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PROLONGED POSTSTRIKE ELEVATION IN TONGUE-FLICKING RATE WITH RAPID ONSET IN GILA MONSTER, *Heloderma suspectum*: RELATION TO DIET AND FORAGING AND IMPLICATIONS FOR EVOLUTION OF CHEMOSENSORY SEARCHING

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Abstract—Experimental tests showed that poststrike elevation in tongue-flicking rate (PETF) and strike-induced chemosensory searching (SICS) in the gila monster last longer than reported for any other lizard. Based on analysis of numbers of tongue-flicks emitted in 5-min intervals, significant PETF was detected in all intervals up to and including minutes 41–45. Using 10-min intervals, PETF lasted though minutes 46–55. Two of eight individuals continued tongue-flicking throughout the 60 min after biting prey, whereas all individuals ceased tongue-flicking in a control condition after minute 35. The apparent presence of PETF lasting at least an hour in some individuals suggests that there may be important individual differences in duration of PETF. PETF and/or SICS are present in all families of autarchoglossan lizards studied except Cordylidae, the only family lacking lingually mediated prey chemical discrimination. However, its duration is known to be greater than 2-min only in Helodermatidae and Varanidae, the living representatives of Varanoidea. That prolonged PETF and SICS are typical of snakes provides another character supporting a possible a varanoid ancestry for Serpentes. Analysis of 1-min intervals showed that PETF occurred in the first minute. A review of the literature suggests that a pause in tongue-flicking and delay of searching movements are absent in lizards and the few nonvenomous colubrid snakes

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tested. The delayed onset of SICS may be a specific adaptation of some viperid snakes to allow potentially dangerous prey to be rendered harmless by venom following voluntary release after envenomation and preceding further physical contact with the prey.

Key Words—Tongue-flicking, poststrike elevation in tongue-flicking, strike-induced chemosensory searching, gila monster, lizard, Squamata, Helodermatidae, snake origin.

INTRODUCTION

Poststrike elevation in tongue-flicking rate and strike-induced chemosensory searching occur in a wide variety of squamate reptiles (reviewed in Cooper, 1994a). In many highly venomous snakes, especially crotaline vipers, envenomation is followed by a predictable behavioral sequence (Chiszar and Scudder, 1980; Chiszar et al., 1983) having five major components: (1) voluntary release of the prey, which appears to be restricted to highly venomous snakes such as elapids and viperids, especially when attacking potentially dangerous prey (Radcliffe et al., 1980); (2) a pause before initiation of tongue-flicking and crawling, presumed to allow time for the venom to incapacitate the prey; (3) an increase in tongue-flicking rate; (4) locomotion while tongue-flicking (the latter two behaviors being necessary to relocate and follow the scent trail of the envenomated prey); and (5) scent-trailing to relocate the prey, which by the time of relocation is very likely to have died or become incapacitated.

The strike-release-trail strategy encompassing all five components appears to be unique to some highly venomous snakes including some viperids, but at least some of the components are more widely distributed among squamates (Cooper, 1994a). In particular, the increase in tongue-flicking rate and concurrent locomotion occur in many lizards and nonvenomous snakes (lizards reviewed by Cooper, 1994a; nonvenomous snakes by Cooper et al., 1989; Cooper, 1991a, 1992a; Burghardt and Chmura, 1993). Component 3 is called poststrike elevation in tongue-flick rate (PETF); components 3 and 4 combined are called strike-induced chemosensory searching (SICS). The increased tongue-flicking serves to sample chemical cues (presumably for delivery to the vomeronasal organ), and the movement serves to bring the squamate into a position to detect and follow the scent trail.

