When Basking Is Not an Option: Thermoregulation of a Viperid Snake Endemic to a Small Island in the South Atlantic of Brazil

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It is broadly accepted that snakes are able to regulate their body temperature (T_b) behaviorally, but fundamental differences in this ability have been suggested to exist between temperate and tropical species. Herein, we examined the thermal ecology of the Golden Lancehead, *Bothrops insularis*, a critically endangered Neotropical crotaline snake endemic to Queimada Grande Island (QGI), southeastern Brazil. We sampled T_b's of individual snakes found in the field and tested which proximal factors, biotic and abiotic, were potentially relevant for their thermoregulatory behavior and T_b selection. We verified whether T_b regulation would be compensated, through the day and/or seasons, by adjustments in the thermoregulatory effort. Finally, we hypothesized that for a Neotropical snake, the thermoregulatory effort would be lower because the thermal quality of habitat is higher compared to species inhabiting temperate zones. In general, *B. insularis* conformed to this hypothesis. However, seasonal declines in the thermal quality of habitat during the colder seasons and during nighttime were compensated by increases in the effectiveness of thermoregulation. Overall, T_b of *B. insularis* is determined largely by environmental variables, particularly air temperature, with some influence of biotic factors, such as body size. Use of open areas for basking, a common thermoregulatory behavior for squamates, was largely avoided; this may be explained by ecological factors, and may be due to foraging constraints and increased risks of predation and dehydration.

GIVEN the pervasive effects of temperature on most biological processes (Du et al., 2000; Hochachka and Somero, 2002; Zhang and Ji, 2004), studies focusing on thermoregulation are pivotal to understanding the ecology of ectothermic organisms (Huey, 1982; Angilletta, 2009). In terrestrial vertebrates, such as reptiles, body temperature (T_b) regulation is largely dependent on the heat gained from the physical environment. This regulation is achieved mainly through the behavioral choice of microclimates (Cowles and Bogert, 1944; Huey et al., 1989; Peterson et al., 1993), although physiological (Dzialowski and O'Connor, 1999) and morphological adjustments (Strugariu and Zamfirescu, 2009) may also play a role.

An ectotherm can either be a perfect thermoregulator (Cowles and Bogert, 1944), achieving nearly complete independence of body temperature from the prevailing ambient temperature, or a complete thermoconformer (Ruibal, 1961). However, the majority of ectotherms usually fit within an intermediate position between these extremes (Huey, 1974; Huey and Slatkin, 1976). Historically, the conceptualization of the thermal biology of reptiles was largely biased toward small diurnal lizards from temperate zones, which usually behave as active thermoregulators (Ruibal, 1961; Huey, 1982). This bias limited the appreciation of the complexity and diversity existing in the thermal interaction of reptiles with the physical environment (Cowles and Bogert, 1944; Pearson, 1954) and led to a simplistic view that most reptiles were ''good'' thermoregulators. A more accurate picture, however, started to emerge as new studies extended to other groups of lizards and snakes (Huey, 1982; Peterson et al., 1993), amphisbaenians (López et al., 2002), chelonids (Dubois et al., 2009), plus the incorporation of methodological and theoretical advances.

Particularly relevant, in this context, was the proposal and subsequent refinements of thermoregulatory indices (Hertz et al., 1993; Christian and Weavers, 1996; Brown and Weatherhead, 2000; Blouin-Demers and Weatherhead, 2001), which allowed for the quantitative comparison among different studies.

Currently, the information available on the thermal ecology of Neotropical squamates does not allow for a truly quantitative assessment of the thermoregulatory effort, which precludes a solid comparison between temperate and tropical species, whose thermoregulatory behavior was likely shaped by different selective pressures (Ruibal, 1961; Anderson et al., 2005). In tropical areas, squamates' T_b's may (Luiselli and Akani, 2002) or may not (Shine and Madsen, 1996) reflect traits associated with the life-history of the animals. For example, some forest species may forego opportunities to bask and instead select microhabitats without reference to their thermal characteristics (i.e., thermoconformity; Rummery et al., 1995; Webb and Shine, 1998; Fitzgerald et al., 2003), while others can exploit transient patches of sunlight within the forest (Vitt et al., 1997) and thermoregulate to some extent. Complicating the matter, depending upon spatial and temporal variation in the costs and benefits associated with active thermoregulation (Huey, 1974; Huey and Slatkin, 1976), intermediate strategies are adopted.

Herein, we investigated the thermal ecology of the Golden Lancehead, *Bothrops insularis,* a critically endangered crotaline snake endemic to the Queimada Grande Island, off southeastern Brazil. Our specific goals were twofold. Firstly, we aimed to identify the proximal factors potentially influencing snakes' T_b, climatic and/or biotic, and infer the possible ecological significance of its fluctuation

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through the day and seasons. Accordingly, we hypothesized that fluctuations in biotic and abiotic parameters, relevant to T_b regulation, would be compensated for, through the day and/or seasons, by adjustments in the thermoregulatory effort. Second, we calculated thermoregulatory indices for *B. insularis* to compare its thermoregulatory behavior with previous studies in other snake species aiming to identify possible benefits and constraints associated with different strategies/locations. Specifically, we tested the hypothesis that in Neotropical regions, the thermoregulatory effort would be lower because the thermal quality of habitat is relatively higher than in temperate zones. An additional motivation is the critical conservation status of the Golden Lancehead (Marques et al., 2004; Machado et al., 2005). This endemic, insular species has a small (less than 2,500 individuals) and declining population (Martins et al., 2008); thus, a better understanding of its thermoregulatory behavior and thermal habitat may prove critical in guiding *in loco* and/or *ex situ* conservation actions.

MATERIALS AND METHODS

Study area and study species.—The Golden Lancehead, *Bothrops insularis* (Squamata: Viperidae), is an endemic crotaline snake from Queimada Grande Island (QGI), off the coast of São Paulo state, southeastern Brazil (46°40′16.57″W, 24°28′35.59″S). The climate at QGI is classified as wet tropical ''Af'' type, according to Köppen-Geiger's system (Peel et al., 2007). *Bothrops insularis* is included within the ''*Bothrops jararaca* species complex'' together with another insular endemic, *B. alcatraz*, from the Alcatrazes Island (Marques et al., 2002a) and the common lancehead of the mainland, *B. jararaca* (Grazziotin et al., 2006). Although these three species are closely related, *B. insularis* differs in many anatomical and ecological traits from the two related species, and even from the majority of the other species of *Bothrops* (*sensu lato*, Amaral, 1921a; Martins et al., 2002; Wüster et al., 2005). Golden Lanceheads feed upon migratory passerine birds (Martins et al., 2001; Marques et al., 2002b, 2012) being highly arboreal (Martins et al. 2001) and predominantly diurnal (Amaral, 1921b; Duarte et al., 1995; Marques et al., 2002b). Moreover, Golden Lanceheads are relatively slender bodied and have a slightly prehensile tail (Martins et al., 2001).

