RESPONSES TO PREY CHEMICALS BY A LACERTID LIZARD, *Podarcis muralis*: PREY CHEMICAL DISCRIMINATION AND POSTSTRIKE ELEVATION IN TONGUE-FLICK RATE

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Abstract—The ability to discriminate prey chemicals from control substances and the presence of a poststrike elevation in tongue-flicking (PETF) rate are experimentally demonstrated in the lacertid lizard, *Podarcis muralis*. The tongue-flick attack score, a composite index of response strength, was significantly higher in response to integumental chemicals from cricket than to cologne or distilled water. The cricket chemicals additionally elicited a significantly greater rate of tongue-flicking and higher proportion of attacks by the lizards than did control stimuli. PETF combined with apparent searching movements strongly suggest the presence of strike-induced chemosensory searching (SICS). Experimental evidence indicates that both PETF and SICS occur in insectivorous representatives of three families of actively foraging autarchoglossan lizards, suggesting their widespread occurrence in such lizards. The adaptive roles of chemosensory behavior in the foraging behavior of *P. muralis* are discussed. It is proposed that these lizards may form chemical search images and that PETF and SICS may have been present in the lacertilian ancestors of snakes.

Key Words—Prey chemicals, tongue-flicking, feeding behavior, Reptilia, Lacertidae, *Podarcis muralis*.

INTRODUCTION

Knowledge about the importance of the chemical senses to lizards for locating and identifying prey is growing rapidly, but our understanding of chemosensory roles in foraging and other behaviors by lacertid lizards is fragmentary. *Lacerta vivipara* may be able to identify the vomodors (Cooper and Burghardt, 1990b)

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of one of its predators, the snake *Vipera berus* (Van Damme et al., 1990); tongue-flicking rates in this lizard increase in cages previously occupied by the predator. Tentative experimental findings were presented by Kahmann (1939) on the use of the vomeronasal organ in feeding. Recently, an ability to discriminate integumentary chemicals of crickets from control substances was confirmed for *Podarcis hispanica* (Cooper, 1990a), but the sample size was very small ($N = 5$).

Lizards in several families of actively foraging insectivores can locate and identify prey by tongue-flicking (partially reviewed by Burghardt, 1970; Halpern, 1991; Simon, 1983; and Cooper, 1990b). Discrimination of prey chemicals has been demonstrated experimentally in representatives of several families of lizards that are insectivorous active foragers or cruising foragers (Regal, 1978), including Anguidae (Cooper, 1990c), Helodermatidae (Cooper, 1989b), Lacertidae (Cooper, 1990a), Scincidae (Loop and Scoville, 1972; Burghardt, 1973; Von Achen and Rakestraw, 1984; Nicoletto, 1985; Cooper and Vitt, 1989), Teiidae (Cooper, in press), Varanidae (Cooper, 1989b), and possibly Cordylidae (gerrhosaurines; Cooper, in press), as well as in a nocturnal gecko (Dial, 1978; Dial et al., 1989) and an herbivorous iguanid (Pedersen, 1988; Krekorian, 1989; Cooper and Alberts, 1990). Accordingly, it may be predicted that typical lacertids, the vast majority of which appear to be actively foraging insectivores, are capable of prey chemical discrimination.

Some lizards that can discriminate prey chemicals also use chemical cues in a manner analogous to strike-induced chemosensory searching (SICS) in rattlesnakes (Chiszar and Scudder, 1980). After striking and envenomating potentially dangerous prey, such as large rodents, rattlesnakes and many other venomous snakes relocate the prey after it has been incapacitated by following the prey's scent trail. Shortly after releasing the envenomated prey, a rattlesnake greatly increases its tongue-flick rate and follows the prey's trail by tongue-flicking (Chiszar and Scudder, 1980).

The elevated tongue-flicking rate and searching behavior constitute SICS; the larger behavior pattern is called the strike–release–trail strategy. Some nonvenomous snakes (Cooper et al., 1989), a varanid lizard (Cooper, 1989c), and a cordylid lizard (Cooper, in press) exhibit behavior similar to SICS despite failure to voluntarily release prey. This was discovered after removal of prey items from their mouths. Because the lizards not only increase their tongue-flicking rates, but also their locomotion, apparently searching for the removed prey (Cooper, 1989c), they show SICS.

