

Prey chemical discrimination and strike-induced chemosensory searching in the lizard *Liolaemus zapallarensis*

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Summary. Experimental tests were conducted to determine whether the ambush foraging iguanian lizard, *Liolaemus zapallarensis*, was capable of discriminating prey chemicals from control substances and whether this lizard exhibits strike-induced chemosensory searching (SICS) or its components after biting prey. The two components of SICS are a poststrike elevation in tongue-flicking rate (PETF) and apparent searching movements for relocation of prey that has been bitten, but released or escaped. *Liolaemus zapallarensis* failed to discriminate prey chemicals from control substances, but exhibited significant PETF lasting one minute. SICS was absent in *L. zapallarensis* because no post-strike movements were observed. The absence of both prey chemical discrimination and SICS exhibited by *L. zapallarensis* is common to all the insectivorous iguanians and ambush foraging lizards studied to date. However, *L. zapallarensis* is the first insectivorous iguanian species shown to exhibit PETF. The results suggest that *L. zapallarensis* does not use the tongue for detection, identification, or relocation of prey while foraging. The possibility does remain that *L. zapallarensis* may be capable of chemically identifying prey once the prey stimuli reach the oral cavity.

Key words. Prey chemicals – tongue-flicking – PETF – SICS – insectivorous – Reptilia Lacertilia – Iguania – Tropiduridae – *Liolaemus zapallarensis*

Introduction

Chemical discrimination of prey based on tongue-flicking prior to attack occurs in several families of lizards (Cooper 1990a). The ability to discriminate prey chemicals in lizards is correlated with foraging mode and may be important to many lizards in locating and identifying prey (Cooper 1989a). Discrimination of prey chemicals from control stimuli is present in several families of active foragers (Cooper 1989a,b, 1990b,c) which move through the environment while seeking their prey and rely on prey chemicals to detect prey (Cooper 1989a,b, 1990c). However, prey chemical discrimination is absent in several families of sit-and-wait foragers: Phrynosomatidae, Polychridae, and Chamaeleonidae (Curio & Mobius 1978; Simon *et al.*

1981; Cooper 1989b,c), which remain immobile much of the time while foraging, and use vision as the primary means of detecting prey. Active foragers are more likely to use chemical cues to relocate and recover prey that has escaped or been released than are ambush foragers.

Strike-induced chemosensory searching (SICS) is a unique squamate chemosensory behavior. SICS consists of a combined increase in tongue-flicking rate and locomotory searching behavior that occurs after a prey item has been bitten and then escapes, is voluntarily released, or is removed from the mouth. The tongue-flicking component of SICS is referred to as poststrike elevation in tongue-flicking (PETF) (Cooper 1991). SICS presumably helps lizards find and follow odor trails of released or escaped prey (Cooper 1989c) and may aid in the location of other individuals of the same prey type that may be in the immediate vicinity (Cooper 1991).

SICS was originally studied in rattlesnakes (Chiszar & Scudder 1980). These snakes strike large prey, then release it voluntarily. Shortly after releasing the envenomated prey, a rattlesnake greatly increases its tongue-flick rate and follows the prey's trail by tongue-flicking. By the time the prey is relocated, it has died or is greatly weakened and no longer poses a threat to the snake. Thus, SICS allows the snake to attack dangerous prey with a greatly reduced chance of being injured (Chiszar & Scudder 1980; Chiszar *et al.* 1982, 1983, 1985, 1986).

Recently, SICS has been demonstrated in two species of nonvenomous snakes that do not use a strike-release-trail strategy (Cooper *et al.* 1989), and in several species of lizards including a varanid, *Varanus exanthematicus* (Cooper 1989c), a cordylid, *Gerrhosaurus nigrolineatus* (Cooper 1992a), and a lacertid, *Podarcis muralis* (Cooper 1991). From these findings Cooper (1989c) hypothesized that SICS may occur in any squamate that uses the lingual-vomeroneasal system extensively during foraging.

This paper reports the first experiments on the possible presence of prey chemical discrimination, PETF, and SICS in a tropidurid lizard, *L. zapallarensis*. The family Tropiduridae is part of the iguanian radiation (Camp 1923; Estes *et al.* 1988), members of which are typically sit-and-wait foragers and have long been believed to use visual, rather than chemical cues in

social behavior and feeding (Evans 1961; Cooper 1989b). Tropicidurids are sit-and-wait foragers, but there is no specific information available on the diet and feeding ecology of the multi-colored swift, *L. zapallarensis*.

