Thermoregulation by a Nocturnal Elapid Snake (*Hoplocephalus bungaroides*) in Southeastern Australia

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ABSTRACT

Studies of reptilian thermoregulation have tended to focus on diurnal heliothermic taxa that display overt thermoregulatory behavior, with nocturnal reptiles attracting less attention. We studied thermoregulation by the broad-headed snake (*Hoplocephalus bungaroides*), a small (mean snout-vent length = 57 cm) nocturnal elapid that spends long periods sequestered in diurnal retreat sites. The snakes selected body temperatures of 28.1°–31.1°C in laboratory thermal gradients. Prey-capture ability (strike speed and accuracy) increased at higher body temperatures over the range 20°–30°C. Using temperature-sensitive radio transmitters, we obtained 7,801 body-temperature measurements of 19 free-ranging snakes. Information on operative environmental temperatures was obtained at the same time. From these data, we quantified the degree to which the snakes exploit the environmental thermal heterogeneity available to them (i.e., the time they spent within their set-point range, relative to the total time that these body temperatures were available to them). Mean body temperatures (both diurnally and nocturnally) differed among seasons but not among different types of retreat sites. Inclement weather prevented snakes from attaining "preferred" body temperatures on 30% of days. However, even when preferred temperatures were available, the snakes exploited this opportunity for only 26% of the time: they remained within retreat sites and rarely emerged to bask. Nonetheless, judicious retreat-site selection resulted in snakes being within their set-point range for 60% of the time at the most crucial time of day (i.e., the 2-h period around dusk, when the opportunity to capture prey is highest). Basking may be rare not only because of its high potential costs (e.g., risk of avian predation) but also because high body

temperatures enhance snake fitness for only a short time each day and can be attained over that short period without the "expense" of heliothermy. Our results suggest that precise thermoregulation may not be widespread among snakes, particularly small nocturnal species that spend long periods sequestered in retreat sites.

Introduction

Since the pioneering work of Cowles and Bogert (1944), numerous studies have demonstrated the complex and often subtle ways in which reptiles can modify their body temperatures by exploiting thermal heterogeneity in the local environment (reviews by Avery 1982; Huey 1982). However, this work is based primarily on a restricted subset of reptilian species: primarily, on diurnal heliothermic temperate-zone Northern Hemisphere lizards (Avery 1982; Huey 1982). One reason that studies of thermoregulation have focused on these species is that they actively and overtly thermoregulate and, thus, maximize an investigator's ability to document organismal "strategies" for thermoregulation (e.g., Bradshaw and Main 1968). Unfortunately, this bias may obscure more general patterns of reptilian thermoregulation for two reasons: (1) many species spend long periods inactive in refugia, where temperatures may be very different to those available on the surface (Huey 1982; Peterson 1987; Huey et al. 1989), and (2) compared with lizards, a significantly higher proportion of snakes (typically, around 50%) are nocturnal (e.g., Huey 1982; Cogger 1992).

To date, few studies have adequately investigated thermoregulation by inactive diurnal or nocturnal squamates (but see Peterson 1987; Huey et al. 1989; Autumn et al. 1994). One central question is the degree to which thermoconformity (i.e., reluctance to show overt thermoregulatory behavior such as basking) results in a significant reduction in the proportion of time that an organism is able to achieve temperatures optimal for key physiological or behavioral processes. For tropical reptiles, this diminution may be trivial in magnitude (e.g., Ruibal 1961; Huey 1982; Hertz et al. 1993; Shine and Madsen 1996). However, it may be significant for temperate-zone species.

In order to adequately determine the extent to which ectotherms exploit their thermal environment, we need information on four variables: (1) the animals' "preferred" body temperature (T_b) range, usually assessed in a "cost-free" environment in the laboratory (Heath 1965; Licht et al. 1966); (2) the range of potential equilibrium body temperatures (operative temperatures: T_e's) that an animal would attain in a

particular microhabitat at a particular time (Porter et al. 1973; Bakken and Gates 1975; Peterson 1987); (3) the animals' physiological state (Regal 1966; Stevenson et al. 1985; Peterson et al. 1993); and (4) the body temperatures actually displayed in the field (i.e., spot temperatures or continuous profiles, see Peterson [1987]). Using these data, we can then calculate indices that describe the extent of active thermoregulation (Hertz et al. 1993; Christian and Weavers 1996).

We studied thermoregulation by a small species of elapid snake (the broad-headed snake, *Hoplocephalus bungaroides*) that lives in a relatively cool and highly seasonal climate and shows strong thermally forced seasonal shifts in retreat-site selection (Webb and Shine 1998b). Broad-headed snakes are active nocturnally but infrequently and, thus, spend long periods of time (both by day and by night) sequestered under stones on exposed cliff edges. The snakes are highly selective in their choice of retreat sites: during spring they select thin rocks fully exposed to solar insolation but avoid shaded and thicker (and thus cooler) rocks (Webb and Shine 1998b). Broad-headed snakes bask infrequently (Webb 1996), but we do not know whether the virtual absence of this behavior reflects high costs (e.g., vulnerability to predation when basking) or low benefits (e.g., snakes sheltering under rocks may be able to exploit their thermal environment efficiently without basking). In this article, we investigate the latter hypothesis by quantifying the extent to which these snakes are able to exploit their thermal environment with and without basking. In addition, the dramatic seasonal shift in habitat use displayed by *H. bungaroides*, whereby the snakes shelter in tree hollows in open woodland during summer (Webb and Shine 1997b), allows us to quantify the extent to which different types of retreat sites influence the snakes' ability to exploit the thermal environment at different times of the year.

Material and Methods

Study Sites and Radiotelemetry

This study was part of a 3-yr (1992–1995) radiotelemetry and 4-yr mark-recapture project that was carried out in Morton National Park, 160 km south of Sydney, New South Wales. In this area, the mean daily maximum air temperatures range from 25.9°C in January (midsummer) to 15.8°C in July (midwinter), while the mean daily minimum air temperatures for these months are 15.9° and 6.0°C, respectively (Bureau of Meteorology 1988). Each year, we radio-tracked 11 snakes at three sites (each approximately 3 km apart), on the western side of a sandstone plateau of 400 m elevation. The plateau is covered by open woodland forest (for a full description, see Black [1988]) except for the exposed western cliff edge (10–30 m wide) where rocks of varying sizes and thicknesses have weathered from the underlying sandstone. The cliff faces are 20–30 m high and are deeply dissected by numerous horizontal crevices. Both sandstone rocks and crevices are abundant and are used as retreat sites by broad-headed snakes (Webb and Shine 1998b).

Temperature-sensitive radio transmitters (Holohil BD-2G, 18 × 9 × 5 mm, 2.2 g, slow pulsing, battery-life 6 mo) were waterproofed and calibrated at 2°C increments from 4° to 40°C before implantation in snakes. Full details of our surgical techniques are given elsewhere (Webb and Shine 1997b). Following surgery, snakes were released at the site of capture and radiotracked for periods of up to 6 mo. Snakes were usually radiotracked from early spring (September) to late summer (February), but release dates varied each year depending on when we could find snakes. Full details of body sizes and sexes of telemetered snakes, release dates, and duration of radio tracking are provided elsewhere (Webb and Shine 1997a, 1997b).

