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FLEXIBLE DEFENSE: CONTEXT-DEPENDENT ANTIPREDATOR RESPONSES OF TWO SPECIES OF AUSTRALIAN ELAPID SNAKES

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ABSTRACT: Snakes exhibit a complex repertoire of defensive responses, shifting from one tactic to another depending upon conditions at the time of encounter with a potential predator. Standardized laboratory trials, controlling factors such as time of day, temperature, and type of encounter, can be used to test predictions about the form of this context dependency. We studied two sympatric species of elapid snakes from southeastern Australia. Although similar in body sizes, habitat use, and nocturnality, small-eyed snakes (*Cryptophis nigrescens*) are wide foragers (and hence, encounter predators under cool conditions at night in relatively open areas), whereas broad-headed snakes (*Hoplocephalus bungaroides*) lie in ambush for long periods within sun-warmed rocky retreat sites (and hence, encounter predators mostly when the snake is warm, and within its retreat). Based on those differences, we predicted that small-eyed snakes would be thermal generalists; that is, temperature would exert relatively little effect on the snakes' locomotor abilities, alertness, and preparedness to flee from threat. Broad-headed snakes would be likely to utilize tactics other than fleeing, and to increase response intensity substantially at higher temperatures. Both species were predicted to exhibit more intense responses at night, and when warm. Data from our laboratory trials supported these predictions: (1) antipredator behaviors of small-eyed snakes were less sensitive to thermal variation than were those of broad-headed snakes, (2) both species relied primarily on fleeing, but broad-headed snakes were more likely to adopt retaliatory behavior than were small-eyed snakes, and (3) both species responded more intensely at night and when warm. These results are consistent with the broader theory that snakes flexibly adjust their antipredator tactics to local conditions.

Key words: Antipredator behavior; *Cryptophis nigrescens*; Elapid; *Hoplocephalus bungaroides*; Nocturnal

PREDATION is a significant source of mortality for many kinds of animals, imposing strong selection on traits such as the ability to recognize and avoid potential predators (Flowers and Graves, 1997; Vermeij, 1982; Wisenden and Millard, 2001). If an encounter does occur, then its outcome (and hence, fitness consequences for the potential prey item) can be affected by the prey's responses (Cooper and Frederick, 2007; Lind and Cresswell, 2005). Depending upon the circumstances, rapid escape (flight), crypsis (immobility) or direct retaliation against attack may be the most effective option (Ajie et al., 2007; Lingle and Pellis, 2002). Venomous snakes are of special interest in this respect, because although venom evolved for capture and immobilization of prey (Deufel and Cundall, 2006; Kardong, 1982; Pough et al., 2004), it can also be used to deter predators (Greene et al., 2000; Rasmussen et al., 1995; Whitaker et al., 2000). Possession of this powerful weapon enables venomous snakes to use a wider range of antipredator responses than would be available to a nonvenomous reptile (Greene, 1988).

The effectiveness of any specific antipredator behavior depends on the context of encounter between predator and prey and, consequently, natural selection may endow animals with a repertoire of responses that can be used flexibly depending on external and

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internal conditions (Duvall et al., 1985; Magalhães et al., 2002; Pollock et al., 2006). Thus, the behavior elicited by a predator's approach varies as a function of multiple factors, including the responding animal's physical condition (Hailey and Davies, 1986), sex and reproductive status (Kissner et al., 1997), body size (Shine et al., 2000), body temperature (Goode and Duvall, 1989; Passek and Gillingham, 1997), feeding history (Herzog and Bailey, 1987), and familiarity with the terrain (Lopez et al., 2000). Also, the type of threat may influence prey response (e.g., the part of the snake's body on which the attack is centered; Langkilde et al., 2004). To predict accurately how snakes will respond to potential predators, all of these factors need to be considered.

Some antipredator responses require greater physical performance and coordination than others, so that any factor affecting the prey's locomotor abilities also will affect its ability to perform such responses. Presumably reflecting this constraint, the body temperature of a reptile can substantially influence its choice of antipredator tactics. For example, a snake that is too cold to flee rapidly from a predator's approach instead may rely on crypsis or threat (Passek and Gillingham, 1997; Shine et al., 2002). Quantifying such facultative shifts in antipredator responses is difficult or impossible under field conditions because the relevant factors covary under natural conditions. For example, it may be impossible to disentangle the effects of body temperature, proximity to retreat site, and time of day on a snake's antipredator behavior in a field-based study: a diurnal snake encountered early in the morning likely will be cold, and close to its overnight retreat. By contrast, laboratory trials with standardized protocols allow tests of individual factors while other variables are controlled (e.g., Llewelyn et al., 2006; Mori and Burghardt, 2001, 2004).

