Strike-Induced Chemosensory Searching: Variation Among Lizards

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STRIKE-INDUCED CHEMOSENSORY SEARCHING: VARIATION AMONG LIZARDS

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ABSTRACT

Strike-induced chemosensory searching (SICS) was found in two families of lizards (Teiidae, Anguidae) but not in two other lizard families (Scincidae, Iguanidae). Experiments on another family (Xenosauridae) were inconclusive as to its possession of SICS. The rate of tongue-flicking was significantly increased after a simulated prey strike compared to controls in *Cnemidophorus sexlineatus* and *Barisia imbricata*. SICS may be part of a complex foraging strategy evolved in certain reptiles rather than part of a generalized chemosensory behavior because two species of skinks did not exhibit SICS in spite of a well developed vomeronasal olfactory apparatus and known abilities to use chemosensation extensively in sexual and individual recognition behaviors. Additional studies in other saurian families are needed to further understand the relationship between SICS and other chemosensory behaviors.

† † †

Strike-induced chemosensory searching (SICS) is a behavior exhibited by certain reptiles that presumably enhances discovery or recovery of prey following a feeding attempt. SICS involves an increased tongue-flicking rate, specifically in response to a feeding attempt rather than simply the rate of tongue-flicking associated with generalized vomeronasal exploration of the environment during searching or other behaviors (Chiszar et al., 1983). Venomous snakes that strike, inject venom, release, and then trail their prey use SICS presumably not only to increase the likelihood of prey capture but also to permit capture of large or dangerous prey without injury (Chiszar et al., 1986; Radcliffe et al., 1986). That SICS also occurs in non-venomous snakes (Cooper et al., 1989) argues against an adaptive origin of SICS linked to evenomation. Furthermore, Cooper (1989a) demonstrated SICS in the lizard *Varanus exanthematicus* and suggested that SICS may be a more generalized chemosensory behavior associated with foraging. Cooper (1990b) reported increased tongue-flicking in response to prey odors in *Tupinambis rufescens* and *Ameiva undulata* of the family Teiidae and *Podarcis hispanica* of the family Lacertidae but did not specifically report SICS. Cooper (1989b) found no tongue-flicking response to prey odors in two iguanids (*Anolis carolinensis* and *Sceloporus malachiticus*) and an agamid (*Calotes mystaceus*).

Various reptile species differ greatly in the degree to which the vomeronasal organ is developed (Parsons, 1970; Pratt, 1948) as well as the degree to which taste or smell is used in general chemosensation (Burghardt, 1970; Simon, 1983). If SICS is a general reptile behavior associated with olfaction rather than gustation, widely foraging species with well-developed vomeronasal organs (Jacobson's organs) might be expected to exhibit SICS, whereas species such as sit-and-wait (ambush) foragers that rely less on olfaction and more on gustation during feeding would not exhibit SICS (Cooper, 1989b).

To examine the hypothesis that SICS is associated with species having highly-developed olfactory senses and to elucidate the distribution of this behavior among other squamates, we examined species in the lizard families Teiidae, Anguidae, Scincidae and Iguanidae. Teiids actively search for prey and have a long, forked tongue and well-developed Jacobson's organ (Burghardt, 1980; Simon, 1983). Anguids tend to be secretive with feeding habits that are less well known, but at least some are active foragers with an ability to discriminate prey odors (Cooper, 1990a). They have a well-developed vomeronasal system (Parsons, 1970;

Pratt, 1948), a forked tongue (Bellairs, 1970) and presumably use olfaction in search of prey. Scincids are a very diverse group but many have well-developed olfactory senses including abilities to discriminate odors among sexes, species, and possibly individuals in behavioral situations (Cooper and Vitt, 1984, 1986). Feeding behavior of skinks is varied; some species are ambush predators whereas others actively search for prey although the well-developed vomeronasal system may be used to search for prey (Bissinger and Simon, 1979; Pratt, 1948; Simon, 1983). Iguanids are also a diverse group but in general they tend to be sit-and-wait predators without elongate tongues (Simon, 1983). Many species of iguanids use tongue-licking behavior to sample environmental cues (Duvall, 1979; Simon, 1983) including recognition of conspecifics (Simon et al., 1981), but iguanids do not seem to use vomeronasal olfaction extensively in food detection. Based on this information one would predict that SICS would occur in teiids but not iguanids if it occurs in any of these lizards. Occurrence of SICS in both anguids and scincids would not be surprising in view of the development of their vomeronasal systems.

