

Chemosensory Recognition of Familiar and Unfamiliar Conspecifics by Juveniles of the Iberian Wall Lizard *Podarcis hispanica*

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Abstract

Chemosensory recognition of familiar conspecifics has been reported in studies with members of several lizard families and may be advantageous to distinguish between intruders and neighbors or group members. However, few species have been studied and information on the ability to discriminate between familiar and unfamiliar conspecifics by chemosensory means is lacking for most lizard families. In this paper we ask whether juveniles of the Iberian wall lizard *Podarcis hispanica* (Lacertidae), can discriminate between chemical signals from familiar conspecifics with whom they have shared a terrarium for several months and those from unfamiliar conspecifics housed in a different terrarium. Experimental trials were conducted by transferring juveniles to a test terrarium with a filter paper substrate. We tested the responses of lizards to paper substrates labeled by familiar cage-mates, unfamiliar conspecifics, or unlabeled. Tongue-flicks and other behaviors in response to pheromonal stimuli were recorded for 10 min. Juveniles directed more chemosensory behavior towards paper substrates bearing chemicals from familiar conspecifics than towards similar paper substrates labeled by unfamiliar conspecifics. These results indicate that juveniles in this lizard species can recognize familiar conspecifics and discriminate between familiar and unfamiliar individuals using only chemical stimuli. We discuss the role of habituation in familiar conspecific recognition and review possible explanations of the functional significance of this type of discrimination in lizards.

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Introduction

Chemical communication is increasingly recognized as an important aspect of reptilian biology (Burghardt 1970, 1980; Mason 1992; Font 1996). Although most research on chemical communication in reptiles has been carried out with

snakes, data are also rapidly accumulating on the chemosensory abilities of lizards (Simon 1983; Cooper 1994). Members of several lizard families can detect pheromones from conspecifics and, in most cases, they respond differentially to chemicals of different categories of individuals (self vs. other, kin vs. non-kin, male vs. female, familiar vs. unfamiliar). However, few species have been studied in most families and information is lacking for the majority of lizard families (Halpern 1992; Cooper 1994).

Lacertids, with over 250 species distributed throughout Africa and most of Eurasia, are a case in point. It has been claimed that visual stimuli play a dominant role in the communication of socially relevant information in this family (e.g. Bauwens et al. 1987). However, this claim is contradicted by recent evidence that ranks lacertids among the most chemosensory of all lizards (Cooper 1996a), and by the results of a handful of laboratory studies supporting a role of the chemical senses in lacertid behavior. Adult *Podarcis hispanica* are capable of discriminating between paper substrates labeled by conspecifics and by sympatric heterospecifics (Gómez et al. 1993). In the same study, male *P. hispanica* exhibited more chemosensory behavior in cages labeled by conspecifics than in their home cages, suggesting a likelihood of pheromonally mediated self-recognition in this species. Similarly, male *Lacerta monticola* discriminate between self-produced scents in fecal pellets and those of other conspecific males (López et al. 1998). Juveniles of *L. vivipara*, a viviparous lacertid, are attracted to shelters containing chemicals of their mother, which indicates an ability for chemosensory mother-offspring recognition (Léna & Fraipont 1998). Thus, although scant, the available evidence suggests that lacertids may be capable of finer chemosensory discriminations than has hitherto been recognized.

Chemosensory recognition of familiar conspecifics may be advantageous to distinguish between intruders and neighbors or group members. Evidence for chemosensory recognition of familiar conspecifics is available for three lizard families, including representatives of Iguanidae (Alberts & Werner 1993; Hanley et al. 1999), Scincidae (Cooper 1996b; Bull et al. 2000), and Gekkonidae (Steele & Cooper 1997). Findings of a previous study suggest that males of the lacertid *L. monticola* may be capable of discriminating fecal pellets of familiar and unfamiliar conspecifics (Aragón et al. 2000). However, the results of this study were not significant, and other lacertid species remain unstudied in controlled laboratory settings. Given that lacertids vary widely in ecology and behavior, studies of additional species may lead to rewarding insights and provide a necessary database for truly comparative research (Burghardt 1993).