In species lacking a strike-release-trail strategy, it has been hypothesized that when prey has escaped, SICS may help relocate the lost prey or other individuals of the same prey type known to be in the vicinity (Cooper et al., 1989; Cooper, 1993; Burghardt and Chmura, 1993). The scant data available show that PETF and/or SICS occur in two families of snakes (Pythonidae, see Cooper, 1991a; Colubridae, see Cooper et al., 1989; Cooper, 1992a; Burghardt and Chmura, 1993) and numerous families of scleroglossan lizards, including

Teiidae, Lacertidae, Scincidae, Anguidae, Helodermatidae, and Varanidae (reviewed by Cooper, 1994a). SICS has not been demonstrated in any iguanian family, but PETF (and perhaps SICS) occurs in an iguanid (Cooper and Alberts, 1993).

The duration of PETF and SICS may be expected to vary widely among taxa, being prolonged in those groups of active foragers capable of scent-trailing as well as detection of prey chemicals in groups having prey that can be located reliably by scent-trailing (Cooper, 1994b). Among viperid snakes, the prey is usually killed and, barring removal by other predators, is reliably available for consumption for a relatively long time. SICS may last over 2 hr in crotalines in the laboratory (Chiszar et al., 1982, 1985). Among small insectivorous lizards, PETF and SICS are much briefer, presumably reflecting a combination of the difficulty of scent-trailing flying insects and greater profitability of searching other patches if brief search fails to detect additional prey. The greatest duration of PETF reported for a lizard is 25–30 min for the varanid *Varanus exanthematicus* (Cooper, 1993). Although *V. exanthematicus* feeds primarily on invertebrates in the field in Senegal (Cisse, 1972), perhaps due to availability, it readily consumes vertebrates, given the opportunity. SICS might have even greater duration in larger varanids that normally eat larger, more easily scent-trailed prey or in the other lizards that have exceptionally well-developed lingual–vomeronasal systems and consume prey that can be located reliably by scent.

In this paper we consider three components of chemosensory searching behavior in squamates. First, we present experimental data on the duration of PETF and SICS (components 3 and 4) in a helodermatid lizard, *Heloderma suspectum*. The gila monster is capable of discriminating prey chemicals from other chemicals (Cooper, 1989a) and exhibits PETF and SICS lasting a minimum of 10 min, the maximum possible time that could have been observed in a previous study (Cooper and Arnett, 1995). We predicted that SICS would be prolonged in the gila monster due to its prolonged active foraging over great distances (Bogert and Del Campo, 1956; Beck, 1990; Beck and Lowe, 1991) and to its diet. The gila monster consumes reptile eggs, eggs and young of ground-nesting birds, and young of small mammals (Bogert and Del Campo, 1956; Jones, 1983; Beck, 1990; Beck and Lowe, 1991). Such prey are unlikely to wander far if they initially escape or are lost. The lizards also might be able to locate juvenile rodents by following scent trails of parents to the nest. Support by prolonged PETF/SICS in varanoid lizards for the proposed varanoid ancestry of snakes is discussed. We review data on the occurrence of a pause after loss or release of prey before beginning to tongue-flick at elevated rates (component 2) and suggest that restriction of the pause to viperids may be a synapomorphic and integral part of the strike-release-trail strategy in that taxon. Finally, we briefly survey the status of knowledge regarding taxonomic distribution of the five components of the strike-release-trail strategy and chemosensory search for prey in squamates.

METHODS AND MATERIALS

The duration of PETF was studied in eight adult gila monsters. Five were obtained from the Arizona Game and Fish Department and were maintained in the laboratory at Indiana University-Purdue University Fort Wayne (IPFW) for several months prior to testing to ensure habituation of the field-captured lizards to laboratory conditions. Several specimens initially refused to eat anything but eggs, but all were eating mice by the time the study was conducted. Each lizard was isolated in a 51 × 26 × 32-cm glass terrarium with a removable locking screen top. In the terrarium were a sand–gravel substrate and a water bowl. Heat lamps were provided to permit the lizards to thermoregulate. Fluorescent lighting cycled on a 12L : 12D schedule. The lizards were fed albino mice (*Mus musculus*) once per week; water was continuously available.

