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Chemosensory discrimination of familiar and unfamiliar conspecifics by lizards: implications of field spatial relationships between males

Abstract The ability of territorial lizards to discriminate between scents of neighbors and non-neighbors might contribute to decreasing the costs of aggressive interactions. To test this hypothesis, we conducted a field study to analyze the spatial relationships between male Iberian rock-lizards, *Lacerta monticola*. We then used the same individuals in a laboratory experiment to test whether male lizards can use chemical cues to discriminate between familiar conspecific males (those whose home ranges overlapped) and unfamiliar conspecific males (those whose home ranges did not overlap, and whose home range centers were at least 50 m apart). Differences in tongue-flick rates in the presence of chemical cues suggested that male *L. monticola* discriminated between odors of familiar and unfamiliar males. The behavioral responses were also dependent on relative differences in body size between the responding male and the unfamiliar male that donated the scent: There was a significant negative correlation between tongue-flick rates emitted in cages of unfamiliar males and the body size differences between males. In contrast, when the donor of the scent was a familiar male, the tongue-flick rate was not dependent on body size differences. These results are compatible with individual discrimination through chemical cues in male *L. monticola*.

Keywords Familiar discrimination · Chemical communication · Lizards · *Lacerta monticola*

Introduction

Communication by chemical signals is widespread among vertebrates (Stoddart 1980; Brown and Macdonald 1985).

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The presence and relative concentration of pheromone components vary among individuals (Alberts 1992), and might, therefore, convey information on individual identity and serve a variety of functions (Halpin 1980). For example, individual odors may deter conspecifics from entering the home area of the marker, especially after negative experiences with the producer of the odor (Halpin 1986). Individual discrimination has been demonstrated within vertebrates in several mammal (Halpin 1986), bird (Whitfield 1987), and salamander (Simon and Madison 1984) species.

In lizards, the chemical senses play important roles in intraspecific communication (Halpern 1992; Mason 1992; Cooper 1994). Several studies have shown pheromonal detection in different species (Cooper and Vitt 1984, 1986; Alberts 1989; Gómez et al. 1993; Cooper et al. 1994). However, individual discrimination has received little attention although some studies suggest discrimination by lizards between their own odors and those of other individuals, as occurs in blue-tongued skinks, *Tiliqua scincoides* (Graves and Halpern 1991), male broad-headed skinks, *Eumeces laticeps* (Cooper 1996), desert iguanas, *Dipsosaurus dorsalis* (Alberts 1992), and the amphisbaenian *Blanus cinereus* (López et al. 1997). Furthermore, discrimination between familiar and unfamiliar individual males has been suggested in male desert iguanas (Glinski and Krekorian 1985) and green iguanas, *Iguana iguana* (Alberts and Werner 1993), and discrimination between scents of familiar and unfamiliar individuals of the opposite sex has been suggested in the broad-headed skink (Cooper 1996), and in male geckos, *Eublepharis macularius* (Steele and Cooper 1997). The ability of territorial lizards to discriminate between neighbors and non-neighbors might help to stabilize social systems by reducing the frequency and intensity of aggressive encounters (Glinski and Krekorian 1985) or by favoring mate location (Cooper 1996).

These studies on discrimination between familiar and unfamiliar individuals were accomplished by housing animals together to create familiar individuals or by maintaining animals individually to create non-familiar

individuals (Halpin 1986; Cooper 1996; Guffey et al. 1998). There is no direct empirical support for chemosensory discrimination among individuals whose actual spatial relationships have been previously determined in the animal's natural environment. By forcing individuals to become familiar, the experimenter could have chosen random pairs of males that would not be neighbors in natural conditions. For example, in contrast to the situation of most laboratory studies on first encounters in territorial animals, free-living juvenile *Anolis aeneus* did not encounter one another at random with respect to size and familiarity. In fact, there were fewer than the expected number of first encounters involving dyads in which one member was doubly disadvantaged (smaller and less familiar with the area) (Stamps 1994). The behavioral responses of individuals may also depend upon other factors such as relative body size, ownership of an area or previous experience (Mathis and Simons 1994; Gosling et al. 1996a, 1996b; Zucker and Murray 1996).