Rationale, Study System, and Predictions

One major axis of ecological variation in snakes involves foraging mode: some species capture most of their prey from ambush, whereas others roam widely across the landscape searching for food (Balent and Andreadis, 1998; Greene et al., 2000; Tsairi and Bouskila, 2004). Although this dichotomy is simplistic, extensive data suggest that many snake species do indeed cluster at one or the other end of this continuum between ambush predation and wide foraging (Greene et al., 2000). Foraging mode also should have important implications for the context in which snakes encounter potential threats of predation (Huey and Pianka, 1981), and hence for the manner in which adaptive forces fashion their antipredator responses. In the present study we focus on two species of medium-sized elapid snakes from southeastern Australia: the small-eyed snake (*Cryptophis* [*Rhinoplocephalus*] *nigrescens*) and the broad-headed snake (*Hoplocephalus bungaroides*). Both species are highly venomous proteroglyphous elapids (one is known to have caused human fatality; Sutherland and Tibballs, 2001) that occur sympatrically over a large area (>40,000 km^2; Cogger, 2000) and attain similar adult snout–vent lengths (SVL; adult SVL of approximately 40–60 cm in our study area; Webb et al., 2003). Although both are nocturnal, take refuge during the day under exfoliated sandstone rocks, and prey upon small vertebrates, especially lizards (Shine, 1977; Webb and Shine, 1998*a*; Webb et al., 2002), these two species utilize distinctly different foraging tactics. The small-eyed snake forages actively across rock outcrops at night in search of sleeping lizards, and may be vulnerable to avian and mammalian predators at this time (Webb and Shine, 2008). Temperatures on the exposed rock outcrops fall rapidly after dusk during most of the year (Webb and Shine, 1998*b*; Webb and Whiting, 2005). Consequently, small-eyed snakes are likely to be traveling across open areas (i.e., rock outcrops) at relatively low body temperatures when they encounter predators. Thermal monitoring of this species in field enclosures showed overnight body temperatures during activity from 15 to 25 °C (Llewelyn et al., 2005). In contrast, broad-headed snakes select the warmest available (sun-heated) rocky retreat sites on these outcrops (Pringle et al., 2003), and radiotracking shows that the snakes remain for days or weeks inside such a site, awaiting the arrival of potential prey (Webb and Shine, 1998*c*). These snakes move about actively only to switch ambush sites, an activity largely restricted to midsummer (Webb

and Shine, 1998*c*). Hence, we expect broad-headed snakes to encounter predators mostly when the snakes are warm, and probably most often within a shelter site offering little opportunity for fleeing.

Because foraging mode and time of activity influence the selective forces acting on snake antipredator behavior (because they affect when and where a snake encounters predators), we can use these attributes to make predictions about the antipredator responses of our study species. The nocturnality and foraging modes of our study species suggest the following predictions:

1. Because both species encounter predators by night rather than by day, both will show more intense and/or effective antipredator responses when tested at night.
2. Both species will use crypsis or bluff when locomotor performance is impaired by low body temperature, switching to more vigorous antipredator responses (such as fleeing or biting) at higher temperatures (as documented in other snakes; Passek and Gillingham, 1997; Shine et al., 2002).
3. Because small-eyed snakes often encounter predators when they are cold, we predict that this species will be a thermal generalist (i.e., temperature will have relatively little effect on the snake's locomotor performance and antipredator behavior). In contrast, because broad-headed snakes are usually warm when they encounter predators, we predict that this species will be a thermal specialist (i.e., its defensive abilities will be more sensitive to temperature).
4. Because small-eyed snakes often encounter predators when they are active and foraging, we predict that this species will rely primarily on fleeing (when this option is available), whereas broad-headed snakes (which are often inside their retreat site when they encounter predators) will rely more heavily on behaviors other than fleeing.

Materials and Methods

Collection and Husbandry

We collected snakes by hand from the Nowra region of New South Wales, Australia (34° 52′ S, 150° 29′ E) by turning cover items during daylight hours. Snakes were housed individually in plastic boxes (300 × 205 × 95 mm) with transparent tops and opaque sides and floor. Each box contained a sheet of paper for cover and a small water bowl. Between trials, snake boxes were placed on heat racks that provided an under-floor thermal gradient (20–30 °C), allowing snakes to thermoregulate behaviorally during daylight hours. The heating was switched off at night to mimic thermal fluctuations in the wild. The heat racks were kept in a temperature-controlled room (17 °C) lit by overhead fluorescent lights during the day (0800 to 1730 h).