All available information suggests that insectivorous iguanian lizards that are strict ambush or sit-and-wait foragers neither discriminate chemical prey cues from chemical control stimuli nor use chemical cues while foraging (Cooper 1989b, 1990b, 1992b). If a strict ambush forager were to strike a prey item and the prey item were to escape, continued ambush tactics would preclude relocation of prey by tongue-flicking in most instances. Cooper (1992b) therefore predicted that SICS and PETF may be absent or reduced in lizards that do not discriminate prey chemicals from control substances and in those that do not use the tongue to detect chemical prey cues while foraging. Here, we predicted that *L. zapallarensis*, would not demonstrate prey chemical discrimination, PETF, or SICS.

Materials and methods

Animals and maintenance

Fifteen adult *L. zapallarensis* were obtained from a commercial dealer. The lizards were allowed to become habituated to the laboratory conditions for at least three weeks prior to the beginning of testing. The experiments were conducted between 1000 and 1600 h when the lizards were active. Each lizard was housed individually in a 51 × 26 × 32 cm glass terrarium with a sand substrate and a plastic shelter. The ambient room temperature was maintained at 28–30°C and heat lamps allowed thermoregulation during the lighted portion of a 12:12 LD light cycle. Water and food were available *ad libitum*. Each lizard ate normally following all experimental condition.

Prey chemical discrimination

The ability of *L. zapallarensis* to discriminate chemical prey stimuli from control stimuli by tongue-flicking was tested experimentally by presentation of chemical stimuli on cotton-tipped applicators (Burghardt 1967; Cooper & Burghardt 1990a). Each of fifteen adults were tested for responses to prey surface chemicals, cologne, and distilled water. Distilled water was an odorless control for reactions to the experimental setting. Cologne was a pungency control, *i.e.*, a control for reactions to a highly volatile stimulus that lacks trophic or social relevance. Stimuli were prepared by immersing the cotton tip of an applicator in distilled water and then adding other stimuli if necessary. Prey chemical stimuli were imparted by pressing the wetted swab on the integument of a domestic cricket and rolling it across the integumentary surface to obtain a chemical sample that was both representative of much of the cricket's surface and evenly distributed on the swab. Cologne (Mennen Skin Bracer, Spice Scent) was added to a moistened swab by brief immersion.

The experiment was conducted on 4 May 1992 between 1000 and 1500 h when the lizards were fully active. The lizards were not fed during the four days before the experiment. Plastic shelters were removed from home terrariums one hour before the first trials began and were not replaced until the end of the experiment. Although the ambient air temperature in the room was only 26°C, sand surface temperatures near the heat lamps were in the low to mid 30s. Although we did not measure lizard body temperatures, they were normally in the low 30s in the laboratory conditions. This is important because tongue-flicking rates in lizards are affected by temperature (Cooper & Vitt 1986). However, there is no evidence that tongue-flick rates to various stimuli are differentially affected.

Each trial was begun by preparing a fresh stimulus, slowly approaching a lizard's terrarium, removing its screen top carefully to avoid noise or mechanical disturbance, and placing the cotton tip of an applicator 1.5 cm anterior to a lizard's snout. Tongue-flicks and bites directed to the swab were recorded for 40 s. Because no tongue-flicks occurred in most trials, after 40 s and again at 50 s, the swab was gently brought into contact with the lizard's anterior labial scales. This procedure often induces tongue-flicking. Tongue-flicks were recorded until the trial was terminated after 60 s.

Variables analyzed were numbers of tongue-flicks, tongue-flick attack scores (TFAS(R)), and number of bites. TFAS(R) combines tongue-flicking and biting in a composite measure of response strength. If no biting occurs, TFAS(R) is the number of tongue-flicks. If a lizard bites, TFAS(R) is the greatest number of tongue-flicks performed by that lizard in any of the experimental conditions plus (trial duration – latency to bite in seconds). In this experiment, trial duration was 40 s for analysis of responses prior to touching a swab to labial scales, 60 s for all data, and 20 s for data after a lizard was touched by a swab. Use of TFAS(R) ensures that biting, indicating a strong predatory response, is weighted more heavily than any amount of tongue-flicking.

The three conditions were presented in an incompletely counter-balanced sequence in which each stimulus was presented to an equal number of lizards in each of the three trials. Because no tongue-flicking or biting occurred in many trials, the assumption of normality required for parametric analysis of variance was violated. Data were analyzed nonparametrically by Friedman two-way analysis of variance (Siegel 1956) using an alpha value of 0.05 and two-tailed tests. Other nonparametric tests were conducted as in Siegel (1956).

PETF and SICS

The experimental design used to investigate the presence of PETF and SICS was that of Cooper (1989c). Fourteen adult *L. zapallarensis* were tested in a partially counterbalanced order in four stimulus conditions. The lizards were not fed for three days prior to each experimental condition to ensure feeding motivation among stimuli. Each lizard was tested once per day. Plastic shelters were removed from the terrariums prior to each experimental condition and replaced immediately at the conclusion of that trial.

