

Do lingual behaviors and locomotion by two gekkotan lizards after experimental loss of bitten prey indicate chemosensory search?

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Abstract. Poststrike elevation in tongue-flicking rate (PETF) and strike-induced chemosensory searching (SICS) were assessed experimentally in two species of gekkonoid lizards belonging to families differing in foraging mode. PETF is an increase in rate of lingual protrusions after a prey item has been bitten and escapes or is removed from the mouth of a squamate reptile, whereas SICS is PETF combined with locomotory searching behavior. *Eublepharis macularius*, the leopard gecko, is an actively, albeit slowly, foraging eublepharid. This species exhibited PETF for a duration of about five minutes based on total lingual protrusions. Labial-licks were initially much more frequent than tongue-flicks. A substantial increase in movement occurred during minutes 5-8, hinting that SICS might be present, but was not quite significant. SICS is likely present, as in other actively foraging lizards, but was not conclusively demonstrated. Handling the lizards induced increased locomotion in both the experimental condition and a control condition, presumably accounting for the apparent delay in onset of increased movement. The tokay gecko, *Gekko gecko*, a gekkonid ambush forager, performed no tongue-flicks, but exhibited PETF based on labial-licks during the first minute. SICS was absent. These findings support the hypothesis that SICS is absent in ambush foraging lizards, which do not use the lingual-vomeronasal system to search for prey. They are suggestive, but equivocal regarding the hypothesis that SICS is present in actively foraging lizards that exhibit lingually mediated prey chemical discrimination. The finding of PETF in *G. gecko* suggests that this species and several iguanians previously found to increase rates of labial-licking after biting prey may be able to detect prey chemicals.

Introduction

Strike-induced chemosensory searching (SICS) is a combined increase in the tongue-flicking rate and in searching behavior involving locomotion that occurs after prey has been bitten, escapes or is removed from the mouth of squamate reptiles. The increase in tongue-flicking rate is referred to as poststrike elevation in tongue-flicking (PETF), which may occur in the absence of locomotion (Cooper, 1991). As a major function of tongue-flicking is chemical sampling (Gove, 1979; Graves and Halpern, 1989; see Cooper, 1994a

for other functions) for analysis by vomerolfaction (Cooper and Burghardt, 1990a). PETF and SICS presumably help lizards find and follow chemical trails of released or escaped prey (Cooper, 1989a) and may aid in locating other individuals of the same prey type that are nearby (Cooper, 1991).

In addition to tongue-flicks that contact substrates in the external environment for chemical sampling, lizards often perform a second type of lingual protrusion called labial-licking. A labial-lick is an outward extension of the tongue from the mouth in which the tongue contacts the labial scales and perhaps immediately adjacent scales surrounding the mouth (DePerno and Cooper, 1993, 1994). Due to recent information suggesting a chemosensory function of labial-licking (DePerno and Cooper, unpublished data), we recorded tongue-flicks, labial-licks, and movements of leopard geckos *Eublepharis macularius* to assess the possible presence of PETF and SICS.

SICS occurs in many snakes and lizards (e.g., Chiszar and Scudder, 1980; reviewed by Cooper, 1994b). The ability of lizards to discriminate prey chemicals is correlated with foraging mode (Cooper, 1989b, 1994b, c, 1995a). Most lizards can be categorized as ambush foragers, which remain immobile much of the time while foraging (Cooper, 1994b, c, 1995a), or active foragers, which move over a wide range while seeking their prey.

PETF or SICS occurs in actively foraging lizards from diverse taxa, including a varanid, *Varanus exanthematicus* (Cooper, 1989a, 1993a), a helodermatid, *Heloderma suspectum* (Cooper et al., 1994; Cooper and Arnett, 1995), a gerrhosaurid, *Gerrhosaurus nigrolineatus* (Cooper, 1992a), a teiid, *Tupinambis nigropunctatus* (Cooper, 1993b), and a lacertid, *Podarcis muralis* (Cooper, 1991). In contrast to these actively foraging lizards, strict ambush foragers neither discriminate chemical prey cues from chemical control stimuli nor use chemical cues while foraging (e.g., Cooper, 1989c, 1990c, 1992b). PETF and SICS appear to be absent in several such families of ambush foragers including Phrynosomatidae (Cooper, 1994a), Chamaeleonidae (Cooper, 1994a), Cordylidae (Cooper et al., 1995), and Polychrotidae (DePerno and Cooper, 1993). In an ambushing tropidurid *Liolaemus zapallarensis*, SICS and lingually mediated prey chemical discrimination are absent. However, PETF lasting one minute is present (DePerno and Cooper, 1994), suggesting an ability to identify prey chemicals that reach the mouth, but not chemosensory search.