Predator Pursuit Experiment

We investigated the antipredator behavior of these snakes in two experiments. Our objective for the first experiment was to simulate an encounter in which the snake was pursued but not seized by a predator. In this experiment, we examined the effect of temperature on snake locomotor performance and utilization of alternative antipredator behaviors (i.e., behaviors other than fleeing) in a terrestrial racetrack. We tested 34 small-eyed snakes (17 males and 17 females; mean SVL = 457 ± 12 mm SE, range 353–610 mm) and 35 broad-headed snakes (17 females and 18 males; mean SVL = 458 ± 23 mm SE, range 244–610 mm). We measured sprint performance and antipredator behaviors of all snakes at three temperatures (10, 20, and 30 °C) with the use of a linear racetrack. We chose these temperatures because they reflect the range of temperatures encountered by these species in the field (Llewelyn et al., 2005; Webb and Shine, 1998*b*). The order of temperature treatments was randomly assigned to each snake. All snakes (in labeled boxes) were placed in constant-temperature incubators 3 h prior to trials. Pilot studies indicated that this length of time allowed snake body temperatures to equilibrate to the temperature set on the incubator. We raced each snake at one temperature per day, giving snakes one full day of rest between successive trials.

Sprint performance.—The racetrack (250 × 17 × 30 cm [L × W × H]) was marked into four 50-cm sections, plus 25-cm sections at each end. The running surface was covered with artificial grass carpet (Astroturf®) to provide traction. All snakes were fasted for

at least 3 d prior to trials in order to ensure that they were postabsorptive when tested.

To begin a trial, the snake was placed at the start of the racetrack by being gently tipped out of its box (i.e., it was not directly handled). The subject was then encouraged to move along the track by being tapped softly on the tail with a paintbrush. For each trial, we raced the subject twice along the racetrack in quick succession (i.e., the second lap was run immediately after the first). When the subject reached the end of the first length of the racetrack it was pushed (with the paintbrush) into a bucket. The subject was then gently tipped back into the start of the track and encouraged to move as before. We video-recorded the snake's sprint performance and behavior from directly above the racetrack. Sprint speed, in body lengths per second, over each 50-cm section of the racetrack was calculated by watching the film frame by frame (25 frames/s). A subject's maximal sprint speed at each test temperature was calculated by taking the mean speed of its two fastest sections in the trial. Per-unit body length speed (i.e., body-lengths/s) was measured in this experiment because it is likely to be more important than absolute speed (i.e., m/s) or endurance in determining a snake's success at escaping a predator or catching prey (Van Damme and Van Dooren, 1999).

Alternative antipredator behaviors (AABs).—As an alternative to fleeing, snakes in the racetrack sometimes exhibited body thrashes (the snake rapidly flings the anterior half of its body sideways), strikes (the snake launches its head directly towards the paintbrush), threat displays (snake flattens its head and neck) and reversals (snake changes direction in the racetrack). We recorded the number of times a snake displayed these AABs in each sprint speed trial. From these data we calculated the total number of all AABs within each trial (i.e., the number of times a subject used any AAB). Our aim in collecting these data was to assess how temperature affected the propensity of snakes to flee versus use AABs.

Captured by Predator Experiment

Our second experiment simulated an encounter during which the snake was seized, and we examined the effects of temperature and time of day on antipredator behavior before and after seizure. We tested the effects of these factors on (1) posture and alertness, (2) low-intensity (slow/weak) antipredator behaviors, and (3) high-intensity (fast/powerful) antipredator behaviors. High- and low-intensity behaviors were grouped separately because they are likely to differ in thermal sensitivity (fast/powerful movements require more physical coordination, and hence are likely to be more sensitive to temperature variation than are slow/small movements).

This experiment tested 36 small-eyed snakes (mean SVL = 452 ± 11 mm SE, range 353–610 mm) and 35 broad-headed snakes (mean SVL = 458 ± 23 mm SE, range 244–610 mm). These were the same individuals as were tested in the sprint performance experiment, plus an additional two small-eyed snakes (one male and one female). Snakes were given a full week to recover from the previous experiment. In each trial, the snake experienced two stages of a predator–prey interaction: (1) initial confrontation (the snake is exposed in close proximity to the predator) and (2) capture (the snake is seized by the predator).

