ÉCOSCIENCE

Estimating the energetic significance of basking behaviour in a temperate-zone turtle[1]

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Abstract: Basking is a common thermoregulatory behaviour in many ectotherms, including reptiles. Because the key physiological processes affecting net energy retention (NER) are temperature dependent, ectotherms have the potential to modulate their energy budget by using basking behaviour. Many aquatic chelonians bask extensively. The energetic significance of basking is, however, largely unknown. We used biologging to measure the body temperature of free-ranging juvenile northern map turtles in Ontario, Canada. We measured the contribution of basking behaviour to the ability of turtles to reach their optimal body temperature for NER. We also used the predicted standard metabolic rate as a proxy to estimate the effects of basking on NER. Our results show that basking is essential for turtles to reach the optimal temperature for NER and suggest that basking behaviour allows turtles to increase their metabolic rate by 17.2 to 30.1%, which should translate into an even greater increase in NER. In addition, our results show that basking behaviour allows turtles to buffer the effects of climatic variations on their T_b and thus potentially on their energy budget. Collectively, our results suggest that basking behaviour has important ramifications for the energy budget, and by extension the fitness, of temperate-zone turtles.
Keywords: basking behaviour, net energy retention, northern map turtle, standard metabolic rate.

Résumé : Se réchauffer au soleil est un comportement de thermorégulation commun chez de nombreux ectothermes, y compris les reptiles. Puisque les processus physiologiques clés ayant un impact sur la rétention d'énergie nette (REN) dépendent de la température, les ectothermes ont le potentiel de moduler leur budget énergétique en utilisant le comportement de réchauffement au soleil. De nombreux chéloniens aquatiques le font énormément. La signification énergétique du réchauffement au soleil est cependant très peu connue. Nous avons utilisé la biotélémétrie pour suivre la température corporelle de tortues géographiques juvéniles en milieu naturel en Ontario, Canada. Nous avons mesuré la contribution du comportement de réchauffement au soleil à la capacité des tortues d'atteindre leur température corporelle optimale pour la REN. Nous avons aussi utilisé le taux métabolique standard prédit comme indicateur pour évaluer les effets de ce comportement sur la REN. Nos résultats montrent que se réchauffer au soleil est essentiel pour les tortues afin d'atteindre la température optimale pour la REN et suggèrent que ce comportement permet aux tortues d'augmenter leur taux métabolique de 17,2 à 30,1 %, ce qui devrait se traduire en une augmentation encore plus grande de la REN. De plus, nos résultats montrent que ce comportement permet aux tortues de réduire les effets des variations climatiques sur leur T_b et ainsi potentiellement sur leur budget énergétique. Dans l'ensemble, nos résultats suggèrent que le comportement de réchauffement au soleil a des ramifications importantes pour le budget énergétique, et par extension sur la valeur adaptative, des tortues des régions tempérées.
Mots-clés : comportement de réchauffement au soleil, rétention d'énergie nette, taux métabolique standard, tortue géographique.

Nomenclature: Le Sueur, 1817.

Introduction

Ectotherms, by definition, have limited capacity for metabolic heat production. Consequently, reptiles faced with important diurnal and seasonal temperature fluctuations, such as in temperate areas, rely largely upon behavioural thermoregulation to maintain their body temperature (T_b) within a specific range. Because T_b dictates the rate of most physiological processes, behavioural thermoregulation is expected to provide numerous physiological benefits that could ultimately increase fitness (Huey & Slatkin, 1976; Huey, 1991). The most important effect of T_b on fitness is likely through modulation of the energy budget (Huey & Slatkin, 1976; Congdon, 1989). The amount of energy available for growth or reproduction depends on many thermally sensitive processes, including metabolic rate (Gatten, 1974;

Kepenis & McManus, 1974), gut passage time (Parmenter, 1981; Avery *et al.,* 1993), and ingestion rate (Kepenis & McManus, 1974; Avery *et al.*, 1993). Thus, ectotherms have the potential to regulate their energy budget by behaviourally adjusting their T_b.