Set-Point Temperatures in the Laboratory

Body temperatures of nine postabsorptive snakes (7 males, 2 nongravid females, mean snout-vent length [SVL] = 63.8 cm, range 55.5–76.0 cm) were measured in identical thermal gradients over 2 d in early spring 1995. We used unfed snakes because this species feeds infrequently in the wild (Webb and Shine 1998a), so that overall patterns of thermal selection are unlikely to be affected greatly by postfeeding thermophily. Each thermal gradient consisted of a painted wooden cage (77 cm long × 30 cm wide × 30 cm high) with a sliding-glass front with an underfloor heating element and air vent at one end. Thermal gradients were placed in a constant-temperature room with an ambient temperature of 17°C. Lighting in the room matched the natural photoperiod, and heating elements within the cages were programmed to come on at sunrise and switch off at dusk. Diurnal floor temperatures within each cage ranged from <20°C to >50°C (means of 17.4° and 52.3°C, respectively).

Thin-gauge copper-constantan thermocouples connected to a Campbell-CR10 data logger were used to monitor snake body temperatures. The end of each thermocouple was covered in Dow Corning 100% flowable silicon and allowed to dry before use. Thermocouple ends were inserted 2–3 cm into the cloacae of snakes and were held in place with glue (5-min epoxy resin) and masking tape on the tail 2 cm below the vent. Both glue and tape were easily removed afterward by soaking the snakes' tails in water. Following attachment of thermocouples, snakes were immediately placed into thermal gradients, and their body temperatures were recorded every 5 min for 2 d. A thin layer of newspaper was placed in each cage for shelter. Snakes usually remained under the newspaper throughout the day and were able to move freely from one end of the gradient to the other. During the day, most snakes remained relatively stationary in coiled postures (diameter of coil <8 cm) while in the gradients. Thus, cloacal temperatures should approximate deep body temperatures.

For each snake, the bounds of the central 50% of the ob-

served body temperatures were used to estimate the set-point range (Hertz et al. 1993; Christian and Weavers 1996).

Effect of Temperature on Performance (Strike Speed and Accuracy)

Broad-headed snakes are sit-and-wait predators that ambush prey (diurnal and nocturnal lizards) that venture near or under rocks used by the snakes (Webb and Shine 1998a). In this species, feeding strikes are initiated from a stationary position, so that prey capture is likely to depend on strike speed and accuracy rather than, for example, crawling speed. We realize that the situation will be far more complex in the field, where responses of both predator (prey-detection ability) and prey (crypsis, tail loss, ability to flee) will ultimately determine whether a feeding strike is successful (see Downes and Shine 1998).

Snake-strike trials were held in a glass arena (44 cm long × 37 cm wide × 20 cm high) with a wooden floor. The wooden floor was raised 6 cm from the bottom of the aquarium, and a rail was attached 4 cm above the floor to allow a clear Perspex lid to slide into place. This design meant that snakes were contained within a 4-cm-high "crevice" during the experiment. A new sheet of paper with 1 cm grid squares was glued onto the floor before each day of testing. Trials were filmed from above with a fixed video camera.

Strike-speed trials were carried out at 20°, 25°, and 30°C, with the test order randomized for each snake. Ten postabsorptive adult broad-headed snakes (six males, four females; mean SVL = 63.1 cm, range 55.5–72.0 cm; mean mass = 71.5 g, range 37.0–143.4 g) were used in the experiment. For each trial, a snake was placed into the "crevice" and a piece of dark cardboard was placed on top of the Perspex lid at one end. Snakes usually sheltered under the cardboard, and we gave them 5 min to settle down before the cardboard was removed. A small dead mouse (the staple diet for captive snakes) was then slowly moved toward the snake; this was repeated until the snake had struck the mouse several times. Trials were terminated after 5 min or when snakes exited the arena.

Trials were analyzed using a video recorder that allowed frame-by-frame playback (25 frames/s). We only analyzed strike speed in instances where snakes actually bit the mice. We followed Greenwald's (1974) protocol for measuring strike speed. Snakes usually initiated strikes from a standstill, so measurements were taken once the snake's head first moved and were terminated as soon as the snake's head appeared to touch the mouse. Thus, we measured the distance moved by the snake's head from frame to frame. These measurements allowed us to determine the average velocity over the entire strike as well as the maximum velocity attained during the strike. Only one measurement of average and maximum velocity (from the single fastest strike) for each snake was included in the final data set. We defined "successful" strikes as those strikes where the snake struck the mouse with an open or closed mouth. The total number of strikes and the number of successful strikes were recorded for each snake at each temperature.

Operative Temperatures

Operative environmental temperatures (T_e's: Bakken and Gates 1975; Bakken 1992) available to broad-headed snakes were estimated by combining temperature data (from rocks and exposed models) with data on the availability of rocks with different thicknesses and degree of shading. We measured temperatures under eight sandstone rocks of different diameters (20–63 cm) and thicknesses (2–16 cm) on a single exposed rock outcrop. Thermocouples were glued to the middle of the underlying rock substratum (T_s) and underside of each rock (T_r) using 5-min epoxy resin. It was physically impossible to place hollow copper-tube models under rocks because of the extremely tight fit (often <6 mm) between the rocks and their underlying rock substrata. To assess the effects of shading on rock temperatures, we artificially shaded four rocks (range of 21–34 cm in diameter, 4–10 cm thick) using square frames (90 cm wide × 50 cm high) covered with two layers of 75%, beige shade cloth. Shaded air temperature 1 m from the ground was also recorded (Christian and Tracy 1985). All thermocouples were multiplexed to a Campbell-CR10 data logger, and temperatures were recorded every 30 min.

Although the patterns of heat flux under rocks are complex (e.g., Kreith 1965; Porter et al. 1973), previous studies have found that rock thickness strongly affects rock temperatures (Huey et al. 1989). Our results support this finding (see below). Thus, we can predict temperatures under rocks of different thicknesses using our thermal data. To estimate the availability of rocks with different thermal characteristics, we measured the size (length and width), thickness, proportion canopy cover (shading), and substrata (soil vs. rock) directly below a total of 1,995 rocks (including 134 rocks used by snakes) along transects (see Webb and Shine [1998b] for full details).

Body temperatures available to snakes in the open (sun vs. shade) or in crevices were estimated using physical models (Peterson et al. 1993). Models were 60-cm-long copper tubes (wall thickness 1.1 mm, diameter 12 mm, painted black) with sealed ends (tight-fitting plastic stoppers). Each model had a single thermocouple suspended in its center and was flattened slightly to ensure that the "ventral" surface made good contact with the substrate (Peterson et al. 1993). Initial tests showed that the models accurately predicted body temperatures of broad-headed snakes (e.g., comparison of temperatures of a model with a dead broad-headed snake on a flat exposed concrete surface from 0800 to 1100 hours on a sunny spring morning: range for both model and snake = 17°–38°C, mean thermal discrepancy between model and snake <0.1°C, and correlation between the two readings $r^2 = 0.97$; 1, 89 df; $P < 0.0001$). One model was placed in full sun on an exposed rock platform near the cliff edge, one model was placed in full

shade (under a large shady tree), and three models were placed 5 cm inside crevices with westerly, easterly, and southerly aspects. During the final field season, we placed one model under a large boulder (170 cm long × 90 cm wide × 36 cm thick) and two models 60 cm inside cliff-top crevices with westerly aspects (thickness of rock above crevices = 60 cm). Temperatures of models were recorded every 20 min using single-channel Hobotemp data loggers.