In this paper I present experimental findings on responses to prey chemicals by a lacertid lizard, *Podarcis muralis*. The topics investigated are (1) the ability to detect and respond differentially to prey chemicals, (2) the presence of one component of SICS, the poststrike elevation in tongue-flicking (PETF),

and (3) the duration of PETF. Roles of chemical cues in lacertid foraging are discussed.

Prey odor discrimination in squamate reptiles appears to be mediated by vomerolfaction (Cooper and Burghardt, 1990c), with the tongue serving as a sampling device that delivers chemicals from the external environment to the mouth, where the chemicals are transferred via the vomeronasal ducts to the vomeronasal organs above the roof of the mouth for sensory analysis. Normal responses to food chemicals require vomeronasal participation (Halpern and Frumin, 1979; Halpern and Kubie, 1980; Graves and Halpern, 1990; Cooper and Alberts, 1991). Thus, tongue-flicking behavior has been used extensively as an observable index of chemosensory investigation (e.g., Burghardt, 1970; Cooper and Burghardt, 1990a; Halpern, 1991) and is so used here.

METHODS AND MATERIALS

Subjects and Maintenance. Sixteen adult *P. muralis* purchased from a commercial dealer were maintained in the laboratory from their arrival on December 27, 1989, for several months before the experiments. This allowed habituation to experimental conditions, especially the close proximity of an experimenter's hand. Each lizard was housed individually in a 30 × 30 × 26-cm glass terrarium containing a water bowl, a wooden shelter board, a sand substrate, and a wire screen top.

Fluorescent lighting was provided during the daylight hours. Air temperatures fluctuated from 22 to 29°C. Because these temperatures were lower than those expected to produce the highest tongue-flicking rates (Cooper and Vitt, 1986; Van Damme et al., 1990), undercage heaters were used to allow the lizards to thermoregulate and to remain fully active even when air temperatures were low. Cloacal temperatures were typically in the low thirties.

The lizards were fed crickets to satiation three times per week. Water was available ad libitum. To prepare the lizards for the experiments, the experimenter would move slowly while feeding and watering them. *Podarcis muralis* is warier than many lizard species, but a sufficient number of individuals became habituated to the experimenter's presence to allow completion of the experiments.

Prey Odor Discrimination. The ability of the lizards to discriminate prey chemicals from control substances was assessed by an experiment with a randomized blocks design in which each individual responded to three stimuli presented on cotton swabs: integumentary chemicals of domestic crickets, cologne (Mennen Skin Bracer, Spice Scent), and distilled water. Stimuli were prepared by initially dipping the cotton tip of a 15-cm wooden applicator in distilled

water; other substances were added when needed by either dipping a moistened swab in cologne or by rolling a moistened cotton over the integument of a cricket. The distilled water condition served as an odorless control to gauge responsiveness to the experimental milieu. Cologne was a pungency control to indicate degree of response to a highly odorous substance lacking trophic or social relevance. Each swab was used only once.

To begin a trial, the experimenter slowly approached a lizard's cage and carefully removed its wire cover to avoid disturbing the lizard. He then placed the cotton tip of the applicator 1–1.5 cm anterior to the lizard's snout. Tongue-flicks directed to the applicator were counted for 60 sec or until the lizard bit the applicator, whichever came first. Timing began when the first tongue-flick occurred. In addition, the presence or absence of biting and latency to biting were recorded; a latency of 60 sec was assigned if a lizard did not bite.

The experiment was conducted between 1200 and 1430 hr Central Standard Time on March 30, 1990. Nine lizards were tested with stimuli presented in random sequence, with approximately equal numbers of individuals tested with each stimulus in each of the three trials. The intertrial interval was ca. 60 min. The air temperature was only 25°C, but the sand and lizards were warmer. Although body temperature strongly affects tongue-flicking rates (Cooper and Vitt, 1986), the relative responsiveness to various chemical stimuli does not appear to be affected over a wide range (20–35°C) of temperatures (Van Damme et al., 1990).