Snake boxes were placed in constant-temperature incubators set at 10, 20, or 30 °C for 3 h prior to testing in order to allow snake body temperatures to equilibrate to incubator temperature. Light globes inside incubators provided bright illumination during daylight hours (30 μmol photons m^{-2} s^{-1}), but were switched off at night between 1730 and 0800 h. Each day we conducted one testing session from 1200 to 1500 h and one between 1800 and 2000 h. Thus, we treated time as a categorical variable with day and night as levels. Every snake was tested once at each of the three temperatures both during the day and night for a total of six trials per subject. Both assignment to incubators and the order that subjects were tested in the temperature and time treatments were randomized.

To begin a trial, we removed the top of the snake box and moved the paper so that the snake was entirely exposed. We recorded the snake's initial body position as either coiled or stretched. Over the next 30 s, we scored the total number of tongue-flicks, whether or not the snake raised its head, threat displayed (i.e., flattened and elevated the rear of the head in

TABLE 1.—Antipredator responses of elapid snakes, showing the system used to derive overall indices of antipredator behaviors. The 11 behavioral variables measured during this study were grouped into three categories for calculation of indices: (1) posture and alertness, (2) low-intensity antipredator behaviors, and (3) high-intensity antipredator behaviors. Each behavioral variable was assigned a weighting. Trials were divided into two stages: an initial phase where the snake was exposed but not touched, and a second stage where the animal was seized and held by the experimenter.

Category	Behavioral variable	Weighting		Stage of trial
		Present or absent	Per occurrence	
Posture and alertness	Coiled body	0 or 2	—	First
	Raised head	2 or 0	—	First
	Tongue flicks	—	1	First
Low-intensity antipredator behaviors	Threat display	2 or 0	—	First
	Slow move	1 or 0	—	First
	Threat display	2 or 0	—	Second
	Slow move	1 or 0	—	Second
High-intensity antipredator behaviors	Flee	10 or 0	—	First
	Bites	—	5	Second
	Wraparounds	—	2	Second
	Body thrashes	—	1	Second

a threat display), moved slowly around the cage, and/or moved rapidly (i.e., attempted to flee). Wearing latex gloves over leather welding gloves for protection, the same researcher (JL) then grasped the snake between the thumb and forefinger at midbody to simulate capture by a predator. The snake was held this way for 30 s, during which time its behavior was scored. We scored slow movement and threat display as before, as well as the number of times the subject body thrashed (as described in the previous experiment), wrapped its body around the observer's fingers (some snakes rapidly coiled and uncoiled around the handler's fingers and hands when picked up) and the number of bites. The latex glove was thoroughly washed in warm soapy water, rinsed in fresh water, and towel dried between trials to remove any scent left by previous subjects.

The behaviors displayed by snakes fell into two groups: categorical variables and continuous variables. Categorical variables represented behaviors that, if adopted, were typically maintained throughout that stage of the trial. Behaviors in this group (such as body positions, threat display, slow move, flee) were scored as either present or absent. The second group (i.e., continuous variables) comprised transitory behaviors (such as tongue flicks, bites, body thrashes, and wraparounds) that could be repeated during a single observation period. For these behaviors, we recorded the number of times that each behavior was performed.

Eleven response variables were recorded in this experiment. Analyzing so many response variables individually would require numerous Bonferroni corrections and lead to an unacceptably high type-II error rate. Thus, we grouped response variables into categories and calculated indices for each category. The 11 response variables were grouped into three categories: (1) posture and alertness, (2) low-intensity antipredator behaviors, and (3) high-intensity antipredator behaviors. The response variables within each category were given a weighting (see Table 1 and below for details and justification) to reflect the variable's importance as an indicator of the snake's performance in that category.

Posture and alertness.—During the first 30 s of the trial, we measured three variables that indicate a snake's level of prior activity and initial alertness: (1) whether the snake was coiled or stretched out at the beginning of a trial, (2) whether it lifted its head from the substrate, and (3) the number of times it flicked its tongue in and out of the mouth. These variables are indicators of the snake's overall alertness rather than antipredator responses per se. In the field, inactive small-eyed and broad-headed snakes are typically found in a tightly coiled body position (J. Llewelyn, personal observation). We calculated overall scores in this category by allocating two points for stretched-out position, two points for head raising, and one point per tongue flick. For example, a snake that was

stretched out, did not raise its head, and tongue flicked three times would be given a score of five (e.g., 2 + 0 + 3).

