

Does gestation or feeding affect the body temperature of the golden lancehead, *Bothrops insularis* (Squamata: Viperidae) under field conditions?

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ABSTRACT. Temperature affects physiological performance in reptiles and, therefore, body temperature (T_b) control is argued to have an important adaptive value. Alterations in T_b due to transient changes in physiological state, as during digestion or gestation, are often linked to the potential benefits of a more precise T_b regulation. However, such thermoregulatory responses in nature remain controversial, particularly for tropical snakes. Herein, we measured T_b of the golden lanceheads, *Bothrops insularis* (Amaral, 1921), at Queimada Grande Island, southeastern Brazil, to test for alteration in selected body temperatures associated with feeding or gestation. We found no evidence that postprandial or gravid snakes selected for higher T_b indicating that, under natural conditions, body temperature regulation in *B. insularis* apparently encompasses other ecological factors beyond physiological state *per se*.

KEY WORDS. Digestion; gravid females; postprandial thermophilic response; snake; thermoregulation; Neotropics.

Ectothermic organisms such as snakes are particularly sensitive to changes in environmental temperature since they depend mainly on external heat resources for the regulation of body temperature (T_b). Metabolic heat production in snakes, except in a few particular situations (HUTCHISON *et al.* 1966, VAN MIEROP & BARNARD 1976, MARCELLINI & PETERS 1982, TATTERSALL *et al.* 2004), is so low that its contribution to the control of T_b is usually negligible (RUBEN 1976). Moreover, a snake's T_b will mainly be determined by the use of thermal features available in the environment at any given time (PETERSON *et al.* 1993). Body temperature can be changed during the performance of different activities. Because physiological performances may have distinctly different thermal optima, snakes are able to improve their performance for a given activity by temporarily changing their preferred T_b (STEVENSON *et al.* 1985, VAN DAMME *et al.* 1991). Well-known examples of such plasticity is the increase in T_b following the ingestion of food (REGAL 1966, SIEVERT & ANDREADIS 1999, BLOUIN-DEMERS & WEATHERHEAD 2001a), referred to as the postprandial thermophilic response, and the maintenance of higher and less variable body temperatures by gravid females (CHARLAND & GREGORY 1990, BROWN & WEATHERHEAD 2000, BLOUIN-DEMERS & WEATHERHEAD 2001b).

Digestion in snakes may last for many days (BENEDICT 1932, ANDRADE *et al.* 1997, WANG *et al.* 2001) causing impaired capacity for locomotion (GARLAND & ARNOLD 1983, FORD & SHUTTLESWORTH 1986), which may constrain their ability to defend themselves

against predators or engage in other ecologically relevant activities. Thus, an increase in the rate of meal digestion by the elevation of T_b (i.e. postprandial thermophilic response) is largely accepted as beneficial for snakes (LILLYWHITE 1987, REINERT 1993, SIEVERT & ANDREADIS 1999, WANG *et al.* 2002). This, indeed, seems to be the case since such responses are commonly found when snakes are tested in thermal gradients, where temperature is the sole variable being manipulated (REGAL 1966, LYSENKO & GILLIS 1980, TOUZEAU & SIEVERT 1993). During gestation, which represents an even longer commitment to an altered physiological state than feeding, the maintenance of adequate T_b is even more crucial than during digestion because failure in this case may compromise embryo development, with direct negative consequences to reproductive success (FOX *et al.* 1961, ANDRADE & ABE 1998). However, despite the importance of temperature in both cases, changes in selected T_b due to digestion or gestation have been rarely documented under field conditions for snakes, particularly in the Neotropics.

Here we report on the effects of feeding and gestation on T_b of the golden lancehead, *Bothrops insularis* (Amaral, 1921), sampled under field conditions in a subtropical region of the South America. The golden lancehead is a critically endangered endemic (MARQUES *et al.* 2004) pitviper from Queimada Grande Island (QGI), located 33 km off the coast of southeast Brazil (24°29'S, 46°40'W), with a total area of 0.43 km². A population of approximately 2,500 individuals dwells within the lowland

forest that covers about 55% of the island (MARTINS *et al.* 2008). The high density of snakes and the limited area of QGI offer a unique opportunity for the gathering of biological data under field conditions. The data presented here were collected within a broader research program devoted to the study and conservation of the species (see www.jararacailhoa.org). Specifically, we tested the prediction that, in nature, gravid and postprandial individuals of *B. insularis* would exhibit higher body temperatures than non-gravid females and fasting specimens, respectively.

