

Thermoregulation in a Nocturnal, Tropical, Arboreal Snake

NANCY L. ANDERSON,^{1,2} THOMAS E. HETHERINGTON, BRAD COUPE,^{1,3} GAD PERRY,^{1,4}
JOSEPH B. WILLIAMS,¹ AND JEFF LEHMAN⁵

¹Department of Evolution, Ecology, and Organismal Biology, The Ohio State University,
1735 Neil Avenue, Columbus, Ohio 43210, USA

³Natural Science Department, Florence A. Black Science Center, Castleton State College, Castleton, Vermont 05735, USA

⁴Department of Range, Wildlife, and Fisheries Management, Texas Tech University,
Box 42125, Lubbock, Texas 79409-2125, USA

⁵Department of Statistics, Ohio State University, 1958 Neil Avenue, Columbus, Ohio 43210, USA

ABSTRACT.—Few studies have focused on the thermal biology of tropical or nocturnal snakes. We recorded preferred body temperatures (T_b) of seven Brown Treesnakes (*Boiga irregularis*) in the laboratory and compared these to operative temperatures obtained with copper models and T_b s obtained by radiotelemetry from 11 free-ranging snakes on Guam. Operative temperatures on Guam did not vary across refuge types, unless the site received direct solar radiation. In a thermal gradient and on Guam, Brown Treesnakes thermoregulated around two distinct temperature ranges (21.3–24.9°C; 28.1–31.3°C). In the gradient, brown treesnakes exhibited elevated T_b into the higher range only in the evening. On Guam, snakes achieved T_b s in the high range only when direct solar radiation was available during the afternoon, a period when snakes were inactive. Higher mean T_b s on sunny days corresponded with observations of basking behavior.

There have been many field studies on the thermal biology of diurnal, temperate snakes (for review, see Peterson et al., 1993) but relatively few on tropical or nocturnal snakes (Shine and Lambeck, 1985; Secor and Nagy, 1994; Henderson and Henderson, 1995; Dorcas and Peterson, 1997; Webb and Shine, 1998; Luiselli and Akani, 2002). Selective pressures shaping thermoregulatory behaviors of ectothermic vertebrates are likely to be different in temperate versus tropical climates. It has been argued that, because of benign thermal conditions, and in contrast to their temperate relatives, tropical ectotherms may spend little, if any, time devoted to behavioral thermoregulation (Shine and Madsen, 1996). This hypothesis was based on studies of relatively large snake species, the Diamond Python (*Morelia spilota*) and the Water Python (*Liasis fuscus*), that exhibit high thermal inertia (Slip and Shine, 1988; Shine and Madsen, 1996). However, it seems likely that smaller tropical snakes with lower thermal inertia may display, and benefit from, thermoregulatory behavior. For example, four semiaquatic colubrid snakes from tropical Africa (*Natriciteres fuliginoides*, *Natriciteres variegata*, *Afonatrix anoscopus*, *Grayia smithii*) were able to maintain high and stable body temperatures (T_b s; mean T_b s: 28.3–32.7°C; SD = 2.5°C) with little thermoregulatory effort (Luiselli

and Akani, 2002). However, gravid females of these species maintained higher and more precise T_b s than nongravid female or male snakes and mean T_b was inversely related to length (SVL) in females, indicating that these tropical snake species thermoregulated under certain circumstances (Luiselli and Akani, 2002). Additional studies of a wider variety of tropical snakes are needed to provide a more complete picture of both the thermal problems confronting ectothermic reptiles and their evolved behavioral responses.

Brown Treesnakes (*Boiga irregularis*) are colubrid snakes native to Papua New Guinea, the Solomon Islands, Indonesia, and coastal Australia that were introduced to the island of Guam in the late 1940s (Rodda et al., 1999). Guam has a stable and moderate tropical climate, and Brown Treesnakes have become very abundant in areas of moist tropical forests on the island. On Guam, these snakes are chiefly arboreal, nocturnally active, remain in refuges during the day, and are catholic in their diet and foraging mode (Rodda et al., 1999). Because of their abundance on Guam and the relative ease of capturing individuals, the Brown Treesnake provides an excellent system for fieldwork on the thermal behavior of a tropical snake.

The only published information available on the thermal preferences of Brown Treesnakes is one study reporting gradients between head and deep body temperatures (1–2°C), mean thermal preference (34.8°C) and mean voluntary maxima (35.2°C) for two captive Brown Treesnakes

² Present address: Lindsay Wildlife Museum, 1931 First Avenue, Walnut Creek, California 94597; E-mail: nanderson@wildlife-museum.org

(Johnson, 1975). The goals of our study were to better document the thermal preferences of Brown Treesnakes and to determine whether these preferences affected diurnal refuge site selection of resting snakes. We accomplished this by comparing the thermal preferences of Brown Treesnakes in the laboratory in a thermal gradient, T_b s and refuge site selection of snakes in the field, and operative temperatures (T_o) measured with copper models placed in different types of refuge sites on Guam.