Data collection.—We carried out the fieldwork on four expeditions (each five days long) in early June (autumn), late August (winter), mid December 2007 (spring), and early March 2008 (summer). Snakes were searched for along a north–south transect (~1500 m) at different times of the day. For each captured snake, we recorded biometrical data (snout–vent length, SVL; tail length, TL; body mass), sex, reproductive status, stomach content, microhabitat use, and time of the day. Before handling, we recorded posture according to Oliveira and Martins (2002; if snakes remained undisturbed after spotted) and made behavioral notes. At the exact place of capture, we also recorded relative humidity (%; Vaisala, Model HMI31), wind (m/s²; Minipa, Model MDA-10), luminosity (lux; Lutron LX-102), air (T_a; °C; ETI, Model EcoTemp), and substrate (T_s; °C; ETI, Model EcoTemp) temperature. Body temperature data was always the first measurement taken after the snake was captured, and this was made by inserting the probe of a digital quick-response thermometer (ETI, Model EcoTemp; 0.1°C resolution and

±1% precision) into the cloaca. Body temperature readings were accepted as valid only if the record occurred within 30 seconds after the beginning of capture. To avoid pseudoreplication, snakes were marked with subcutaneous ID microchips (Trovan, ID-100).

Operative environmental temperatures (T_e).—We sampled operative temperatures using physical models constructed with water-filled copper pipes, 40 cm long and 4 cm in diameter. Models were painted with golden metal paint to approximate the reflectance of Golden Lancehead snakes (Peterson et al., 1993). We verified the accuracy of these models by comparing their thermal profile to a freshly dead snake, *B. jararaca*, with body proportions similar to *B. insularis*. Snake carcasses and the copper model temperature were sampled under a variety of conditions for heat exchange/equilibration likely to occur in the wild (exposed, sheltered, during sunny or rainy days). Temperature readings were taken every 15 min for 24 h using a temperature datalogger (Tidbit, Hobo, Onset) previously inserted inside the snake carcass and in the model. Carcasses and models temperatures were highly correlated (Pearson linear regression, snake carcass = −0.0350 + (0.990 * T_e model), r^2 = 0.973; $F_{1,90}$ = 3205.9; P < 0,001), indicating that our physical models were adequate for sampling operative temperatures (T_e; see Brown and Weatherhead, 2000; Row and Blouin-Demers, 2006).

At the beginning of the study, eight physical models were distributed at the QGI to continuously sample the available T_e's in the most representative thermal sites available to *B. insularis* (see Row and Blouin-Demers, 2006). We placed these physical models fully exposed to solar radiation in an open area of QGI (at different orientations), on the ground inside the forested area in full shade, and at 1, 2, 5, and 7 m heights onto the arboreal stratum where some individuals were seen previously. The temperature of the models were sampled every 15 min using dataloggers (Tidbit, Hobo, Onset) previously inserted into them. Only the records taken during the months in which fieldwork was carried out were used to calculate mean, maximum, and minimum values of T_e per season (Table 1).

Preferred body temperature (T_{set} interval).—Preferred body temperature is usually determined in thermal gradients in the laboratory. However, because we were not allowed to remove specimens from the island (according to the current Brazilian legislation), we measured the T_{set} interval of *B. insularis* in a thermal gradient built in the field, similar to the method used by Shine et al. (2002; see also Hertz et al., 1993). Our thermal gradient was built in a 123 × 233 cm area limited by 100 m high concrete walls (an abandoned water reservoir), top-covered with canvas (Sombrite) to homogenize light level and prevent the snakes from escaping. The ground was covered homogeneously with 3–5 cm of local forest litter. A temperature gradient was created by two electric heater/fans (Mondial A-02, 1500 W) placed at the opposite ends of the arena. One of these units had the ventilation and heating function turned on, while the other had only the ventilation. Under our field conditions, the temperature gradient was influenced by the time of the day and by season. Thus, during winter our gradient temperature attained minimum and maximum temperatures varying from 24.5°C to 34.5°C (for the time interval between 1200 and 1500 h) and from 19.8°C to 28°C (from 1500 to

Table 1. Operative Environmental Temperatures (T_e; mean $\pm$ SE, maximum, and mininum values), and Thermal Quality (d_e; mean $\pm$ SE, and maximum values) of the Four Main Habitats Available to *Bothrops insularis* at Queimada Grande Island throughout the Seasons (°C). Percentage equal to zero (% = 0) or higher (% > 0) indicate the proportion of time in which T_e equaled or exceeded T_{set}, respectively.

