Thermoregulation and habitat selection in wood turtles *Glyptemys insculpta*: chasing the sun slowly

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Summary

1. It is widely accepted that reptiles are able to regulate behaviourally their body temperature (T_b) , but this generalization is primarily based on studies of lizards and snakes in the temperate zone. Because the precision of T_b regulation may vary considerably between taxa and over geographical ranges, studies of semi-terrestrial turtles in climatic extremes are relevant to the understanding of reptilian thermoregulation.

2. We studied thermoregulation in 21 free-ranging wood turtles (*Glyptemys insculpta*) at the northern limit of their range in Québec, using miniature data loggers to measure their internal $T_{\rm b}$ and external temperature ($T_{\rm ext}$) continuously. We simultaneously recorded the available operative environmental temperature ($T_{\rm e}$) using 23 physical models randomly moved within each habitat type, and we located turtles using radiotelemetry.

3. The habitat used by wood turtles was thermally constraining and the target temperature (T_{set}) was only achievable by basking during a short 5-h time window on sunny days. Wood turtles did show thermoregulatory abilities, as determined by the difference between turtle T_b distribution and the null distribution of T_e that resulted in T_b closer to T_{set} . Although most individuals regulated their T_b between 09.00 h and 16.00 h on sunny days, regulation was imprecise, as indicated by an index of thermoregulation precision (| $T_b - T_{set}$ |).

4. The comparison of habitat use to availability indicated selection of open habitats. The hourly mean shuttling index ($|T_{ext} - T_b|$) suggested that turtles used sun/shade shuttling from 09.00 to 16.00 h to elevate their T_b above mean T_e .

5. Based on laboratory respirometry data, turtles increased their metabolic rate by 20-26% over thermoconformity, and thus likely increased their energy gain which is assumed to be constrained by processing rate at climatic extremes.

Key-words: behavioural thermoregulation, biologging, energetics, terrestrial turtle

Introduction

Temperature reflects the average kinetic energy of a biochemical system, so changes in temperature dramatically alter the rate of all physiological functions (Beitinger & Fitzpatrick 1979). For this reason, body temperature (T_b) regulation is inextricably linked to the ecology of ectotherms (Heatwole & Taylor 1987; Berman & Quinn 1991). Moreover, understanding how living organisms respond to temperature is a key step to predict the consequences of climate change on populations (Parmesan & Yohe 2003; Kearney, Shine & Porter 2009). Thermoregulation

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should aim to maintain T_b as close as possible to an optimal temperature (T_o ; Huey & Slatkin 1976) where fitness is maximized through improvements in performance (Huey & Kingsolver 1989). Because reptiles generate negligible amounts of body heat and have limited physiological control over T_b , they regulate their T_b largely through habitat selection and behaviour. The exception is one of the largest (> 500 kg) reptile, the leatherback turtle, which can remain warm in near-freezing water (James, Davenport & Hays 2006). Thus, for most reptiles we expect a strong link between habitat use and thermoregulation (Blouin-Demers & Weatherhead 2002), especially at climatic extremes where the environment is constraining (Blouin-Demers & Weatherhead 2001). Here our general goal is to explore the relationship between thermoregulation and habitat use in wood turtles, *Glyptemys insculpta* (Le Conte, 1830[1829]), near the northern limit of their range.

Reptiles are able to regulate their $T_{\rm b}$ to some extent (Avery 1982; Huey 1982; Hertz, Huey & Stevenson 1993), but the precision of $T_{\rm b}$ regulation varies considerably (Adolph 1990; Rummery et al. 1995; Dorcas & Peterson 1998). Since the ecological costs and physiological benefits associated with thermoregulation are largely independent (Huey & Slatkin 1976), the evolutionarily optimal temperature may be different from the physiological optimum. Thus, variation in the costbenefit ratio is assumed to underlie variation in thermoregulatory precision. The cost-benefit model of thermoregulation (Huey & Slatkin 1976) predicts that thermoregulation should cease when the costs outweigh the benefits. Two costs of thermoregulation are predation risk (Pianka & Pianka 1970; Huey 1982) and the reduction in time for other nonthermoregulatory activities such as foraging (Huey & Slatkin 1976; Gregory, Crampton & Skebo 1999). The primary benefit of thermoregulation is the improvement in physiological performances, which can be grouped in two broad categories: locomotory (Huey 1982; Stevenson, Peterson & Tsuji 1985; Blouin-Demers, Weatherhead & McCracken 2003) and energy intake (Beaupre, Dunham & Overall 1993; van Marken Lichtenbelt, Vogel & Wesselingh 1997; Niu, Zhang & Sun 1999).