MATERIALS AND METHODS

Thermal Preferences.—We used seven Brown Treesnakes captured on Guam (four males, two females, one unknown; mean body mass [BM] = 286 g, range 145–914 g) for the thermal gradient study. Snakes were housed at Ohio State University for > 6 months prior to the experiment (air temperature [T_a] 24–29°C; 12:12 h light cycle) and fed one mouse every 2–3 weeks. Water was provided ad libitum, and snakes were fasted for 5–10 days prior to placement in the thermal gradient. We anesthetized each snake with a 5 mg/kg intracardiac dose of propofol (RapinoveTM, Mallinckrodt Veterinary, Inc., Mundelein, IL; Anderson et al., 1999) and implanted temperature-sensitive radio transmitters (model BD-2GT, Holohil, Corp., Canada) into the coelomic cavity (Reinert and Cundall, 1982) from one day to two weeks prior to placement in the gradient. The short recovery time was chosen to mimic conditions in the field study. Transmitters did not exceed 1.4% of BM and were calibrated in a water bath from 23–39°C at 4°C increments against a thermometer with a certificate traceable to the National Institute of Standards and Technology ($\pm 0.1^\circ\text{C}$). Linear regression of temperatures as predicted by the radio-transmitters and actual temperatures yielded R^2 -values ≥ 0.99 ; temperatures were accurate to within 0.1°C .

The thermal gradient was 1.71 m long and 0.6 m wide and was divided into nine equal (190 \times 600 mm) sections of increasing floor temperatures (range: 21–43°C; increments: 2–3°C). Each section was continuously heated with mylar heat tape (Bush Herpetological Supply, Neodesha, Kansas). Snakes were placed individually in a thermal gradient for periods of 5–7 days, between August 1997 and June 1998. Lighting in the room matched the natural photoperiod in Columbus, Ohio, and varied from approximately 10 h of light in the winter to 14 h of light in the summer. Because Brown Treesnakes usually seek enclosed refuge sites during the day on Guam, we provided contiguous hide boxes (190 \times 320 \times 105 mm) along one wall of the gradient. In pilot work, snakes were observed and videotaped moving from hide box to hide box and to leave hide boxes to drink from a water dish during

scotophase and photophase. Thermocouples were used to measure the floor temperature for each section. We used a Telonics receiver and an analog/digital converter (models TR-4 and TDP-2, respectively, Telonics, Mesa, Arizona) to measure the period between pulses of the radio-transmitters. Voltages from the TDP-2 and the maximum and minimum floor temperatures were recorded every 5 min with a data logger (Model LI-1000, Li-cor^R Lincoln, Nebraska). We used regression equations from water bath calibrations to convert pulse periods to T_b .

For data analysis, we partitioned, a priori, each 24-h cycle into three, 8-h periods beginning at 1800 h (dusk). We selected these periods to coincide with the natural activity patterns of Brown Treesnakes on Guam (i.e., 1800–0200 h: active foraging period; 0200–1000 h: end of foraging period and location of refuge site; 1000–1800 h: resting in refuge site [Rodda et al., 1999]). Body temperature patterns of gradient snakes fell into one of two distinct patterns described by Petersen (1987). Smooth T_b patterns showed little to no change in T_b ($\pm 0.5^\circ\text{C}$) over a 24-h period. During smooth patterns, snakes were mostly inactive but did move between adjacent hide boxes and left hide boxes to drink water. Such movements within the gradient were not associated with changes in snake T_b . Plateau T_b patterns were characterized by a short, rapid heating phase ($> 1^\circ\text{C}$ per 5 min) that coincided with snakes moving to hide boxes at the warm end of the gradient, followed by an extended period of elevated and stable T_b during which some snakes were videotaped exploring the entire gradient. Plateau patterns ended with an abrupt cooling phase. Because T_b changed so rapidly at the beginning and end of plateau patterns (maximum of 6.7°C in 5 min) we chose to collect temperature data every 5 min. To avoid pseudoreplication, we selected one “representative” 24-h cycle for each pattern for each snake. Because T_b patterns were repeatable within individuals, selection of any one 24-h period for each snake affected results by $< 1^\circ\text{C}$. We calculated mean T_b for smooth patterns from all T_b measurements recorded every 5 min for each 8-h time period for each snake. The preferred T_b range for plateau patterns was calculated as the mean of the maximum T_b and four 5-min sample points (two before and two after the maximum T_b) that a snake achieved during a plateau phase. This parameter minimized the damping effect derived from averaging T_b over 8 h when the elevated portion of the plateau phase was limited to < 4 h. Because normal probability plots showed that distributions of T_b data were normal, we used the grand mean $T_b \pm 2$ SD to determine the preferred T_b ranges for smooth and plateau patterns. We

TABLE 1. Results from models and factors tested by a SAS proc mixed model used to simulate operative temperatures of refugia occupied by Brown Treesnakes (*Boiga irregularis*) using operative temperatures recorded by representative copper models placed throughout the study site on Guam.

Models	Degrees of freedom	F-value	P-value	Tested factors
Time category	2	243.65	< 0.0001	Morning, afternoon, evening
Weather type	3	4.83	0.0042	Sunny, partly sunny, rain, other
Refuge site	11	16.22	< 0.0001	Full sun, underground, ground, tree, epiphyte, branch, Pandanus (multiple heights and thickness of fronds), Pandanus roots
Time category × weather type	6	8.98	< 0.0001	N/A
Time category × refuge site	22	40.22	< 0.0001	N/A
Weather type × refuge site	33	0.71	0.8636	N/A
Air temperature	1	4.87	0.0307	Continuous data

compared these ranges to the central 50% of all T_b s chosen by Brown Treesnakes for their entire stay in the gradient (set point temperature as defined by Hertz et al. [1993]) for both smooth and plateau patterns.