The other three individuals were housed and tested at the Cincinnati Zoo (CZ). Prior to testing, these lizards were removed from their home cages and placed in separate 51 × 26 × 32-cm glass terraria having slate bottoms. No tops, sand, gravel, or water bowls were placed in the cages. Prior to the experiment, the lizards were fed mice once per week and had continuous access to water.

Experimental demonstrations of PETF and SICS in species that do not voluntarily release bitten prey typically incorporate four experimental conditions, including controls, for effects of the experimental context, the sight of prey, and mechanical disturbance caused by experimental removal of the prey from the predator's mouth (e.g., Cooper, 1989b, 1991b; Cooper et al., 1989). Because the presence of PETF and SICS already had been established and the mechanical disturbance condition was found to elicit much higher tongue-flicking rates than the other control conditions, the usual experimental protocol was abbreviated to establish the duration of PETF. As in a study of PETF in *Varanus exanthematicus* (Cooper, 1993), control conditions for effects of experimental context and sight of the prey were omitted.

The two conditions used in the present study were the strike and mechanical disturbance control conditions. In the strike condition a recently killed mouse held in forceps was presented to a lizard, which was allowed to approach, investigate, and bite the mouse. As soon as the lizard bit, the experimenter separated lizard and mouse by pulling steadily on the forceps. If the lizard did not release the mouse, the experimenter gently pushed against the lizard in the opposite direction with a second pair of forceps. To induce several individuals to release the prey, it was necessary to gently pull the mouse upward until the front legs of the gila monster were lifted slightly off the substrate, which reliably induced voluntary release. To control for possible effects of mechanical disturbance caused by inducing the lizard to release the mouse, a mouse was presented as above and the gila monster was allowed to approach and investigate the mouse. However, when the gila monster opened its mouth and prepared to bite the mouse, the mouse was immediately removed, preventing oral contact, and the lizard was simultaneously pushed away from the mouse with another pair of forceps.

To begin a trial, an experimenter slowly approached a lizard's cage, carefully removed the lid and water bowl (if present), and moved away. Twenty minutes later, the experimenter returned and slowly positioned a mouse 20 cm anterior to the lizard's snout. As soon as a lizard released a bitten mouse or had been pushed after preparing to bite, the experimenter began recording tongue-flicks for 60 min at 1-min intervals. Observations were made between 1100 and 1530 hr at IPFW and between 0900 and 1630 hr at CZ. Ambient temperatures were 24–27°C at IPFW and 28–30°C at CZ.

Each individual was tested once per day in a repeated measures design in which the two stimulus conditions were presented in counterbalanced sequence. Due to extreme nonnormality indicated by the presence of many zero values of tongue-flicking in minutes near the end of the 60-min observation period, the statistical analysis was conducted using the nonparametric Wilcoxon matched-pairs signed-ranks test (Hollander and Wolfe, 1973). As the hypothesis tested was directional, all tests of significance were one-tailed with $\alpha = 0.05$ unless stated otherwise (Siegel, 1956). Data were analyzed for 1-, 5-, and 10-min intervals. The 1-min intervals were useful for determining the onset of PETF. The 5- and 10-min intervals allowed detection of somewhat smaller differences cumulated over longer intervals, especially when the initially high tongue-flicking rates had declined and PETF and SICS were waning. In addition, binomial tests were conducted to assess the significance of frequency of minutes in which an individual's tongue-flicking rate exceeded that of all individuals in the control group (Hollander and Wolfe, 1973).

RESULTS

Mean tongue-flicking rates were highest in both conditions in the initial minutes (Figure 1). They declined gradually thereafter, reaching zero in the control condition by minute 35. In the strike condition, the mean tongue-flicking rate decreased from values in the low 40s and high 30s per minute during the first 5 min to 3–7/min by minute 37, but some individuals continued tongue-flicking in every minute, and the mean rate showed no further detectable decline. Although many individuals failed to tongue-flick in the latter minutes, two individuals continued tongue-flicking at substantial rates even in the final few minutes. Movements were not recorded, but tongue-flicking and locomotion were closely associated throughout the observation period.