MATERIALS AND METHODS

We attempted to examine SICS in ten species in five families (Table I). *Xenosaurus grandis* (Xenosauridae) did not respond to the experimental protocol, so we report on results of species in the other four families. Prior to experimentation, lizards were maintained at 27–30°C and fed crickets or grasshoppers, and occasionally mealworms. Lizards were kept individually in terraria of appropriate size and provided water *ad libitum*. Terraria were fitted with lights for thermoregulation as needed, and lizards appeared to be healthy at the time of the experiments. Tests were conducted on individuals within two weeks of capture. These lizards responded well to captivity with regular feeding activity.

The occurrence of SICS was tested using procedures modified from Cooper (1989a). Briefly, lizards were kept in terraria and given one of four test treatments (randomized) each day. These treatments consisted of three controls to exclude increased tongue-flicking as a response to the experimental situation and one experimental test of SICS (i.e. response to having food pulled away after a feeding attempt). Test one (disturbance control) involved showing the forceps and experimenter's hand to the subject; test two (sight-cue control) included showing a prey item (cricket or grass-

Table I Summary of lizard species examined for presence of SICS behavior. Each test consisted of 4 trials on 1–8 individuals (indicated by n).

Family	**Locality Source**	**General Response (mean tongue flicks)**			
Species		**Test 1**	**Test 2**	**Test 3**	**Test 4 (exp)**
Teiidae					
Cnemidophorus sexlineatus, n = 8	Western Nebraska	2.4	1.9	3.0	48.1
Scincidae					
Eumeces copei, n = 1	Cahuacan, Mexico	3.0	1.3	1.7	2.7
Eumeces obsoletus, n=1	Western Nebraska	0.0	1.0	1.0	2.0
Anguidae					
Barisia imbricata, n = 1	Cahuacan, Mexico	1.3	0.7	1.7	8.3
Iguanidae					
Sceloporus mucronatus, n=2	El Capulin, Mexico	0.0	0.0	0.0	0.0
Sceloporus torquatus, n = 1	nr. Mexico City	0.0	0.0	0.0	0.0
Sceloporus horridus, n = 1	Zitlala, Guerrero	0.0	0.0	0.0	0.0
Sceloporus grammicus, n = 3	San Juan Tetla, Puebla	0.0	0.0	0.0	0.0
Sceloporus formosus, n = 1	Acatlan, Guerrero	0.0	0.0	0.0	0.0
Xenosauridae					
Xenosaurus grandis, n = 2	Cuautlapan, Veracruz	no response to protocol			

hopper) held in forceps inside the terrarium in full view of the lizard subject for 10 seconds; test three (attempted strike) consisted of allowing or coaxing the subject to advance in an attempt to strike the prey, which was removed at the last moment. The experimental test of SICS (test 4) consisted of allowing the subject to strike the prey after which the prey item was withdrawn from the mouth to prevent ingestion. Although we have no assurance that a lizard's response to test 4 was toward chemosensation of the prey rather than handling, we have no reason to suggest that it wasn't. Furthermore, we did not observe tongue-flicking in response to handling during routine husbandry.

We counted the number of tongue flicks in a one-minute interval following each trial. The presence of SICS was demonstrated if there was a significant increase in the number of tongue flicks following the experimental test compared to the control tests. We never observed a delayed SICS response (i.e. one beginning after one minute that did not appear before one minute). Response was sufficiently distinctive that a qualitative response was evident, but a significant increase in number of tongue flicks ($p < 0.05$) over all controls verified the qualitative responses.

