Journal of Chemical Ecology, Vol. 10, No. 10, 1984

RESPONSES BY KING SNAKES (*Lampropeltis getulus*) TO CHEMICALS FROM COLUBRID AND CROTALINE SNAKES

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(Received December 1, 1983; revised March 12, 1984)

Abstract—Four litters of king snakes (*Lampropeltis getulus*), a snake-eating species, were tested for responses to chemicals from colubrid and crotaline snakes. King snakes presented with swabs rubbed against the dorsal skin of living snakes and with swabs treated with methylene chloride extracts of shed snake skins tongue-flicked more to swabs from a northern copperhead (*Agkistrodon contortrix*), a crotaline, than to swabs from some colubrid snakes or to blank swabs. Six out of 10 king snakes in one litter attacked and attempted to ingest swabs treated with snake skin chemicals, implicating these chemicals as feeding stimuli for these ophiophagous snakes. Ingestively naive king snakes presented with plain air and snake odors in an olfactometer tongue-flicked more to snake odors. This study and others suggest that crotaline and colubrid snakes can be distinguished by chemical cues.

Key Words—Colubridae, Crotalinae, snake skin chemicals, king snakes, chemical aposematism.

INTRODUCTION

King snakes (*Lampropeltis getulus*) consume a diversity of vertebrates—mammals, amphibians, birds, lizards, and snakes (Clark, 1949; Hamilton and Pollack, 1956). Numerous crotaline (Crotalinae) and some colubrid (Colubridae) snakes respond to king snakes with fleeing, body posturing, biting, or other defensive behaviors (Bogert, 1941; Chiszar et al., 1978; Marchisin, 1980;

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0098-0331/84/1000-1509$03.50/0

Weldon, 1982; Weldon and Burghardt, 1979). Chemicals from king snakes elicit these responses. The involvement of chemicals perceived by king snakes from prey snakes or, indeed, from any of the many vertebrates on which king snakes feed is less clear.

Brock and Myers (1979) tested a litter of 11 ingestively naive *L. getulus* for responses to chemicals from 19 stimulus species. Extracts on cotton swabs from an annelid, arthropods, fishes, amphibians, a mammal, several lizards, and the banded water snake (*Nerodia fasciata*) were presented to king snakes, and tongue-flicks (a presumed measure of a snakes' arousal to chemical stimuli) were counted. Brock and Meyers observed no significant differences in tongue-flick rates by *Lampropeltis* to these substances (see also Burghardt, 1970, p. 288), and they concluded that cues other than chemicals are important in the recognition of king snake prey.

Williams and Brisbin (1978) tested 13 adult *L. getulus* to extract swabs from three potential prey species—mouse, chicken, and rat snake (*Elaphe* sp.)— in addition to swabs treated with human hand rinse or physiological saline solutions. These king snakes has been fed only mice for 2–10 years, yet they recognized all prey odors, tongue-flicking more to these stimuli. Although kingsnakes tongue-flicked more to mouse odors, their responses to the mouse, the chicken, and the snake were not significantly different. Thus, whether king snakes discriminate among chemicals from these classes of vertebrate prey is uncertain.

Observations of interactions between *Lampropeltis* and some crotaline snakes have led some investigators to suspect that king snakes avoid these venomous serpents and that crotaline chemicals elicit this response (Cowles, 1938). Bogert (1941), who established that rattlesnakes (*Crotalus* spp.) respond defensively to king snake skin chemicals, also noted king snakes' attempts to escape from rattlesnakes. Other authors have remarked on king snakes' fear of rattlesnakes (Cowles, 1938) or other crotalines, such as copperheads (*Agkistrodon contortrix*) (Meade, 1940) and cottonmouth moccasins (*A. piscivorus*) (Neill, 1947). Neill (1947, p. 205) wrote: "*Lampropeltis getulus getulus* is loath to attack a cottonmouth, under captive conditions. A tame hungry king snake, placed in a cage with a moccasin two-thirds its length, usually becomes frightened, rooting about the cage in a desperate effort to escape." Our laboratory observations of the occasional display by king snakes (*Lampropeltis getulus holbrooki* and *Lampropeltis g. niger*) of sudden withdrawal and flight from northern copperheads (*Agkistrodon contortrix mokasen*) are in agreement with these reports. It is the purpose of this study to examine whether king snakes (1) perceive chemicals from other snake species and (2) discriminate between chemicals from some crotaline and nonvenomous colubrid snakes.