A trial was begun when the investigator slowly approached the terrarium, removed the lid of the terrarium, and positioned one of the experimental stimuli approximately twenty centimeters anterior to the lizard's snout for fifteen seconds, except as noted below.

The string condition consisted of visual presentation of hand-held string, which was used in other conditions to tether live crickets (*Acheta domesticus*). The string condition served as a disturbance control for effects of the presence of the experimenter's hand, string, and opening the lid of the cage on the lizard's tongue-flicking rate.

The visual condition consisted of visual presentation of a live cricket. In this condition the tethered cricket was shown to the lizard for fifteen seconds without allowing the lizard to approach, tongue-flick the prey directly, or attack the prey. If the lizard approached the prey, the prey was immediately removed from the terrarium.

The pull condition served as a control for the effects of removing bitten prey from a lizard's mouth. In this condition the tethered cricket was presented to the lizard until the lizard showed signs of preparing to attack. The prey was then immediately removed from the terrarium and the lizard simultaneously grasped and pulled away from the prey, before any oral contact with the prey occurred.

In the strike condition, the lizard was allowed to bite the prey item. The prey was pulled out of the lizard's mouth immediately after having been bitten. This was accomplished by grasping the lizard with two fingers directly behind the head and simultaneously pulling the string in order to remove the bitten prey. Forced removal of prey from a lizard's mouth is a somewhat drastic experimental procedure that requires contact with the lizard, but is necessary for demonstration of PETF in species that do not voluntarily release their prey (Cooper 1991). Although forced removal of prey might seem likely to have behavioral effects beyond those on tongue-flicking, such as increased locomotion, the disturbance does not elicit the full SICS response (Cooper *et al.* 1989).

After termination of the experimental stimuli, tongue-flicks and putative searching movements were counted in all conditions. A

searching movement began when the lizard crawled and ended when the lizard stopped moving. Tongue-flicks and searching movements were recorded for two minutes. PETF was considered to be present if there was a significantly higher number of tongue-flicks in the strike condition than in all three of the control conditions. SICS was present if PETF was accompanied by a significant higher number of searching movements in the strike condition than in all three of the control conditions (Cooper 1991).

Data for PETF and SICS were nonnormal due to the presence of many zero values and the variances were intractably heterogeneous. Therefore, they were analyzed nonparametrically by a Friedman two-way analysis of variance for each minute (Siegel 1956) followed by multiple comparisons (Hollander & Wolfe 1973; Zar 1974). Statistical tests are two-tailed with $\alpha = 0.05$ unless stated otherwise.

Results

Prey chemical discrimination

The lizards exhibited low tongue-flick rates in all conditions, even after being stimulated by contact with swabs, and the lizards rarely bit the swabs (Table 1). Most tongue-flicks were typical straight extensions outside the oral cavity, but some individuals extended their tongues only enough to lick either their anterior or lateral labial scales. Such labial-licks were observed only after contact with swabs following either biting, tongue-flicking, or being touched on the labials by swabs.

Prior to touching of the labial scales with a swab, the most frequent response was no tongue-flicking. Only 3 of the 15 lizards tongue-flicked in the cricket condition, 6 in the cologne condition, and 2 in the distilled water condition. Only 2 individuals bit swabs, both in the cologne condition; one of them bit prior to any lingual protrusions. The main stimulus effect was not significant for either tongue-flick rate ($X^2 = 3.07$, $df = 2$, $P > 0.10$) or TFAS(R) ($X^2 = 5.63$, $df = 2$, $P > 0.10$). Total ranks of responses elicited by cricket stimuli and distilled water were nearly identical.

Responses to cologne were slightly stronger than the cricket and distilled water stimuli, but not markedly. Both individuals that bit, and only those individuals, subsequently performed labial-licks. Addi-

tional signs that some lizards detected cologne were that 2 individuals opened their mouths and one shook its head, both rare responses in other contexts. Combining biting, opening mouths, and head-shaking as indications of reactions to cologne, 5 individuals reacted to cologne and none reacted to either of the other stimuli. Under the hypothesis that cologne, being volatile, is more likely than the other stimuli to be detected even in the absence of tongue-flicking, cologne is significantly more likely to be detected than either cricket stimuli or distilled water (sign tests, $P = 0.03$ each).