Season Habitat	T_e			d_e		% = 0	% > 0
	Maximum	Mean	Minimum	Mean	Maximum		
Autumn							
	46.3	21.7 ± 0.16	12.2	5.1 ± 0.18	24.3	4.8	27.9
Forest–ground	28.3	19.7 ± 0.05	15.3	2.3 ± 0.05	6.2	6.7	23
Forest–1 m	28.7	19.4 ± 0.05	15.1	2.6 ± 0.09	6.4	6.1	22.4
Forest–2 m	30.1	18.7 ± 0.07	14.5	2.9 ± 0.09	6.6	4.9	12.8
Forest–5 m	29.1	18.4 ± 0.05	13.6	3.2 ± 0.06	6.7	5.4	18.6
Forest–7 m	29	19.5 ± 0.05	14.7	2.5 ± 0.06	7.3	1.2	28.3
Winter							
Open area	44	19.2 ± 0.13	9.9	5.8 ± 0.15	22.1	2.5	24
Forest–ground	29.4	16.9 ± 0.03	13.8	3.8 ± 0.05	7.6	1.9	4.3
Forest–1 m	31.1	16.6 ± 0.04	13.3	4.3 ± 0.05	9.5	1.4	5.5
Forest–2 m	30.7	17 ± 0.08	12.9	4.2 ± 0.05	9.1	2.2	9.6
Forest–5 m	30.1	15.7 ± 0.05	12.2	5.2 ± 0.07	8.5	1.4	5.4
Forest–7 m	31.8	16.8 ± 0.05	13	4.3 ± 0.06	9.9	1.7	6.9
Spring							
Open area	55.6	27.2 ± 0.14	14.8	8.1 ± 0.51	29.3	7.2	46.5
Forest–ground	35.2	24 ± 0.04	20.1	2.1 ± 0.08	4.8	21.8	15.5
Forest–1 m	36.3	23.7 ± 0.05	19.8	2.3 ± 0.09	8.5	15.4	12.7
Forest–2 m	36.7	23.5 ± 0.05	18.8	2.5 ± 0.08	6	10.2	20.3
Forest–5 m	33.7	22.6 ± 0.04	18.3	2.8 ± 0.1	6.5	12.8	7.6
Forest–7 m	35.1	23.8 ± 0.04	19.4	2.6 ± 0.09	5.4	19.5	16.6
Summer							
Open area	50.9	27.5 ± 0.11	20.9	3.9 ± 0.19	24.3	10.9	39
Forest–ground	31.8	23.7 ± 0.03	19.8	1.8 ± 0.04	5	12.7	10.6
Forest–1 m	30.4	23.4 ± 0.03	19.5	2 ± 0.05	5.4	10.7	7.9
Forest–2 m	30.7	23.3 ± 0.04	18.8	2.4 ± 0.05	6	7.4	13.2
Forest–5 m	29.8	22.5 ± 0.03	18.3	2.8 ± 0.05	6.4	8	6.4
Forest–7 m	33.6	24 ± 0.04	19.7	2 ± 0.05	6.4	5.3	21.6

1800 h); during summer the gradient ranged from 25.5°C to 38°C (from 1200 to 1500 h) and from 24.8°C to 35.8°C (from 1500 to 1800 h).

In winter and in summer, four (SVL = 705 ± 18.8 mm) and three (SVL = 580.3 ± 44.4 mm) adult non-reproductive Golden Lanceheads, respectively, were placed in the arena (between 1000 to 1200 h) and allowed to acclimatize for two hours. Thereafter, we recorded their skin T_b's, at mid body, every 15 minutes for three hours (between 1400 to 1800 h) with an infrared thermometer (ETI–TN2; 0.2°C resolution and ±2% precision) to avoid the disturbance of multiple cloacal measurements. Also, we had previously verified that superficial and core temperatures of snakes not exposed to intense radiative heat exchange rates (as during basking) were not significantly different. Sampling period was planned to coincide with the time that *B. insularis* is most active (Amaral, 1921b; Duarte et al., 1995; Marques et al., 2002b).

We used the 25% and 75% quartiles as the lower and upper temperatures delimiting the preferred temperature interval (Hertz et al., 1993). The amplitude of the T_{set} recorded in winter and in summer differed considerably (see Results), and, therefore, we attempted to calculate all thermoregulatory indices separated by seasons. Since preferred body temperature could not be determined for the

autumn and spring, due to logistic limitations, we assumed that values calculated for the winter and summer, respectively, were valid for those seasons.

Thermoregulatory indices.—The following indices were used to evaluate the thermal quality of each microhabitat, the accuracy of thermoregulation (i.e., extent to which field T_b's overlap T_{set} interval), and the effectiveness of thermoregulation (i.e., improvement of accuracy with respect to non-regulating models; see Hertz et al., 1993 for a detailed discussion):

(a) Thermal quality of habitat (d_e): computed as the mean of the absolute values of the deviations of T_e's from T_{set} interval (d_e = [T_e−upper limit of T_{set}] for T_e's above T_{set} interval, d_e = [lower limit of T_{set}−T_e] for T_e's below T_{set} interval, and d_e = 0 for T_e's within T_{set} interval).

(b) Accuracy of thermoregulation: d_b (same as above but for measured T_b's).

(c) Effectiveness of thermoregulation of Hertz et al. (1993): $E = 1-(d_b/d_e)$.

The value of *E* generally ranges between 0 (when snakes do not thermoregulate and their deviations from preferred range are similar to those of models) and 1 (when snakes

thermoregulate carefully and their deviations from preferred range are much smaller than those of models: Hertz et al., 1993). Considering a possible constraint of the E of Hertz et al. (1993; see Blouin-Demers and Weatherhead, 2001 for details), we also used another index of effectiveness of thermoregulation ($E = d_e–d_b$; Blouin-Demers and Weatherhead, 2001). In E of Blouin-Demers and Weatherhead (2001), positive numbers represent animals that thermoregulate to some extent, zero represents perfect thermoconformity, and negative values represent animals that avoid thermally favorable habitats (Blouin-Demers and Weatherhead, 2001).

Statistical analyses.—Before running any parametric test, the premises of normality and homoscedasticity were checked, and in the case they were violated, data were log (base 10) transformed. If even after log transformation the data persisted in violating the assumptions required by the parametric tests, non-parametric procedures were applied on the original values. All statistical tests were performed in the R program (R Development Core Team, 2009), and, unless otherwise noted, data are presented as mean ± standard error (SE).

We used a multiple regression model to test the influence of environmental factors recorded in the exact location of capture of each individual (T_a, relative humidity, wind speed, luminosity, height of the substrate) on T_b of the snakes. Substrate temperature (T_s) was excluded from the regression model because it was highly correlated with T_a and therefore violated one of the assumptions of our model. Subsequently, environmental variables that did not have significant influence on the model, i.e., that explained little variation of the T_b, were discarded. We also verified the influence of season, sex, and body size on T_b variation using mixed model analysis.

To calculate E values, we considered all the deviations (d_b and d_e) calculated from individual T_b measurement and the respective T_e. E values were averaged for each season in order to identify a possible seasonal variation and, within each season, for day and night to check for a possible circadian difference. To estimate confidence intervals for E, we used the bootstrap procedure suggested by Hertz et al. (1993; see also Diaz, 1997). We drew random samples with replacement from the empirical distributions of T_b and T_e and then computed the E values in the two modes described above. This process was repeated 1000 times to set confidence intervals.

