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# Size-Dependent Chemosensory Responses to Familiar and Unfamiliar Conspecific Faecal Pellets by the Iberian Rock-Lizard, *Lacerta monticola*

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# Abstract

We conducted a field study to analyse the social relationships between males of the Iberian rock lizard (Lacerta monticola). The degree of familiarity was determined based on the degree of overlap between their home ranges. We then designed a laboratory experiment to test whether the same males were able to discriminate between familiar and unfamiliar conspecifics using faecal pellet odours. Differential tongue-flick rates suggest that large males (snout-to-vent length, SVL > 75 mm), at least, may discriminate between odours of familiar and unfamiliar males. The behavioural responses were dependent on relative differences in body size between the responding male and the male that donated the faecal pellet. Thus, as responding small males increased in size relative to their corresponding familiar male, their rate of tongue-flicking significantly decreased; this was not the case in response to unfamiliar males. In contrast, there were no significant correlations between the response of large males to familiar or unfamiliar male stimuli, regardless of size differences. These results suggest that chemical cues contained in faecal pellets allow individual recognition in male L. monticola, and that the response depends on body size. We suggest that faecal pellets might be used to scent-mark home ranges, which would contribute to lowering the costs of aggressive interactions.

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## Introduction

Communication by chemical signals plays an important role in the intra-specific communication of many vertebrates (Stoddart 1980), including reptiles (Hal-

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pern 1992; Mason 1992; Cooper 1994). In lizards, pheromonal recognition has been documented in several studies (Cooper & Vitt 1984; Alberts 1989; Gómez et al. 1993; Cooper et al. 1994). The presence and relative concentration of pheromone components varies among individuals (Alberts 1992). Therefore, these differences may serve a variety of other functions and convey information on individual identity (Halpin 1986). For example, individual odours may deter conspecifics from entering the home area of the marker (Halpin 1980). The ability to discriminate between neighbours and non-neighbours could help to stabilize social systems by reducing the frequency and intensity of aggressive encounters (Glinski & Krekorian 1985). However, only a few studies of reptiles have suggested discrimination between own and other individuals odours (Graves & Halpern 1991; Alberts 1992; Cooper 1996; López et al. 1997), or discrimination between familiar and unfamiliar individuals (Glinski & Krekorian 1985; Alberts & Werner 1993; Cooper 1996; Steele & Cooper 1997; Bull et al. 2000).

In several lizards and snakes, faecal pellets may also work, alone or in combination with glandular secretions, as sources of chemical components (Duvall 1979; Simon 1983; Duvall et al. 1987; Carpenter & Duvall 1995). However, although the pheromonal activity of glandular secretions of lizards has been well studied (Alberts 1989, 1992; Mason 1992), only a few studies have examined the possible role of excrements in intra-specific communication among lizards. Chemical signals from faecal pellets are used in intra-specific communication in salamanders (e.g. Jaeger et al. 1986; Ovaska & Davis 1992). Additionally, a few previous studies of the lizards Sceloporus occidentalis (Duvall et al. 1987) and Lacerta monticola (López et al. 1998) suggest that there is a composite signal arising from the faecal pellets that may play an important role in communication between males. In these lizards, and in the gecko Coleonyx variegatus (Carpenter & Duvall 1995), faecal pellets may be used as scent marks. They might give information on individuals, and the ability to discriminate the faecal pellets of individual neighbours from non-neighbours through chemosensory senses may minimise agonistic encounters (Gosling 1982, 1990). If less aggression is shown towards neighbours, then this may be an example of 'dear enemy' recognition (Fisher 1954). Such behaviour may minimize the energy expended on aggressive acts and reduce the frequency of escalated contests between neighbours (Jaeger 1981; Glinski & Krekorian 1985).