In this paper we experimentally investigate whether juveniles of the Iberian wall lizard, *Podarcis hispanica*, housed in small groups can recognize chemical signals from members of their own group and distinguish them from those of unfamiliar individuals belonging to another group. The results reported here provide the first conclusive demonstration of familiar conspecific recognition in a lacertid lizard. However, the direction of the discrimination in this species is opposite to that found in most previous studies of familiar conspecific recognition in lizards. We discuss possible reasons for the discrepancies between this and

previous studies and examine alternative hypotheses regarding the functional significance of familiar conspecific recognition in lizards.

Materials and Methods

The Iberian wall lizard, *Podarcis hispanica*, is a small (50–70 mm adult snout–vent length) diurnal heliothermic lizard found mainly in rocky habitats throughout the Iberian Peninsula, the Mediterranean coast of France, and northwest Africa. Subjects for this experiment were 10 juvenile *P. hispanica* (four males, six females) caught by hand at several sites around the city of Valencia (Spain) in July and Aug. 1997. Because eggs in this area first hatch out in July (Font, unpubl. data), the juveniles were less than 1 mo old at the time of capture. The lizards were collected from locations several kilometers apart and thus they probably belonged to different clutches and had never encountered one another prior to their arriving in the laboratory. Juveniles were tentatively sexed by counting ventral scales (Braña 1996) and individually identified by noting distinctive features of body coloration and design. All animal care and experimentation was conducted according to ABS/ASAB guidelines.

In the laboratory, groups of two to three juveniles of the same or different sex, matched for size, were housed in four glass terraria (50 × 25 × 30 cm) with an artificial grass substrate, a water dish, and rocks for basking and shelter. Each terrarium contained one or two additional juveniles that did not participate in the chemical discrimination tests. At least one juvenile of each sex was present in every terrarium. The terraria were held in a temperature-controlled room at ambient humidity, where light was supplied by fluorescent bulbs on a 14 h light : 10 h dark cycle. A 40-W incandescent lamp suspended over a basking rock provided additional heat and light during the light phase of the photoperiod. The terraria were lined with soft-board screens on three sides to provide visual isolation from lizards in adjacent terraria. Because all the terraria were kept in the same room, lizards could presumably detect odors, but not non-volatile vomodors (Cooper & Burghardt 1990) from conspecifics housed in neighboring terraria. Lizards were fed to satiation three times per week, the diet being small mealworm (*Tenebrio molitor*) larvae, supplemented occasionally with fruitflies and other small insects.

Experimental trials were conducted in Dec. 1997, more than 4 mos after the groups had been established. Trials consisted of gently picking up a juvenile and transferring it to a test terrarium (40 × 20 × 25 cm) for a 10-min observation period. The test terrarium was kept in the colony room under the same light, temperature and humidity conditions as the holding terraria. The floor of the test terrarium was covered with a filter paper substrate bearing chemical stimuli corresponding to one of three stimulus conditions. Paper substrates were prepared by placing an odor donor in the test terrarium in the evening preceding an experimental trial and allowing it to remain there until 10 min before the trial. Shed skin, feces and other obvious visual stimuli left by the odor donor were removed by gently brushing the paper substrate prior to the trial. For control

trials, the test terrarium was fitted with a clean paper substrate. Two lizards (one male, one female) acted only as donors of chemical stimuli. Each of the remaining eight juveniles was tested three times, once with a clean paper substrate (control), once with a paper substrate bearing chemical stimuli from a familiar cage-mate (i.e. another lizard in the same group), and once with a paper substrate with chemical stimuli from an unfamiliar conspecific (i.e. a lizard from another group). Familiar and unfamiliar odor donors were of the same sex, which in all but two cases also agreed with the sex of the respondent lizard. Each lizard was tested only once per day with an inter-trial interval of 2 d. The order of stimulus presentation was partially counterbalanced to avoid sequential bias. At the end of each trial, the paper substrate was discarded and the terrarium was washed thoroughly with water and alcohol to eliminate residual chemical traces. Trials were conducted between 15:00 h and 18:30 h (local time) when lizards were fully active. Room temperature at the time of testing was maintained at 25–26°C thus minimizing variability arising from thermal dependence of tongue-flick rates (Cooper & Vitt 1986).