In reptiles, behavioural thermoregulation is common and includes behaviours such as selecting appropriate activity times (Crawford, Spotila & Standora, 1983; Sinervo & Adolph, 1994) and thermal microenvironments (Huey *et al.*, 1989; Adolph, 1990) as well as postural adjustments (Boyer, 1965; Seebacher, 1999). One of the most conspicuous thermoregulatory behaviours in ectotherms is basking: the exposure of at least part of the body to solar radiation while the animal is immobile. This behaviour is especially pronounced in freshwater turtles (Boyer, 1965). Indeed, many freshwater turtles commonly bask either at the surface of the water (aquatic basking) or completely emerged on substrates such as logs or rocks (atmospheric basking). Basking may serve multiple purposes, including enhancing

vitamin metabolism (Ferguson *et al*., 2003), desiccating leeches (Ernst, 1971), and creating fevers to fight infection (Monagas & Gatten, 1983). In addition, in temperate-zone freshwater turtles, basking yields important thermal benefits (Grayson & Dorcas, 2004; Bulté & Blouin-Demers, 2010), suggesting that the energetic benefits would also be high. The energetic significance of this conspicuous basking behaviour under natural conditions, however, remains largely unknown. In this study, we used biologging technology to measure T_b in free-ranging northern map turtles (*Graptemys geographica*) at the northern limit of their range. Our primary objective was to estimate the energetic significance of basking behaviour. We determined the extent to which basking behaviour allows these turtles to maintain the estimated optimal T_b for energy assimilation. We estimated the relative increase in energy assimilation that is realized by basking. Our second objective was to determine if northern map turtles use their thermal environment to maximize energy assimilation. We estimated the relative change in energy assimilation that turtles would experience if they were using all the available opportunities to maintain their T_b within the optimal range for energy assimilation. Determining how much reptiles deviate from optimal thermoregulation offers insights on the cost of thermoregulation (Blouin-Demers & Weatherhead, 2001). Basking behaviour in chelonians is particularly interesting from a cost–benefit perspective because this behaviour occurs largely outside the water in many turtles, including the northern map turtle. Thus, basking behaviour is mutually exclusive with other imperative activities, including foraging and mating, which both occur in water. As a third objective, we examined the effect of weather on basking behaviour and its energetic significance.

Methods

BIOLOGGING AND QUANTIFICATION OF BASKING BEHAVIOUR

We studied northern map turtles in Lake Opinicon, a small mesotrophic lake at the Queen's University Biological Station 100 km south of Ottawa, Ontario, Canada. From mid April to early May 2005 and 2006, we captured northern map turtles at a communal hibernation site. We surgically implanted temperature data loggers (Thermocron iButton DS 2422; Dallas Semiconductor, Sunnyvale, California, USA) in the abdominal cavity of 14 juvenile females (9 in 2005 and 5 in 2006). Details of the anaesthetic and surgical procedures are provided by Edwards and Blouin-Demers (2007). The loggers recorded T_b every 25 min between May and October. Each turtle with an implanted logger was also equipped with a radio-transmitter (SI-2FT or SB-2FT; Holohil Systems, Carp, Ontario, Canada). The radio-transmitters were bolted to the rear marginal scutes using stainless steel bolts. The combination of logger and radio-transmitter did not exceed 5% of the turtle's mass. The fall or spring following logger implantation, we recaptured turtles to remove the transmitters and the loggers. Analyses were performed on T_b collected between May 15 and August 15 of each year.

The turtles used in this study were small and thus rapidly reached thermal equilibrium with water when submerged.

