A reluctant heliotherm: thermal ecology of the arboreal snake *Hoplocephalus stephensii* (Elapidae) in dense forest

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Abstract

Dense forests exhibit little thermal heterogeneity, and hence pose substantial difficulties for behavioral regulation of body temperatures by ectotherms. The problems are exacerbated for nocturnally active secretive taxa that spend most of their time hidden deep within shaded retreat-sites, such as our study organism *Hoplocephalus stephensii* in wet sclerophyll forests and rainforests of near-coastal eastern Australia. In laboratory studies these elapid snakes selected temperatures around 28°C if these levels were available within retreat-sites, but rarely basked. Body temperatures of radio-tracked snakes in the field were well below these "preferred" levels, and generally around 24°C during the active season. Nonetheless, the radio-tracked snakes consistently maintained body temperatures slightly higher than shaded air temperatures, primarily by microhabitat selection (elevated tree hollows) and occasional covert basking. The snakes exploited higher radiation levels available in the tree canopy; a snake's height in the tree was positively correlated with its body temperature. Calculated thermoregulatory indices (Am. Nat. 142 (1993) 796) confirm the low thermal quality of the habitat, and the trend for snake body temperatures to fall midway between shaded air temperatures and the animals' set-point range. Thus, *H. stephensii* will bask covertly when conditions permit, but rarely do so in the field. Our study shows the potential danger of extrapolating laboratory observations of thermal preferenda to the field, and clarifies the thermal constraints influencing ectotherms in forest habitats.
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1. Introduction

Terrestrial ectotherms exploit an immense diversity of habitats, and thus experience a vast array of thermal environments. Especially in the mid-latitudes, operative temperatures during daylight hours may span a wide range, and the spatial scale of heterogeneity in these temperatures facilitates precise regulation of body temperatures. In particular, heliotherms that shuttle between sun and shade can maintain relatively high, invariant temperatures for much of the day. Thermoregulatory tactics in such animals have attracted intense

scientific scrutiny, with many studies emphasizing the precision and subtlety of temperature regulation (Huey, 1974, 1991; Peterson et al., 1993). Many habitats, however, impose substantial impediments to behavioral thermoregulation. For example, thermal heterogeneity may be very limited for animals that are active nocturnally, or occupy dense forests where direct sunlight rarely penetrates to the forest floor (Vitt et al., 1997). Such animals may thus be forced to forego precise thermoregulation, either because the costs would exceed the benefits (Huey, 1974; Huey and Slatkin, 1976) or more simply, because there is no opportunity to regulate temperatures behaviorally within this situation.

Despite the focus of most reptilian thermal studies on diurnal actively thermoregulating lizards (Avery, 1982), many taxa (including most aquatic ectotherms) have

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little opportunity to control their own body temperatures by behavioral means. For example, a high proportion of snake species are nocturnal, or spend much of their time hidden within retreat-sites that typically offer only limited thermal variation (Webb and Shine, 1998b; Kearney and Predavec, 2000; Kearney, 2002). What characteristics of thermal biology should we expect to see in such an ectotherm? One possibility is the evolution of passive thermoconformity, with the animals forgoing opportunities to bask and instead, selecting microhabitats without reference to their thermal consequences. For example, some lizards that inhabit dense forests display body-temperature regimes almost identical to shaded air (operative) temperatures recorded at random sites within the habitat (Rummery et al., 1995). At the other extreme, forest ectotherms may exploit transient patches of sunlight within the forest, and thus maintain relatively high, stable temperatures by selecting appropriate habitats and by expending substantial effort in thermoregulation (Vitt et al., 1997; Klingenbök et al., 2000).

Presumably, many forest ectotherms adopt a strategy intermediate between these two extremes, depending upon spatial and temporal variation in the costs and benefits associated with active thermoregulation (Huey, 1974; Huey and Slatkin, 1976). The thermoregulatory tactics of terrestrial ectotherms in dense forests will thus fall along a continuum from passive thermoconformity to behaviorally regulated stenothermy. If we are to understand the thermal challenges imposed by such environments, and the ways that animals have responded to those challenges, we will need detailed studies on environmental and body-temperature regimes of species covering a wide range of phylogenetic lineages, body forms and sizes, and ecologies. The present study provides such data for a hitherto poorly known study organism: a secretive highly arboreal elapid snake from dense forests in eastern Australia. We measured body temperatures of radio-tracked snakes together with shaded air temperatures, and also quantified thermal preferenda of captive animals. Using these data, we explore the degree to which these animals attempted to, and were able to, regulate their body temperatures in the face of the severe thermal challenges posed by this habitat.