METHODS AND MATERIALS

Swab Presentations. In experiment I, eight black king snakes, *Lampropeltis getulus niger* [snout–vent length (SVL) = 18.0–23.5 cm $\overline{X}$ = 22.9 cm]. hatched from eggs laid by a female captured in Knox County, Tennessee, were tested at three months of age. Snakes were individually housed in 31 × 16 × 8-cm clear plastic boxes with lids. They had free access to water and had been fed a small live mouse every 7–9 days. One snake had occasionally refused food, but all snakes fed at least four days before testing began. None of the snakes was exposed to stimuli from other snake species prior to testing. The temperature of the testing and housing room was 22–24° C.

Snakes were tested once to each of four stimuli (three snakes and a control) in a Latin-square design. Each snake was tested once each day for four consecutive days. Tests were run between 1400 and 1600 hr.

Skin chemicals were collected on cotton swabs from adult females of three snake species sympatric with the king snakes: eastern garter snake, *Thamnophis sirtalis sirtalis* (Colubridae); speckled king snake, *Lampropeltis getulus holbrooki* (Colubridae); and northern copperhead, *Agkistrodon contortrix mokasen* (Crotalinae). A swab was dipped into methylene chloride (CH_2Cl_2) and rubbed against the dorsal surface of a snake while the snake's head and vent were held. Control (blank) swabs were dipped into CH_2Cl_2 without further treatment. Swabs were air-dried at least 7 min before being presented to the snakes. Similar methods of obtaining snake-scented stimuli have been used in other tests of snakes' responses to chemicals (Bogert, 1941; Marchisin, 1980; Weldon, 1982; Weldon and Burghardt, 1979).

Subjects were tested in their home cages after removal of water dishes and paper towel shelters. A sheet of paper was taped around a snake's cage to extend the cage walls vertically and prevent snakes from crawling upwards during testing. Swabs were held in front of a snake's snout (about 2 cm away) for 2 min while all tongue-flicks were hand-counted. No attempt was made to touch the snakes with the swabs, but occasionally a snake would itself touch a swab or the wooden handle of it.

In experiment II, seven speckled king snakes, *Lampropeltis g. holbrooki* (SVL = 21.5–23.0 cm; $\overline{X}$ = 22.1 cm), hatched from eggs laid by a female captured in Shelby County, Tennessee, were tested at three months of age. They were maintained and tested as described for snakes in the first experiment.

Adult females of three species were stimulus snakes: black rat snake, *Elaphe obsoleta obsoleta* (Colubridae); speckled king snake, *Lampropeltis g. holbrooki* (Colubridae); and northern copperhead, *Agkistrodon contortrix mokasen* (Crotalinae). All are sympatric with the king snakes tested.

Shed skins of stimulus snakes were collected within two days of ecdysis. The skins were weighed, wrapped in aluminum foil, and stored in a freezer at −1°C. Within several months, skins were extracted in a Soxhlet apparatus with CH_2Cl_2 for two days each. A viscous yellow residue of skin extract remained after CH_2Cl_2 was removed at reduced pressure (water aspiration). Extractions of the skins of *Elaphe* (3.10 g), *Lampropeltis* (1.42 g), and *Agkistrodon* (3.25 g) yielded 4.2%, 16.2%, and 5.0%, respectively, of the skins' weights in residue.