MATERIAL AND METHODS

Field work was carried out during regular visits to QGI during the years of 2007-2008. Excursions typically lasted for 3-5 days and were planned to sample snakes during all seasons. Air temperature and humidity from an open area at QGI were sampled continuously by a meteorological station (HOBOWare® 2.2, Onset Computer Co.) installed at the site. Climate at QGI can be classified as wet tropical "Af" type, according to Köppen-Geiger's system (PEEL *et al.* 2007). Average air temperature measured during the study period was around 27°C (21-38°C, min-max) during the hottest month (March), and around 18°C (15-27°C, min-max) during the coldest month (August). The average monthly relative humidity was always higher than 90%.

Snakes were searched for along a main transect (~1500 m) at different times of the day. Upon capture, cloacal T_b was measured within 30 secs with a quick response temperature probe sensor (ETI – EcoTemp model; $\pm 1\%$ precision and 0.1°C resolution) inserted into the snake's cloaca. Snout-vent-length (SVL), body mass, reproductive stage, posture, time of the day, height of substrate, and activity (ambushing, moving or resting) were also recorded. Female snakes were carefully examined by palpation and were classified as gravid if they were found bearing embryos. Postprandial individuals were induced to regurgitate the stomach contents and, if the prey items maintained structural integrity, i.e. with the body wall not ruptured, we considered that ingestion had occurred within the previous 48 hours (see ANDRADE *et al.* 1997), and these snakes were classified as postprandial.

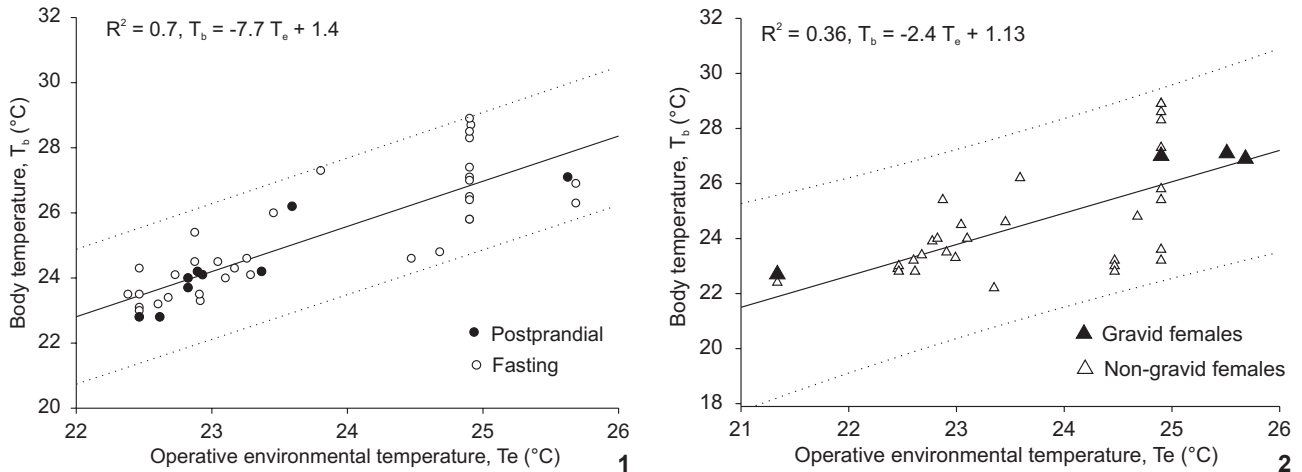
Operative environmental temperatures (T_e) was sampled using copper "snake" models ($n = 6$) filled with water and painted to match the colour of golden lanceheads (see BROWN & WEATHERHEAD 2000, ROW & BLOUIN-DEMERS 2006). Models were distributed at random across QGI in order to sample the possible thermal habitats used by the snakes (e.g. open and forested areas, different altitudinal gradients on the vegetation, and retreat sites; see MARTINS *et al.* 2008 for details about habitats available at the QGI). Temperature of the models were recorded continuously throughout the study period once every 16 min using temperature dataloggers (StowAway®, TidBit®) placed inside of them (resulting in 5760 values for T_e). The thermal accuracy of the models was determined against fresh snake carcasses under a