RESULTS

Only *Cnemidophorus sexlineatus* and *Barisia imbricata* exhibited increased tongue-flick rates in response to striking a prey item (Fig. 1). Both of these species showed only modest tongue-flick rates to the controls, but each demonstrated a distinct increase in tongue-flicks following removal of a prey item. The response was much stronger in *Cnemidophorus* than in *Barisia*. Clearly, *Cnemidophorus* exhibited a classical strike-induced chemosensory searching response with a rate of tongue-flicking ten times greater after biting a prey compared to responses to any of the controls. A general heightened awareness to presence of food was also evident following test four (strike) in *Cnemidophorus*. Individuals actively searched for the prey by visually and chemically (with tongue-flicks) testing the environment while moving about the enclosure. The response of *Barisia* was less pronounced but a tongue-flick rate clearly elevated by 6.9 times the average response to controls suggested that SICS also occurs in this species. The lizard would move around after test 4, appearing to investigate the surroundings but with a much slower and more deliberate pace than was evident in *Cnemidophorus*.

Although both *Eumeces copei* and *E. obsoletus* occasionally flicked their tongues in the air, this behavior was uncommon and more typical in response to usual feeding on prey on the substrate. Skinks were frequently seen to lick their labial scales after feeding and extend the tongue a couple of times but we saw no increase in use of the tongue in response to the experimental protocol, nor any general increased alertness directed toward searching for food. Similarly, SICS did not occur in any of the species of *Sceloporus* that we examined. These lizards struck voraciously at the prey in test four as often and as frequently as it was offered, but did not use a tongue-flicking response. They appeared to lick their lips a couple of times and seemed to "yawn" or stretch their mouths open. Whether this was associated with an attempt to increase chemosensation

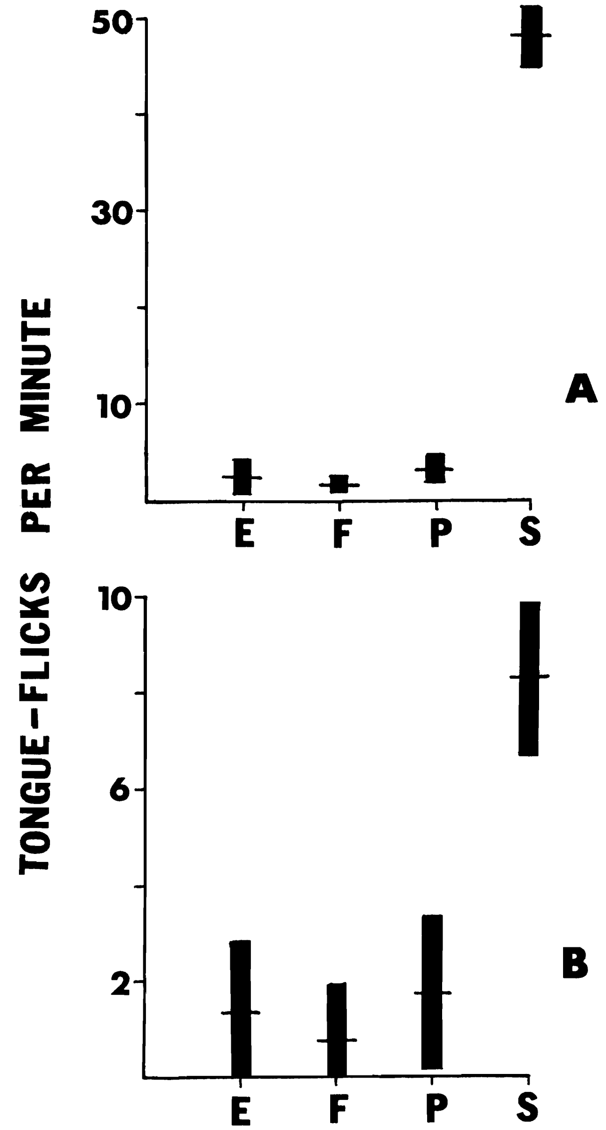

Figure 1. Response of *Cnemidophorus sexlineatus* (A) and *Barisia imbricata* (B) in tongue-flicking behavior to experimental protocol: E = presentation of empty forceps for 10 sec. F = presentation of forceps with insect food. P = presentation of food in forceps but retracted just prior to lizard striking food. S = lizard allowed to strike prey, but prey then removed. Data shown are means (horizontal lines) ± 2 SE (vertical bars).