Solutions of 50 mg skin extract/ml of CH_2Cl_2 were prepared for each species' extract. Cotton swabs were dipped into the solutions and air-dried for 7–10 min. Swabs from each stimulus snake were then wrapped in aluminum foil and stored (−1°C) for several days before being presented to the king snakes. Control swabs were dipped into CH_2Cl_2 and stored in an identical fashion.

In experiment III, ten black king snakes, *Lampropeltis g. niger* (SVL = 19.5–23.5 cm; $\overline{X}$ = 22.7 cm), hatched from a clutch of eggs collected in Knox County, Tennessee, were tested at four months of age. They were fed a small mouse every 5–8 days, and each snake ate one mouse five days before testing began.

A female Central American black and yellow rat snake, *Spilotes pullatus* (Colubridae); a female garter snake, *Thamnophis fulvus* (Colubridae); and a prairie rattlesnake, *Crotalus viridis viridis* (Crotalinae) (sex unknown) were the stimulus snakes. None of these species is sympatric with the king snakes tested. The shed skins of the stimulus snakes were stored and extracted as described for the preceding experiment. Extractions of *Thamnophis* (1.33 g), *Spilotes* (3.16 g), and *Crotalus* (11.50 g) skins yielded 6.2% 5.5%, and 8.9%, respectively, of the skins' weights in residue. Solutions of snake skin extracts were prepared as described above.

In experiment IV, five king snakes from those tested in experiment III were tested four months later to swabs treated with snake skin chemical solutions of *Thamnophis fulvus*; a female banded water snake, *Nerodia fasciata* (Colubridae); and a female timber rattlesnake, *Crotalus horridus horridus* (Crotalinae); only the latter two species are sympatric with the king snakes tested. Solutions of *T. fulvus* skin chemicals were prepared from what remained after the first series of swab preparations. The *Crotalus* (2.56 g) and *Nerodia* (5.50 g) skins yielded 5.1% and 2.4% of their weights on extraction, respectively.

Olfactometer Experiment. The purpose of this experiment was to test king snakes' responses to airborne snake chemicals.

Seven ingestively naive *Lampropeltis g. holbrooki* (SVL = 19.0–24.0 cm; $\overline{X}$ = 21.0 cm), hatched from eggs laid by a female captured in Shelby County,

Tennessee, were tested three weeks after hatching. Other than the postponement of feeding until after testing, snakes were maintained as were those described in the previous experiments.

Snakes were tested once to each of four conditions (three snakes and a control) for four consecutive days in a Latin-square design. The stimulus snakes were a female northern copperhead, *Agkistrodon contortrix mokasen* (SVL = 79 cm); a female speckled king snake, *Lampropeltis g. holbrooki* (SVL = 106 cm); and a male plains garter snake, *Thamnophis radix* (SVL = 59 cm). Tests were run between 1200 and 1700 hr.

The apparatus and methods of odor presentation were similar to those described by Weldon (1982) for tests of *Thamnophis sirtalis* to snake odors. Air flow was generated by a Manostat varistaltic pump. Air passed through Teflon and Tygon tubing to a charcoal air filter and air flowmeter. A tube from the flowmeter connected to a glass bifurcation and stopcock, which directed air through either of two arms leading to two 1.9 liter jars. One arm directed air to a control jar containing cotton soaked in distilled water. The other arm connected to one of three jars containing stimulus snakes. From the control jar and each stimulus snake jar, an air outflow tube directed the airstream into a 14 × 10 × 6-cm plastic container placed inside a soundproof observation chamber (International Acoustics Co.). A test snake was placed into a plastic container, which was fitted with a glass top for overhead viewing of snakes in the chamber. Two tubes from the olfactometer were inserted into holes in the upper rim of the plastic container. One tube delivered air from the control jar; the other conducted air that had passed through one of the stimulus snake jars. Different plastic containers were used for each stimulus condition. Each container was washed with soap and water and dried after each test.