Lacerta monticola is a small diurnal lacertid lizard found in rocky habitats of high mountains on the Iberian Peninsula. Males defend territories against other males, but overlap between home ranges is extensive, and agonistic encounters occur during the mating season (Martín and Salvador 1993, 1997). However, despite the close spatial association between males, few interactions occur (e.g., number of agonistic interactions/month per lizard observed during May and June 1997: mean±SE= 1.2±0.3). Males that are frequently engaged in agonistic interactions may incur greater energetic and survival costs (Marler and Moore 1988, 1989). Therefore, mechanisms that reduce the frequency of aggressive encounters would be advantageous. The potential savings in energy may be especially important in *L. monticola* because this species has a short period of annual activity.

Previous studies with *L. monticola* suggest that composite signaling (visual and olfactory), arising from the fecal pellets, plays an important role in intraspecific communication between males (López et al. 1998). Male *L. monticola* detected and discriminated between self-produced scents in fecal pellets and those of other conspecific males through chemoreception (López et al. 1998). As in other reptiles (Alberts and Werner 1993), femoral secretions may play an important role in communication in this species (Aragón et al., in press). We hypothesized that one of the possible mechanisms to reduce costs of agonistic interactions could be the capacity to discriminate between the scents of individual familiar neighbors and unfamiliar non-neighbors.

To address this hypothesis, we first studied the spatial relationships between male *L. monticola* in the field, by determining the percentage of overlap between their natural home ranges which presumably reflects the degree of familiarity between males. We then used the same individuals in a laboratory study of their chemosensory discrimination capabilities. The aim of this experiment was to emulate a natural situation in which experimental lizards were intruders in a conspecific's home range. We specifically analyzed the ability of males to discriminate between signals arising from scents of familiar and unfamiliar conspecific males when the responding male is in an unknown area previously occupied by another male that had been present long enough to simulate scent-marking characteristic of resident males. We also tested whether the movement rate of a non-resident male could be affected by the presence of scents of a resident male.

Methods

Species and study site

We conducted field work from May to June 1997 at "Alto del Telégrafo" (Guadarrama Mountains, central Spain) at an elevation of 1,900 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 and Salvador 1992). In the study area, *L. monticola* is found between 1,750 and 2,350 m elevation. Mature individuals are approximately between 61–90 mm in snout-vent length (SVL). Lizards are active from May–October, mating in May–June and producing a single clutch in July (Elvira and Vigal 1985).

Field study

To determine the spatial relationship between individual male lizards, we conducted a field study in a 0.3-ha plot (80×40 m) that was divided into 32 quadrants of 100-m^2 each to form a grid. Lizards (males: $n=42$; females: $n=40$) were captured by noosing, and individually marked with paint on the back, and remarked when necessary. To determine home ranges of males, we recorded on a map the position of every individual captured or sighted with respect to the grid marks (x-y coordinate within the plot). Censuses were performed each day during May and June 1997 from 0800 to 1500 hours GMT. To ensure independence of data, the time interval between locations was at least 2 h. Home range for each lizard was defined by the convex polygon surrounding the points on the map (Rose 1982; Christian and Waldschmidt 1984). In a previous study, we determined the minimum number of locations that represented an adequate sample size for this species by plotting the number of locations against cumulative home range, and converting to percentage of maximum area (Martín and Salvador 1997; see Rose 1982 for methods). Approximately ten sightings for males described 80% of the home range estimated with all the sightings, and we considered this the minimum number of sightings to represent adequately home range size in this population (Martín and Salvador 1997). Thus, in this paper, we used only home range data that fulfilled these requirements (number of sightings: mean±SE=12.5±1.8, $n=29$). Lizards with less than ten sightings were transients or those with most of their home range outside the study plot. We used the computer program RANGES V (written by R. Kenward, Institute of Terrestrial Ecology, Wareham, UK) (Larkin and Halkin 1994) to determine home range size and degree of overlap between individuals. The home range centers were determined with the kernel fix estimator included in the RANGES V computer program; this is the equivalent Gaussian Kernel estimator (Worton 1989) and is more robust than the simple arithmetic mean. We considered familiar lizards to be those whose home ranges overlapped, and unfamiliar lizards to be those whose home ranges did not overlap, and whose home range centers were at least 50 m apart.

