Temperature selection in wood turtles (*Glyptemys insculpta*) and its implications for energetics¹

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Abstract: For turtles in northern climates, the primary function of body temperature (T_b) regulation should be to maximize energy gain. The increase in energy gain with T_b is explained primarily by the increase in food consumption and passage rate, both of which have thermal reaction norms similar to that of metabolic rate. We measured T_b continuously for fed and food-deprived wood turtles (*Glyptemys insculpta*) in a dry thermal gradient and in an enclosure with access to water containers and infra-red radiation during the photophase. We also measured the increase in metabolic rate with T_b to estimate the increase in energy gain with increasing T_b . In the thermal gradient, fed juveniles maintained higher T_b . In the enclosure, feeding had no significant effect on T_b selection when infra-red radiation was available only 5 h·d⁻¹ fed juveniles maintained higher T_b . Metabolic rate increased exponentially with T_b with a Q_{10} of 1.96 ± 0.10 (SD). We argue that, for turtles, the 95th percentile of selected T_b (T_{upper}) better approximates the optimal T_b for energy gain than the preferred T_b range (25th to 75th percentiles of selected T_b) commonly used in other studies. T_{upper} remained at 30 °C in all treatments, although T_b became increasingly skewed towards T_{upper} for fed turtles and when infra-red radiation was limited. We conclude that T_{upper} approximates the optimal T_b that fed turtles try to maintain. *Keywords*: metabolic rate, optimal temperature, postprandial thermophily, thermoregulation, wood turtles.

Résumé : Pour des tortues en climat nordique, la fonction première de la régulation de la température corporelle (T_b) devrait être de maximiser le gain d'énergie. On explique l'augmentation du gain d'énergie avec T_b principalement par l'augmentation de la consommation de nourriture et du taux de passage, les 2 ayant des normes de réactions thermiques similaires à celles du métabolisme. Nous avons mesuré T_b en continu pour des tortues des bois (*Glyptemys insculpta*) alimentées et privées de nourriture, dans un gradient thermique sec et dans un enclos avec accès à des contenants d'eau et de la radiation infrarouge durant la photophase. Nous avons aussi mesuré l'augmentation du taux métabolique avec T_b pour évaluer l'augmentation du gain d'énergie avec l'augmentation de T_b . Dans le gradient thermique, les juvéniles alimentés ont maintenu une T_b plus élevée. Dans l'enclos, la nourriture n'avait aucun effet significatif sur la sélection de T_b lorsque la radiation infrarouge était disponible 10 h·d⁻¹, mais lorsque la radiation infrarouge était disponible seulement 5 h·d⁻¹ les juvéniles alimentés ont maintenu une T_b plus élevée. Le taux métabolique a augmenté exponentiellement avec T_b avec un Q_{10} de 1.96 ± 0.10 (SD). Nous soutenons que, pour des tortues, le 95^e centile de la T_b sélectionnée (T_{upper}) est un meilleur estimé de la T_b optimale pour le gain d'énergie que l'étendue préferentielle de T_b (25^e au 75^e centile de la T_b sélectionnée) qui est généralement utilisée dans d'autres études. T_{upper} est demeurée à 30 °C dans tous les traitements, bien que T_b soit devenue de plus en plus biaisée vers T_{upper} pour les tortues alimentées et lorsque la radiation infrarouge était limitée. Nous concluons que T_{upper} se rapproche de la T_b optimale que les tortues alimentées tentent de maintenir.

Mots-clés : taux métabolique, température optimale, thermophilie postprandiale, thermorégulation, tortues des bois.

Nomenclature: Holman & Fritz, 2001.