Energy intake is often more sensitive to T_b than locomotion (Huey 1982; Stevenson *et al.* 1985; Angilletta Jr, Hill & Robson 2002) and the benefit of enhanced locomotion is likely to be trivial for turtles that do not use rapid locomotion to capture food or to escape predators (Harding & Bloomer 1979; Ernst 2001). Moreover, turtles are long-lived iteroparous organisms with low and unpredictable annual reproductive success and high adult survival (Congdon, Dunham & Sels 1993; Ernst, Barbour & Lovich 1994). Fitness is thus likely to be tied more closely to energy gain than to locomotion in turtles. Therefore, the cost-benefit relationship of thermoregulation likely differs for turtles compared to lizards and snakes from which most of our understanding of reptilian thermoregulation is drawn.

The main benefit of thermoregulation for freshwater turtles, increased energy gain, should be higher in climatic extremes. At high latitudes, temperature can be viewed as an ecological resource (Magnuson, Crowder & Medvick 1979; Tracy & Christian 1986) that may limit growth and reproduction of ectotherms more than food availability because food processing rate is constrained by low temperatures and short growing seasons (Congdon 1989; Grant & Porter 1992; Niewiarowski 2001). Indeed, studies have shown that growth of turtles (Koper & Brooks 2000) and snakes (Brown & Weatherhead 2000), and clutch frequency in turtles (Rollinson & Brooks 2007), increase with air temperature (T_a) in northern climates. An increase in energy gain through careful regulation of $T_{\rm b}$, metabolism, and food processing capacity should increase allocation to growth and reproduction, allowing for earlier age at maturity and higher fecundity and clutch frequency in turtles. In southern Canada, only 7% of female wood turtles reproduce annually (Foscarini 1994).

To demonstrate thermoregulation, two criteria must be met. First, the distribution of $T_{\rm b}$ must differ significantly from a null or random distribution which represents $T_{\rm b}$ of hypothetical thermoconforming animals (Hertz et al. 1993; Wills & Beaupre 2000). Second, $T_{\rm b}$ of the animals must deviate directionally from the null distribution such that $T_{\rm b}$ approaches the target temperature (Hertz et al. 1993). For instance, behavioural thermoregulation has recently been demonstrated in loggerhead sea turtles at the limit of their breeding range with turtles actively selecting patches of warm water (Schofield et al. 2009). Thermoregulation might similarly be expected in freshwater turtles at climatic extremes. In this study, we used miniature data loggers to measure available operative environmental temperatures (T_e) , internal T_b , and external carapace temperatures (T_{ext}) in wood turtles. We assume that the $T_{\rm b}$ that turtles seek to maintain $(T_{\rm set})$ is 30 °C, based on their choice in a laboratory thermal gradient (Dubois, Blouin-Demers & Thomas 2008). Based on costbenefit arguments, we predicted that wood turtles would be precise thermoregulators. In addition, there is a strong link between habitat use and thermoregulation (Adolph 1990; Grover 1996; Blouin-Demers & Weatherhead 2002). Wood turtles prefer open habitats such as alder stands (Kaufmann 1992; Compton, Rhymer & McCollough 2002; Arvisais et al. 2004) which may be driven by thermoregulation needs (Tuttle 1996; Arvisais 2000; Compton et al. 2002). We predicted that wood turtles would select open habitats and use sun/shade shuttling to regulate $T_{\rm b}$ close to $T_{\rm set}$.

Materials and methods

STUDY SITE

We conducted this study during summer 2004 in Brome-Missisquoi County in southern Québec. The study area was a 7-km section of meandering river surrounded by flood plains and higher nonflooded terraces. Half of the study site was open habitat: active or abandoned hay fields, successional fields with herbaceous and shrub vegetation, wetlands, and lawns. The other half was closed woodland habitat dominated by alder (*Alnus rugosa*) stands or mixed deciduous forest.

CAPTURE, RADIOTELEMETRY, AND BODY TEMPERATURE MEASUREMENT

Turtles were captured by hand and marked with a unique code by carapace notching (Cagle 1939). Adult males were recognized by their concave plastron and longer, thicker pre-anal tail (Lovich, Ernst & McBreen 1990; Brooks *et al.* 1992). Individuals smaller than 160 mm carapace length were considered juveniles.

