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Temperature Dependent Defensive Behavior in Three Species of North American Colubrid Snakes

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The antipredator response employed by a snake may be constrained, in part, by environmental temperature, and the biochemical processes and physiology that control behavior and metabolism are generally temperature dependent (Lillywhite, 1987). Therefore, it may be adaptive to use different antipredator responses at different temperatures. For example, rapid movement (flight) may not be possible at low temperatures and therefore a defensive display may be a more feasible alternative (Schieffelin and de Queiroz, 1991).

Studies on agamid and iguanid lizards suggest that colder animals generally opt for defensive displays rather than flight (Hertz et al., 1982; Crowley and Pietruszka, 1983). In snakes, the antipredator behavior of garter snakes (genus *Thamnophis*) has received the most attention but relatively few studies have examined the role of temperature on these behaviors. Fitch (1965) and Heckrotte (1967) commented that *T. sirtalis* are more likely to aggressively defend themselves at cold temperatures (<18 C) than to attempt flight but provided no quantitative data. Arnold and Bennett's (1984) quantitative study of *T. radix* showed the same pattern, with increased "aggressive" defen-

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TABLE 1. Scoring system used for the various behaviors associated with each body component.

Component	Scoring scheme	Score
Tail	no display	0
	coil	1
	vibration (buzz)	2
Body	tight coil (passive)	0
	loose coil (aggressive)	1
Head	hidden under a coil	1
	exposed	2
	strike position and/or hiss	3
	closed mouth strike	4
	open mouth strike	5
	bite (teeth embedded in hand)	6

sive reactions at low temperatures (15 C) and increased flight response at higher temperatures. Goode and Duvall (1989) found a similar result in free-ranging prairie rattlesnakes (*Crotalus viridis*). However, this has not been the case in all studies. Schieffelin and de Queiroz (1991) found that garter snakes (*T. sirtalis*) demonstrated less aggressiveness at lower temperatures (10 C) than at higher temperatures (20–30 C). The purpose of our study was to test the effects of temperature on the antipredator responses of some common North American snakes other than those of *Thamnophis*.

We used nine snakes representing three genera of the Family Colubridae: two adult and one subadult captive-born Sonoran gopher snakes (*Pituophis melanoleucus affinis*), two wild caught adult and one captive-born juvenile blue racer (*Coluber constrictor foxii*), and three wild caught adult prairie kingsnakes (*Lampropeltis calligaster calligaster*). The adult blue racers and kingsnakes had been in captivity for three and four months respectively. None of the snakes used in the study were handled for three weeks prior to the experimental trials and were disturbed only for water changes and feeding. None of the snakes were tame.

Prior to the experiment the snakes were maintained at approximately 28 C on a 12 L:12 D photoperiod. The snakes, except the juvenile blue racer, were housed separately in glass aquaria with dimensions of 50 cm × 26 cm × 30 cm. The juvenile blue racer was housed in a plastic shoe box measuring 30 cm × 15 cm × 8 cm. All trials were conducted in the snake's own cage to avoid any displacement response or exploratory behavior that could be associated with a foreign arena. Water bowls and shelters were removed from the snake's cage prior to each trial. Because presence of food in the digestive tract can affect defensive behavior (Herzog and Bailey, 1987), the snakes were fasted for one week prior to the onset of the experimental trials.

The snakes were placed in an environmental room (while in their own cages) four to six hours prior to any trials being performed. Trials were run at 10, 15, 20, and 30 C (±0.5 C). The 10, 15, and 20 C trials were conducted in the environmental room and the 30 C trials were conducted in a separate room. Because trial order can affect snake defensive behavior (Arnold and Bennett, 1984), we tested the three species in different trial orders. *Coluber constrictor* were trialed in order of increasing temperature (10, 15, 20, and 30 C), *L. calligaster* were trialed in order of decreasing temperature (30, 20, 15, and 10 C), and *P. melanoleucus* trials were in the order 15, 10, 30, and 20 C. Each of the nine snakes was tested once at each of the four temperatures for a total of 36 trials. At least two days passed between successive trials for each snake and all trials were performed in the afternoon between 1200 and 1600 h.

Herzog et al. (1989) found that a human hand was an effective stimulus for eliciting defensive responses in snakes, so this was used as the stimulus in our study. Each trial consisted of first touching the snake with a bare hand to try to elicit defensive behavior. If or when this was achieved, a hand with closed fist was thrust toward the snake at approximately one thrust per second. This procedure was continued until the snake's defensive behaviors had been recorded (usually within 30 sec).

Each snake was given a separate score for its head, body, and tail defensive displays following the protocols used by Schieffelin and de Queiroz (1991), Ar-

TABLE 2. Mean defensive scores and standard errors of three species at three temperatures and the results of a Kruskal-Wallis test showing nonsignificant differences in scores between species at each temperature.

