

## INTRASPECIFIC CHEMICAL RECOGNITION IN THE LIZARD *Liolaemus tenuis*

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**Abstract**—Experimental tests were conducted to determine whether females and males of the tree-dwelling lizard *Liolaemus tenuis* (Tropiduridae) show intraspecific chemical recognition during breeding and postreproductive seasons. Animals were individually maintained in plastic enclosures for one week. Thereafter, the number of tongue-flicks that a lizard performed in the enclosure of a male, a female, its own home enclosure, and a control (unused) enclosure were recorded. In both seasons, males and females made fewer tongue-flicks in their home enclosures than in any other one, indicating a recognition of a familiar place, probably a chemical self-recognition. Conspecific chemical recognition was season dependent. During the post-reproductive season, lizards tongue-flicked at similar rates in conspecific and control enclosures, while during the breeding season enclosures of females elicited more tongue-flicks by both sexes, and the overall tongue-flick rates were higher than in the postreproductive season. Results are discussed within the context of the social system of the species.

**Key Words**—*Liolaemus* lizards, conspecific chemical recognition, tongue-flick.

### INTRODUCTION

In recent years it has become clear that reptiles depend on more than vision for their orientation and communication. The importance of chemoreception for gathering information from the environment is now widely recognized (for reviews see Halpern, 1992; Mason, 1992). To sample the environment, squamates protrude their tongues to obtain chemical samples by touching either a

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substrate or the air, and then deliver these samples to the vomeronasal organ (Halpern, 1992). Much of our knowledge of squamate chemoreception and correlated behavioral phenomena pertains to snakes, which possess highly sensitive vomeronasal organs and utilize chemical stimuli in diverse ecological situations. Nevertheless, chemoreception is also widespread in lizards (Halpern, 1992; Mason, 1992; Cooper, 1994), although its use varies among lizard families (for reviews see Mason, 1992; Cooper, 1994). Because *Liolaemus* lizards (Tropiduridae) are sit-and-wait foragers, they would not be expected to detect prey chemicals (De Perno and Cooper, 1995; Cooper, 1994; 1995). However, no studies have been published of conspecific chemical recognition in any of the more than 150 species in this genus (Etheridge, 1995), nor in any other tropidurid.

Chemical secretions used in intraspecific communication may come from specific glands, such as urodaeal (Cooper and Trauth, 1992) and femoral glands (Alberts, 1993), from the body surface (Mason and Gutzke, 1990; Steele and Cooper, 1997), or from feces (Werner et al., 1987). One diagnostic characteristic of Tropiduridae is the presence of precloacal or preanal pores (Frost and Etheridge, 1989), which in most *Liolaemus* are only present in males (Donoso-Barros, 1966). These pores have been described as similar to sebaceous glands and more active during the breeding season (Donoso-Barros, 1966), when secretions appear enlarged and more reddish (A. Labra, personal observations). In gekkonid lizards these pores are openings of precloacal glands that produce holocrine secretions (Maderson, 1972), and in amphisbaenians these pores are associated with pheromonal secretions (Cooper et al., 1994). Therefore, even though it is not clear whether precloacal pores of *Liolaemus* are homologous with those described for other species, pheromone secretion is a distinct possibility.

The tree-dwelling *Liolaemus tenuis* is highly sexually dimorphic, males being more colorful and larger than females. The species has a polygynous mating system; males are territorial and females establish hierarchies based on agonistic behaviors inside a territory (Manzur and Fuentes, 1979). The widespread occurrence of pheromonal communication in lizards, the presence of precloacal pores in males with potential for deposition of pheromones on substrates, and observations that both sexes of *L. tenuis* tongue-flick the substrate after arriving at new locations (A. Labra, personal observation) suggest that *L. tenuis* might be responsive to conspecific chemical compounds. In this report, we present results of a study on intraspecific chemical recognition by *L. tenuis*. Because the rate of tongue-flick has been widely used as a good indicator of chemosensory investigation and discrimination of stimuli by squamates (Cooper and Burghardt, 1990a; Cooper, 1994, 1998), we recorded tongue-flicking performed by males and females in enclosures belonging to males or to females and within their own enclosures and control (unused) enclosures. During this investigation we addressed three questions: (1) Do individuals of *L. tenuis* show intraspecific

- chemical recognition, particularly towards males, which have precloacal pores?
- (2) Does *L. tenuis* show seasonal changes in intraspecific chemical recognition?
  - (3) Is chemical recognition dependent on sex?