Seven males, females, and juveniles (21 turtles; 330-1200 g; 132-215 mm carapace length) were equipped with radiotransmitters and temperature data loggers. Turtles were injected with ketamine intramuscularly (40 mg kg⁻¹) 30 min before surgery and were maintained at a surgical plane of anaesthesia with isoflurane. A temperature data logger (Dallas iButton thermochron (Sunnyvale, California, USA) model DS1921L; 3 g) was implanted in the coelomic cavity through an incision made just anterior to the hind leg. After surgery, turtles were kept under observation for 5 to 7 days before release at their capture site. A radiotransmitter (Holohil Systems, Carp, Ontario, Canada, model AI-2F for adults or model SI-2F for juveniles) was affixed with stainless steel bolts to the posterior margin of the carapace for adult males and juveniles, and to the anterior margin for adult females to minimize interference during copulation. A second temperature data logger was mounted on top of the radiotransmitter. The implanted logger was used to measure internal $T_{\rm b}$ and the second logger to measure $T_{\rm ext}$. All data loggers used in the study were calibrated in a water bath from 5 °C to 50 °C. The protocol was approved by the Animal Care Committee at the Université de Sherbrooke (DT14) and permits were provided by the Société Faune et Parcs du Québec.

TELEMETRY AND TEMPERATURE RECORDING

Turtles were located two to four times weekly from 1 June to 2 August for a total of 478 locations. Each day, the tracking sequence was chosen randomly to ensure that individuals were located at different times from 08.00 to 19.00 h. The implanted data loggers recorded $T_{\rm b}$ at 30-min intervals from 24 June to 4 August. The data loggers mounted on the radiotransmitters recorded temperature at 10-min intervals and were downloaded ~ every 15 days because of their limited storage capacity (2048 readings).

HABITAT USE

Turtle locations were mapped with a global positioning system (GPS) with 3–10 m accuracy (mean = $8 \cdot 2$ m). During a pilot study, we noted vegetation cover at 452 turtle locations and paired random points within a 50-m radius (see below) of the turtles' locations to define cover type classes as forest, alder, shrub (< 2 m tall), herbaceous, graminoid (hayfield, flood plain, and wetlands), bare ground (lawn and bare soil), and river. In 2004, we characterized 478 turtle locations (21 to 25 characterizations per individual, mean = 23.5).

We characterized all available habitats within the study site with digital orthophotos (1:5000 scale) in ARCVIEW 3·2 (ESRI, Redlands, California, USA). Turtles were located at most 250 m from the river. We superimposed a grid, composed of 25×25 m squares, on a 250-m buffer area bordering the river. We determined the proportion of each of the 2838 grid squares covered by closed habitat (alder and forest), open habitat (shrub, herbaceous, graminoid, and bare ground), and river to the nearest 20%.

To determine the habitats available to turtles, we developed an index that we term *truly available habitat area* (TAHA). Because 75% of movements between consecutive locations were ≤ 50 m, we considered that all habitats within a 50-m radius of a turtle's location were available. Therefore, we used the 100-m wide corridor linking successive locations as the TAHA. All 1822 grid squares encompassed in the TAHA were ground truthed: we recorded the proportion of each cover type (forest, alder, shrub, herbaceous and graminoid) to the nearest 20%.

We compared habitat use to habitat availability at two scales: the entire study site and the TAHA. The first scale was to test whether turtles' TAHA were randomly dispersed in the study site, while the second scale was to test whether turtles were randomly located in their TAHA. At the study site scale, habitat availability was the sum of the grid squares in the study site and habitat use was the sum of grid squares in TAHA of all turtles. At the TAHA scale, habitat availability was the sum of grid squares in turtles' TAHA and habitat use was the sum of turtles' locations. For this analysis, the five terrestrial cover types were classified as closed habitat (alder and forest) and open habitat (shrub, herbaceous, graminoid, and bare ground) and χ^2 tests were used to compare availability to use at each scale.

