The Role of Chemoreception in the Prey Selection of Neonate Reptiles

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INTRODUCTION

The role of chemoreception in the prey selection of neonate reptiles was the focus of our research on ten species of Kansas snakes and two species of Kansas lizards. Recent investigators, most notably Burghardt (1970b, 1971, 1973) have demonstrated innate chemical preferences in certain snakes and lizards for the kinds of prey normally eaten in the wild. However, such innate feeding preferences are subject to some degree of variation, including geographic variation paralleling those in the animals' natural diets (Burghardt 1970a; Arnold 1977). Furthermore, distinct polymorphism within local populations, even within broods, has been demonstrated, apparently serving to prevent overspecialization, thereby permitting better utilization of available food resources (Arnold 1977; Burghardt 1975; Gove and Burghardt 1975).

Elimination of visual and olfactory senses results in unaltered prey attacks in at least some kinds of snakes (Wilde 1938; Burghardt and Hess 1968; Burghardt 1970b). Snakes with vomeronasal nerve lesions fail to respond differentially to chemical cues (Halpern and Frumin 1979). Therefore, the primary receptor of this chemical information appears to be the vomeronasal system: the tongue, Jacobson's organ, and associated nerves. This system likely evolved as primitive lizards accidently picked up chemicals with the tongue while drinking, eating, and mating. With increased sensitivity of Jacobson's organ and concomitant facilitating manipulations of the tongue, the system became proficient at responding to airborne chemicals (Gove 1979). Since the tongue transmits the chemical cues to Jacobson's organ, the number of tongue flicks elicited by an odoriferous object, as well as actual attacks, seem to be reliable measures of the reptile's interest in the object (Burghardt 1967).

Past works have dealt predominantly with natricines (Burghardt 1967, 1969, 1975; Burghardt and Hess 1968; Sheffield *et al.* 1968). While these snakes displayed a strong response when tested (many tongue flicks and attacks) others, such as *Lampropeltis getulus*, appear to be less responsive to this methodology (Brock and Myers 1979). Exploration of saurian chemosensory mechanisms, although scant, has shown innate predisposition to chemical stimuli in some species of *Eumeces* (Loop and Scoville 1972; Burghardt 1973) and *Gerrhonotus* (Burghardt 1977).

The innateness of the behavior implies an evolutionary origin; thus one might expect a phylogenetic basis for the differential reliance upon this sensory system. Our objectives were to determine whether the chemoreceptive responses to prey odors that have been shown for some reptiles are of widespread occurrence in squamates and whether these responses differ among species and among higher taxa regardless of life histories.

METHODS

Subjects. — Twenty-three broods of snakes, representing ten species (one hundred and thirty-four individuals), and four broods of lizards representing two species (thirty-one individuals) were born in captivity to gravid females captured in central or eastern Kansas (Table 1). The females were kept in individual containers until parturition, and subsequently released. Each brood was housed collectively in the container in which they were born. The lizards and small snakes (*Storeria dekayi* and *Diadophis punctatus*) were kept in gallon jars in moist wood frass with moistened plastic wrap. Larger snakes were housed in wooden cages (30 × 30 × 60 cm) with screen fronts which held small water containers and open boxes full of wood frass. Experimental animals were maintained in a concrete building with natural lighting, temperature, and humidity.

Preparation. — A variety of prey animals were collected (Table 2). Although most investigators have followed Burghardt's extract preparation technique (1968), Carr and Gregory (1976) suggest that since reptiles presumably respond to odors emanating from the surface of the prey, rubbing a moistened cotton swab over the prey

TABLE 1.   Data on reptiles at time of testing.