In most studies of discrimination between familiar and unfamiliar conspecifics through chemosensory investigation, the main experimental approach has been to house individuals together until habituation occurs (Halpin 1986; Lai & Johnston 1994; Cooper 1996; Guffey et al. 1998). There is a lack of evidence for chemosensory discrimination among individuals whose actual spatial and social relationships have been previously determined in the field. In addition, the behavioural responses of individuals may depend upon other factors, such as relative body size and ownership of an area (Mathis 1990; Mathis & Simons 1994; Zucker & Murray 1996). Agonistic behaviour could be influenced by the body size of the resident, thus, when encountering a scent mark, larger individuals tend to become more aggressive and smaller individuals become more submissive (Mathis & Simons 1994). Lacerta monticola is a small diurnal lacertid lizard found mainly in rocky habitats of some high mountains of the Iberian Peninsula. Males of this species defend territories against other males, but overlap between home ranges is extensive and agonistic encounters occur during the mating season (Martín & Salvador 1993a, 1997). Given this high spatial overlap between males, the frequency of agonistic interactions should be higher than that which we have observed in the field (unpubl. data). Males which are frequently engaged in agonistic interactions may incur energetic and survival costs (Marler & Moore 1989). Therefore, mechanisms of reducing the frequency of aggressive encounters would be advantageous. Male *L. monticola* can detect and discriminate between self-produced scents in faecal pellets and those of other conspecific males (López et al. 1998). We hypothesized that, if males also have the capacity to discriminate the faecal pellets of neighbours from non-neighbours through chemosensory senses, faecal scent marks might minimize the costs of agonistic interactions.

In this paper, we firstly analysed, in the field, the social relationships between male *L. monticola*, by initially determining familiarity between males based on the overlap between their natural home ranges. Next, we used these same individuals in a laboratory experiment to study the ability of males to discriminate between signals arising from faecal pellets of familiar and unfamiliar conspecific males when the responding male is in his own cage. We therefore designed our experiment to mimic a natural situation in which a male lizard detects a conspecific faecal pellet in his own home range.

# **Materials and Methods**

#### Species and Study Site

We conducted field work between May and July 1997 at 'Alto del Telégrafo' (Guadarrama Mountains, Central Spain) at an elevation of 1900 m. Patches of large granite rocks and scree interspersed by shrubs (*Cytisus oromediterraneus* and *Juniperus communis*) were dominant at the study site, together with meadows of *Festuca* and other grasses (Martín & Salvador 1992). In the study area, *L. monticola* is found between 1750 and 2350 m elevation. Mature individuals are approximately between 61 and 90 mm snout-to-vent length (SVL). Lizards are active from May to Oct., mating in May and June, and producing a single clutch in July (Elvira & Vigal 1985).

# **Field Study**

To determine the relationship (familiar or unfamiliar) between individual male lizards, we conducted a field study in a 0.3-ha plot  $(80 \times 40 \text{ m})$  that was divided into 32 quadrants of  $100 \text{ m}^2$  each to form a grid. Lizards were captured by noosing, individually marked with paint marks on the back and re-marked when necessary. To estimate home range size, we recorded on a map the position of every individual captured or sighted with respect to the grid marks. Censuses were performed each day during June 1997 from 08:00 h to 15:00 h GMT. To ensure

independence of data, the time interval between localizations was of at least 3 h, but most of the localizations were distributed throughout the whole month. The home range for each lizard was defined by the convex polygon surrounding the 100% of the points on the map (Rose 1982; Christian & Waldschmidt 1984). We previously determined the minimum number of localizations that represent an adequate sample size for this species by plotting the number of locations against cumulative home range, and converting to a percentage of the maximum area (Rose 1982). Approximately 10 sightings for males described 80% of the home range estimated with all the sightings, and we considered this the minimum number of sightings to adequately represent home range size in this population (Martín & Salvador 1997). Thus, in this paper, we used only home range data which fulfilled these requirements (number of sightings:  $\bar{x} \pm SE = 12.5 \pm 1.8$ ). We used the computer program RANGES V (R. Kenward, Institute of Terrestrial Ecology, Wareham, UK) (Larkin & Halkin 1994) to determine home range size and the overlap between individuals. Familiarity (i.e. vicinity) between males was established by the degree of space overlap between their home ranges. We considered familiar males to be those whose home ranges overlapped, and unfamiliar males to be those whose home ranges did not, and whose home range centres were far apart (at least 50 m). This was to ensure that individuals had not previously been in contact. Lizards with contiguous but non-overlapping home ranges were not operationally considered familiars.