Cooper (1992b) hypothesized that SICS may occur in any actively foraging squamate, but that SICS and PETF may be absent or reduced in ambush-foraging lizards. For active foragers, tongue-flicking during locomotion increases the probability of encountering the escaped prey's scent trail. In contrast, a strict ambush forager that continued ambush foraging after bitten prey escaped, would not be able to relocate the prey by tongue-flicking.

We predicted that members of two closely related families of geckos, Eublepharidae and Gekkonidae, that differ in foraging mode would also differ in presence or absence of PETF and/or SICS. In the classification of Kluge (1987), all geckos are placed in

Gekkota, Eublepharidae is the sister taxon of all other geckos, and Gekkonidae includes the remaining geckos except Pygopodidae, which are the snake-like pygopodids and the diploactyls. Within Gekkonidae, the typical nocturnal geckos are gekkonines. Eublepharids are active foragers that tongue-flick extensively during foraging (Evans, 1961; Vogel, 1979) and are able to detect and discriminate prey chemicals (Dial, 1978, 1990; Dial et al., 1989; Cooper, 1995a). On the other hand, gekkonids are typically ambushers that have highly developed olfactory and vomeronasal systems (Gabe and Saint Girons, 1976), but are believed to use primarily visual, rather than vomerolfactory cues in social behavior and feeding (Evans, 1961; Brillet, 1990; Cooper, 1995a).

Foraging mode is usually stable within lizards families (Cooper, 1994b, c). However, Gekkonidae is a huge family in which the foraging behavior of many species has not been studied. Ambush foraging occurs in a large majority of species, but some variation has been reported (Cooper, 1994b, c). Eublepharids appear to be active foragers with the exception of *Aeluroscalabotes felinus*, which is at the base of the family tree (Grismer, 1988). Thus, active foraging is derived in other eublepharids, but ambush foraging is very likely plesiomorphic in gekkonine gekkonids (contrary to Cooper, 1994c; see Cooper, 1995b). We predicted that the leopard gecko, *Eublepharis macularius*, an actively foraging eublepharid, would exhibit PETF and/or SICS. However, given the slow movements of foraging eublepharids relative to members of many actively foraging lizards and their recent evolution of active foraging, it was likely that SICS would not be as strongly expressed as in active foragers such as teiids. We predicted that the tokay gecko, *Gekko gecko*, an ambush foraging gekkonine (Vitt and Price, 1982), would not exhibit SICS.

PETF and SICS were studied experimentally in the laboratory using a standardized experimental protocol. In the main experimental condition, a lizard is allowed to bite prey, which is then forcibly removed from its mouth (e.g., Cooper, 1989a; Cooper et al., 1989). Other control conditions are included to assess effects of the experimental setting, sight and perhaps smell of prey, and forced removal of prey on tongue-flicking and movement rates.

Materials and methods

Twelve adult *G. gecko* were obtained from a commercial dealer. Sixty captive-born *E. macularius* were obtained from researchers. Sample sizes for the experiments were 12 for *G. gecko* and 16 for *E. macularius*. The lizards were habituated to the laboratory conditions for at least four weeks prior to the beginning of testing. Each *G. gecko* was housed individually in a 51 × 26 × 32 cm glass terrarium with a wire mesh cover and a cedar bark substrate. Each *E. macularius* was isolated in a 41 × 28 × 23 cm plastic terrarium with a ventilated plastic cover and a plastic shelter. Ambient temperature for both species was maintained at 27–30°C and heat lamps allowed thermoregulation during

the lighted portion of a 12:12 L:D cycle. Water and food were available *ad libitum*. Each lizard ate crickets normally following all conditions.

The experimental design used to investigate the presence of PETF and SICS in both species was that of Cooper (1989a, 1992a, b). Both species were tested in a partially counterbalanced order in four stimulus conditions in one experiment; two additional experiments with *E. macularius* were abbreviated to the two primary conditions. The lizards were not fed for three days prior to each experimental condition to ensure equal feeding motivation for each stimulus condition. Each lizard was tested once per day. To prevent the lizards from hiding from the experimenter, the plastic shelters were removed from the terrariums of *E. macularius* twenty minutes prior to each experimental condition. The shelters were replaced immediately at the conclusion of that trial. A trial began when the investigator slowly approached the terrarium, removed the lid of the terrarium, and positioned one of the four experimental stimuli approximately twenty centimeters anterior to the lizard's snout for fifteen seconds, except as noted below.