Field Body Temperatures

Continuous body temperatures (T_b's) of three snakes under rocks, three snakes in crevices, and seven snakes in tree hollows were recorded during the 1993–1994 and 1994–1995 field seasons using an automated system (see Rummery et al. [1995] for details). Body temperatures of four of these snakes were recorded when the snakes were using different retreat sites, so overall we have continuous body temperature measurements for nine different adult snakes (five males, four nongravid females). Additional information on daily body temperatures of another 10 snakes was obtained by recording the period between pulse intervals with a stopwatch over 2 d in 1992 and 8 d in 1993. We defined "diurnal" temperatures to be those recorded between 0800 hours and sunset, and "nocturnal" temperatures as those taken over the rest of the day. Exact times of sunset for Sydney (Lomb 1994) were used in all analyses.

Indices of Thermoregulation

Exploitation Index. Christian and Weavers (1996) showed that plots that superimpose T_b's, T_e's, and the set-point range over the whole day are extremely useful for describing thermoregulation by ectotherms. These plots can be visually inspected to assess daily patterns (Peterson 1987) or can be used to describe the extent to which the animals exploit their thermal environment. The index of thermal exploitation (Ex) is the time in which T_b's are within the set-point range divided by the time available for the animal to have its T_b within the set-point range (Christian and Weavers 1996). We used this methodology to describe thermoregulation by broad-headed snakes. Cool, overcast, or rainy days (where maximum T_e's < 28.1°C) and days where snakes could only attain preferred body temperatures for <1 h were excluded from the analysis. For the remaining days, we calculated the amount of time that each snake could have achieved its T_b within the set-point range. Snakes in the cliff-top habitat had access to a variety of rocks of different thicknesses and crevices of different aspects, and so could potentially maintain preferred body temperatures for long periods by basking early in the morning and then retreating under rocks or into crevices later in the day. The maximum time that these snakes could achieve temperatures within their set-point range was determined by examining T_e data for rocks, exposed models, and models in crevices. Snakes using tree hollows also had considerable opportunities for ther-

moregulation. Most trees selected by snakes were large and contained more than two hollow branches (Webb and Shine 1997a). Broad-headed snakes are agile climbers, and so could potentially crawl to exposed sites on tree branches to exploit patches of sunlight both early in the morning and late in the afternoon. However, we were unable place snake models in these places (most hollows used by the snakes were located >15 m from the ground, see Webb and Shine [1997a]). Instead, we used T_e data from our cliff-top site (T_e's of models in full sun and full shade) to estimate the maximum time that snakes in tree hollows could spend in their set-point range.

We calculated the degree of thermal exploitation over two time periods: (1) the hour before sunset plus the hour after sunset and (2) the rest of the day. The former measure provides an index of the snakes' degree of thermal exploitation of its ambient thermal environment at dusk, which is likely to be the most critical time of day for prey capture (see below). Our statistical analyses are based on mean values for each snake in each type of retreat site rather than treating successive measurements on the same snake within a given type of retreat site as independent measures. We adopted this technique to avoid pseudoreplication (Hurlbert 1984). However, we treated data for the same snake in different types of retreat sites (e.g., crevice vs. tree hollow) as separate samples. Given that thermal variances were similar among snakes and among retreat-site categories, this procedure should not introduce any significant bias into our analyses (Leger and Didrichson 1994).

Hertz Index. Visual inspection of plots that superimpose T_b's, T_e's, and T_{set} (see Figs. 1–3) reveal how snake T_b's (and T_e's) deviate from T_{set} during different times of the day. We calculated the magnitude of these deviations using the methods of Hertz et al. (1993), but our analysis was restricted to T_b data obtained from nine snakes using cliff-top habitats (six in crevices, three under rocks) during six different spring days over a 3-yr period (1992–1994). For each snake we calculated d_b, the deviation of T_b from T_{set} (note that a T_b within T_{set} is assigned a value of zero), and d_e, the mean deviation between T_e's and the set-point range (see Hertz et al. 1993). The index d_e describes the thermal quality of the habitat; a large d_e means that the animal must thermoregulate carefully if it is to maintain its T_b within the set-point range. Our analysis was restricted to cliff-top habitats because to calculate d_e a good estimate of T_e's in the habitat is required. In our study, T_e's were measured in the exposed cliff habitat but not the arboreal habitat. To estimate the mean T_e in this habitat (a requirement of the analysis, see Hertz et al. [1993] for full details of methodology), we used our data on availability of exposed basking sites and rocks with different thermal characteristics (see Webb and Shine [1998b] and results below). A mean T_e for snake models was obtained by assuming that snakes had equal access to crevices with different aspects. This assumption is not unrealistic; at our study sites, the western-facing cliff edges are deeply dissected so that crevices with easterly and southerly
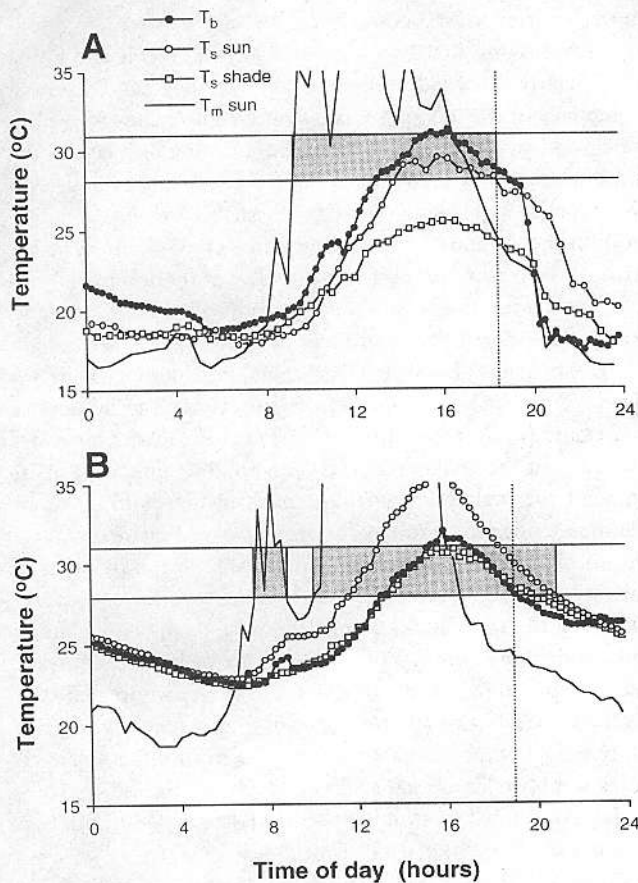
Figure 1. Body temperatures of two nongravid female broad-headed snakes using rocks during spring (A) and summer (B). The snake monitored in spring (November 13, 1993) was under a thin (10-cm-thick) exposed rock, whereas the snake monitored during summer (January 22, 1994) was under a thin (10-cm-thick) shaded rock. T_b = snake body temperature, T_s sun = substratum temperature under a 10-cm-thick exposed rock, T_s shade = substratum temperature under a 10-cm-thick shaded rock, and T_m sun = a snake model in full sun. The vertical dotted lines show the times of local sunset. The solid horizontal lines show the upper and lower limits of the set-point range (as measured in the laboratory). The shaded section between these lines represents the time periods for which the snakes could potentially attain body temperatures within this range, on the basis of available T_e's.

aspects are found relatively close (<5 m away) to those with northerly and westerly aspects. However, the cliff-top shaded sites were less common (76.6% of all rocks were in exposed locations), so models in full sun and full shade were weighted according to the availability of these sites. Similarly, thermal data from rocks were weighted according to their availability in the habitat, but we restricted our sample to rocks with rock substrata since telemetered snakes avoided rocks lying on soil (Webb and Shine 1998b). Last, we calculated a third index proposed by Hertz et al. (1993) that describes the effectiveness of thermoregulation: $E = 1 - (d_b/d_e)$. Values of zero indicate no thermoregulation, whereas values near 1 indicate precise

thermoregulation. This index allows us to address the question, How carefully do broad-headed snakes thermoregulate?