Introduction

Temperature affects the speed of physiological reactions (Beitinger & Fitzpatrick, 1979; Huey, 1982). For heterotherms such as reptiles, physiological performance typically increases with temperature up to an optimal temperature (T_o) after which it decreases sharply (Huey, 1982). The primary function of behavioural regulation of body temperature (T_b) is to maximize energy gain rather than locomotory performance, and reptiles do so by regulating T_b to approach T_o whenever possible (Huey & Slatkin,

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1976; Angilletta, Hill & Robson, 2002). Regulating T_b to maximize the rate of energy acquisition, rather than locomotory performance, may be particularly important for turtles at northern latitudes, for 2 main reasons. First, turtles are largely protected from predation by their hard carapace and do not use rapid locomotion to capture food (Harding & Bloomer, 1979; Ernst, 2001). Second, for reptiles at northern latitudes food processing rate may be more constrained by temperature than by food availability (Congdon, 1989; Grant & Porter, 1992; Koper & Brooks, 2000). The general goal of our study was to explore the energetic implications of T_b selection by fed and fasted wood turtles.

In many reptiles, absorptive (fed) individuals select higher T_b than post-absorptive (fasted) individuals (Lang,

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1979; Heatwole & Taylor, 1987; Dorcas, Peterson & Flint, 1997; Blouin-Demers & Weatherhead, 2001a), although a few exceptions exist (Knight, Layfield & Brooks, 1990; Brown & Brooks, 1991). High T_b allows absorptive individuals to speed the processing rate (Stevenson, Peterson & Tsuji, 1985; Waldschmidt, Jones & Porter, 1986; Angilletta, 2001) and increase the rate of energy gain (Spencer, Thompson & Hume, 1998; Niu, Zhang & Sun, 1999). For this reason, we predicted that juvenile and adult male wood turtles would select higher T_b during the photophase when fed *ad libitum* than when fasted. In addition, we predicted that when basking time was limited, as commonly occurs in nature due to cloud cover and shade, fed turtles would regulate T_b more tightly around T_o in an effort to maximize food processing rate.

Over the range of body temperatures where heterotherms are active and feed voluntarily, the increase in net energy gain with temperature is explained primarily by the increase in food consumption and its passage rate (Greenwald & Kanter, 1979; Waldschmidt, Jones & Porter, 1986; Zimmerman & Tracy, 1989; Spencer, Thompson & Hume, 1998; Du, Yan & Ji, 2000; Koper & Brooks, 2000; Angilletta, 2001). In several reptiles, the thermal dependence of food consumption or passage rate is similar to the increase in metabolic rate with T_b at temperatures below T_o (Stevenson, Peterson & Tsuji, 1985; Dorcas, Peterson & Flint, 1997; Niu, Zhang & Sun, 1999). The correlation between food consumption and metabolic rate arises because digestive processes that influence digestion and passage rate (e.g., secretion, peristalsis) depend on metabolic rate (Skoczylas, 1978). Therefore, when food is available ad libitum, energy gain appears to be constrained by processes that are tightly correlated with metabolic rate. Andrews (1982) argued that metabolic rate limits growth rate in reptiles because both are related to body mass with a similar power. Thus, metabolic rate and food processing rate increase with T_b and should reflect the relative increase in energy gain, as long as T_b does not exceed T_o and food is not limiting (see Appendix I for a justification). For most reptiles, the increase in metabolic rate with T_{b} has a Q_{10} value between 2 and 3 (Bennett & Dawson, 1976). We predicted that the metabolic rate of juvenile and adult male wood turtles would increase with T_{b} with a Q_{10} value between 2 and 3 within the range of T_{b} for activity (16-32 °C; Ernst, 1986; Tuttle, 1996).

The concept of preferred (or set point) body temperature (T_{set}) has been used widely to estimate the T_b that maximizes physiological performance (Dawson, 1975; Stevenson, Peterson & Tsuji, 1985; Hertz, Huey & Stevenson, 1993; Autumn & De Nardo, 1995; Christian & Weavers, 1996; Shine & Madsen, 1996; Bedford & Christian, 1998; Brown & Weatherhead, 2000; Blouin-Demers & Weatherhead, 2001b). T_{set} is typically defined as the mean (Pough & Gans, 1982) or the central range (25th to 75th quartiles; Hertz, Huey & Stevenson, 1993) of selected T_b in an environment devoid of thermoregulation costs. These methods may be appropriate for the estimation of T_b that maximizes locomotion, but we argue that they may not be appropriate for estimating T_b that maximizes energy gain. Using a range of T_b implies that physiologi-