Laboratory study

During July 1997, we captured by noosing 19 adult male *L. monticola* for which we knew spatial relationship with other individu-

als. Males were weighed and their SVLs were measured (SVL: mean±SE=75±1 mm, range=67–80 mm; body mass: mean±SE= 8.1±0.2 g, range=6–10 g). They were individually housed at "El Ventorrillo" Field Station (Navacerrada, Madrid Province) 5 km from the capture site in outdoor plastic cages (60×40 cm) containing sand substrate and rocks for cover. The cages were covered with a metal net to prevent entry of predators (mainly jays). Food (mealworms and crickets) dusted with a multivitamin powder was provided daily and water was provided ad libitum. Lizards ate food rapidly, and food that was not eaten was removed immediately to avoid any influence of food remains on subsequent tests. Males were held in their home cages for at least 1 week before testing to allow familiarization with the novel environment. All the animals were healthy during the trials. At the end of the experiments, they were released to their last sighting locations prior to the last capture.

To begin a trial, we took one individual male lizard from his cage and placed him gently in the middle of a cage previously occupied by a familiar male or unfamiliar male, or in an empty clean control cage. Each lizard was tested in all three conditions in a random order of presentation. The duration of each trial was 15 min. In a previous study with *L. monticola*, we demonstrated that males can discriminate among odors from their own fecal pellets, those of unfamiliar lizards, an odorless control, and a pungency control (López et al. 1998). Therefore, in the present study a pungency control was not necessary. Furthermore, cologne would not have been an appropriate control in this experiment. In a previous study, when tongues of lizards contacted the pungency control stimuli (cotton swab impregnated with cologne), lizards frequently exhibited lip licking and jaw rubbing. Such behavior could have affected a successful comparison between treatments in the present experimental design because lizards sometimes licked scent-bearing substrates.

We performed 57 trials (19 individuals×3 treatments). In each trial, the donor lizard was drawn out of its homecage a few seconds before the beginning of the trial and returned at the end. To ensure that the odors of lizards (e.g., fecal pellets, femoral secretion) were present in each test cage, the trials began after at least 1 week of captivity. After each trial, the cages were cleaned thoroughly with water for 20 min and dried at the outdoor temperature. The sand and rocks were replaced to avoid odor contamination in successive trials. We waited for another week with the donor lizard inside the cage before another test. All trials were made in outdoor conditions during June and early July 1997 on sunny days between 0900–1200 hours GMT. Lizards were allowed to bask for at least 2 h before trials. No lizard was tested more than once per day.

Experiments were recorded on videotape (Hi-8 format, 25 frames/s) using a video camera aligned perpendicularly over the center of the terraria. The experimenter was not present during filming, to ensure that the behavior of animals was not affected by human presence. From the videotapes, we noted the time that the lizards spent moving or motionless. Because differences in tongue-flicking rates can indicate chemosensory discrimination in lizards (Cooper and Burghardt 1990), we also recorded the total number of tongue-flicks emitted, tongue-flicks directed to the ground, and tongue-flicks directed to the rocks. To determine possible changes through time in rate of response for each variable, we divided the 15-min period into three periods of 5 min each.

Data analysis

We used analysis of variance for a two-factor experiment with repeated measures on both factors to assess variation in dependent variables among treatment conditions and time periods (within-subjects factors). The interaction between treatment and time was included to determine whether the responses to the different treatments changed with time spent in the cage. Differences between conditions were assessed a posteriori using Tukey's honestly significant difference (HSD) test. We previously tested dependent variables for normality with Kolmogorov-Smirnov tests and for homogeneity of variance using Hartley's tests. Pearson's correlations were conducted between tongue-flick rates and the body size differences between the responding male and the corresponding familiar or unfamiliar male (Sokal and Rohlf 1995). The average body size differences between the test and the donor males were not significantly different for the familiar and unfamiliar trials (F=0.002, df=1,36, P<0.96).