For instance, painted turtles of equal size to our juvenile northern map turtles (*ca* 400 g) need approximately 11 min to cool 10 °C when submerged in water (Costanzo, 1982). We thus assumed that any time a turtle's T_b was above the maximum surface temperature of the water (S_{max}), the turtle was emerged and thus basking. We calculated hourly mean T_b for each individual. From the hourly means, we calculated the percentage of time spent basking for each individual as the percentage of T_b measurements exceeding S_{max}. Thus, we obtained a single measurement of time spent basking per individual per year. In our calculation of the percentage of time spent basking, we excluded nighttime T_b measurements (1900 to 0700) because basking only occurs during the day. To obtain hourly measurements of S_{max}, we measured water surface temperature at four locations in the lake with temperature loggers (Thermocron iButton DL 1922; Dallas Semiconductor, Sunnyvale, California, USA). We calculated hourly S_{max} as the maximum surface temperature of the 4 locations. The 4 locations were: 1 deep (7 m) open water site, 2 shallow open water sites (2–3 m), and 1 shallow (1 m) marsh. These sites were selected to capture the range of possible surface temperatures in the lake.

STANDARD METABOLIC RATE AND NET ENERGY RETENTION

We predicted the standard metabolic rate (SMR) of turtles from their T_b and used it as a proxy to estimate the effects of T_b on net energy retention (NER), the amount of energy available for growth and reproduction. Although predicting SMR from T_b is a linear transformation of T_b, SMR provides a better basis for interpreting the energetic implications of thermoregulation. Indeed, the physiological processes responsible for digestion, and thus energy retention, depend on metabolic rate (Dubois, Blouin-Demers & Thomas, 2008; Dubois *et al*., 2009). In addition, below the optimal temperature for NER, NER increases faster with T_b than SMR (Dubois, Blouin-Demers & Thomas, 2008). Thus, we argue that SMR is a conservative proxy to determine the relative change in NER with T_b as long as T_b is below the optimum temperature for NER (Dubois, Blouin-Demers & Thomas, 2008). Dubois, Blouin-Demers, and Thomas (2008) demonstrated that the optimal temperature (T_o) for NER matches the upper voluntary maximum T_b selected in a thermal gradient (T_{set}). In northern map turtles, T_{set} is between 28.7 and 32.5 °C (Bulté & Blouin-Demers, 2010). When predicting SMR from T_b, we excluded the T_b measurements above the upper bound of T_{set} (32.5 °C). T_b was above T_{set} only 2% of the time during the active season, indicating that at our latitude opportunities to maintain T_b above 32.5 °C are rare. We excluded these data because, in reptiles, SMR varies with T_b at a similar rate to food consumption or food passage only at T_b below T_o. Thus, at T_b above T_o the relationship between SMR and T_b no longer estimates the relationship between NER and T_b (Dubois, Blouin-Demers & Thomas, 2008).

As part of another study, we measured oxygen consumption in northern map turtles at 4 temperatures (14, 20, 26, and 32 °C) using open flow respirometry (see Bulté & Blouin-Demers, 2008 for details) in 6 juvenile females ranging in mass from 136 to 544 g and derived a predictive equation (Log $V0_2 = -6.40 + 3.36*\log T_b$; $R^2 = 0.76$) that

we used to predict SMR from T_b. We performed our respirometry measurements in June and July 2006.

DETERMINING THE ENERGETIC SIGNIFICANCE OF BASKING AND THE MAXIMAL NET ENERGY RETENTION

To quantify the energetic significance of basking, for each individual we calculated the relative change in SMR that turtles would experience if they could not bask to raise their T_b above S_{max}. To predict the SMR of turtles unable to bask, we used the realized field T_b of the turtles (measured with the implanted loggers) and replaced all the mean hourly T_b that were above S_{max} by S_{max} for the same hour. We thus "removed" the basking events from the actual field T_b measurements and predicted SMR from these modified data.

To determine if map turtles were thermoregulating to maximize NER, we measured the T_b that turtles could have achieved in the lake and at basking sites. We measured water temperature hourly with temperature loggers at 13 locations in Lake Opinicon. These locations were selected with the aim of representing the various habitats and depths available to turtles in Lake Opinicon. To determine the body temperatures available to turtles when basking, we used copper models of the same size and colour as juvenile females (Edwards & Blouin-Demers, 2007). The models were filled with water and placed on rocks and logs fully exposed to the sun because we wanted to capture the maximum available temperatures during basking. Model temperatures were also measured hourly with temperature loggers. Because the models were not used for the entire active season, we predicted temperature of models at basking sites with predictive equations based on microclimate data collected at a weather station located on the shore of Lake Opinicon. We used multiple regressions with air temperature, solar radiation, wind speed, and wind direction to obtain equations predicting the temperatures of all models at all times (Blouin-Demers & Weatherhead, 2001). The predictive equations explained most of the variation in model temperature ($R^2 > 0.81$).