The string condition was a control for the effects of the presence of the experimenter's hand, the string, and opening the lid of the cage on the lizard's tongue-flicking rate. In the string condition, the string used to tether the live crickets (*Acheta domesticus*) in the other conditions was visually presented to the lizard for 15 s and then removed. In the visual condition, a tethered cricket was presented visually to a lizard for 15 s and then removed. If the lizard approached, the cricket was immediately removed from the terrarium. The lizard was not allowed to tongue-flick or attack the cricket, but could see and perhaps smell it. The pull condition served as a control for any effects of removing the bitten cricket from the lizard's mouth, i.e., a mechanical disturbance control. In this condition the tethered cricket was presented to the lizard until the lizard showed signs of preparing for imminent attack. The cricket was then immediately removed from the terrarium and the lizard simultaneously grasped and pulled away from the prey, preventing any oral contact with the cricket. In the experimental condition, the strike condition, the lizard was allowed to bite the tethered cricket, but the cricket was removed from the lizard's mouth as quickly as possible to prevent mastication and swallowing. Removal was accomplished by grasping the lizard with two fingers behind the head and simultaneously pulling the string to remove the bitten cricket.

All experiments were conducted between 17:00 and 21:00 h under red light. The nocturnal *Eublepharis macularius* was tested in three separate experiments. In experiments 1 and 2 lingual protrusions were recorded for five and ten consecutive minutes, respectively, following removal of experimental stimuli. Two categories of lingual protrusions were recorded: tongue-flicks, which were directed to substrates, and labial-licks, in which the tongue contacted the labial scales and possibly adjacent scales, but not other substrates. In experiment 3 duration of movements in seconds was recorded for ten minutes. All four experimental conditions were used in experiment 1, but only the pull and strike conditions were used in experiments 2 and 3. Another difference was that lizards were disturbed minimally by handling in experiments 2 and 3, the lizards being

nudged with one finger, not grasped and pulled as described above. Minimal handling was used to reduce possible increases in movement noted in experiment 1 that might have been induced by relatively rough handling during removal of bitten prey from a lizard's mouth. Excessive movement in control conditions could obscure effects of biting prey on both lingual protrusions and movement. Because lizards were selected for experiments independently of inclusion in previous experiments, some individuals may have participated in more than one experiment.

The experiment for *G. gecko* was conducted in red light conditions between 18:00 and 20:00 h. Tongue-flicks, labial-licks, and number of movements were recorded for five min in all conditions. Number of bouts of locomotion was used rather than time moving because preliminary data indicated that movements were very brief, typically lasting less than one second. PETF was present if there was a significantly higher number of combined tongue-flicks and labial-licks in the strike condition than in each of the three control conditions. SICS was present if PETF was accompanied by a significantly higher number of searching movements in the strike condition than in the control conditions (Cooper, 1991).

Data for PETF and SICS were nonnormal due to the presence of many zero values. Therefore, they were analyzed nonparametrically by a Friedman two-way analysis of variance for each minute (Siegel, 1956) followed by multiple comparisons (Hollander and Wolfe, 1973; Zar, 1974). The Friedman two-way analysis of variance tests were two-tailed unless stated otherwise. A Wilcoxon signed-ranks matched-pairs test was used to examine the differences between the strike and pull conditions for data on time spent moving data in experiment 3 for *E. macularius*. The Wilcoxon test was also used to analyze the differences between the strike and pull conditions for the tongue-flick and labial-lick data in the 10-min minimal disturbance experiment (experiment 3) for *E. macularius*. The Wilcoxon tests were one-tailed unless stated otherwise. Because several tests for main effects were conducted for time intervals, alpha was set at 0.01 for these tests. For the multiple comparison tests, $\alpha = 0.05$.

Results

Eublepharis macularius

Experiment 1: Typical Experiment Disturbance. Most of the lingual protrusions were labial-licks. Labial-licks occurred at highest frequency in the first minute and declined rapidly thereafter, whereas numbers of tongue-flicks were fairly stable throughout the five minutes. The main treatment effect for combined tongue-flicks and labial-licks (fig. 1a) in minutes 1, 2, 3 and 5 under red light conditions was highly significant (minute 1, $\chi^2_r = 32.23$, $df = 3$, $P < 0.001$; minute 2, $\chi^2_r = 24.70$, $df = 3$, $P < 0.001$; minute 3, $\chi^2_r = 15.68$, $df = 3$, $P < 0.001$; minute 5, $\chi^2_r = 12.96$; $df = 3$, $P < 0.01$). The main treatment effect during minute 4 was not significant ($\chi^2_r = 5.31$; $df = 3$; $P > 0.10$).