Results

Field study

The home range size of the males used in the experiment ranged from 8.5 m² to 441.8 m² (mean±SE=113.5± 27.5 m², n=19), and there was no significant correlation between home range size and SVL (Pearson's correlation: r=0.05, F=0.03, df=1,17, P=0.85). Male home ranges overlap with a high number of other males (number of overlapping males/male: mean±SE=13.7±2.4). For those males whose areas overlapped with other males, the degree of overlap between home ranges ranged from 0.2 to 54.8% (mean±SE=23.3±5.5%).

Laboratory experiment

All lizards emitted tongue-flicks in all conditions and there were significant differences in total tongue-flick rates among conditions (F=6.87, df=2,36, P=0.003; Fig. 1) and among the successive periods of 5 min (F=41.79, df=2,36, P<0.0001). These effects cannot be interpreted simply, because there was a significant interaction between conditions and periods (F=2.70, df=4,72, P=0.036). The total tongue-flick rates in the first period were significantly higher than in the other two periods in all the conditions (Tukey's HSD test: P<0.0001 in all cases; Fig. 1). Considering only the first time period, the cages of both familiar and unfamiliar males elicited significantly higher total tongue-flick rates than the control cages (control vs familiar: P<0.001; control vs unfamil-
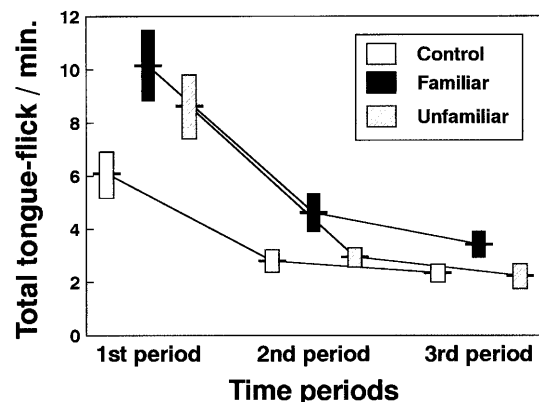

Fig. 1 Total tongue-flick rates (mean±1SE) for male *Lacerta monticola* in a clean control cage and in cages with scents from a familiar or an unfamiliar male during three successive periods of 5 min
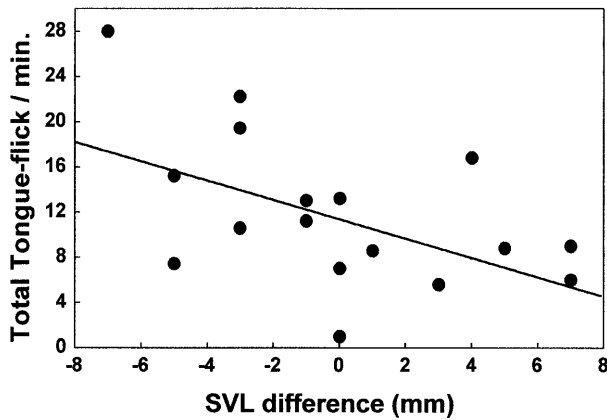
Fig. 2 Relationship between the SVL size difference (experimental lizard size–donor lizard size) and the total tongue-flick rate emitted in the first 10 min spent in cages with scents from an unfamiliar male
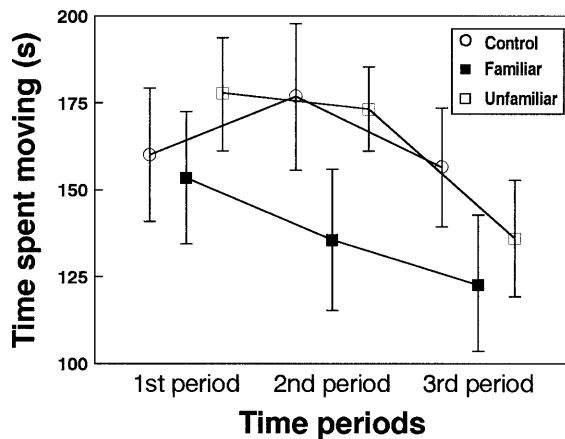