OPERATIVE ENVIRONMENTAL TEMPERATURES

Operative environmental temperature (T_e) integrates the effects of T_{a} , wind, and solar radiation to infer the temperature that an ectotherm would attain at a given point and time (Bakken & Gates 1975). We used 23 rectangular water-filled plastic containers $(180 \times 10 \times 60 \text{ mm})$ painted to approximate the colour and reflectance of a wood turtle carapace to act as ' T_e thermometers' (Tracy 1982; Bakken 1992). These models did not reproduce the exact size and shape of wood turtles, but studies have demonstrated that model shape, size, and colour have minor effects on T_e (< 1 °C on mean T_e ; Vitt & Sartorius 1999; Shine & Kearney 2001). A data logger placed in each model recorded temperature at 30-min intervals. We confirmed the accuracy of T_e measures by recording simultaneously the temperatures of four models and four turtles (carapace length 145–182 mm, mass 452–1050 g) on bare ground in an outdoor enclosure.

The expected null distribution of T_b for thermoconforming animals can be obtained by randomly sampling the thermal environment (Hertz *et al.* 1993). We reduced the number of models required to sample adequately spatial and temporal variation in T_e over the entire study site by using a combination of stratified and random sampling. We placed four models in each of the five cover types, one model on bare ground to measure the maximal available T_e , and two data loggers in the river. Models were randomly moved within their cover type once a day (5 days week⁻¹) to capture spatial heterogeneity encountered by a randomly moving turtle within a given cover type.

The null T_e distribution of a thermoconforming control for each turtle was obtained by first randomly picking one of the 23 models where the probability that a particular model was picked reflected the proportional vegetation cover type available in the TAHA of a given turtle. Once a model was chosen, the entire model's temperature data set (2048 readings) was used. Loggers in models and in turtles recorded temperatures during identical time periods, so picking the entire model's temperature data set allows us to control for temporal variation in model and turtle samples, revealing the spatial variation only. This procedure was repeated 150 times with replacement to generate the null T_e distribution for a given turtle.

THERMOREGULATION ANALYSES

Thermoregulation indices are often based on differences between an average animal's T_b and an average control's T_e (Hertz *et al.* 1993; Brown & Weatherhead 2000; Blouin-Demers & Weatherhead 2001). Hertz *et al.* (1993) argued that mean values can be misleading because they lose information about underlying distributions and variability. This is especially relevant for T_b and T_e distributions which are rarely normally distributed (Dewitt & Friedman 1979; Wills & Beaupre 2000). We tested for differences between T_b and null T_e distributions with Kolmogorov–Smirnov tests (Blouin-Demers & Weatherhead 2008) and used the *D*-statistic as a thermal selection index (TSI) to quantify the extent of departure from thermoconformity.

We then verified that turtles' T_b deviated directionally from thermoconformity such that T_b approached T_{set} . T_{set} should approximate T_o and is often defined as the central 50% range (25– 75% quartiles) of preferred T_b of post-absorptive animals in a thermal gradient (Hertz *et al.* 1993; Christian & Weavers 1996; Blouin-Demers & Weatherhead 2001). Due to low T_a and a short growing season at

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our northern latitude, the ability to digest and pass food rather than to find and ingest food is likely to limit energy acquisition (Congdon 1989; Koper & Brooks 2000; Niewiarowski 2001), so we expect T_{set} to maximize food processing rate. As argued elsewhere (Dubois *et al.* 2008), energy intake from processed food increases much faster than metabolic rate, thus increasing net energy retention at T_b below T_o . We defined T_{set} (30 °C) based on the upper selected T_b (95% percentile) of fed animals in laboratory settings, which more closely approximates T_o for energy acquisition compared to a range of preferred T_b that assumes a performance plateau (Dubois *et al.* 2008). Our approach is thus similar to that used by Huey and Slatkin (1976). We calculated the accuracy of T_b (d_b) by the deviation of T_b from T_{set} (] $T_b - T_{set}$]; Hertz *et al.* 1993).

To analyse the use of sun/shade shuttling as a behavioural adjustment for thermoregulation, we created a shuttling index based on our continuous temperature recordings. The shuttling index was the absolute difference between a turtle's external temperature (T_{ext}) and its internal T_b (| $T_{ext} - T_b$ |). Without solar radiation, T_{ext} should track T_b such that $T_{ext} \approx T_b$. T_{ext} and T_b should deviate when a turtle moves into the sun ($T_{ext} > T_b$) or when a turtle moves into the shade after basking ($T_{ext} < T_b$).

STATISTICAL ANALYSES

Sunny and cloudy days (> 5 h and \leq 5 h of sun, respectively) were analysed separately because they represent different thermal conditions. Thermoregulation analyses were restricted to temperature data from six each for males, females, and juveniles, and from 22 physical models. We lost one juvenile turtle and one physical model and two implanted data loggers failed. T_{ext} data were incomplete for most individuals (4761 to 5709 T_{ext} /turtle) because of data logger loss or impossibility of downloading before the memory was full.