cal performance is stable inside that range, as is often the case with locomotion performance (Huey, 1982; Huey & Bennett, 1987; Blouin-Demers, Weatherhead & McCracken, 2003). Available data, however, indicate that food consumption, passage rate, and growth rate of ectotherms typically increase continuously to a peak To and decrease steeply thereafter with no performance plateau (Lillywhite, Licht & Chelgren, 1973; Stevenson, Peterson & Tsuji, 1985; Dorcas, Peterson & Flint, 1997; Niu, Zhang & Sun, 1999), although there are exceptions to this pattern (Kepenis & McManus, 1974; Waldschmidt, Jones & Porter, 1986; Ji, Du & Sun, 1996; Du, Yan & Ji, 2000). Thus, to maximize their energy gain, absorptive animals should select T_b that tend toward T_o , but should rarely allow T_b to exceed \overline{T}_o because the loss in performance (*i.e.*, the decrease in the rate of energy gain) is much steeper for temperatures exceeding T_o than for temperatures below T_o (Huey & Slatkin, 1976). For this reason, we expected the distribution of T_b for fed turtles to be negatively skewed (Dewitt & Friedman, 1979). In this context, the upper body temperature (T_{upper}) selected by animals in a thermal gradient, defined as the 95th percentile to exclude the most extreme T_b , should match T_o of digestive performance and hence energy acquisition. T_o for digestive performance of turtles and snakes is 29–30 °C (Parmenter, 1980; Stevenson, Peterson & Tsuji, 1985; Vandamme, Bauwens & Verheyen, 1991; Dorcas, Peterson & Flint, 1997), and T_o for developmental and growth rate for turtles is 30–31 °C (Niu, Zhang & Sun, 1999; Holt, 2000). Therefore, we predicted that T_{upper} would lie close to 30 °C and would match T_o for energy acquisition.

Methods

STUDY ANIMALS

Eight adult male (452-1128 g) and 8 juvenile (230-321 g) wood turtles (*Glyptemys insculpta*) were captured by hand or with dip nets in spring 2004 in Brome-Missisquoi County, southern Quebec, Canada. Each turtle was marked with a unique code by notching the carapace (Cagle, 1939). Adult males were identified by their concave plastron and longer, thicker preanal tail (Harding & Bloomer, 1979; Lovich, Ernst & McBreen, 1990; Farrell & Graham, 1991; Brooks et al., 1992). Individuals below 160 mm of carapace length could not be sexed and were classified as juveniles. Turtles were weighed $(\pm 1 \text{ g})$ with a digital balance, and maximum carapace and plastron lengths were measured $(\pm 1 \text{ mm})$ with a tree caliper. Turtles were brought to the Université de Sherbrooke for experiments and later released at their exact capture locations. Our procedures were approved by the Animal Care Committee at the Université de Sherbrooke (DT14), and capture permits were provided by the Société Faune et Parcs du Québec.

Turtles were kept in an indoor animal housing facility at 16–23 °C on a 15:9 (D:L) photoperiod, reproducing natural summer conditions. However, to facilitate metabolic measurements (see below), we shifted the turtles' photoperiod by $1 \text{ h}\cdot\text{d}^{-1}$ over a 3-week period so that lights turned on at 2300 and off at 1400. Adult males and juveniles were kept in separate communal enclosures (244 × 183 cm) where they had access to 3 water containers (183 × 70 × 10 cm) and 2 infra-red heating lamps (175 W). The lamps provided

an operative temperature of 40 $^{\circ}$ C in a 1-m² area at one end of the enclosure. Trout chow was provided *ad libitum* during the 3-week acclimation period.

To measure T_b , each turtle was equipped with a small temperature data logger (thermochron; model IBBat, Alpha Mach Inc., St-Hilaire, Quebec, Canada; 1 g) glued to the skin in the hind leg cavity. Thermochrons were calibrated prior to and after their use in a water bath at 3 temperatures. T_b was recorded every 30 min.