#### METHODS AND MATERIALS

*Animals and Their Maintenance.* *L. tenuis* was collected at El Ingenio (30°46'S; 70°15'W; 1850 m) near Santiago, Chile. Twenty-one lizards (14 males, 7 females) were obtained during the postreproductive season in February and March 1997. During the breeding season, in October and November 1997, twenty-one lizards (11 males, 10 females) were collected. Animals were transported to the University of Chile and placed in a large outdoor vivarium exposed to ambient temperatures and natural photoperiod. Within the vivarium, lizards were housed individually in soil-filled plastic enclosures (30 × 19 × 10 cm) that were covered with thin plastic transparent mesh enabling lizards to climb. Because *L. tenuis* has been described as tree-dwelling, each enclosure contained a piece of water-washed tree bark (18 × 5 cm) of *Quillaja saponaria* (Rosaceae), one of the most common tree species at the capture site. The bark was used both as basking site and as shelter. Enclosures also contained a small bowl of water. Animals were fed mealworms every other day.

*Experimental Design.* Lizards remained in their enclosures for one week prior to experimentation. This allowed habituation to the experimental enclosures and deposition of chemical compounds, potentially active as pheromones. After the period, lizards were removed from their enclosures and maintained individually in fabric bags for 45 min; thereafter, their behaviors were recorded in two consecutive stages. In stage I, lizards were placed individually in one of the four experimental enclosure types: the empty home enclosure of a male (M), the empty home enclosure of a female (F), the home enclosure of the tested individual (H), or an empty control untreated enclosure (C). Thus, a lizard tested in a conspecific enclosure was exposed only to chemical signals and not to visual stimuli from a conspecific, since the owner was removed. After a lizard's behavior was recorded in stage I, it was removed and returned to its own fabric bag, where it remained for another 45 min. Thereafter, it was placed again in its home enclosure, and its behavior was recorded again (stage II). In some trials, while a lizard was maintained in its fabric bag between stages, its home enclosure was used to test the response of another individual in a conspecific enclosure. The process did not take longer than 20 min. Preliminary results indicated that the owner did not show differences in behavior upon returning to its home enclosure previously used by a conspecific.

The experimental enclosure was placed in a sunny patch, behind a curtain that had a hole through which the observer could watch the lizards. After the

first tongue-flick, the behavior was recorded for 10 min. The following variables were registered:

1. Tongue-flick (TF): the lizard extrudes and rapidly retracts its tongue, regardless of whether the tongue touches the substrate or is waved in the air.
2. Motion time: the time that animals remained in motion (minutes), which included adjustment in body posture, head movements (scanning), and displacements of the body's center of gravity through the habitat.
3. Latency to the first tongue-flick: the time period between placement of the lizard in the enclosure and onset of the first tongue-flick (minutes).

If the lizard retreated under the bark or failed to extrude the tongue within 45 min, the trial was canceled and postponed to a later date. Two males in the postreproductive season failed to tongue-flick and were discarded from the analysis. Only one two-stage trial per day was conducted for a given individual. Lizards had at least one day to rest before they were tested under a different experimental condition. Each animal was tested randomly in the four experimental conditions of stage I. With this design, the behavior of each animal was recorded in eight conditions (four in each stage). During experiments, handling was minimized to reduce stress and was similar in all trials. Experiments were restricted to late morning and early afternoon, at which times ambient temperatures were in the 30s (°C). When lowland *Liolaemus* have no constraints for thermoregulation, as was the case of *L. tenuis* in these experiments, lizards do not show seasonal changes in selected body temperature (Labra, 1998). Thus, experimental conditions ensured that lizards were fully active, not heat-stressed, and with similar body temperatures among seasons. All the animals were returned to the field after the experiments were finished.

