THE OPHIOPHAGE DEFENSIVE RESPONSE IN CROTALINE SNAKES: EXTENSION TO NEW TAXA

PAUL J. WELDON and GORDON M. BURGHARDT

Departments of Zoology and Psychology
University of Tennessee
Knoxville, Tennessee 37916

Abstract—A total of 21 new taxa of New World pit vipers (Serpentes: Crotalinae) responded by elevating the middle portion of the body in a defensive posture (body bridge) when exposed to the skin substances of certain colubrid snakes (Colubridae). Newborn snakes from two of the three species tested gave the response. Several new species of colubrid snakes also are documented as capable of eliciting a response, and it is suggested that the term *ophiophage defensive response* be used to denote body bridging and associated defensive behaviors instead of the restrictive "kingsnake defense posture." Most of the snakes which elicit the response in crotaline snakes are known to feed on lizards and/or snakes. There is no apparent correlation between the stimulus snakes' ability to elicit a response in the crotaline snakes and sympatry with the crotaline snakes.

Key Words—Snake behavior, chemoreception, predator–prey, kairomone, Colubridae, Crotalinae, ophiophage, defensive response.

INTRODUCTION

Klauber (1927) and Cowles (1938) provided the first reports of an unusual defensive posturing in rattlesnakes (genus *Crotalus*) to the presence of kingsnakes (*Lampropeltis getulus*), notorious ophiophagous snakes. This response, originally referred to as the "kingsnake defense posture" by Cowles (1938), is characterized by the elevation of the middle portion of the body to form a bend (body bridge), which directs body blows toward an advancing kingsnake, a decided contrast to the vertical coiling position assumed by rattlesnakes to other types of perturbations. By presenting rattlesnakes with sticks smeared with cloacal sac contents or rubbed against the dorsal and ventral surfaces of stimulus snakes, Bogert (1941) showed that chemical cues from

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the dorsal skin of *Lampropeltis getulus* are necessary and sufficient to elicit a response. *Masticophis flagellum piceus* (= *Coluber f. frenatum*) and *Pseustes sulfureus* also elicited a response, but a number of boid, crotaline, and non-ophiophagous colubrid snakes did not. Rattlesnakes also respond by body bridging to the scent of the spotted skunk, *Spilogale putorious*, (Cowles, 1938). 1-Butanethiol, once believed to be the primary malodorous constituent of the scent of the common skunk, *Mephitis mephitis*, (Aldrich, 1896) evoked a response only when accompanied by tactile stimulation (Cowles and Phelan, 1958). However, a recent reanalysis of the scent of *M. mephitis* by Andersen and Bernstein (1975) failed to indicate the presence of 1-butanethiol; this may account for the partial response with the snakes.

The species of New World pit vipers which respond to *Lampropeltis* species by body bridging and other defensive behaviors has been extended, through several reports, to include members of the genera *Agkistrodon* (Neill, 1947; Carpenter and Gillingham, 1975) and *Sistrurus* (Inger, cited in Burghardt, 1970; Carpenter and Gillingham, 1975) in addition to a number of species and subspecies within the genus *Crotalus* (Meade, 1940; Bogert, 1941; Klauber, 1956; Carpenter and Gillingham, 1975). Carpenter and Gillingham (1975) have tabulated the species known to respond and have suggested that body bridging may be a behavioral characteristic of the subfamily Crotalinae. They were unsuccessful in eliciting a response from a variety of colubrid snakes when placed in encounters with kingsnakes.

This is a preliminary report from our survey of body bridging in crotaline snakes in response to the skin substances of ophiophagous or possibly ophiophagous snakes.