Overall responsiveness in the three conditions was measured by the tongue-flick attack score for repeated measures experiments, TFAS(R) (Cooper and Burghardt, 1990a). If the lizard does not bite, TFAS(R) is the number of tongue-flicks it emits during the trial. If it bites, TFAS(R) is the maximum number of tongue-flicks emitted by that individual lizard in any of the three trials plus (60 − latency to bite in seconds). The stronger weight of biting than any amount of tongue-flicking in TFAS(R) reflects a conviction that a predatory attack is a stronger indication of feeding motivation than is chemosensory investigation by tongue-flicking. Numbers of tongue-flicks, latency to bite, and numbers of individuals biting in the three conditions were also compared.

Differences among stimulus conditions in TFAS(R) and number of tongue-flicks were tested for significance by analysis of variance for a single-factor experiment with a repeated measures design (Winer, 1962). Individual comparisons between pairs of means were made using Student-Newman-Keuls tests. Homogeneity of variance was tested by Hartley's tests for heterogeneity followed by logarithmic transformation where needed. Latency differences were examined by nonparametric Friedman two-way analysis of variance because the distribution of latency was nonnormal. The difference in number of lizards biting in response to cricket stimuli and the other two stimuli was assessed by a

binomial test (Siegel, 1956). Tests were two-tailed unless otherwise stated, with $\alpha = 0.05$.

PETF. In previous related studies of lizards and nonvenomous snakes (Cooper, 1989c, 1991b; Cooper et al., 1989), apparent searching movements have been noted qualitatively; only the increase in tongue-flicking rate has been treated quantitatively. Because tongue-flick rates might increase in the absence of search involving locomotion, it is important to distinguish the tongue-flicking behavior from SICS. The increase in tongue-flicking rate after the prey has been removed from the mouth of an animal is the poststrike elevation in tongue-flicking (PETF; Cooper, 1992).

The effect of biting on tongue-flicking rate was determined by counting tongue-flicks emitted in 10 consecutive minutes in four experimental conditions. In the strike condition, a cricket was tied to a white thread (ca. 25 cm) and was lowered to a position just above the sand 10 cm anterior to a lizard's snout. Immediately after the lizard bit the cricket, the experimenter removed the cricket from the lizard's mouth as gently as possible and immediately began counting tongue-flicks. The cricket was presented in the same way in the pull condition, but after the lizard approached and was poised to bite the cricket, the experimenter removed the cricket with one hand and simultaneously moved the lizard a short distance (as if separating it from bitten prey) with the other hand, then began counting tongue-flicks. In the sight condition, a cricket was held at the far side of the cage in clear view of the lizard. The cricket was removed after 10 sec or sooner if the lizard approached it. The lizard was not allowed to tongue-flick it. The string condition was similar to the sight condition except that no cricket was tied to the string. Counting of tongue-flicks was initiated upon removal of the experimental stimuli in the last two conditions.

Forced removal of prey from a lizard's mouth is a somewhat drastic experimental procedure that requires contact with the lizard. It seems likely to have behavioral effects beyond those on tongue-flicking. However, this procedure is necessary for demonstration of PETF in species that do not voluntarily release prey. The pull condition serves as a control for handling effects. In this condition, the lizard is allowed to tongue-flick the cricket. It is hoped that the only important difference from the strike condition is the absence of chemical and possibly other cues associated with biting. In a study of garter snakes, an additional control for the effects of tactile stimuli during biting was used to show that the chemical cues received during biting produced PETF (Cooper et al., 1989). The sight condition is a control for the effect of seeing the prey on tongue-flicking rates. Tongue-flicking rates expected in the experimental setting are revealed in the string condition. For further discussion of the experimental procedures and interpretation of results, see Cooper et al. (1989) and Cooper (1989c).

A repeated measures (randomized blocks) design in which each lizard responded in four conditions was used, with a partially counterbalanced sequence of presentation. Lizards were tested only once a day, two days after having been fed to satiation. Eight lizards were tested, all of which had been subjects in the study of prey odor discrimination. The experiment was conducted at 1200–1500 hr CST between April 6 and 18, 1990. Although the experiment was conducted at air temperatures of 25–27°C, the lizards were active and their bodies were warmer than the air temperature.

