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Thermoconformity strategy in the freshwater turtle *Hydromedusa tectifera* (*Testudines, Chelidae*) in its southern distribution area



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ABSTRACT

Ectotherm species are not capable of generating metabolic heat; therefore, they present different strategies for regulating their body temperatures, ranging from a precise degree of thermoregulation to a passive thermoconformity with ambient temperatures. In reptiles, aerial basking is the most common mechanism for gaining heat. However, among aquatic reptiles, such as freshwater turtles, aquatic basking is also frequent. *Hydromedusa tectifera* is a turtle of exclusively aquatic and nocturnal habits widely distributed in South America. We studied the relationship between body temperature (Tb) of *H. tectifera* and its habitat, and explored the effects of sex, life stage and body size and mass on Tb. Fieldwork was conducted in two streams of a mountain area of central Argentina. We recorded cloacal temperature, size and mass of 84 turtles. We also determined individuals' sex and life stage (adult/juvenile). Regarding ambient temperatures, we measured water temperature on the surface (Tsurf) and at depth of turtle capture (Tdepth) and air temperature. Mean Tb was 18.58 °C (Min = 10.20 °C; Max = 25.70 °C). Tsurf and Tdepth were highly correlated. Multi-model analysis using Akaike criterion indicated that Tb was strongly associated with water temperature, whereas air temperature and body size and mass did not show a significant effect. There was also no effect of turtle sex or life stage on Tb. Our results indicate that *H. tectifera* is a thermoconformer and eurythermal species. A nocturnal pattern of activity and a fully aquatic lifestyle are suggested as determinant factors.

1. Introduction

Body temperature is a key factor in metabolic processes, affecting important biological and ecological functions, such as digestion (Parmenter, 1980), locomotion (Claussen et al., 2002), growth (Frazer et al., 1993), response to predators (Weetman et al., 1998), habitat selection (Dubois et al., 2009), and competition (Cadi and Joly, 2003). Therefore, because most ectotherms such as reptiles are not able to regulate their body temperature by metabolic heat production, performing their activities within a range of temperatures that optimize their behavioural and physiological performance is a crucial challenge (Vitt and Caldwell, 2009).

Reptiles use a variety of thermoregulation strategies that range from thermoconformity to a precise degree of thermoregulation. In the former, body temperature is not regulated by behaviour, and therefore matches environmental temperature (Huey, 1982; Manning and Grigg, 1997; Souza and Martins, 2006; Ibargüengoytía et al., 2010), whereas in the latter, individuals can adjust and maintain body temperature within a narrow range (Huey, 1982; Edwards and Blouin-Demers, 2007;

Hill et al., 2012). Species can also be thermally generalists (eurythermal), i.e. they can live under a wide temperature range, or thermally specialists (stenothermal), i.e. they need to maintain a narrow range of body temperatures to keep their functional performance (Huey, 1982; Hill et al., 2012). The thermoregulation mechanism most frequently observed in reptiles consists of allocating some time to aerial basking in order to elevate their body temperature (Pough et al., 1998; Cadi and Joly, 2003; Lillywhite, 2014).

Some reptile species present a nocturnal activity pattern. At night hours, the environment provides constrained opportunities for behavioural thermoregulation due to the absence of solar radiation. Therefore, during activity hours, nocturnal species tend to present body temperatures strongly correlated to ambient (e.g. air, water) temperatures (Pianka and Pianka, 1976; Pianka and Huey, 1978; Autumn et al., 1994; Webb and Shine, 1998; Shen et al., 2013). This in turn results in nocturnal species showing relatively lower and more variable field-active body temperatures than diurnal species (Vitt and Caldwell, 2009).

In addition to environmental characteristics and activity patterns, intrinsic factors such as body size, sex and ontogeny may also influence

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the thermal relationships of an organism (Maia-Carneiro and Rocha, 2013). Because the surface-to-volume ratio affects heat exchange with the environment through thermal inertia, body size may be important in determining body temperature (Seebacher and Shine, 2006; Vitt and Caldwell, 2009; Fitzgerald and Nelson, 2011; McMaster and Downs, 2013). Moreover, life stage or sex may drive to differences in body temperature because of size differences or different basking behaviour (Grayson and Dorcas, 2004; Bulté and Blouin-Demers, 2010; Maia-Carneiro and Rocha, 2013).