is speculative. *Sceloporus* did not use the tongue in the typical tongue-flicking manner observed in the other species. We conclude that SICS does not occur in these iguanids. We had great difficulty in our experiments in inducing *Xenosaurus* to respond to our experimental protocol. Little is known about the feeding behavior of *Xenosaurus*. We were unsuccessful in getting *Xenosaurus* to feed or even show an interest in food presented them, even though we have successfully kept them in captivity on a diet of mealworms, crickets, and grasshoppers.

DISCUSSION

Clearly, *Cnemidophorus* and *Barisia* exhibit classical SICS and if representative of other species of their respective families, strike-induced chemosensory searching can be extended to the Teiidae and Anguidae in addition to the Varanidae and snakes known previously (Cooper, 1989a). Cooper (1990a; 1990b) reported increased tongue flicks and prey odor detection in two teiids, a lacertid, and an anguid but did not specifically relate these observations to the occurrence of SICS. Nevertheless, Cooper *(in litt.)* corroborates the occurrence of SICS in teiids and anguids. Contrary to our results on *Eumeces*, Cooper *(in litt.)* found SICS in the broad-headed skink *(Eumeces laticeps)*. Like Cooper (1989b), we did not find SICS in iguanids.

Assuming that the behavior in these three families of lizards is homologous and indeed homologous to SICS in snakes, we agree with Cooper (1989) that this specific behavioral strategy is more primitive than previously thought and is perhaps an ancestral characteristic. Cooper (1989a) pointed out the possibility that SICS evolved in lizards ancestral to snakes (i.e. the platynotans of McDowell, 1972), but our observations extending SICS to lizard families beyond the platynotans indicate that SICS may have evolved earlier than Cooper (1989a) suggested or evolved several times.

Camp (1923) divided lizards into two major groups, the ascalabotans (including Iguanidae) and the autarchoglossans (including Anguidae, Scincidae, Teiidae, Varanidae and Xenosauridae). Autarchoglossans are known to use chemoreception along with vision whereas ascalabotans use vision much more (Simon, 1983). Similarly, the Jacobson's organ (vomeronasal olfactory system) is much more extensively developed in autarchoglossans compared to ascalabotans (Bellairs, 1970; Pratt, 1948). The exact phylogenetic basis for SICS is yet to be determined because relatively few species have been examined, but SICS likely evolved in ancestors of lizards (e.g. ancestors of autarchoglossans) rather than in snakes or strictly snake ancestors. Additional studies are needed to elucidate further the occurrence of SICS in various lizard groups. It would be especially interesting to know if tongue-flicking behavior associated with foraging that Dial (1978) observed in geckos of the genus *Coleonyx* is related to SICS and indeed whether or not the Gekkonidae exhibit SICS.

Our observations further suggest that SICS is a relatively specialized behavior and not simply a part of the general chemosensory repertoire. Thus, rather than being associated with general chemosensory abilities, including a well-developed vomeronasal system, SICS may be a specific component of a complex foraging strategy. This possibility is suggested by our data on *Eumeces*. In spite of the generally high level of olfactory chemoreception in *Eumeces* including a well-developed Jacobson's organ (Pratt, 1948) as well as the use of chemoreception in various behaviors for sexual to individual recognition (Cooper and Vitt, 1984, 1986), we failed to discern a specific increase of tongue-flicking behavior in response to feeding. Cooper *(in litt.)* finds SICS in *Eumeces laticeps*, a large, frequently arboreal skink. Both *E. copei* and *E. obsoletus* are terrestrial and may not use SICS in foraging. This may indicate that strike-induced chemosensory searching is a complex behavior exhibited in specific rather than general olfactory situations as suggested by Cooper (1989a).

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