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Discrimination of Femoral Gland Secretions from Familiar and Unfamiliar Conspecifics by Male Iberian Rock-Lizards, Lacerta monticola

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Intraspecific communication by chemical signals is widespread among vertebrates (Stoddart, 1980), including reptiles (Halpern, 1992; Mason, 1992; Cooper, 1994). In many lizards, secretions from skin (Mason and Gutzke, 1990), cloaca (Cooper and Trauth, 1992), or femoral pores (Alberts, 1990, 1993) play an important role in pheromonal communication. The femoral pores are epidermal structures located on the ventral surface of the thigh of many saurians and are connected to glands that produce copious amounts of holocrine secretion (Mason, 1992). Femoral secretions are composed primarily of proteins (Cole, 1966; Fergusson et al., 1985; Alberts, 1990, 1991, 1993), which have low volatility, suggesting that perception could occur by the vomeronasal organ (Halpern, 1987) rather than by nasal olfaction (Wilson, 1970). Components of low volatility are likely to work in the absence of the signalers because of their durability (Alberts and Werner, 1993). Femoral pores are larger in males than in females, are regulated by androgens, and present a peak of activity in the breeding season (Mason, 1992). Additionally, the ventral location of the femoral pores suggests that secretions are passively deposited on the substrate as lizards move through their home ranges (Fergusson et al., 1985). Therefore, femoral gland secretions could advertise residence in a home range and could convey information about social status and competitive ability of the sender, thus reducing costs of agonistic encoun-

When discrimination between conspecifics occurs, the relative concentrations of chemical components should be variable among individuals (Beecher, 1989). The electrophoretic patterns of femoral gland proteins differ consistently among individuals of the desert iguana, Dipsosaurus dorsalis (Alberts, 1990), which are able to detect and respond differentially to their own femoral gland secretions and those of unfamiliar conspecifics (Alberts, 1992). Male green iguanas, Iguana iguana, use chemical cues from femoral gland secretions to discriminate between familiar and unfamiliar conspecific males (Alberts and Werner, 1993).

The vomeronasal organ is well developed in Squamates, and within this group, *Lacertidae* is one of the families in which it is best developed (see Halpern, 1992). Although there are several studies that have suggested the role of femoral gland secretions of lacertids in pheromonal communication (e.g., Gómez et al., 1993), there is a lack of direct empirical support.

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The Iberian rock-lizard, Lacerta monticola, is a small diurnal lacertid lizard endemic to the Iberian Peninsula that occurs mainly in rocky habitats of high mountains. Mature individuals range from 61-90 mm snout-vent length (SVL). They are active from May-October, mating in May-June, and produce a single clutch in July (Elvira and Vigal, 1985). Males defend territories against other males, but overlap between home ranges is extensive, and agonistic encounters occur during the mating season (Martín and Salvador, 1993a, 1997). However, individuals with higher agonistic interaction levels may incur greater energetic and survival costs (Marler and Moore, 1989). Therefore, mechanisms of reducing the frequency of aggressive encounters would be advantageous. The ability of territorial lizards to discriminate between neighbors and nonneighbors might help to reduce the frequency and intensity of aggressive encounters (Glinski and Krekorian, 1985).

Tongue flicking (a behavior associated with the vomeronasal organ) reflects chemosensory investigation of a stimulus (Halpern, 1992). Tongue-flick rates have been often analyzed in chemosensory discrimination experiments (Cooper, 1994; Cooper and Burghardt, 1990). In a previous study, differential tongueflick rates indicated that male L. monticola were able to detect and discriminate between chemicals arising from their own excrement and that of other males (López et al., 1998; Aragón et al., 2000). Moreover, the fecal pellets act as a composite signal (visual and chemical) in the intraspecific communication of this lizard (López et al., 1998), which also occurs with the excrements of the lizard Sceloporus occidentalis (Duvall et al., 1987). In this study, we present the results of the first direct evidence of discrimination of femoral secretions in Lacertidae. We performed a laboratory study to examine (1) whether male L. monticola are able to detect and discriminate their own femoral secretions from those of other males and (2) whether male L. monticola are able to discriminate the femoral secretions of familiar males from those of unfamiliar males.

