

Body temperature of free-living freshwater turtles, *Hydromedusa maximiliani* (Testudines, Chelidae)

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Abstract. Field body temperatures of the Maximilian's snake-necked turtle, *Hydromedusa maximiliani*, a small freshwater turtle species endemic to Atlantic rainforest mountainous regions in Brazil, were studied. Turtle body temperatures and water temperatures were significantly related, but turtle body temperature averaged 1°C higher than stream water temperature, this difference being statistically significant. A multivariate model revealed that only water temperature was significantly related to turtle body temperature while body size had no effect. There was no effect of sex and life stage on turtle body temperature, implying that water temperature was the main factor determining body temperatures. Thermoconformity was verified for all sampled individuals. The broad implications of these results are also discussed.

Habitat temperature is an important resource for turtle life-history strategies because of its effect on turtle body temperature. Thus, environmental temperatures play a key role in determining turtle behavior on local and regional scales, from selecting available sites for habitat use and feeding behavior (Brow and Brooks, 1991; Nieuwolt, 1996) to shaping population structure and geographical distribution patterns (Litzgus et al., 1999; Ewert et al., 2005). Thus, species must deal daily with oscillating habitat conditions with the goal of reaching optimal conditions for routine behavioral or physiological activities (Huey and Slatkin, 1976; Meek and Avery, 1988; Janzen et al., 1992). This situation may be particularly difficult in habitats with limited optimum basking (e.g. few available sunny places), as in the Brazilian rainforests.

For freshwater turtles species, the most common and widespread behavior for increasing body temperature is basking (but see Manning and Grigg, 1997), with turtles selecting available sites (logs, stones, river beaches)

for thermoregulation (Meek and Avery, 1988; Grayson and Dorcas, 2004). Although basking is recorded as a common behavior for several neotropical freshwater turtles (Pritchard and Trebbau, 1984; Lacher et al., 1986; Cabrera, 1998), available data on body temperature for free-living species are primarily anecdotal (Brattstrom, 1965; Yamashita, 1990). For captive animals, Lacher et al. (1986) verified that body temperatures for *Kinosternon scorpioides*, *Trachemys scripta*, *Acanthochelys spixii*, *Phrynops geoffroanus*, and *Podocnemis expansa* frequently were lower than water or substrate temperature, suggesting that these species must rely on basking to optimize their body temperature. Interestingly, the Neotropical freshwater turtles species mentioned above are found in large rivers or regions with open vegetation (Pritchard and Trebbau, 1984; Cabrera, 1998; Souza, *in press*), which offer areas exposed to sunlight where basking behavior is possible.

Maximilian's snake-necked turtle, *Hydromedusa maximiliani*, is a small (<200 mm straight-line carapace length; <520 g body mass) freshwater turtle species endemic to Atlantic rainforest mountainous regions from southeastern and southern northeastern Brazil (Souza and Abe, 1997, 1998). Natural habitat for the species includes streams with clear and cold water as well as sandy and rocky bottoms, within pri-

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mary forest at over above 600 meters above sea level. Little sunlight reaches the streams inhabited by this species because of the dense canopy, the closed understory, and the common broad-leaved plants along streams banks (Souza and Abe, 1998; Souza, 2005). Semi-aquatic turtles and tortoises living in shady habitats thermoregulate by exploring the thermal gradient in the area (forest-gap, forest-edge) for avoidance overheating (Donaldson and Echternacht, 2005; Luiselli, 2005). Thus, for this forest-dwelling freshwater turtle, a higher body temperature in relation to water or substrate could be expected if the species was engaged in basking behavior in forest gaps or if some physiological mechanism was involved. This paper examines the thermal ecology of a free-living freshwater turtle species by analysis of the relationships between turtle body temperature and that of the species' aquatic habitat.