Fig. 3 Time (s) (mean±1SE) spent moving by male *L. monticola* in a clean control cage, and in cages with scents from a familiar an unfamiliar male during three successive periods of 5 min

iar: $P=0.02$), but there were no significant differences between familiar and unfamiliar cages ($P=0.34$). In the second period, the cages of familiar males elicited significantly higher total tongue-flick rates than the control ($P=0.021$) and unfamiliar cages ($P<0.05$) but there were no significant differences between control and unfamiliar cages ($P=0.99$). Considering the third time period, there were no significant differences between treatments ($P>0.05$ in all cases).

In the first 10 min, when differences in tongue-flick rates between conditions were greater, there was a significant negative correlation between total tongue-flick rates emitted in the unfamiliar-male cages and the difference between the male SVLs ($r=-0.49$, $F=5.29$, $df=1,17$, $P=0.03$; Fig. 2). In contrast, the corresponding correlation was not significant in tests conducted in cages of familiar males ($r=-0.07$, $F=0.09$, $df=1,17$, $P=0.76$). However, in the first 10 min, there was a significant negative correlation between total tongue-flick rates emitted in the familiar-male cages and the degree of overlap ob-

served in the field between the home ranges of the responding and familiar male ($r=-0.51$, $F=6.00$, $df=1,17$, $P=0.02$).

Tongue-flicks emitted to rocks differed significantly among conditions (repeated-measures ANOVA: $F=5.51$, $df=2,36$, $P<0.01$) and time periods ($F=27.65$, $df=2,36$, $P<0.0001$), and the interaction was not significant ($F=1.53$, $df=4,72$, $P=0.20$). A significantly higher tongue-flick rate directed to rocks occurred in cages of familiar males than in the other conditions ($P<0.045$ in both cases), but the difference between the control and unfamiliar-male conditions was not significant ($P=0.70$). Tongue-flicks emitted to the ground differed significantly among time periods ($F=27.65$, $df=2,36$, $P<0.0001$) but the condition effect ($F=2.33$, $df=2,36$, $P=0.11$) and the interaction ($F=1.48$, $df=4,72$, $P=0.21$) were not significant.

Males spent less time moving around the enclosure as the experiment progressed ($F=3.64$, $df=2,36$, $P=0.036$; Fig. 3), but this behavior was not significantly affected by the different scent conditions ($F=1.53$, $df=2,36$, $P=0.22$), nor was the interaction between conditions and periods significant ($F=1.27$, $df=4,72$, $P=0.28$). Males decreased their movement rate over time. Time spent moving was significantly greater during the first than during the third period (Tukey test: $P=0.013$), and greater during the second than during the third period ($P=0.02$), but the differences between the first and the second periods was not significantly different ($P=0.96$).

Discussion

Many lizards obtain information on conspecifics by tongue-flicking (Mason 1992; Cooper 1994). Our results show that male *L. monticola* can detect conspecific odors, tongue-flicking more than to a clean control. In a previous study, male *L. monticola* detected and discriminated between self-produced scents contained in fecal pellets and those of other conspecific males, a clean control, and a pungency control (López et al. 1998). In the present experiment, the higher total tongue-flick rate in the cage of familiar males than in the cage of unfamiliar males suggests that male *L. monticola* can also discriminate between familiar and unfamiliar conspecific males. Our findings agree with those for several other lizards such as iguanas (Alberts and Werner 1993), skinks (Cooper 1996), and geckos (Steele and Cooper 1997).