Results

Temperatures Selected by Snakes in the Laboratory

We discarded data for two snakes that remained at the cold end of the gradient throughout the experiment. Thus, our analysis is based on the data from seven snakes. For these animals, lower (28.1°C) and upper (31.1°C) set-point body temperatures were very similar on all 3 d (one-factor repeated-
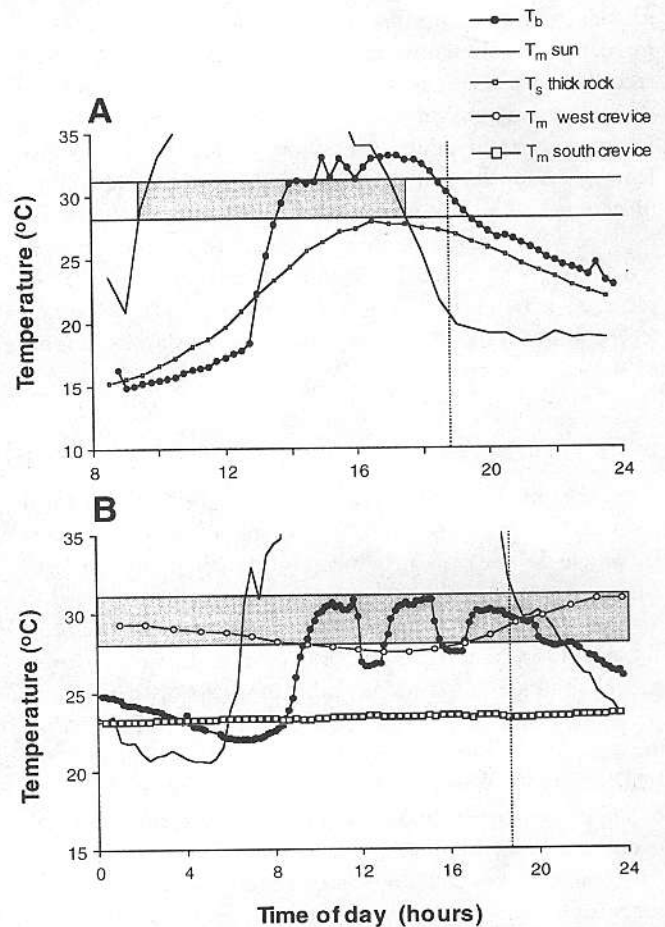

Figure 2. Body temperatures of two male broad-headed snakes using crevices during spring (A) and summer (B). The snake monitored during spring (November 10, 1994) was in a crevice 1 m below the cliff top, while the snake monitored during summer (December 19, 1994) was in a crevice approximately 5 m below the cliff top. T_b = snake body temperature, T_m = snake model in full sun, T_s thick rock = substratum temperature under an exposed 16-cm-thick rock, T_m west crevice = snake model 60 cm inside an exposed cliff top crevice with a westerly aspect, T_m south crevice = snake model 60 cm inside an exposed cliff top crevice with a southerly aspect. See caption to Figure 3 for explanations of other symbols.
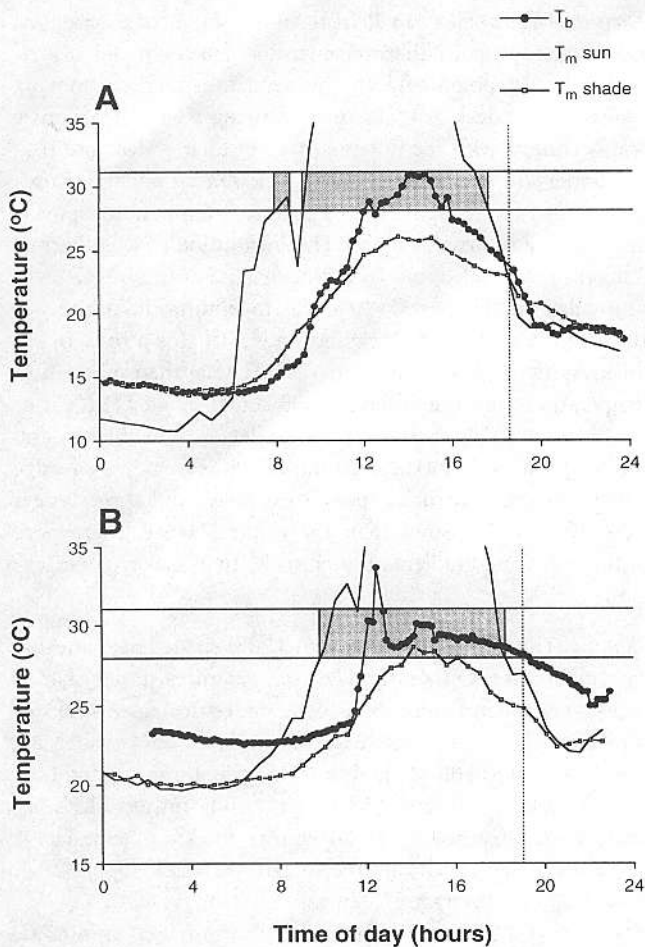
Figure 3. Body temperatures of a nongravid female broad-headed snake using tree hollows in open woodland during (A) spring (November 26, 1993) and (B) summer (January 20, 1993). T_b = snake body temperature, T_m = snake model in full sun, T_m shade = snake model in full shade. See caption to Figure 1 for explanations of other symbols.

measures ANOVAs: 2, 6 df; $P > 0.05$ for both variables). Lower and upper set-point temperatures showed a similar range during the 3 d (lower set-point temperatures: 23.5°–32.2°, 23.3°–32.6°, and 24.4°–30.6°C; upper set-point temperatures: 28.8°–33.9°, 26.1°–33.3°, and 27.5°–34.6°C). Minimum and maximum T_b's of snakes were also similar on all 3 d (one-factor repeated-measures ANOVAs: 2, 6 df; $P > 0.05$ for both variables).