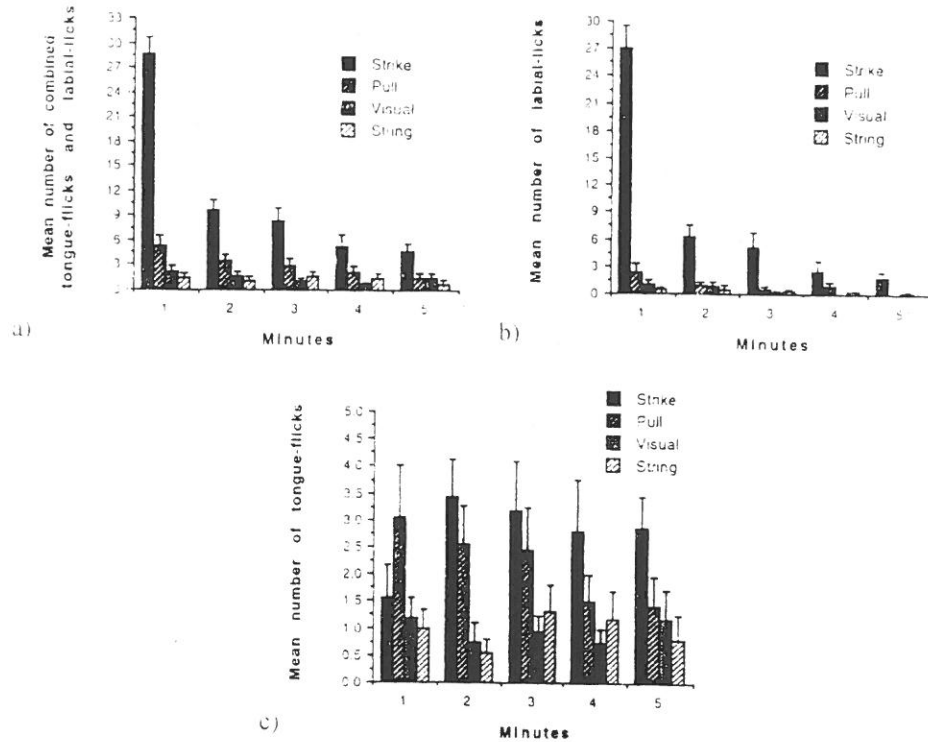


Figure 1. The mean (\pm SE) numbers of a) combined tongue-flicks and labial-licks, b) labial-licks, and c) tongue-flicks emitted by *Eublepharis macularius* for five minutes following removal of bitten prey in experiment 1 in the four experimental conditions.

During minute one there were significantly greater numbers of combined tongue-flicks and labial-licks in the strike condition than in each of the other conditions ($P < 0.001$ each). In addition, there were significantly more combined lingual protrusions in the pull condition than in the string condition ($P < 0.024$ one-tailed). There were no significant differences in labial-licks between other conditions during minute one. During minute two there was significantly greater number of combined tongue-flicks and labial-licks in the strike condition than in the pull condition ($P < 0.01$) and in the visual and string conditions ($P < 0.001$). In addition, there were significantly more combined lingual protrusions in the pull condition than in the string condition ($P < 0.024$ one-tailed). During minutes three and five there were significantly greater numbers of combined tongue-flicks and labial-licks in the strike condition than in the pull condition ($P < 0.01$ each), the visual condition ($P < 0.001$; $P < 0.01$), and the string condition ($P < 0.001$; $P < 0.001$). There were no significant differences in combined tongue-flicks and labial-licks between other conditions during minute three or five (fig. 1a).

The main treatment effect for labial-licks (fig. 1b) was highly significant during minutes 1, 2 (minute 1, $\chi^2 = 29.10$, $df = 3$, $P < 0.001$; minute 2, $\chi^2 = 18.53$, $df = 3$,

$P < 0.001$) and suggestive during minute 5 ($\chi^2 = 10.82$, $df = 3$, $P < 0.02$). The main treatment effect during minute 4 was not significant (minute 4, $\chi^2 = 3.43$; $df = 3$; $P > 0.10$). During minutes one and two there were significantly greater numbers of labial-licks in the strike condition than in each of the other conditions ($P < 0.001$ each). There were no significant differences in labial-licks between other conditions during minute one or two. During minute five there were significantly greater numbers of labial-licks in the strike condition than in the pull condition ($P < 0.01$), the visual condition ($P < 0.01$), and the string condition ($P < 0.01$). There were no significant differences in labial-licks between other conditions during minute five (fig. 1b).