2. Materials and methods

2.1. Study species

Stephen's Banded Snakes *Hoplocephalus stephensii* are slender to moderately built snakes found in coastal and hinterland forests from the central coast of New South Wales to south-eastern Queensland in eastern Australia. Maximum adult snout-vent length is ∼1 m and max-

imum mass is ∼250 g (Fitzgerald et al., 2002a). The species is arboreal, with prolonged sequestration periods in tree hollows during a ∼3 month overwintering period and for extended periods (mean = 8 days) during the active season (September–May; Fitzgerald et al., 2002b). Wildlife conservation authorities rate Stephen's Banded Snake as vulnerable in New South Wales and rare in Queensland. To obtain basic ecological data for *H. stephensii* and to identify possible impacts of silvicultural practices upon the species, we undertook a radio-tracking study in a forest principally managed for timber production.

2.2. Study area

Whian Whian State Forest (WWSF) 30 km north-east of Lismore in north-eastern New South Wales forms part of an 11,000 ha continuous tract of forest, including Nightcap National Park. Sixteen snakes were radio-tracked over varying periods (mean = 287 days, SE 43 days) from April 1997 to May 1999 at three sites with varied disturbance histories and forest types (wet sclerophyll forest; rainforest; or ecotones between these associations). Vegetation, topography and climate of the study area are described in detail elsewhere (CSIRO, 1996; Fitzgerald et al., 2002a; Fitzgerald, 2003).

2.3. Radiotelemetry

Snakes used in this study were captured on roads at night (9), while locating other radio-tracked snakes (5) or in trees (2). Radio-tracked snakes were adults (6 male, 10 female) measuring from 62 to 80.7 cm snout-vent length; snake mass varied from 70 to 149 g at the time of first capture. Snakes were surgically implanted with miniature temperature-sensitive radiotransmitters (Holohil Canada; BD2-GT1, PD-2T and SB-2T) following techniques used by Reinert and Cundall (1982) and modified by Webb and Shine (1997a, b) and Whitaker (1999). Transmitters were placed intraperitoneally; details of surgical procedures are provided elsewhere (Fitzgerald et al., 2002a). Before implantation transmitters were calibrated in a water bath at 5°C increments from 5°C to 40°C. Pulse intervals were measured in the field using a stopwatch whenever we located telemetered snakes, and later converted to temperature.

2.4. Laboratory study

We used a laboratory thermal gradient to identify thermal preferenda in a situation that allowed thermoregulation without overt basking. Five snakes containing radiotransmitters were placed alone and unfed in a 1.5 m long wooden cage designed to simulate a tree hollow. Perforations in the cage top provided limited illumination. Beneath-substrate heating and a suspended

150 W reflector lamp, both close to one end of the cage, produced a linear gradient from 18°C to 40°C on the cage substrate. Night temperatures fell to shaded air levels (16–18°C). Only daytime temperatures (0800–1800 h; $n = 83$) were used to establish the range of preferred body temperatures (T_b) because, as in the field, opportunities for elevating T_b were only available by day. Following the scheme developed by Hertz et al. (1993), the median 50% of daytime temperatures selected by five snakes was used as the set-point range (T_{set} range) to facilitate comparison with related studies (Webb and Shine, 1998a; Blouin-Demers and Weather-head, 2001).

2.5. Fieldwork

Snakes were released at their site of capture, generally <48 h after transmitter implantation. Monitoring took place every 2–3 days during the active season and less often during winter. At these times we also recorded shaded air temperature (T_a) at 2 m above the ground. Because direct sunlight rarely penetrates the canopy at this site, we use shaded air temperatures rather than temperatures inside physical models to estimate operative temperatures; in the absence of direct solar radiation the two methods provide identical results (Peterson et al., 1993). The only microhabitat in which models would have been appropriate was in exposed positions within the main canopy, but we were unable to access these sites (canopy height exceeds 35 m throughout most of the study site). We also placed data loggers (Hobo-temp; Hastings Data Loggers) in a tree hollow ($n = 1$, duration = 76 days in summer 1997–98) and at ground level (10 cm beneath ground surface, $n = 7$, average duration = 60 days in summer 1998–99).

3. Results

3.1. Thermoregulatory behavior of captive snakes

Captive *H. stephensii* exhibited long periods of inactivity, even during summer. Even very long term (>10 years) captives rarely emerged from their hide-boxes, and the only snakes that basked overtly were post-feeding, in late pregnancy, or in the few days prior to ecdysis. Even in those situations, snakes would rarely expose their entire body, and then only for brief periods (generally <10 min).

Nonetheless, captive snakes given access to a thermal gradient within the retreat-site selected relatively high daytime temperatures (21.6–34.4°C; $n = 83$; see Fig. 1). Most records were in a much narrower range; the median 50% bounds were 27.8–29.3°C (used as the T_{set} range in our subsequent calculations) and the median 75% bounds were 25.9–30.0°C. Individual mean values
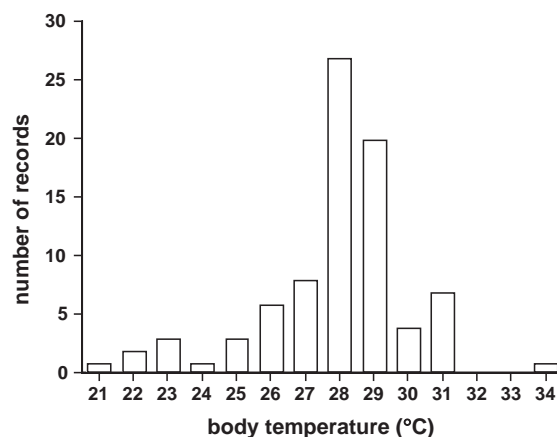

Fig. 1. Frequency distribution of daytime body temperatures selected by Stephens' Banded Snakes in a thermal gradient in the laboratory.

for daytime temperatures of five snakes were 26.9°C, 27.2°C, 28.2°C, 28.8°C, 29.2°C, and 29.2°C.