During May 1999, we captured 40 adult male L. monticola (SVL, $\bar{x} + 1$ SE = $6\hat{8}.9 + 0.9$ mm) by noosing at "Alto del Telégrafo" (Guadarrama mountains, Central Spain) at an elevation of 1900 m. Male lizards were housed in pairs at "El Ventorrillo" Field Station (Navacerrada, Madrid Province) 5 km from the capture site in outdoor cages (60 × 40 cm) containing sand substrate and rocks for cover. Food and water were provided ad libitum. To ensure that lizards had not been in previous contact, distances between capture sites of each pair of males were at least 500 m. Individuals were healthy during the trials and, at the end of the experiments, were released at the capture site. To create familiar individuals, pairs of males were housed together for at least two weeks before testing began (Cooper, 1996). We considered males that were housed in different cages to be unfamiliar. In each pair, one of the males was used as the experimental individual and the other as the donor of the femoral gland secretions.

To examine the hypotheses of self-recognition and familiar discrimination based only on femoral secretions, we compared the number of tongue flicks emitted by 20 males in their own cages in response to

stimuli arising from cotton swabs impregnated with (1) the lizard's own femoral secretion, (2) femoral secretion from an unfamiliar conspecific male, (3) femoral secretion from a familiar conspecific male, (4) cologne (pungency control), or (5) deionized water (odorless control; Cooper and Burghardt, 1990). Water was used to gauge baseline tongue-flick rates in the experimental situation. Cologne was used to test for possible discrimination between an unfamiliar conspecific stimuli and a novel strong stimuli without biological relevance. We prepared the control stimuli by dipping the cotton tip (1 cm) of a wooden applicator (50 cm) in deionized water or cologne. We gently pressed the femoral pores of the lizards to express secretions and then collected femoral secretions by rubbing the pores with cotton swabs impregnated in distilled water. We attempted to use the same amount of femoral secretion in each stimulus. We used the femoral secretion of one leg in one trial and the other leg in the next trial to ensure a new stimulus in each trial. Femoral secretions from donor lizards were used in the trials immediately after collection to avoid fading of the stimuli. The own stimuli condition was exceptional because we waited 1 h until the beginning of the trial to avoid fright responses. This would not result in a dilution of the stimulus since femoral secretions, in which volatility of components are low, are long lasting (Alberts and Werner, 1993).

Lizards were tested with each stimulus once, and the order of presentation was randomized. We conducted trials during June 1999, coinciding with the mating season of lizards in their original natural population, in outdoor sunny conditions between 0900-1200 h GMT, when lizards were fully active. Each individual was allowed to bask for at least 2 h 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 h of basking (Martin and Salvador, 1993b). After at least two hours of basking, 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. Lizards permitted approach and testing without fleeing. We recorded total tongue flicks, tongue flicks directed to the swab, and tongue flicks directed elsewhere for 60 sec, 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 among conditions in number of tongue flicks and latency to the first tongue flick, we used nonparametric Friedman two-way AN-OVA by ranks because data were either not normally distributed or variances were not homogeneous as determined by Hartley's F_{max} tests. Significance levels for the multiple tests were calculated by using the sequential Bonferroni adjustment of Rice (1989) for multiple comparisons (Chandler, 1995). Pairwise comparisons were planned using nonparametric multiple comparison procedures (Sokal and Rohlf, 1995).

All lizards emitted tongue flicks to the swab in all conditions. There were significant differences among treatments in the total number of tongue flicks (Friedman two-way ANOVA, χ , $^2 = 30.57$, df = 4, P < 0.001). Tongue flicks elicited by cologne were significantly

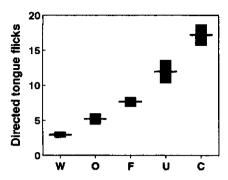


FIG. 1. Tongue flicks (mean \pm 1 SE) emitted in 1 min by male *Lacerta monticola* directed to cotton swabs bearing deionized water (odorless control) (W), chemical stimuli from their own femoral gland secretion (O), femoral gland secretions of familiar males (F) or unfamiliar males (U), and cologne (pungency control) (C).

higher than in the rest of the conditions (P < 0.01 in all cases), but there were no significant differences between the rest of conditions (P > 0.05 in all cases).