Validation of Copper Models.—Operative temperatures were measured using copper tubing (16 mm diameter, 1.5 mm wall thickness, 20 cm length) painted to match the estimated solar absorptivity of Brown Treesnakes using a flat gray paint (Sherwin Williams Province Blue flat exterior paint) as suggested by Peterson et al. (1993). To test the accuracy of the copper models in estimating snake T_b , we compared the temperature of a copper model to a live Brown Treesnake (134 g) implanted with one of the temperature sensitive radio-transmitters used in the field study. The copper model and snake (in a wire mesh enclosure) were placed outdoors on the grass in the sun on a partly cloudy day in Columbus, Ohio. Model and snake T_b were measured every 5 min for 60 min. Snake T_b varied by 2.5°C during the trial period. Snake temperature was on average 0.16°C less than the copper model, a nonsignificant difference (paired *t*-test, $P = 0.212$). We also tested four copper models against two Brown Treesnake cadavers (estimated body masses: 60 and 100 g) placed in a different location on partly shaded grass. We measured temperatures with thermocouples every 10 min for 50 min. The cadaver T_b and copper model T_e s were not significantly different (Friedman, $P > 0.133$). The temperatures of the cadavers and copper models remained between 34.1–34.3°C during the last 20 min of the trial.

Field Study Site.—This study was conducted in typhoon-impacted limestone rain forest in the Northwest Field region of Andersen Air Force Base (AAFB), Guam, from 6 November to 15 December 1997. The mean T_a and relative

humidity recorded at AAFB for this time period were 26.7°C (range: 23–32°C) and 72.3% (range: 40–100%; AAFB, unpubl. data). Rainfall averaged 4 mm/day (range: 0–52 mm) during the study (AAFB, unpubl. data).

To document the range of available T_e s at our study site on Guam, we placed copper models throughout the environment: direct sun (hottest), 300 mm underground (coolest), 10 m high in a thinly leafed deciduous tree, and 1.5 m high on a horizontal branch under typical forest canopy. We also positioned models in sites similar to refuge sites selected by snakes: Pandanus leaves (1.5–3.5 m height; most common refuge site [Anderson, 2002]), in the detritus collected in the cone shaped roots of Pandanus, on the ground under fallen logs, and inside the base (600 mm diameter) of an epiphyte. We logged all model temperatures every 30 min for 10–14 days with a Campbell data logger (Campbell Scientific, Inc., Logan, Utah). Opportunistically, we placed copper models in refuge sites after snakes left. We calculated the means, maxima, and minima for T_e for each site, and used a SAS proc mixed repeated-measures model with Bonferroni's correction ($\alpha < 0.05$) to test for effects of time category, weather type, refuge site, and T_a on T_e (Table 1).

Field Measurement of Snake T_b s.—We collected 10 female and one male, adult Brown Treesnakes using traps and visual surveys. We weighed snakes (BM = 115 g, range 99–140 g) with spring scales (0–300 g, Pesola™, Pesola, Switzerland), anesthetized them, and implanted radio transmitters as previously described. Transmitters were < 1.8% of BM. R^2 -values for linear calibration of transmitters were ≥ 0.99 ($\pm 0.1^\circ\text{C}$). To check for drift, we recalibrated three of four transmitters (one transmitter was not recovered; transmitters were reused during the

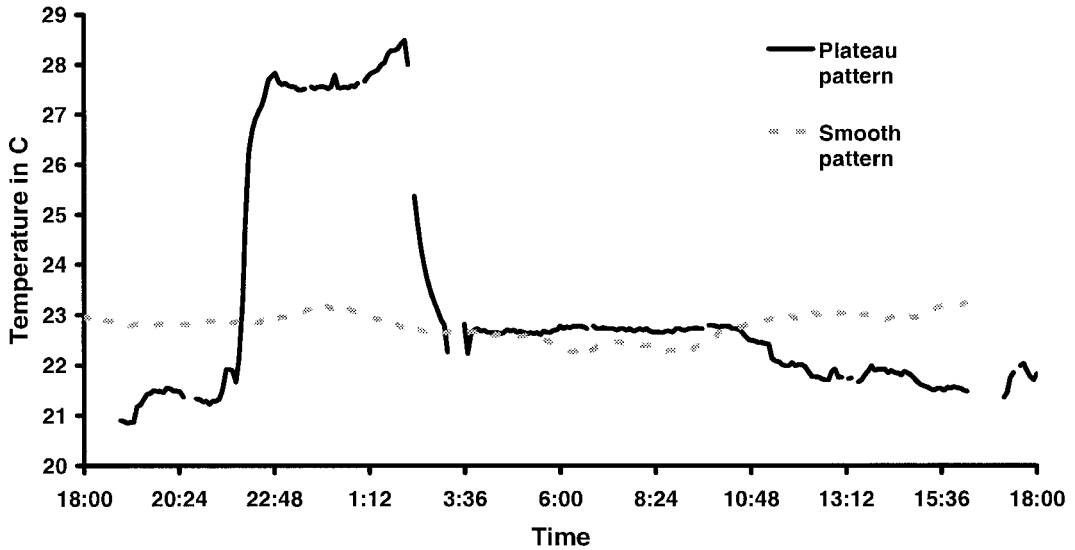


FIG. 1. Smooth and plateau body temperature patterns for a Brown Treesnake (*Boiga irregularis*) in a thermal gradient. Discontinuities in the plateau pattern line represent occasional lapses in data logger function.

study) at the end of the study ($R^2 = 1.0$). Drift accounted for temperature changes of $\pm 0.1^\circ\text{C}$. We returned snakes to the site of capture and released them by laying the untied snake bag on top of sturdy vegetation and allowing the snake to leave the bag on its own.