Temp.	Species	Mean	SE	Test statistic	*P* values
10 C	*C. constrictor*	1.00	0.962	H = 2.00	*P* = 0.368
	L. calligaster	1.00			
	P. melanoleucus	2.66			
15 C	*C. constrictor*	6.66	1.49	H = 0.865	*P* = 0.649
	L. calligaster	4.66			
	P. melanoleucus	4.66			
20 C	*C. constrictor*	5.66	1.67	H = 0.023	*P* = 0.988
	L. calligaster	6.00			
	P. melanoleucus	7.00			
30 C	*C. constrictor*	5.33	1.45	H = 0.655	*P* = 0.721
	P. calligaster	7.66			
	P. melanoleucus	7.66			

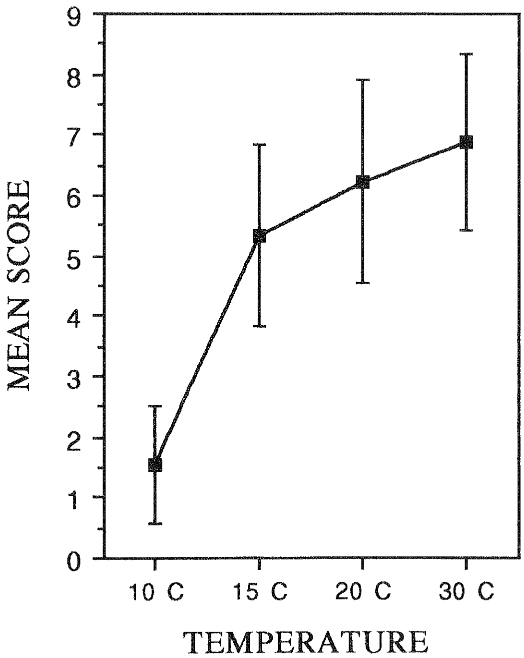

FIG. 1. Pooled mean defensive scores and standard error bars for *Coluber constrictor, Lampropeltis calligaster,* and *Pituophis melanoleucus* at four temperatures.

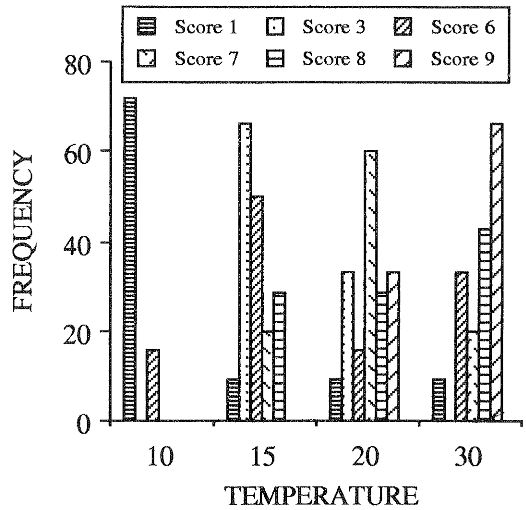

FIG. 2. Frequency histograms of overall defensive scores in the snake species *Coluber constrictor, Lampropeltis calligaster,* and *Pituophis melanoleucus* at four temperatures.

nold and Bennett (1984), and Herzog and Burghardt (1986), but the scoring scheme was altered slightly to accommodate the displays given by the particular species tested (Table 1). The score for each body region was summed to give a total defensive score at each temperature for each snake for each of the 36 trials. If a snake showed more than one type of defensive strategy then the defense that merited the higher score was used. The lowest possible score was one and the highest possible score was nine.

The score variation between each of the three snake genera at each of the four temperatures was first compared using a non-parametric Kruskal-Wallis test due to small sample size and non-normality of the data. Interspecific differences at each temperature were minor and non-significant (Table 2). We concluded therefore, that all three species were experiencing a similar temperature effect, at least quantitatively, so we pooled defensive scores of the three species for each temperature and calculated average scores from the pooled data (Fig. 1). Kruskal-Wallis comparisons of the pooled data revealed that defensive responses were significantly lower at 10 C than at 15, 20, and 30 C (H = 8.500, $P = 0.002$; H = 6.500, $P = 0.001$; H = 6.00, $P = 0.001$; respectively), but did not differ significantly among the higher temperatures (15 C × 20 C, H = 29.500, $P = 0.322$; 15 C × 30 C, H = 23.000, $P = 0.114$; 20 C × 30 C, H = 33.000, $P = 0.499$: see Fig. 2). We conclude, therefore, that defensive behavior of the three colubrid snake species tested was significantly affected by temperature.

At 10 C the snakes appeared to be sluggish and almost uniformly relied upon passive defensive strategies (head hidden, no tail display, and a tight coil), and several of the snakes defecated and sprayed musk on their backs. One *P. melanoleucus affinis* attempted to strike but was unable to do so effectively. At 15 C the snakes were more apt to strike, although most were either closed or open mouth strikes that did not make contact with the stimulus, and there were few recorded bites. The snakes' strikes tended to be directed to either side of the stimulus or only lightly touch the stimulus, suggesting it was bluff behavior as Arnold and Bennett (1984) found in garter snakes. Many terrestrial snakes will coil, puff up their bodies, and keep their head elevated to appear much larger than they are (Greene, 1979), in an attempt to intimidate or startle the attacker. Defensive scores at 20 C and 30 C were higher than at 15 C, but not significantly so. However, at 20 C and 30 C there were many more responses recorded as bites.

These results support the hypothesis that snakes employ more passive defensive displays at lower temperatures. The possible adaptive significance of these defensive reactions has been considered by Schieffelin and de Queiroz (1991) but it is important to note that our results (as well as those of Schieffelin and de Queiroz) appear to contradict earlier studies in garter snakes by Fitch (1965), Heckrotte (1967), and Arnold and Bennett (1984), and work on lizards by Hertz et al. (1982) and Crowley and Pietruszka (1983). Interpretations of the adaptive significance of thermally-induced shifts in defensive displays are problematical at present, in light of these contradictory results. What we can say is that the general feeling among herpetologists that colder reptiles are more aggressive may not be a general trend and more detailed studies are needed.

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