Species	Capture site of gravid female (Kansas county)	Brood size	Age (days)	Temp. (C)	Time (CDT)
Eumeces fasciatus	Johnson	6	4	31	1600
	Johnson	11	5	29	1430
Ophisaurus attenuatus	Johnson	3	<7	28	1400
	Johnson	11	<7	27	2000
Coluber constrictor	Johnson	5	8	22	1100
	Johnson	8	6	28	1400
Lampropeltis calligaster	Johnson	5	14	23	1630
Diadophis punctatus	Johnson	3	6	29	1630
	Johnson	1	5	29	1715
	Douglas	2	6	29	1745
	Johnson	1	7	28	1830
	Douglas	2	4	27	1845
	Douglas	2	6	26	1915
	Johnson	2	3	26	2000
	Johnson	4	3	25	2030
Storeria dekayi	Douglas	9	6	33	1500
	Douglas	15	4	32	2000
	Douglas	7	3	32	1330
	Douglas	12	5	38	1600
	Douglas	13	4	31	1400
Thamnophis sirtalis	Douglas	8	6	28	1530
	Douglas	7	6	27	1830
Thamnophis radix	Unknown[a]	8	4	28	1500
Nerodia sipedon	Douglas	5	5	23	1600
Agkistrodon contortrix	Douglas	5	<7	25	1600
Sistrurus catenatus	Unknown[a]	5	<7	25	1500
Crotalus viridis	Unknown[a]	5	<7	26	1300

[a] Captured in central Kansas, county unknown.

surface results in an equally valid test. Therefore, cotton spindles (5 × 12 mm) were soaked in distilled water and rubbed over the surfaces of the live prey animals. These swabs were freshly prepared just before testing and rerubbed on the prey item every five minutes. Each cotton spindle was suspended on thread tied to a dowel. The investigator could thus manipulate the swab without being seen.

Ingestively naive reptiles less than fourteen days old were used since feeding responses can be modified by experience (Burghardt *et al.* 1973; Arnold 1978). While some individuals had already shed their natal skins, none were experiencing ecdysis at the time of testing. Each reptile was removed from its cage and placed in a straight-sided glass gallon container which was covered with cloth to prevent distracting visual stimuli. All individuals were tested in this container. A habituation time of five minutes was allowed. Each individual was presented a series of prey swabs by slowly lowering the swab to within 2 cm of its snout, taking care to prevent accidental swab contact with the container. During each sixty second presentation, tongue flicks were counted, differentiating between those that touched the swab and those that did not. The number of attacks and the elapsed time before attack (attack latency) were also recorded. If no attacks or touching tongue flicks were made within thirty seconds, the swab was gently touched to the subject's snout once. The swab was removed immediately upon attack. Prey swabs were presented in random order, with a distilled water swab serving as a control. A one minute rest period elapsed between each presentation. Our results show no effects of desensitization or carry-over interest to successive stimuli due to order of presentation. The testing chamber was wiped out with distilled water after each experimental reptile was removed. Additional testing information can be found in Table 1.

Scoring. — Burghardt's tongue flick-attack score (1967), an arbitrary value system based on the number of tongue flicks and length of attack latencies, was used to calculate a "response profile" for each species (Table 2). This score is based on the assumption that an attack is a more significant response than any number of tongue flicks, and that a more desirable stimulus leads to an attack with a shorter latency than a less desirable stimulus. The formula for attacking reptiles is represented by:

$$\text{Score} = \text{base unit} + (60\text{-attack latency})$$

The base unit is the maximum number of touching tongue flicks given by any individual of the experimental group tested to any of the stimuli in a sixty second trial. An attacking reptile was given a score identical to the base unit for that species plus the trial length minus the attack latency. A reptile which did not attack was given a score identical with the number of tongue flicks emitted towards the swab. Czaplicki (1975) found a high test-retest reliability when this scoring method was used ($r = .86$). To eliminate responses other than those elicited by swabs (e.g., exploratory tongue flicking), only those tongue flicks which touched the swabs were used.

Results

In all species a preference was shown for one or more types of prey items over the control swab. Using the Wilcoxon Signed Ranks Test to investigate differences between the control and the most preferred swab (those with the highest tongue flick-attack score for each species), we determined that for four species the difference was significant ($P < 0.05$) (Fig. 1). In addition, *Diadophis punctatus* showed a significant response ($P < 0.03$) to a swab other than the one receiving the highest tongue flick-attack score. Although comparison was not possible with the Wilcoxon Signed Ranks Test for *Thamnophis sirtalis*, a paired *t*-test showed highly significant results ($P < 0.005$). Preferred stimuli generally corresponded to the prey species in the natural diet as indicated by food samples from the local population.