METHODS AND MATERIALS

The testing procedure entailed the presentation of cotton balls attached with clips on the end of 1-m wooden rods to individual snakes. The experimental ball was moistened with methanol, a solvent found to be suitable for collecting skin substances from the various species that elicit the defensive posture, and rubbed against the dorsal surface of a stimulus snakes. A fresh ball was presented to a crotaline snake by placing it a few cm from the snout. If no response appeared after the first minute, the snout or anterior trunk of the snake, depending upon the position the snake was in at the time of testing, was lightly tapped and observations continued for another minute. A control ball, moistened only with methanol, was presented to each subject in an identical fashion. For approximately half the snakes tested, the presentation of the experimental preceded that of the control ball; the remaining snakes were tested with the control ball first. On a subsequent day, the order of control and experimental presentations was reversed in a counterbalanced design.

Zoos and private collections were the source of the majority of specimens tested in this study. Observations were conducted either in the snakes' home cages, where water bowls and shelters were removed prior to testing, or in large plastic or metal cans. All of the substrates used for observations of the snakes' behavior were flat surfaces on which any postural responses could readily be discerned. Body bridging, the elevation of the trunk of the snake, was used as the sole criterion for a response. The methanol used as a solvent to collect the skin substances, and present on both control and experimental balls, probably constituted an aversive stimulus, as did the visual effects of the presentations and the tactile stimulation involved in the snakes touching or being touched by the cotton balls. Thus, under the conditions encountered in this study, escape, head-hiding, and other behaviors which may be associated with body bridging, could not reliably be recorded as a positive response.

Approximate total length was recorded for each snake tested together with information on the individuals' history and sex where available.

Skin extracts were taken from whichever snakes (of those known or suspected to elicit a response) were available at each facility visited. Extracts from the suspected stimulus snakes were tested first with a known responder.

RESULTS

We report here only those previously undocumented taxa of crotaline snakes that exhibited a body-bridging response in one or more individuals. Because of the relatively small sample size for many of the taxa tested, the lack of a response should not be taken as conclusive evidence that a response does not occur in a particular species or subspecies (see Discussion). For each taxon, the number of individuals tested, the number observed to respond, and their approximate total lengths are shown in Table 1.

In addition to the adult and juvenile specimens listed in Table 1, we tested three litters of crotaline snakes with the skin substances of ophiophagous snakes. Since we were primarily concerned with the reaction of these snakes in their first exposure to ophiophage chemicals, the testing of litters involved the presentation of only one series of control and experimental balls such that half received the experimental ball first and half received the control ball first.

One litter of four captive-born cantils, *Agkistrodon bilineatus bilineatus*, each 43 days old and approximately 15 cm total length at the time of testing, were tested with the skin substances from *Lampropeltis getulus bolbrooki*. None of these snakes exhibited body bridging during the test sessions. Of a litter of eleven captive-born western diamondback rattlesnakes, *Crotalus atrox*, each 21 days old and about 22 cm total length, three exhibited body bridging when tested with an extract from *Lampropeltis getulus niger*. One litter of five northern copperheads, *Agkistrodon contortrix mokasen*, each ap-

TABLE 1. PREVIOUSLY UNREPORTED TAXA EXHIBITING BODY BRIDGING

Test taxa (Crotalinae)	Snakes tested		Snakes responded		Stimulus taxa (Colubridae)
	Number	Total length (cm)	Number	Total length (cm)	
Agkistrodon bilineatus bilineatus	4	60–75	2	60–75	Lampropeltis g. niger[a] L. g. splendida
A. contortrix contortrix	2	45–60	1	60	Lampropeltis g. holbrooki
A. c. mokasen	6	60–90	4	60	Lampropeltis g. holbrooki L. g. floridana[a] L. g. niger Drymarchon corais couperi
A. c. pictigaster	3	45–60	1	60	Lampropeltis g. floridana[a]
Bothrops alternatus	1	30	1	30	Lampropeltis mexicana alterna[a]
B. asper	1	120	1	120	Lampropeltis getulus holbrooki[a]
B. melanurus	2	30–35	1	30	Lampropeltis getulus holbrooki[a]
B. neuwiedi	4	55–90	1	90	Masticophis taeniatus ornatus[a]
B. undulatus	4	30–60	2	45–60	Coluber c. constrictor[a] Drymarchon corais couperi[a] Lampropeltis getulus holbrooki[a]