We video-recorded each trial using a Panasonic S-VHS video camera and recorder with a temporal resolution of 50 frames/s. From the videotaped sequences we recorded the lizards' behavior with the aid of a portable computer equipped with event-recording software. We scored all occurrences of the following behaviors:

1 Tongue-flick: tongue-flicking, which indicates lingually mediated chemical sampling from vomerolfaction, is a widely used index of chemosensory investigation in squamate reptiles (Burghardt 1970; Graves & Halpern 1989; Cooper & Burghardt 1990; Halpern 1992). During a tongue-flick the lizard extrudes and rapidly retracts its tongue, either waving it in the air or touching the substrate or some other object with it. We therefore distinguished two types of tongue-flicks:

- air-licks: tongue extrusions into the air;
- tongue-touches: tongue extrusions that contact the substrate or the walls of the test terrarium. During tongue-touches directed at the substrate the head is typically tipped downward from the neck with the snout pointing slightly down.

2 Foot-shake: the lizard raises then lowers one or both forelegs several times in rapid sequence. Foot-shaking has been considered a putative appeasement display in lacertids (Steward 1965; Verbeek 1972; Thoen et al. 1986; Gómez et al. 1993).

3 Escape attempt: the lizard rubs its snout against the walls of the test terrarium, attempts to climb up the walls, or runs directly into them (see also Gómez et al. 1993).

4 Locomotion: two measures of locomotion were used:

- number of moves;
- time spent moving.

The significance of differences among stimulus conditions was tested using non-parametric Friedman two-way analysis of variance. Following detection of significant main stimulus effects, differences between pairs of stimuli were tested for significance using multiple comparison procedures (Siegel & Castellan 1988).

Alpha was 0.05 and significance tests were two-tailed. Data are presented as mean \pm SE.

Results

Responses to the paper substrate bearing different chemical stimuli are shown in Table 1. In the control condition, one lizard did not perform any air-licks and two did not perform any tongue-touches. All lizards performed air-licks and tongue-touches in the familiar and unfamiliar conditions. A non-parametric analysis of variance revealed a statistically significant difference among conditions for tongue-touches (Friedman's test, $F_r = 15.06$, $p < 0.01$), but not for air-licks ($F_r = 0.25$, ns). Seven of eight lizards directed more tongue-touches to paper substrates labeled by familiar than unfamiliar conspecifics, and there was one tie. In pair-wise comparisons of stimulus condition, lizards directed significantly more tongue-touches to paper substrates labeled by familiar conspecifics than to paper substrates labeled by unfamiliar conspecifics or to the blank control ($p < 0.05$ each comparison). Similarly, lizards directed more tongue-touches to paper substrates labeled by unfamiliar conspecifics than to the control ($p < 0.05$). The results were substantially similar regardless of whether the tested lizard and the odor donor were of the same or different sex. However, the small sample size precluded meaningful tests of differences between same-sex and different-sex trials. Thus, lizards showed a significantly stronger response, as measured by the number of tongue-touches, to the stimulus from a familiar cage-mate than to the stimulus from an unfamiliar conspecific, regardless of sex.

Table 1: Response of eight juvenile *Podarcis hispanica* to unlabeled (control) paper substrates and to substrates labeled by unfamiliar or familiar conspecifics. Numbers of tongue-touches differ significantly among all three stimulus conditions. Differences among stimulus conditions for the remaining variables are not statistically significant

Stimulus condition	Air-licks	Tongue-touches	Escape attempts	Number of moves	Time spent moving (s)
Control					
Mean	29.13	12.63	5.75	10.88	26.25
SE	8.85	5.87	3.24	5.39	14.75
Range	0–75	0–42	0–23	1–40	2–119
Unfamiliar					
Mean	33.88	32.75	5.50	16.75	37.38
SE	7.36	9.17	2.55	6.42	11.31
Range	6–66	5–71	0–17	0–41	0–88
Familiar					
Mean	39.63	72.25	8.75	24.38	70.25
SE	6.57	13.32	2.60	6.02	15.11
Range	8–73	9–123	0–17	0–46	0–130

Foot-shaking was infrequent and was observed only in lizards exposed to conspecific chemical stimuli. Three lizards performed foot-shakes in the unfamiliar and one in the familiar condition, but none performed foot-shakes in the control condition. None of the other behaviors recorded (escape attempts, number of moves, and time spent moving) showed significant differences among stimulus conditions.