The airstream in the olfactometer was directed from the control jar to a jar containing a stimulus snake by turning the stopcock in the glass bifurcation. During control sessions, where only plain air was presented throughout the trials, the airstream was interrupted momentarily by turning the stopcock to a disconnected arm of a glass bifurcation; this corresponded to a momentary disruption of airflow during tests with stimulus snakes where air was directed from the control jar to a jar containing a stimulus snake. Air was delivered at 400 ml/min.

Test snakes were exposed to plain air for nine minutes during an acclimation period. After 9 min of plain air presentation, baseline data on tongue-flicking and accumlated activity time (scored whenever a snake's head or body moved) were recorded on an Esterline-Angus event recorder for one more minute. After 10 min of plain air presentation, a turn of the stopcock directed air through a jar containing a stimulus snake or (if a control session) a

continuation of plain air. Tongue-flicks and activity were recorded for 5 min after the stopcock was switched. Temperature in the observation chamber was 24° C.

RESULTS

A two-tailed Kruskal-Wallis test on data from experiment I (Table 1) detected overall significant differences in tongue-flick rates ($H = 54$; $P << 0.05$). An STP a posteriori test (Sokal and Rohlf, 1981) detected significantly higher tongue-flick rates to *Agkistrodon* odors than to *Lampropeltis* odors or plain swabs ($P < 0.05$, in both cases). No other significant differences among treatment groups were detected.

A two-tailed Kruskal-Wallis test on the results of experiment II (Table 2) detected overall significant differences in tongue-flicking ($H = 975.5$; $P << 0.05$). An STP test detected significantly greater tongue-flicking by king snakes to the *Agkistrodon* vs. the *Elaphe*, *Lampropeltis*, and control conditions ($P < 0.05$, in both cases). No other significant differences among treatment groups were detected.

It was surprising to find in experiment III that six out of 10 snakes struck at and attempted to ingest swabs laden with snake skin chemicals. In some cases snakes wrapped themselves around the swab handle while grasping the cotton swab tip in the mouth (Figure 1). In the first test with this litter, four attacks were directed at *Thamnophis* swabs, three attacks at *Spilotes* swabs, and one snake, who attacked both of these, once attacked a *Crotalus* swab. No attacks on control swabs occurred.

When attacks on swabs occurred, tongue-flicks could not be counted and trials were terminated. Snakes were placed under running water to induce them to release their grasp on swabs. Snakes were returned to their home cages and tested to another stimulus condition the following day.

During experiment IV, two attacks on *Thamnophis* swabs, and one attack each on the *Nerodia* and *Crotalus* swabs, occurred. Only two of five snakes tested attacked swabs; both individuals had attacked swabs during the previous test. Again, no attacks on control swabs occurred.

TABLE 1. MEAN TONGUE-FLICKS PER MINUTE BY EIGHT *Lampropeltis getulus* FOR 2 MINUTES TO BLANK SWABS AND SWABS FRESHLY RUBBED AGAINST DORSAL SKINS OF STIMULUS SNAKES (±1 SD)

Agkistrodon contortrix	*Lampropeltis getulus*	*Thamnophis sirtalis*	Blank
38.1 ± 16.8	22.2 ± 10.9	29.8 ± 2.6	19.7 ± 3.1

TABLE 2. MEAN TONGUE-FLICKS PER MINUTE BY SEVEN *Lampropeltis getulus* FOR 2 MINUTES TO BLANK SWABS AND SWABS DIPPED IN SOLUTIONS OF SNAKE SKIN CHEMICALS EXTRACTED WITH METHYLENE CHLORIDE (±1 SD)

Agkistrodon contortrix	*Lampropeltis getulus*	*Elaphe obsoleta*	Blank
31.9 ± 13.1	22.3 ± 10.7	23.3 ± 10.8	22.1 ± 11.5

A Kruskal-Wallis test on tongue-flicking data for the first minute of experimental air presentation in the olfactometer experiment fell short of detecting significant overall differences among treatment groups (Figure 2) ($H = 10.4$; $0.20 > P > 0.10$). An STP test detected significantly greater tongue-flicking during this period to each of the stimulus snakes than to plain air, and more tongue-flicking to *Lampropeltis* odors than those from *Thamnophis* ($P \ll 0.05$ for all comparisons).