RESULTS

We recorded 173 T_b values from 85 males (SVL = 580 ± 79.5 mm, mass = 79.3 ± 26.7 g), including 13 juveniles (SVL = 441.8 ± 55.9 mm, mass = 41.8 ± 13.4 g), and 88 females (SVL = 716.6 ± 107 mm, mass = 181.1 ± 75.4 g), 14 of which were juveniles (SVL = 514 ± 67.8 mm, mass = 65.9 ± 30 g; Fig. 1). Mean T_b of each group did not differ within seasons ($F_{3,170}$ = 2.01, P = 0.11). Most snakes (80.3%) were hunting in a coiled posture, whereas the remaining snakes were moving.

Variation in T_b's through the day and seasons.—Golden Lanceheads showed T_b values ranging from 15.8 to 30.1°C (mean = 22.05 ± 0.25°C) year round (Fig. 2, Table 2). Body temperatures were significantly higher than environmental temperatures ($T_b \times T_e$: Wilcoxon signed rank test, W = −6772,
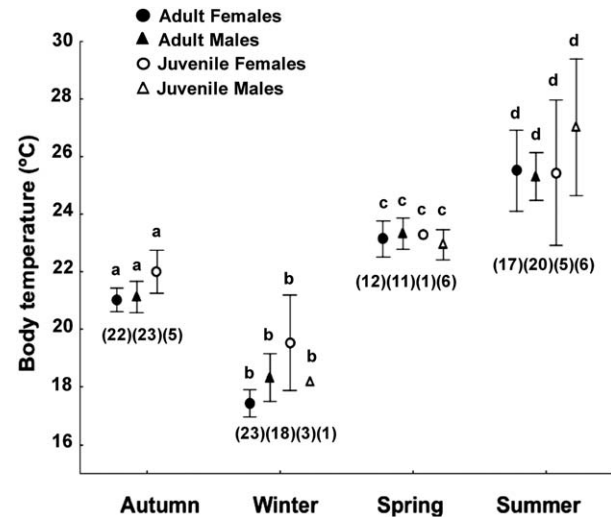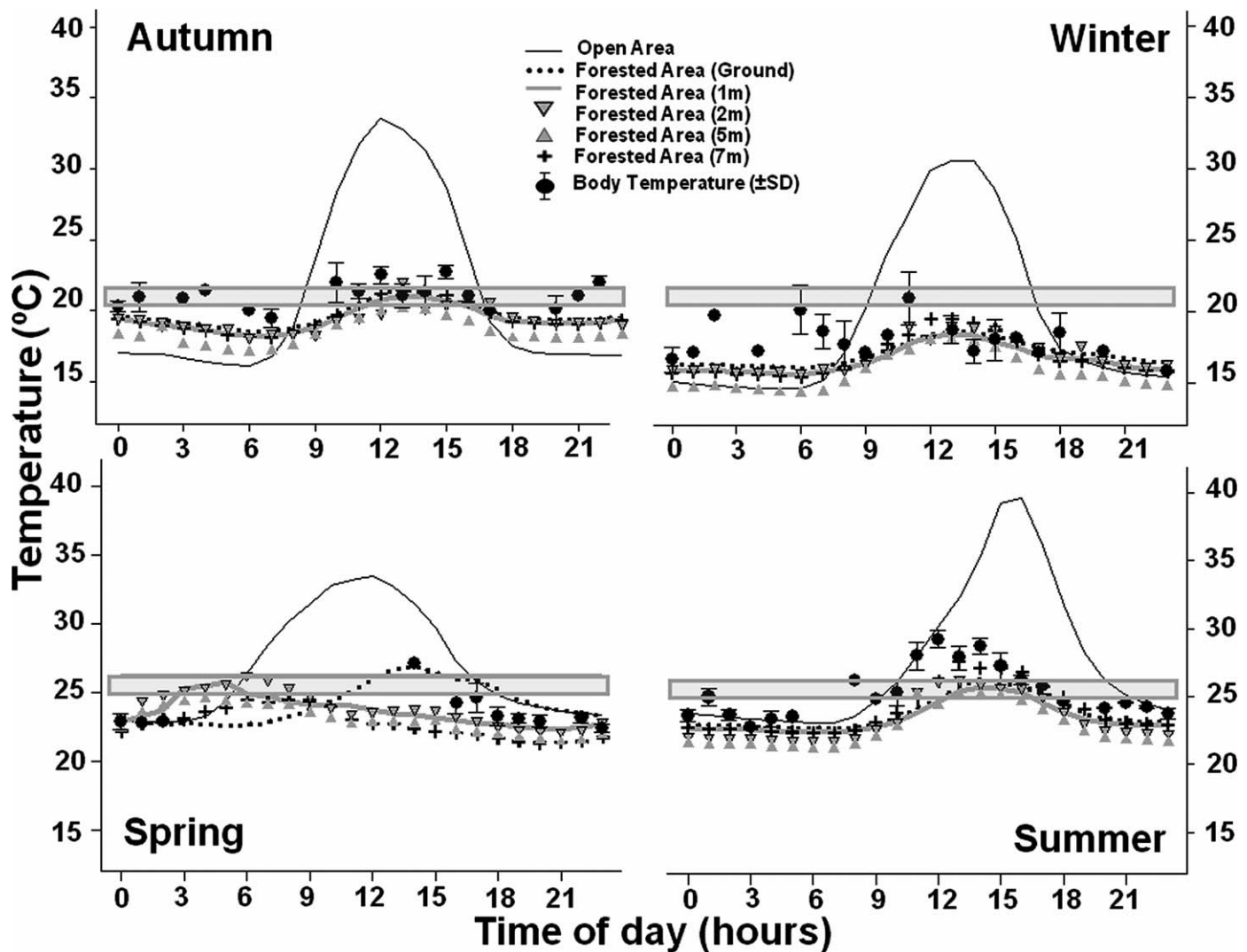

Fig. 1. Mean (±SE) body temperature of *Bothrops insularis* at Queimada Grande Island, separated for juveniles and adults, males and females, and seasons. Significant differences were found among all seasons, while no difference was found within any season (i.e., different letters denote significant differences). Juvenile males were not found in autumn.

$P < 0.001$; $T_b \times T_a$: Wilcoxon signed rank test, W = −9740, $P < 0.001$; $T_b \times T_s$: Wilcoxon signed rank test, W = −9594, $P < 0.001$; Tables 2, 3) considering all seasons together. All T_b values were within the range of available T_e's (Fig. 3).