Lizards. — *Eumeces fasciatus* responded strongly to grasshoppers and spiders (Table 2). Although grasshoppers received the most atten-

tion, they are outnumbered two : one by spiders in stomach contents (Fitch 1954). Perhaps this is because as adults, most grasshoppers are too large for even an adult skink to subdue and ingest. Spiders and orthopterans combined comprise the bulk of the diet in the wild. Only 6% of the skinks attacked harvestman swabs, compared to 47% that attacked the grasshopper swab. Harvestmen constitute a minor food source in the local population.

Ophisaurus attenuatus likewise showed a strong response to spider ($P < 0.015$) and orthopteran swabs (grasshopper $P < 0.003$), (cricket $P < 0.003$). Orthopterans comprise 58% of their diet, spiders 12.5%, in a food sample of a local population (Fitch, pers. comm.). Although the cricket swab elicited as many attacks as the spider swab, the spider trials were characterized by shorter attack latencies and more tongue flicks.

Snakes. — *Coluber constrictor* showed minimal responses to all prey swabs. Of the three prey offered, worms are not included in their natural diets, mice are often eaten, but crickets are the most frequently consumed prey (Fitch 1963). The mouse swab elicited the strongest response, although that was negligible. No attacks were made on any swab.

Lampropeltis calligaster eats mainly small mammals and reptiles (Fitch 1978). While the mouse swab surprisingly aroused no more interest than the distilled water swab, the swabs of red sided garter snake and eastern yellow bellied racer did elicit some response as expected. Since ringneck snakes have been found in stomach and scat contents (Fitch 1978), it is somewhat surprising that ringneck swabs received so little attention (Table 2). No attacks were made.

The diet of local populations of *Diadophis punctatus* is composed almost exclusively of earthworms (Fitch 1975). While the earthworm swab did elicit the strongest response, the snail swab received almost as much interest and was significant at $P < 0.03$. No attacks were made.

Storeria dekayi showed an overwhelming preference for the earthworm swab ($P < 0.0001$), supporting Collins' (1974) assessment that locally they eat primarily earthworms. There was a weaker, but still significant ($P < 0.01$) response to the pond snail (Table 2).

Thamnophis sirtalis preys chiefly on mammals, frogs and worms (Fitch 1965). Fish are not well represented in the diet of the local popula-

TABLE 2.   Tongue-flick attack (TFA) scores for 12 species of Kansas reptiles.