Starting the morning following release, we used a Telonics receiver and an analog/digital converter (models TR-4 and TDP-2, respectively, Telonics, Mesa, AZ) to record the period between pulses of the radio-transmitters three times a day (once in each of the following time periods: 0600–0830, 1130–1500, 1800–2200 h) for 9–13 days. We used regression equations from water bath calibrations to convert pulse periods to T_b . We calculated the means, maxima, and minima for T_b and used a SAS proc mixed repeated-measures model with Bonferroni's correction ($\alpha < 0.05$) to test for effects of time category and refuge type on T_b . We located snake refuge sites daily and recorded their position with a global positioning unit (± 2.2 m [Anderson, 2002]). Every 4–5 days, we captured each snake for weighing and palpation for stomach contents. We immediately released the snakes as described above.

Field behavior of snakes during this study appeared normal. Study snakes moved similar distances (mean = 47.1 m, SE = 7.2 m [Anderson, 2002]) to Brown Treesnakes in previous telemetry studies (mean = 54.0 m [Tobin et al., 1999]; mean = 43.8 m [Santana-Bendix, M.A., unpubl. data]), and distances moved did not change in response to surgery or handling (Anderson, 2002). All snakes maintained or gained weight during the study.

Comparison of T_e to Snake T_b .—We used a one-way analysis of variance (ANOVA) to compare snake T_b s to T_e s measured by “matched” copper models (models placed in the same type of refuge site, measured at the same time of day, under the same weather conditions, and with T_a within 0.5°C). To test for potential basking behavior, we used the following four ANOVA sample groups: snake T_b with and without direct solar radiation available and “matched” model T_e with and without direct solar radiation available.

We used a Licor data logger to record radio transmitter pulse intervals every 5 min for seven snakes for time periods ranging from 2–28 h. In four cases, simultaneous copper model data were collected from the same type of refuge site and other preferred refuge types located within 50 m of a snake. Interference from nearby military communications centers prevented more consistent continuous recording of snake and operative temperatures.

Unless otherwise stated, Minitab Release 13 (Minitab, Inc., State College, Pennsylvania) was used to perform statistics on all data. When an ANOVA was performed, we used a Tukey's correction for multiple comparisons ($\alpha = 0.05$). Statistical significance was set at $P < 0.05$.

RESULTS

Behavior of Snakes in Gradient.—Once established in the gradient, captive Brown Treesnakes showed two T_b patterns (smooth and plateau). Only smooth patterns were observed during the first 7 h of afternoon and last 7 h of morning time periods (Fig. 1). All snakes maintained T_b

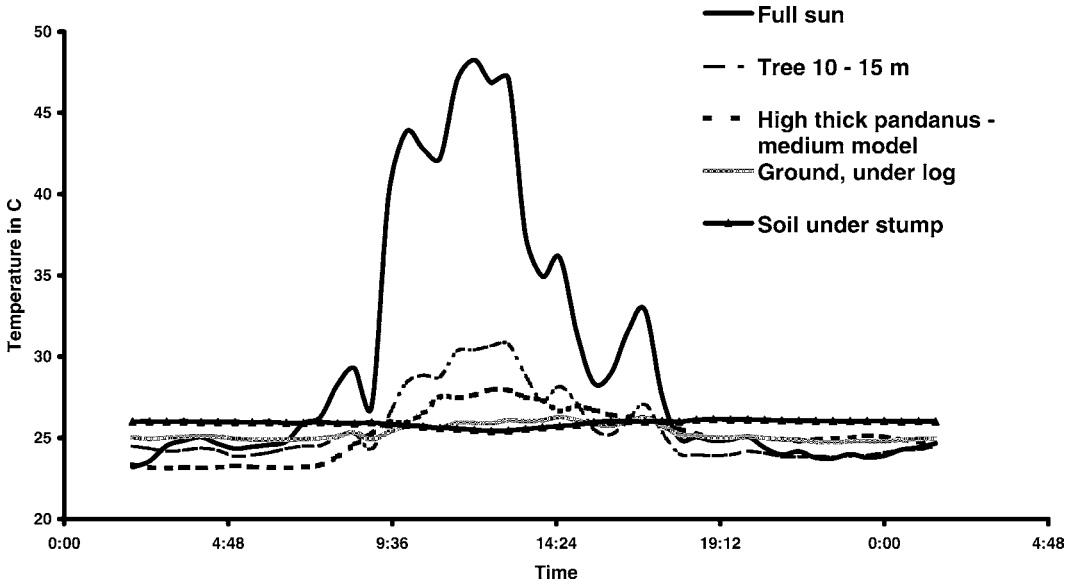


FIG. 2. Daily temperature variation of painted copper models placed throughout the study site on Guam. Model temperatures represent the operative temperatures available to Brown Treesnakes (*Boiga irregularis*) at the study site.

between 21 and 25°C during all smooth patterns. Four snakes showing smooth patterns were observed resting in the coolest section of the gradient for at least part of a day on 15 occasions; hence, these snakes may have chosen temperatures even lower than those provided in this experiment.

Plateau temperature patterns were observed in four snakes and only occurred once per 24-h period (between 1700 and 0325 h) for any individual. Plateau patterns commenced with a rapid rise in T_b ($\geq 3^\circ\text{C}$ in ≤ 15 min) and were followed by 3.5 ± 1 h where T_b was maintained between 28 and 32°C (Fig. 1). The end of the plateau pattern was defined as the time when T_b first rapidly decreased to the level observed in the smooth pattern. Frequency of plateau patterns varied from nightly to only once during the study period.