3.2. Environmental temperatures

Shaded air temperatures (T_a) at the study site exhibited significant variation among hours within the day, and more significant variation among seasons. Shaded air temperature during winter ranged from 8°C to 20°C with a mean of 15.5°C (SE 2.19°C), whereas the active season T_a ranged from 10°C to 29.5°C; overall mean value was 21.6°C (SE 0.10°C). Fig. 2 illustrates mean T_a as a function of season and time of day. To facilitate comparisons with body temperature, we calculated the mean shaded air temperature recorded when body temperatures were taken for each snake in each season (spring, September–November; summer, December–February; autumn, March–May; winter, June–August) and treated these as independent data points for the analysis. Statistical tests on these data showed that mean T_a varied significantly among seasons, and 2-hourly mean T_a varied significantly throughout the day (two-factor ANOVA with season and time interval as factors, season: $F_{3,167} = 71.91$, $P < 0.001$; 2-hourly time interval: $F_{4,167} = 5.60$, $P < 0.0001$; Fig. 2) but with no significant interaction between these two timescales ($F_{11,167} = 1.44$, $P = 0.16$).

Continuous records from data loggers also revealed low and relatively invariant environmental temperatures. Air temperatures measured hourly in an open vertical hollow 2 m above the ground in a live Crabapple tree (*Schizomeria ovata*) used by three of our radio-tracked snakes averaged 20.6°C (SE = 0.07°C), with a range from 13.4°C to 37.9°C (monitored 6 November 1997–20 January 1998). Mean daily temperature was 21.6°C (SE 0.10°C) and nightly mean was 19.5°C
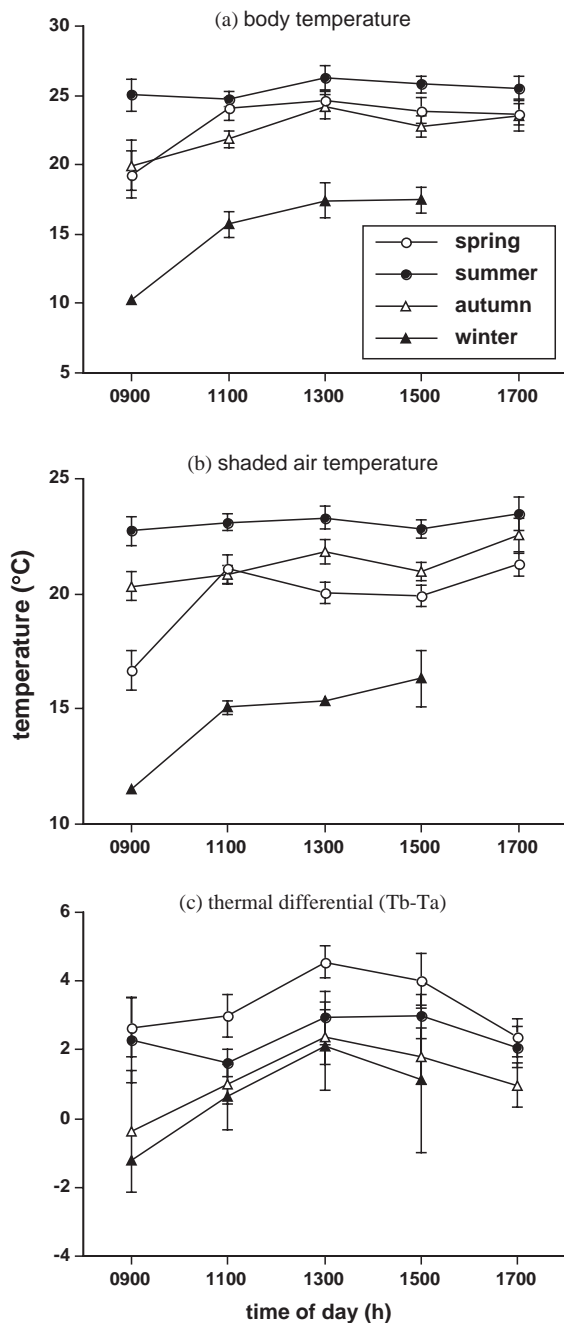
Fig. 2. Fluctuations in temperature regimes as a function of season (spring, September–November; summer, December–February; autumn, March–May; winter, June–August) and time of day (in 2-h blocks): (a) mean body temperatures of radio-tracked Stephens' Banded Snakes; (b) shaded air temperatures (shaded air measured 2 m above the ground, taken at the same time as telemetered snakes were located); and (c) disparity between snake body temperatures and simultaneously measured shaded air temperatures. Each data point shows the mean value for a telemetered snake over a single season (e.g. spring 1998).