Prey swab	Number of attacks	Mean TFA score ± SE
Eumeces fasciatus ($P < 0.023$, N = 17)[a]		
Distilled water	1	3.24 ± 3.11
Harvestman (*Leiobunum vittatum*)	1	4.71 ± 3.37
Differential grasshopper (*Melanoplus differentialis*)	8	16.41 ± 5.16
House spider (*Achaeranea tepidariorum*)	3	8.71 ± 4.79
Ophisaurus attenuatus ($P < 0.015$, N = 14)[a]		
Distilled water	0	0.43 ± 0.20
Differential grasshopper (*Melanoplus differentialis*)	3	21.21 ± 9.17
Cricket (*Acheta assimilis*)	5	26.21 ± 8.46
Prairie wolf spider (*Lycosa rabida*)	5	28.36 ± 9.59
Coluber constrictor ($t = 1.39$, N = 13, $P < 0.10$)[b]		
Distilled water	0	0.00 ± 0.00
Cricket (*Acheta assimilis*)	0	0.15 ± 0.10
House mouse (*Mus musculus*)	0	0.85 ± 0.61
Earthworm (*Allolobophora caliginosa*)	0	0.15 ± 0.15
Lampropeltis calligaster ($P < 0.18$, N = 5)[a]		
Distilled water	0	0.20 ± 0.20
House mouse (*Mus musculus*)	0	0.20 ± 0.20
Red-sided garter snake (*Thamnophis sirtalis*)	0	1.80 ± 1.36
Eastern yellow-bellied racer (*Coluber constrictor*)	0	1.40 ± 0.87
Prairie ringneck snake (*Diadophis punctatus*)	0	0.20 ± 0.20
Diadophis punctatus ($P < 0.14$, N = 17)[a]		
Distilled water	0	0.71 ± 0.37
Pond snail (*Physa hawni*)	0	2.06 ± 0.52
Mealworm (*Tenebrio molitor*)	0	0.24 ± 0.18
Earthworm (*Allolobophora caliginosa*)	0	2.59 ± 1.27
Storeria dekayi ($P < 0.0001$, N = 56)[a]		
Distilled water	0	1.02 ± 0.25
Pond snail (*Physa hawni*)	0	2.14 ± 0.43
Earthworm (*Allolobophora caliginosa*)	0	12.46 ± 1.90
Mealworm (*Tenebrio molitor*)	0	1.46 ± 0.26
Thamnophis sirtalis ($t = 3.25$, N = 15, $P < 0.005$)[b]		
Distilled water	0	0.00 ± 0.00
Bullfrog (*Rana catesbeiana*)	0	3.60 ± 1.45
Earthworm (*Allolobophora caliginosa*)	5	25.00 ± 7.70
Red shiner (*Notropus lutrensis*)	1	9.20 ± 4.54
Mealworm (*Tenebrio molitor*)	0	1.87 ± 1.27
Thamnophis radix ($P < 0.052$, N = 8)[a]		
Distilled water	0	0.50 ± 0.27
Earthworm (*Allolobophora caliginosa*)	2	17.63 ± 8.29
Red shiner (*Notropus lutrensis*)	0	5.25 ± 0.84
Pond snail (*Physa hawni*)	3	20.63 ± 10.09
House mouse (*Mus musculus*)	0	3.38 ± 1.25
Nerodia sipedon ($t = 1.48$, N = 5, $P < 0.15$)[b]		
Distilled water	0	0.00 ± 0.00
Red shiner (*Notropus lutrensis*)	0	3.20 ± 1.85
Leopard frog (*Rana pipiens*)	0	4.40 ± 2.98
Tree frog (*Hyla chrysoscelis*)	0	2.60 ± 1.66
Agkistrodon contortrix ($t = 1.57$, N = 5, $P < 0.10$)[b]		
Distilled water	0	0.00 ± 0.00
House mouse (*Mus musculus*)	0	1.00 ± 1.00
Cricket frog (*Acris crepitans*)	0	0.80 ± 0.80
Prairie ringneck snake (*Diadophis punctatus*)	0	5.00 ± 1.84
Western slender glass lizard (*Ophisaurus attenuatus*)	0	6.40 ± 4.07

TABLE 2. Continued.

Prey swab	Number of attacks	Mean TFA score ± SE
Sistrurus catenatus ($P < 0.110$, N = 5)[a]		
Distilled water	0	0.80 ± 0.80
Bullfrog (*Rana catesbeiana*)	0	0.00 ± 0.00
Prairie vole (*Microtus ochrogaster*)	0	3.20 ± 1.53
White-footed mouse (*Peromyscus leucopus*)	0	0.80 ± 0.49
House mouse (*Mus musculus*)	0	0.00 ± 0.00
Fence lizard (*Sceloporus undulatus*)	0	2.20 ± 1.74
Crotalus viridis ($P < 0.110$, N = 5)[a]		
Distilled water	0	0.40 ± 0.40
Leopard frog (*Rana pipiens*)	0	3.80 ± 3.80
Prairie vole (*Microtus ochrogaster*)	0	6.20 ± 3.92
White-footed mouse (*Peromyscus leucopus*)	0	2.20 ± 2.20
House mouse (*Mus musculus*)	0	11.20 ± 6.11

[a] Wilcoxon Signed Ranks Test between distilled water swab (control) and prey swab with highest mean TFA score.