Normal probability plots indicated that T_b data were normally distributed. We used a one-way ANOVA to determine whether mean T_b during the smooth pattern varied between the morning ($N = 7$), afternoon ($N = 7$), and evening ($N = 7$) time periods. We found no difference between any time period ($P = 0.44$); thus, we used grand mean T_b measured during smooth patterns ± 2 SD to determine preferred T_b ranges during smooth patterns (21.3–24.9°C). This range was almost identical to the range of central 50% of all T_b measurements recorded during all smooth T_b patterns (first quartile: 21.4°C, third quartile: 24.9°C). The mean ± 2 SD for the preferred T_b

preference range for the plateau phase (28.1–31.3°C) was also virtually identical to the central 50% of all T_b measurements recorded during plateau patterns (first quartile: 28.2°C, third quartile 31.4°C).

Thermal Characteristics of Refugia on Guam.—Representative 24-h period T_e profiles of various sites on Guam are shown in Figure 2. The full sun model approached 50°C during midday, whereas T_e s measured under the forest canopy were more moderate (22–30°C) during daylight hours. At night, T_e s at all sites were similar (22–27°C; Fig. 2). The only statistically significant differences in mean T_e s between refuge sites occurred in the afternoon when the full sun model was warmer than all other models and the tree model was warmer than the soil, ground, and Pandanus root models (Table 2). In the morning and evening, all models (including full sun) were within 1.6°C of each other.

To evaluate the thermal quality of the environment, we compared T_e to preferred temperature ranges for smooth and plateau patterns. During the morning and evening, all models were $< 1.2^\circ\text{C}$ warmer than the preferred T_b range for the smooth pattern. In the afternoon, all models were 0.6–11.3°C warmer than the preferred T_b range for the smooth pattern. In the morning and evening, all models were cooler than the preferred T_b range for the plateau phase. For the afternoon, only the tree site was within this range; the full sun site was hotter, and the rest of the models were cooler. Therefore, preferred T_b

TABLE 2. Adjusted mean (calculated by repeated measures SAS proc mixed model), maximum, and minimum temperatures ($^{\circ}\text{C}$) of copper models (T_e) placed in sites representative of Brown Treesnake refugia. In addition, a copper model was placed in full sun site to represent the maximum afternoon environmental temperature. The "All" category results were calculated after combining the model data from different sites.

Site	Morning model temperatures			Afternoon model temperatures			Evening model temperatures		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum
All	20.86	24.92	39.99	23.88	27.73	50.85	21.61	24.96	29.41
Full sun	20.86	25.13	39.99	23.88	36.17	50.85	21.61	24.41	29.41
Underground/soil	25.43	25.93	26.20	24.9	25.53	26.15	25.59	25.95	26.21
Ground	23.51	24.83	25.74	24.89	25.75	28.96	24.11	25.02	26.26
Tree, 10 m	22.45	24.74	30.80	23.88	28.1	32.76	22.95	24.65	26.71
Epiphyte	22.69	24.53	27.08	24.38	26.0	29.1	23.24	24.75	26.31
Branch 1.5 m thin, high	22.24	24.65	28.64	23.98	27.62	31.77	22.89	24.97	26.48
<i>Pandanus</i> 3.5 m thick, high	21.80	24.85	27.62	24.22	27.46	29.54	22.24	25.0	26.42
<i>Pandanus</i> 3.5 m thick, low	22.11	24.83	27.17	24.26	26.94	28.14	22.82	25.08	26.42
<i>Pandanus</i> 1.5 m	22.07	24.82	26.89	24.28	26.91	28.44	22.76	25.13	26.51
<i>Pandanus</i> roots	22.34	24.72	25.87	24.16	25.56	26.39	23.27	24.8	25.6

for the plateau pattern was only available in sites located in direct sun (full sun, tree) in the afternoon time period.

Field Temperatures of Snakes.—In general, Brown Treesnakes used only the lower range of available T_e , taking advantage of the coolest available temperatures. Mean afternoon T_b was 1.1°C warmer than mean evening T_b ($SE = 0.30$, $P = 0.0003$) and 1.6°C warmer than mean morning T_b ($SE = 0.32$, $P < 0.0001$; Table 3). Mean evening T_b was 0.5°C warmer than mean morning T_b ($SE = 0.18$, $P = 0.006$; Table 3). The only significant difference in T_b between refuge sites within a time period was limited to the afternoon when snakes in *Pandanus*, vine, and ground sites were approximately 2°C warmer than snakes in underground sites. Above the ground within a time period, snakes experienced similar mean T_b regardless of refuge site. The means reported in Table 3 are adjusted means from the repeated-measures model that accounts for environmental factors. Therefore, if all datapoints for snake T_b s for a particular refuge type were collected under similar weather conditions (i.e., sunny days), the

model corrects for the average weather condition; thus, the adjusted mean may be outside the limits of the data collected.

In the afternoon and evening, average T_b s associated with the different refuge types were 0.2 – 4.0°C and 0.3 – 1.3°C warmer than the preferred T_b range for captive snakes displaying the smooth thermal profile. In the morning, T_b was 0.3 – 1.0°C warmer than the preferred T_b range for the smooth pattern except for snakes in tree, epiphyte, and ground refugia. Based on average T_b , only snakes in tree refuge sites achieved preferred T_b for the plateau pattern during any time period. However, individual snakes achieved T_b s within the preferred T_b range for the plateau pattern during 57% of afternoon time periods. The large variability in T_b s was associated with the availability of solar radiation (Fig. 3). Snake T_b was $> 1.0^{\circ}\text{C}$ over T_a only when direct solar radiation was available. In addition, mean T_b with direct solar radiation available was 1.3 – 1.9°C warmer than T_b (no direct solar radiation available) and T_e (with or without direct solar radiation available). No difference was observed

TABLE 3. Adjusted mean (calculated by repeated measures SAS proc mixed model), maximum, and minimum body temperatures ($^{\circ}\text{C}$) of Brown Treesnakes (T_b) in different types of refugia. The All category results were calculated after combining the T_b data from different sites.