Snakes' T_b's showed significant seasonal variation (linear mixed model, $F_{3,170}$ = 224.6, $P < 0.0001$; Tukey's *post hoc* test: T_b in summer > T_b in spring > T_b in autumn > T_b in winter; Table 2, Fig. 2). However, the activity pattern through the year, conferred by the number of captures (standardized by time spent collecting) across seasons, was not affected by the variation of the T_b's (Chi-square test: χ^2_3 = 3.68, P = 0.29). Also, T_b's showed a more defined cycle (unimodal) in summer (Fig. 2). The lowest T_b's were registered during winter nights, while the highest T_b's were recorded during the summer at midday (Fig. 2). Diurnal T_b's of the Golden Lanceheads were significantly higher than nocturnal T_b's in the spring (Holm-Sidak test, df = 5,22, t = 3.4, $P < 0.05$) and summer (Holm-Sidak test, df = 24,23, t = 10.6, $P < 0.05$) but not in autumn and winter.

Preferred body temperature (T_{set} interval).—Preferred body temperatures (25 to 75 percentiles) ranged from 20.4°C to 21.7°C in winter and from 24.9°C to 26.3°C in summer.

Operative environmental temperatures (T_e) and thermal quality of habitat (d_e).—The operative environmental temperatures (T_e's) of all seasons combined (n = 53,574) ranged from 9°C to 55.6°C, with a mean of 21.6 ± 0.46°C (Table 2). T_e values differed significantly among seasons (Kruskal-Wallis test, H_3 = 149.2, $P < 0.001$), except between spring and summer (Tukey's *post hoc* test, P = 0.56). Pooling all microhabitats together, the mean d_e was higher (i.e., low thermal quality) in winter than in all other seasons (Table 1). During autumn, spring, and summer, the mean d_e values in the forested areas showed lower deviations (i.e., closer to zero) indicating that T_e's were closer to T_{set} interval (Table 1). In general, environmental temperatures allowed *B. insularis* to reach preferred body temperature during the daytime (d_e percentages within or above the T_{set} interval, Table 1).

Fig. 2. Hourly mean ($\pm$ SE) of the operative environmental temperatures (T_e) and body temperatures (T_b) for *Bothrops insularis* registered at Queimada Grande Island. T_b's differed significantly among seasons (summer > spring > autumn > winter). Gray boxes represent the range of preferred body temperature (T_{set} interval, see text for details).

However, the duration at which T_e was high enough to allow T_b's to reach preferred body temperature was shorter during the winter compared to autumn, spring, and summer and for forested areas compared to open areas (Table 1).

Thermoregulatory indices.—The mean deviation of T_b from the preferred range (d_b) was 1.35°C. The mean deviation of the operative temperatures from the preferred range (d_e) was 1.48°C. The indices of effectiveness of thermoregulation (E)

Table 2. Body (T_b), Air (T_a), Substrate (T_s), and Operative Environmental (T_e) Temperatures (°C; mean $\pm$ SE; min–max) Registered for *Bothrops insularis* at Queimada Grande Island. Percentage, number, and sex (σ = males; φ = females) of snakes found on the ground or on vegetation.

Seasons	T_b	T_a	T_s	On the ground	On vegetation
Autumn	21.1 $\pm$ 0.15 (18.8–23.6) ($n = 50$)	20.5 $\pm$ 0.15 (18.3–23) ($n = 50$)	20.4 $\pm$ 0.16 (17.8–23.3) ($n = 50$)	72% (15 σ, 21 φ)	28% (8 σ, 6 φ)
Winter	17.9 $\pm$ 0.21 (15.8–20.9) ($n = 45$)	17.6 $\pm$ 0.29 (15–23.5) ($n = 45$)	17.6 $\pm$ 0.27 (15.1–23.2) ($n = 45$)	67% (13 σ, 17 φ)	33% (6 σ, 9 φ)
Spring	23.4 $\pm$ 0.22 (22.4–27.1) ($n = 29$)	23 $\pm$ 0.11 (22.4–24.7) ($n = 29$)	22.9 $\pm$ 0.11 (22.2–24.7) ($n = 29$)	71% (12 σ, 8 φ)	29% (4 σ, 5φ)
Summer	25.7 $\pm$ 0.3 (22.2–30.1) ($n = 49$)	24.6 $\pm$ 0.28 (22.3–30) ($n = 49$)	24.6 $\pm$ 0.28 (22.1–30) ($n = 49$)	49% (14 σ, 10 φ)	51% (13 σ, 12 φ)

Table 3. Statistical Results Comparing Body Temperatures (T_b) of *Bothrops insularis* and Temperatures of the Surrounding Microenvironment Where Snakes Were Found. T_a = air temperature; T_s = substrate temperature. U-test of Mann-Whitney was performed for $T_b \times T_b$ comparisons. Wilcoxon Signed Rank Test was performed for $T_b \times T_a$ and $T_b \times T_s$ comparisons.

Classes	Autumn	Winter	Spring	Summer
T_b on ground × T_b on vegetation	U = 70, P = 0.425	U = 208, P = 0.682	U = 73, P = 0.591	U = 274, P = 0.603
T_b on ground × T_a 20 cm of the ground	Z = 2.62, P < 0.05	Z = 1.36, P = 0.173	Z = 2.58, **P < 0.05**	Z = 4.28, **P < 0.0001**
T_b on vegetation × T_a 20 cm of the vegetation	Z = 3.52, P < 0.05	Z = 2.55, **P < 0.05**	Z = 1.82, P = 0.068	Z = 3.67, **P < 0.05**
T_b on ground × T_s of the ground	Z = 2.55, P < 0.05	Z = 1.47, P = 0.139	Z = 3.06, **P < 0.05**	Z = 4.04, **P < 0.0001**
T_b on vegetation × T_s of the vegetation	Z = 1.88, P = 0.059	Z = 2.6, **P < 0.05**	Z = 2.1, **P < 0.05**	Z = 3.83, **P < 0.05**

calculated following Hertz et al. (1993) and Blouin-Demers and Weatherhead (2001) were similarly low (0.09 vs. 0.13, respectively). Therefore, in both cases, they indicate Golden Lanceheads are thermoconformers.

Additionally, T_b and T_e were calculated from bootstrap resampling data (computing d_b and d_e, and then E). Following this procedure, calculated d_b and d_e were 1.04 and 1.17, respectively, and the confidence intervals (95%) for E varied between −0.17 and 0.31 (considering $E = 1 − d_b/d_e$) and between −0.15 and 0.41 (considering $E = d_e–d_b$). Comparing thermoregulatory indices calculated from the original data and those bootstrapped, the latter indicates *B. insularis* as a modest/weak thermoregulator.