To control for repeated measures on individuals and some missing values, we used nested linear mixed models with individual intercepts as a random factor, thus separating individual and treatment effects. Models were fitted by the lme function with restricted maximum log-likelihood (REML) in software R (R project version $1\cdot9\cdot1$). The significance of each independent variable was tested with type III sums of squares. Normality of residuals was checked with quantile–quantile normal plots and distribution histograms. Data are presented as means ± 1 SD.

Results

OPERATIVE ENVIRONMENTAL TEMPERATURES

In the outdoor enclosure, T_b of turtles were highly correlated with the temperatures of physical models recorded simultaneously (r = 0.99, $F_{1,24} = 1346.3$, P < 0.001). Although the mean temperature of models was significantly higher than that of turtles (0.44 ± 0.28 °C, paired t = 3.126, P = 0.002), this difference was less than the measurement error of the data loggers (± 0.5 °C). Therefore, we conclude that our physical models adequately predict available T_e for wood turtles.

HABITAT THERMAL QUALITY AND HETEROGENEITY

We recorded 49 152 T_e from 22 physical models. We first calculated the hourly mean T_e of each cover type during cloudy (n = 18) and sunny (n = 24) days (Fig. 1). Terrestrial



Fig. 1. Hourly mean operative environmental temperature (T_c) available to wood turtles in Québec (a) on cloudy days and (b) on sunny days. The dashed line represents T_{set} for wood turtles.

cover types were thermally homogeneous from 20.00 to 08.00 h and offered lower T_e than the river (15.6 ± 1.9 °C and 19.5 ± 0.9 °C, respectively). From 09.00 to 19.00 h, the hourly mean T_e in terrestrial cover types exceeded T_e in the river only for shrub, herbaceous, and graminoid covers from 12.00 to 17.00 h on sunny days. The hourly mean T_e exceeded T_{set} only on bare ground on sunny days from 11.00 to 18.00 h. During that time, 86% of bare ground T_e exceeded T_{set} , while only 3% of shrub and graminoid T_e exceeded T_{set} and T_e never exceeded T_{set} in other cover types. Turtles can attain T_{set} only during sunny days by basking on bare ground.

The thermal heterogeneity of terrestrial cover types from 09.00 to 19.00 h was evaluated with a mixed model nested ANCOVA where T_e was the dependent variable, time of day, cover type (forest, alder, shrub, herbaceous, and graminoid), and their interaction were predictor variables, and individual physical model intercept was a random factor. We conducted separate analyses for sunny and cloudy days. For both sunny and cloudy days, mean T_e was significantly affected by time of day (P < 0.001), but not by cover type (P = 0.21 and P = 0.41, respectively). The interaction between time of day and cover type was significant for sunny days (P < 0.001), but not for cloudy days (P = 0.92; Table 1). Thus, not surprisingly, cover types were thermally heterogeneous only on sunny days, and thermal heterogeneity varied with time of day, with a peak at 14.00 h (Fig. 1).

Table 1. Mixed model nested ANCOVA for the effects of terrestrial cover type and time of day on mean environmental temperature available for wood turtles in Québec on sunny and cloudy days (09.00–19.00 h)

Random effects		Fixed effects				
Level	Residual variance	Predictor	d.f.	F	Р	
Cloudy days		Cloudy days				
Among models	0.25 (12.0%)	Cover type	4, 14	1.084	0.42	
Within models	1.84 (88.0%)	Time of day	10, 1715	11.562	< 0.0001	
		Cover type \times time of day	40, 1715	0.719	0.91	
Sunny days		Sunny days				
Among models	0.46 (15.2%)	Cover type	4, 14	1.840	0.18	
Within models	2.56 (84.8%)	Time of day	10, 5548	52.201	< 0.0001	
		Cover type × time of day	40, 5548	2.088	< 0.0001	

THERMOREGULATION ANALYSES

We recorded 36 864 T_b and 92 741 T_{ext} from 18 turtles. We first compared the distribution of T_b to the null T_e distribution representing the expected T_b distribution for a thermoconforming turtle randomly moving within its TAHA. The T_b and null T_e distributions of the 18 turtles were pooled three ways: (i) complete data set (00.00 to 23.00 h), (ii) cloudy days (09.00 to 18.00 h), and (iii) sunny days (09.00 to 18.00 h). For the three data sets, the null T_e distribution encompassed turtles' T_b distribution, indicating that the null T_e distribution adequately reflected the temperatures that were available to turtles (Fig. 2). The Kolmogorov–Smirnov tests indicated that the distribution of T_b was significantly different from the null T_e distribution for the complete data set (D = 0.22, P < 0.001), cloudy days (D = 0.17, P < 0.001), and sunny days (D = 0.25, P < 0.001).

