do with the localization of chemical stimuli sources rather than with actual discrimination (Cooper 1998). Hence, the absence of differential tongue-flicking does not necessarily exclude chemical discrimination (e.g. Labra & Niemeyer 2004). Our results support this view and offer concluding evidence that chemical discrimination can take place in the absence of significant differences in chemosensory exploration (i.e. tongue-flicking).

Scent-mark Function in Lizards

Traditional hypotheses, such as the scent-fence hypothesis, claim that scent marks act as chemical repellents that prevent trespassing by certain individuals (Wyatt 2003). Our results seem to argue against this hypothesis as males never avoided scent-marked areas. Furthermore, the fact that males were able to assess rival size on the basis of their scent marks supports the idea that these signals may mediate competitor assessment in this species (Gosling & Roberts 2001). Like other lacertid lizards (e.g. Edsman 1990), *P. hispanica* males actively defend areas around themselves and nearby females, and agonistic encounters are very frequent, and can be very costly, during the breeding season (Gil et al. 1988; López & Martín 2001). Thus, male *P. hispanica* are likely to benefit from communicating their competitive ability as a way to minimize the costs of agonistic encounters. However, our results show that males were attracted to scent-marked areas only when marked by similar or larger males (Fig. 1), a result that is difficult to explain if scent marks act exclusively to mediate competitor assessment.

In lizards, the presence of conspecifics in a territory may be a cue to resource availability (e.g. presence of potential mates, refuges, food, basking places), or absence of predators (e.g. Stamps 1988; Graves & Duvall 1995), and it has been proposed that scent marks may function as social attractors for conspecifics (e.g. López & Martín 2001). However, in our study experimental lizards were not attracted by all scent-marked areas, but only by those marked by males of similar or higher competitive ability. Male competitive ability correlates with territory resource quality in many lizard species (e.g. Haenel et al. 2003). Thus, if a territory scent marked by a relatively large male usually signifies high resource value (e.g. more females; Haenel et al. 2003), males may use their assessment of rival status as a proxy to territory resource quality and explore it regardless of asymmetries in competitive ability. This is not to say that information concerning the competitive ability of potential competitors is ignored by receivers. Male mating strategies are not necessarily fixed or unconditional but may adjust to varying costs and benefits (e.g. Gross 1996; Shuster & Wade 2003; Plaistow et al. 2004; Shine et al. 2005). Hence, a receiver's decision to enter a territory does not imply it will contest the resident male for its resources. Alternatively, receivers may decide to enter a scent-marked territory and try to sneak, but escape upon encountering a resident male (Gross 1996). Irrespective of whether male assessment of rival competitive ability serves to minimize the costs of agonistic interactions, our results suggest that male *P. hispanica* may use scent marks to indirectly assess territory resource quality. It would be interesting to pursue this possibility in future research, and to investigate how scent marks that provide simultaneous and inextricable information about associated costs and benefits fit into existing theoretical models concerning territory establishment (e.g. Stamps & Krishnan 2001) and honesty and deception in animal communication systems (e.g. Hurd & Enquist 2005; Searcy & Nowicki 2005).

Seasonal Change in Male Response to Scent-marked Areas

In contrast to the early breeding season, males in the late breeding season were not attracted to areas scent marked by other males (Fig. 1), which could reflect the existence of a seasonal shift in the cost-to-benefit balance of entering or exploring scent-marked areas (e.g. Fawcett & Johnstone 2003). There are theoretical reasons to expect seasonal changes in both the benefits and the costs of intruding a scent-marked area as the reproductive season progresses. For example, the average net reproductive value of *P. hispanica* females is considerably lower towards the end of the breeding season because of reduced reproductive returns of second clutches (e.g. Castilla & Bauwens 2000), a seasonal decline in female receptivity (e.g. Baird Day et al. 2001), and a decrease in female marginal value with successive matings (López & Martín 2002). Seasonal variation in female receptivity has been shown to trigger changes in territorial behaviour in several lizard species (e.g. Stamps & Crews 1976; Ruby 1978; Baird Day et al. 2001; Aragón et al. 2001c). However, a decrease in female reproductive value is also likely to drive a decrease in male intrasexual aggression (e.g. Stamps & Crews 1976; Ruby 1978; Baird Day et al. 2001), and thus in the costs of intruding a rival's territory. Given the available evidence, it is difficult to predict whether this drop could offset the decrease in the benefits of exploiting a scent-marked area.

Alternative explanations could involve seasonal changes in scent-mark composition, signaller marking behaviour and/or receiver motivation to intrude a marked territory. The actual mechanism that allows *P. hispanica* to chemically derive information about rival competitive ability is unknown. In mammals, at least some of the pheromonal compounds involved in scent marking are controlled by androgens, and reflect the physiological state and/or dominance status of the signaller (Wyatt 2003). In lizards, there is evidence that testosterone levels may affect not only scent-mark production (e.g. Alberts et al. 1992; Mason 1992) but also scent-marking behaviour (Martins et al. 2006). Male lizard territorial behaviour and aggressive behaviour are also under direct endocrine control (e.g. Moore & Lindzey 1992; Adkins-Regan 2005). Thus, an endocrine-based seasonal change in marking rate, scent-mark composition and/or male territorial behaviour (e.g. male motivation to intrude a scent-marked territory) could explain

why experimental males in the late breeding season were not attracted to areas marked by similar or larger males. It must be noted that our results on this point rest on a single comparison between two consecutive reproductive seasons. Therefore, and because of the possibility of seasonal effects, our results should be taken with caution until confirmed by future studies. As a corollary, the fact that male lizard social behaviour may vary substantially over the breeding season should warn against interpretations based on results that are restricted to a specific moment of the breeding period.

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