					Stimulus snake
Crotalus adamanteus	4	60–90	2	60–90	*Lampropeltis triangulum sinaloae*[a]
					Drymarchon corais couperi
C. enyo enyo[b]	1	40	1	40	*Lampropeltis getulus holbrooki*[a]
C. molossus molossus	1	80	1	80	*Lampropeltis getulus holbrooki*[a]
C. m. nigrescens	3	60	2	60	*Lampropeltis triangulum sinaloae*
					Coluber c. constrictor[a]
C. polystictus	1	30	1	30	*Lampropeltis triangulum nelsoni*
C. pricei pricei	1	30	1	30	*Lampropeltis triangulum niger*[a]
C. ruber lucasensis[b]	2	30–90	1	30	*Lampropeltis mexicana alterna*[a]
					L. getulus holbrooki[a]
C. scutulatus salvini	4	60–70	1	60	*Drymarchon corais couperi*[a]
C. stejnegeri	1	40	1	40	*Lampropeltis triangulum nelsoni*
					L. getulus holbrooki[a]
C. tigris	3	60–75	1	60	*Coluber c. constrictor*[a]
C. viridis concolor	1	60	1	60	*Lampropeltis getulus niger*[a]
C. willardi willardi	2	45–60	1	45	*Masticophis taeniatus ornatus*[a]

[a] Sympatry between the test snake and this stimulus snake is unlikely.
[b] Bogert (1941) also found that *Crotalus enyo* and *C. ruber* exhibited a response; however, no subspecies were indicated.

proximately 15 cm total length, was found under a rock with an adult female in Cumberland County, Tennessee, during August 1977. It is unlikely that these snakes had had previous experience with any ophiophagous snakes, since the young generally do not disperse until several to many days after birth (Fitch, 1960). When tested with the skin extract from *Lampropeltis getulus holbrooki* 16 days after their capture, two out of five individuals responded by body bridging.

DISCUSSION

Previous studies of body bridging in crotaline snakes have concentrated on responses to subspecies of *Lampropeltis getulus*. Inger (unpublished) and Carpenter and Gillingham (1975) also found *Lampropeltis calligaster calligaster* to be effective. Thus, the term "kingsnake defense posture" has been used to refer to this behavior. Bogert (1941), however, stated that *Masticophis flagellum piceus* and *Pseustes sulfureus* also possess skin substances capable of eliciting the response. Aside from a few new subspecies of *Lampropeltis getulus*, we have observed that the dorsal skin of *Drymarchon corais couperi* (independently discovered earlier by Marchisin, personal communication), *Coluber constrictor constrictor, Masticophis taeniatus ornatus, Lampropeltis mexicana alterna, L. triangulum nelsoni,* and *L. t. sinaloae,* mostly known snake feeders, possess similar properties, and undoubtedly other such species will be discovered. Hence, we propose the term *ophiophage defensive response* to denote the body bridging and associated defensive behaviors of crotaline snakes and, should similar antipredator responses occur in other groups, of other snake taxa as well.

Actual body bridging has been used to establish the occurrence of a response in crotaline snakes to ophiophagous snakes; we also conservatively used trunk elevation as an indication of a response in this survey. From other reports on the ophiophage defensive response and our own observations, however, it is clear that recognition of predatory snakes through chemical cues may be manifest by other behaviors such as escape, head-hiding, and thrashing. Thus, body bridging represents just one of a constellation of recalcitrant reactions to ophiophagous snakes. A more complete inventory of responses and precise quantitative analysis, perhaps derived from actual encounters between snakes, would be useful. This would best be done with a common species available for repeated testing in controlled settings, conditions that did not prevail in the present study.