To compare the hourly variation in T_b and available T_e , we calculated the hourly mean T_b for turtles with the same three data sets. These hourly mean T_b were superimposed on the hourly mean T_e for bare ground, river, and terrestrial cover type weighted by availability of the cover types in turtles' TAHA (Fig. 3). Turtle T_b was always higher than terrestrial cover type T_e . From 20.00 to 08.00 h, turtles maintained T_b intermediate between terrestrial cover types and river T_e , suggesting that they partitioned their time between the river and terrestrial habitats. During daytime, turtle T_b exceeded river T_e from 10.00 to 17.00 h on sunny days, whereas T_b only marginally exceeded river T_e on cloudy days. After 15.00 h on sunny days, turtle T_b decreased more or less in concert with bare ground T_e and approached available T_e in terrestrial cover types and river around 18.00 h.

To gain information on interindividual and hourly variation in thermal selection, we compared the hourly T_b and null T_e distributions separately for each of the 18 turtles with Kolmogorov–Smirnov tests. We used data for sunny days (09.00 to 18.00 h) when opportunities for thermoregulation are present. Figure 4 presents the number of turtles with an hourly T_b distribution significantly different from their hourly null T_e distribution (D > 0.262, P < 0.05), which suggests active thermoregulation. From 09.00 to 16.00 h, the number of thermoregulating turtles varied between 12 and 15



Fig. 2. Distribution of $T_{\rm b}$ and null distribution of $T_{\rm e}$ for wood turtles from June to August in Québec: (a) complete data set (00.00–23.00 h), (b) cloudy days (09.00–18.00 h), and (c) sunny days (09.00–18.00 h). Black bars represent $T_{\rm b}$ distributions and grey bars represent available $T_{\rm e}$ for thermoconforming controls. The dashed line represents $T_{\rm set}$ for wood turtles.

(67-83% of individuals), while it was much lower late in the afternoon when the sun was lower [7 (39% of individuals) at 17.00 h and 6 (33% of individuals) at 18.00 h].

We verified that the departure from thermoconformity was towards T_{set} with the D-statistic (our TSI). We used TSI as an

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Fig. 3. Hourly mean $T_{\rm b}$ of wood turtles and $T_{\rm e}$ on bare ground, in river, and in terrestrial habitats from June to August in Québec: (a) complete data set (00.00–23.00 h), (b) cloudy days (09.00–18.00 h), and (c) sunny days (09.00–18.00 h). The dashed line represents $T_{\rm set}$ for wood turtles.



Fig. 4. Number of individuals with an hourly distribution of body temperatures different from thermoconformity (Kolmogorov–Smirnov test D > 0.262, P < 0.05) for wood turtles in Québec on sunny days (09.00–18.00 h).

explanatory variable, along with time of day and their interaction, to explain variation in individual hourly mean d_b . The mixed model nested ANCOVA, with individual turtle intercept as a random factor, indicated that TSI and time of day both



Fig. 5. (a) Hourly mean deviations of T_b from $T_{set}(d_b)$ on sunny days (09.00–18.00 h) in Québec. (b) Individual mean d_b as a function of mean thermal selection index (TSI) from 11.00 to 16.00 h on sunny days. The dashed line indicates the threshold above which TSI values represent a significant departure from thermoconformity. The black triangles indicate the mean d_b on both figures.

had an effect on d_b (P < 0.001), and there was no interaction between TSI and time of day (P = 0.75; Table 2). d_b was negatively correlated with TSI (-6.12 ± 0.44). Mean d_b decreased with time of day from 09.00 to 13.00 h, was stable between 13.00 h and 16.00 h, and increased from 17.00 to 18.00 h (Fig. 5). Mean d_b for all turtles on sunny days (09.00 to 18.00 h) was 7.1, and it decreased to 5.9 between 11.00 h and 16.00 h, when it was possible for turtles to attain their T_{set} (Fig. 5).