Leopard geckos tongue-flicked at low rates ($< 4/\text{min}$) with substantially higher rates in the strike and pull conditions (fig. 1c). The main treatment effect for tongue-flicks was significant only during minute 2 ($\chi^2 = 15.32$, $df = 3$, $P < 0.005$). During minutes 1, 3, 4, and 5 the main effect was not significant (minute 1, $\chi^2 = 2.57$; minute 3, $\chi^2 = 3.53$; minute 4, $\chi^2 = 1.93$; $df = 3$ and $P > 0.10$ each; minute 5, $\chi^2 = 6.28$, $df = 3$, $0.05 < P < 0.10$). There were significantly greater numbers of tongue-flicks in the strike condition in minute two than in the visual and string conditions ($P < 0.001$ each), but not in the pull condition ($P > 0.05$). Significantly more tongue-flicks occurred in the pull condition than in the visual and string conditions ($P < 0.01$ each), but numbers of tongue-flicks in the visual and string conditions did not differ significantly.

Experiment 2: Lingual Protrusions after Minimal Disturbance. The differences in number of combined tongue-flicks and labial-licks emitted by *E. macularius*, under red light conditions with minimal disturbance (fig. 2a), between the strike and pull conditions were significant during minutes 1-4 (minute 1, $T = 0$, $n = 16$, $P < 0.001$; minute 2, $T = 1$, $n = 15$, $P < 0.001$; minute 3, $T = 4$, $n = 15$, $P < 0.001$; minute 4, $T = 14$, $n = 15$, $P < 0.005$) and suggestive during minutes 5-6 (minute 5, $T = 19.5$, $n = 14$, $P < 0.025$; minute 6, $T = 30$, $n = 16$, $P < 0.05$). The differences in combined tongue-flicks and labial-licks between the strike and pull conditions during minutes 7-10 were not significant (minute 7, $T = 36$, $n = 16$, $P > 0.05$; minute 8, $T = 23.5$, $n = 13$, $P > 0.05$; minute 9, $T = 21$, $n = 12$, $P > 0.05$; minute 10, $T = 19$, $n = 12$, $P > 0.05$).

The differences in number of labial-licks between the strike and pull conditions (fig. 2b) were significant during minutes 1, 2, 5, and 6 and approached significance in minutes 3, 4, and 7 (minute 1, $T = 0$, $n = 16$, $P < 0.001$; minute 2, $T = 1.5$, $n = 14$, $P < 0.0025$; minute 3, $T = 11$, $n = 14$, $P < 0.025$; minute 4, $T = 13$, $n = 11$, $P = 0.025$; minute 5, $T = 7.5$, $n = 12$, $P < 0.01$; minute 6, $T = 0$, $n = 11$, $P < 0.001$; minute 7, $T = 6$, $n = 9$, $P < 0.05$). Few individuals labial-licked in the final three minutes, and differences between conditions were not significant then (minute 8, $T = 6$, $n = 6$; minute 9, $T = 2$, $n = 5$; minute 10, $T = 4$, $n = 4$; $P > 0.10$ each).

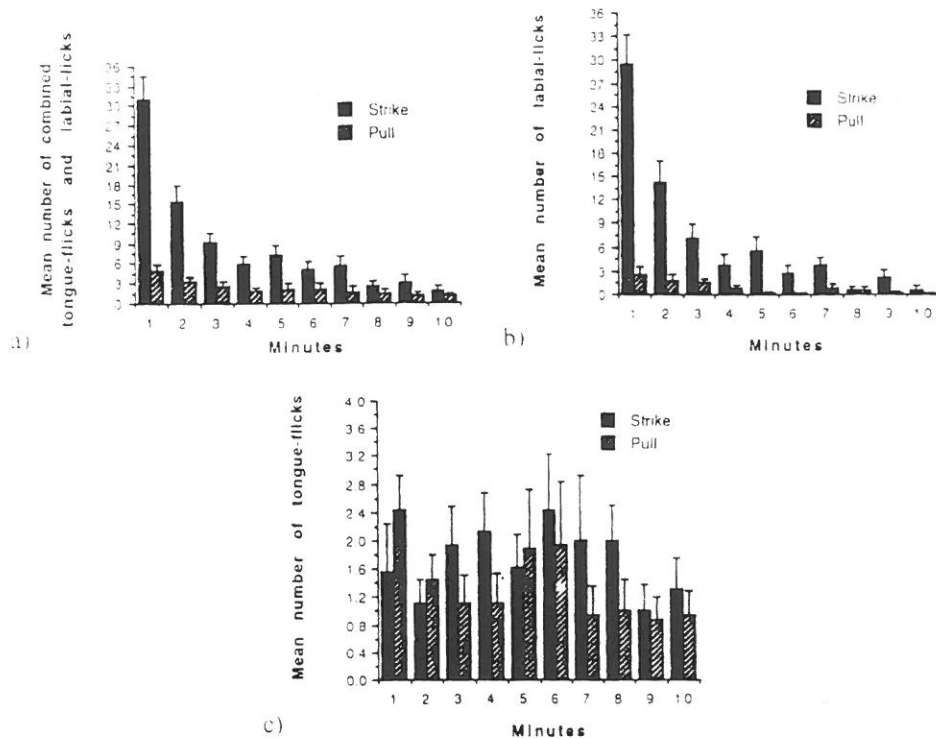


Figure 2. The mean (\pm SE) numbers of a) combined tongue-flicks and labial-licks, b) labial-licks, and c) tongue-flicks emitted by *Eublepharis macularius* for ten minutes following removal of bitten prey with minimal disturbance to the lizard in experiment 2 in the strike and pull conditions.