The number of tongue flicks directed to swabs differed significantly among conditions (Friedman twoway ANOVA, $\chi_2^2 = 59.30$, df = 4, P < 0.001; Fig. 1). Pairwise nonparametric comparisons showed significant differences in the number of directed tongue flicks between all conditions (at least P < 0.05 in all cases; i.e., each condition differed significantly from each other condition). The own femoral secretion elicited a significantly higher number of tongue flicks than deionized water (P < 0.05) and significantly lower than the familiar stimuli (P < 0.05). The nonfamiliar male femoral secretion elicited a significantly higher number of tongue flicks than familiar stimuli (P < 0.05) and their own femoral secretion (P < 0.01). Variances of the number of tongue flicks directed to the cotton swabs with stimuli from familiar and unfamiliar conspecific were significantly heterogeneous $(F_{\text{max}} = 6.18, \text{ df} = 1.19, P = 0.002).$

Treatments did not differ significantly in tongue flicks not directed to the cotton swab (Friedman two-way ANOVA, χ ,² = 9.14, df = 4, P < 0.057). There were also no significant differences among conditions in the mean latency to the first tongue flick (Friedman two-way ANOVA, χ ,² = 8.36, df = 4, P < 0.07; Fig. 2). However, variances of latency to the first tongue flick were significantly heterogeneous in response to familiar and unfamiliar stimuli (F_{max} = 6.22, df = 1,19, P < 0.001).

The results of our experiment indicate that male *L. monticola* can detect and discriminate between odors from their own femoral gland secretions and those of other conspecific males. The fact that the number of tongue flicks directed to swabs with femoral gland secretions was significantly higher than to the deionized water condition demonstrates that males can detect conspecific femoral gland secretions. The numbers of tongue flicks directed to the swabs were significantly greater in response to femoral gland secretion of other males (familiar or unfamiliar) than to their own secretions, indicating that male *L. monticola* are able to discriminate between their own secretions and

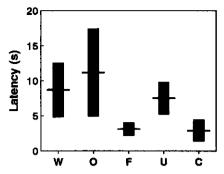


FIG. 2. Latency in seconds (mean \pm 1 SE) to first tongue flick by male *Lacerta monticola* in response to deionized water (odorless control) (W), chemical stimuli from their own femoral secretions (O), femoral gland secretions of familiar males (F) or unfamiliar males (U), and to cologne (pungency control) (C).

chemical stimuli from the femoral glands of other males.

In addition, our results also show self-detection because significant differences were observed between responses to self-stimuli and both deionized water and familiar stimuli. In animals capable of self-recognition, scent marks are commonly used to advertise home ranges or territories (Stoddart, 1980; Halpin, 1986; Hepper, 1986). The scincid lizard Tiliqua scincoides discriminates between substrates marked with their own chemical signals and those marked by other conspecifics (Graves and Halpern, 1991), and tongueflicking discrimination of self from unfamiliar individuals in desert iguanas, D. dorsalis, almost invariably involved direct contact with the substrate (Alberts, 1989, 1992). Also, male L. monticola detect and discriminate between self-produced scents and those of other conspecific males contained in fecal pellets (López et al., 1998; Aragón et al., 2000), deposited on the substrate on selected sites (e.g., relatively higher positions on rocks) of their home ranges.

Male *L. monticola* are able to discriminate between femoral gland secretions of familiar and unfamiliar conspecifics. Evidence for this is that tongue flicks directed to cotton swabs were significantly higher in response to unfamiliar femoral gland secretion than to familiar stimuli. In addition, variances of both directed tongue flicks and latency were greater in the unfamiliar than in the familiar stimulus condition which corroborates such discrimination.

The responses to pungency control were significantly different to the unfamiliar stimuli, suggesting that male *L. monticola* discriminate the unfamiliar conspecific odors from other novel stimuli without biological relevance. The higher response to the cologne might simply suggest that a novel strange stimulus also elicit more chemosensory investigation. The fact that the strongest response to femoral gland secretion was directed to the unfamiliar male secretion suggests that, when two males encounter, the resident male may exhibit "dear enemy" recognition based on chemicals. As do male *Anolis carolinensis* (Qualls and Jaeger, 1991) and male desert iguanas, *Dipsosaurus dorsalis* (Glinski and Krekorian, 1985), resident male *L. monticola* might show a more aggressive response to-

ward strangers than toward neighbors, but whether they do so is unknown. Nevertheless, an alternative, but nonexclusive, explanation for our results is that because nonneighbor males never interacted before, resident males might need more information about the competitive ability of the unfamiliar male and hence exhibit a higher tongue-flick rate.

Chemicals arising from fecal pellets seem to play an important role in intraspecific communication of *L. monticola* (López et al., 1998; Aragón et al., 2000), and femoral gland secretions have the potential to do this. Thus, both types of stimulus working together could provide more accurate information on conspecifics. The ability to discriminate between odors of familiar and unfamiliar conspecific males may contribute to stabilization of their social system by lowering the costs of aggressive interactions. Our results point out the need of further studies on the existence of individual recognition and dear enemy recognition behavior when two males encounter.