Discussion

In this study, juvenile *Podarcis hispanica* lizards directed more chemosensory behavior (i.e. tongue-touches) towards paper substrates bearing chemicals from conspecifics than towards clean paper substrates. This result indicates an ability to distinguish pheromones from non-pheromonal chemical cues and extends the findings of a previous study showing that adults of this species tongue-flick at higher rates on paper substrates labeled by conspecifics than on paper substrates sprayed with water or cologne (Gómez et al. 1993). Juveniles also directed more tongue-touches towards paper substrates labeled by familiar cage-mates than towards paper substrates labeled by unfamiliar conspecifics. This result demonstrates that juvenile *P. hispanica* are capable of discriminating between the chemicals of conspecifics with whom they have shared living quarters for several months and those of conspecifics housed in a different terrarium.

That lizards can recognize familiar conspecifics pheromonally and discriminate between the pheromones of unfamiliar individuals and those of familiar cage-mates agrees with data for other lizard species (Alberts & Werner 1993; Cooper 1996b; Steele & Cooper 1997; Hanley et al. 1999; Bull et al. 2000). However, unlike the present study, in other species the discrimination is revealed by elevated numbers of tongue-flicks towards stimuli from unfamiliar conspecifics. Thus, adult male green iguanas, *Iguana iguana*, tongue-flick at a higher rate in response to femoral gland secretions of unfamiliar than familiar males (Alberts & Werner 1993). Juveniles of another iguanid species, *Ctenosaura similis*, tongue-flick more towards burrows and basking sites previously occupied by an unfamiliar conspecific than towards similar stimuli labeled by conspecifics with whom they have interacted for 3 d (Hanley et al. 1999). Sub-adults of *Egernia stokesii*, a gregarious skink from Australia, also tongue-flick more in response to paper substrates or scats from non-group members than to similar stimuli from group members (Bull et al. 2000). Males of the broad-headed skink, *Eumeces laticeps*, tongue-flick at a significantly greater rate towards pheromones of unfamiliar than familiar females (Cooper 1996b). Similarly, in male leopard geckos, *Eublepharis macularius*, chemical stimuli from unfamiliar females elicit more tongue-flicks than chemical stimuli from female cage-mates (Steele & Cooper 1997).

Possible exceptions to the pattern of greater responsiveness to chemicals from unfamiliar conspecifics have also been reported. Young and adult females of two Australian skink species, *Tiliqua rugosa* and *Egernia stokesii*, direct more tongue-flicks to gauze bags containing unrelated but familiar individuals than to bags

containing unrelated, unfamiliar individuals, although the difference did not reach statistical significance (Main & Bull 1996). In a field study of *Varanus griseus*, adult males were found to react differently to tracks left by familiar and unfamiliar conspecifics, with tracks from familiar individuals eliciting chemosensory investigation more often than similar tracks from unfamiliar individuals (Tsellarius & Men'shikov 1994). Results from these two studies, together with our own on *P. hispanica*, suggest that under some circumstances lizards direct more chemosensory investigation to chemicals from familiar than unfamiliar conspecifics. Further investigation is needed to decide whether the discrepancies between these and other studies are due to procedural differences or rather reflect interspecific variability in chemosensory responses.