variety of conditions (rainy, sunny, day, night) and in all cases they agreed with the snake's thermal properties with great accuracy (Pearson linear regression; snake carcass = $-0.035 + (0.99 * T_e)$ model); $r^2 = 0.973$; $F_{1,90} = 3205.9$; $p < 0,001$).

To check whether body temperature of gravid or postprandial snakes was significantly different from the rest of the population, we constructed a "null model" by fitting a linear regression (minimum square method) between T_b and T_e for all non-gravid females ($n = 28$) and fasting individuals ($n = 33$) found at the same season (see details below). In this regression, T_e values were taken from the physical model located at the most similar habitat to where the snake was found and at the same time (± 16 min, due to the sampling interval) for which T_b was recorded. We then checked whether T_b of gravid or postprandial snakes would fit within the 95% confidence interval calculated for the general relationship between T_b and T_e for the non-gravid and fasting snakes. Afterward, we performed a Student's t-test on the calculated residuals for the regression line comparing postprandial vs. fasting individuals within the appropriate season to test whether differences in T_b would occur independently of T_e . Finally, we selected fasting ($n = 9$) and non-gravid females ($n = 5$) with similar body size and whose T_b was recorded under conditions (microhabitat, posture, daytime, season, and T_e) identical to the postprandial and gravid snakes, respectively, and tested for significant differences in T_b using a Student's t-test. Whenever necessary, to adhere to assumptions of normality and homoscedascity, data were \log_{10} transformed before statistical analysis. All statistical procedures were applied according to ZAR (1996) using the SigmaStat statistical software (SSI, Richmond, CA, USA). Unless specified otherwise, all values are presented as mean \pm SE, and differences were accepted as statistically significant when $p \leq 0.05$.

RESULTS

We found nine individuals of the golden lancehead that had recently eaten (Tab. I). From all of them, we recovered the ingested prey and found that they had eaten, in all cases, the seasonal migrant bird (Passeriformes) *Elaenia chilensis* Hellmayr, 1927 (average meal mass equal to 18% of the snake body mass). All postprandial snakes were found during the summer (February/March) within the forested area, as previously observed (MARTINS *et al.* 2008). None of the postprandial individuals were found to deviate significantly from the general relationship between T_b and T_e for the season (Fig. 1) (i.e., all of their T_b values fell within the 95% confidence interval for the regression). Corroborating this, the test on the residual values for this regression did not show any significant difference between postprandial and fasting snakes (Student's t-test, $t_{36} = -1.65$, $p = 0.11$). Finally, the direct comparison between postprandial and fasting individuals, recorded under similar conditions, also revealed no significant difference in T_b (Student's t-test, $t_{16} = 0.2$, $p = 0.84$; Fig. 3).



Figures 1-2. Least square regression lines (solid) and 95% prediction intervals (dotted) for the relationship between body temperature and operative environmental temperature (of the same microenvironment where each snake was found) for free-ranging golden lanceheads, *B. insularis*. (1) Open and solid circles indicate fasting ($n = 33$) and postprandial ($n = 9$) snakes, respectively (all individuals found during summer). (2) Open and solid triangles indicate non-gravid ($n = 33$) and gravid ($n = 4$) females, respectively (sampled during spring/summer). Notice that body temperature values of postprandial and gravid individuals always fell within the 95% confidence intervals for the respective season.

Four gravid females of the golden lancehead, all of them found in the forested area, had their T_b sampled (Tab. I). Two of them were found in late spring (December) and contained four and five embryos, whereas the other two were found in late summer (March) and contained four embryos each. In none of these cases did body temperature deviate from the general relationship between T_b and T_e for the two seasons combined (Fig. 2) or for each of them considered separately (not shown). The comparison between T_b values recorded for gravid snakes compared to those recorded for non-gravid females, found under similar conditions, did not reveal a significant difference (Student's t -test, $t_7 = -0.02$, $p = 0.98$, see Tab. I and Fig. 3).