In previous studies, resident male *L. monticola* showed a higher tongue-flick rate in the presence of the unfamiliar stimuli (Aragón et al., 2000, in press). In contrast, in this study, intruder male *L. monticola* directed a higher tongue-flick rate to familiar than to unfamiliar stimuli. This response is, however, similar to the stronger response by intruder individuals of the lacertid *Podarcis hispanica* (Font and Desfilis 2000) and by non-resident meadow voles, *Microtus pennsylvanicus*, to familiar conspecifics (Ferkin 1988). Many studies in which experimental individuals are residents replicate the cost-benefit

relationship that favors territory defense (Fox and Baird 1992). However, few studies have examined the response of experimental individuals as intruders to familiar and unfamiliar resident odors as in the present study. Our results suggest that the balance between costs and benefits might differ between residents and intruders since intruders have do not an area to defend during the trials. These findings indicate the need for further studies to examine the interaction of the response of resident and intruder individuals to familiar and unfamiliar conspecifics in staged encounters.

That both the total tongue-flick rates and the movement rates decreased with time in all conditions indicates that the exploratory behavior of males was higher in the first 10 min, which is probably enough time for lizards to obtain an important part of the information available through the chemical cues. Similar results were obtained in the ocellated skink, *Chalcides ocellatus*, in which the exploratory response to a new cage was stabilized over a 10-min period (Graves and Halpern 1990).

That there were significant differences among conditions in tongue-flick rates emitted to rocks, but not in those emitted to the ground, suggests that individuals obtained chemical information from fecal pellets and/or femoral secretions. Feces are deposited on rocks at specific sites and act as composite signals (visual and chemical) that play an important role in the intraspecific communication of *L. monticola* (López et al. 1998). Our field observations suggest that males also deposit femoral secretions on rocks as do other lizard species (Alberts 1989).

The finding that, in the first 10 min, the total tongue-flick rate in response to scents of unfamiliar males decreased significantly as the difference in body size between responding individuals and donors increased is similar to the size-dependent response to chemical cues reported for a salamander (Mathis and Simons 1994). Size dependence might be a consequence of a correlation between body size and concentrations of chemical components of the excrement and body, and/or femoral secretions. If so, concentration of chemicals could be used to assess the competitive ability of the donor as indicated by body size. The cost of encountering the male that has deposited the chemical mark depends on the competitive ability of both the issuer and the receiver (Gosling et al. 1996a, 1996b). Thus, when a large male detects a smaller opponent, more information on the detected male may be unnecessary because the probability of success in an agonistic interaction is high for the large male. In contrast, when a male is smaller in size than the signaler, he might require more information on the other male, and hence a higher tongue-flick rate, to decide whether to avoid a possible agonistic interaction with the opponent. A study of the interactions between free-living juvenile *A. aeneus* settlers suggested that smaller individuals were able to avoid encounters with larger individuals with which they were likely to lose interactions (Stamps 1994) but this ability has not been shown to depend on chemical cues. Other factors contributing to the greater chemosensory investigation of cues from larger donors might include the presence in the chemicals of information regarding physical condition and attempts to become familiar with the scent to permit subsequent rapid identification of the donor.

The total tongue-flick rate decreased with the difference in body size between test and donor lizards for scents from unfamiliar males, but not in the presence of scents from familiar males. This suggests that the test males were already familiar with the scents of males with whom their home ranges overlapped, and thus did not require additional information about body size or condition. Similarly, in the first 10 min, the total tongue-flick rate decreased with the degree of overlap between the home ranges of individuals, which might reflect the need for more information about infrequently encountered individuals than about those encountered more frequently.

Our results show that male *L. monticola* are able to discriminate between chemical scents from familiar and unfamiliar males. Additionally, in the absence of the signalers, the behavioral responses depend on the relative size of unfamiliar males or on spatial overlap between familiar individuals. These results show that male *L. monticola* discriminate at least between classes of individuals, which is compatible with the possibility of individual discrimination. Gosling (1982, 1986) hypothesized that individual recognition is combined with the ability to learn the status of individual conspecifics through repeated encounters. In territorial systems and dominance hierarchies, individual recognition may help to reduce the intensity and frequency of agonistic encounters. Therefore, the ability of male *L. monticola* to discriminate among individual neighbors and non-neighbors might reduce the costs of aggression (Marler and Moore 1988, 1989) and may play an important role in the organization of their social system.

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