[b] One-sided paired *t*-test between control and swab with highest TFA score.

tion. The strong response to earthworm swabs (Table 2) corresponds to their natural preference. The comparisons between the earthworm swab and all other prey swabs were significant ($P < 0.05$). One might expect a higher response towards the frog swab as well. Perhaps frogs are not included in the juvenile diet, as the availability of small frogs is greatly reduced by the time the hatchling snakes are feeding.

Thamnophis radix feeds upon amphibians, worms, fish and rodents (Collins 1974). Gastropods are not known to be a regular food source. Consequently, the one unexpected result of our tests was the well defined preference for the snail swab (Table 2). Since snails are abundant and easily caught, their absence from the available samples of this snake's food is puzzling. Burghardt (1969), in testing *Thamnophis sirtalis* with slugs, found that although the snakes might attack the slug, they rejected it immediately and quickly learned to avoid it. Since ingestion could not be accomplished in our experiments, it is not known if snail rejection and subsequent aversion would follow. Another congener, *Thamnophis elegans*, displayed both geographic variation and intrapopulation polymorphism in its predisposition to eat slugs (Arnold 1977). In our study there was no bimodal distribution of feeding scores and therefore no polymorphic response to snails. Perhaps in this species juvenile prey preference differs from that of the adult. The earthworm swab also elicited a strong response ($P < 0.02$), as would be expected, since worms are prominent in food samples. While the fish received a lower score, it was significant at $P < 0.01$.

Locally, *Nerodia sipedon* feeds on frogs and fish (Fitch, pers. comm.). While responses were made to all three stimuli, the swab from the leopard frog, one of the two most frequently consumed foods of local populations, (Fitch, pers. comm.) was the most preferred in these tests. No attacks were made (Table 2).

Agkistrodon contortrix eats rodents, frogs, certain insects, lizards and snakes (Fitch 1960). Fitch found that ringneck snakes comprised 8% of the adult's diet, but are one of the primary foods of the hatchlings. Accordingly, a high response was elicited by the ringneck swab, although the glass lizard swab scored a higher tongue flick-attack score. The glass lizard constituted 2% of food eaten, but house mice and cricket frogs were rarely taken. The strong response to the glass lizard (Table 2) may well indicate a preference for this prey, but the low percentage found in their stomachs may reflect the difficulty involved in catching such an evasive animal. No attacks were made.

Sistrurus catenatus is primarily a rodent eater, although frogs, lizards and snakes are also eaten (Fitch, pers. comm.). In this study, the prairie vole swab received the most tongue flicks, while the fence lizard swab attracted moderate attention (Table 2). No attacks were made.

Mammals are reported to be the common food for *Crotalus viridis* (Collins 1974). Frogs are not
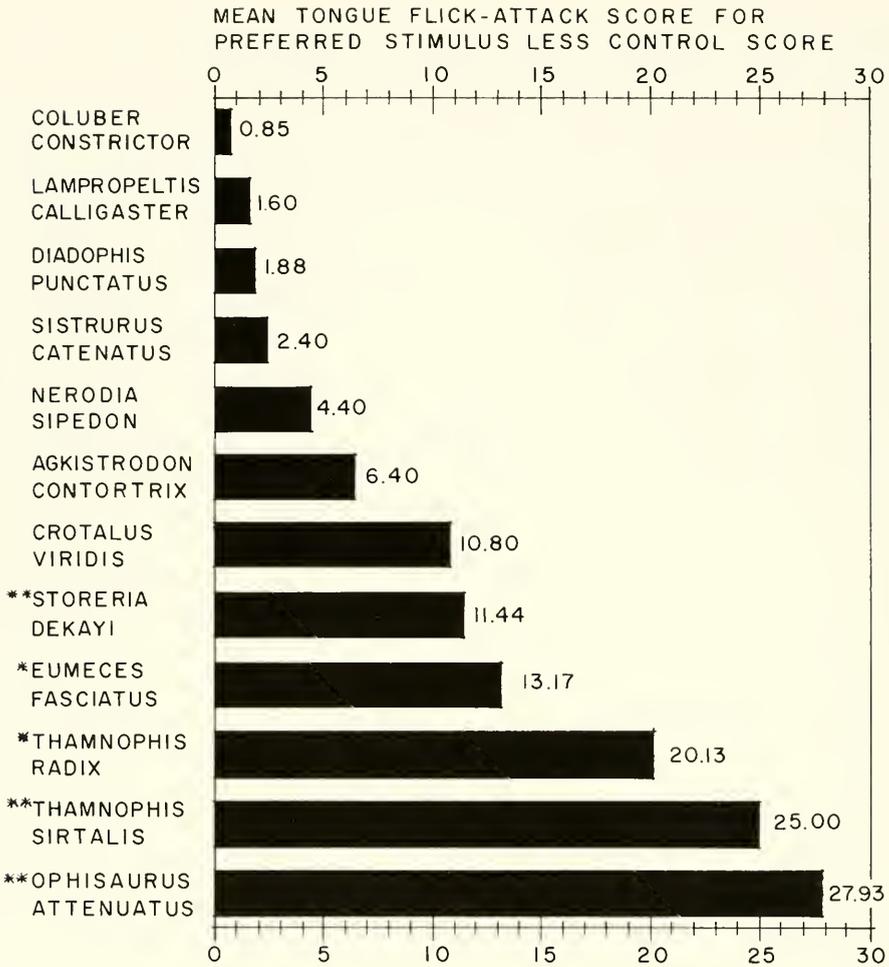
Fig. 1. The difference between the tongue flick-attack scores for the most preferred prey stimulus (the one with the highest tongue flick-attack score) and the distilled water control swab for twelve species of previously unfed Kansas reptiles. Levels of chemosensory dependence are indicated, tending to conform to subfamily groupings.