#### **Experimental Procedure**

During July 1997, we noosed 23 sexually mature male L. monticola in the study plot, for which we knew their relationship (familiar or unfamiliar) with other individuals. Males were weighed and their snout-to-vent length (SVL) was measured (SVL:  $\bar{x} \pm 1$  SE = 74.7  $\pm$  0.7 mm, range = 67–80 mm; body mass:  $\bar{x} \pm 1$  $SE = 8.1 \pm 0.2$  g, range = 6–10 g). For this study, individuals with SVLs below and above the mean in the population were classified as small (SVL < 75 mm) and large (SVL > 75 mm), respectively. These size categories also corresponded, approximately, with age categories (unpubl. data). This separation allowed us to test for differential responses to chemical signals since it is generally assumed that size is correlated with the competitive ability of lizards (e.g. Tokarz 1985; Olsson 1992; Zucker & Murray 1996). Lizards were individually housed at 'El Ventorrillo' Field Station (Navacerrada, Madrid Province), 5 km from the capture site in outdoor plastic cages ( $60 \times 40$  cm) containing sand substrate and rocks for cover. Food (mealworms and crickets dusted with a multivitamin powder) and water were provided ad libitum. Lizards were held in their home cages for at least 1 wk before testing for familiarization to the laboratory conditions. All the animals were healthy during the trials and, at the end of the experiments, were released to their initial sighting location.

We collected faecal pellets from lizards immediately after their capture to be used as sources of chemosensory stimuli. Metal forceps were used to collect pellets, which were then cleaned with 96% ethanol after use to avoid contamination. Pellets were placed in small sealed and labelled glass vials and then frozen (Jaeger et al. 1986). They were thawed them at room temperature for 30 min before use; fresh gloves were used when handling each pellet to avoid contaminating them with human odours (Ovaska & Davis 1992).

To examine the hypothesis that male lizards can distinguish between faecal pellets from familiar and unfamiliar males based only on chemical cues, we compared the number of tongue flicks emitted by 23 males in their own cages in response to stimuli arising from cotton swabs impregnated with: (i) a faecal pellet from a conspecific familiar male; (ii) a faecal pellet from a conspecific unfamiliar male; and (iii) deionized water (odourless control) (Cooper & Burghardt 1990). Water was used to gauge baseline tongue-flick rates in the experimental situation. In a previous study with *L. monticola* lizards we have demonstrated that males can discriminate between odours from their own faecal pellets, those of unfamiliar lizards, an odourless control and a pungency control (López et al. 1998). Therefore, in the present study, which further examined the ability to discriminate between familiar and unfamiliar conspecifics, we considered that it was not necessary to include either the lizard's own faeces stimuli or a pungency control.

We prepared stimuli by dipping the cotton tip (1 cm) of a wooden applicator (50 cm) in deionized water. We added other stimuli by rolling the moistened cotton over the wet faecal pellets. We used a new stimulus in each trial. Every lizard responded to each stimulus once in a counterbalanced sequence; the order of presentation was randomized and no lizard was tested more than once per day.

Trials were conducted in outdoor conditions during July 1997 (coinciding with the mating season of lizards in their original natural population), between 09:00 h and 12:00 h GMT, when lizards were fully active. Each individual was allowed to bask for at least 2 hours before trials. We had measured the temperature of lizards in previous experiments, showing that they were able to attain a body temperature within the activity temperature range of the species after 2 hours of basking (Martín & Salvador 1993b). Following this basking time, one of the experimenters slowly approached a lizard's cage and slowly moved the cotton swab to a position 2 cm anterior to the lizard's snout. We recorded total tongue flicks, tongue flicks directed to the swab, and tongue flicks directed elsewhere for 60 s, beginning with the first tongue flick. We also recorded the latency to the first tongue flick, computed as the period elapsed between placing the swab in the cage and the first tongue extrusion.

To examine differences in the number of tongue flicks elicited among conditions, we used repeated measures two-way ANOVA's (Sokal & Rohlf 1995) with treatment as the within-subjects factor, and two categories of male body size (small vs. large) as the between-subjects factor. The interaction between treatment and size was included to determine whether the responses to faecal pellets were dependent on male body size. We previously tested dependent variables for normality with Kolmogorov–Smirnov's tests and for homogeneity of variances using Hartley's tests. Latencies to the first tongue flick had significant heterogeneous variances; thus, these data were analysed using non-parametric Friedman twoway ANOVA (Siegel & Castellan 1988). Pairwise comparisons of central tendency were planned using Tukey's honest significant difference tests for parametric analyses and a non-parametric multiple comparison procedure for non-parametric analyses (Sokal & Rohlf 1995). Spearman rank correlations were conducted between tongue-flick rates emitted in response to other male faecal stimuli and the difference between the SVL of each responding male and the SVL of the faecal donor male (Siegel & Castellan 1988).