Effect of Temperature on Strike Performance (Speed and Accuracy)

Nine of 10 snakes readily bit the dead mouse when it was moved toward them. One snake did not bite the mouse during any of the trials, and a second snake failed to bite during the 25°C trials. Hence, we have data for nine snakes at 20° and 30°C and eight snakes at 25°C. Our measures of snake size

(SVL, mass) were not correlated with our measures of strike speed (either for the entire strike or for the fastest part of strike: $P > 0.05$ for all correlation analyses). Overall, snakes struck faster at higher temperatures (repeated-measures ANOVA for all strikes: $F_{2,12} = 5.85$, $P < 0.017$; for the fastest part of the strike: $F_{2, 12} = 4.16$, $P < 0.05$; see Fig. 4).

To examine the effect of temperature on strike accuracy, we excluded data from snakes that struck less than three times in a trial. Hence, we analyzed data for eight snakes at each temperature. The proportion of successful strikes made by snakes increased with temperature (repeated-measures ANOVA for the proportion of successful strikes: $F_{2, 14} = 7.28$, $P < 0.05$). Overall, snakes struck faster and more accurately at higher temperatures (see Fig. 4).
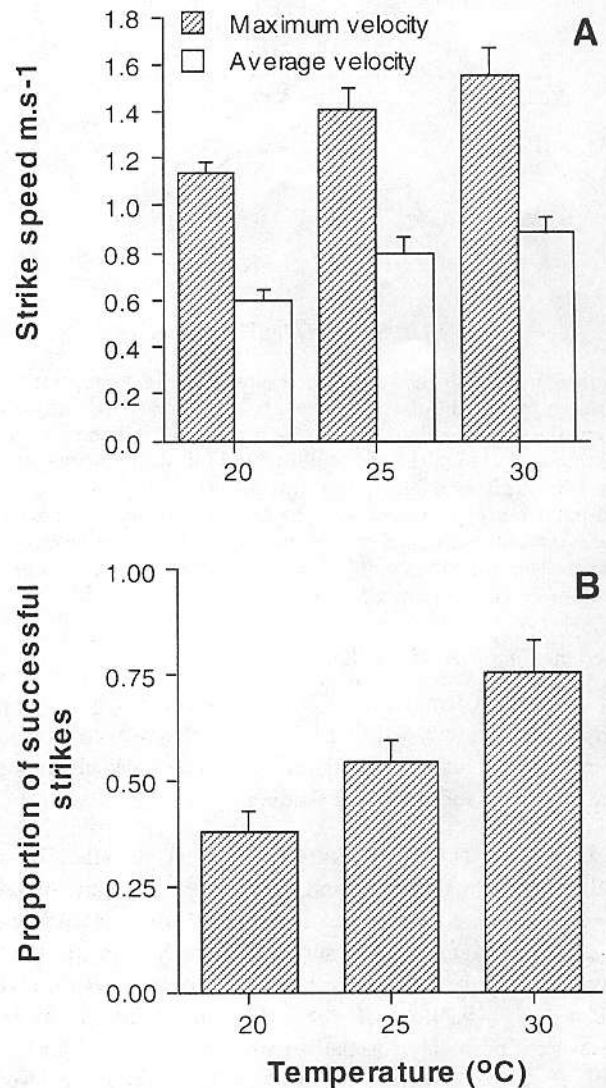

Figure 4. Changes in (A) speed of the feeding strikes and (B) accuracy of the feeding strikes of captive broad-headed snakes as a function of the body temperatures of the snakes when tested. Values are means and SEs. See text for description of arena and statistical analysis of results.
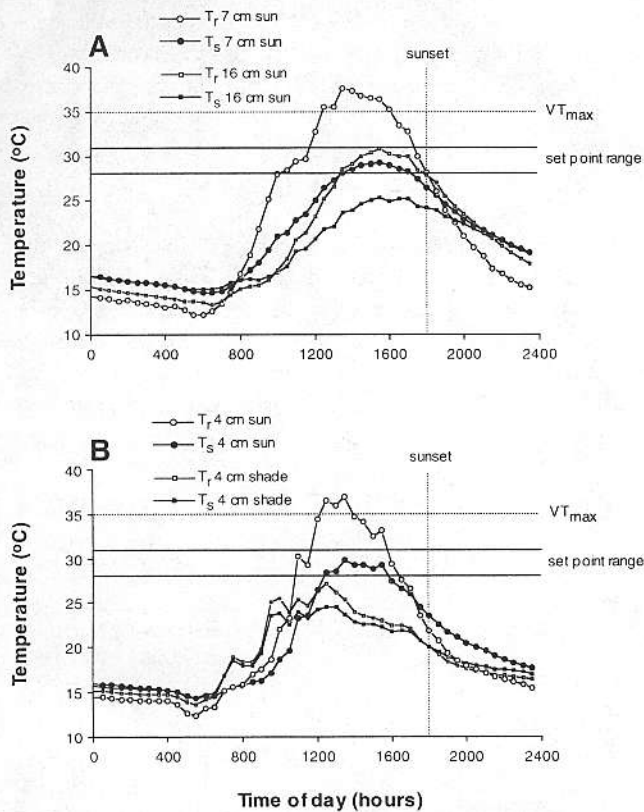
Figure 5. Daily cycle of rock (T_r) and substratum (T_s) temperatures during a fine spring day (October 31, 1994) for (A) a thin rock (7 cm thick) and a thick rock (16 cm thick) in full sun and for (B) thin rocks (4 cm thick) in full sun and full shade for the same day. Solid horizontal lines indicate the preferred temperature range (set-point range) of the snakes, the dotted horizontal line is the snakes' voluntary thermal maximum (VT$_{max}$) based on laboratory studies. The dotted vertical line is the time of sunset. Measurements were taken at 30-min intervals.

Thermal Characteristics of Rocks

On sunny days temperatures underneath rocks showed clear daily cycles due to radiant heating, and differences in thermal regimes of potential retreat sites were largely dependent on rock thickness and degree of shading.

Rock Thickness. Thick rocks heated more slowly than thin rocks, so that the thermal minima and maxima, and the times of day at which they were achieved, all depended on rock thickness (Fig. 5). For example, on a sunny day on October 31, 1994, maximum temperatures were negatively correlated with rock thickness ($r^2 = 0.74$; 1, 6 df; $P < 0.01$) while minimum temperatures were positively correlated with thickness ($r^2 = 0.55$; 1, 6 df; $P < 0.05$). Very thin rocks (<5 cm thick) achieved their thermal minima and maxima earlier in the day (typically, around 0600 and 1400 hours, respectively) than did thicker rocks (at 16 cm thick, typically around 0700 and 1700 hours, respectively). During spring, temperatures under thick rocks never warmed to the snakes' preferred range.

Thermal Heterogeneity in Retreat Sites. Some rocks provided more heterogeneous thermal microhabitats than did others. Snakes could potentially thermoregulate either by moving closer to the edges of rocks or by moving so as to maximize bodily contact with the upper surface of their retreat site (i.e., the underside of the overlying rock). On sunny days, rock temperatures were higher than substratum temperatures, while the reverse was true at night. The magnitude of this thermal difference depended on rock thickness. For example, on a sunny day on October 31, 1994, the maximum difference was 10.2°C for a rock 2 cm thick and only 5.4°C for a rock 16 cm thick. At night, rock temperatures were cooler than substratum temperatures, but the difference was much smaller (1.8°C under a 16-cm-thick rock vs. 2.4°C under a 2-cm-thick rock). Although we did not take continual measurements of edge temperatures under rocks, spot checks revealed that rock edges were often 3°C warmer than the center. Hence, there were distinct thermal gradients under rocks that snakes could exploit.