As for most ectotherms, aerial basking serves as the main mechanism to achieve thermoregulation in aquatic turtles (Brown and Brooks, 1991; Moore and Seigel, 2006; Edwards and Blouin-Demers, 2007; Ben-Ezra et al., 2008). However, aquatic basking is highly relevant for some species. For instance, when thermal stratification occurs in the water body, individuals use the sectors where water is warmest to regulate their body temperature (e.g. by selecting the position in the water column) (Spotila et al., 1984; Chessman, 1987; Bulté et al., 2010; Fitzgerald and Nelson, 2011; Picard et al., 2011). Nevertheless, some freshwater turtles do not regulate their body temperature efficiently and are rather thermoconformers (Manning and Grigg, 1997; Souza and Martins, 2006; Shen et al., 2013).

The South American chelid genus *Hydromedusa* is currently represented by two freshwater turtle species: *Hydromedusa maximiliani* and *H. tectifera*, the latter being the least studied (Souza, 2004). Both species exhibit an exclusively aquatic habit, preferring small lakes and slow-current portions of rivers, as frequently observed in species of the family *Chelidae* (Cabrera, 1998, 2015). Souza and Martins (2006) described a thermoconformity strategy in *H. maximiliani* individuals inhabiting a portion of the Atlantic Forest of southeastern Brazil. *Hydromedusa tectifera* has a southern and wider distribution, ranging from Paraguay and southern Brazil to central-eastern Argentina. The thermal biology of *H. tectifera* is not deeply known, although the importance of water temperature in terms of annual activity pattern has been shown for this species (Lescano et al., 2008). In addition, unlike *H. maximiliani*, *H. tectifera* has a crepuscular-nocturnal activity pattern (Cabrera, 1998; Lescano et al., 2008).

The aim of this study was to determine the relationship between body temperature of *H. tectifera* and its habitat during activity hours of individuals at the southern extreme of its distribution range, in a mountainous area of central Argentina. In addition, we evaluated the influence of body size variables on body temperature, and explored possible differences between sexes and life stage groups.

Based on the absence of solar radiation during the activity hours of this species, along with its exclusively aquatic habit, we hypothesize that these turtles are not able to vary their body temperature with respect to water temperature due to the lack of heat sources. Thus, we predict a thermoconformity strategy in *H. tectifera*, i.e. body temperature of individuals will not differ significantly from water temperature. Furthermore, given the largely aquatic habits of *H. tectifera* we do not expect to find any direct influence of air temperature on body temperature.

Since *H. tectifera* is a relatively small-sized species (< 300 mm straight-line carapace length; < 2000 g body mass), we hypothesize that individuals present a null thermal inertia effect (Fitzgerald and Nelson, 2011; McMaster and Downs, 2013). Hence, we do not expect to find an effect of body size on body temperature. Likewise, no effect of sex is foreseen, since there are no important morphometric differences between males and females.

2. Materials and methods

2.1. Study site

Fieldwork was carried out in a stretch of Toro Muerto and Tanti streams, in a mountain area of Córdoba province, Argentina, at 800 m a.s.l. (Toro Muerto: 31°23′12,94″S; 64°36′08,56″W; Tanti:

31°21′21,41″S; 64°34′01.73″W). Both streams flow irregularly over granitic rock, with mean depth being 70–100 cm. The physiognomy of the surrounding vegetation is that of sierras secondary forest and thorny shrublands, typical of the Chaco region (Cabrera, 1976; Luti et al., 1979). The sites present a low tree cover, with a consequently reduced shaded area. Annual rainfall is 800 mm, being concentrated mainly in spring and summer. Mean annual temperature is 18.9 °C (Capitanelli, 1979), mean minimum temperature is 9.8 °C and mean maximum temperature is 21.5 °C, with peak values in summer that may exceed 38 °C and frosts in winter (Bonino et al., 2009).