We used 2 methods to validate the use of external temperature loggers to measure T_b . In 2003, we implanted an iButton thermochron (model DS1921L, Maxim Integrated Products, Sunnyvale, California, USA; 3 g) in the coelomic cavity of 1 turtle (Edwards & Blouin-Demers, 2007). We then compared coelomic T_b to T_b recorded in the hind leg cavity. In 2004, we measured cloacal temperatures before and after each O_2 consumption and thermal gradient trial using a type-T thermocouple (model HH203A, Omega Engineering Inc., Stamford, Connecticut, USA).

TEMPERATURE SELECTION

We first measured temperature selection by allowing solitary individuals to move freely in a thermal gradient. The gradient (16 °C to 40 °C) was established in a box (244 × 60 × 60 cm) with a 4-mm-thick aluminium plate floor and plastic walls by circulating cooled water in copper tubing under one end of the floor and by heating the opposite end with heating cables. Turtles were left in the gradient for 24 h, but only the last 10 h (photophase) were considered for the T_b selection analysis. Hence, our results apply to the photophase only. Each turtle was tested once under fasted and twice under fed treatments (see below).

We also measured temperature selection by turtles that were housed in groups in the communal enclosures. The enclosure trials more closely reproduced natural conditions by providing access to water containers and basking sites. In the communal enclosures, turtles were subjected to 3 treatments of either 8 or 16 d, each preceded by a 5-d acclimation period. For the fasted treatment, turtles fasted for 5 d to ensure that they were post-absorptive. They were then placed in the enclosure for 8 d, during which time the heat lamps were turned on for 10 $h \cdot d^{-1}$. In the fed treatment, turtles were provided with food ad libitum for 16 d and the heat lamps were turned on for $10 \text{ h} \cdot \text{d}^{-1}$. In the time-constraint treatment, turtles were provided with food ad libitum for 16 d and heat lamps were turned on for $5 \text{ h} \cdot \text{d}^{-1}$. For analysis, we used T_b recorded during the photophase only, when heat lamps were turned on, excluding the first 90 min. During that time period, air temperature (T_a) in the enclosures varied from 20 to 23 °C, whereas water temperature (T_{water}) varied from 17 to 20 °C.

MEASUREMENT OF O_2 CONSUMPTION

Turtles were weighed and placed individually in opaque metabolic chambers (0.5 L for juveniles; 5 L for adults), which were then placed in a controlled-temperature refrigerator. Moist room air was pumped through each metabolic chamber during the first 3 h of the acclimation period. This period corresponded with the photophase and allowed T_b to equilibrate with the chamber temperature. At the begin-

ning of the scotophase, air was passed through a drierite scrubber and dry air was pumped through each chamber (200 mL·min⁻¹). A 100-mL·min⁻¹ subsample was then directed first through a drierite scrubber and then through an oxygen analyzer (Sable Systems FC-1, Henderson, Nevada, USA). The recording of O₂ concentration started after an additional 2-h acclimation period corresponding to the scotophase. A computerized data acquisition system (Sable Systems Datacan V, Henderson, Nevada, USA) controlled valves to calibrate the oxygen analyzers at the start and end of each trial with fresh scrubbed air $(20.94\% O_2)$ before reading and storing O2 concentration in the chamber outflow at 20-s intervals over \bar{a} 4-h trial. The resulting O₂ concentration curves were transformed to O_2 consumption using Equation [4a] from Withers (1977). To exclude bouts of activity, we calculated O_2 consumption $(V_{O_2} \text{ in } mL \cdot h^{-1} \cdot g^{-1})$ for each temperature as the average of the lowest V_{O_2} during a 30-min period. Trials where V_{O_2} never stabilized were excluded (14 of 80 trials). Each animal was tested at 5 experimental temperatures (16, 20, 24, 28, and 32 °C) covering the range of temperatures at which turtles are active in the field (Ernst, 1986; Tuttle, 1996). Because turtles had access to food in the enclosures prior to metabolic trials, our measures represent resting metabolic rate.