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Predation by Goldfish (Carassius auratus) on Eggs and Larvae of the Eastern Long-Toed Salamander (Ambystoma macrodactylum columbianum)

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Amphibian biodiversity is declining worldwide for a variety of reasons (Wake, 1991; Blaustein, 1994; Blaustein et al., 1994). In western North America, exotic fish introductions are one factor responsible for such declines (Hayes and Jennings, 1986). Predatory fish have adverse effects on the dispersal (Bradford et al., 1993; Fellers and Drost, 1993), reproduction (Gamradt and Kats, 1996), and distribution (Bradford, 1989) of western amphibians. The primary cause suggested for these detrimental effects is increased predation rates because native prey species lack defenses and behaviors that are effective against introduced predators (Maloney and McLean, 1995; Gamradt and Kats, 1996; Kiesecker and Blaustein, 1997).

Fish predation on amphibian larvae is well documented among native (Petranka, 1983; Kats et al., 1988; Petranka and Kennedy, 1999; Smith et al. 1999) and nonnative predator-prey assemblages (Gamradt and Kats, 1996). In many aquatic ecosystems, fish can completely eliminate amphibian larvae (Heyer et al., 1975). However, fish predation on amphibian eggs is considered uncommon because the mucoid egg capsule often makes eggs noxious (Duellman and Trueb, 1986), unpalatable (Kats et al., 1988; Denton and Beebee, 1991), or toxic (Mosher et al., 1964; Licht, 1969; Pavelka et al., 1977). Ward and Sexton (1981) and Semlitsch (1988) demonstrated that both fish and nonfish predators will not consume intact eggs of the spotted salamander, Ambystoma maculatum, but readily ingest them when the outer jelly coat is removed. Invertebrate predators commonly prey on amphibian eggs (Murphy, 1961; Diamond, 1996; Gamradt and Kats, 1996; Majecki and Majecka, 1996; Axelsson et al., 1997) by bypassing ingestion of the egg jelly (but see Axelsson et al., 1997). To our knowledge, only four species of fish (Gambusia affinis, Gasterosteus aculeatus, Salmo clarkii, and Lepomis macrochirus) are known to eat amphibian eggs (Licht, 1969; Grubb, 1972; Semlitsch, 1988). However, oophagy among these fish species is still limited by the size, firmness (Grubb, 1972), or toxicity (Licht, 1969; Semlitsch, 1988; Gamradt and Kats, 1996) of the egg and its outer jelly coat.

Goldfish, Carassius auratus, are among the most popular fish in the pet trade and are widely established throughout the United States and southern Canada (Lee et al., 1980; Page and Burr, 1991). Monello and Wright (1999) hypothesized that the widespread introduction of exotic fish into permanent, artificial ponds in northern Idaho has resulted in the elimination of amphibians native to those areas and is in part a result of the consumption of amphibian eggs by goldfish. Our purpose was to determine whether introduced goldfish prey on the eggs and larvae of the eastern long-toed salamander, Ambystoma macrodactylum columbianum, one of the most common amphibians found in northern Idaho (Nussbaum et al., 1983; Monello and Wright, 1999).

We used a 3×2 factorial design replicated four times to determine whether goldfish prey on eggs of the long-toed salamander. Treatments consisted of either no fish, one medium-sized goldfish [mean snoutfork length (SFL) \pm SE = 94.85 \pm 2.18, Mass (M) = 19.08 \pm 1.45], or one large goldfish (SFL = 143.96 \pm 4.14, $M = 63.05 \pm 5.10$). Each of these treatments was crossed with food (goldfish flakes) provided ad libitum daily or no food added. We could not include small goldfish (SFL = 66.20 mm ± 1.70 mm, M = $6.75 \text{ g} \pm 0.51 \text{ g}$) as a treatment because this size class was uncommon in the population. We obtained goldfish and eggs of the long-toed salamander from two ponds 10 km east of Moscow, Idaho (46°50'N, 117°20'W). Egg strands of the long-toed salamander are typically wrapped around emergent vegetation on the pond shore and easily break apart when separated from the vegetation. Because of this, we counted and placed one unbroken egg strand (mean eggs/strand \pm SE = 17.68 \pm 1.00), attached to their original vegetation, in separate 11.4-liter plastic aquariums. We placed the aquaria (N = 24) on the bank of a local pond, covered them with chicken wire, and changed

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