In these experiments different enclosures were used instead of cotton swabs bearing conspecific chemicals (Cooper, 1998) because in pilot experiments with swabs lizards showed signs of stress and failed to show TF towards the swabs during more than 20 min.

*Analysis.* To test the effect of season, sex, condition (a total of eight conditions, four in each stage), and their interactions on number of tongue-flicks, motion time, and latency to the first tongue-flick, data were analyzed by parametric analysis of variance with a three-factor design and repeated measurements for condition (Edwards, 1968). After the ANOVA, Tukey's tests were used for individual comparisons. Even though two of the data sets were not normally distributed (female's latency in her own enclosure during breeding season and male's latency in the control during postreproductive season), and data of tongue-flick in males' enclosures showed heterogeneity of variance, ANOVA was used because it is robust enough to perform well even if the data deviate from the requirements of normality, homoscedasticity, and additivity (Zar, 1984). As a check of this procedure, a nonparametric approach was used. Data were ranked and ANOVA was used as described above with a posteriori test for multiple

comparisons (Zar, 1984). This latter approach was used to analyze differences among conditions, considering season and sex as a block and excluding variability within the block. Additionally, the original data were log transformed, and an ANOVA was performed. Since the results obtained with different approaches were consistent, only results of parametric tests were presented. Finally, Pearson correlations were used to test relationships between variables.

## RESULTS

When animals were placed in any of the experimental enclosures, they spent a short time (about 1 min) breathing rapidly, possibly due to the stress of being handled. However, exploratory behavior began soon thereafter. There was a tendency towards longer latency to first tongue-flick by lizards placed in the control enclosures and shorter latency when they were tested in their home enclosures in stage I (Figure 1). Nevertheless, there was no significant effect of any factor or interaction of factors on latency to the first tongue-flick ( $P > 0.05$ ).

Results for tongue-flick are presented in Table 1. During the breeding sea-

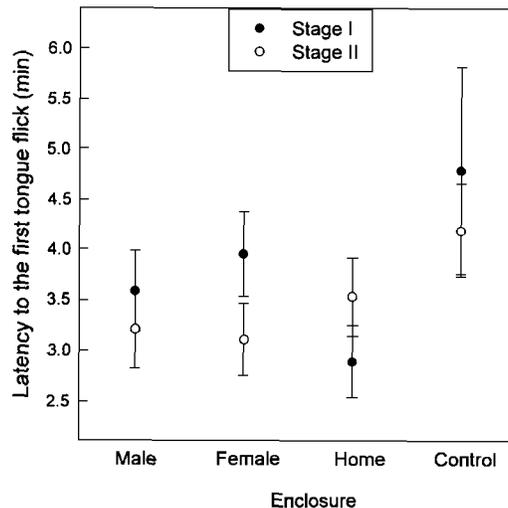


FIG. 1. Mean  $\pm$  SE latency time to the first tongue-flick exhibited by *Liolaemus tenuis* in the two stages of the experiments. In stage I, animals were placed in one of the following conditions: male, female, home, or control enclosure. In stage II, animals were returned to their home enclosures after being tested in stage I. Test period lasted 10 min. Since sex and season did not have any effect in the latency to the first TF, data for both sexes and seasons were pooled.

TABLE 1. TONGUE-FLICKS MADE IN TWO SEASONS BY MALE AND FEMALE *Liotaemus tenuis* IN DIFFERENT CONDITIONS<sup>a</sup>