Carpenter and Gillingham (1975) have suggested that body bridging may be a behavioral characteristic of the subfamily Crotalinae. Body bridging as a defensive maneuver also has been reported in the elapid snakes, *Vermicella annulata* (Bustard, 1969) and *Denisonia maculata* (Johnson, 1970) in response to human molestation, and it is possible that they respond similarly to other perturbations. Given the limitations imposed by an elongate, limbless

Bauplan, it is not surprising to find some convergence in ophidian defensive postures and displays (Greene, 1977). We regard both the behavioral response, postural or otherwise, and its release by chemical stimuli as the unique features of the ophiophage defensive response. This is underscored by the fact that the scent of the spotted skunk elicits a response (Cowles, 1938), although the adaptive significance of the defensive response in this context remains to be investigated beyond Cowles' inconclusive observations on rattlesnake–skunk interactions. Nevertheless, the increasing number of crotaline snakes shown to respond to ophiophage skin substances lends tentative support to Carpenter and Gillingham's suggestion that the response may be a behavioral characteristic of the subfamily Crotalinae. It would thus be interesting to ascertain whether the strictly arboreal varieties, such as some *Bothrops* species, exhibit responses and, if so, in what form. Body bridging, at least, would seem to be an inappropriate defensive behavior for a species occurring among branches since purchase could easily be lost. If body bridging turns out to be ubiquitous in all crotaline species except for arboreal ones, the response could still be viewed as an ancestral crotaline response secondarily lost in species living where the response is no longer adaptive.

More fundamental is assessment of whether this response has been acquired convergently, due perhaps to some crotaline-peculiar chemosensory capacity, or has been generated in a common ancestor. This will depend upon the extension of our knowledge to new taxa, a consideration of the ecologies of the various species, and, ideally, the establishment of neuroanatomical and muscular correlates of this behavior.

A lack of responsiveness in crotalines to ophiophagous snakes, primarily *Lampropeltis* species, has been noted by others and probably accounts for some of the discrepancies which have appeared in the literature as to which species react. Bogert (1941) observed the attenuation of a response in individuals that had been in captivity and repeatedly exposed to the odor of predatory snakes. Carpenter and Gillingham (1975) stated that some of the snakes in their study that had been in captivity for several months exhibited no or weak responses to encounters with kingsnakes. It is unclear whether the lack of response or its decrease can be attributed to captive conditions per se or to repeated testing with ophiophagous snakes or their skin substances. In this regard, we have observed very dramatic responses with some crotalines that had been in captivity for several years.

The size or age of the snake may be another determinant of responsiveness to ophiophage cues. Bogert (1941) stated that large specimens of *Crotalus atrox* failed to react to kingsnakes, whereas juvenile and young adults responded without exception. Carpenter and Gillingham (1975) noted that individuals of *Agkistrodon contortrix laticinctus* that were larger than the kingsnakes in their study did not exhibit body bridging, although no measurements are given for either crotalines or kingsnakes. It is possible that larger

specimens are either less responsive or require more in the way of visual or tactile stimulation, in addition to chemical stimulation, to potentiate a response.

Our preliminary tests with litters of pit vipers point to behavioral polymorphism as one basis for the apparent variations in responsiveness. The relatively low ratio of snakes responding to the ophiophage skin substances may, in part, be attributed to our use of body bridging as the response criterion. As pointed out above, recognition of predatory snakes may be manifest in other forms. Carpenter and Gillingham (1975), for example, describe body flips of small *Agkistrodon c. laticinctus* in response to kingsnakes. From our data on neonates, however, it is clear that the response is not dependent upon previous experience with predatory snakes, an obvious advantage since the first encounter with an ophiophage could be the last, especially for smaller individuals.

We were successful in eliciting body bridging responses in a geographically diverse assemblage of New World crotaline snakes, including several species of the genus *Bothrops* (previously unreported), using a few species of ophiophagous snakes. In some cases the stimulus snakes used could be sympatric with the crotalines tested, but in many cases they would not be. In one case, *Crotalus stejnegeri*, a rare species known from a restricted area in southern Mexico, exhibited body bridging to the skin extract of *Lampropeltis g. holbrooki*, a subspecies indigenous to central United States. Other examples of response to allopatric stimulus snakes can be seen in Table 1. Bogert (1941) also found that several species of *Crotalus* from the western United States responded to *Lampropeltis g. getulus* from the eastern United States. Thus it appears that sympatry with the crotaline snakes is not essential when considering which snakes are capable of eliciting a defensive response. This suggests that (1) the crotaline chemoreceptors possess low specificity for the chemicals from the various predators, (2) the chemicals from the predators are the same or similar substances, or (3) different chemicals and chemoreceptors elicit the same response.