Probability values are from Wilcoxon Signed Ranks Test for all species but *Thamnophis sirtalis* for which a paired *t*-test was used (* = $P < 0.05$, ** = $P < 0.01$).

normally eaten. The house mouse swab elicited the greatest response in these tests. As was true of the other pit vipers tested, no attacks were made (Table 2).

DISCUSSION

Our experiments follow the general pattern of many previous investigators over the past two decades, but, in choosing potential prey species from which to obtain odoriferous test swabs, we were guided, in most instances, by the results of large-scale food-habit studies on the same local populations from which our experimental neonates were drawn. Also notable are the large number of species and individuals tested, and the inclusion of species not tested before. It was hoped that the inclusion of ecologically diverse types of reptiles for study under the same experimental conditions would enhance the value of the results, allowing phylogenetic comparisons of chemoreceptive responsiveness.

In their test on six families of lizards, Bissinger and Simon (1979) noted that the difference in frequency of tongue extrusions in different families might indicate the relative importance of the vomeronasal system. Accordingly, mean responses to preferred prey swabs provide the basis for comparing each species' differential sensitivity to chemical cues. Fig. 1 shows the difference in the tongue flick-attack scores between the most preferred type of swab (the one receiving the highest tongue flick-attack score) and the distilled water control swab for each of the twelve species. These responses vary among the species and could represent the relative importance of chemoreception in the selection of prey. While only a tentative indication, this does suggest an interesting pattern. Ranked by their levels of selective chemical discrimination, the reptiles are generally arranged into subfamilies (based on Dowling's [1975] classification).

The three species with the lowest response scores, *Coluber constrictor, Lampropeltis calligaster,* and *Diadophis punctatus,* belong to the subfamily Colubrinae. *Coluber constrictor,* a snake of open grassland, appears to rely largely on sight (Collins 1974). Movement of nearly any small animal stimulates the racer to pursue and attack. Olfaction appears to play a minor role in the finding and capture of prey.

Diadophis punctatus is thought to depend on smell for prey detection, and its secretive life under rocks seems to confirm this. However, under the conditions of our experiments, the odor of its primary prey evoked little response, although a lower scoring swab did elicit a significant response.