Site	Number of samples	Morning snake temperatures			Afternoon snake temperatures			Evening snake temperatures		
		Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum
All	347	21.29	25.16	32.62	24.52	26.75	32.91	22.00	25.65	27.50
<i>Pandanus</i>	229	21.68	25.17	26.13	24.52	27.16	31.14	22.81	25.61	27.50
<i>Pandanus</i> roots	12	22.16	25.39	26.27	26.77	26.49	29.10	23.04	25.39	25.88
Vine mass	33	24.03	25.88	25.55	27.45	27.60	32.91	23.86	25.70	26.35
Bush	20	21.29	25.25	25.89	26.11	26.83	29.32	24.52	25.70	26.38
Tree	6	23.95	24.22	24.38	28.58	28.87	29.06	25.34	25.87	26.26
Epiphyte	7	24.16	24.60	25.02	25.18	25.19	26.61	24.85	25.57	26.04
Ground	24	21.97	24.91	27.12	27.11	27.82	32.06	22.00	25.16	26.26
Underground	16	23.69	25.84	25.88	24.76	25.07	28.57	24.31	26.20	26.25

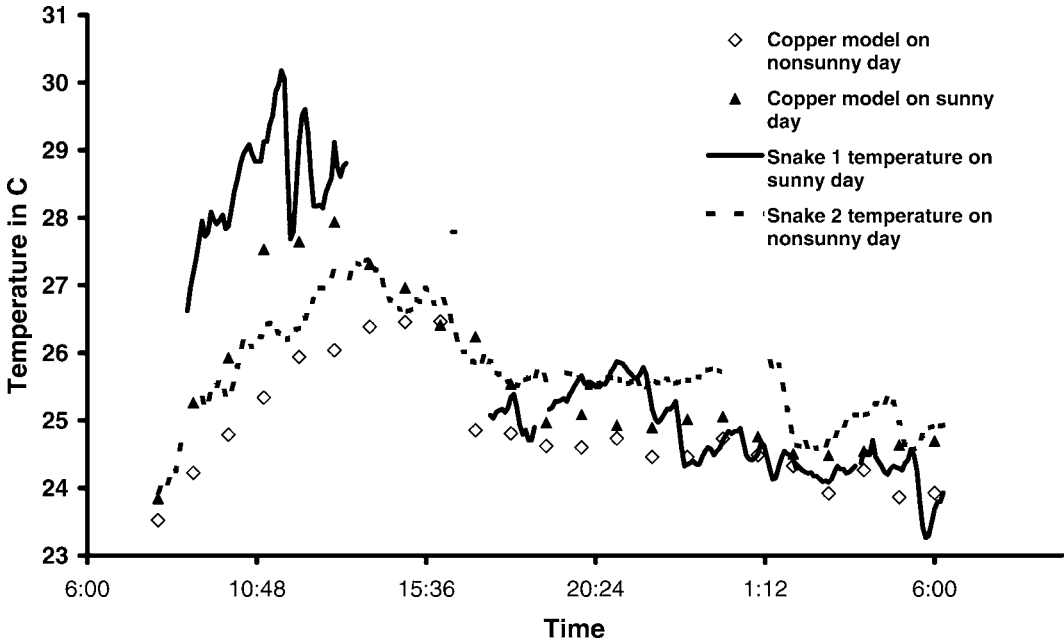


FIG. 3. Typical 24-h body temperature (T_b) traces from two Brown Treesnakes and operative temperatures from two copper models in *Pandanus* refuge sites on Guam. The T_b s from the warmer snake (B3) were recorded on a day with direct solar radiation available most of the day. The T_b s from the cooler snake (B1) were recorded on a day when there was significant cloud cover. Discontinuities in the plateau pattern line represent occasional lapses in data logger function.

between T_b when solar radiation was not available and $T_{e,s}$ whether solar radiation was available or not ($P < 0.0001$) indicating that snake use of solar radiation produced the temperature differences. Indeed, five Brown Treesnakes (six observations) with T_b s $> 0.6^\circ\text{C}$ above T_e were observed basking (i.e., loose loops of coils positioned outside the confines of refuge sites into direct sunlight) in the afternoon time period on sunny days. Basking behavior in Brown Treesnakes was easily recognizable and unusual because, aside from these six observations, the snakes were always tightly coiled in the most protected and thus shaded part of a refuge site. We did not observe this unusual posture on nonsunny days or in "cool" snakes.

DISCUSSION

Both our field and gradient findings suggest that Brown Treesnakes prefer T_b s below $35\text{--}36^\circ\text{C}$. This is in agreement with reports of snakes in general avoiding $T_b > 35^\circ\text{C}$ (Lillywhite, 1987). The preferred T_b range for captive snakes displaying smooth thermal profiles fell within the lower end of gradient T_b ranges reported for many snakes in a wide variety of genera (Lillywhite, 1987) and was similar to the range of field T_b s of the nocturnally foraging boid

Corallus enydris (Henderson and Henderson, 1995). Because of the limitations of $T_{e,s}$ offered by the gradient in this study, Brown Treesnakes might at times prefer even lower T_b s. The preferred T_b range for captive snakes displaying plateau thermal profiles was comparable to the general preferred T_b range for active snakes ($28\text{--}34^\circ\text{C}$) across taxonomic lines (Lillywhite, 1987) but was cooler than T_b s recorded from two basking Brown Treesnakes tested in an outdoor enclosure ($32\text{--}37.9^\circ\text{C}$; Johnson, 1975).