2.2. Capture of specimens and measurements

Sampling was conducted between September 2014 and August 2015, and consisted of 13 surveys, covering the entire annual range of climatic conditions. A total of 84 individuals (51 males, 15 females and 18 juveniles) were located by visual encounter surveys and caught from the beginning of sunset, just before the start of the time of greatest activity of the individuals. Turtles were captured by hand along both margins of a 2-km stream stretch. Cloacal temperature was used to estimate body temperature (Tb) (Luiselli, 2005; Souza and Martins, 2006; Edwards and Blouin-Demers, 2007), which was recorded immediately after capture of each turtle using a fast-reading digital thermometer (accuracy \pm 0.01 °C, TES-1300, TES Electrical Electronic Corp., Taipei, Taiwan). In addition, temperature of surface water (Tsurf; measured at 5 cm in depth) and at capture depth (Tdepth), and air temperature (Tair) at 100 cm above the ground were recorded at the capture site. Maximum length and width of carapace and plastron were measured as body size variables using a vernier calliper (accuracy \pm 0.1 cm, TESA, Renens, Swiss). Body mass was measured using a spring scale (accuracy ± 0.1 g, Pesola®, Schindellegi, Switzerland). Sex was determined by identifying male secondary sexual characters: plastron concavity and a tail longer than females (Cabrera, 1998). Turtles were also classified according to life stage as adults or juveniles based on body mass: individuals with a body mass < 300 g were considered juveniles (i.e., secondary sex characters were not evident in individuals smaller than 300 g). Finally, each turtle was marked by marginal scute notching for individual identification and then released at the capture site. We did not record Tb from recaptured individuals to avoid pseudoreplication (Luiselli, 2005; Souza and Martins, 2006). We were authorized by the government environmental agencies for scientific capture (Secretaria de Ambiente y Cambio Climático, Gob. de la Prov. de Córdoba).

2.3. Statistical analyses

Multiple linear regression analyses were performed to examine the relationships among Tb (dependent variable) and water temperature, Tair and turtle body variables. We then developed a model set composed of all possible combinations of these variables, excluding interactions. We used Akaike information criterion (AIC) to assess the relative support of the models. AIC trades off explanatory power versus number of predictors; parsimonious models explaining the greatest variation have the lowest AIC values. We considered the model with the lowest AIC as the "best AIC" model. To compare candidate models we calculated delta AIC (Δ AIC) values, since models with similar AIC values (Δ AIC < 2) are equally good candidates (Burnham and Anderson, 2002; Mazerolle, 2006). In addition, we calculated the Akaike weight (ωi) for each model, which represents the probability that a model is the best in the whole set of candidate models (Mazerolle, 2006). We examined all models that had $\Delta AIC < 2$ and compared them. Finally, we ranked variables according to their relative importance by summing the Akaike weight ($\Sigma \omega i$) from all model combinations where the variable occurred. The larger the sum of the weight value, the more important the variable relative to the other variables.

Before performing the multiple regression analyses, we tested the

Table 1
Summary of body temperature, body mass and body size variables measured on *Hydromedusa tectifera* individuals, including males and females, adults and juveniles. Tb: body temperature; \(\overline{X} \): mean; Min: minimum; Max: maximum; SD: standard deviation.

	Male X (Min-Max; SD)	Female \overline{X} (Min-Max; SD)	Adult \overline{X} (Min-Max; SD)	Juvenile \overline{X} (Min-Max; D)	Total \overline{X} (Min-Max; SD)
Tb (°C)	17.78 (10.2–25.7; 4.15)	18.78 (14.3–24.0; 3.55)	18.0 (10.2–25.1;4.0)	20.74 (14.4–25.7; 3.41)	18.58 (10.2–25.7; 4.02)
Body mass (g)	750.41 (312.0-1350.0;	1070.67 (320.0-1990.0;	823.2 (312.0-1990.0;	143.06 (33.0-292.0;	667.45 (33.0-1990.0;
	289.0)	550.3)	384.39)	70.42)	442.22)
Carapace width (cm)	12.78 (10.0–16.5; 1.6)	14.07 (9.2–17.7; 2.56)	13.07 (9.2–17.7; 1.92)	7.83 (4.5–10.2; 1.51)	11.95 (4.5–17.7; 2.83)
Carapace length (cm)	19.47 (13.4–26.3; 2.97)	20.61 (13.6–27.0; 4.77)	19.93 (13.4–27.0; 3.45)	10.19 (5.7–14.4; 2.28)	17.69 (5.7–27.0; 5.09)
Plastron width (cm)	9.55 (7.4-14.9; 1.38)	10.65 (6.8-13.5; 2.29)	9.80 (6.8-14.9; 1.68)	5.42 (3.0-7.6; 1.18)	8.86 (3.0-14.9; 2.4)
Plastron length (cm)	14.56 (10.6–19.5; 2.12)	16.47 (10.8–20.6; 3.41)	14.99 (10.6–20.6; 2.57)	8.08 (4.5–11.2; 1.82)	13.51 (4.5–20.6; 3.74)

existence of correlation between the explanatory variables. Of those pairs of variables that showed a high correlation (Pearson coefficient r>0.60) we selected the one with greatest explanatory power in previous preliminary models, discarding the rest for later analysis. Thus, multicollinearity did not bias our analysis because Pearson's correlation among independent variables were all r<0.60.