To generate the thermal profile of a turtle maximizing NER for every hour during the active season, we used the available temperature (water temperature or physical model temperature) closest to T_{set} as our measure of T_b. Thus, when all available temperatures were below T_{set}, we used the maximum available temperature as T_b, and when available temperatures were above or within T_{set} for growth, we used the upper limit of T_{set} (32.5 °C) as T_b. As before, to determine the T_b of turtles in the absence of basking behaviour, we replaced all the T_b measurements above S_{max} with the mean surface temperature of the lake for the corresponding hour.

Results

Mean plastron length of turtles at recovery of the loggers was 138 mm (range: 123 to 151 mm), and there was no difference in percentage increase in plastron length between 2005 and 2006 (t-test: $t_{12} = 0.47$, $P = 0.65$, Table I). The percentage of mass uptake, however, was greater in 2005 than in 2006 (t-test: $t_{12} = 2.52$, $P = 0.03$, Table I). The average mass at recovery in 2005 was 467 g (range: 384 to 558 g) compared to 379 g (range: 298 to 495 g) in 2006 (Table I).

The mean surface temperature of the lake was higher in 2005 than in 2006, except in May (Figure 1). Overall, juvenile female northern map turtles were able to raise T_b substantially above S_{max} (Figure 2). The percentage of T_b measurements above S_{max} during daylight hours was

TABLE I. Mean (range) mass and length at implantation and recovery of juvenile female northern map turtles (n = 14 individuals) from Lake Opinicon, Ontario, Canada in 2005 and 2006.

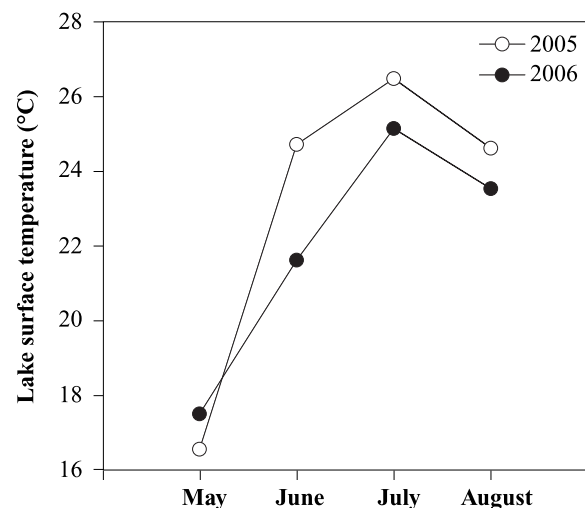|		2005	2006
Mass (g)	Implantation	325 (260–376)	299 (250–376)
	Recovery	467 (384–558)	379 (298–495)
Plastron length (mm)	Implantation	127 (123–134)	121 (114–136)
	Recovery	141 (132–151)	132 (123–148)

FIGURE 1. Monthly mean surface water temperature in Lake Opinicon, Ontario, Canada in 2005 and 2006.
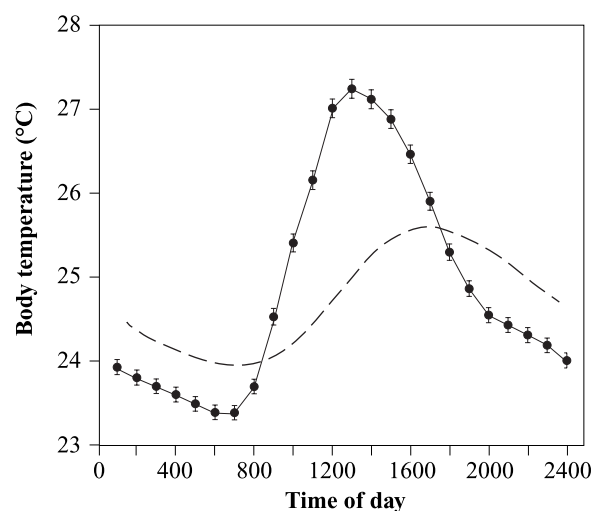