A similar picture has emerged from a few other kairomone systems involving the recognition of predators by actual or potential prey animals. Reed (1969) observed a fright response in several North American fish of the families Cyrinidae, Poecilidae, and Cyprinodontidae to chemicals from predatory fish, including two South American cichlids, *Astronotus ocellatus* and *Cichlasoma severum*. Müller-Schwarze (1972) tested the avoidance responses of naive black-tailed deer (*Odocoileus hemionus*) from the United States to droppings from the African lion (*Panthera leo*), the Bengal tiger (*Panthera tigris tigris*), the snow leopard (*Panthera unica*), the mountain lion (*Felis concolor*), and the coyote (*Canis latrans*). Only the mountain lion and coyote occur sympatrically with the deer. Although the odors of the mountain lion and coyote elicited the most consistent avoidance response, the odors from the snow leopard, African lion, mountain lion, and coyote did not differ in their

effect. The Florida apple snail, *Pomacea paludosa*, exhibits a burial response to some fresh-water turtle predators sympatric with it in addition to several turtles which are not, including a terrestrial turtle. *Gopherus polyphemus* (Synder and Snyder, 1971). Lastly, several marine gastropods (Clark, 1958; Yarnall, 1964; Ansell, 1969; Weldon, unpublished) and at least one anemone (Ward, 1965) exibit flight responses to chemicals emanating from predatory asteroids and/or gastropods that are and are not sympatric with them. Yarnall (1964) has suggested that the chemicals responsible for the elicitation of the flight responses are related to some common feature of the physiology of the predators, and indeed this appears to be true of other systems in which actual or potential prey recognize predators through chemical cues.

Mauzey et al. (1968) have hypothesized that the substances from predaceous asteroids that elicit escape responses in other echinoderms may have a dietary origin. This is a possibility with the crotaline–colubrid interaction, as most of the snakes that elicit the defensive reponse are known to be snake and/or lizard feeders (see Wright and Wright, 1957, for the diets of *Coluber c. constrictor, Drymarchon c. couperi, Lampropeltis c. calligaster, L. getulus* ssp., *Masticophis f. piceus, M. t. ornatus*; Mole, 1924 for *Pseustes sulfureus*; and Gehlbach and Baker, 1962, for *L. mexicana alterna. Lampropeltis t. sinaloae* has been reported as feeding on reptile eggs [Zweifel and Norris, 1955], and we know of no information on the diet of *L. t. nelsoni*).

We feel that these observations call for a broader consideration of the ophiophage defensive response by focusing not only on the species exhibiting a response, but also on the species eliciting it. Are the substances from the various predatory snakes which elicit a response the same or similar substances? Are they related to the diet of the snake or produced de novo? These are some of the questions that we hope to consider in future investigations.

Note Added in Proof. Chiszar et al. (1978) have found that rattlesnakes (*Crotalus viridis*) and water moccasins (*Agkistrodon piscivorus*) exhibit less tongue flicking when placed into a cage previously occupied by a kingsnake (*Lampropeltis getulus*) than in a cage previously occupied by a hognose snake (*Heterodon nasicus*) or in an open-field situation. The disruption of exploration by the odor of kingsnakes as measured by tongue flicking was more dramatic in water moccasins

than in rattlesnakes. This is said to correlate with the extent to which the species overlap in nature, although the particular subspecies of *Lampropeltis* used in their study ranges from central Texas to central Mexico, and the subspecies of *Agkistrodon* from Virginia to central Alabama (Conant, 1975). No body bridging was observed in the pit vipers during the sessions in which they were exposed to kingsnake odor.

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