For each minute, the significances of differences among conditions were assessed by nonparametric Friedman two-way analysis of variance (Siegel, 1956), which was necessary because the tongue-flicking distributions were non-normal due to frequent zero values. When the main condition effect was significant, individual comparisons were made between pairs of conditions (Hollander and Wolfe, 1973). Binomial tests were conducted to determine the significance of differences in numbers of days of greater relative magnitude for selected comparisons between conditions. Alpha was 0.05 and tests of significance were two-tailed except as noted.

RESULTS

Prey Odor Discrimination. The lizards tongue-flicked in all conditions, but emitted the most tongue-flicks in cricket trials and bit only in response to cricket stimuli, resulting in high TFAS(R) values for the cricket condition (Table 1). Variances of TFAS(R) were heterogeneous for the raw data (Hartley's $F_{max} = 15.76$; $df = 3, 8$; $P < 0.01$), but logarithmic transformation yielded homogeneity ($F_{max} = 2.49$; $df = 3, 8$; $P > 0.10$). The main condition effect for the transformed TFAS(R) data was highly significant ($F = 18.83$; $df = 2, 16$; $P < 0.002$). TFAS(R) was significantly greater in the cricket condition than in either the cologne or distilled water condition ($P < 0.01$ each), but did not differ between the two control conditions ($P > 0.10$).

The lizards tongue-flicked at a much higher mean rate in response to cricket stimuli than to the control stimuli; for the two control groups the means were similar but variance was somewhat larger in response to distilled water because two individuals emitted 85% of all tongue-flicks in that condition. Variances of tongue-flicks were heterogeneous for the raw data ($F_{max} = 11.65$; $df = 3, 8$; $P < 0.01$), but the heterogeneity was removed by logarithmic transformation ($F_{max} = 1.92$; $df = 3, 8$; $P > 0.10$). The stimulus effect was significant ($F = 9.39$; $df = 2, 16$; $P < 0.01$); with significantly more tongue-flicks emitted in response to cricket stimuli than to cologne ($P < 0.05$) or distilled water ($P < 0.01$).

TABLE 1. RESPONSES BY NINE ADULT *Podarcis muralis* TO CHEMICAL STIMULI
PRESENTED ON COTTON-TIPPED APPLICATORS

	Cricket	Cologne	Distilled water
TFAS(R)			
Mean	45.56	11.67	9.33
SE	8.97	2.26	3.38
Range	19–101	3–24	1–33
Tongue-flicks			
Mean	30.56	11.67	9.33
SE	7.72	2.26	3.38
Range	7–83	3–24	1–33
Latency			
Mean	48.56	60	60
SE	6.39	0	0
Range	8–60		
Number biting	3	0	0

Three lizards bit swabs bearing cricket stimuli; no bites occurred in trials with control stimuli. Thus, no significant difference in number of lizards biting occurred between the cricket condition and either of the control conditions taken individually. However, biting is predicted to be more frequent in response to prey stimuli. If it is assumed that there is an equal chance of a lizard biting in each condition, the probability that a given lizard that bites will do so in the cricket condition is 0.333 and the combined probability of it biting in one of the other conditions is 0.667. The likelihood of all three biting in the cricket condition is thus only 0.037 (one-tailed), indicating a significantly higher frequency of biting in response to cricket stimuli than to the combined controls. Latency to bite did not differ significantly among conditions ($\chi_r^2 = 1.50$, $df = 2$, $P > 0.10$).

PETF. The highest mean tongue-flicking rates occurred in the strike condition throughout the experiment except in minutes 2 and 6, when the means were higher in the pull condition (Table 2). There was also a tie for the highest mean between the strike and pull conditions in the fourth minute. During each of the first six minutes the pull condition elicited higher total tongue-flicks rates than did the sight and string conditions and had the individual emitting the greatest number of tongue-flicks among these conditions (binomial $P = 0.016$ for each comparison, one-tailed). In addition, the sight condition elicited higher tongue-flicking rates than did the string condition and had the individual emitting the greatest number of tongue-flicks for the two conditions in each of the

TABLE 2. MEANS, STANDARD ERRORS (SE), AND RANGES OF NUMBERS OF TONGUE-FLICKS EMITTED BY *Podarcis Muralis* DURING TEN CONSECUTIVE MINUTES IN FOUR EXPERIMENTAL CONDITIONS