Finally, when E values were calculated separately for each season and day and night, we found that Golden Lanceheads thermoregulated more effectively during autumn and winter than during warmer seasons (Fig. 4A) and during the night compared to day (Fig. 4B).

Biotic and physical determinants of T_b.—Body temperature (T_b) was highly correlated with T_a and T_s ($T_b \times T_a$: Spearman correlation test, $r_s = 0.96$, $n = 168$, $P < 0.0001$; $T_b \times T_s$: $r_s = 0.95$, $n = 170$, $P < 0.0001$). Indeed, the equation best describing the overall T_b variation was the one including only T_a (multiple regression model, $r^2 = 0.92$, $F_{1,168} = 1939.7$, $P < 0.0001$). Also, T_b tended to decrease with the increase in body mass (linear mixed model, $F_{1,170} = 5.97$, $P < 0.05$; Fig. 1). The best-fit model did not include T_e, sex, and interactions because previous analyses of these data failed to find any influence of these factors on T_b.

Body temperature of the snakes on the ground versus T_b of those at various heights in the vegetation did not differ significantly within any season (Table 3), neither number of individuals found at these substrates differed among seasons (Table 2). Snakes found on the ground had T_b values significantly higher than T_a and T_s in all seasons, except winter (Table 3). For those individuals on the vegetation, T_b was significantly higher than T_a and T_s for all seasons, except for spring and autumn (Table 3).

In winter, the differences (delta T) between the T_b's and microenvironmental temperatures where Golden Lanceheads were located (i.e., T_b–T_a and T_b–T_s) were significantly higher at night (1800–0600 h) than during the day (0600–1800 h; Holm-Sidak test, df = 9,35, t = 2.61, $P < 0.05$).
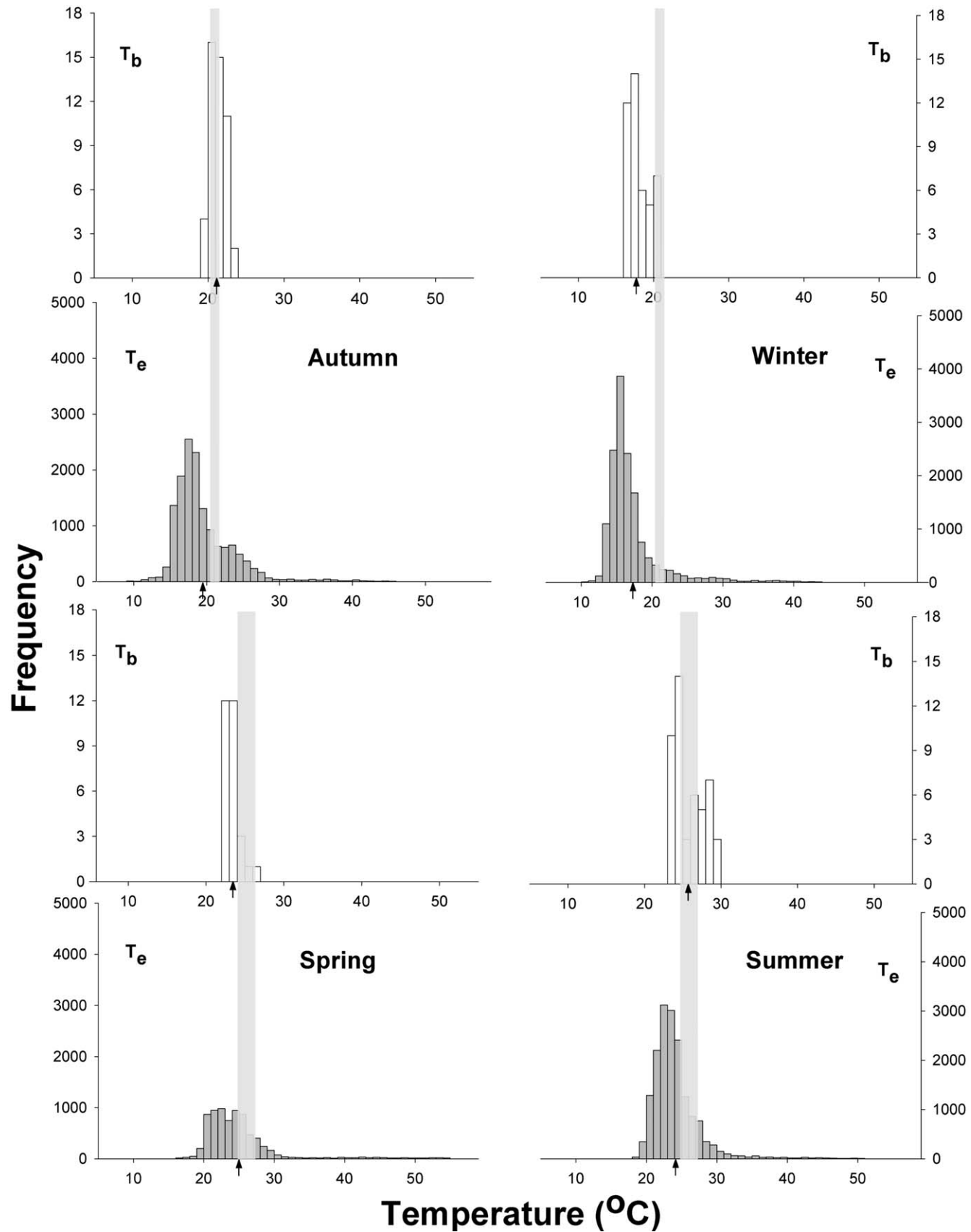
DISCUSSION

Effectiveness of thermoregulation and seasonal variation.—Effectiveness of thermoregulation calculated according to Hertz et al. (1993) and Blouin-Demers and Weatherhead (2001) indicated Golden Lanceheads to be strong thermoconformers, while the bootstrap resampling analyses indicates the species as a modest/weak thermoregulator. The congruency between the two thermoregulatory indices, the correlation between T_b and T_a, and our failure to observe any active thermoregulatory behavior gives stronger support for the thermoconformity of *B. insularis*. Nevertheless, when E was calculated separately by seasons, Golden Lanceheads were found to thermoregulate more effectively when the thermal quality of the habitat decreased during colder seasons. During the warmer seasons, preferred body temperature was achieved mostly passively because environmental temperatures largely overlapped (and sometimes exceeded) the preferred body temperature. Therefore, the thermoconformity label for *B. insularis* may not be completely accurate for all seasons.