Season and sex	N	Stage I				Stage II			
		Male (M)	Female (F)	Home (H)	Control (C)	M-H	F-H	H-H	C-H
Post-reproductive									
Male	12	20.58 ± 3.57	19.08 ± 2.49	9.50 ± 0.81	21.17 ± 3.99	4.67 ± 1.22	5.33 ± 0.80	4.83 ± 1.21	5.58 ± 1.11
Female	7	15.86 ± 2.54	14.14 ± 2.84	9.14 ± 1.16	13.71 ± 2.35	7.71 ± 1.29	7.71 ± 1.82	6.43 ± 1.82	5.29 ± 1.11
Breeding									
Male	10	23.10 ± 2.15	32.40 ± 7.64	10.70 ± 1.40	25.40 ± 3.37	6.50 ± 0.99	6.50 ± 1.65	5.50 ± 1.08	6.30 ± 1.72
Female	11	22.09 ± 0.83	27.00 ± 2.46	13.45 ± 2.06	22.73 ± 2.18	5.45 ± 0.73	8.82 ± 1.17	6.45 ± 1.04	7.36 ± 0.54
Overall mean ± SE	40	20.80 ± 1.31	23.72 ± 2.38	10.82 ± 0.76	21.35 ± 1.69	5.88 ± 0.54	7.00 ± 0.67	5.73 ± 0.61	6.20 ± 0.59

<sup>a</sup>Stage I: Tested enclosures of Male (M), Female (F), Control (C) and the Home (H). Stage II: M-H: home enclosure after male's enclosure. F-H: home enclosure after female's enclosure. H-H: home enclosure after home enclosure and C-H: home enclosure after control enclosure. N = sample size. The period of recording was 10 min. Values are means ± standard errors. The overall mean of each treatment is indicated also.

TABLE 2. REPEATED-MEASURES ANALYSIS OF VARIANCE OF EFFECTS OF SEX (MALE VERSUS FEMALE), SEASON (BREEDING VERSUS POSTREPRODUCTIVE), EXPERIMENTAL CONDITION (DIFFERENT ENCLOSURES, INCLUDING RESULTS OF STAGES I AND II), AND THEIR INTERACTION UPON TONGUE-FLICK

Source of variation	<i>F</i>	<i>df</i>	<i>P</i>
Between subjects			
Season	6.833	1,36	0.013
Sex	0.373	1,36	0.545
Season × sex	0.117	1,36	0.735
Within subjects			
Condition	51.626	7,252	<<0.0001
Condition × season	4.366	7,252	0.0001
Condition × sex	2.060	7,252	0.048
Condition × season × sex	0.465	7,252	0.859

son lizards exhibited a significantly higher number of TF than during the postreproductive season (Table 2). Males and females did not show a significant difference in TF (Table 2). The experimental condition had a significant effect upon tongue-flicking. A Tukey test indicated that lizards exhibited significantly more TF in any novel environment than in their home enclosure (compare in Table 1 data for H with data for M, F, or C), and there were no significant differences of TF among M, F, and C enclosures. The number of TF when lizards were placed for the first time in their home enclosure was significantly higher than the number of TF recorded in stage II (compare in Table 1 data for H with M-H, F-H, H-H, and C-H). TF recorded in the different conditions of stage II did not differ significantly among them, and they were significantly lower than those recorded in any stage I condition (Table 1).

The interaction between season and experimental condition was significant (Table 2); female enclosures elicited significantly more TF in the breeding than in the postreproductive season, and in the latter season, lizards exhibited a similar number of TF in any novel enclosure (Figure 2). The interaction between sex and condition was significant (Table 2). Males showed more TF in a novel enclosure than females, but not in home enclosures in either stage. However, the interaction between season, sex, and experimental condition was not significant (Table 2).

The number of TF performed in the air during both seasons was much lower than those performed on the substrate, 25 (1.5% of total) and 4 (0.16% of total) during postreproductive and breeding season, respectively. A Pearson correlation of the pooled data of the number of TF and latency to the first tongue-flick indicated that the two variables were not correlated ( $r = 0.063$ ;  $P = 0.26$ ;  $N = 320$ ).

The first TF was always preceded by movements of the head (scanning).