FIGURE 2. Mean hourly body temperature (2005 and 2006 combined) of juvenile female northern map turtles (n = 14 individuals) from Lake Opinicon, Ontario, Canada. Hourly mean maximum (n = 4 sites) water surface temperature is indicated by the dashed line. Error bars indicate standard error.

higher in 2006 than in 2005 (*t*-test; $t_{11} = -2.26$, $P = 0.04$). In 2005, 43.6% (range: 36.7 to 51.5%) of the T_b measurements exceeded S_{max}, compared to 53.0% (range: 40.0 to 67.8%) in 2006. In 2005, S_{max} was within T_{set} 28% of the daylight hours compared to 5.4% in 2006. The percentage of T_b measurements within T_{set} during daylight hours was higher in 2005 than in 2006 (*t*-test; $t_{11} = 3.04$, $P = 0.01$). In 2005, 24% (range: 17.8 to 30.8%) of the T_b measurements were within T_{set}, compared to 18% (range: 14 to 20.5%) in 2006 (Figure 3). When T_b could not exceed S_{max} (*i.e.*, we removed basking events by substituting S_{max} for T_b when T_b exceeded S_{max}), T_b measurements within T_{set} during daylight hours declined to 5.0% (range: 3.7 to 6.6%) in 2005 and to 0.1 % (range: 0 to 0.3%) in 2006 (Figure 4). The available body temperatures sampled throughout the lake indicated that turtles would have been able to maintain their T_b within T_{set} 50.2 % of the daylight hours in 2005 and 41.2% of the daylight hours in 2006.

In 2005, 82% of the T_b measurements within T_{set} of map turtles occurred when T_b exceeded S_{max} (*i.e.*, when turtles were basking) compared to 99% in 2006. The SMR predicted from the actual field T_b of map turtles was higher than the SMR predicted from the modified data in which we removed basking by preventing T_b from exceeding S_{max}. The relative decrease in SMR was greater in 2006 than in 2005. When T_b could not exceed S_{max} (*i.e.*, when we removed the basking events), predicted SMR of map turtles decreased by 20.2% (range: 17.1 to 26.0%) in 2005 and by 27.7% (range: 21.2 to 30.2%) in 2006. Always selecting the available temperatures that maximize NER (perfect thermoregulation with respect to energy acquisition) would translate to a mean increase in predicted SMR of 33.2% (range: 24.4 to 41.9 %) compared to the SMR experienced by map turtles in Lake Opinicon.