Fasting snakes included adult male and females, the non-gravid group included only adult females. For all groups the most common posture was coiled with the head lying over the body in an apparent alert/ambushing posture (OLIVEIRA & MARTINS 2001).

DISCUSSION

Mean body temperature for postprandial snakes fit the general relationship observed between T_b and T_e for fasting snakes indicating that *B. insularis* did not modify its thermoregulatory behaviour during digestion. The absence of differences between fed and fasting snakes also indicates that heat conductance was not altered (by postural changes, for example) and/or by postprandial thermogenesis (see TATTERSALL *et al.* 2004). Corroborating these findings, the residual analysis and the direct comparison of postprandial and fasting individuals (under similar conditions) also failed to identify any significant difference in T_b that could be attributed to a postprandial thermophilic response. Indeed, T_b values for postprandial and fasting snakes were found to completely overlap each other (Fig. 3).

One possible explanation for the lack of a postprandial thermophilic response in *B. insularis* may be related to micro-

Table I. Body temperature of free-ranging golden lanceheads, *B. insularis*. Gravid and postprandial individuals were compared to non-gravid females and fasting specimens, respectively, found under similar conditions. No significant difference was found for any of the pairwise comparisons (Student's t -test, see text for details). Mean \pm Standard Error.

Variable	Postprandial	Fasting	Gravid females	Non-gravid females
Body Mass (g)	99.8 \pm 16.3	103.2 \pm 15.9	205.6 \pm 12.8	191.8 \pm 13.7
Snout-vent-length (mm)	633.7 \pm 23.3	624.4 \pm 27.7	742.6 \pm 26.3	805.0 \pm 28.2
Body temperature, T_b ($^{\circ}$ C)	24.3 \pm 0.4	24.2 \pm 0.3	25.9 \pm 1.0	25.9 \pm 1.1
Operative Environmental Temperature, T_e ($^{\circ}$ C)	23.2 \pm 0.3	23.4 \pm 0.5	24.3 \pm 1	24.2 \pm 0.7
n	9	9	4	5

habitat use. Golden lanceheads are strict forest dwellers rarely venturing in open areas or forest edge zones to bask (MARTINS *et al.* 2008), even during digestion when an increase in body temperature is thought to be beneficial (ANDRADE *et al.* 2004). On the other hand, snakes that exhibit a postprandial thermophilic response, such as *Pantherophis obsoletus* (Say, 1823), are known to bask in open areas more often during digestion than during fasting (BLOUIN-DEMERS & WEATHERHEAD 2001a). Although the habitat of *B. insularis* provides thermoregulatory opportunities for T_b to be elevated, this possibility would imply shuttling behaviour, which is constrained by the hindered locomotor ability of postprandial snakes (FORD & SHUTTLESWORTH 1986). Also, since four raptor species, *Rupornis magnirostris* (Gmelin, 1788) (Accipitridae), *Falco peregrinus* Tunstall, 1771, *Caracara plancus* (Miller, 1777), and *Milvago chimachima* (Vieillot, 1816) (Falconidae) are found on QGI (A. Macarrão, Universidade Estadual Paulista “Júlio de Mesquita Filho”, unpubl. data), the exposure of *B. insularis* in open areas may increase predation risk. Finally, prey consumed by the golden lanceheads – *Elaenia mesoleuca* (Deppe, 1830) and *Turdus flavipes* Vieillot, 1818 (AMARAL 1921); *E. chilensis*, and *Turdus* sp., (A. Macarrão, unpubl. data) – are more abundant inside the lowland forest (O.A.V. Marques and A. Macarrão pers. comm.) and time spent basking in open areas may impair foraging success. In combination, these factors seem to agree with the observation that the postprandial thermophilic response is commonly reported by experimental studies in thermal gradients (WALL & SHINE 2008). Conversely, in natural conditions, animals face many other constraints and factors besides temperature (e.g. predators, prey availability, climatic factors), and become considerably more elusive. In fact, for the colubrid snake *P. obsoletus*, a postprandial thermophilic response was observed in the laboratory but not clearly in the field (BLOUIN-DEMERS & WEATHERHEAD 2001a).