The two thermoregulatory patterns (smooth and plateau) displayed by captive Brown Treesnakes in this study were associated with mean T_b s differing by 6.8°C . Use of the mean of all gradient T_b s would have resulted in one mid-range, preferred T_b and a large SD that would not have described the observed bimodal thermoregulatory pattern. Although several studies of various species of snakes have reported different T_b patterns displayed by individual animals in the field in different circumstances (smooth, oscillating, inverted, plateau) and compared them to preferred T_b ranges obtained from gradient work, these studies did not provide detailed information about patterns of T_b s observed in captive snakes (Peterson, 1987; Dorcas and Peterson, 1997; Brown and Weatherhead, 2000; Whitaker and Shine, 2002). We

suspect that the thermoregulatory patterns of Brown Treesnakes observed in our thermal gradient may not be unique. More detailed observations of T_b patterns in gradients may find this phenomenon in other species as well.

Because snakes in a gradient have access to a wide variation of T_c without constraints, such as solar availability or predation, many researchers consider T_b s selected in a gradient to be the species' preferred T_b . Our captive snakes typically chose daytime temperatures cooler than, and nighttime temperatures warmer than, those available on Guam at the respective times. If indeed these gradient preferences represent preferred T_b s, there would appear to be a frequent mismatch between preferred and possible body temperatures of Brown Treesnakes on Guam that suggests that the environment imposes a temporal constraint on T_b . Alternatively, at least two studies (Cogger, 1974; Gregory, 2001) have suggested that captive reptiles choose cooler T_b s than conspecifics in the field. The authors attributed the difference to stress and a decrease in food consumption or body condition. Gregory (2001) found that gravid garter snakes (*Thamnophis sirtalis*) chose cooler T_b s than wild conspecifics, although he did not find a difference between T_b of captive and free-ranging gravid females of the closely related *Thamnophis elegans* living at the same study site. Cogger (1974) found that captive agamid lizards (*Amphibolurus fordii*) chose cooler T_b s, but food availability was markedly decreased in the captive population compared to the free-ranging populations. We suggest that the T_b preferences recorded in the gradient in this study were indicative of T_b preferences of free-ranging Brown Treesnakes on Guam because preferred T_b range for shady and sunlit patterns of the wild snakes were similar in magnitude to the captive snakes. The only difference between captive and wild Brown Treesnakes was the time that the snakes could achieve preferred T_b range for plateau patterns. In addition, the captive snakes in our study were probably under less stress than the food-deprived and gravid animals in the studies of Cogger (1974) or Gregory (2001). The nutritional state of Brown Treesnakes in the laboratory was similar to snakes on Guam and none of the snakes in our study were gravid. Also, after plateau temperature patterns, snakes in the gradient returned to the same preferred T_b range for smooth patterns and the variation in preferred T_b range for smooth patterns between all snakes was small, further indicating that snakes in the gradient were free to thermoregulate. Further research on Guam with a large naturalistic enclosure equipped with artificially heated and cooled refuge sites is needed to make a final determination of whether gradient temperature preferences of

Brown Treesnakes are similar to free-ranging Brown Treesnakes.

Our copper model data from Guam concur with Plummer's (1993) report from Arkansas that T_c s varied $< 1^\circ\text{C}$ in the forest understory during summer as well as with Stevenson's (1985) conclusion based on heat transfer models that the T_a in tropical forests varies as little as 1°C . It appears that in the shaded understory of tropical forests, the only option that arboreal snakes may have for significantly changing T_b may be to bask or retreat underground. We did observe basking behavior in Brown Treesnakes, and the higher mean T_b s we recorded on sunny days correlated with our observations that, on sunny afternoons, Brown Treesnakes position coils outside of refuge sites and into direct sunlight. These data provide evidence that the Brown Treesnake, a tropical species living in a warm, thermally stable environment, actively thermoregulates. However, not all tropical arboreal snakes may take advantage of opportunities to raise T_b by basking. Stephen's Banded Snakes (*Hoplocephalus stephensi*), arboreal tropical elapid snakes from eastern Australia, were not observed to bask even though the opportunity existed and consequently did not maintain high constant T_b s (Fitzgerald et al., 2002).

We also found little difference between T_a and T_c of matched refuge sites during the foraging period for Brown Treesnakes. This is likely true in other tropical forests, which suggests that moderately sized, tropical, nocturnal, and arboreal snakes may sacrifice little thermally by choosing to forage rather than remain in their arboreal refuge sites. Trade-offs in T_b were more significant for three species of nocturnal snakes living in temperate zones (Sidewinders, *Crotalus cerastes* [Secor and Nagy, 1994]; Rubber Boas, *Charina bottae* [Dorcas and Peterson, 1997]; and Broad-Headed Snakes, *Hoplocephalus bungaroides* [Webb and Shine, 1998]) whose subterranean or enclosed refugia were $5\text{--}10^\circ\text{C}$ warmer than surface temperatures. Our data suggest that there may be few thermal constraints on the behavior of actively foraging nocturnal snakes living in tropical climates. Luiselli and Akani (2002) provided comparable data demonstrating that four species of diurnal African colubrid snakes maintained relatively high and stable T_b s while active in an aquatic environment, a type of environment that often provides significant thermal challenges to temperate species of snakes (Blouin-Demers and Weatherhead, 2001).

More studies are needed on nocturnal, arboreal, and tropical snakes to better understand the selective pressures shaping the thermoregulatory behaviors of snakes. Future research should attempt to determine why some nocturnal snakes bask in the middle of the day. Basic information

about T_b -dependent parameters such as rate of digestion, metabolic rate, locomotory physiology and immune responses will be needed to begin to understand the costs and benefits associated with basking in nocturnally active snakes.