During the interval after the snout was touched by a swab, no individuals bit. A higher proportion of individuals tongue-flicked in the initial 40 s than in the cricket and distilled water conditions, but not in the cologne condition. In the cricket condition, 12 lizards tongue-flicked at least once, a significantly greater proportion than in the initial 40 s (McNemar test, $P < 0.01$). In the water condition, 7 individuals tongue-flicked once or more, and the proportion of individuals tongue-flicking was significantly higher than in the initial 40 s (McNemar test, $P = 0.03$). Only 7 individuals tongue-flicked in the cologne condition, one more than in the first 40 s. However, of these 7, 6 had not tongue-flicked earlier.

After lizards were touched by a swab, the pattern of rank sums differed from that in the initial time period in that the rank sums were nearly equal for cologne and distilled water, but indicated somewhat stronger response to cricket stimuli. However, the condition effect was not significant ($X^2 = 3.73$, $df = 2$, $P > 0.10$, tongue-flicks = TFAS(R) in the absence of any biting). Ordinal data for the entire 60 s revealed no indication of prey chemical discrimination for tongue-flicks ($X^2 = 1.73$, $df = 2$, $P > 0.10$) or for the TFAS(R) ($X^2 = 1.60$, $df = 2$, $P > 0.10$).

Labial-licks occurred either after biting or after contact with swabs, but never prior to biting or other direct contact. In the initial 40 s 2 individuals performed labial-licks in 3 trials. One lizard in the cricket condition licked its labials twice after contacting the swab by tongue-flicking. In the cologne condition, both individuals that bit subsequently performed labial-licks. One of these licked its labials in the cricket condition. Labial-licks occurred in a significantly higher proportion of trials in the cologne condition following biting than in trials in which biting did not occur (Fisher test, $P < 0.02$). In the final 20 s two individuals licked their labial scales, one in the cricket condition and one in the cologne condition. For the entire 60 s two lizards licked their labials in the cricket condition, three in the cologne condition, and none in the distilled water condition.

Results of statistical analysis for total lingual protrusions, the sum of labial-licks and tongue-flicks, are similar to those based on tongue-flicks alone. In the initial 40 s, there is no significant variation among conditions ($X^2 = 2.03$, $df = 2$, $P > 0.10$ for lingual protrusions and $X^2 = 2.10$, $df = 2$, $P > 0.10$ for an inclusive TFAS(R)). Statistical values in the final 20 s were

Table 1 Responses by 15 adult *Liolaemus zapallarensis* during the initial 40 s of exposure to stimuli on cotton-tipped applicators. n = number of individuals with nonzero responses

	Cricket	Cologne	Water
<i>Tongue-flicks</i>			
$\bar{x}$	0.2	1.1	0.3
SE	0.1	0.5	0.3
n	3	6	2
<i>TFAS(R)</i>			
$\bar{x}$	0.2	3.5	0.3
SE	0.1	2.0	0.3
n	3	7	2
<i>Labial-licks</i>			
$\bar{x}$	0.1	0.7	0.0
SE	0.1	0.5	—
n	1	2	0

identical for tongue-flicks and total lingual protrusions. For the entire 60 s trial no differences among conditions were apparent ($X^2_r = 2.03$, $df = 2$, $P > 0.10$) for both lingual protrusions and the inclusive TFAS(R).

PETF and SICS

Liolaemus zapallarensis exhibited two distinct lingual behaviors, labial-licking and tongue-flicking. The number of tongue-flicks (Fig. 1), labial-licks (Fig. 2), and their combined values (Fig. 3), varied significantly among all conditions only during minute one. No movement was observed during any of the conditions during minute one or minute two.

The main treatment effect for tongue-flicks in minute one was highly significant ($n = 14$, $X^2_r = 14.19$; $df = 3$; $p < 0.001$). In minute one the number of tongue-flicks in the strike condition was significantly greater than in the pull condition ($p < 0.05$), the visual condition ($p < 0.025$), and the string condition ($p < 0.025$).

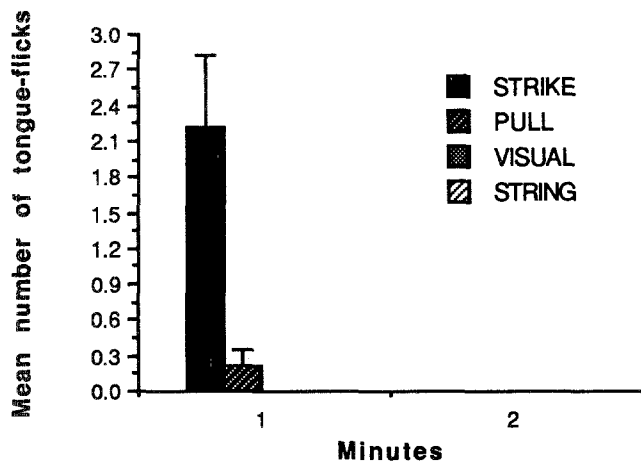


Fig. 1 The mean number of tongue-flicks emitted by *Liolaemus zapallarensis* for two minutes following the removal of the experimental stimuli