Shading. The degree to which a rock was shaded also affected its temperature. On sunny days, temperatures under shaded rocks were much cooler than those under unshaded rocks of similar thickness (see Fig. 5). For example, on October 24, 1994, diurnal (0800–2000 hours) temperatures under four shaded rocks (4–10 cm thick) were significantly cooler than those under exposed rocks of similar thickness (one-factor ANOVAs; maximum T_s: means of 25.0° vs. 30.9°C, $F_{1, 6} = 19.2$, $P < 0.01$; for average T_s: means of 21.3° vs. 24.7°C, $F_{1, 6} = 10.6$, $P = 0.02$; for maximum T_r: means of 26.3° vs. 40.3°C, $F_{1, 5} = 195.3$, $P < 0.001$; for average T_r: means of 22.1° vs. 30.9°C, $F_{1, 5} = 36.3$, $P < 0.01$). During spring, temperatures under shaded rocks never warmed to the snakes' preferred range.

Availability of Retreat Sites

Full details on the availability of snake retreat sites (rocks and crevices) are presented elsewhere (Webb and Shine 1998b), but key results are given here. Rocks exposed to full sun (with rock or soil substrata) were readily available to snakes (76.6% of all rocks were exposed). Thus, exposed basking sites were abundant on the sparsely vegetated cliff edge (Webb 1996). Because temperatures under rocks are largely influenced by weather and rock thickness, snakes trying to achieve set-point temperatures would have to select thin (15 cm thick) exposed rocks during spring. Although such rocks were reasonably abundant (32% of available rocks, see Webb and Shine [1998b]), very thin rocks (<4 cm thick) could still exceed T_{set} on warm spring days (see Fig. 5). Thus, in order to maintain set-point temperatures, the snakes have to choose retreat sites carefully.

Field Body Temperatures

We obtained a total of 7,801 body temperature measurements from 19 snakes (12 males, seven nongravid females) on 79

Table 1: Grand means of diurnal (0800 hours–sunset) and nocturnal (sunset–0800 hours) body temperatures of telemetered *Hoplocephalus bungaroides* recorded on sunny days

Season and Retreat Site	Day				Night			
	N	Mean	SD	Range	N	Mean	SD	Range
Spring:								
Rock	6	25.7	5.8	12.7–35.3	2	19.3	4.3	12.2–29.5
Crevice	10	25.6	5.1	13.7–34.8	1	22.2	3.6	14.5–31.0
Tree	3	24.2	5.5	11.4–34.9	2	17.8	3.6	10.5–30.5
Summer:								
Rock	1	26.7	3.9	18.4–35.0	1	22.6	3.1	18.0–32.3
Crevice	4	27.3	3.4	17.5–33.9	1	23.8	3.3	17.7–33.9
Tree	6	25.9	4.4	16.5–35.2	4	21.6	4.3	12.5–34.1
Autumn:								
Rock	1	20.8	3.8	12.8–28.8	1	18.1	2.6	12.6–26.6
Crevice	1	18.3	6.4	11.8–28.5	1	16.4	3.5	11.9–27.0
Tree	1	21.8	2.5	14.3–29.4	1	19.0	2.3	13.2–23.1

Note. Body temperatures of free-ranging broad-headed snakes were recorded during spring (September–November), summer (December–February), and autumn (March–May). Exact times for sunset were used; these ranged from 1700 to 1830 hours in autumn, 1740 to 1850 hours in spring, and 1850 to 1910 hours in summer. N = number of individual snakes for which we have at least 8 h of continuous data on body temperatures.

sunny days during the study (118 snake days, mean = 6.2 d/snake, SD = 8.0, range 1–30 d). Table 1 shows the grand means of body temperatures of telemetered snakes in the three most commonly used retreat sites (rocks, crevices, and tree hollows) during spring, summer, and autumn.

Effects of Season and Retreat Site

To investigate whether body temperatures of snakes varied with time of year or type of retreat site, we used a two-factor ANOVA with mean daily body temperatures from individual snakes as the independent variables. We restricted our analysis to spring and summer, the two seasons where we had large sample sizes. Mean body temperatures of snakes were significantly lower in spring than in summer (means of 25.2° vs. 27.5°C). The analysis revealed a significant effect of season ($F_{1, 24}$ = 6.7, P = 0.02), whereas the other factors (retreat site, interaction between season and retreat site) were nonsignificant. A similar analysis using minimum body temperatures of snakes also showed strong seasonal effects ($F_{1, 24}$ = 24.3, P < 0.0001), but no effects of retreat site or interaction between the two factors. Snakes had lower minimum body temperatures in spring than in summer (means of 15.0° vs. 21.6°C). Maximum body temperatures of snakes were similar in spring and summer (means of 32.0° vs. 33.5°C) and did not differ among retreat sites, with no significant interaction between the two factors.

Did snakes exhibit differences in nocturnal body temperatures between seasons or among retreat sites? A two-factor ANOVA using mean nighttime body temperatures of snakes as the independent variable revealed a barely significant effect

of season ($F_{1, 5}$ = 6.7, P = 0.05), with no effect of retreat site and a nonsignificant interaction term. Mean nocturnal temperatures of snakes were lower in spring than in summer (means of 19.1° vs. 23.2°C). Interestingly, minimum nocturnal body temperatures of snakes did not differ among seasons, whereas maximum body temperatures did ($F_{1, 5}$ = 10.5, P = 0.02). At night, snakes attained higher body temperatures in summer than in spring (30.8° vs. 26.3°C).

Effects of Weather and Time of Day

During cool, cloudy days, snakes had low body temperatures (<25°C) and showed the smooth pattern described by Peterson (1987). On sunny days, snake body temperatures varied depending on the type of retreat selected and the time of year. Snakes under rocks tracked heating and cooling rates of rocks (Fig. 1). In most cases, body temperatures of snakes under rocks only fell within the set-point range when the temperatures under rocks were within this range. In consequence, snake body temperatures often rose above the set-point range on warm days (Fig. 1). Because rocks heated more slowly than exposed snake models, maximum temperatures of snakes under rocks were not attained until after midday during spring and summer (Fig. 5).

During spring, many snakes selected crevices with westerly aspects near the tops of cliffs, and these were not exposed to direct insolation until after midday (see Webb and Shine 1998b). Snakes using these crevices did not attain preferred body temperatures until midafternoon (Fig. 2). During hot weather in summer, model temperatures deep inside (60 cm) cliff-top crevices with westerly aspects remained within the

snakes' set-point range for long periods of time (up to 17 h/d, see Fig. 2). However, during summer, the snakes selected crevices lower down the cliffs; these crevices were cooler than cliff-top crevices because of increased shading by vegetation (Webb and Shine 1998b). One snake that used a crevice halfway down the cliff basked early in the morning, and then retreated into the crevice to maintain temperatures within its set-point range (Fig. 2B).

During spring, snakes sheltering in tree hollows attained preferred body temperatures for relatively short periods of the afternoon (Fig. 3). For example, a snake that used a low-lying hollow branch near the cliff edge in November 1992 maintained a relatively high constant body temperature by moving along portions of the branch that lay in direct sunlight. Presumably snakes can maintain preferred body temperatures by exploiting thermal gradients within the hollows. During summer, snakes sheltering in tree hollows attained preferred body temperatures after midday, and occasionally snakes basked in direct sun before retreating inside their branches (Fig. 3). Snakes using tree hollows during summer consistently exhibited relatively high body temperatures at dusk (Fig. 3).