Paradoxical results are not restricted to discrimination of familiar vs. unfamiliar chemicals and have also been found in studies dealing with other chemosensory discriminations (see also Allen et al. 1984). The response by reptiles to their own pheromones is usually indicated by a greater number of tongue-flicks being directed to chemicals from other conspecifics than to their own chemicals (e.g. *Nerodia sipedon*, Scudder et al. 1980; *Sceloporus jarrovi*, Bissinger & Simon 1981; *Thamnophis sirtalis*, Halpin 1990; *Tiliqua scincoides*, Graves & Halpern 1991; *Iguana iguana*, Alberts & Werner 1993; *Podarcis hispanica*, Gómez et al. 1993; *Eumeces laticeps*, Cooper 1996b; *Blanus cinereus*, López et al. 1997; *Liolaemus tenuis*, Labra & Niemeyer 1999). However, male *Eublepharis macularius* emit more tongue-flicks in response to their own pheromones than to those from other males (Steele & Cooper 1997; see also Alberts 1992). Several studies have shown that male lizards tongue-flick at higher rates in response to female than to male pheromones (e.g. *Eumeces laticeps*, Cooper & Vitt 1984; *Gerrhosaurus nigrolineatus*, Cooper & Trauth 1992; *Ameiva exsul*, Bofill & Lewis 1999; *Liolaemus tenuis*, Labra & Niemeyer 1999). Yet, males of the cordylid *Cordylus cordylus* exhibit higher tongue-flick rates when responding to male pheromones (Cooper et al. 1996). The response to cologne, a pungent odor control widely used in studies of pheromonal communication and chemical food discrimination in reptiles, is also paradoxical. Whereas a majority of studies report a lower chemosensory response to cologne than to pheromones or chemical food stimuli, others find just the opposite result (e.g. *Blanus cinereus*, López & Salvador 1992; see also López & Martín 1994). In all these experiments, a significant difference in the response to two or more stimuli is taken to imply detection of the chemical stimuli tested. However, there is no theory that predicts the direction of the difference. Collectively, these results underscore the need for more empirical and theoretical work that will allow predictions to be made concerning the direction of the discrimination.

In a recent paper, Hanley et al. (1999) raised the point that the direction and degree of response to unfamiliar vs. familiar chemical cues may be predicted from knowledge of the social relationship between familiar associates. In rodents, the amount of time an animal devotes to investigating a familiar cue has been shown to depend on its own competitive ability relative to that of the producer of the cue (Gosling et al. 1996). Similarly, the response of juvenile black iguanas, *Ctenosaura*

similis, to chemicals of familiar conspecifics seems to be influenced by the social relationship between the respondent lizard and the odor donor (Hanley et al. 1999). Iguanas tongue-flick more in response to chemicals from unfamiliar than familiar conspecifics, whereas *P. hispanica* juveniles show the opposite pattern of response. Perhaps the different results obtained with *C. similis* and *P. hispanica* may be explained by considering the social relationships of the juveniles to each other in nature. Juvenile iguanas show affiliative social behavior (Burghardt et al. 1977; Mora 1991; Hanley et al. 1999), whereas no such affiliative behaviors have been observed in juvenile lacertids. Natal dispersal in lacertids occurs mainly at the juvenile stage and is completed within the first few days after birth (Clobert et al. 1994). Juveniles establish exclusive territories from which other juveniles are aggressively displaced (e.g. Civantos 2000). In captivity, juveniles behave aggressively towards one another and casualties are relatively common when several lizards are kept in the same terrarium for an extended period of time (Font & Desfilis, unpubl. data). Hanley et al. (1999) did not observe any physical contact between the juvenile iguanas that were housed together for 3 d in their experiment. In contrast, physical contact usually resulting from agonistic interactions was frequent among juvenile *P. hispanica* from the same terrarium. Interestingly, the only iguanas that tongue-flicked in response to the chemical stimuli of familiar conspecifics in the study by Hanley et al. (1999) were those that had previously displayed aggression towards other juveniles. Thus, the overall higher rate of chemosensory investigation towards chemicals from familiar conspecifics shown by *P. hispanica* juveniles may be a response to familiar individuals who are likely to be aggressive.