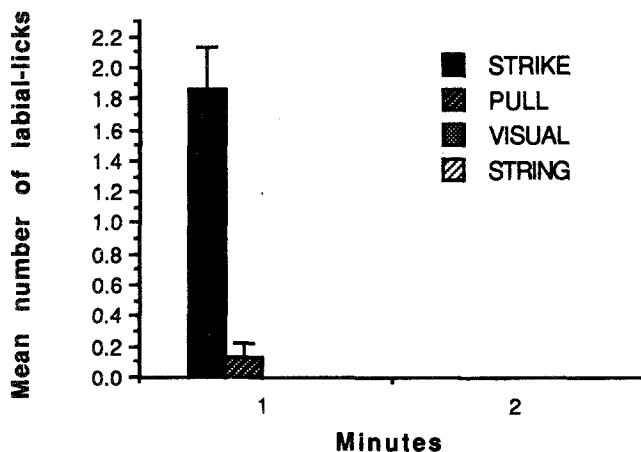


Fig. 2 The mean number of labial-licks emitted by *Liolaemus zapallarensis* for two minutes following the removal of the experimental stimuli

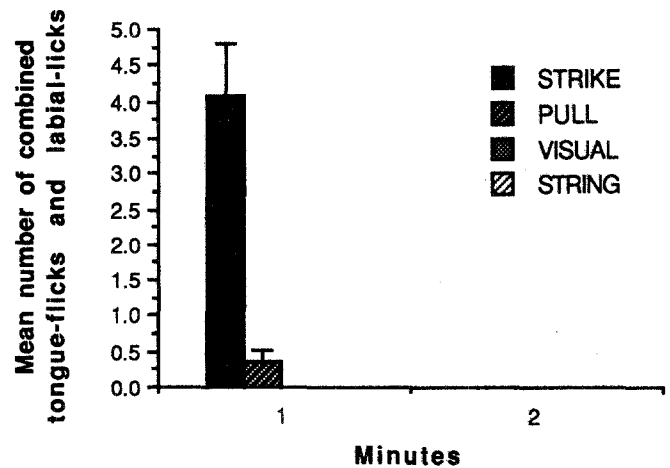


Fig. 3 The mean number of combined tongue-flicks and labial-licks emitted by *Liolaemus zapallarensis* for two minutes following the removal of the experimental stimuli

No other differences were significant between pairs of conditions. No tongue-flicks were observed in any of the four test conditions during minute two (Fig. 1).

The main treatment effect for labial-licks during minute one was highly significant ($X^2_r = 17.85$; $df = 3$; $p < 0.001$). There were significantly greater numbers of labial-licks in the strike condition than in the pull condition ($p < 0.025$), the visual condition ($p < 0.005$), and the string condition ($p < 0.005$). There were no significant differences in labial-licks between other conditions. No labial-licks were observed in any of the four test conditions during minute two (Fig. 2).

The main treatment effect for tongue-flicks and labial-licks combined during minute one was highly significant ($X^2_r = 18.71$; $df = 3$; $p < 0.001$). Differences in the strike condition than in the pull condition, in the visual condition, and in the string condition were all significant ($p < 0.05$). No other pairs of conditions differed significantly during minute one. No tongue-flicks or labial-licks were observed in any of the four test conditions during minute two (Fig. 3).

Discussion

Prey chemical discrimination

The results evince no indication of linguistically mediated prey chemical discrimination by *L. zapallarensis*. This is apparent from the absence of significantly greater responses to cricket stimuli than to either cologne or distilled water in any of the analyses. Differences did not approach significance in the direction predicted for prey chemical discrimination, null probabilities being greater, usually substantially greater, than 0.3 for the Friedman two-way analyses of variance.

Furthermore, the probability of rejecting a false null hypothesis is quite high in studies of this sort, even using considerably smaller sample sizes (Cooper 1989b, 1994). Based on previous studies using the same design,

a power analysis can be conducted to gauge the probability of making a type II error (Winer 1962). The phi function for such experiments has been estimated to be 0.59 (Cooper 1989b). For this value, the probability of a type II error with a sample size of fifteen is less than 0.1. Given this strong statistical power and the failure of the results to even closely approach significance, we conclude that *L. zapallarensis* did not discriminate prey chemicals from the control substances.

Absence of prey chemical discrimination by *L. zapallarensis* is consistent with previous findings for lizards belonging to insectivorous iguanian families and to scleroglossan families that forage by ambush. As in other iguanians studied (Cooper 1989b), most individuals do not tongue-flick the swabs at all unless the swab is first brought into contact with the labial scales, which presumably induces transfer of the chemical stimuli to the vomeronasal organs (Graves & Halpern 1989).