King snakes were active 93%, 94%, 86%, and 97% of the minute before the stopcock was switched for the *Thamnophis*, *Agkistrodon*, *Lampropeltis*, and control conditions, respectively. Snakes were active 91%, 80%, 95%, and

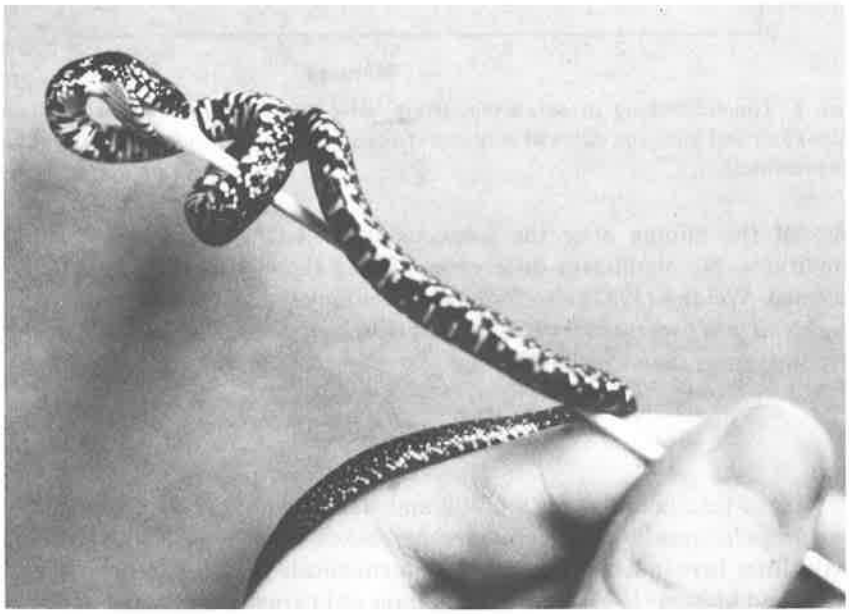

FIG. 1. *Lampropeltis getulus* (23 cm snout-vent length) ingesting a swab dipped into solution of *Thamnophis fulvus* shed skin extract.