(SE 0.08°C). Seven subsoil (10 cm) data loggers yielded similar values; mean values ranged from 19.4°C to 21.4°C over the period 8 February–9 April 1999.

3.3. Snake body temperatures: behavioral observations

H. stephensii spend most of their time hidden deep within secure retreat-sites, even during the active season (Fitzgerald et al., 2002a). Radio-tracked snakes were recorded as basking (exposed to solar radiation either directly or inside hollows exposed to the sun) on only 80 of 991 occasions when we located telemetered snakes during the active season. On 43 of these occasions snakes were seen openly basking. The other 37 cases involved snakes in concealed situations but with body temperatures substantially ($> 7.5^{\circ}$C) higher than shaded air temperatures. The latter observations were all of snakes in trees: 18 in trunk or branch hollows in dead stags, and 19 in upper canopy vegetation. Mean height above ground for these cases was 23.34 m (SE 5.51 m), with a range of 5–35 m.

Radio-tracked snakes were only recorded as active (moving or stretched out in a posture that indicated previous movement) on 44 of 991 (4.4%) active-season observations. When active during the day, snakes were mainly (68%) in terrestrial locations. Body temperatures of active snakes ranged from 12.8°C to 31.5°C with an overall mean of 22.0°C (SE 0.69°C, $n = 39$). Females were warmer than males at this time (female: mean 23.1°C, SE 0.67°C; male: mean 20.1°C, SE 0.98°C; one-factor ANOVA with sex as the factor: $F_{1,42} = 6.65$, $P < 0.05$). Snakes were active at shaded air temperatures from 15.5°C to 28°C, highly correlated with snake T_b ($r = 0.70$, $P < 0.001$, df $= 42$; see Table 1 for correlation analyses for overall data on individual snakes).

3.4. Temporal variation in snake body temperatures

H. stephensii in WWSF were generally active from September to May, after remaining inactive in tree hollows during winter (Fitzgerald et al., 2002a). Mean winter body temperature (T_b) for individual snakes varied from 13.2°C to 21.5°C, with an overall mean of 16.5°C (SE $= 1.04^{\circ}$C), close to T_a (mean 15.3°C, SE 0.16°C). Over the rest of the year (i.e. active season), the mean overall snake T_b was 24.0°C (SE $= 0.15^{\circ}$C; range of all records during the active season 11.1–37.8°C). Analysis revealed relatively little variation in snake body temperatures within the active season, the same pattern as recorded for shaded air temperatures. Fig. 2 illustrates that snake T_b was relatively low and similar to T_a. In seasons with low shaded air temperatures, radio-tracked snakes exhibited low body temperatures (using mean values per snake per season, $n = 57$, $r = 0.80$, $P < 0.001$).

Table 1
Correlations between height above ground and snake body temperature for radio-tracked Stephen's Banded Snakes

Snake ID (active season)	T_b vs. height above ground r; P-value	T_b vs. T_a r; P-value	$T_{(b-a)}$ vs. height above ground r; P-value	N
F121 (97–98)	0.81; <0.001	0.38; <0.05	0.55; <0.001	24
F200 (97–98)	0.01; >0.05	0.31; <0.05	0.22; >0.05	45
F200 (98–99)	0.34; <0.001	0.68; <0.001	0.57; <0.001	75
F019 (98–99)	0.60; <0.001	0.38; <0.05	0.56; <0.001	44
F141 (98–99)	0.36; <0.05	0.53; <0.001	0.40; <0.05	40
F190 (97–98)	0.33; <0.05	0.32; <0.05	0.59; <0.001	46
F978 (97–98)	0.098; >0.05	0.59; <0.001	−0.28; >0.05	47
F978 (98–99)	−0.15; >0.05	0.46; <0.001	0.13; >0.05	67
F299 (98–99)	0.23; <0.05	0.57; <0.05	0.43; <0.001	94
F338 (98–99)	0.50; <0.001	0.51; <0.001	0.35; <0.05	62
M919 (97–98)	0.32; >0.05	0.60; <0.001	0.58; <0.05	27
M919 (98–99)	0.21; >0.05	0.56; <0.001	0.39; <0.001	73
M271 (97–98)	0.29; >0.05	0.09; >0.05	0.29; >0.05	38
M938 (97–98)	0.21; >0.05	0.37; <0.05	0.35; <0.05	37
M938 (98–99)	0.19; >0.05	0.52; <0.001	0.30; <0.05	55
M057 (97–98)	0.35; <0.05	0.50; <0.001	0.50; <0.001	64
M057 (98–99)	0.09; >0.05	0.62; <0.001	0.28; <0.05	69
M351 (96–97)	0.52; >0.05	0.86; <0.001	0.42; >0.05	13
M351 (97–98)	0.33; <0.05	0.63; <0.001	0.28; >0.05	47

Note: Table shows results from least-squares linear regression of: (1) height above ground vs. snake body temperature; (2) body temperature vs. shaded air temperature; and (3) height above ground vs. extent to which body temperature exceeded shaded air temperature. These analyses were performed separately for data on each radio-tracked animal. In the column for Snake ID, sex is indicated by F = female, M = male. Active season shows years when snake was monitored.