The failure to investigate swabs by tongue-flicking differs markedly from the behavior of typical actively foraging scleroglossans, which tongue-flick at much higher rates both in experimental trials and in the field (Evans 1961; Cooper 1989a,b; Cooper & Vitt 1989). The negative findings of the present study strongly suggest that in *L. zapallarensis* the tongue does not participate in detection or identification of prey during foraging. All available evidence, although it is limited, indicates that the presence or absence of lingually mediated prey chemical discrimination is fixed within lizard families. Thus, its absence is probably typical of members of the family Tropiduridae.

Because neither cologne nor prey chemicals elicited stronger responses than distilled water, there is no evidence from the nonparametric anovas that the lizards even detected these chemicals. For cologne, however, the presence of biting, opening the mouth, and head-shaking and the associated statistical differences from other conditions in the initial 40 s suggest that the lizards did detect cologne. Tongue-flicking was not necessary for this detection, the response occurring prior or in the complete absence of tongue-flicks. Because the olfactory and vomeronasal system of turtles appear to be about equally sensitive to a variety of volatile substances (Shoji & Kurihara 1991), detection of volatile substances from cologne may be mediated by either olfaction or vomerolfaction (Cooper & Burgardt 1990b).

The increases in proportions of individuals tongue-flicking in the cricket and distilled water conditions after swabs contacted the labial scales were not necessarily responses to chemical stimuli. Lingual investigation instead might have been elicited by mechanical stimulation or by water in the swab. Although these factors both might account for some of the increase in responsiveness, there is a hint that the lizards may have detected prey chemicals. All 7 individuals that tongue-flicked in the water condition in the last 20 s also did so in the cricket condition, but an additional 5 tongue-flicked in the cricket condition (sign test, $P = 0.06$, two-tailed).

Even if the lizards did detect the chemicals, there is no indication that they discriminated them from cologne. A sign test similar to the above gives $P = 0.12$ (two-tailed) for the difference between proportions tongue-flicking in the cricket and cologne conditions after being touched by a swab. Even this nonsignificant probability is misleadingly low because most individuals that responded to cologne before being touched by the swab did not respond further after being touched. Proportions of lizards tongue-flicking in the two conditions during the entire trial were quite similar (Table 1). There is thus no evidence of prey chemical discrimination after being touched by a swab. Such evidence, were it found, would not indicate that *L. zapallarensis* used the tongue to sample prey chemicals from the external environment.

Labial-licks, as they occurred only after direct contact with a swab, could also reflect responses to chemicals or fluids on the swab or to mechanical stimulation. The complete absence of labial-licks in the water condition suggests that the response is to chemical stimuli, but the infrequent occurrence of labial-licks in the other conditions precludes strong inference.

PETF and SICS

The significantly higher tongue-flick rate in the strike condition as compared to any of the three other conditions for min 1 (Fig. 1) demonstrates that PETF exists in *L. zapallarensis* for one minute. That *L. zapallarensis* did not exhibit any tongue-flicks, labial-licks, or movements during minute two shows that the response is of brief duration.

These results are consistent with the prediction that PETF should be brief in squamates, such as insectivorous lizards, that feed on prey not likely to be located by scent trailing (Cooper 1992b). PETF is quite brief or absent in the insectivorous lizards studied to date; a lacertid, *Podarcis muralis* (1 min; Cooper 1991); a scincid, *Eumeces laticeps* (1 min; Cooper 1992b); a cordylid, *Gerrhosaurus nigrolineatus* (2 min; Cooper 1992a); a polychrid, *Anolis carolinensis* (absent; C. S. DePerno & W. E. Cooper unpubl.); a tropidurid, *Liolaemus zapallarensis* (1 min; this study); a eublepharid, *Eublepharis macularius* (absent; C. S. DePerno & W. E. Cooper unpubl.); and a gekkonid, *Gekko gecko* (absent; C. S. DePerno & W. E. Cooper unpubl.).

Labial-licking, a licking of the labial scales around the mouth, was nearly as frequent as tongue-flicking directed to the external environment. The function of labial-licking is largely unknown, but it may serve as a cleaning behavior or for chemical sampling of labials. Such licking could be a response to vomeronasal stimulation as a result of biting prey and may lead to further delivery of prey chemicals already sampled by the tongue or present on the labials (Graves & Halpern 1989; Cooper 1994). Given the absence of searching movements, it is unclear whether labial-licking affects subsequent responses to prey.