Degree of Exploitation of Thermal Environment

Whole Day. Body temperatures of 19 individual snakes were recorded on 91 different days. On 27 of these days (i.e., 29.7%), overcast or rainy weather prevented snakes from attaining body temperatures in their set-point range. During the remaining 64 d, continuous measurements of snake body temperatures and operative temperatures enabled us to calculate the number of hours per day that a snake in a given season could possibly achieve its set-point range, the number of hours that snakes actually did remain within this range, and the index Ex (the degree to which the snakes exploited their available thermal environment: see Christian and Weavers [1996]). The most striking result is that mean Ex indices were low (<50%) regardless of the type of retreat selected by snakes or the time of year (Table 2). However, variability among snakes was high, and four snakes never attained preferred body temperatures, although set-point temperatures were achievable.

When we compared the two seasons with large sample sizes (spring and summer), we found that snakes could potentially attain preferred body temperatures for longer periods during summer than spring (6.6 vs. 11.0 h; two-factor ANOVA: $F_{1, 21}$ = 13.6, $P < 0.01$). This analysis revealed a barely significant effect of retreat site ($F_{2, 21}$ = 3.6, $P = 0.05$, but post hoc tests showed no differences among the three types of retreat sites). Despite the strong seasonal effects, the mean time that snakes actually spent in their preferred range was not significantly different in spring or summer (1.9 vs. 3.1 h; two-factor ANOVA: $F_{1, 21}$ = 2.2, $P > 0.05$) or among snakes using different retreat sites, and there was no significant interaction between the two factors. In fact, Ex indices of snakes were remarkably similar in spring and summer (29.0% vs. 30.0%) and among

habitat types (see Table 2). During summer and spring, there was a highly significant positive correlation between the time spent by individual snakes in the set-point range and the time available for snakes to attain preferred body temperatures (r^2 = 0.86; 1, 26 df; $P < 0.0001$).

Dusk. Do snakes exploit the thermal environment more in the 2-h period around dusk than they do in the rest of the day? We used a paired analysis to compare Ex indices of individual snakes for dusk with the rest of the day. Overall, snakes had higher Ex indices around dusk compared with the rest of the day (59.9% vs. 25.6%; paired *t*-test: $t_{1, 26}$ = 3.64, $P = 0.001$). During spring and summer, snakes utilizing different retreat sites had similar Ex values around dusk (Table 2). Overall dusk Ex values for spring and summer were remarkably similar (41.6% vs. 41.0%). During autumn, Ex values for the whole day and dusk were generally low (Table 2), but the small sample size makes these results hard to interpret.

The Hertz Index

Do broad-headed snakes thermoregulate more carefully in the evening or are T_e's within the set-point range more abundant at this time? To investigate this question, we calculated the indices suggested by Hertz et al. (1993). If we consider the entire day, we find that broad-headed snakes do not thermoregulate very carefully (Table 3). In contrast, if we partition the day into three equal 4-h periods (morning, afternoon, and evening), a more complex pattern of thermoregulation is revealed. During the afternoon, the average deviation of T_e from T_{set} (i.e., d_e) was relatively low, so that even nonthermoregulating snakes would attain T_b's close to T_{set}. In contrast, during the morning and evening, average T_e's were below T_{set}, so that snakes would have to select specific microsites in order to attain T_b's close to T_{set}. Clearly, during the morning, snakes did not thermoregulate (d_b was much higher than d_e, Table 3). In contrast, snakes clearly thermoregulated during the evening (d_b was closer to T_{set} than d_e), and the value of E (0.53) suggests that broad-headed snakes were moderately effective thermoregulators at this time.

Behavior of Snakes in Retreat Sites

We routinely observed broad-headed snakes making subtle movements in their retreat sites during daylight hours (e.g., moving to the edges of rocks or crevices during the morning and afternoon). Clearly, the snakes could have extended the time spent in their preferred body-temperature range by basking, but they rarely did so. During 3 yr of fieldwork (513 observations of 25 radio-tagged snakes), we only observed snakes basking or part-basking (body loops extended from crevices or rocks) on 15 occasions (12 individual snakes, six males, six females). Thus, the relatively low Ex values for broad-headed snakes were related to the snakes' reluctance to bask,

Table 2: Mean time that body temperatures within the set-point range were obtained by free-ranging broad-headed snakes using three types of retreat sites in three different seasons

Season and Retreat Site	No. of Days	Time T_{set} Possible (h)	Time T_{set} Exploited (h)	Ex	% of Dusks T_{set} Possible	Dusk Ex
Spring:						
Rock (3)	10	6.3	3.1	49.2	66.6	92.4
Crevice (9)	4	7.4	1.8	24.3	75.0	49.7
Tree (3)	9	4.9	1.4	28.6	22.2	90.5
Summer:						
Rock (1)	7	10.6	3.3	31.1	71.4	47.6
Crevice (4)	9	13.8	3.7	22.5	100.0	82.6
Tree (7)	15	9.5	3.1	32.6	75.0	58.7
Autumn:						
Rock (1)	14	4.5	.1	2.2	57.1	.0
Crevice (1)	2	2.5	.3	12.0	50.0	50.0
Tree (1)	8	4.0	.1	2.5	25.0	.0

Note. Numbers of snakes using each type of retreat site for which we have body temperature data are listed in parentheses. The table shows the mean number of hours per day that set-point temperatures were achievable. The index Ex is the ratio of the two preceding columns (×100) and represents the percentage of the available time in the set-point range that is exploited by the snakes. The percentage of days with temperatures within the set-point range (T_{set}) at dusk (1 h before and 1 h after sunset) is also shown. The index Dusk Ex indicates the degree of exploitation of set-point temperatures around dusk by the snakes.

Discussion

The thermoregulatory behavior of *Hoplocephalus bungaroides* is very different from the precise heliothermic thermoregulation typical of diurnal lizards (Avery 1982). Many diurnal lizards bask in sunlight early in the morning and then shuttle between sun and shade in order to maintain relatively high and stable body temperatures (e.g., Bradshaw and Main 1968). In contrast, broad-headed snakes select thermally suitable retreat sites where they remain for entire days and sometimes even weeks (Webb and Shine 1997b). As a consequence of this relatively sedentary behavior, the snakes do not fully exploit the thermal opportunities available in their environment. During spring, snakes could maximize the time spent in their set-point range in two ways: they could move among rocks of different thicknesses at different times of the day or on days with different weather conditions (e.g., moving from a thin rock to a thicker rock on a hot day or at midday) or they could bask beside their retreat sites (rocks and crevices) during the morning and then retreat to their shelters later in the day. Basking in the morning followed by retreat to shelter sites is common among diurnal snakes (e.g., Peterson 1987) but rarely occurs in *H. bungaroides*. Our measurements of the availability of rocks in full sun coupled with T_e's show that snakes could easily achieve high body temperatures simply by basking beside rocks or crevices.