Mean body temperatures of individual snakes varied significantly with time (two-factor ANOVA with season and time of day as factors, season: $F_{3,167} = 29.51$, $P < 0.001$; 2-hourly time interval: $F_{4,167} = 4.74$, $P < 0.002$), but with no significant interaction between these two timescales ($F_{11,167} = 0.58$, $P = 0.84$; see Fig. 2). The extent to which snake body temperatures exceeded shaded air temperatures (measured at the same time as the snake's temperature was determined) also varied with season ($F_{3,167} = 5.51$, $P < 0.002$) and time of day ($F_{4,167} = 2.84$, $P < 0.03$), with no significant interaction between these two timescales ($F_{11,167} = 0.20$, $P = 1.00$). In winter, snake and shaded air temperatures were lower, and more similar to each other, than was the case during the other seasons (Fig. 2). Body temperatures were similar throughout the active season, so that the lower shaded air temperatures in spring meant that the disparity between snake and shaded air temperatures was highest at this time of year (Fig. 2).

3.5. Sex differences in snake body temperatures

Overall mean body temperatures were higher for female (23.93°C) than for male (22.41°C) *H. stephensii*. A three-factor ANOVA incorporating snake sex as well as season and time of day showed that female snakes were consistently warmer than were males monitored at the same times (sex: $F_{1,150} = 6.94$, $P < 0.01$; main effects

of season and time of day similar to above; all interactions $P > 0.66$). Shaded air temperatures measured at the same times as these body temperatures did not differ between the sexes ($F_{1,150} = 1.13$, $P = 0.29$), and thus, the amount by which snakes were warmer than shaded air conditions was greater for females than for males ($F_{1,150} = 5.03$, $P < 0.03$; in both latter analyses, main effects of season and time have $P < 0.05$, but all interaction effects have $P > 0.56$).

3.6. Spatial variation in snake body temperatures

Given the low variance in shaded air temperatures within the study site (Fig. 2), the only arboreal microhabitat where snakes could potentially achieve much higher body temperatures was high in the trees, where the forest canopy was exposed to incident radiation. Hence, we focus on the relationship between snake body temperature and height above ground. Including winter, snakes were in arboreal positions on 82% of all observations (Fitzgerald et al., 2002a). Snake T_b was not correlated with height above ground during winter ($r = 0.12$, $P > 0.05$), but as predicted, snake T_b was correlated with height above ground during the active season (Fig. 3; mean body temperature vs. height above ground, $n = 9$ height categories, $r = 0.26$, $P < 0.001$). However, such a correlation could arise because of concurrent temporal variation in microhabitat
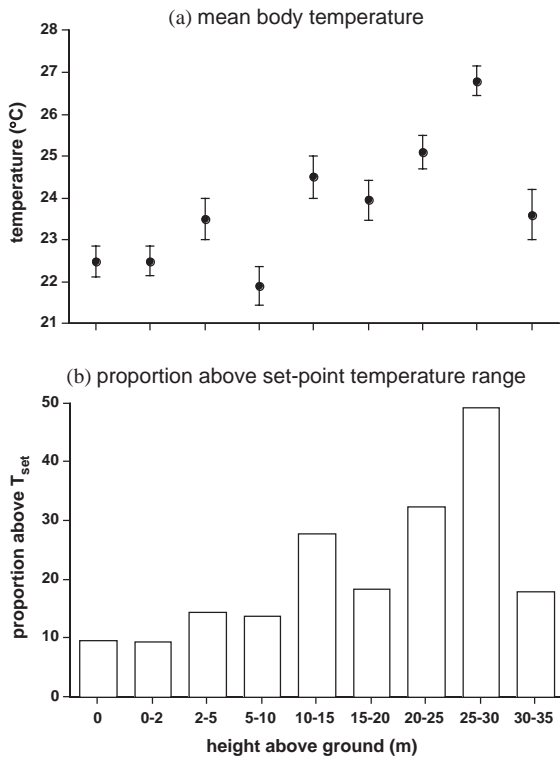
Fig. 3. Body temperatures of radio-tracked Stephens' Banded Snakes as a function of the height above ground at which the snakes were located when their temperatures were recorded by telemetry: (a) mean body temperatures for each height category; (b) proportion of all body-temperature records exceeding the snakes' set-point minimum temperature (27.8°C) as measured in the laboratory. See text for statistical analysis.

use and shaded air temperatures. To overcome this problem, we calculated correlations between height above ground and body temperature separately for individual snakes in each active season. The calculated correlations were statistically significant ($P < 0.05$) in 10 of 18 such data sets (snake-seasons), and the difference between T_b and T_a was significantly correlated with height above ground in 13 of 18 snake-seasons (Table 1).