Tongue-flick rates were lower than in experiment 1 (fig. 2c). Although mean numbers of tongue-flicks did not differ significantly between conditions in most minutes, the total number of tongue-flicks for the group was consistently greater in the strike condition than in the pull condition after the first two minutes (fig. 2c). The mean number of tongue-flicks was greater in the strike condition in 7 of the last eight minutes (sign test, $P = 0.035$, one-tailed) and in the final five minutes (sign test, $P = 0.031$).

The difference in number of tongue-flicks between the strike and pull conditions under red light with minimal disturbance was not significant in any minute and only approached significance in minute 8 (minute 1, $T = 24.5$, $n = 13$, $P > 0.10$; minute 2, $T = 53$, $n = 15$, $P > 0.10$; minute 3, $T = 25$, $n = 12$, $P > 0.10$; minute 4, $T = 23$, $n = 12$, $P > 0.10$; minute 5, $T = 37$; $n = 12$, $P > 0.10$; minute 6, $T = 27$, $n = 11$, $P > 0.10$; minute 7, $T = 27$, $n = 11$, $P > 0.10$; minute 8, $T = 12.5$; $n = 10$, $P < 0.05$; minute 9, $T = 27$, $n = 10$, $P > 0.10$; minute 10, $T = 23.5$, $n = 10$, $P > 0.10$).

Experiment 3: Movement after Minimal Disturbance. The leopard geckos spent substantial periods in motion, especially in the strike condition (fig. 3). More time was

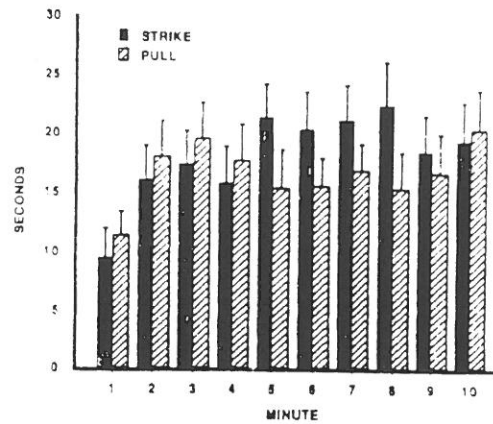


Figure 3. Mean number of seconds spent moving (\pm SE) by *Eublepharis macularius* for ten minutes following removal of bitten prey with minimal disturbance to the lizard (experiment 3) in the strike and pull conditions.

spent moving in the strike condition than in the pull condition, but only after a delay of several minutes during which movement rates were fairly high in both conditions (fig. 3). The leopard geckos spent more seconds moving in the pull condition than in the strike condition during the first four minutes, but the differences were small and did not approach significance (minutes 1-2, $T = 48.5$, $n = 15$, $P > 0.10$; minutes 3-4, $T = 41.0$, $n = 15$, $P > 0.10$).

In the succeeding four minutes geckos spent more time moving in the strike condition, although the differences were not quite significant using the stringent 0.01 alpha level (minutes 5-6, $T = 27$, $n = 16$, $P < 0.025$; minutes 7-8, $T = 30.5$, $n = 16$, $P < 0.05$). Additionally the mean time spent moving was greater for five consecutive minutes beginning with minute five. During minutes 9-10 the lizards in both conditions spent approximately equal times moving ($T = 56$, $n = 16$, $P > 0.10$).

Gekko gecko

Gekko gecko exhibited labial-licking but no tongue-flicks in which the ventral pallets of the tongue contacted a substrate. The main treatment effect for labial-licks (fig. 4) was significant in minute one ($\chi^2 = 19.38$, $df = 3$, $P < 0.001$), and number of labial-licks was significantly greater in the strike condition than in any of the other conditions ($P < 0.001$ each). No other differences were significant between pairs of conditions in minute one. The main treatment effects for labial-licks in minutes 2-5 were not significant (minute 2, $\chi^2 = 7.35$; minute 3, $\chi^2 = 0.60$; minute 4, $\chi^2 = 0.60$; minute 5, $\chi^2 = 0.15$; $df = 3$; $P > 0.05$ each).