Lampropeltis calligaster, unlike the natricines usually used in these works, is a constrictor. Other investigators using colubrid constrictors have found their responses towards test swabs differ somewhat from that of natricines. Brock and Myers (1979) were unable to find any significant difference between the control and prey swabs for ingestively naive *L. getulus.* However, Williams and Brisbin (1978) found that adult *L. getulus* had an innate preference for certain prey extracts despite restricted diets. Burghardt and Abeshaheen (1971), working with another colubrid constrictor, *Elaphe vulpina,* found that, in contrast to a garter snake's immediate attack and ingestion of prey, *E. vulpina* moved more deliberately and hesitantly, often taking several hours

to constrict and ingest the prey. Perhaps a sixty second trial is insufficient for such snakes.

The importance of the vomeronasal system to the Crotalinae seems not to be strongly associated with prey detection. Previous work on rattlesnakes (Chiszar and Radcliffe 1976; Chiszar *et al.* 1978) has demonstrated that visual or thermal signals are needed to elicit attacks and relatively few tongue flicks are emitted prior to striking. Once the strike has occurred, however, tongue flicking is initiated and continues while the snake trails the stricken prey and investigates the carcass, presumably to locate the head. Tongue flicking again commences after the prey is swallowed, perhaps to detect any remaining prey in the vicinity. However, rattlesnakes are able to detect prey solely by chemical cues (Cowles and Phelan 1958). The lack of any attacks by the crotalines that we tested supports the supposition that visual or thermal cues are necessary to elicit a strike, even though detection can be accomplished by odor alone.

The fourth snake in an intermediate position is a natricine, *Nerodia sipedon.* Unlike the other natricine tested, *N. sipedon* exhibited a relatively low degree of tongue flicking and made no prey attacks. Burghardt (1968) has reported similar findings for this species. Because this snake generally feeds in the water, volatile chemical cues may not be as useful as visual or tactile cues. Drummond (1979) suggests that this species responds to and integrates visual and chemical cues. Out of the water attacks can be elicited from experienced snakes by visual stimuli alone. When the snake is submerged, visual and/or mechanical stimuli are adequate. Attack frequency increases when diffuse chemical cues accompany visual ones. However, attack can be induced by chemical cues alone.

The three snakes with the highest response scores, *Storeria dekayi, Thamnophis sirtalis,* and *Thamnophis radix,* are terrestrial natricine non-constrictors that overpower, hold and swallow their prey. Their high response scores corroborate previous findings based on essentially the same testing technique (Burghardt 1967, 1969, 1970a, 1971; Burghardt and Hess 1968). Prey attacks were common and tongue flick activity was among the highest of all the snake species tested, suggesting a strong dependence on chemosensory methods of prey selection. Sheffield *et al.* (1968) note that prey attacks were always

preceded by at least one tongue flick that actually touched the swab, and we noted only two exceptions among the one hundred sixty-five individuals tested in this study. One *E. fasciatus* attacked a harvestman swab immediately upon introduction, and an *O. attenuatus* likewise attacked a cricket swab. These attacks were not surprising since many lizards are known to respond to visual cues, including movement. However, Chiszar *et al.* (1976) noted that juvenile *Thamnophis* flick their tongue more often than do adults. It is possible that other senses gradually replace some of the dependence on chemoreceptian during ontogeny (Burghardt 1969; Burghardt and Pruitt 1975). That would explain how a garter snake could catch swiftly moving prey such as a frog, which would seldom remain motionless to permit close approach and preliminary tongue flicks by the predator.

Lizards are generally thought to be less dependent on Jacobson's organ than snakes. Terrestrial lizards, however, usually have better developed olfactory/vomeronasal organs and concomitant decreased vision as compared with arboreal lizards (Gravelle 1980). *E. fasciatus* exhibited a relatively strong chemical preference when tested, placing it among the natricines in response scores. While Loop and Scoville (1972) found no differential tongue flicking or prey attack behavior in a congener, *E. inexpectatus*, our findings support the conclusion of Burghardt (1973) that there is innate chemical recognition of prey. Burghardt also noted, as we did, the very low rate of tongue flicking in *Eumeces* compared with snakes in similar tests.

Ophisaurus attenuatus displayed the highest level of response of all the species tested, both in terms of tongue flicks and attacks. This is consistent with the theory that those lizards showing a lack of elaborate visual communication use Jacobson's organ more frequently (Bissinger and Simon 1979). Furthermore, Gove (1979) demonstrates that the tongue flick pattern of these lizards are more similar to snakes than are most lizards.