3.7. Indices of thermoregulation

Hertz et al. (1993) suggested a series of indices to compare temperatures potentially available in the field to those exhibited by snakes either in the laboratory or in the field. While Hertz et al. (1993) use T_e as a measure of average available operative temperatures, we use T_a = shaded air temperature. To facilitate comparison between studies we retain d_e to represent the difference between T_a and the upper or lower bounds of T_{set}.

Where T_a falls within the bounds of T_{set} range $d_e = 0$. Thus, these methods enable us to quantify:

(a) *Thermal quality of the environment* ($[d_e]$, the extent to which shaded air temperatures $[T_a]$ deviate from the snake's set-point range $[T_{set}$ range] in the laboratory). Our field data show that the overall range of available temperatures on average fell $\sim 7.0°C$ below the snake's thermal preferenda with mean T_a values of 20.8°C vs. 27.8°C (the lower bounds of T_{set} range as measured in the laboratory). The difference between T_a and the lower bounds of T_{set} range during the active season (d_e) averaged 5.73°C; was greatest in winter (mean = 12.69-°C), and varied significantly between seasons (one-factor ANOVA with season as the factor, $F_{1,112} = 496.87$, $P < 0.001$). Thus, WWSF provides a challenging thermal environment with average shaded air temperatures much cooler than the snakes' T_{set} range.

(b) *Precision of thermoregulation* (variance in T_b). Variance overall for active season T_b was 23.1°C ($n = 991$; winter T_b variance = 20.0°C, $n = 123$). These high values suggest that *H. stephensii* do not thermoregulate precisely in the field.

(c) *Accuracy of thermoregulation* (d_b = difference between T_b and T_{set} range). Mean values for thermoregulatory accuracy varied among seasons (overall mean daily $d_b = 5.7°C$, active season mean = 4.7°C, winter = 11.4°C), indicating that the snakes did not thermoregulate precisely. They typically managed to remain about 3°C or 4°C warmer than shaded air temperatures, but remained about 3°C or 4°C below their thermal preferenda.

(d) *Effectiveness of thermoregulation* (extent to which T_b are closer to T_{set} range than to T_a). Hertz et al. (1993) use $E = 1 - ($mean $d_b/$mean $d_e)$ to measure this trait, where E = effectiveness of thermoregulation, d_b is the difference between T_b and the upper or lower bounds of T_{set} range, and d_e is the difference between T_a and the upper or lower bounds of T_{set} range. Mean d_b and d_e are used to calculate this index. "When animals do not thermoregulate, mean d_b and mean d_e will be similar and E will approach zero…when animals thermoregulate carefully and successfully, mean d_b will be smaller than mean d_e and E will approach one" (Hertz et al., 1993, pp. 802–803).

Blouin-Demers and Weatherhead (2001) argue that the ratio nature of this variable is less useful in quantifying the effectiveness of thermoregulation than a simple difference between d_b and d_e (i.e. $d_e - d_b$) which "…should be used to quantify the extent of departure from perfect thermoconformity". Because mean d_b is close to mean d_e in our study, the two methods of calculation provide very similar results; mean seasonal E values are strongly correlated with $d_e - d_b$ values ($r = 0.93$, $P < 0.05$, df = 4). Our data show that the temperatures exhibited by *H. stephensii* in the field are generally closer to shaded air temperatures than to the

snakes' set-point range (mean $T_b - T_a = 3.5°C$; mean $T_b - T_{set}$ range $= 5.7°C$). The Blouin-Demers and Weatherhead (2001) effectiveness of thermoregulation index $(d_e - d_b)$ varied significantly among seasons ($F_{5,969} = 18.5$, $P < 0.001$). Overall mean $d_e - d_b$ averaged 0.19 (active season $= 0.10$; in winter $= 1.3$).

(e) A non-parametric alternative index of the effectiveness of thermoregulation is the percentage of observations where $T_b \geqslant T_{set}$ range. Body temperatures $\geqslant$ the upper bounds of T_{set} range were recorded on 22.98% of 991 observations in the active season, and 1.6% of 123 observations in winter. Shaded air temperatures reached the range of set-point temperatures on only 0.05% of all records (0% in winter, 0.05% in the active season). Soil temperatures never reached the lower bounds of T_{set} range. Tree temperatures within T_{set} range were only available on 2.33% of observations ($n = 1801$).