DATA ANALYSIS

We calculated the 5th, 25th, 50th, 75th, and 95th percentiles of the T_b distribution for each individual in each treatment. We then used the median values of all individuals to establish the value of the 5 percentiles for a given group in each treatment.

One adult male was excluded from T_b selection analyses because its temperature logger failed. Turtles were checked daily for the presence of their loggers, and the T_b recorded during the day when a turtle had lost its logger were excluded from analysis.

Oxygen consumption data were linearized using logarithmic models (Clarke & Fraser, 2004). The Q_{10} was established using the slope of the log (V_{O_2}) as a function of log (T_b) (Schmidt-Nielsen, 1997).

To control for repeated measures on individuals and some missing values, we used linear mixed models and included individual as a random factor, thus separating individual and treatment effects. Models were fitted by the restricted maximum log-likelihood (REML) procedure in R (R project version 1.9.1), and the significance of each independent variable was tested using a type III sum of squares. The normality of data and residual distributions were checked with quantile-quantile normal plots and distribution histograms. All means are reported \pm SE.

Results

BODY TEMPERATURE MEASUREMENT

External T_b measured in the hind leg cavity was highly correlated with internal T_b measured in the coelom $(r = 0.96, F_{1, 46} = 1063, P < 0.001)$ and with cloacal temperature $(r = 0.98, F_{1, 290} = 10\ 210, P < 0.001)$. Mean external T_b was significantly different from mean internal T_b (paired t = 4.20, df = 47, P < 0.001) but not significantly

different from mean cloacal temperature (paired t = 0.15, df = 291, P = 0.88). Because the mean difference between external and internal T_b (0.25 ± 0.41 °C) was less than the measurement error of the data loggers (± 0.5 °C), we conclude that external T_b measured in the hind leg cavity is an acceptable proxy for internal T_b.

MEAN SELECTED T_B

During the photophase in the thermal gradient, mean T_b was significantly higher in the fed treatment compared to the fasted treatment for juveniles $(3.45 \pm 0.59 \text{ °C})$, but not for adult males $(0.27 \pm 0.87 \text{ °C})$; Figure 1). Mean differences between treatments are the coefficients of the mixed model nested ANOVA (treatment: $F_{1, 11} = 20.51$, P < 0.001; age group $F_{1, 13} = 0.04$, P = 0.84; treatment × age group: $F_{1, 11} = 13.26$, P = 0.004).

During the photophase in the enclosures, there was no significant difference in mean T_b between fed and fasted individuals for either adult males $(2.75 \pm 1.43 \text{ °C})$ or juveniles $(0.73 \pm 1.00 \text{ °C})$ when heat lamps were on for 10 h·d⁻¹. Fed juveniles had higher mean T_b than fasted juveniles when heat lamps were on for 5 h·d⁻¹ ($2.56 \pm 0.96 \text{ °C}$), but this was not the case for adult males $(0.51 \pm 1.49 \text{ °C})$. Mean differences between treatments are the coefficients of the mixed model nested ANOVA (treatment: $F_{2,23} = 4.08$, P = 0.03; age group: $F_{1,13} = 2.92$, P = 0.11; treatment × age group: $F_{2,23} = 3.60$, P = 0.04).

OXYGEN CONSUMPTION

Oxygen consumption (V_{O_2} ; mL $O_2 \cdot h^{-1} \cdot g^{-1}$) increased with body temperature (Figure 2; $\log[T_b]$: $F_{47} = 4.16$, P = 0.04), but was unaffected by mass ($\log[mass]$: $F_{47} = 0.002$, P = 0.96), and there was no interaction between mass and temperature. Mass was then excluded from the model to calculate the effect of T_b on mass specific oxygen consumption. The equation describing the relation was

$$\log(V_{O_2}) = -3.70 + 1.92(\log[T_b])$$
[1]

with a Q_{10} value of 1.92 ± 0.10 .