Basking may be rare because it involves significant costs or few benefits for this species (Huey and Slatkin 1976). These costs are clearly not related to a lack of thermally suitable microclimates, as is the case for many forest-dwelling lizards (e.g., Huey 1974; Huey and Slatkin 1976; Rummery et al. 1995). Instead, the exposed nature of the sandstone cliff edge means that basking (even relatively close to retreat sites) may substantially increase the risk of predation. Presumably, small snakes like *H. bungaroides* are vulnerable to birds of prey if they move

Table 3: Mean body (T_b) and operative (T_e) temperatures, deviations of body (d_b) and operative (d_e) temperatures from T_{set}, and E, the effectiveness of temperature regulation by broad-headed snakes using cliff-top habitats during spring

	Whole Day	Morning	Afternoon	Evening
T_b	25.6 ± .4	19.6 ± .5	28.9 ± .4	27.5 ± .4
T_e	26.8 ± .3	25.1 ± .6	30.9 ± .6	24.1 ± .7
d_b	3.7 ± .3	8.6 ± .5	1.5 ± .2	1.9 ± .3
d_e	3.4 ± .2	4.0 ± .4	2.2 ± .2	4.1 ± .4
E	−.08	−1.15	.32	.53

Note. Operative temperatures and body temperatures of nine snakes (three snakes under rocks, six snakes in crevices) were recorded every 30 min during spring. Values listed are means and SEs for the entire 12-h d (0830–2000 hours), morning (0830–1200 hours), afternoon (1230–1600 hours), and evening (1630–2000 hours). Note that $E = 1 − (d_b/d_e)$. Values of E close to one show careful thermoregulation, while values near zero show thermoconformity. Negative values of E suggest avoidance of set-point temperatures (see Hertz et al. [1993] for full details).

as can be clearly seen from the temperature profiles of snakes and models (Figs. 1–3). This lack of basking by broad-headed snakes was not due to lack of suitable basking sites since rocks exposed to direct sunlight were abundant on the cliff edge.

around on exposed cliff edges during the day. Numerous species of diurnal avian snake predators have been recorded in Morton National Park, including nine species of raptors (Fox 1988). At our study sites, kookaburras (*Dacelo gigas*), whistling kites (*Milvus sphenurus*), brown falcons (*Falco subniger*), and wedge-tailed eagles (*Aquila audax*) were commonly seen near the cliffs.

An alternative explanation for the broad-headed snake's low exploitation of the thermal environment is that maintaining set-point temperatures for extended periods during the day has few benefits. All of our radio-tagged snakes fed infrequently in the field (Webb and Shine 1998a) and were nongravid. Laboratory experiments have demonstrated thermophilic responses to feeding in several snake taxa (Peterson et al. 1993), but in the field, such responses may be modified by constraints imposed by the thermal environment (Peterson 1987; Beck 1996) or vulnerability to predators (Lysenko and Gillis 1980; Beck 1996). Indeed, available evidence suggests that careful, prolonged thermoregulation by snakes is most obvious in gravid females (e.g., Charland and Gregory 1990; Peterson et al. 1993; Reinert 1993; Charland 1995).

Because of the snakes' general immobility in retreat sites, they usually did not attain preferred body temperatures until after midday. For snakes under rocks, the delay was primarily due to the heating profiles of rocks and the high correlation between rock temperatures and snake temperatures (Webb and Shine 1998b). For snakes sheltering in crevices, the delayed heating was brought about by the snakes' reluctance to move outside their crevices and because the crevices they selected (those with westerly aspects) did not receive direct sunlight until after midday. Although we have no operative-temperature data for hollow tree branches, the snakes could presumably have basked outside the branches much earlier in the day. They did not. The overall effect of the delay in heating shown by broad-headed snakes was that their body temperatures were relatively high around dusk when nocturnal prey are most active. Similar diel patterns of thermoregulation, whereby animals delay heating until late in the day, have been documented in nocturnal fossorial skinks in the laboratory (Bennett and John-Alder 1986; Andrews and Kenney 1990). The most plausible explanation for the delay in heating shown by some nocturnal species, including *H. bungaroides*, is that high body temperatures around dusk facilitate foraging at that time.

During spring, broad-headed snakes in our study area fed mainly on one species of nocturnal gecko (*Oedura lesueurii*; Webb and Shine 1998a) that is most active around dusk (Schlesinger and Shine 1994). Hence, snakes with high body temperatures at this time would maximize their ability to capture prey because higher temperatures enable snakes to strike faster and more accurately (Fig. 4; see also Greenwald 1974). Velvet geckos also select "hot rocks" (Webb and Shine 1988a), and selection of such rocks by broad-headed snakes may increase their probability of encountering prey. Interestingly, the snakes' reluctance to move outside their retreat sites may minimize odor deposits that could alert velvet geckos to the snakes' presence (Downes and Shine 1998). During summer, the snakes fed on small nocturnal mammals (Webb and Shine 1998a). Snakes with high body temperatures may enhance their chances of capturing a fast-moving mammal that enters the same tree hollow as the snake. Elevated temperatures at dusk may also facilitate locomotor performance (at least for the first few minutes), thereby reducing vulnerability to avian predation (e.g., Christian and Tracy 1981).

In conclusion, our study suggests that broad-headed snakes may exploit the available thermal environment in a rather different fashion than do previously studied diurnal snakes (e.g., Peterson et al. 1993) and lizards (e.g., Christian and Weavers 1996). Our calculations of the degree of thermal exploitation suggest that the snakes' thermoconformity (i.e., its restriction to retreat sites and reluctance to bask) considerably reduces the proportion of time that the snakes spend within their preferred range of body temperatures. However, this restriction is actually quite minor for the time period (around dusk) that is likely to be most important biologically to these snakes (in terms of prey capture and the snake's ability to move between retreat sites). Thus, the snakes select retreat sites that enable them to attain high body temperatures around sunset. In this way, the snakes avoid the metabolic costs of maintaining high body temperatures throughout much of the day and the vulnerability to avian predation that could arise from basking in exposed positions. The extent of thermoregulation shown by these small ectotherms may be modified by environmental costs (such as risk of predation) as well as by the time-dependence of the benefits of attaining high body temperatures. This conclusion mirrors that from previous discussions (Huey 1974; Huey and Slatkin 1976).

In combination with previous work, our data suggest that reptile species may vary considerably in the degree to which individuals attempt to maximize the time spent in their preferred thermal range (e.g., Porter et al. 1973; Huey et al. 1989). In particular, many snake species may not thermoregulate precisely under field conditions, at least for much of the day. The proportion of nocturnal species tends to be higher in snakes than in lizards (Huey 1982), and reliance on diurnal retreat sites for thermoregulation is likely to be widespread among nocturnal snakes. We suggest that complex time-dependencies of thermal exploitation may well be a general feature of nocturnal reptiles. Diurnal species that are careful, precise thermoregulators have attracted most attention, but they represent only a subset—perhaps, a minority—of snakes. If indeed most snake species only thermoregulate actively when the benefits of doing so exceed the associated costs (e.g., Huey 1974; Huey and Slatkin 1976), we predict that simple optimality criteria (e.g., maintain body temperatures within the set-point range for as long a time as possible each day) will not be generally applicable to these animals. Additional studies on the thermal biology of nocturnal snake species would be valuable and would help to evaluate the generality of our results.

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