Our observation that the effectiveness of thermoregulation tends to improve as the thermal quality of the habitat decreases through the seasons seems to be paralleled by the variation noted in the circadian cycle. Indeed, *B. insularis* thermoregulated more effectively during the night of all seasons, when the thermal quality of habitat decreased, than during the day. One possible explanation for this is related to prey capture. Golden Lanceheads are more diurnal than all other species of *Bothrops* (*sensu lato*; Amaral, 1921b; Duarte et al., 1995; Martins et al., 2002) probably to match with the activity period of migrant passerine birds that represent more than 80% of their diet (Martins et al., 2002; Marques et al., 2012). Most of individuals (80.3%) found in the field were hunting. Thus, during the day, the Golden Lancehead microhabitat selection presumably may be driven by foraging considerations even in detriment of more thermally favorable sites, while, during the night, such a conflict would not be at play (see also our comments on the avoidance of open areas for basking below). Thermoregulatory consequences possibly also driven by foraging constraints were also reported for *Gloydius shedaoensis* (Shine et al., 2003) and *Pseudechis porphyriacus* (Shine and Lambeck, 1990).

A seasonal change in thermoregulatory behavior was previously reported by Chiaraviglio et al. (2003) for *Boa constrictor occidentalis*. In this species, snakes were more easily found during the cold season because they become more exposed due to basking (Chiaraviglio et al., 2003), providing evidence that the seasonal decrease in the thermal quality of the habitat was compensated by a greater thermoregulatory effort. This pattern seems to be similar to what we have documented for the Golden Lancehead (higher effectiveness of thermoregulation in the coldest season); however, we fail to find any seasonal difference associated with behavioral thermoregulation, such as basking. Also, in milk snakes, *Lampropeltis triangulum*, which inhabit open forests in North America, thermoregulatory effort was increased when the thermal quality of the habitat decreases seasonally. However, differently from what occurs

Fig. 3. Frequency of body temperatures (T_b; white bars) distribution for *Bothrops insularis* and operative environmental temperatures (T_e; dark gray bars) recorded at different seasons. Light gray vertical bars represent the range of preferred body temperature (T_{set} interval, see text for details) for the snakes. Arrows indicate mean T_b or T_e.
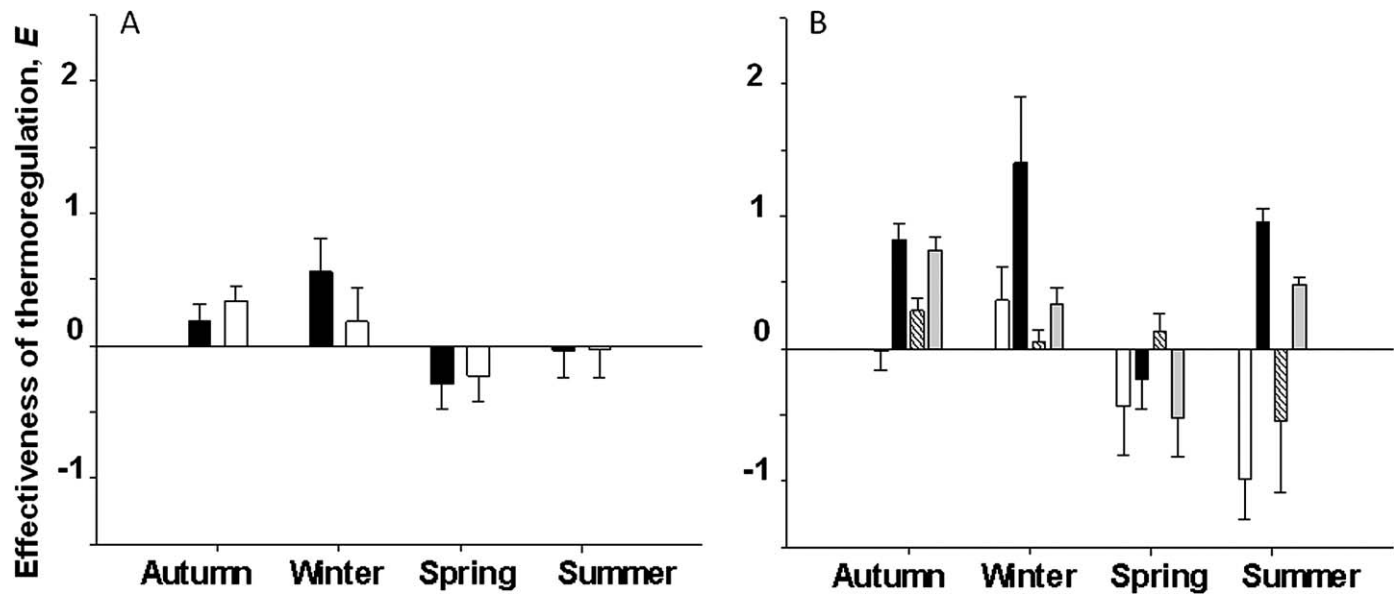
Fig. 4. Index of effectiveness of thermoregulation (*E*) for *Bothrops insularis* through the year (A) and the circadian cycle (B). (A) Black and white bars represent mean *E* calculated according to Blouin-Demers and Weatherhead (2001) and Hertz et al. (1993), respectively. (B) White and black bars depict *E* values calculated according to Blouin-Demers and Weatherhead (2001) during day (0600–1800 h) and night (1800–0600 h), respectively. Also, in (B) *E* values calculated according to Hertz et al. (1993) are depicted by dashed and gray bars for day (0600–1800 h) and night (1800–0600 h), respectively.

with *B. insularis*, the costs of thermoconformity for *L. triangulum* were higher than the benefits provided by a more active thermoregulation (Row and Blouin-Demers, 2006).

One possible way to compensate for the decline in the thermal quality of the habitat through the year, or even lower T_e's within the forested areas, could involve vertical migration similar to red-sided garter snakes (Shine et al., 2005). *Bothrops insularis* is semi-arboreal (Martins et al., 2001) and, therefore, is able to exploit forest strata in search of suitable thermal sites, as suggested for the arboreal elapid snake *Hoplocephalus stephensii* (see Fitzgerald et al., 2003). Nevertheless, our data do not provide any support for such a suggestion because we did not find a higher proportion of individuals on vegetation during colder seasons. Moreover, mean T_b of snakes found on vegetation versus those found on the ground was not significantly different in any season.