Low-intensity antipredator behaviors.—Antipredator behaviors that do not require fast or powerful movements were used in the calculation of the low-intensity indices. In the initial confrontation stage of a trial, snakes were awarded two points if they threat displayed and one point if they moved slowly (< one body length/10 s). The same behaviors and same weightings were used in the second capture stage of the trial (i.e., the 30 s following picking up the snake). Threat displays are a specific antipredator behavior, so were weighted more heavily than moving slowly (a more general behavior that may not be a response to the predator). To illustrate the scoring procedure, a snake that threat displayed and moved slowly in both stages of the trial would score six points in that trial (i.e., 2 + 1 + 2 + 1).

High-intensity antipredator behaviors.—Behaviors that require fast and/or powerful movements were used to calculate the high-intensity indices. Only one of these variables (flee, = moving at > one body length/5 s) was exhibited during the initial stage of the trial (i.e., prior to picking up the snake). If a snake attempted to flee it scored 10 points. The second stage of the trial elicited other high intensity behaviors (bites, wraparounds, and body thrashes). Snakes were awarded five points per bite, two points per wraparound and one point per body thrash. These weightings were designed to reflect the physiological costs and escalation of each behavior. For example, fleeing requires rapid and highly coordinated movement for a few seconds at least, so this behavior scored highly. Biting represents an escalated retaliatory behavior, and so bites were awarded a higher score than wraparounds or body thrashes. Wraparounds require a snake to rapidly move its body around the predator and constrict, whereas body thrashes only require fast sideways movements. Hence, wraparounds were allocated a higher score than body thrashes. The following example illustrates the scoring procedure: a snake that attempted to flee, gave one bite, one wraparound, and one body thrash would score 18 for that trial (i.e., 10 + 5 + 2 + 1).

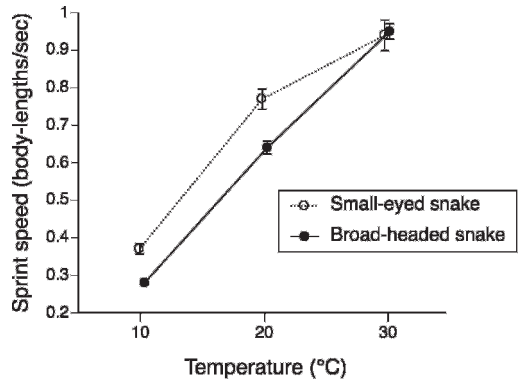

FIG. 1.—Maximal sprint speed of two species of elapid snakes at three temperatures, when tested in a terrestrial racetrack. Each point indicates mean maximal sprint speed and associated standard error.

Analysis

We analyzed the results of these experiments with the use of repeated-measures ANOVAs. When the assumption of sphericity was not met, we compensated for this violation by adjusting the degrees of freedom (Quinn and Keough, 2002). The Huynh-Feldt adjustment to degrees of freedom was used when estimated epsilons were greater than 0.75, and the Greenhouse–Geisser adjustment was used when estimated epsilons were less than 0.75. The main factors in our analyses were species (both experiments), temperature (both experiments) and time of testing (only the second experiment). We were primarily interested in testing (1) whether time of day and temperature had significant effects on antipredator behavior, and (2) whether species were affected differently by temperature (i.e., species × temperature interaction). When the effect of temperature on antipredator behavior was found to differ between species, we used post hoc profile analysis to identify over which temperature intervals the species differed (Quinn and Keough, 2002). Because profile analysis represents multiple tests on the same data set, *P* values from profile analyses were adjusted using sequential Bonferroni corrections (Holm's method).

RESULTS

Predator Pursuit Experiment

Sprint performance.—The snakes moved faster at higher temperatures ($F_{1.9,128.0}$ =

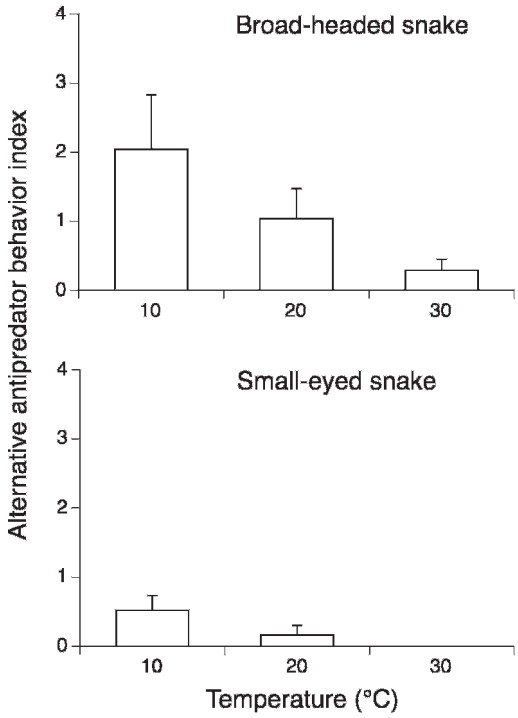

FIG. 2.—Alternative antipredator behavior index scores of two species of elapid snakes at three temperatures, when tested in a terrestrial racetrack. Each histogram shows the mean value and associated standard error.