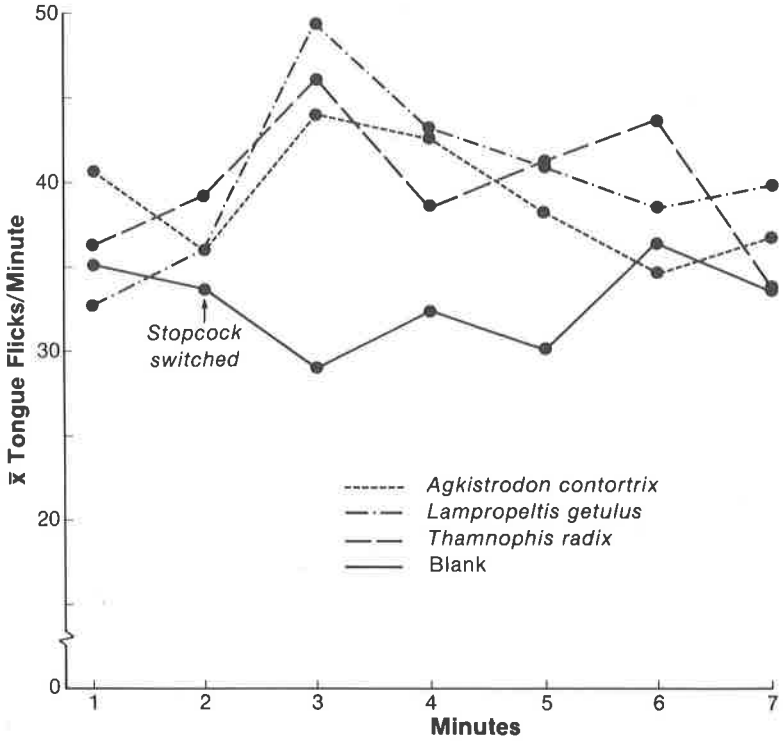

FIG. 2. Tongue-flicking of seven ingestively naive *Lampropeltis getulus* to plain (blank) air and airborne odors of stimulus snakes. Scoring began after 9 min of plain air presentation.

86% of the minute after the stopcock was switched for each of these conditions. No significant differences among these scores (sec/min) were detected. Weldon (1982) also found the accumulated activity time of *Thamnophis sirtalis* presented with snake odors to be less sensitive an indicator of responsiveness than tongue-flicking.

DISCUSSION

These results and those of Williams and Brisbin (1978) indicate that *Lampropeltis getulus* chemically perceive snakes. Further, tests with one king snake litter here indicate that snake skin chemicals elicit predatory attacks. Brock and Meyers (1979) reported that three of 11 king snakes struck at swabs in nine of 220 trials, and one snake seized a control swab and a skink (*Leiolopisma laterale*) -scented swab in its mouth. However, swab attacks by

their king snakes were accompanied by tail vibrations, and they were interpreted to be defensive rather than prey oriented. Since in our study (1) tail vibrations were not observed prior to most attacks, (2) ingestion was attempted after swab tips were grasped, and (3) no attacks on control swabs were observed, we believe that these attacks were prey oriented.

The different methods by which snake chemical samples were obtained by Brock and Meyers, where swabs were dipped into hot water in which snakes had been immersed, and those used here, may account for the discrepant results. Since snake skin chemicals are predominantly lipoidal (Ahern and Downing, 1974; Roberts and Helmkamp, 1982; Roberts and Lillywhite, 1983; Schell and Weldon, in preparation) their water solubility will be low. Our methods undoubtedly provided more concentrated chemical samples.

Individual, interlitter, or subspecific variation in responses to snake chemicals may account for different results in tests with king snakes. These possibilities are underscored by the failure of king snakes from all but one litter tested here to attack swabs, and not all snakes from this litter attacked swabs. In any case, Soxhlet extraction of shed snake skins appears suitable to obtain behaviorally active snake skin chemicals. Ahern and Downing (1974) obtained up to 8% in weight of chloroform–methanol extractable lipids from Florida indigo snake (*Drymarchon corais*) shed skins, and Roberts and Lillywhite (1983) removed 2–12.5% of shed skin weights in lipids from several snake species using different solvent systems. These yields are comparable to those obtained here. By collecting snake shed skin chemicals, samples of uniform concentration may be presented in other tests of the behavioral significance of these substances. Graves and Duvall (1983) recently reported that prairie rattlesnakes (*Crotalus viridis viridis*) respond by mouth gaping to conspecific shed skin chemicals obtained by CH_2Cl_2 extraction, although they did not report extraction yields or the concentration(s) of skin chemical solutions presented to snakes.

Observations of tongue-flicking in the olfactometer confirmed that king snakes perceive airborne snake chemicals. Similar olfactometric tests of a litter of 14 three-week-old, ingestively naive black racers (*Coluber constrictor*), another ophiophagous species, to the same stimuli presented to king snakes gave similar results (Weldon, unpublished). Other snakes respond by tongue-flicking or other behaviors to airborne chemicals from prey (Burghardt, 1977; Burghardt and Abesheenan, 1971; Dunbar, 1979; Halpern and Kubie, 1983) or from other snakes. Cowles and Phelan (1958) observed increased heart rates in rattlesnakes presented with king snake odors in an olfactometer. Weldon (1982) found that garter snakes (*Thamnophis sirtalis*) tongue-flick more to airborne odors from a king snake (*Lampropeltis getulus*) than to those from a rat snake (*Elaphe obsoleta*) or to plain air. The present

results add to the growing list of airborne stimuli known to be perceived by snakes. It is unclear, however, whether king snakes discriminate among snake taxa when presented airborne chemicals.