Acknowledgments.—This research was supported by funds from the Biological Resources Division of the United States Geological Service and the Kansas City Herpetological Society. S. Beaupre, C. Petersen, S. Secor, and M. Dorcas made invaluable comments on early drafts of the manuscript. We thank the United States Air Force for granting access to the study site and S. Kot and M. Doles for providing study animals. The research reported here complies with The Principles of Animal Care, publication 86-23 (revised 1985) of the National Institutes of Health (USA) and with current laws of the state of Ohio (USA).

LITERATURE CITED

- ANDERSON, N. L. 2002. Thermal Preferences, Metabolic Rate, and Water Flux of the Brown Treesnake (*Boiga irregularis*) in the Laboratory and on Guam. Unpubl. Ph. D. diss., Ohio State Univ., Columbus.
- ANDERSON, N. L., R. F. WACK, L. CALLOWAY, T. E. HETHERINGTON, AND J. B. WILLIAMS. 1999. Cardiopulmonary effects and efficacy of propofol as an anesthetic agent in Brown Tree Snakes, *Boiga irregularis*. Bulletin of the Association of Reptile and Amphibian Veterinarians 9:9–15.
- BLOUIN-DEMERS, G., AND P. J. WEATHERHEAD. 2001. Thermal ecology of Black Rat Snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology 82:3025–3043.
- BROWN, G. P., AND P. J. WEATHERHEAD. 2000. Thermal ecology and sexual size dimorphism in Northern Water Snakes, *Nerodia sipedon*. Ecological Monographs 70:311–330.
- COGGER, H. G. 1974. Thermal relations of the Mallee Dragon *Amphibolurus fordi* (Lacertilia: Agamidae). Australian Journal of Zoology 22:319–339.
- DORCAS, M. E., AND C. R. PETERSON. 1997. Head-body temperature differences in free-ranging rubber boas. Journal of Herpetology 31:87–93.
- FITZGERALD, M., R. SHINE, AND F. LEMCKERT. 2002. Radiotelemetric study of habitat use by the arboreal snake *Hoplocephalus stephensii* (Elapidae) in eastern Australia. Copeia 2:321–332.
- GREGORY, P. T. 2001. Feeding, thermoregulation, and offspring viability in gravid Garter Snakes (*Thamnophis sirtalis*): what makes laboratory results believable? Copeia 2:365–371.
- HENDERSON, R. W., AND K. Y. HENDERSON. 1995. Altitudinal variation in body temperature in foraging tree boas (*Corallus enhydris*) on Grenada. Caribbean Journal of Science 31(1–2):73–76.
- HERTZ, P. E., R. B. HUEY, AND R. D. STEVENSON. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. American Naturalist 142:796–818.
- JOHNSON, C. R. 1975. Thermoregulation in the Papuan-New Guinean boid and colubrid snakes, *Candoia carinata*, *Candoia aspera*, and *Boiga irregularis*. Zoology Journal of the Linnaeus Society 56:283–290.
- LILLYWHITE, H. B. 1987. Temperature, energetics, and physiological ecology. In R. A. Siegel, J. T. Collins, and S. S. Novak, (eds.), Snakes: Ecology and Evolutionary Biology, pp. 422–477. Macmillan Publ. Co., New York.
- LUISELLI, L., AND G. C. AKANI. 2002. Is thermoregulation really unimportant for tropical reptiles? Comparative study of four sympatric snake species from Africa. Acta Oecologica 23:59–68.
- PETERSON, C. R. 1987. Daily variation in the body temperatures of free-ranging garter snakes. Ecology 68:160–169.
- PETERSON, C. R., R. A. GIBSON, AND M. E. DORCAS. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. In R. A. Siegel and J. T. Collins (eds.), Snakes: Ecology and Behavior, pp. 241–314. McGraw-Hill, New York.
- PLUMMER, M. P. 1993. Thermal ecology of rough green snakes (*Opheodrys aestivus*). Journal of Herpetology 27:254–260.
- REINART, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. Copeia 3:702–703.
- RODDA, G. H., Y. SAWAI, D. CHIZAR, AND H. TANAKA. 1999. Problem Snake Management, the Habu and the Brown Treesnake. Comstock Publishing Assoc., Ithaca, NY.
- SECOR, S. M., AND K. A. NAGY. 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. Ecology 75:1600–1614.
- SHINE, R., AND R. LAMBECK. 1985. A radiotelemetric study of movements, thermoregulation and habitat utilization of arafura filesnakes (Serpentes: Acrochordidae). Herpetologica 41:351–361.
- SHINE, R., AND T. MADSEN. 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. Physiological Zoology 69:252–269.
- SLIP, D. J., AND R. SHINE. 1988. Thermoregulation of free-ranging Diamond Pythons, *Morelia spilota* (Serpentes, Boidae). Copeia 1988:984–995.
- STEVENSON, R. D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. American Naturalist 126:362–386.
- TOBIN, M. E., R. T. SUGIHARA, P. A. POCHOP, AND M. A. LINNELL. 1999. Nightly and seasonal movements of *Boiga irregularis* on Guam. Journal of Herpetology 33:281–291.
- WEBB, J. K., AND R. SHINE. 1998. Thermoregulation by a nocturnal elapid snake (*Hoplocephalus bungaroides*) in southeastern Australia. Physiological Zoology 71:680–692.
- WHITAKER, P. B., AND R. SHINE. 2002. Thermal biology and activity patterns of the Eastern Brownsnake (*Pseudonaja textilis*): a radiotelemetric study. Herpetologica 58:436–452.

Accepted: 5 November 2004.