Prey chemical discrimination, PETF, and SICS in iguanian ambush foragers

Liolaemus zapallarensis is the first insectivorous iguanian species shown to exhibit PETF. However, the prey chemical responses of this species are in most respects typical for ambush foraging insectivorous iguanian lizards. These lizards failed to discriminate prey chemicals from control stimuli, tongue-flicked at very low rates even after biting prey, and did not exhibit searching movements. It is clear that they did not use chemical cues to identify prey prior to attack or to relocate prey that had been removed. Iguanian insectivores appear to attack their prey with no preliminary tongue-flicking or other apparent chemosensory investigation (Simon *et al.* 1981). It was apparent through behavioral observations of *L. zapallarensis* that they responded primarily to visual stimulation and not chemical cues. Vision is the dominant sense for lizards in several iguanian families; extensive use of vision may be of primary importance in iguanid feeding, territorial and courtship behaviors (Underwood 1951, 1970; Burghardt 1964; Bellairs 1970).

Despite the basic similarities of chemosensory responses by prey to those of other iguanian ambush foragers, the findings of PETF and elevated labial-licking in the minute after removal of prey are unique for iguanians and ambush foragers studied to date. Although, *L. zapallarensis* employs the tongue neither to detect prey while foraging nor while performing searching movements during attempts to relocate prey, it is possible that the brief increases in tongue-flicking rate and labial-licking may be functional after prey has been lost. One function might be further transfer of prey chemicals to the vomeronasal organs. Continuing stimulation might enhance attention to appropriate prey stimuli during visual search for escaped prey. Alternatively, as noted above, the minimal tongue-flicking and labial-licking could represent responses to nonchemical, likely mechanical stimuli and might serve for cleaning or other functions.

The results indicate that *L. zapallarensis* does not use chemical cues obtained by tongue-flicking to locate prey, but the possibility remains that this species can identify prey chemically once chemical stimuli reach the mouth. The presence of both prey chemical discrimination and PETF in an iguanid herbivore, *Dipsosaurus dorsalis* (Cooper & Alberts 1990) suggests that other iguanians may possess latent abilities to identify prey based on lingually sampled chemical stimuli.

Both PETF and increased labial-licking in the strike condition may indicate that *L. zapallarensis* responded to prey chemicals sampled by biting. Although mechanical stimuli might account for the observed increase in lingual protrusion, previous studies in another lizard and snake have demonstrated that increased tongue-flicking after oral mechanical and chemical stimulation is a specific response to chemical stimuli (Cooper *et al.* 1989; Cooper 1992b). Further study is needed to determine whether such latency prey chemical discrimination

occurs in *L. zapallarensis* and other lizards that do not tongue-flick while foraging.

Acknowledgements

This research project was partially supported by the Biology Department at Indiana University-Purdue University Fort Wayne. We are grateful to Carla Barrett for the care and maintenance of the lizards used during this experiment.

References

- Bellairs A (1970) The Life of Reptiles. Vol 2. New York: Universe Books
- Burghardt GM (1964) Effects of prey size and movement on the feeding behavior of the lizards *Anolis carolinensis* and *Eumeces fasciatus*. *Copeia* 1964:576–578
- Burghardt GM (1967) Chemical-cue preferences of inexperienced snakes: comparative aspects. *Science* 157:718–721
- Camp CL (1923) Classification of the lizards. *Bull Amer Mus Nat Hist* 48:289–481
- Chiszar D, Scudder KM (1980) Chemosensory searching by rattlesnakes during predatory episodes. Pp 125–139 in Müller-Schwarze D, Silverstein RM (eds) Chemical Signals: Vertebrates and Aquatic Invertebrates. New York: Plenum Press
- Chiszar D, Radcliffe CW, O'Connell B, Smith HM (1982) Analysis of the behavioral sequence emitted by rattlesnakes during feeding episodes. II. Duration or strike-induced chemosensory searching in rattlesnakes (*Crotalus viridis*, *C. enyo*). *Behav Neural Biol* 34:261–270
- Chiszar D, Radcliffe CW, Scudder KM, Duvall D (1983) Strike-induced chemosensory searching by rattlesnakes: the role of envenomation-related chemical cues in the post strike environment. Pp 1–28 in Müller-Schwarze D, Silverstein RM (eds) Chemical Signals in Vertebrates. Vol. 3. New York: Plenum Press
- Chiszar D, Radcliffe CW, Overstreet R, Poole T, Byers T (1985) Duration of strike-induced chemosensory searching in cottonmouths (*Agkistrodon piscivorus*) and a test of the hypothesis that striking prey creates a specific search image. *Can J Zool* 63:1057–1061
- Chiszar D, Radcliffe CW, Byers T, Stoops R (1986) Prey capture behavior in nine venomous snakes. *Psychol Rec* 36:433–438
- Cooper WE Jr (1989a) Prey odor discrimination in the varanoid lizards *Heloderma suspectum* and *Varanus exanthematicus*. *Ethology* 81:250–258
- Cooper WE Jr (1989b) Absence of prey odor discrimination by iguanid and agamid lizards in applicator tests. *Copeia* 1989:472–478
- Cooper WE Jr (1989c) Strike-induced chemosensory searching occurs in lizards. *J Chem Ecol* 15:1311–1320
- Cooper WE Jr (1990a) Prey odor discrimination by lizards and snakes. Pp 533–538 in Macdonald DW, Müller-Schwarze D, Natynczuk SE (eds) Chemical Signals in Vertebrates. Vol 5. Oxford: Oxford University Press
- Cooper WE Jr (1990b) Prey odor detection by teiid and lacertid lizards and the relationship of prey odor detection to foraging mode in lizard families. *Copeia* 1990:237–242
- Cooper WE Jr (1990c) Prey odor discrimination by anguid lizards. *Herpetologica* 46:183–190
- Cooper WE Jr (1991) Responses to prey chemicals by a lacertid lizard, *Podarcis muralis*: prey chemical discrimination and post-strike elevation in tongue-flick rate. *J Chem Ecol* 17:849–863
- Cooper WE Jr (1992a) Prey odor discrimination and poststrike elevation in tongue flicking by a cordylid lizard, *Gerrhosaurus nigrilineatus*. *Copeia* 1992:146–154
- Cooper WE Jr (1992b) Elevation in tongue-flick rate after biting prey in the broad-headed skink, *Eumeces laticeps*. *J Chem Ecol* 18:455–467