From October 2003 to April 2005, individuals of *H. maximiliani* were hand captured in four streams from Parque Estadual de Carlos Botelho (24°00'-24°15'S, 47°45'-48°10'W), São Paulo State, southeastern Brazil, as part of a long-term project on the ecology of the species (see Souza and Abe, 1998 for a more detailed area description). Captured animals were marked by marginal scute notching for individual identification (Cagle, 1939) and released at the same point of capture. Turtles were grouped by sex (male, female, and juvenile), identified by their external body characteristics (plastron concavity, tail length) and body size (Souza, 1995; Souza and Abe, 1997, 1998). For each captured turtle, body size (plastron length) was measured with calipers to the nearest 0.1 mm, and body mass was measured with a spring scale to the nearest 0.5 grams. Turtle body temperature (T_b) was immediately recorded after animal capture by using a rapid-recording cloacal thermometer (EHDigitalTemp™; Ribeirão Preto, SP, Brasil; 0.1°C precision). Water temperature (T_w) was recorded by mercury thermometer (0.2°C precision) at the point of turtle capture, and cloacal thermometer data was calibrated with it. Body temperatures from recaptured turtles were not recorded in order to avoid data pseudo-replication. Multiple linear regression analysis was performed to examine the relationships among body temperature (dependent variable) and turtle size and mass, while analysis of covariance (with T_w as covariate) was employed to check for the effects of the sex and water temperature on turtle temperature. Since ectotherms must depend upon getting heat from the physical environment, turtles should regulate T_b through physiological processes or choosing an appropriate microclimate (Grayson and Dorcas, 2004; Donaldson and Echternacht, 2005; Luiselli, 2005). To assess thermoregulatory behavior

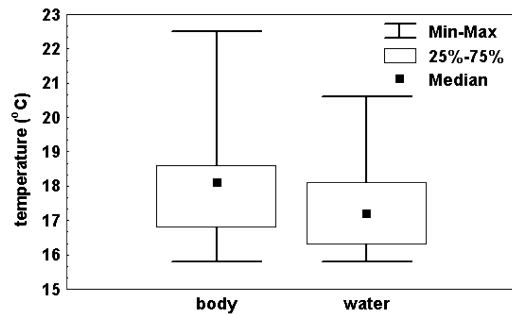


Figure 1. Body temperature ($n = 45$) and water temperature ($n = 45$) for *Hydromedusa maximiliani* from Parque Estadual de Carlos Botelho, southeastern Brazil.

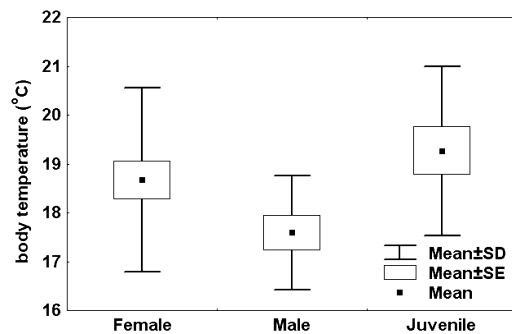


Figure 2. Body temperature for females ($n = 23$), males ($n = 10$), and juveniles ($n = 12$) *Hydromedusa maximiliani* from Parque Estadual de Carlos Botelho, southeastern Brazil.

in *H. maximiliani* the slope of the body vs. water temperature regression was carried as an estimate of the species' thermoregulatory strategy (k ; Huey and Slatkin, 1976). A t -test was used to determine if turtles exhibit a passive or thermoconformity strategy (slopes significantly different than 0) or a thermoregulation strategy (slopes not significantly different than 0) (Zar, 1999). Data normality was checked prior to analysis (Zar, 1999).

Body temperature was recorded from forty-five activity turtles living in streams from an Atlantic rainforest area. There was a significant positive relationship between turtle body and water temperature ($T_b = -4.42 + 1.32T_w$; $r = 0.81$; $P < 0.001$). However, turtle body temperature averaged 1°C higher ($18.6 \pm 1.8^\circ\text{C}$; $n = 45$) than stream water temperature ($17.4 \pm 1.1^\circ\text{C}$; $n = 45$) ($U = 607$; $P = 0.001$) (fig. 1). By the multivariate model, only water temperature ($\beta = 0.784$; $P < 0.001$) was significantly related to turtle body temperature while body

size (for plastron length: $\beta = -0.240$; for mass: $\beta = 0.180$) had no effect. Although juvenile body temperature was higher ($19.3 \pm 1.7^\circ\text{C}$; $n = 12$) than for both males ($17.6 \pm 1.2^\circ\text{C}$; $n = 10$) and females ($18.7 \pm 1.9^\circ\text{C}$; $n = 23$), analysis of covariance showed no effect of sex and life stage on turtle body temperature ($F_{2,41} = 1.89$; $P > 0.05$) (fig. 2), implying that water temperature was the main factor determining body temperatures ($F_{1,41} = 74.26$; $P < 0.001$). Thermoconformity was verified for all sampled individuals (slope: 1.32; $t_{45} = 9.04$; $P < 0.0001$), with no sex-life stage influence (males: slope = 1.13; $t = 6.21$; $P < 0.001$; $n = 10$; females: slope = 1.25; $t = 5.17$; $P < 0.0001$; $n = 23$; juveniles: slope = 1.36; $t = 6.02$; $P < 0.001$; $n = 12$).