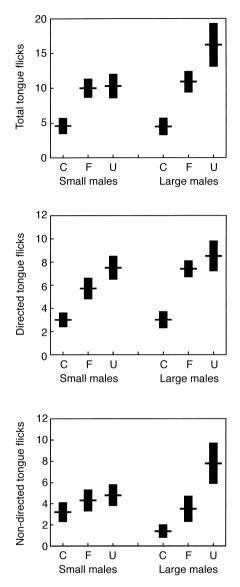
# Results

In the field, home range size of the lizards used in the experiment varied between 8.5 m<sup>2</sup> and 441.8 m<sup>2</sup> ( $\bar{x} \pm SE = 113.5 \pm 27.5 \text{ m}^2$ ), and for those individuals whose areas overlapped, the degree of overlap between home ranges varied from 0.2% to 54.8% ( $\bar{x} \pm SE = 23.3 \pm 5.5\%$ ).

In the laboratory experiment, all lizards emitted tongue flicks in all conditions. There were significant differences among conditions in total tongue-flick rates (repeated measures ANOVA: within factor,  $F_{2,42} = 24.95$ , p < 0.0001; Fig. 1a) but there were no significant differences between the two categories of male body size (between factor:  $F_{1,21} = 1.29$ , p = 0.27). However, there was a significant interaction between conditions and body size categories ( $F_{2,42} = 3.27$ , p < 0.05). In both body size categories, the total tongue-flick rates were significantly higher in the presence of the familiar and unfamiliar stimuli than in the control stimuli (Tukey test: p < 0.03 in all cases). In small males (n = 13), there were no significant differences between responses to familiar and unfamiliar stimuli (p = 0.99), whereas in large males (n = 10), the responses to familiar and unfamiliar stimuli approached significant differences (p = 0.076). The large males had significantly higher total tongue-flick rates to faecal pellets of unfamiliar males than did smaller individuals (p = 0.021).

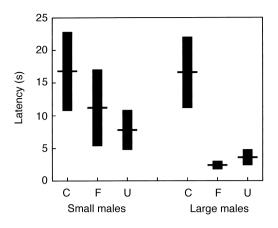
Tongue-flick rates directed to the swabs were significantly different among conditions (repeated measures ANOVA:  $F_{2,42} = 21.87$ , p < 0.0001; Fig. 1b) but there were no significant differences between the two body size categories ( $F_{1,21} = 1.02$ , p = 0.32), or for the interaction between treatments and body size ( $F_{2,42} = 0.61$ , p = 0.54). Tongue-flicks rates directed to the swabs were significantly higher for familiar (Tukey test: p < 0.001) and unfamiliar stimuli (p < 0.0001) than for the control stimuli, but there were no significant differences between familiar and unfamiliar stimuli (p = 0.16).

There were significant differences among conditions in tongue-flick rates directed elsewhere (repeated measures ANOVA  $F_{2,42} = 8.41$ , p =0.0008; Fig. 1c). There were no significant differences between body size categories ( $F_{1,21} = 0.01$ , p =0.91), although there was a significant interaction between conditions and body size ( $F_{2,42} = 3.46$ , p =0.04). In the small males, the tongue flicks directed elsewhere did not differ among conditions (Tukey test: p > 0.70 in all cases). For large males, there were no significant differences between the control and familiar conditions (p > 0.70). However, the control and the unfamiliar conditions did differ significantly (p < 0.001), whereas the familiar and the unfamiliar conditions were only marginally different (p = 0.056).



*Fig. 1:* Tongue-flick rates ( $\bar{x} \pm 1$  SE) emitted by small (SVL < 75 mm) and large (SVL > 75 mm) male *L. monticola* in response to deionized water (odourless control) (C) and chemical stimuli from faecal pellets of a familiar (F) or of a unfamiliar male (U)

Variances in the latency to first tongue flick were significantly heterogeneous (Hartley's test:  $F_{max} = 75.18$ , df = 3, 22, p < 0.0001). The mean latency differed significantly among conditions (Friedman ANOVA:  $\chi^2 = 9.02$ , p =0.011; Fig. 2). However, when analysed by size classes, only latencies of large males were signifi-



*Fig. 2:* Latency ( $\bar{x} \pm 1$  SE) to first tongue flick when deionized water (odourless control) (C) and chemical stimuli from faecal pellets of a familiar (F) or of a unfamiliar (U) male were presented to small (SVL < 75 mm) and large (SVL > 75 mm) male *L. monticola* 

cantly different among conditions ( $\chi^2 = 6.86$ , p =0.03), whereas latencies of small males were not ( $\chi^2 = 2.94$ , p =0.23). In large males, the latency in response to deionized water was significantly longer than to unfamiliar stimuli (p =0.04), and to familiar stimuli (p =0.036), but the latencies to familiar and unfamiliar stimuli were not significantly different (p =0.29).