Minute	Mean				SE				Range			
	Strike	Pull	Sight	String	Strike	Pull	Sight	String	Strike	Pull	Sight	String
1	17.88	6.50	4.25	1.75	1.36	1.58	1.74	1.75	12–22	2–15	0–12	0–4
2	4.00	4.25	3.00	1.00	1.36	1.51	1.34	1.00	0–12	0–12	0–9	0–3
3	8.63	5.25	2.13	0.88	2.65	2.36	0.74	0.48	0–19	0–21	0–6	0–3
4	3.63	3.63	0.88	0.25	1.24	2.03	0.44	0.25	0–8	0–15	0–3	0–2
5	2.63	2.50	0.75	0.25	1.16	1.16	0.41	0.25	0–8	0–8	0–3	0–2
6	2.50	2.75	0.50	0.38	1.72	1.35	0.38	0.18	0–14	0–9	0–3	0–1
7	3.50	0.88	2.13	2.83	1.31	0.48	1.74	0.58	0–11	0–3	0–14	0–4
8	3.75	1.00	1.13	0.38	1.87	0.87	0.99	0.26	0–15	0–7	0–8	0–2
9	1.88	0.50	0.75	0.75	1.26	0.50	0.49	0.62	0–10	0–4	0–4	0–5
10	1.50	0.50	0.25	0.63	0.57	0.33	0.16	0.50	0–5	0–2	0–1	0–4

first six minutes (binomial $P = 0.016$ for each comparison, one-tailed). Overall, there were more tongue-flicks in the sight condition than in the string condition in eight of ten minutes, with one tie and one reversal [P (8 of 9) $= 0.035$, one-tailed].

Despite these consistent differences, numbers of tongue-flicks varied significantly among conditions only during the first three minutes. In the first minute, the main effect was significant ($\chi^2_r = 18.56$, $df = 3$, $P < 0.001$). Significantly more tongue-flicks were emitted in the strike condition than in the pull ($P < 0.05$, one-tailed), sight ($P < 0.01$), and string ($P < 0.01$), and string ($P < 0.01$) conditions. There were no significant differences among the three control conditions. The main effect was only marginally significant during the second minute ($\chi^2_r = 6.45$, $df = 3$, $P < 0.05$, one-tailed) and the numbers of tongue-flicks were not significantly greater in the strike condition than in the control conditions. The only significant difference was a greater response in the pull than in the string condition ($P < 0.05$, one-tailed). During the third minute, the tongue-flicking rate differed significantly among conditions ($\chi^2_r = 7.91$, $df = 3$, $P < 0.05$), but PETF was absent because the number of tongue-flicks in the strike condition was significantly greater than that in only the string condition ($P < 0.05$). The sole other significant difference was that more tongue-flicks occurred in the pull condition than in the string condition ($P < 0.05$, one-tailed). The nonsignificant main effects for the remaining minutes all had probability values greater than 0.10 and χ^2_r values with three degrees of freedom of 4.35, 1.88, 1.39, 1.48, 2.29, 0.56, and 2.59, consecutively).

Although movements were not quantified, individuals that tongue-flicked at high rates crawled while doing so. The locomotion, which presumably in part indicated searching movements, decreased greatly after the first few minutes, as did tongue-flicking. Most individuals that did not tongue-flick during a given minute were also still at that time. Differences among conditions, therefore, were closely related to the proportions of lizards that tongue-flicked (Figure 1). During the first few minutes, high proportions of lizards tongue-flicked in all conditions. Thereafter, the proportions fell rapidly in the three control conditions. They also decreased in the strike condition and became increasingly variable in the later minutes, but remained higher than in the control conditions throughout the experimental interval. Some individual lizards tongue-flicked in the early minutes, remained quiescent for several minutes, then tongue-flicked again later.