Movements were infrequent (fig. 5). Observed movements almost all resulted in the repositioning of the lizard on the wall of the terrarium to orient downward. The main

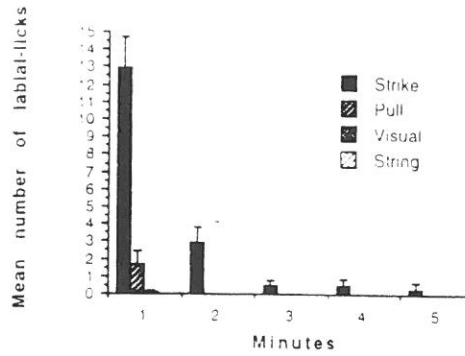


Figure 4. The mean (\pm SE) numbers of labial-licks emitted by *Gekko gecko* for five minutes following removal of bitten prey in the four experimental conditions.

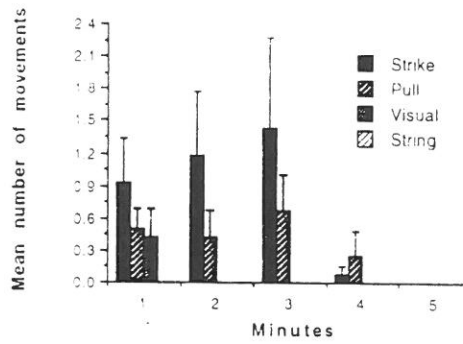


Figure 5. The mean number of movements (\pm SE) performed by *Gekko gecko* for five minutes in the four experimental conditions.

treatment effect for number of movements (fig. 5) was not significant during any minute (minute 1, $\chi_r^2 = 2.88$; minute 2, $\chi_r^2 = 3.60$; minute 3, $\chi_r^2 = 2.48$; minute 4, $\chi_r^2 = 0.02$; minute 5, $\chi_r^2 = 0.00$; $df = 3$; $P > 0.10$ each).

Discussion

Labial-licking and PETF

The function of labial-licking is largely unknown, but it is often observed after eating, suggesting a grooming function (Cooper, 1994a). Another major function may be chemosensory, perhaps to aid further delivery of chemicals on the tongue to the vomeronasal ducts or to sample chemicals on the labials. Leopard geckos rubbed inside the mouth and on the labials by a cotton swab labial-lick at higher rates if the swab

bears prey chemicals than water alone (DePerno and Cooper, unpublished data). This shows that labial-licking is a response to the chemical stimuli, not merely grooming in response to mechanical stimulation. Thus, labial-licking may be indicative of chemosensory investigation. Given the high movement rates exhibited by *E. macularius* (although perhaps not specific to the strike condition), it is possible that labial-licking may aid relocation of prey during search for chemical prey stimuli on environmental substrates. On the other hand, it has recently been suggested that labial-licking may function to clear previously sampled chemicals from the vomeronasal organ (Desfilis et al., 1993). Although the rapid rise and decline in labial-licking is consistent with such a purging function, that labial-licking remained significantly elevated for several minutes suggests that labial-licking may indicate ongoing response to prey chemicals.

Because our unpublished data show that labial-licking increases in response to prey chemicals, we now believe that labial-licks and/or tongue-flicks indicate PETF. This criterion seems appropriate for lizards, such as leopard geckos, that are capable of lingually mediated prey chemical discrimination. However, it remains questionable for lizards not known to identify prey chemicals by lingual sampling.

In a study of PETF and SICS in the iguanian lizard *Anolis carolinensis*, we did not consider a significant elevation in labial-licking after biting to be evidence for PETF; only significantly increased tongue-flicking was taken to indicate PETF (DePerno and Cooper, 1994). Using the relaxed criterion including labial-licking, even anoles would exhibit PETF. Anoles do not tongue-flick prior to attacking prey or exhibit lingually mediated prey chemical discrimination in experiments (Cooper, 1989c). However, increased labial-licking suggests that they might detect them. Whether they can identify prey chemicals introduced into the mouth, rather than merely detect them, by vomerofaction is not known. Until this has been determined experimentally, significant elevation of labial-licking in such taxa should be considered only as possible evidence of PETF. In no case yet studied does this suspension of judgement affect interpretations regarding the presence of SICS because all species showing significant increases in searching movements after losing prey also are capable of prey chemical discrimination (DePerno and Cooper, 1993, 1994; Cooper, 1994b, c).

Eublepharis macularius

PETF lasting several minutes consisted primarily of rapid labial-licking in the first minute followed by a more nearly equal mixture of labial-licking and tongue-flicking in the next several minutes. Movement appeared to increase after attacks on prey in minutes 5-6 and 7-8; the differences were significant at $\alpha = 0.025$ and 0.05, respectively, but were not significant using the 0.01 alpha level. The apparent increase in movement had an unusually delayed onset, being detectable only after several minutes.