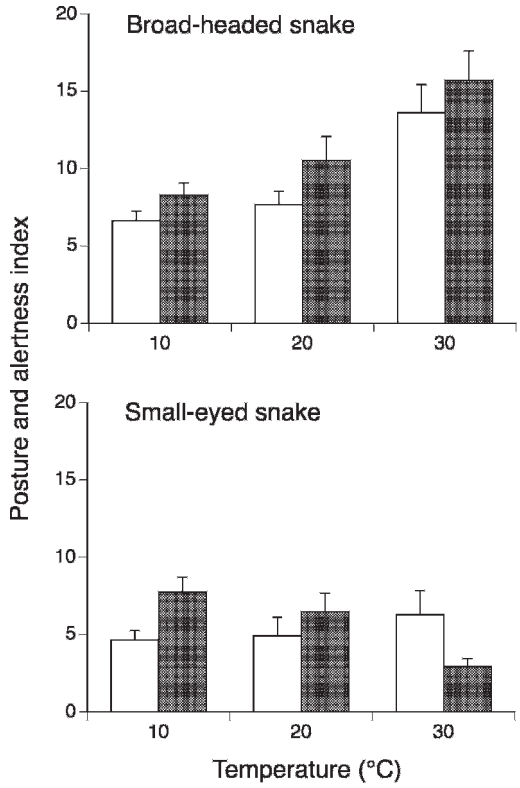

FIG. 3.—Posture and alertness index scores of two species of elapid snakes tested at three temperatures during the day and at night. Open histograms indicate measurements taken during daylight hours and shaded histograms indicate measurements taken at night. Each histogram shows the mean value and associated standard error.

515.51, $P < 0.0001$; Fig. 1). However, the rate at which sprint speed increased with temperature differed between species (temperature × species interaction, $F_{1.9,128.0} = 6.59$, $P = 0.019$) because between 20 and 30 °C, the speed of broad-headed snakes increased more than did that of small-eyed snakes (Fig. 1). Profile analysis confirmed that the increase in sprint speed between 20 and 30 °C was greater for broad-headed snakes than small-eyed snakes ($F_{1,66} = 12.30$, $P = 0.0016$), whereas the rate of increase between 10 and 20 °C was similar in the two species ($F_{1,66} = 2.04$, $P = 0.16$).

Alternative antipredator behaviors.—When exposed in the presence of a potential threat, both species responded primarily by fleeing (27 of 34 small-eyed snakes and 22 of 35 broad-headed snakes did not use AABs in any trial). Alternative antipredator behaviors were increasingly adopted at lower temperatures (Fig. 2; $F_{1.39,93.13} = 7.90$, $P = 0.025$), and the effect of temperature did not differ significantly between species ($F_{1.39,93.13} = 2.44$, $P = 0.09$). Broad-headed snakes exhibited AABs more often than did small-eyed snakes ($F_{1,67} = 4.22$, $P = 0.04$; Fig. 2).

Captured by Predator Experiment

Posture and alertness.—The effect of temperature on posture and alertness differed between species ($F_{1.88,112.68} = 16.08$, $P = 0.0001$). Broad-headed snakes were more alert at higher temperatures, whereas small-eyed snakes displayed little variation between test temperatures (Fig. 3). Profile analysis confirmed that posture and alertness increased more rapidly in broad-headed snakes than small-eyed snakes between 20 and 30 °C ($F_{1,66} = 17.46$, $P = 0.002$; Fig. 3), whereas the rate of increase in this response from 10 to