Additionally, an analysis of covariance, with water temperature as covariate, was employed to check for the effects of sex (male/female) and life stage (juveniles and adults) on body temperature (Luiselli, 2005; Souza and Martins, 2006).

We also checked for residual normality using a QQ plot and tested variance homogeneity by relating residuals and predicted values. All statistical analyses were performed using InfoStat Version 2015 (Di Rienzo et al., 2015).

3. Results

Mean body temperature (Tb) was 18.58 °C, ranging between 10.2 and 25.7 °C (Table 1). Mean water temperature at capture depth (Tdepth) was 18.64 °C (min 10.5 – max 25.5 °C); these values were highly similar to those of surface water temperature (Tsurf) (\overline{x} = 18.65 °C; min 10.5 – max 25.5 °C). Mean air temperature (Tair) was 15.36 °C (min 3.2 – max 24.8 °C). On average, turtles were captured at 36.57 cm in depth, within a range of 4–107 cm.

A high correlation was detected between surface (Tsurf) and depth (Tdepth) water temperatures (r > 0.90; p < 0.05); as well as among the five body size and mass variables (r = 0.90; p < 0.05). Hence, only Tdepth and maximum carapace length were used for further analyses, given their highest explaining power on the response variable (Tb). Although air temperature (Tair) also showed a high correlation with Tsurf and T depth (r = 0.87; p < 0.05) it was not excluded from further analyses since it represents the thermal offer of the terrestrial habitat during H. tectifera activity hours.

Four multiple regression models had $\Delta AIC < 2$ (Table 2). All of these models included Tdepth as a predictor variable. The sum of the Akaike weights of the four models that contained Tdepth amounted to

Table 2 Models explaining *Hydromedusa tectifera* body temperature ordered according to Akaike information criteria (AIC). K: number of parameters used in each model; Δ AIC: difference between AIC of a model and AIC of the best model; ω i: Akaike weight of the model; Tdepth: water temperature at capture depth; Tair: air temperature.

Model	K	AIC	ΔAIC	ωί
Tdepth + Tair + Carapace length	3	22.50	0.00	0.293
Tdepth + Tair	2	22.65	0.15	0.272
Tdepth	1	22.82	0.32	0.250
Tdepth + Carapace length	2	23.44	0.94	0.183
Tair	1	357.14	334.64	0.000
Tair + Carapace length	2	359.14	336.64	0.000
Carapace length	1	470.24	447.74	0.000

 $\Sigma\omega i=0.998$, revealing the great importance of Tdepth with respect to the remaining measured variables, either associated with turtle body size (carapace length) or the environment (Tair). The multiple linear regression analysis of the first model, which presented the lowest AIC value and included all three independent variables (Tdepth, Tair and Carapace length; Table 2), indicated that Tdepth was the only variable that had a significant effect on Tb (n=84; R²=1; Table 3). Accordingly, a simple regression analysis showed a positive and highly significant effect of Tdepth on Tb (p=<0.0001; R²=0.996; n=84), with the parameters slope and intercept being $\beta=1.00$ and $\alpha=0.02$, respectively (Fig. 1). This strong relationship was maintained throughout the surveyed annual period (Fig. 2).

4. Discussion

Water temperature was the variable that best explained body temperature, indicating that *H. tectifera* is a thermoconformer species. Our data consisted of measurements taken from 84 individuals in the field; to our knowledge, this is the highest number of individuals sampled in studies on thermal biology of turtles that include body temperature measurements, which provides robustness to our conclusions.

Two different factors appear as determinants to explain the observed thermoconformity in *H. tectifera*: first, the activity pattern of this species, i.e. it is largely nocturnal and develop most of its activities in the water (Cabrera, 1998); second, the habitat characteristics, i.e. the thermal homogeneity of the streams it inhabits. During field work, 92.6% of the captured individuals were found at night and 99% were found in the water, which is consistent with previous records about the habits of this species (Cabrera, 1998; Lescano et al., 2008; Bonino et al., 2009).