In other actively foraging lizards the onset of SICS is immediate and clearcut (e.g., *Heloderma suspectum*, Cooper et al., 1995; *Varanus exanthematicus*, Cooper, 1989a; *Podarcis muralis*, Cooper, 1991; *Eumeces laticeps*, Cooper, 1992b). Despite care taken

to minimize disturbance, movement rates were extensive in both the strike and pull conditions in experiment three. The leopard geckos spent roughly 30% of the time moving slowly and deliberately, as does another eublepharid species (*Coleonyx variegatus*, Kingsbury, 1989), in both conditions. Movement in both strike and pull conditions was far greater than in any species characterized as an ambush forager for which the presence of SICS has been tested (DePerno and Cooper, 1993, 1994; Cooper, 1994a; Cooper et al., 1995).

Either mechanical or other experimental disturbance factors may account for much of the movement exhibited in both conditions. Since tongue-flicking is elevated during searching movements (Cooper, 1993; Cooper and Arnett, 1995; pers. obs.), movements induced by experimental disturbances may have masked differences in tongue-flicking as well as increases in movement attributable to biting prey. If the increase in movement is a real effect, the delayed onset of SICS might be an experimental artifact in which high movement rates in the pull condition mask a typical rapid onset.

It is not clear whether the extensive, long-lasting movements observed represent 1) defensive behaviors such as shelter-seeking or escape in the strike condition, the pull condition, or both, 2) a search for food in one or both of the conditions, or 3) some combination of defense, prey search, or some other behavior. Because cages were opened almost exclusively at feeding times for over a year prior to the experiments, the mere presence of the experimenter might have induced conditioned search. Such search might have been prolonged because multiple prey were released into the cages at feeding times. However, such behavior has not been reported in other lizards. Given the high movement rate in the control condition for mechanical disturbance (pull), it appears that a different experimental procedure may be needed to better evaluate the PETF, SICS, and their temporal characteristics in *E. macularius*.

All previous data show that PETF and SICS are present in actively foraging lizards. Data exist for at most a few species per family, but PETF or SICS has now been confirmed in all species tested in all speciose families of actively foraging carnivorous lizards (reviewed by Cooper, 1994b, this paper) except Gymnophthalmidae, in which no species have been studied, and Eublepharidae. PETF is present in *E. macularius*, but is unlike that of some other active foragers in that the rate of tongue-flicking is quite low and the major contributor to PETF is labial-licking.

The combination of an increase in lingual protrusions and an apparent, but equivocal, increase in movement after experimental removal of bitten prey, suggest that SICS may be present, but do not conclusively establish it. If present, SICS may be atypical in *E. macularius* due to its slow locomotion and low rates of tongue-flicking a substrate. Lizards in most actively foraging families move considerably faster, covering wider areas per unit time (personal observation). If SICS occurs in eublepharids, the present findings are sufficient to establish that it is less strikingly expressed than in families such as Varanidae and Helodermatidae (Cooper, 1989a, 1993; Cooper et al., 1994; Cooper and Arnett, 1995).

Increases in the two types of lingual protrusion and in lingual protrusion versus locomotion were asynchronous. The rapid rise of labial-licking might indicate further assessment of chemical cues already received and possibly even a period of visual search. A following phase of active search could be indicated by the onset of increases in tongue-flicking and locomotion.

Gekko gecko

An increase in rate of labial-licking, possibly indicating PETF, lasted one minute, but could not have contributed to relocating prey by chemosensory means in the absence of tongue-flicking directed to substrates that might bear prey chemicals. Given the complete absence of tongue-flicking and the very low frequency of movement, there is no evidence of SICS in *G. gecko*. The infrequent brief movements could not have contributed to chemosensory searching involving lingual sampling because no tongue-flicking was observed before, during, or after the movement. The downward orientation following movement might possibly represent repositioning order to ambush prey using visual rather than chemosensory search. However, because the experimenter's head was typically above the lizard, turning to a downward orientation might equally well have been an antipredatory response.

The results for *G. gecko* are consistent with data from similar studies involving ambush-foraging iguanians, in that no SICS is evident. SICS is absent in all tested species in seven families of ambush foragers (DePerno and Cooper, 1993, 1994; Cooper, 1994a, b; Cooper et al., in press; this paper). The absence SICS in *G. gecko* supports the hypothesis that this behavior is absent in lizards incapable of discriminating prey chemicals from control substances and in those that do not use the tongue to detect prey chemicals during foraging (Cooper, 1992b).

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