The proportion of individuals tongue-flicking was consistently higher in the strike condition than in the control conditions. It was higher than in the pull condition in nine of ten minutes (binomial $P = 0.02$, one-tailed), including the last seven minutes (binomial $P = 0.008$). The proportion tongue-flicking in the strike condition was higher than in the sight and string conditions in all ten minutes (binomial $P = 0.001$ for each comparison, one-tailed). Higher pro-
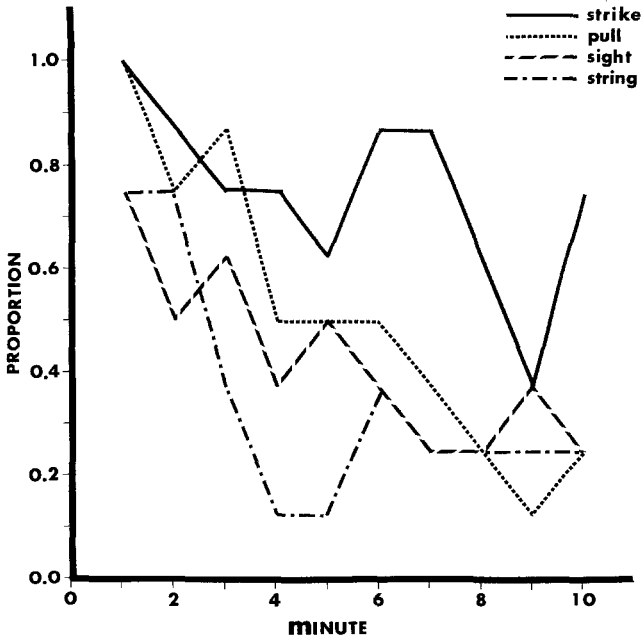
FIG. 1. Proportions of individuals of *Podarcis muralis* tongue-flicking at least once in the four experimental conditions.

portions tongue-flicked in the pull condition than in the other control conditions during the first seven days. For each comparison, the proportion was higher on six days for the pull condition, with a tie occurring on the remaining day. These differences are significant by a binomial (sign) test ($P = 0.016$, one-tailed). The proportions tongue-flicking were similar in the sight and string conditions, with ties on five days. Although greater proportions tongue-flicked in the sight condition than in the string condition in four of the remaining five days, the two conditions did not differ significantly (binomial $P = 0.19$, one-tailed).

DISCUSSION

Prey Odor Discrimination. Podarcis muralis readily detects prey chemicals and discriminates them from trophically irrelevant chemical stimuli. These results extend the previous findings for *P. hispanica* (Cooper, 1990a) to another lacertid species. In both species TFAS and numbers of tongue-flicks were significantly higher in response to prey chemicals than to control stimuli. However, *P. muralis* had TFAS and numbers of tongue-flicks over twice as great as those of *P. hispanica*. Reasons for these differences may include differences in

temperature (Cooper and Vitt, 1986), lighting, and random effects in small samples, as well as true interspecific differences.

Both biting and tongue-flicking contributed substantially to the difference between responses to prey chemicals and control chemicals. In this respect the responses of *P. muralis* are most similar to those of the varanid *Varanus exanthematicus* (Cooper, 1989b) and the anguid *Elgaria coerulea* (Cooper, 1990c), but it is now obvious that interspecific differences in the relative importance of biting and tongue-flicking exist among congeners. This is known in *Podarcis* (Cooper, 1990a, this paper) and *Elgaria* (Cooper, 1990c). Although the experimental conditions and procedures are similar in these cases, some of the apparent differences may reflect differential (defensive) responses to experimenters and uncontrolled experimental variables extraneous to chemosensory analysis and response.

Whatever the cause of the interspecific differences, it now seems likely that detection and recognition of prey chemicals are widespread in Lacertidae. The results agree with previous findings for lizard families consisting largely of active foragers (Cooper, 1989a, 1990a; Cooper and Vitt, 1989). Because information is available for only one or at most a few species per family, it will be important to determine the extent to which these responses to prey chemicals are phylogeneticaly constrained or are responsive to changes in foraging mode. Within families, most species have a similar foraging mode (Huey and Pianka, 1981; Vitt and Price, 1982); the crucial tests will require study of species that have evolved foraging modes atypical for their families.