Biotic and physical determinants of T_b.—Although there are criticisms in comparing snakes' T_b with immediate surrounding temperatures (see Huey, 1982; Dreisig, 1984; Hertz et al., 1993), Peterson et al. (1993) argue that differences between snakes' T_b and air and substrate temperatures around the site occupied by the animal would be informative in the sense of analyzing heat exchange patterns. For example, the temperature differential can be expected to be lower during periods of low radiation levels, such as during the night, than during high radiation periods, as during the day (Peterson et al., 1993). However, for *B. insularis* we observed the opposite trend, as the difference between T_b's and the environment (T_a and T_s) was higher at night than during the day. This pattern could be related to the occurrence of behavioral and/or physiological adjustments in heat exchange rates in order to maintain, during the night, part of the heat gained during the day. This pattern could be related to the occurrence of circadian adjustments of regional blood flow (Amiel et al., 2011) and changes in posture, i.e., coiling at night (Ayers and Shine, 1997),

causing part of the heat gained during the day to be maintained during the night. However, contrary to what could be anticipated, we found a much greater proportion of Golden Lanceheads coiled during the day (83%, $n = 84$) than during the night (61.8%, $n = 68$). This pattern may be related to the hunting coiled posture (see Oliveira and Martins, 2002) adopted during the day by *B. insularis*.

Body size affected the T_b of Golden Lanceheads, with juveniles exhibiting higher and more variable T_b's than adult ones. In fact, juveniles of many ectotherms are subjected to faster heating rates and reach equilibrium temperature in a much shorter time than adults due to their small body mass to surface ratio (Porter and Tracy, 1983; Stevenson, 1985). Although juveniles may bask more often than adults of certain snakes (Blouin-Demers and Weatherhead, 2001), *B. insularis* was not observed basking. Feeding and pregnancy, known to cause a thermophilic response in some snakes (Peterson et al., 1993), was previously found not to affect field T_b of *B. insularis* (Bovo et al., 2010).

Thermoregulatory behavior and habitat use.—Despite the fact that *B. insularis* increased their *E* during colder seasons, this response did not suffice to prevent a significant seasonal lowering of mean T_b during winter and autumn. Thus, it is likely that the costs of a more active thermoregulatory behavior, particularly the use of open areas where basking would allow for the rapid elevation of T_b, were greater than the possible benefits derived from keeping T_b within preferred body temperature for a longer period (see also Huey, 1974; Hertz, 1974; Lee, 1980). Avoiding areas where preferred body temperature is available has been reported for other snake species and may be related to the presence of predators or low availability of prey (Huey and Slatkin, 1976; Crowder and Magnuson, 1983). In the case of Golden Lanceheads, both factors might be involved. Falcons and owls are potential predators of *B. insularis*, and they are commonly reported in open areas (see Duarte et al., 1995;

Bovo et al., 2010) while the typical prey of *B. insularis* are not (Bovo et al., 2010; A. Macarrão, pers. comm.). Finally, although higher temperatures may enhance performance on the speed and precision of the strike, and consequently foraging success, in many snake species (Huey, 1982; Shine et al., 2002), the immobility required by ambush hunters may exceed the benefit of a more precise thermoregulation. Keeping the T_b high seems to be essential for the success of active foragers (Huey and Pianka, 1981), but not for sit-and-wait snakes that spend extended periods of time ambushing prey in relative immobility (Huey, 1982; Mori et al., 2002). This seems to apply to *B. insularis* (present study) and at least another insular pitviper, *G. shedaoensis*, from China (Shine and Sun, 2002).

The behavioral thermoregulation of inland Bearded Dragons (*Pogona vitticeps*, Agamidae) was recently found to be affected by situations imposing different locomotory costs (Cadena and Tattersall, 2009). Although no similar data exist for snakes, it seems plausible that the energetic expenditure associated with shuttling between forested and open areas would likely represent a considerable portion of the energy budget of a sit-and-wait predator as the Golden Lancehead. Also, in open areas *B. insularis* would experience greater exposure to wind, which may increase cooling and/or desiccation (Sun et al., 2001). While convective cooling could be compensated by the heat gained from solar radiation, desiccation would be made worse with the direct exposure to sunlight (Ladyman and Bradshaw, 2003). Although we cannot ascertain the relevance of such risks for the Golden Lancehead, QGI has no permanent source of freshwater and water economy is likely to be a challenge.

Concluding remarks.—Grand mean T_b of *B. insularis* (22.05°C), averaged for all seasons, is among the lowest values ever reported for a viperid snake (see reviews in Brattstrom, 1965; Lillywhite, 1987; Mori et al., 2002). Mean T_b of the Golden Lacehead is also lower than that recorded for *B. jararaca* (commonly above 25°C; Sazima, 1992). *Bothrops jararaca* is the sister species of *B. insularis* (Grazziotin et al., 2006), whose separation happened around 11,000 years ago due to the rise in sea level (Marques et al., 2002a; Wüster et al., 2005). Therefore, the differences in regard to thermoregulatory behavior between *B. jararaca* and *B. insularis* may involve differences in environmental parameters (which impose thermal constraints) between the insular and mainland habitats and/or a relatively rapid evolutionary change following the separation of the ancestral clade.

The hypothesis that tropical reptiles may devote little time to behavioral thermoregulation (Shine and Madsen, 1996) seems to agree with studies conducted in tropical snakes (Shine and Madsen, 1996; Luiselli and Akani, 2002; Anderson et al., 2005; present study). However, it should be noted that this hypothesis was largely based on studies focusing on Australian snakes with high thermal inertia, without regard to strong evidence showing that open habitat ectotherms also invest considerable time basking (Ruibal, 1961). Also, it has been shown that thermoregulatory effort in semiaquatic colubrid snakes from Africa may acquire increased importance under given circumstances, for example during pregnancy (Luiselli and Akani, 2002). Similarly, we have shown that a species identified broadly as a thermoconformer may, in fact, encompass subtle seasonal and circadian differences in their effectiveness of thermoregulation. Therefore, generalizations about thermoregulation in tropical snakes should also consider the possible cost–benefit tradeoffs under a given ecological circumstances along with macroclimate considerations.

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