 $\mathrm{T}_{\mathrm{UPPER}}$ and distribution of T_{B}

T_{upper} was 30 °C for all treatments, except for fasted juveniles (26 °C) and fed adult males (27 °C) in the thermal gradient. In the thermal gradient, the distribution of T_b for absorptive juveniles shifted to higher temperature, as indicated by the higher percentiles in the fed compared to the fasted treatments (Figure 3). As the mean T_b increased among treatments for juveniles in the enclosure, the 50th and 75^{th} percentiles shifted higher, but the value of T_{upper} remained stable at 30 °C (Figure 3). For adult males in the thermal gradient, the 75th and 95th percentiles shifted lower, indicating a tighter distribution around the median (Figure 3). In the enclosure, all percentiles, except the 95th, shifted higher for adult males that had access to food and 10 $h \cdot d^{-1}$ of heat lamps (fed treatment), compared to the other treatments (Figure 3). As for juveniles, the increase of mean T_b for adult males, although not significant, resulted in a shift of the 50th and 75th closer to the 95th percentile, while the T_{upper} remained stable at 30 °C.



FIGURE 1. Mean selected T_b of juvenile and adult male wood turtles in a thermal gradient and indoor enclosures for treatments where feeding status and availability of heat lamps differed. Mean T_b was calculated for each individual under each treatment. These means were then used to compute the population mean for each group (horizontal line in vertical boxes). Vertical boxes indicate the range in individual mean T_b , and the vertical line indicates the range of individual T_b . Letters indicate significant differences between treatments.



FIGURE 2. Oxygen consumption as a function of body temperature for adult male (open circles) and juvenile (filled circles) wood turtles. Axis scales are logarithmic, and each point represents the mean resting metabolic rate of an individual at a given temperature. The regression line was constructed based on the equation $\log(V_{O_2}) = -3.70 + 1.92(\log[T_b])$.



FIGURE 3. Percentiles (5th, 25th, 50th, 75th, and 95th) of body temperatures for juvenile and adult male wood turtles in a thermal gradient (white bars) and an indoor enclosure (grey bars) under treatments where feeding status and availability of heat lamps differed. Each value represents the median of all individual values of a given percentile for each group in a given treatment.



FIGURE 4. Net energy intake (gross energy intake × assimilation efficiency), net energy retention, and metabolic energy expenditure as a function of temperature for an 88 g *Trachemys scripta*. See Appendix I for Q_{10} and assimilation efficiency values. Note that net energy retention increases exponentially with increasing temperature, as do net energy intake and metabolic rate.

The distributions of T_b in the enclosures were generally wider than the ones obtained in the thermal gradient. The difference was the selection of $T_b \leq 20$ °C in the enclosure. These low T_b correspond with T_{water} (17–20 °C). Because T_a generally oscillated between 20 and 23 °C when heat lamps were turned on, we assume that $T_b \leq 20$ °C are associated with bathing.

Discussion

As predicted, fed juveniles selected higher mean T_b compared to fasted juvenile wood turtles in the thermal gradient during the photophase. The mean selected T_b of juveniles when fasted (23.1 °C) matches the T_b of 3 adult male wood turtles in another laboratory study (23.5 °C; Cabanac & Bernieri, 2000), while their mean selected T_b when fed (26.6 °C) approaches the mean T_b measured for 2 wood turtles in another study (27.5 °C; Nutting & Graham, 1993). During longer trials in enclosures, fed juveniles selected higher mean T_b only when basking time was constrained to 5 h·d⁻¹, which is the time period when operative temperatures ≥ 30 °C are available during summer in our study area (Dubois, 2006). This suggests that juveniles selected higher T_b as a compensatory mechanism to increase food passage rate and to make up for the processing rate limitation imposed by the short basking time and low T_a (16–17 °C) while heat lamps were off. Our metabolic rate calculations indicate that juveniles increase their rate of energy acquisition by selecting T_b closer to T_{upper} when fed.