Analysis by 1-min intervals revealed significantly more tongue-flicks in the strike condition in the initial minute ($T = 3$, $N = 8$, $P < 0.02$). Significantly greater tongue-flicking rates were observed in the first three minutes (Table 1; min 2: $T = 1$, $N = 8$, $P < 0.01$; min 3: $T = 5$, $N = 8$, $P < 0.04$). Although the difference between conditions was not significant in minutes 4 and 5 due to elevated tongue-flicking in the control condition (Table 1; min 4: $T = 15$, $N = 8$, $P > 0.05$; min 5: $T = 7$, $N = 7$, $P > 0.05$), they were significant in 21 of the first 30 min. Although the difference was significant thereafter only in minute 34, more tongue-flicks were emitted in the strike condition in every one of the

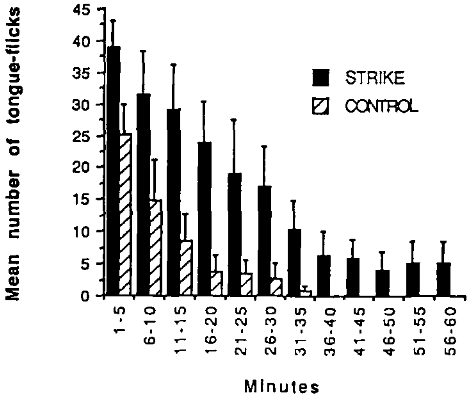

FIG 1. Mean numbers of tongue-flicks emitted by *Heloderma suspectum* in 5-min intervals in the strike and control conditions. Error bars represent 1.0 SE.

TABLE 1. MEANS, STANDARD ERRORS, AND RANGES OF NUMBERS OF TONGUE-FLICKS IN STRIKE AND CONTROL CONDITIONS FOR FIVE INITIAL 1-MINUTE INTERVALS

	Strike			Control		
Min	Mean	SE	Range	Mean	SE	Range
1	41.9	4.1	19-56	22.4	2.3	14-32
2	38.8	2.4	29-51	21.6	3.4	9-38
3	38.4	3.7	26-60	25.6	4.6	14-40
4	36.0	5.4	4-55	31.4	5.9	4-56
5	39.2	5.2	12-61	25.1	5.3	0-45

60 min. Of the two individuals that tongue-flicked in the strike condition during the final 10 min, one tongue-flicked in nine of the ten, the other in all 10. For each of these two individuals, we conducted a binomial test for the presence of PETF in minutes 51–60 using a null hypothesis that tongue-flicking rate by the individual and the maximum rate for any individual in the control group were equal. Both individuals tongue-flicked at significantly greater than control levels during the final 10 min ($P = 0.011$ and $P = 0.001$).

Analysis of data for 5- and 10-min intervals revealed the presence of SICS well after the last detectable time based on 1-minute intervals. In all 5-min intervals, up to and including minutes 41–45, tongue-flicking rates were significantly higher in the strike condition than in the control condition (Figure 1; 1-5: $T = 3$, $P < 0.02$; 6–10: $T = 1$, $P < 0.008$; 11–15: $T = 3$, $P < 0.02$; 16–20: $T = 3$, $P < 0.02$; 21–25: $T = 2$, $P < 0.024$; 26–30: $T = 1$, $P < 0.032$; 31–35: $T = 1$, $P < 0.032$; 36–40: $T = 0$, $P < 0.016$; 41–45: $T = 0$, $P < 0.032$; 46–50: $T = 0$, $P > 0.05$; 51–55: $T = 0$, $P > 0.05$; 56–60: $T = 0$, $P > 0.05$; due to tied values, effective sample sizes were eight in the first four intervals, seven in the fifth, six in the next three intervals, then five, four, four, and three in the last four intervals). Analyses for 10-min intervals were concordant with those for 5-min intervals in revealing significantly greater tongue-flicking in the strike condition in all intervals up to and including minutes 41–50, but not in the final 10 min (Figure 2; 1–10: $T = 1$, $P < 0.008$; 11–20: $T = 3$, $P < 0.02$; 21–30: $T = 1$, $P < 0.02$; 31–40: $T = 0$, $P < 0.016$; 41–50: $T = 0$, $P < 0.016$: 51–60: $T = 0$, $P > 0.05$; due to tied values, effective sample sizes were eight, eight, seven, six, six, and four). To further resolve the duration of PETF, the interval 46–55 was analyzed, revealing significantly greater tongue-flicking in the strike condition than in the control condition ($T = 0$, $P < 0.032$, after ties were removed, effective $N = 5$).