Body temperature in *Hydromedusa maximiliani* was related to the water temperature in the stream. Although Yamashita (1990) reported that *H. maximiliani* sometimes engages in aerial basking, such behavior must be extremely scarce since we observed no animal out of water in a decade visiting the same study area. Although terrestrial chelonian species living in forest environments may be faced with a low risk of overheating, they must be engaged in behavioral thermoregulatory strategies that optimize activity temperature while avoiding possible predation in open regions or minimizing desiccation in dry areas (Luiselli, 2005). Thus, the typical thermal gradient present in terrestrial habitats can be exploited by these organisms (by behavioral and physiological means) to mitigate situations of excess body temperature. *Hydromedusa maximiliani* apparently leaves the water only during the rainy season, when temporary or intermittent water systems are connected with the main watercourses, or during nesting forays (Souza and Abe, 1997). Thus, this species is not to exploit a broad thermal gradient in its thermoregulatory strategy because the habitat is linear (i.e., a river channel).

Given the heavy understory and forest canopy that creates a very shady habitat, aerial basking behavior for this turtle is possible only in forest gaps along the stream course. Studies focusing

on the use of gaps versus non-gaps by these turtles would be interesting. Also, aquatic basking by using warmer surface water as suggested by Lacher et al. (1986) for some neotropical turtles and common in others chelid species (Chessman, 1987; Manning and Grigg, 1997), probably does not occur in *H. maximiliani* because the inhabited streams are so shallow (25 cm mean depth) and with fast flow. Hence, water temperatures are quite uniform. The thermoconformity strategy found for this species reflects these observations.

Neither sex and life stage nor body size explained the higher body temperature than water temperature in this species. Body temperature of ectotherms and, by consequence, temperature-dependent physiological performance, can drive several biological processes, including metabolism and food ingestion and food digestion rates (Hammond et al., 1988; Congdon, 1989; Zimmerman and Tracy, 1989; Brow and Brooks, 1991). Energy intake from food can be accelerated in ectotherm individuals exhibiting higher body temperatures (Hammond et al., 1988; Zimmerman and Tracy, 1989; Brow and Brooks, 1991) and thus, food energy can be incorporated more rapidly and efficiently. Living in an environment where water temperature is relatively low (18°C) and constant year-round, even during summer, the maintenance of a higher body temperature in relation to water temperature is likely advantageous for *H. maximiliani*.

According to Luiselli (2005), thermoconformity could be advantageous for forest tortoises by saving energy through reduce searching for sunny areas. However, in non-forested areas tortoises may have an extra cost looking for shady shelters. Animals in this situation could expend energy in locomotion and their movements might increase their conspicuousness to predators. In addition, if the available microhabitats for thermoregulation are unsuitable for food acquisition, energy input would be reduced (Huey and Slatkin, 1976). Thus, a trade-off among thermoregulatory activity, predator

avoidance, and energy intake should be pronounced in ectotherms. Dispersal behavior in *H. maximiliani* is limited to <10 meters/day (Souza, 1995; Souza and Abe, 1997) and during winter season (June to August), few individuals are seen or captured, suggesting significant seasonality in turtle activity (Souza, 1995; Souza and Abe, 1997). The sedentary behavior verified for this turtle could result in low energy expenditure during daily activities. Since the species is omnivorous (Souza, 1995; Souza and Abe, 1998) and food is probably not scarce in the habitat, energy intake may not be limiting over the life span of the species.

The thermoconformity strategy detected in the present study for *H. maximiliani* suggests a pattern of geographical variation in species body temperature given that the present studied population is located at the extreme south portion of species geographical range, where habitat temperature is low when compared to northern areas. *Hydromedusa maximiliani* is associated with pristine forested habitat but the species range encompasses regions of intense development in Brazil and one of the most endangered ecosystems in the world (Myers et al., 2000). Edge effects that are a consequence of extensive deforestation could be severe for this species, since a thermoregulatory strategy apparently is absent. Studies of thermoregulation in this species in open or disturbed habitats would be informative.

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