In small males, there was a significant negative correlation between the rate of directed tongue flicks emitted in response to familiar male stimuli and the difference in SVL of each responding male and the SVL of its corresponding familiar male (Spearman correlation:  $r_s = -0.60$ , p =0.038). Thus, smaller males tongue-flicked more in response to the scent of relative larger males. However, there was no significant correlation for small males between directed tongue-flick rates in response to unfamiliar males stimuli and the SVL differences (Spearman correlation:  $r_s = -0.10$ , p =0.75). In contrast, for large males, there were no significant correlations between the response to familiar or unfamiliar males' stimuli and the SVL differences (p > 0.50 in all cases).

# Discussion

In many lizards, tongue-flicking allows an individual to obtain information about conspecifics (Halpern 1992; Mason 1992; Cooper 1994). In fact, there are studies on tongue-flicking responses of lizards reporting that functional (vs. sealed) vomeronasal ducts are necessary for accurate discrimination of prey chemicals and pheromones (Graves & Halpern 1990; Cooper & Alberts 1991). Our results show that male *L. monticola* can distinguish conspecific odours from a control. In a previous study, male *L. monticola* discriminated between self-produced scents contained in faecal pellets and those of other conspecific males and, additionally, the behavioural responses differed between stimuli (López et al. 1998). In the present experiment, the total tongue-flick rate, and the tongue-flick rate directed elsewhere, of large males to the faecal stimuli of an unfamiliar male is higher (although only marginally significant) than to the faecal stimuli of a familiar male. These results suggest that at least large male *L. monticola* can also discriminate between odours contained in faecal pellets of familiar and unfamiliar conspecific males.

Familiar discrimination has been demonstrated in other lizard species. Male green iguanas, Iguana iguana, are capable of distinguishing the femoral gland secretions of unfamiliar males from controls, their own secretions, and those of familiar males (Alberts & Werner 1993). Recent work shows that both sexes of broad-headed skinks (Eumeces laticeps) can discriminate between chemical stimuli of familiar and unfamiliar individuals of the opposite sex and that males can distinguish their own cloacal chemicals from those of unfamiliar males (Cooper 1996). Our experiment suggests that, in addition to femoral and cloacal secretions, lizards may also be able to discriminate between familiar and unfamiliar individuals based on chemicals from faecal pellets. Nevertheless, the information arising from faecal pellets may be incomplete. Thus, in a natural situation faecal pellets could act in conjunction with other chemical stimuli or with the natural visual stimuli that is disturbed when using the impregnated cotton swabs. Possibly for one or both reasons, the differences found in our experiment are not highly significant. However, faecal pellets act as a composite signal (visual and chemical) and the visual location of the pellet might elicit the search of other chemical signals such as femoral secretions (López et al. 1998). Thus, the higher number of undirected tongue flicks in response to unfamiliar stimuli suggests either that unfamiliar volatiles induced non-directed tongue-flicking or that contact with the faecal stimuli of unfamiliar males induced chemosensory search for the source of the chemicals away from the swab, or both.

Our findings support the hypothesis of 'dear enemy recognition' (Jaeger 1981; Qualls & Jaeger 1991); chemical stimuli from the odours of unfamiliar males would provoke a greater aggressiveness than those from familiar males. Other studies showed that territorial male desert iguanas, Dipsosaurus dorsalis, quickly reacted aggressively to unfamiliar males, whereas neighbours were ignored (Glinski & Krekorian 1985). Moreover, as the distance increased between two males, the likelihood of mutual challenge displays increased and the latency to mutual challenge displays decreased. (Glinski & Krekorian 1985). Likewise, in our experiment, the latency to the first tongue flick in response to the control stimuli was significantly longer than to unfamiliar stimuli and marginally longer than to familiar stimuli. Thus, when a conspecific odour was present, male lizards began an exploratory behaviour earlier than when the deionized water was present. This behaviour could allow male lizards to obtain information on other individuals as soon as possible, based on chemicals cues. If an individual is at a size disadvantage relative to the donor of the signal it should retreat from this area quickly to avoid possible injury.