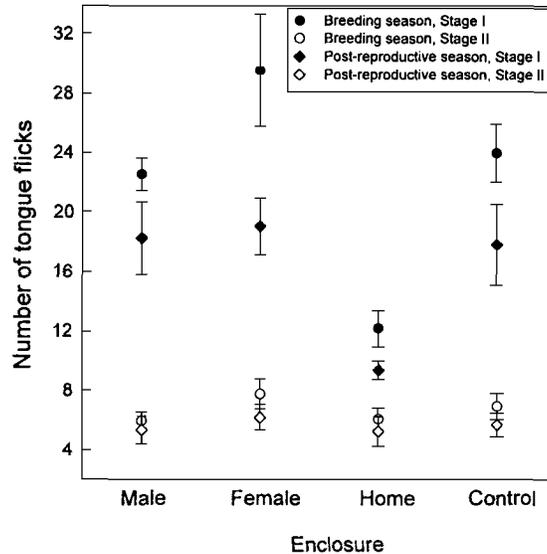


FIG. 2. Mean  $\pm$  SE number of tongue-flicks exhibited by *Liolaemus tenuis* in two seasons (postreproductive and breeding) in the two stages of the experiments. The stages are explained in Figure 1 legend. Test period lasted 10 min. Since males and females did not show differences in TF, data for both sexes were pooled.

However, the only factor affecting motion time was experimental condition (Table 3). Animals spent significantly more time performing some movement during stage I than during stage II (Figure 3). Nevertheless, the time that animals spent moving in their home enclosures in stage I did not differ from any other experimental condition (Figure 3).

Motion time and TF showed a significant and positive relationship ( $r = 0.58$ ;  $P < 0.05$ ;  $N = 320$ ). In contrast, motion time was not correlated with the latency to the first tongue-flicking ( $r = 0.091$ ;  $P = 0.105$ ;  $N = 320$ ).

#### DISCUSSION

The experiments described show that both sexes of *L. tenuis* respond differently to their home enclosures than to enclosures belonging to conspecifics during both seasons. Both sexes also showed no overall differences in the behaviors recorded. Lizards showed lower TF in their home enclosures than in any novel enclosure. The close relationship reported between tongue-flicking and vomerolfaction (Cooper, 1998) suggests that chemical compounds or vomodors (*sensu* Cooper and Burghardt, 1990b) are likely involved in this home recog-

TABLE 3. REPEATED-MEASURES ANALYSIS OF VARIANCE OF EFFECTS OF SEX (MALE VERSUS FEMALE), SEASON (BREEDING VERSUS POSTREPRODUCTIVE), EXPERIMENTAL CONDITION (DIFFERENT ENCLOSURES, INCLUDING RESULTS OF STAGES I AND II), AND THEIR INTERACTION UPON MOTION TIME

Source of variation	<i>F</i>	<i>df</i>	<i>P</i>
Between subjects			
Season	1.121	1,36	0.297
Sex	3.231	1,36	0.081
Season × sex	0.001	1,36	0.982
Within subjects			
Condition	8.493	7,252	<<0.001
Condition × season	0.894	7,252	0.512
Condition × sex	0.786	7,252	0.599
Condition × season × sex	0.755	7,252	0.626

dition, probably recognition of self-produced pheromones or pheromones produced by other individuals. Pheromonally mediated self-recognition might allow the maintenance of a territory at a lower cost by reducing visual displays and/or aggression among conspecifics. These factors may be important selective forces

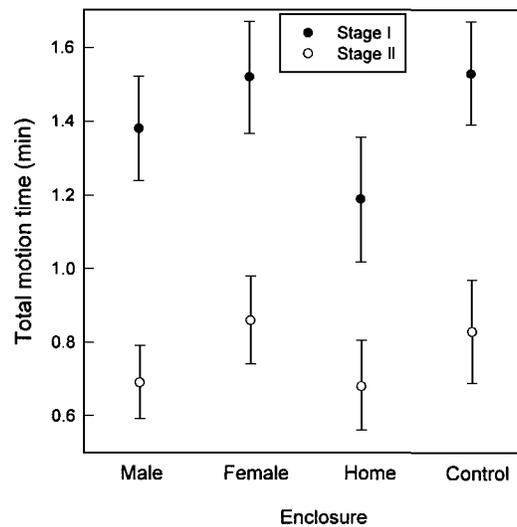


FIG. 3. Mean  $\pm$  SE total motion time exhibited by *Liolaemus tenuis* in the two stages of the experiments. The stages are explained in Figure 1 legend. Test period lasted 10 min. Since sex and season did not have any effect in the latency to the first TF, data for both sexes and seasons were pooled.

for chemical self-recognition, which has been observed in different lizard families such as Iguanidae (Alberts, 1992), Phrynosomatidae (De Fazio et al., 1977), Polychrotidae (Greenberg, 1985), Scincidae (Graves and Halpern, 1991), and now in Tropicuridae.