The nocturnal activity of these turtles prevents them from gaining heat by common air basking. However, some nocturnal reptile species that during activity hours show thermoconformity perform thermoregulation during day-time by selecting retreat sites according to their thermal quality or by making postural shifts inside them (Huey et al., 1989; Schlesinger and Shine, 1994; Webb and Shine, 1998; Kearney and Predavec, 2000; Kearney, 2001). The thermal properties of the day-time

Table 3 Multiple linear regression analysis of the best model obtained using Akaike information criteria (AIC). β : slope; Tdepth: water temperature at capture depth; Tair: air temperature

Variable	β	P	
Tdepth	0,98	< 0,0001	
Tair	0,02	0,0952	
Carapace length	0,01	0,1543	

The analysis of covariance showed no effect of sex (F = 0.03; p = 0.87; $R^2 = 1.00$; n = 66) or life stage (F = 1.23; p = 0.27; $R^2 = 1.00$; n = 84) on turtle body temperature, indicating that water temperature was the main factor determining body temperatures.

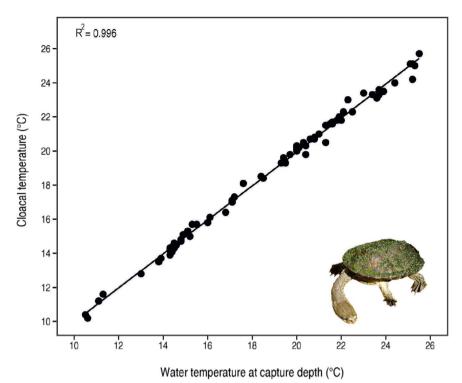


Fig. 1. Body temperature of *Hydromedusa tectifera* relative to water temperature at capture depth. Solid line shows least squares regression line.

retreat sites selected may significantly impact the physiological capabilities of the species and, therefore, their ecological performance (Kearney and Predavec, 2000). This aspect remains unknown for *H. tectifera*; therefore, future studies should attempt to elucidate if *H. tectifera* performs some degree of thermoregulation during day-time or continues as a thermoconformer on retreat sites, in order to more deeply understand its thermal biology and the underlying mechanisms that allow successful functioning with no thermoregulation strategies while active.

The high correlation found between surface water temperature and water temperature of turtles capture depth (r>0.9) indicates a thermal homogeneity of the streams. Additionally, there is evidence that the depth at which turtles are captured does not differ significantly from the available depth of streams at the study site (ANOVA: p=0.9522; F

= 0.0036; capture depth mean = 40.68 ± 2.85 , n = 118; available depth mean = 40.93 ± 2.94 , n = 111; Lescano JN, unpublished data). Based on the thermal homogeneity of the aquatic environment, we discard the possibility that individuals perform microhabitat selection in the water (Chessman, 1987; Hertz et al., 1993; Fitzgerald and Nelson, 2011; Picard et al., 2011). Hence, the interaction of the activity pattern with the environmental characteristics largely constrains the possibilities for conducting behavioural thermoregulation, thus determining thermoconformity in *H. tectifera*.

H. tectifera is not the only freshwater turtle species with an exclusively aquatic habit coupled with a thermoconformist strategy. Indeed, the same characteristics were reported for *H. maximiliani*, in southern Brazil (Souza and Martins, 2006) and *Emydura signata* in eastern Australia (Manning and Grigg, 1997). Nevertheless, this fully

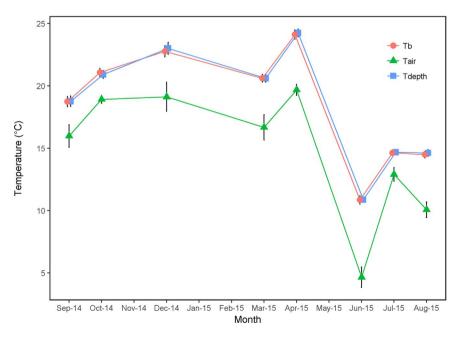


Fig. 2. Variation of temperature measurements grouped per month. Tb: body temperature; Tdepth: water temperature at capture depth; Tair: air temperature. Symbols and bars represent mean and S.E. values, respectively.

aquatic life style characterized by a lack of aerial basking activities is not always associated with thermoconformity. For example, *Sternotherus odoratus, Emydura macquarii, Graptemys geografica* and *Trachemys scripta* take advantage of the thermal heterogeneity of water bodies by performing aquatic thermoregulation (Webb, 1978; Spotila et al., 1984; Chessman, 1987; Bulté et al., 2010; Picard et al., 2011).