Mean T_b during the photophase was not affected by the availability of food or basking time in adult males, as was the case in other studies where no postprandrial thermophily was detected (Knight, Layfield & Brooks, 1990; Brown & Brooks, 1991). This suggests that adult males did not need to maximize their energy gain as much as juveniles. Growth is almost nil in adult turtles (Wilbur, 1975; Lovich, Ernst & McBreen, 1990), fat reserves needed for hibernation are generally small for reptiles (2 to 3% of annual energy budget; Gregory, 1982), and males do not have to produce large egg clutches. Thus, maximizing energy gain is probably much less important for adult males than for juveniles.

Within the range of T_b experienced by active wood turtles (16 to 32 °C; Ernst, 1986; Tuttle, 1996), the thermal sensitivity of metabolism ($Q_{10} = 1.92 \pm 0.10$) was the same as the lower bound of the usual range for reptiles (between 2 and 3; Bennett & Dawson, 1976). Since the rate of energy gain is thought to be constrained by metabolism (Andrews, 1982), the energetic benefit of T_b regulation close to T_o is expected to increase with the thermal sensitivity of metabolic rate. Hence, the low thermal sensitivity of metabolism could partially explain the imprecise T_b regulation observed in this study. Also, the wider distributions of T_b selected in enclosures, partially due to access to cool water (≤ 20 °C), suggest a trade-off between hydration and the need for elevated T_b to speed food processing rate.

Since the metabolic rate increased continuously with $T_{\rm b}$, the rate of energy gain of fed turtles would be expected

to increase continuously with T_b up to T_o after which digestive performance decreases steeply while metabolic rate continues to increase. In that context, using a wide and variable range of T_b (e.g., 25–75th percentiles; Figure 3) to estimate T_o is inappropriate for animals whose fitness is tightly linked to energy acquisition. For example, the 25–75th percentiles range of fed juveniles in the thermal gradient (24– 29 °C) would mean no variation in the rate of energy gain for fed turtles at 24 °C and 29 °C, while the metabolic rate increases by 44% over this temperature range. Most studies, however, show that food intake increases exponentially to a T_b of ~30 °C, which results in a consistent increase in the net energy available for growth and reproduction up to ~30 °C (see Appendix I). Thus, we argue that it is more appropriate to use T_{upper} to estimate T_o of turtles.

 T_{upper} of fed turtles during the photophase was 30 °C as predicted, except for adult males in the thermal gradient (27 °C). T_{upper} corresponds to the maximal cloacal temperatures recorded in free-ranging wood turtles (30–32 °C; Ernst, 1986; Farrell & Graham, 1991; Ross et al., 1991; Tuttle, 1996). T_{upper} is also similar to the T_o for digestive performance of other reptiles (29–30 °C; food intake: Parmenter, 1980; digestion rate: Stevenson, Peterson & Tsuji, 1985; gut passage rate: Vandamme, Bauwens & Verheyen, 1991; passage rate: Dorcas, Peterson & Flint, 1997) and T_0 for developmental and growth rate of other turtles (Niu, Zhang & Sun, 1999; Holt, 2000). Moreover, T_{upper} was stable among treatments, while the frequency of T_b close to T_{upper} increased as turtles maintained higher mean T_b (Figure 3). This suggests that T_{upper} corresponds to T_o , after which food passage rate decreases sharply, as is the case in other reptiles for which T_b selection and digestive performance have been measured (Stevenson, Peterson & Tsuji, 1985; Dorcas, Peterson & Flint, 1997; Du, Yan & Ji, 2000). Similarly, the upper avoidance temperature for bluegill sunfish correlates with the temperature at which growth rate declines (Beitinger & Fitzpatrick, 1979).

In northern latitudes, temperature probably limits the energy acquisition of reptiles more than food availability (Congdon, 1989; Grant & Porter, 1992; Koper & Brooks, 2000). Thus, T_{upper} and the equation of metabolic rate as a function of T_b obtained in this study can be used to evaluate the processing advantage incurred through thermoregulation for field active turtles in northern latitudes.

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In this paper, we argue that the increase in metabolic rate (MR) with increasing body temperature (T_b) roughly parallels the increase in energy intake with T_b and, thus, the net energy that is available to an ectotherm for growth or reproduction. If this inference is correct, then the slope of the relationship between MR and T_b can be used to indicate the benefit of thermoregulating at levels up to, but not exceeding, the optimal body temperature. Here we provide empirical support for this argument.