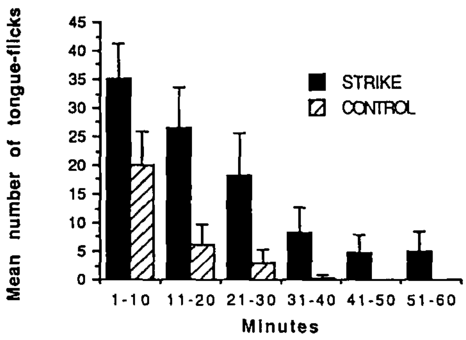

Fig. 2. Mean numbers of tongue-flicks emitted by *Heloderma suspectum* in 10-min intervals in the strike and control conditions. Error bars represent 1.0 SE.

There was substantial variation among individuals in duration of PETF. Numbers of individuals that tongue-flicked during 5-min intervals were zero in the control condition for all intervals beginning at 36–40. In the strike condition, the numbers of individuals tongue-flicking were six in minutes 36–50, five in minutes 41–45, four in minutes 46–50 and 51–55, and three in minutes 55–60. These data alone are sufficient to account for the pattern of significance observed in these intervals.

DISCUSSION

Duration of PETF. The prediction that PETF (component 3) is of longer duration in *H. suspectum* than in most other lizards was verified. Because movements and tongue-flicking were closely associated, SICS has a long duration, similar and perhaps identical to that of PETF. The analyses using five- and ten-min intervals showed that the minimum duration of which PETF was significant for the group was 41–45 min by the 5-min intervals and 46–55 min by the 10-min intervals. However, PETF may last even longer in some individuals, as shown by its presence during the final 10 min in two individuals. Thus, PETF is present for 46–55 min in the group, and some residual group effects remain after 60 min. PETF persists for at least 60 min and perhaps longer in some individuals.

High initial rates of tongue-flicking in both conditions reflect an immediate effect of mechanical disturbance and of biting prey on tongue-flicking. No baseline rates were measured in the present study, but tongue-flicking in the first minutes was far above baseline rates and above rates observed for the two additional control conditions in the demonstration of the existence of PETF in *H. suspectum* (Cooper and Arnett, 1994). Thus, there was no detectable pause before the onset of a high tongue-flick rate.

Although the temporal trends in tongue-flicking rates show a smooth decline for the 5- and 10-min intervals in Figures 1 and 2, the mean tongue-flicking rates in both conditions show some degree of independent waxing and waning from minute to minute (Table 1) as some individuals increased, decreased, or stopped tongue-flicking, sometimes momentarily, accounting for the numerous changes between significance and nonsignificance in the first 30 min. The data for 1-min intervals were useful primarily for detecting the onset of PETF and trends in the initial and final minutes.

PETF and SICS (components 3 and 4) last considerably longer in the gila monster than in any other lizard yet studied. As suggested above, the nature of the prey, which are immobile or have very limited mobility, greatly enhances the probability that a chemosensory search for prey lost in the immediate vicinity will eventually be successful. Prolonged PETF is thus favored. In addition, the dispersed distribution of bird, mammal, and reptile nests requires chemosensory search over wide areas (Bogert and Del Campo, 1956; Jones, 1983; Beck, 1990, Beck and Lowe, 1991). An ability to follow prey scent trails would allow gila monsters to follow scent trails of adult rodents to nests containing edible young.