Discussion

The main objective of our study was to quantify the energetic significance of basking behaviour in a temperate-zone turtle. Our results suggest that basking behaviour deeply affects the energy budget of northern map turtles. We showed that basking behaviour is essential for juvenile female northern map turtles to reach their optimum temperature for NER. Indeed, turtles were basking at least 91% of the time (both years combined) when T_b was within T_{set}.
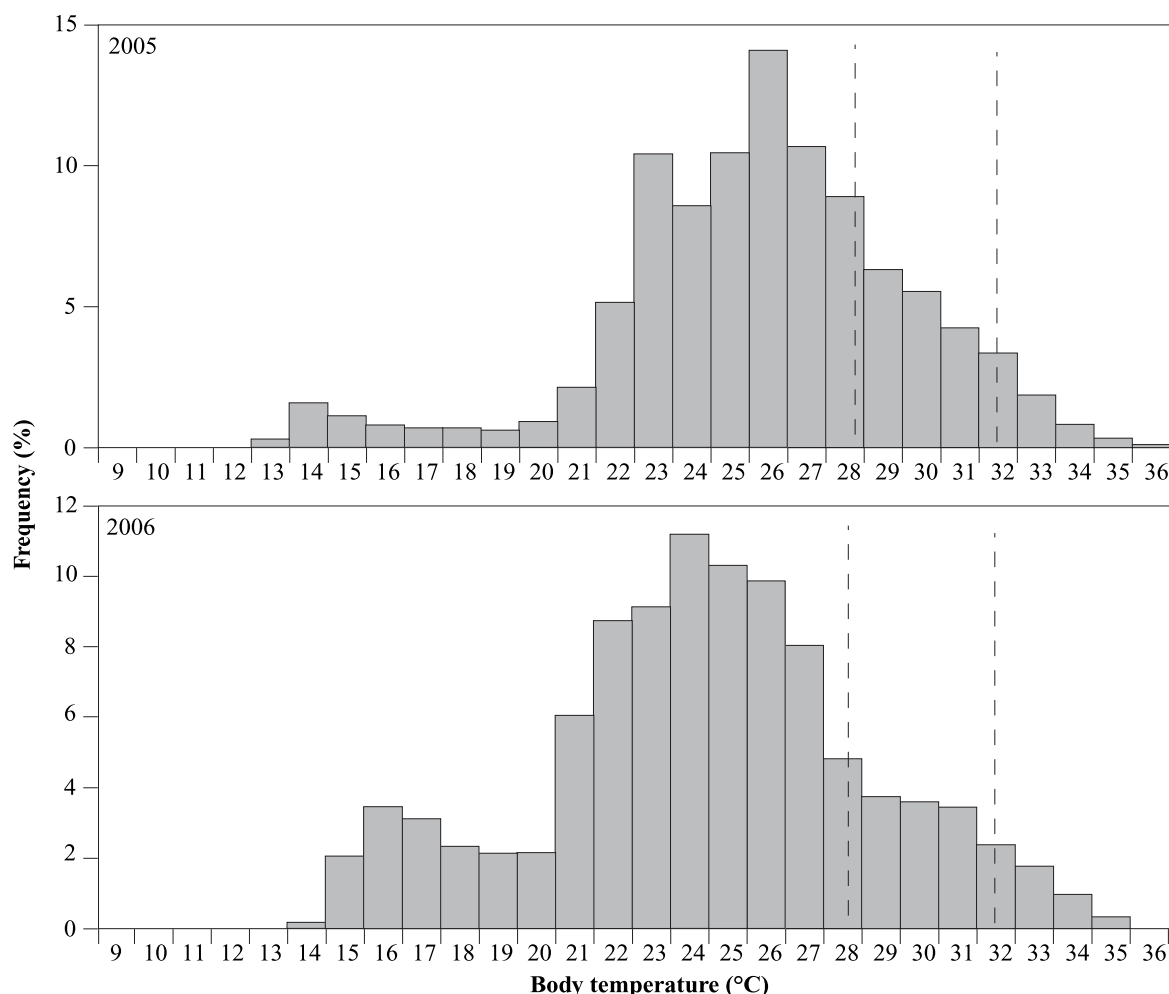