It has often been assumed that habituation may be responsible for the differential response of lizards to chemicals from different categories of individuals (e.g. Cooper 1996b). If lizards spend less time investigating chemicals to which they have been previously exposed, the finding of an increased tongue-flick rate to chemicals from unfamiliar conspecifics in previous studies may have been simply a heightened response of lizards to novel stimuli, not necessarily recognized as pheromonal. However, habituation can be eliminated as an explanation for the chemosensory behavior of *P. hispanica*, because juveniles performed more tongue-touches in the presence of chemicals from familiar cage-mates than in the presence of similar chemicals from unfamiliar individuals. This is just the opposite of what would be expected if habituation were the mechanism underlying the lizards' ability to make this discrimination. The preferential response by juvenile *P. hispanica* to chemicals of familiar individuals may be explained by assuming that discrimination of familiar vs. unfamiliar conspecifics takes place with the first few tongue-touches. Additional tongue-touches may then be used for further assessment of chemicals from familiar conspecifics that could possibly yield information regarding social status, sex, or individual identity of the odor donor (see also Steele & Cooper 1997; Bofill & Lewis 1999). This enhanced chemosensory investigation would be of no use in the case of chemicals from unfamiliar lizards about whom the respondent lizard has no prior information.

The functional significance of familiar conspecific recognition in *P. hispanica* is obscure given that this species lacks parental care and juveniles do not show any affiliative behaviors after hatching. Previous studies have attributed this ability to natural selection favoring individuals who can recognize neighbors (Glinski & Krekorian 1985) or, in gregarious species, group members (Hanley et al. 1999; Bull et al. 2000), or those who can relocate their mates (Cooper 1996b). The latter interpretation seems unlikely because the present study was based on the response of juvenile, non reproductive individuals, and tests were conducted outside the normal spring mating period. A more likely interpretation is that lizards use information about familiarity to reduce the frequency and intensity of agonistic encounters with neighbors with whom they have previously interacted (Glinski & Krekorian 1985). Many lizards occupy territories from which trophic and sexual competitors are excluded (Stamps 1977; Martins 1994). Lizards may acquire information about the chemical signatures of neighboring territory holders and use this information to recognize territorial boundaries or to distinguish between intruders and neighbors, thereby saving time and energy in interactions with conspecifics. However, an alternative remains: that pheromonally based recognition of familiar individuals in this and perhaps in other studies using lizards is an epiphenomenon of some other recognition system, such as individual recognition. In several iguanid lizards the presence and relative concentration of pheromonal components show consistent individual differences which may convey information on the individual identity of the odor donor (Alberts 1991, 1992). Nevertheless, the ability of a lizard to individually recognize a conspecific does not necessarily dictate that it will show an operationally different response to that individual. Thus, it is possible that lizards may be able to individually recognize the chemical signatures of different conspecifics even if the experimental design only reveals a differential response to a few broad categories of individuals, such as familiar and unfamiliar. The results of the present study are consistent with the existence of individual recognition abilities in *P. hispanica*, although they cannot rule out an alternative explanation based on more limited discrimination abilities.

Although the present study did not address the question of what sensory modalities are involved in discrimination of familiar and unfamiliar conspecifics, there is little doubt that, under the conditions of this experiment, olfaction and vomerolfaction are of primary importance. The finding of a significant stimulus effect for tongue-touches but not for air-licks suggests that chemicals involved in this type of recognition are non-volatile and therefore likely to be perceived through vomerolfaction (Burghardt 1980; Halpern 1992). Chemicals used for intraspecific communication in lizards may come from the body surface, from the cloacal region, or from specialized organs such as femoral glands (Mason 1992). The presence of well-developed femoral glands suited for deposition of pheromones on rocky substrates suggests that this may be an important source of semiochemicals in male lacertids. However, femoral glands are not active in juveniles of either sex, and none of the lizards that we used appeared to be producing femoral gland secretions at the time the experiment was conducted. Fecal pellets, alone or in

combination with glandular secretions, are also a source of pheromones in some lizards (Duvall et al. 1987; Carpenter & Duvall 1995; Bull et al. 1999). Males of the lacertid *Lacerta monticola* can discriminate between their own fecal pellets and those from other males (López et al. 1998). In fact, a recent study suggested that chemical stimuli contained in fecal pellets may allow discrimination of familiar vs. unfamiliar conspecifics in this species, although the effect was restricted to large males and then only marginally significant (Aragón et al. 2000). Because fecal pellets were removed from paper substrates in our experiment, we infer that cloacal exudates or skin secretions passively transferred by donor lizards as they moved over the paper substrates may be the source of chemicals supporting discrimination of familiar vs. unfamiliar conspecifics in *P. hispanica*.

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