PETF and SICS occur in numerous families of autarchoglossan lizards (reviewed by Cooper, 1994a), but the duration of PETF among all the families studied is greater than 2 min only in Helodermatidae and Varanidae (Cooper, 1993, and this paper). In these two families, the duration is intermediate to that of other lizards and venomous snakes. Phylogenetic relationships among major families of autarchoglossan lizards in which PETF and/or SICS have been studied are shown in Figure 3. Although PETF occurs in all of these families except Cordylidae (Cooper, 1994a, unpublished data for Cordylidae), the only two

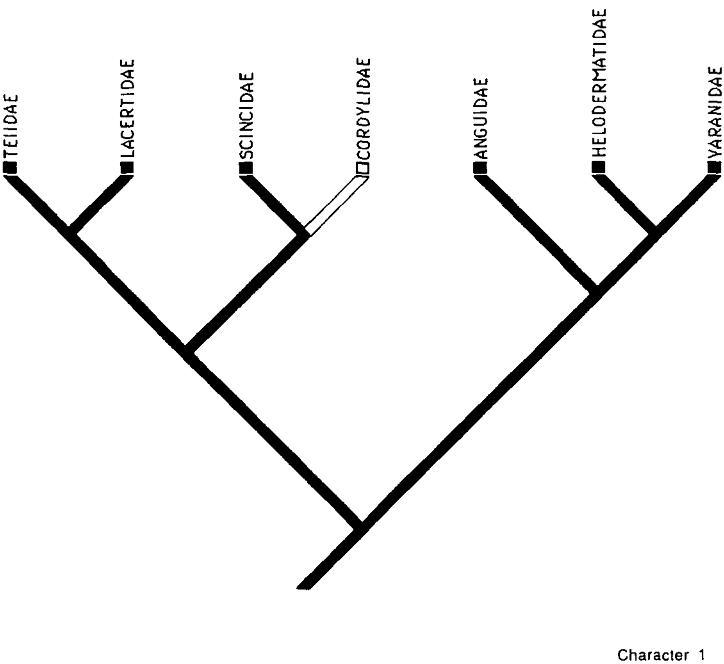

Fig. 3. The phylogeny of major families of autarchoglossan lizards for which data on PETF and/or SICS are available. Helodermatidae and Varanidae are the living families of Varanoidea, which probably includes snakes, which are the only squamates other than varanoid lizards known to have prolonged SICS.

families in which PETF lasts more than a few minutes, Varanidae and Helodermatidae, are very close relatives that constitute the living representatives of Varanoidea. Despite the limitation of data to one species from each of two families, the remarkable stability of chemosensory behaviors such as prey chemical discrimination within lizard families (Cooper, 1994a,c) suggests that long-lasting PETF may be a synapomorphy of varanoid lizards, at least of their extant families.

The phylogenetic relationship of snakes to other squamates remains poorly understood. It is widely accepted that snakes are included in Scleroglossa, which also includes autarchoglossans, gekkonoideans, and amphisbaenians (Estes et al., 1988). However, the relationship of snakes to other taxa within Scleroglossa is uncertain. On the basis of lingual structure, McDowell (1972) hypothesized a varanoid ancestry for snakes. Using more lingual characters and later a combination of lingual and other chemosensory characters, Schwenk (1988, 1993) presented evidence suggesting a sister group relationship between snakes and Varanidae. There is thus a possibility that long-lasting PETF may be a plesiomorphic heritage from varanoid lizards. Data on the existence and duration of PETF and SICS are needed in a wide variety of snake taxa. PETF has been observed to last for more than 2 hr in a colubrid (*Elaphe g. guttata*; Cooper, unpublished observations, $N = 2$), but almost no information is available for less advanced snakes. PETF occurs in a pythonid (Cooper, 1991a), but no data exist on its duration. Studies of scolecophidians and several henophidian families will be crucial to determination of the history of PETF and SICS in snakes.