Net energy retention (NER) at a given temperature is determined by the balance between energy intake and expenditure. This relationship is quantified as

> NER = (energy intake * assimilation efficiency) - (MR + urinary energy)

Because urinary energy losses (or urate losses) are generally < 5% of energy intake (Beaupre *et al.*, 1993), net energy retention can be approximated by

NER = (energy intake * assimilation efficiency) - MR

How NER varies over the range of temperatures at which ectotherms are active and feed voluntarily thus depends on the Q_{10} of food energy intake, the relationship between assimilation efficiency and food intake, and the Q_{10} of MR.

For turtles, the Q_{10} for food intake varies from 1.9 to 4.4 over temperatures ranging from 15 to 30 °C (Kepenis & McManus, 1974; Parmenter, 1980; Avery *et al.*, 1993; Spencer, Thompson & Hume, 1998; Niu, Zhang & Sun, 1999). This range of Q_{10} for food intake also applies to lizards and snakes (*e.g.*, Greenwald & Kanter, 1979; Harwood, 1979; Stevenson, Peterson & Tsuji, 1985; Waldschmidt, Jones & Porter, 1986; Vandamme, Bauwens & Verheyen, 1991; Dorcas, Peterson & Flint, 1997; Du, Yan & Ji, 2000; Angilletta, 2001), suggesting that those values are typical of most reptiles.

With the exception of a single study where Q_{10} exceeded 4.0 ($Q_{10} = 5.1$; Litzgus & Hopkins, 2003), the Q_{10} for stan-

dard MR for turtles varies from 1.6 to 3.3 over temperatures ranging from 15 to 30 °C (Gatten, 1974; 1978; Hailey & Loveridge, 1997; Niu, Zhang & Sun, 1998; Steyermark & Spotila, 2000; Litzgus & Hopkins, 2003). This range of Q_{10} for metabolic rate also broadly applies to lizards and snakes (Smith, 1976; Stevenson, Peterson & Tsuji, 1985; Beaupre, Dunham & Overall, 1993; Bedford & Christian, 1998; Angilletta, 2001; McCue & Lillywhite, 2002; Dorcas, Hopkins & Roe, 2004), again suggesting that those values are typical of most reptiles.

Assimilation efficiency, or apparent digestible coefficient, may decrease as food intake increases and passage time decreases, although this pattern is far from clear in the literature. For carnivorous species, assimilation efficiency lies in the range of 79.7 to 98.3% at 20 °C and 84.3 to 98.5% at 30 °C (Kepenis & McManus, 1974; Avery *et al.*, 1993; Zhang, Niu & Sun, 1996; Spencer, Thompson & Hume, 1998). For herbivorous species, assimilation efficiency is lower due to the high fibre content of the food; efficiency ranges from 40% at 20 °C to 49% at 30 °C (Spencer, Thompson & Hume, 1998). Therefore, assimilation efficiency is less sensitive to body temperature than metabolic rate or food intake.

As temperature increases, energy intake and energy expenditure increase, but assimilation efficiency may decline. The lowest level of NER is thus set by a combination of the lowest Q₁₀ for energy intake, the highest Q₁₀ for MR, and the lowest level of assimilation efficiency. To show how NER varies with temperature given the unfavourable combination of a low Q_{10} for energy intake (1.9), a high Q_{10} for MR (3.3), and the greatest loss of assimilation efficiency (98.3% at 20 °C; 84.3% at 30 °C), we used data for an 88 g Trachemys (= Pseudemys) scripta. At 20 °C, energy intake would be 20.55 kJ·d⁻¹ (Avery et al., 1993) and standard MR would be $0.0109 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ or $0.53 \text{ kJ} \cdot \text{d}^{-1}$ given 23.0 J·mL O₂⁻¹ (Gatten, 1974). Even under the most unfavourable combination, NER increases rapidly with increasing T_b and closely parallels energy intake because metabolic energy expenditure represents only 2-5% of energy intake (Figure 4).