Thermoregulatory changes associated with reproductive stage are relatively well documented in squamates (BEUCHAT 1986, CHARLAND & GREGORY 1990, BLOUIN-DEMERS & WEATHERHEAD 2001b). Particularly, the elevation and relative stability of T_b during gestation have been pointed out as important mechanisms ensuring the proper development of the embryos (SCHWARZKOPF & SHINE 1991, BROWN & WEATHERHEAD 2000), and, ultimately, improving fitness (ROCK *et al.* 2000). Nonetheless, while this response holds for some snakes species (e.g. BROWN & WEATHERHEAD 2000, LADYMAN *et al.* 2003) including tropical ones (LUISELLI & AKANI 2002, CHIARAVIGLIO 2006), it is absent in others (SANDERS & JACOB 1981, ISAAC & GREGORY 2004). For *B. insularis* we found that the T_b of gravid females conformed to the general relationship between T_b and T_e , which indicates no change in thermoregulatory behaviour. However, three out of four gravid females were found at temperatures (T_b and T_e) higher than the majority of the individuals (the remaining one being found at night at a considerably colder temperature) (Fig. 2). At first glance, this observation could suggest that gravid

females selected relatively warmer sites. This idea, however, was not supported by the direct comparison between the T_b of gravid and non-gravid females found under identical conditions (Fig. 3). Therefore, the reasonable conclusion would be that gestation had no detectable effect on the thermoregulation of free-ranging golden lancehead. Due to our limited sample size, however, such conclusion should be taken with the outmost caution because the power of our statistical test was far below (0.05) the desired level (0.8).

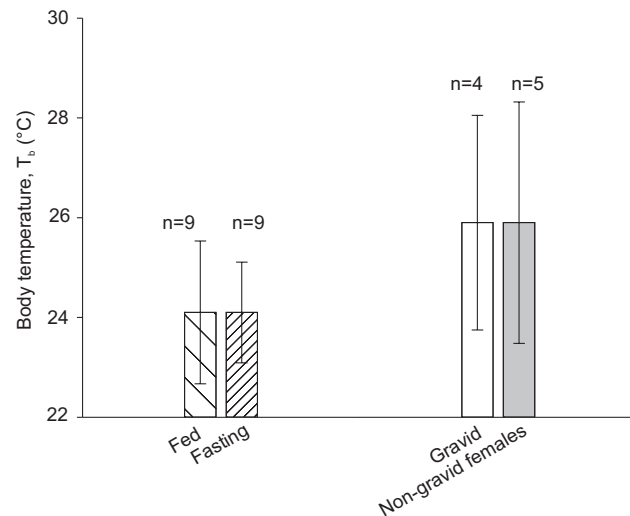


Figure 3. Body temperature comparison between postprandial vs. fasting and gravid vs. non-gravid females of free-ranging golden lanceheads, *B. insularis*, found under similar conditions. Columns = Mean. Bars = Standard Error.

In summary, we were unable to find any indication that gestation or feeding cause *B. insularis* to modify its thermoregulatory behaviour. We are fully aware that our conclusions rest on a fragile data base formed by the sampling of T_b values from a small number of individual snakes. Ideally, long-term body temperature monitoring using radiotelemetry and temperature sensitive implanted devices would provide a more effective way to test for the questions approached here. However, we report on conditions that are infrequently encountered in nature and for which there are few and controversial reports available. This, combined with the fact that fieldwork opportunities at QGI are very limited due to costs and to the inhospitability of the location (AMARAL 1921), prompt us to report the present results. Also, the endemic and insular nature of the golden lancehead, the fact that it is critically endangered (MARQUES *et al.* 2004, MACHADO *et al.* 2005), and has experienced declining population size in recent years (MARTINS *et al.* 2008), makes it urgent that any biological information about this species be made available.

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