The absence of a pause (component 2) of 1 or 2 min after prey was removed before gila monsters began to tongue-flick at elevated rates was consistent with findings for all lizards yet studied that exhibit PETF (Iguanidae, Cooper and Alberts, 1993; Lacertidae, Cooper, 1991b; Teiidae, Cooper, 1994; Scincidae, Cooper, 1992b; Gerrhosauridae, Cooper, 1992c; Anguidae, Cooper, unpublished data; Varanidae, Cooper, 1989b, 1993). The lack of delayed onset of PETF distinguishes PETF in lizards and colubrid snakes (Cooper et al., 1989; Cooper, 1992; Burghardt and Chmura, 1993) from that in viperid snakes (Chiszar and Scudder, 1980).

Components of Chemosensory Search for Prey. The five components of chemosensory searching by squamate reptiles outlined earlier as following oral contact with prey also contain elements that are used in searching for prey prior to chemosensory detection, prior to location of the prey after detection, and after swallowing induces elevated tongue-flicking rates. Thus, the components may be considered as a simple, general framework for investigation of chemosensory behaviors related to feeding.

Component 1, the voluntary release of prey, may occur occasionally in various taxa, especially in response to strong defenses. Nevertheless, reliable release of prey is known only in highly toxic viperid and elapid snakes (e.g., Chiszar and Scudder, 1980; Chiszar et al., 1983), presumably because the prey can be captured and ingested with high probability followed release because venom prevents their escape. Although phylogenetic relationships are poorly known, it is believed that Viperidae is the sister group of the remaining families of Caenophidia, the higher snakes (Dessauer et al., 1987), and that viperids are the oldest extant caenophidians (Cadle, 1988). The widespread occurrence of voluntary release in Viperidae suggests its origin within Viperidae or its common ancestor. Thus, voluntary release may be an adaptation to avoid injury that evolved in Viperidae and is a synapomorphy of many viperids that consume dangerous prey, especially rodents. However, its complete distribution in Viperidae is unknown, and voluntary release does not occur in several vipers that are rodent specialists (Chiszar and Radcliffe, 1989). One such species, the jumping viper, *Porthidium nummifer*, has skin folds that cover the facial pits and eyes as the prey is held, reducing the vulnerability of the head to injury (Chiszar and Radcliffe, 1989). Whether voluntary release in elapids is plesiomorphic or convergent is unknown and unlikely to be resolved until the phylogeny of caenophidian families is clarified. Determination of its presence or absence in Atractaspidae would also be useful.

Component 2, the pause in tongue-flicking and movement before initiation of SICS, is known only in Viperidae. It is absent in lizards and in the few species of nonvenomous snakes studied. PETF appeared rapidly in three species of colubrids (Cooper et al., 1989; Cooper, 1992a; Burghardt and Chmura, 1993). Only in the pythonid *Python regius* has a delay of PETF been observed (Cooper, 1991a). In that species the delay was much longer than that observed in crotaline snakes. Furthermore, the delay is not comparable to that of crotalines but is an artifact of the experimental design and analysis. The ball pythons began tongue-flicking at fairly high rates immediately in the strike condition, but also did so in a control condition for the effects of seeing the prey. In the first minute, they actually tongue-flicked at twice the rate performed in the mechanical disturbance control condition, but PETF was considered absent due to the lack of significantly greater tongue-flicking in the strike condition than in all of the control conditions.