The effect of body size on body temperature is expected only in large reptiles due to the effect of thermal inertia (Seebacher and Shine, 2006), which has been demonstrated in both terrestrial and aquatic turtles (Fitzgerald and Nelson, 2011; McMaster and Downs, 2013). In addition, ectotherms experience a twofold higher rate of heat transfer in the water than in the air, which severely constrains their thermoregulatory capabilities when they are in the water (Fitzgerald and Nelson, 2011). Hence, the relatively small body size of H. tectifera (Table 1) probably undergoes a fast heating and cooling rate (Seebacher and Shine, 2006; Fitzgerald and Nelson, 2011). Therefore, a rapid equilibrium of body temperature with water is likely to occur, making individuals of this species more prone to thermoconformity as they spend most of their time in the water. The effect of body size also depends on basking time in species that perform such activity (Lefevre and Brooks, 1995). Hence, the lack of influence of body size on body temperature in H. tectifera is also consistent with its lack of basking habits (Souza and Martins, 2006).

The comparison of body temperature between male and female adults, and between these and juveniles of H. tectifera indicates an equal thermoconformer behaviour of these groups. Similarities in body temperature of males, females and juveniles has already been reported in several turtle species (Luiselli, 2005; Souza and Martins, 2006; Rowe and Dalgarn, 2010; Feaga and Haas, 2015). An effect of sex on thermoregulation occurs when there is a strong sexual size dimorphism (Bulté and Blouin-Demers, 2010; Maia-Carneiro and Rocha, 2013), or because of differences in basking behaviour between sexes (Grayson and Dorcas, 2004) that may be driven by gravid females (Millar et al., 2012). Although H. tectifera presents a slight sexual size dimorphism (Table 1), our results indicate it is not enough for accounting for an effect of thermal inertia. Moreover, no basking behaviour has been found in this species; therefore, basking does not play a role in its thermal biology. Furthermore, differences on body temperature between adults and juveniles may be caused by differences in size, through the exclusion of juveniles from thermally suitable sites by adults or by greater metabolic requirements of juveniles (Rhen and Lang, 1999; Maia-Carneiro and Rocha, 2013). Hence, the lack of differences in body temperatures between adults and juveniles of H. tectifera provides additional evidence of the scarce thermal requirements of this species.

The thermal breadth found in active individuals suggests that H. tectifera is a thermal generalist (eurythermal). Body temperatures of active individuals ranged between 10.1 °C and 25.7 °C (Mean = 18.58; Table 1; Fig. 1). Accordingly, records of individuals mating under water temperatures as low as 16.5 °C and 9 °C (Lescano et al., 2007) reflect the species capacity to perform activities within a wide temperature range. Likewise, the extensive latitudinal distribution of this species. from the southeast of Brazil to central Argentina, might also an indirect indicator of its thermal tolerance. Therefore, H. tectifera seems to have physiological mechanisms that allow it to remain active under this wide temperature variation. This characteristic makes the species capable of proliferating in diverse environments, also suggesting an invasiveness potential when introduced into new streams. In turn, the body temperatures found in H. tectifera are relatively low (Table 1) with respect to other freshwater turtles, such as Sternotherus odoratus (Picard et al., 2011), Glyptemys muhlenbergii (Pittman and Dorcas, 2009) and Chrysemys picta (Edwards and Blouin-Demers, 2007), although similar to that of other turtles of fully aquatic habit, such as Clemmys guttata (Yagi and Litzgus, 2013), Platysternon megacephalum (Shen et al., 2013) and H. maximiliani (Souza and Martins, 2006). Although several turtle species tolerate temperatures just above freezing (Rasmussen and Litzgus,

2010), it occurs during overwintering, whereas *H. tectifera* remains active during the cooler seasons at low water temperatures (Lescano et al., 2008).

This thermoconformity strategy is energetically conservative, and therefore may be associated with a low metabolic rate. This is reflected by the sedentary activities of this species, since it generally remains at the bottom of streams in sectors of low or no current, while performing prey capture by slowly stalking and suction feeding. Both species of the genus *Hydromedusa* exhibit thermoconformity (Souza and Martins, 2006); thus, their close relationship might suggest a genetic determination for this behaviour.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtherbio.2017.07.008.

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