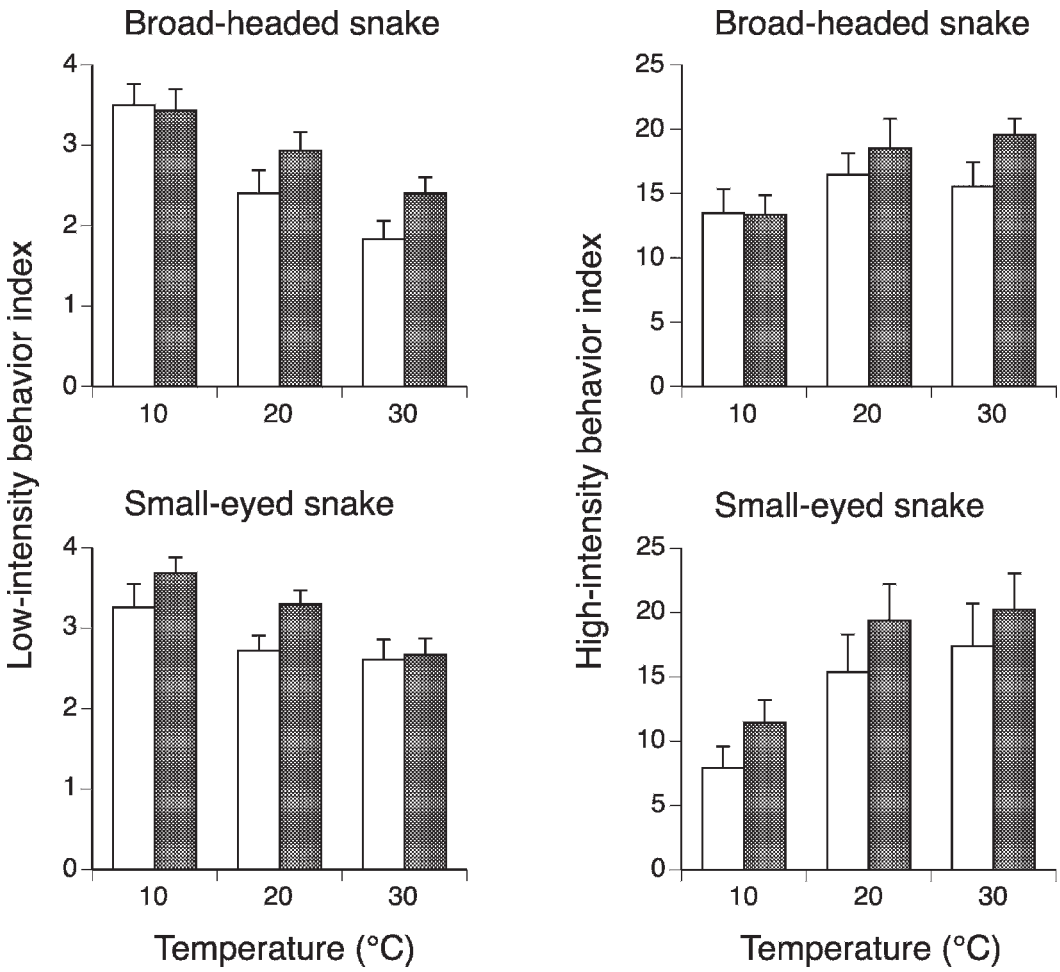

FIG. 4.—Antipredator behavior index scores of two species of elapid snakes tested at three temperatures during the day and at night. Open histograms indicate measurements taken during daylight hours and shaded histograms indicate measurements taken at night. Each histogram shows the mean value and associated standard error. Left-hand panels show low-intensity behaviors, and right-hand panels show high-intensity behaviors. See text and Table 1 for definitions.

20 °C did not differ significantly between the two species ($F_{1,62} = 3.36$, $P = 0.07$).

The effect of time of testing on posture and alertness did not differ significantly between species ($F_{2,120} = 1.37$, $P = 0.25$). Although both species tended to be more alert by night than by day (Fig. 3), this trend fell short of statistical significance ($F_{1,120} = 3.33$, $P = 0.07$).

Low-intensity antipredator behaviors.—Lower test temperatures and nocturnal tests significantly increased the rate of low-intensity antipredator behaviors exhibited by these snakes (thermal effect, $F_{2,138} = 31.99$, $P = 0.0001$; night vs. day effect, $F_{1,138} = 14.15$, $P = 0.0004$; Fig. 4). Neither temperature nor time of testing affected the two species differently ($P > 0.15$ in both cases).

High-intensity antipredator behaviors.—Higher test temperatures and nocturnal tests significantly increased the rate of high-intensity antipredator behaviors shown by these snakes (thermal effect, $F_{2,138} = 16.61$, $P = 0.0001$; night vs. day effect, $F_{1,138} = 4.21$, $P = 0.04$; Fig. 4). Neither temperature nor time of testing was found to affect species differently ($P > 0.2$ in both cases).