The results of swab presentations where swabs were not seized (and where tongue-flicks could be counted throughout an entire trial) also indicate that *Lampropeltis* perceives snake skin chemicals. Because king snakes tongue-flicked more to copperhead odors than to other stimuli, we suggest that *Lampropeltis* distinguishes between chemicals from copperheads and some colubrid snakes. The significance of such a discrimination is open to speculation.

Cowles (1938) believed that a fear of rattlesnakes permits king snakes to avoid defensive body blows when attacked. Rattlesnakes and other crotalines also bite king snakes. Although king snakes generally are resistant to crotaline venom (Bonnett and Guttman, 1971, and references therein) occasional deaths and severe wounding from crotaline bites have been reported (Allyn, 1937; Marchisin, 1980). By recognizing crotalines, then, king snakes could avoid body blows or (more likely, we believe) envenomating bites. Our experimental results are ambiguous with respect to crotaline avoidance by king snakes since we did not measure appropriate behaviors.

The idea that crotaline snakes are detected by chemical cues, or that crotaline and colubrid snakes are chemically distinguishable, is suggested from reports of other vertebrates' reactions to snakes. Hennessey and Owings (1979) found that California ground squirrels (*Spermophilus beecheyi douglasi*) respond more defensively by sand kicking and other behaviors to northern Pacific rattlesnakes (*Crotalus viridis oreganus*; Crotalinae) in perforated plastic bags than to those in sealed bags or to Pacific gopher snakes (*Pituophis melanoleucus catenifer*; Colubridae) in sealed or perforated bags. These authors believe that squirrels distinguish between chemicals from these snakes. Anecdotal accounts suggest that American alligators (*Alligator mississippiensis*), occasional snake predators, also distinguish between crotaline and colubrid snakes. McIlhenny (1935, pp. 44–45) states that alligators vigorously shake cottonmouth moccasins (*Agkistrodon piscivorus*) after grasping them, making it difficult for snakes to bite. Nonvenomous colubrid snakes, on the other hand, are grasped and devoured without shaking (see also Neill, 1971, p. 240). Freshly killed snake carcasses without heads and skins were treated as were the living snakes, leading McIlhenny (cited in Klauber, 1972, p. 1110) to suspect that crotaline chemicals elicit head-shaking attacks. These observations call for more rigorous tests of the involvement of chemical cues.

Chemical aposematism may be widespread, but few cases of vertebrate chemicals acting as aposematic signals, and few examples of vertebrate mimicry where aposematic chemicals are involved, are known (Eisner and

Grant, 1981; see also Czaplicki et al., 1975). Rubinoff and Kropach (1970) believe that the venomous yellow bellied sea snake, *Pelamis platurus* (Elapidae), is chemically aposematic because snake pieces, even with skins removed, were refused by several predatory Pacific fishes. We suggest that crotaline snakes are chemically aposematic if, as indicated by some reports, crotaline chemicals cause potential predators to adopt special prey-handling techniques or abstain from attacking. Further observations of interactions between crotalines and their predators and prey, stimulus control studies, and elucidations of snake skin chemicals are needed.

Acknowledgments—G.M. Burghardt made facilities available to us during this study. I.L. Brisbin, Jr., G.M. Burghardt, H. Drummond, A.C. Echternacht, D.H. Owings, and R.H Wainberg commented on the manuscript, and D. Duvall and A.C. Echternacht provided rattlesnake shed skins. This study was conducted while P.J.W. was supported by a Hilton Smith Fellowship from the University of Tennessee and NSF grants (BNS 78-14196 and BNS 82-17569) to G.M. Burghardt.

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