FIGURE 3. Frequency distribution of estimated body temperatures of juvenile female northern map turtles (*n* = 14) in Lake Opinicon, Ontario, Canada between the hours of 0700 and 1900 in 2005 and 2006. The dashed lines indicate the estimated optimal temperature range for net energy retention.
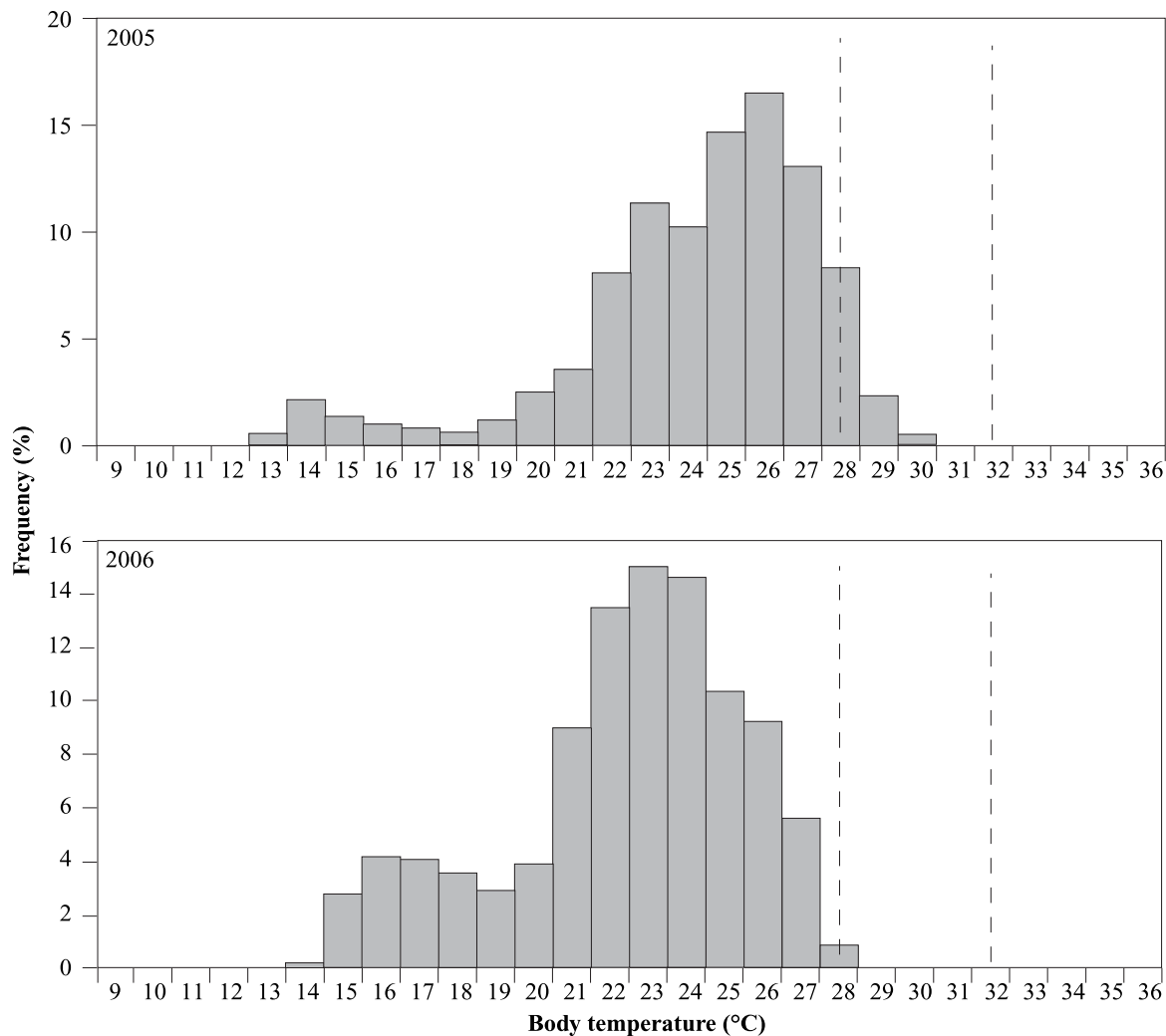
FIGURE 4. Frequency distribution of estimated juvenile female northern map turtle ($n = 14$) body temperatures when basking is excluded in Lake Opinicon, Ontario, Canada between the hours of 0700 and 1900 in 2005 and 2006. The dashed lines indicate the estimated optimal temperature range for net energy retention.

In addition, if map turtles had not been able to bask they would have sustained decreases in SMR ranging from 17.2 to 30.1%. Such decreases in SMR would conceivably be accompanied by an even greater decrease in NER because the Q_{10} for NER is typically greater than for SMR (Dubois, Blouin-Demers & Thomas, 2008).