The lower motion time coupled with reduced TF in stage II indicates an overall reduction of exploratory behavior. This might be due to habituation to handling (Gómez et al., 1993), or be a consequence of recent chemosensory investigation during stage I. During the habituation period lizards only explored their territories, having no possibility to contrast signals of their territories with those of other lizards. Animals placed in any enclosure in stage I might "establish" differences or similarity with signals of their home enclosures based on the recall and contrast of chemicals or/and other signals.

Seasonal differences in chemical exploratory behavior were observed that were not coupled with differences in motion time. During the postreproductive season, the overall rate of TF was lower than in the breeding season and lizards did not discriminate among the different unfamiliar enclosures (Figure 2). In contrast, in reproductive season both sexes showed recognition toward females, and female enclosures elicited more TF. These seasonal behavioral differences might be related to seasonal physiological differences. In the autumn (postreproductive season), *L. tenuis* is preparing itself for hibernation and probably conspecific recognition is not a priority. In contrast, a higher chemical exploratory behavior exhibited during the breeding season would be important for reproduction-related behaviors, such as mate searching and territory establishment (Moore and Lindlezy, 1992; Whittier and Tokarz, 1992). For a reproductive and polygynous *L. tenuis* male, the detection of a female would be important, since males may initiate behaviors to attract a female to its territory. Consexual chemical recognition of females can be understood considering that females exhibit agonistic behavior inside a male's territory and tend to establish hierarchies (Manzur and Fuentes, 1979). Chemical recognition might help to reduce agonistic encounters among females inside a male's territory.

Intraspecific recognition in *L. tenuis* appears to be mainly mediated by non-volatile substances, since most TF were performed to the substrate rather than to the air. Tongue flicking is a requisite for gathering and transporting these substances to the vomeronasal organ (Halpern, 1992; Cooper, 1994). Additionally, the latency to the first TF was similar among experimental conditions, including the control. If the chemical cues had been volatile, a relationship between latency to the first TF and the number of TF (Cooper et al., 1994) or differences in TF between the conspecific and control enclosures would be expected. Alternatively, it is known that lizards can also recognize a territory by visual cues, such as feces (Duvall et al., 1987) or UV light absorbed by pheromones (Alberts, 1989). Since *L. tenuis* had a similar number of TF in conspecific enclosures and enclosures lacking visual signals of the presence of other lizards, visual cues probably were

not an important source of information in these experiments. For the recognition of the home enclosure, minimal structural or chemical differences between the bark present could have been used by lizards as signals to determine a site as familiar. However, bark was not the main site used for chemical recognition, since most of TF were performed directly to the soil and less than 30% to the bark.

It remains unclear where the pheromones involved in intraspecific chemical recognition in *L. tenuis* are produced. Tropicidurid lizards lack femoral glands (Frost and Etheridge, 1989), one of the most studied pheromone-producing glands in lizards (Mason, 1992; Alberts, 1993). However, the precloacal pores of *L. tenuis* males have a histology similar to femoral glands (Labra and Niemeyer, unpublished data), and they are a potential source of pheromones for males. Because neither sex displayed higher TF in male enclosures, even in the breeding season, it is not clear whether precloacal secretions of *L. tenuis* males are involved in territorial marking, male recognition, and female attraction. It is possible that pheromonal products might be detected and identified without prolonged chemosensory investigation.

Females of *L. tenuis* lack precloacal pores and urodaeal glands are a hypothetical source of pheromones for females. These glands, present only in the cloaca of females (Mason, 1992), produce lipid secretions acting as pheromones in *Eumeces laticeps* (Cooper et al., 1986) and *Gerrhosaurus nigrolineatus* (Cooper and Garstka, 1987). Further research is needed to determine the site of pheromone production in both sexes of *L. tenuis*.

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