PETF. The high level of tongue-flicking in the strike condition indicates that PETF occurs in *P. muralis*. PETF is now known to occur in all three species of actively foraging insectivorous lizards that have been studied (Cooper, 1989c, in press, this paper). Its demonstrated duration is brief in *P. muralis*, only 1 min, even shorter than the 2-min interval of PETF in a cordylid species (Cooper, in press). PETF was significant in a varanid (Cooper, 1989c) during the first 2 min but was not examined thereafter.

Although significant levels of PETF might be detected over a somewhat longer interval by using a larger sample size, it is clear that the major increase in tongue-flicking rate attributable to biting begins almost immediately and wanes rapidly. The criterion I have adopted for the existence of SICS in a particular minute is a combined significance of the condition effect and significantly higher number of tongue-flicks in the strike condition than in each of the three control conditions. This is a conservative criterion that could obscure some important findings.

The data on numbers of minutes in which more tongue-flicks were emitted and the greater proportion of lizards tongue-flicking in the strike condition than in the control conditions show that effects of biting last considerably longer than 2 min, some slight residual effects being manifest throughout the 10-min trials.

The sequelae of biting are thus a rapid increase in tongue-flicking and searching movements, followed by a rapid decrease in these behaviors, with a final, more prolonged interval of intermittent chemical monitoring at a reduced rate of tongue-flicking.

Roles of Prey Chemicals in Lacertid Foraging Behavior. As actively foraging insectivores, most lacertid species presumably search for prey that may be cryptic or hidden from view. The ability to respond selectively to prey chemicals must enhance the ability of these lizards to locate and confirm the identity of such prey. Some species of lacertids have been characterized as ambush foragers (Huey and Pianka, 1981) and would thus be expected not to use chemical cues to locate prey. These species would seemingly be good candidates for testing the intrafamilial responsiveness of reliance on prey chemical discrimination to changes in foraging. However, the movement frequencies of the putative lacertid ambush foragers are higher than those of typical phrynosomatid and polychrid (both formerly iguanid; Frost and Etheridge, 1989) ambush foragers, suggesting that prey chemical discrimination could retain importance for these lizards. Use of chemical cues intermediate to that of typical ambush and active foragers is currently unknown, but seems a distinct possibility in such cases.

The temporal pattern of responses to chemical cues in the PETF experiment is readily interpretable in terms of their probable adaptive significance in foraging. Having bitten prey that has escaped, a lizard has also sampled prey chemicals that may be used in an attempt to relocate the prey that is known to be in the vicinity. Insect prey, even if injured, are not nearly as likely to be captured by following a scent trail as are the envenomated prey of rattlesnakes. Furthermore, actively foraging lizards search for prey briefly in one area and then move to another for further search. Therefore, rapid tongue-flicking and searching movements should be beneficial only briefly, presumably explaining the brevity of these responses in *P. muralis*. This contrasts markedly with the prolonged chemosensory searching in rattlesnakes, which may last for hours (Chiszar et al., 1982, 1985) while the snake attempts to relocate envenomated prey that is unlikely to escape.

The longer-lasting intermittent tongue-flicking in *P. muralis* could be explained by periodic fluctuation of neural response to the prey chemicals to levels above threshold for tongue-flicking. Regardless of the physiological mechanism, such chemosensory investigation could be, but is not necessarily, adaptive. In a lizard that is likely to have moved to a new area to forage within a few minutes, any remaining responses to a specific prey chemical pattern might aid in the location of other individuals of the prey type likely to be in the area. This suggests the possibility that the lizards may form a chemical search image, as reported for a viperid snake by Chiszar et al. (1985).

Because PETF was accompanied by apparent searching movements, *P.*

muralis very likely shows SICS, as suggested previously in *V. exanthematicus* (Cooper et al., 1989) and *G. nigrolineatus* (Cooper, in press). The presence of PETF and very probably of SICS in three families representing the lacertoid, scincoid, and varanoid branches of Autarchoglossa (Estes et al., 1988) suggests that these behaviors are quite widespread in autarchoglossan lizards. Thus, SICS, which has been hypothesized to be a preadaptation for evolution of the strike–release–trail strategy in highly venomous viperid snakes (Cooper et al., 1989), may have been present in the lacertilian ancestors of snakes. The prediction that PETF and SICS are present in families of actively foraging lizards has now been supported for all three families studied.

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