Other studies, addressing different questions, have used techniques similar to those used here. However, future investigators should be aware of several problematic areas. One involves the arbitrary age at which the hatchlings are tested. Postnatal onset of hunger following absorption of stored yolk material may take a short or relatively long time in different species and individuals. Moreover, tests to date are based on adult food preferences. It is known that the young of some species prefer different prey than do the adults (Mushinsky and Lotz 1980). If more were known about juvenile diets, utilization of prey items which would generate maximum responses could be assured.

Furthermore, we tentatively conclude that various obscure inhibiting factors altered results to varying degrees, depending on the species and perhaps on the individual. The gentle momentary handling involved in transferring the animal to the experimental container may have involved psychological stress that resulted in suppression of the normal responses to food far beyond the five-minute adjustment period in some hypersensitive kinds. In the more secretive kinds that normally spend their time in burrows or beneath sheltering objects, the experimental container's lack of the necessary thigmotactic stimuli may have inhibited feeding behavior. Differential responses to light intensities and to temperatures may also have been involved.

Finally, most studies have not differentiated between tongue flicks which touched the swab and those which did not . To minimize the risk of confusing tongue flicks not directly stimulated by the odor of the swab, such as exploratory tongue flicks, only those flicks touching the swab were used. This measures response to chemicals of low volatility. Sheffield *et al.* (1968) showed that nonvolatile macromolecules were the attack stimulus for *Thamnophis.* Cowles and Phelan (1958) theorized that the external nares, receiving olfactory stimuli, were highly sensitive but of low discrimination, alerting the snake to visual stimuli of movements and initiating lingual air sampling and subsequent specific analysis by Jacobson's organ. In other words, olfaction conveys volatile information from a distance, while Jacobson's organ is most sensitive to proximal compounds of low volatility. Indeed either the tongue or lips must touch the object before an attack is released (Sheffield *et al.* 1968). Presumably then, touching tongue flicks are more significant indicators of interest than non-touching tongue flicks. Once the prey is inside the mouth, gustation mediates which prey are suitable for swallowing (Burghardt 1969). If prey moves on after detection, a snake may trail it utilizing Jacobson's organ. However, *Elaphe* (Burghardt and Abeshaheen 1971) and *Nerodia* (Dunbar 1979) have demonstrated discrimination of prey on the

basis of volatile chemical cues alone. In our tests, the constrictor *L. calligaster* displayed substantial discriminatory behavior when both touching and non-touching tongue flicks are considered. By contrast, only a weak response was made directly towards the swab. On the other hand, *N. sipedon*, similarly appraised on the basis of all tongue flicks made, responded more to the control than to the scented swabs. Clearly more investigation is needed to determine the most meaningful scoring procedure to use.

With some reservations due to the foregoing constraints, we conclude that purposeful tongue extrusions and attacks do consistently vary among species, the pattern generally following subfamily groupings. This may well suggest a phylogenetic relationship of the differential dependence on chemoreception in the selection of prey.

Summary

Inexperienced young of two lizard and ten snake species from Kansas were presented with cotton swabs scented with body surface odors of various animals including the preferred prey species of each kind of reptile. Distilled water swabs were used as controls. The number of tongue flicks, attacks and attack latencies were recorded. In all cases a preference was shown for one or more prey swabs over the water control swab, generally corresponding to the diet of the local population. This supports earlier findings that suggest innate chemical preferences.

On the basis of tongue flicks and attacks, various levels of discriminatory behavior were recorded, suggesting the relative importance of chemoreception in prey selection for each species. The reptiles tested can be ranked according to their levels of responsivity to chemical stimuli. Tending to conform with subfamily groupings, the colubrinae show the lowest level of discriminatory behavior, natricines, the highest level for snakes, and crotalines, intermediate between the two. The saurian *Eumeces* ranks among the natricines, but *Ophisaurus attenuatus* responded above all the other species tested in exhibiting the highest effectiveness of this sensory modality.

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