4. Discussion

Our data paint a picture of a heliotherm that accords a low priority to precise thermoregulation, living in a habitat that gives little opportunity for such precision. The low body temperatures exhibited by free-ranging *H. stephensii* (especially relative to their thermal preferenda in captivity) thus reflect two separate but interacting phenomena. The first involves environmental constraint: heliothermy is difficult in the dense forests occupied by these snakes, because of the low degree of penetration of sunlight through the dense canopy. Sunny terrestrial sites are available but are rarely exploited by snakes, possibly due to the risks of predation in such locations. The second and equally important factor, however, is a characteristic of the study species: the snake's reluctance to expose its body in any overt basking. Although the study area offers relatively limited opportunities for frequent basking, some terrestrial reptiles at the same site maintain high and relatively invariant temperatures by overt heliothermy (e.g. land mullet *Egernia major*—Klingenbök et al., 2000; red-bellied black snake *Pseudechis porphyriacus*—Shine, 1987). In the case of *H. stephensii*, in contrast, the snake's dependence on covert rather than overt thermoregulation results in body-temperature regimes that fall midway between air temperatures and the snake's set-point range.

The mean diurnal body temperature for *H. stephensii* in the laboratory (28.4°C) was slightly lower than mean selected temperatures reported for 11 other species of Australian elapid snakes (29.4–34.5°C: Lillywhite, 1980; Greer, 1997, Table 7.9). The mean active season field T_b for *H. stephensii* (24.0°C) also lies close to the lower limit of mean field body temperatures reported for nine elapid species (23.4–31.1°C: Greer, 1997, Table 7.8). All of these taxa come from more southern latitudes, and

hence cooler climates, than the WWSF study area. For example, *Austrelaps superbus* and *A. ramsayi* from south-eastern Australia had mean active season T_b around 27°C (Rohr and Malone, 2001). Overall mean T_b for insular *Notechis scutatus* off South Australia was 25.5°C (Schwaner, 1989). Body temperatures of free-ranging red-bellied black snakes from three widely separated study areas in eastern Australia generally ranged from 28°C to 31°C (Shine, 1987). Thus, *H. stephensii* exhibited slightly lower body temperatures, both in the field and the laboratory, than did previously studied Australian elapids. Unfortunately, almost all of these taxa are diurnal, and higher body temperatures in diurnal than nocturnal elapid species is not surprising.

The most powerful comparison comes with other nocturnal elapid species. These have attracted little previous study, with the most extensive research focusing on a close relative of *H. stephensii*, the broad-headed snake *H. bungaroides* (Webb and Shine, 1998a, b). The comparison between these two congeners reveals similarities as well as differences. The median 50% of body temperatures of *H. stephensii* in a laboratory thermal gradient (T_{set} range $= 27.8–29.3°C$) were broadly similar to (but slightly lower than) those reported for *H. bungaroides* (T_{set} range $= 28.1–31.1°C$). Webb and Shine (1998a) report active season daily mean T_b of *H. bungaroides* in various retreat-sites ranging from 18.3°C to 27.3°C. Mean daily active season T_b for *H. stephensii* was 24.0°C; for *H. bungaroides* 25.6°C. Overall daily field T_b range was from 11.4°C to 35.3°C for *H. bungaroides* vs. 11.1–37.8°C. for *H. stephensii.* Like *H. stephensii*, *H. bungaroides* spends long periods sequestered in retreat-sites (including tree-hollows), and rarely basks overtly (Webb and Shine, 1998c). Unlike *H. stephensii*, however, *H. bungaroides* inhabits an environment of relatively open eucalypt woodland and sun-exposed sandstone ridges, which offer much greater thermal heterogeneity and, hence, the opportunity for snakes to attain body temperatures within their set-point range. Indeed, habitat selection by *H. bungaroides* is largely driven by thermal preferenda, at least during cooler times of the year (Webb and Shine, 1997b, 1998a, b), offering a remarkable contrast with *H. stephensii* in this respect. In parts of its geographic range where rock outcrops occur within forests, *H. stephensii* uses crevices under exfoliated rocks as retreat-sites (R. Withey, pers. comm.). The thermal biology of *H. stephensii* in such a site would be of great interest; based on our laboratory studies, we predict that the snakes would maintain high and relatively constant temperatures if such warm, protected sites were available.

Large hollow-bearing trees play a major role in the ecology of *H. stephensii*, with radio-tracked snakes moving between these (relatively scarce) large emergent

trees throughout the year and spending long periods within them (Fitzgerald et al., 2002a, b). Clearly, these trees provide several important benefits to the snakes, including food resources and protection from predators. However, our thermal data suggest that these large trees also offer the only opportunity for a secretive arboreal snake to attain relatively high body temperatures, by covert basking in hollows within the insolated canopy. The thermal significance of these large trees reinforces the importance of this dwindling resource for the conservation of viable populations of Stephens' Banded Snakes (Fitzgerald et al., 2002a); a stand of even-aged regrowth trees, no matter how dense, is unlikely to provide the kinds of thermoregulatory opportunities exploited by this species at WWSF.

The indices proposed by Hertz et al. (1993) provide a useful scheme to quantify aspects of the thermal interaction between ectotherms and their environment, and hence facilitate comparisons among studies. Our calculations using the Hertz et al. (1993) method did not incorporate any correction factors to allow for the fact that relatively large ectotherms do not heat and cool instantaneously. This thermal inertia means that a given shaded air temperature might deviate from operative (available) temperature if the former measure changes too quickly for the animal to reach thermal equilibrium (Hertz et al., 1993). Given the low rates of change in shaded air temperature in our study area, high rates of heat transfer in snakes because of their high surface area to volume ratio, and the small differences between shaded air and observed body temperatures, however, this imprecision should have little effect on our calculated values.