Even in a highly venomous elapid snake, tongue-flicking rates appeared to be elevated in the first minute following release of envenomated prey (O'Connell et al., 1985). This immediate rise in tongue-flicking after biting in all taxa observed, except Viperidae, differs from the suspension of tongue-flicking and motionlessness by viperids for a minute or two after releasing prey (Chiszar and Scudder, 1980). Although data for additional taxa are needed to be conclusive, all existing data are consistent with the hypothesis that the delayed onset of tongue-flicking is a synapomorphy of some viperid snakes. That it may not characterize all viperids that exhibit SICS is suggested by the appearance of elevated tongue-flicking in the first minute after release by *Lachesis muta* (Chiszar et al., 1989).

Despite the limited phylogenetic base, the data provide tentative support for the initial interpretation of the pause by Chiszar and Scudder (1980) as an adaptation to delay further contact with dangerous prey subsequent to envenomation until the prey has been rendered harmless by the venom. The delay is made possible by voluntary release and probably evolved in conjunction with it. Thus, the pause between envenomation and tongue-flicking is a functionally important characteristic of the highly specialized SICS of viperids.

Component 3, an increased tongue-flicking rate, is widespread among actively foraging lizards and nonvenomous snakes as well as in venomous snakes. Tongue-flicking serves to sample the environment for prey chemicals even before any prey has been detected in all families of actively foraging lizards. All of these families are able to distinguish prey chemicals from control chemicals (Cooper, 1994a,c). Lingually mediated prey chemical discrimination is an important means of detecting and locating prey. In the context of PETF and SICS, as well as after swallowing prey (Chiszar et al., 1980; Cooper et al., 1989), the increased tongue-flicking represents more intense chemosensory investigation, enhancing the probability of relocating the prey or other prey items of the same type.

Component 4, locomotion, is necessary to search a region for chemical cues and to follow any scent trails encountered. Tongue-flicking occurs at elevated rates during locomotion in lizards whether or not prey has been attacked recently (e.g., Burghardt et al., 1986). Movement alone may help locate prey by visual means, but movement must be combined with tongue-flicking to permit the lingual sampling of chemical cues needed for initial detection of prey and to detect and follow scent trails of prey already contacted.

Component 5, scent-trailing, may also occur in the context of the strike-release-trail strategy or prior to any direct contact with the prey. It has been observed in various venomous and nonvenomous snakes belonging to several major taxa (reviewed by Halpern, 1992). There is reason to believe that the chemosensory capacity for scent-trailing prey is widespread among autarchoglossan lizards. Prey chemical discrimination has been demonstrated in all autarchoglossan families studied except Cordylidae (references above plus Gerrhosauridae, Cooper, 1992c). Males of the scincid *Eumeces laticeps* can follow female pheromone trails by tongue-flicking (Cooper and Vitt, 1986). Because skinks possess tongues less specialized for chemical sampling (McDowell, 1972) and vomeronasal organs having a lower percentage of chemoreceptor cells in the sensory epithelium (Gabe and Saint Girons, 1976) than do members of several other autarchoglossan families, the chemosensory capacity for scent-trailing prey may exist in various families showing lingual specialization such as forking and elongation and having high percentages of vomeronasal chemoreceptor cells.

The possible existence of such trailing ability has not been demonstrated in any lizard, but should be investigated due to its importance for both initial location of prey and relocation of lost prey. Whether scent-trailing, as opposed to local search in the vicinity of prey chemical cues, is profitable depends on several factors, including the density and mobility of prey. Scent-trailing should be favored when the prey is regionally scarce but locally dense, when there is a large energetic payoff per prey item, and when presence of the trail reliably indicates the continued presence of prey in the area. Due to their diets and the long durations of PETF, the lizards most likely to scent-trail prey are helodermatids and varanids. *Heloderma suspectum*, presumably using chemical cues, can detect eggs placed under sand (Bogert and Del Campo, 1956). There is anecdotal field evidence that *Varanus komodoensis* follows prey trails in the field (Auffenberg, 1981) and laboratory evidence that *V. bengalensis* uses chemical cues to detect hidden food (Auffenberg, 1984). Opportunities for studies of scent-trailing prey and the influence of foraging variables in lizards abound.

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