The significant difference between the two categories of male body size in the total tongue-flick rates to unfamiliar stimuli suggests that the response to chemical cues may depend on the absolute body size (Mathis & Simons 1994). This result agrees with a previous study using L. monticola, in which absolute body size affected chemosensory investigation of the responding male (López et al. 1998). An interesting finding of this study is that the directed tongue-flick rates of small lizards in response to familiar male stimuli decreased significantly with the difference in body size between responding individuals and donors. This suggests that male L. monticola may assess conspecific body size on the basis of chemical cues arising from the faecal pellets alone, and that size asymmetries between males might occur even in the absence of the signaller. The cost that would suppose to find the male which has deposited the chemical mark is going to depend on the competitive ability of the issuing male as well as of the receiving male (Gosling et al. 1996a,b). Thus, when a large male detects a smaller possible opponent, more information on the detected male may be unnecessary because the probability of success in an agonistic interaction is higher for the large male. In contrast, when a male is smaller than the signaller, he might require more information, and hence a higher tongue-flick rate, about the other male to decide whether to avoid a possible agonistic interaction.

Interestingly, the directed tongue-flick rate decreased with the difference in male body size in the presence of familiar, but not unfamiliar stimuli, suggesting individual recognition of familiar males. Lizards probably have prior experience with familiar males who overlap in their home ranges. Thus, males might learn to associate individual odours with positive or negative experiences with the producers of the odour (Halpin 1986). For this reason, behavioural responses are going to depend on the relative competitive abilities and social status of males. If the familiar opponent is greater in size, he also should be dominant, which would suppose a high risk of injury to the smaller opponent in a aggressive encounter. Thus, males might recognize individuals, and their associated status, rather than just differences in body size. Conversely, when the opponent is an unfamiliar male, individual recognition is not possible (i.e. there would not be differences in tongue-flick rates to different individuals). Our results suggest that males might use memorized information about the competitive ability of opponents (Johnston 1993; Gosling et al. 1996b). However, some studies with mice indicate an alternative mechanism for which intruders could innately assess their own competitive ability if kept alone, and therefore without prior experience of competitors (Gosling et al. 1996a,b). Alternatively, or in addition, because our tests were performed in the own home cages of the responding individuals, the determinant factor in a contest with an unfamiliar individual could be the advantage of being resident, whereas if body size differences are not greater they may be less important (e.g. Cooper & Vitt 1987). To test the possibility of self-assessment of their own competitive ability, it would be interesting to also examine the response of the experimental males in the home cages of the unfamiliar donor males. Thus, the responding male would play the role of intruder and, in this context, the response might depend on his competitive ability. These findings point out the need for further studies of chemosensory individual discrimination which consider the body size, social status and residency condition of the responding and donor individuals.

The ability to discriminate between chemical stimuli from neighbour and non-neighbour males, and that the behavioural responses depend on the size of males in the absence of the signallers, suggest individual recognition in *L. monti-cola*. In these circumstances, faecal pellets might be used to scent-mark home ranges or territories. Besides, faeces of male *L. monticola* act as composite signals, have an aggregated spatial distribution and are placed on selected sites. This may confer an advantage because these characteristics allow faecal pellets to be located visually by conspecifics over a longer distance than by chemical signals alone (López et al. 1998). Taking the findings of this and the previous study together, the question that arises is, in which part of the home range are faeces located? The aggregated spatial distribution of faeces could indicate that faeces are located in the border, as has been reported in mammals (Johnson 1973; Kruuk et al. 1984; Mills & Gorman 1987; Allen et al. 1999), or that males have scent-marked their core area more than the rest of the home range.

In territorial behaviour and dominance hierarchies, individual recognition reduces the intensity and frequency of agonistic encounters (Glinski & Krekorian 1985). Gosling (1982, 1986) hypothesised that individual recognition systems are combined with the ability to learn the status of individual conspecifics through repeated encounters. Therefore, the ability of male *L. monticola* to recognize faecal pellets of familiar individuals might be used to reduce the costs of aggressive interactions. A male that finds the faeces of a conspecific might assess his relative competitive ability with respect to the signaller and then decide whether to retreat from this area to avoid an agonistic encounter, or to face a possible fight, being in possession of previous information on the contestant.

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