The reluctance of *H. stephensii* to expose itself fully to bask has interesting methodological implications. If our laboratory thermal gradient had been designed such that an animal would need to be exposed while basking (as is often the case), we would have concluded that *H. stephensii* is a thermoconformer or has low thermal preferenda. This conclusion in turn would affect the interpretation of field data. Instead, the reality is more complex. The major phylogenetic shift in thermal biology for *H. stephensii* relative to previously studied elapids is not in its acceptance of thermoconformity or tolerance of substantially lower body temperatures. Instead, it lies in the species' reluctance to engage in overt basking, combined with its occupancy of a thermal environment where covert basking opportunities are scarce. Thus, conclusions about the thermoregulatory tactics of this species will depend upon (1) the kind of thermal gradient used to assess thermal behavior in the laboratory; and (2) the nature of the habitat used for the field study (e.g. presence or absence of exposed rock outcrops). Changing either the laboratory setup or the field site would substantially modify our quantitative estimates of all the parameters in the Hertz et al. (1993)

model, as well as our overall conclusions about thermoregulatory tactics in the study species.

In terms of Huey and Slatkin's (1976) cost-benefit model for reptile thermoregulation, *H. stephensii* behaves as though overt basking entails a high cost and/or a low benefit. Both of these inferences are consistent with the species' ecology. Observations of captive snakes suggest that the benefits of basking are likely to be greatest for animals that have recently fed, are about to slough or are gravid (see above). The higher basking frequency of reproductive females may explain the trend for higher temperatures in this sex than in simultaneously monitored male snakes. Similar increases in basking frequency as a result of pregnancy, feeding and sloughing are probably seen in many other squamate taxa (Slip and Shine, 1988; Beck, 1996), but *H. stephensii* is unusual in that it feeds rarely, grows slowly (and thus, sloughs rarely) and females reproduce on a much less-than-annual schedule (Fitzgerald, 2003). Thus, the factors that enhance the benefits of basking apply infrequently to most free-ranging *H. stephensii*. Additionally, the movement pattern of *H. stephensii* (long-distance nocturnal forays through cool often-wet undergrowth: Fitzgerald et al., 2002b) mean that any advantages of high diurnal temperatures would be trivial at best, because the snake would rapidly equilibrate with shaded air temperatures as it moved across the forest floor. The congeneric *H. bungaroides* provides a strong contrast in this respect, because its foraging strategy (remaining immobile beneath a sun-warmed rock, lying in wait for active lizards) means that the snake can coil and thus retain heat (Ayers and Shine, 1997), and it remains in a warm microhabitat throughout the peak foraging period. Thus, high afternoon temperatures can influence the snake's ability to capture prey early in the evening (Webb and Shine, 1998a) whereas the ecology of *H. stephensii* means that elevated body temperatures during daylight hours do not confer such benefit.

The costs of basking may also be high for *H. stephensii*. Because it has a "slow" life-history (slow growth, late maturation, infrequent reproduction), theoretical models predict intense selection for any attribute that enhances survival rates of adults (e.g. Reed and Shine, 2002). Selection of lower body temperatures may confer advantages by reducing energetic costs (Huey, 1991; Peterson et al., 1993).

Predation is likely to be the most significant source of mortality in this population (Fitzgerald, 2003). The dorsal coloration of *H. stephensii* makes it highly cryptic against the forest vegetation, in keeping with this idea. No predators of this species are recorded, but diurnal potential predators include kookaburras, gray goshawks, lace monitors and red-bellied black snakes. Potential nocturnal predators include frogmouths, owls and quolls. Behavioral traits (such as long periods of

inactivity, and reluctance to leave retreat-sites during daylight hours) may reflect the same kind of selection. Even if predation is rare, adult *H. stephensii* may be unwilling to accept even a minor risk in exchange for higher temperatures.

More generally, much of the interspecific variation in thermoregulatory tactics among squamate reptiles may reflect differences in species-specific costs and benefits of thermoregulation rather than variation among habitats. A single environment often contains reptile species that exhibit a wide range of thermoregulatory strategies. This is true in WWSF, with reptile taxa running the gamut from thermoconformers (e.g. *Hypsilurus spinipes*—Rummery et al., 1995) through to diurnal heliotherms (*E. major*—Klingenbök et al., 2000; *P. porphyriacus*—Shine, 1987). Within this continuum, *H. stephensii* displays a facultative tactic whereby high body temperatures are selected only when the animal is able to do so without exposing itself to potential predators. These snakes select sheltered positions within large emergent trees where they can obtain access to solar radiation that is unattainable beneath the forest canopy, thus obtaining the benefits of higher body temperatures with low risk.

Acknowledgements

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