- Cooper WE Jr (1994) Multiple functions of extraoral lingual behavior in iguanian lizards: prey capture, grooming, and swallowing, but not prey discrimination. *Anim Behav*: in press
- Cooper WE Jr, Alberts AC (1990) Responses to chemical food stimuli by an herbivorous actively foraging lizard, *Dipsosaurus dorsalis*. *Herpetologica* 46:259–266
- Cooper WE Jr, Burghardt GM (1990a) A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. *J Chem Ecol* 16:45–65
- Cooper WE Jr, Burghardt GM (1990b) Vomerolfaction and vomodor. *J Chem Ecol* 16:103–105
- Cooper WE Jr, Vitt LJ (1986) Thermal dependence of tongue-flicking and comments on use of tongue-flicking as an index of squamate behavior. *Ethology* 71:177–186
- Cooper WE Jr, Vitt LJ (1989) Prey odor discrimination by the broad-headed skink (*Eumeces laticeps*). *J Exp Zool* 249:11–16
- Cooper WE Jr, McDowell SG, Ruffer J (1989) Strike-induced chemosensory searching in the colubrid snakes *Elaphe g. guttata* and *Thamnophis sirtalis*. *Ethology* 81:19–28
- Curio E, Mobius H (1978) Versuche zum Nachweis eines Riechvermögens von *Anolis l. lineatopus* (Rept., Iguanidae). *Z Tierpsychol* 47:281–292
- Estes R, De Queiroz K, Gauthier J (1988) Phylogenetic relationships within Squamata. Pp 119–281 in Estes R, Pregill G (eds) *Phylogenetic Relationships of the Lizard Families, Essays Commemorating Charles L. Camp*. Stanford: Stanford University Press
- Evans LT (1961) Structure as related to behavior in the organization of populations of reptiles. Pp 148–178 in Blair WF (ed.) *Vertebrate Speciation*. Houston, TX: University of Texas Press
- Graves BM, Halpern M (1989) Chemical access to the vomeronasal organs of the lizard *Chalcides ocellatus*. *J Exp Zool* 249:150–157
- Hollander M, Wolfe DA (1973) *Nonparametric Statistical Methods*. New York: John Wiley & Sons
- Shoji T, Kurihara K (1991) Sensitivity and transduction mechanisms of responses to general odorants in turtle vomeronasal system. *J Gen Physiol* 98:909–919
- Siegel S (1956) *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill
- Simon CA, Gravelle K, Bissinger BE, Eiss I, Ruibal R (1981) The role of chemoreception in the iguanid lizard *Sceloporus jarrovi*. *Anim Behav* 29:46–54
- Underwood G (1951) Reptilian retinas. *Nature* 167:183–185
- Underwood G (1970) The eye. Pp 1–97 in Gans C (ed.) *Biology of the Reptilia*. Vol 2. London: Academic Press
- Winer BJ (1962) *Statistical Principles in Experimental Design*. New York: McGraw Hill
- Zar JH (1974) *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall Inc