Although basking behaviour clearly brings some important energetic benefits, our estimates indicate that juvenile northern map turtles are not thermoregulating to the maximum extent possible to increase NER. A hypothetical turtle maximizing NER via perfect thermoregulation would be able to increase its SMR by 33.2% according to our estimates. The disinclination of turtles to maximize NER in their thermal environment could reflect limited thermoregulation opportunities, a trade-off between thermoregulation and other activities, or a trade-off between competing physiological processes. Basking competition (Lovich, 1988) seems an unlikely explanation for the disinclination of map turtles to maximize NER because map turtles commonly bask on top of one another and basking

sites do not appear to be limited in our study area (G. Bulté, pers. observ.). We did not measure the availability of the achievable T_b in the environment, so we cannot rule out the possibility that turtles could not thermoregulate to maximize NER because of limited opportunities to bask, but as explained above this seems unlikely given the availability of basking sites in Lake Opinicon. We did measure achievable T_b in environments that were seemingly broadly available to turtles, however.

A more probable explanation for imperfect thermoregulation is that turtles are not maximizing NER through basking due to a trade-off between the costs and benefits of thermoregulation (Huey & Slatkin, 1976). Basking behaviour occurs largely out of the water in map turtles. This behaviour thus conflicts with other activities, including foraging. In our modelling of the maximal NER that could be achieved through perfect thermoregulation, we assumed that foraging time only represents a minor portion of map turtle time budget and that T_b is the limiting factor on NER. We felt this was reasonable because foraging time is likely short

relative to processing time in freshwater turtles (Congdon, 1989). For instance, the predicted digestive turnover rate at 27 °C in the painted turtle (*Chrysemys picta*) is 42 h (Parmenter, 1981). At our study site, the density of banded mystery snails (*Viviparus georgianus*) and zebra mussels (*Dreissena polymorpha*), the main prey items of map turtles, averaged 35 and 2592 individuals·m^{-2}, respectively (Bulté, Gravel & Blouin-Demers, 2008). Thus, the time required for turtles to fill their digestive tract is likely much shorter than the digestive turnover. During daylight hours, map turtles spend on average at least 46.0% of their time basking. The high proportion of the time budget devoted to basking supports the idea that T_b is an important bottleneck on NER. To maximize NER via thermoregulation, however, map turtles would have to be basking on average 73.8% of the time during daylight hours. Such an important time investment in basking could conceivably impede foraging time or other activities. In addition, although NER is likely the most important benefit of basking in turtles, other key physiological processes, such as immunological processes, may be maximized at different T_b than NER. Thus, the realized T_b of map turtles may also represent a trade-off between multiple optima (Angilletta, Niewiarowski & Navas, 2002). Dubois *et al.* (2009) performed the same analysis with wood turtles at similar latitude. They found that if wood turtles were using the thermal environment to maximize NER, they would increase their NER by up to 93%. This interspecific difference in potential NER suggests that costs of thermoregulation are lower in northern map turtles than in wood turtles.

We found marked differences in basking behaviour and its energetic significance between the 2 y of the study. In the cooler year (2006), turtles spent nearly 10% more time basking during the day, but their T_b was 11% less often within T_{set} than in the warmer year (2005). The mass increase of turtles was on average 20% higher in the warmer year. Thus, according to our estimates, turtles plausibly experienced lower NER due to lower T_b in the cooler year. The mean predicted SMR was 13% lower in the cooler year. These results support the idea that weather is a strong determinant of the energy budget of reptiles (Sinervo & Adolph, 1994; Angilletta, 2001). Nevertheless, basking behaviour seemingly allows turtles to buffer the effects of weather on NER. Indeed, the predicted SMR would have been 22% lower in the cooler year, as opposed to 13%, without the possibility of basking.

Collectively our data suggest that basking behaviour has considerable energetic implications. Basking behaviour has important ramifications for the energy budget, and by extension the fitness, of temperate-zone turtles. Indeed, NER dictates the energy available for growth and reproduction. These results were not entirely unexpected, because the thermal significance of basking behaviour in temperate-zone turtles has already been established (Grayson & Dorcas, 2004; Bulté & Blouin-Demers, 2010). Yet, to our knowledge the energetic significance of basking had never been quantified. In addition, our results show that basking behaviour allows turtles to buffer the effects of seasonal variation in environmental temperature on their T_b, and thus by extension on their energy budget.

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