DISCUSSION

Overall, our data strongly support the hypothesis of context dependency in antipred-

ator responses. The behavioral responses exhibited by the snakes were modified by body temperature and time of testing. Presumably reflecting their substantial similarities in morphology, physiology, and ecology, the two species responded in broadly similar ways to thermal conditions (i.e., adopting more vigorous responses at higher temperatures) and times of day (with nocturnal trials tending to elicit more intense responses). In other respects, however, the two species diverged significantly. Generally, our data on antipredator tactics of these two elapid snake species accord well with predictions based on other facets of their biology:

1. The snakes showed more intense and/or effective antipredator responses when tested at night than if tested during daylight hours, as expected from the hypothesis that behaviors will be manifested most effectively under the conditions in which they are most often required in nature.
2. Both species utilized immobility (crypsis) or bluff when cold, switching to more vigorous antipredator responses (such as fleeing or biting) at higher temperatures, as expected under the hypothesis that snakes will match their antipredator tactics to thermally driven shifts in their locomotor capacity.
3. Sprint speeds and alertness of small-eyed snakes declined less rapidly at lower temperature than did those of broad-headed snakes (Figs. 1 and 3), as expected under the hypothesis that the ability to escape at low temperatures will be more important to the fitness of a nocturnal active forager (that frequently encounters predators when cold) than an ambush hunter (that typically maintains higher temperatures).
4. Broad-headed snakes were less likely to rely on fleeing than were small-eyed snakes (Fig. 2). That difference is consistent with the hypothesis that snakes adopt responses most suitable to the context in which they most often encounter predators (i.e., inside a crevice for broad-headed snakes vs. an open area for small-eyed snakes).

The effects of test temperature on choice of antipredator tactics appear to be phylogenetically conservative among ectothermic vertebrates. In both sets of trials that we conducted, warm snakes relied primarily on behaviors whose performance is highly dependent upon the snake's body temperature, whereas cool snakes increased their utilization of behaviors that are not as thermally sensitive. For example, in the predator pursuit experiment, warm snakes relied primarily on fleeing. In the captured-by-predator experiment where fleeing was not an option, both species matched their antipredator responses to their physiological capacities by utilizing high-intensity behaviors (e.g., biting, wrapping around, and body thrashing) only when tested under warm conditions. At low body temperatures, in contrast, the snakes primarily exhibited low-intensity antipredator behaviors (e.g., threat displaying and moving slowly). A similar switch from highly active antipredator responses to more static/slow responses as body temperature decreases appears to be widespread amongst ectotherms, including invertebrates (Miyatake et al., 2008), fish (Weetman et al., 1998), amphibians (Gomes et al., 2002), lizards (Cooper, 2003; Hertz et al., 1982) and snakes (Shine et al., 2002). These temperature-induced changes in antipredator strategies are likely compensatory adjustments; if the ability of a potential prey item to perform vigorous antipredator behaviors is impaired by low body temperature, it adopts less thermally sensitive antipredator tactics under such conditions rather than attempting to use behaviors for which its performance levels are likely to be poor (Hertz et al., 1982).

Although the antipredator response of both species was affected similarly by temperature, broad-headed snakes were more sensitive to temperature changes than were small-eyed snakes in two measures: sprint performance (Fig. 1), and posture and alertness (Fig. 3). As noted above, the snakes' foraging modes may explain this divergence. Small-eyed snakes are active foragers and thus are exposed to predation risk over a wide range of body temperatures (Downes, 2002; Llewelyn et al., 2005; Shine, 1984). In contrast, broad-headed snakes are ambush predators that rarely leave their shelter sites and thus can be more selective with regards

to when (and under what conditions) they leave their shelter site (Webb and Shine, 1998*a*; Webb et al., 2003). As a consequence, small-eyed snakes need to function effectively at both warm and cool body temperatures, whereas broad-headed snakes simply avoid activity when conditions are unfavorable.

Our results suggest that time of day also influences the antipredator responses of reptiles. Although circadian variation in performance is well documented in humans (e.g., Atkinson and Reilly, 1996; Folkard and Rosen, 1990), this factor is rarely considered in analogous studies of other animals (Llewelyn et al., 2006). The nocturnal snakes that we studied tended to perform antipredator behaviors more effectively at night than by day. Although consistent with the hypothesis that animals match antipredator responses to activity schedules, the evidence is weak. To evaluate this hypothesis more robustly, we could exploit the many shifts between nocturnal and diurnal habits within squamate phylogeny to conduct comparative analysis designed to detect nonrandom association between antipredator responses and activity times.

In summary, the results of our study lend support to the hypothesis that natural selection has endowed snakes with a flexible repertoire of antipredator behaviors that are best suited to the conditions under which the animals are most likely to encounter a predator. Importantly, a snake's time of activity and foraging mode influence when and where it will encounter predators. Consequently, antipredator behaviors are likely to covary with these two factors.

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