HABITAT SELECTION AND SUN/SHADE SHUTTLING

Turtles' TAHAs were nonrandomly located within the study site ($\chi^2 = 1584.9$, d.f. = 2, P < 0.001), with a preference for open habitats and river (Fig. 6). At the TAHA scale, we compared habitat use on sunny (n = 380 locations) and cloudy days (n = 98 locations). Turtles were more often located in terrestrial habitat on sunny days (75%) than on cloudy days $(62\%; \chi^2 = 6.97, d.f. = 1, P < 0.01;$ Fig. 6). When turtles were on land, the proportion of locations in closed habitats compared to open habitats was not different on sunny and cloudy days ($\chi^2 = 0.30$, d.f. = 1, P = 0.61; Fig. 6). We thus compared terrestrial habitat use to availability by pooling cloudy and sunny days. Turtles showed a strong preference for open habitats ($\chi^2 = 68.60$, d.f. = 1, P < 0.001; Fig. 6). We observed basking behaviour in 8% (36/478) of telemetry locations: turtles flattened the vegetation or used already flattened vegetation or bare ground to bask.

Table 2. Mixed model nested ANCOVA for the effects of thermal selection index (TSI) and time of day on mean deviation of body temperatures from the T_{set} (d_b) of wood turtles in Québec on sunny days (09.00–18.00h)

Random effects		Fixed effects				
Level	Residual variance	Predictor	d.f.	F	Р	
Among individuals	0.85 (63.0%)	TSI	1, 143	27.68	< 0.0001	
		Time of day	9, 143	20.35	< 0.0001	
Within individuals	0.50 (37.0%)	TSI × time of day	9, 143	0.66	0.75	



Fig. 6. (a) Relative availability of closed and open habitats and river in the study site (black bars) and in pooled wood turtle truly available habitat areas (TAHA; dark grey bars) from June to August in Québec. (b) Relative frequency of turtle locations in river and terrestrial habitats on cloudy days (hatched bars) and on sunny days (light grey bars). (c) Relative availability of closed and open terrestrial habitats in pooled turtle TAHAs (dark grey bars) in comparison with the relative frequency of turtle terrestrial locations in both habitat types on cloudy days (hatched bars) and on sunny days (light grey bars).

We also tested the use of sun/shade shuttling as a behavioural adjustment for thermoregulation on sunny days (09.00 to 18.00 h). We used the hourly mean shuttling index as a dependent variable in a mixed model nested ANOVA, with time of day as an explanatory variable and individual turtle intercept as a random factor. Time of day had an effect on the shuttling index ($F_{9,134} = 14.1986$, P < 0.001; Fig. 7). The



Fig. 7. Hourly mean shuttling index $(|T_{ext} - T_b|)$ as a function of time of day for wood turtles on sunny days (09.00–18.00 h) in Québec. The letters indicate significant differences in hourly mean shuttling index based on the 95% confident intervals of the mixed model nested ANOVA coefficients.

homogeneous grouping based on 95 % confidence intervals of the model coefficients of each hour indicated that the shuttling index was higher from 10.00 to 12.00 h when turtles were warming up, intermediate at 09.00 h and between 13.00 h and 16.00 h, and lower from 17.00 to 18.00 h when the sun was low.

INTERNAL BODY TEMPERATURE AND EXTERNAL CARAPACE TEMPERATURE

For the 18 free-ranging turtles during sunny days (09.00 to 18.00 h), the internal body temperature (T_b) and external carapace temperature (T_{ext}) were correlated $(r = 0.93, F_{1,23853} = 15.5900, P < 0.001)$, but the residuals ranged from -20 to +8 °C. T_{ext} (20.3 ± 5.95 °C) was significantly higher than T_b [18.7 ± 6.00 °C; paired t test : $t_{(23854)} = 40.7154$, P < 0.001). The distribution of T_b (9.8 to 34.5 °C) was significantly different from the distribution of T_{ext} (11.0 to 44.0 °C; Kolmogorov–Smirnov test: D = 0.17, P < 0.001).

Discussion

The low $T_{\rm e}$ generally available under different vegetation cover types indicates that habitat thermal quality is relatively low for wood turtles at our study site and that turtles must exert careful habitat selection if they are to achieve $T_{\rm b}$ close to

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 T_{set} . This suggests that while regulation of T_{b} close to T_{set} will bring a benefit over thermoconformity, primarily through an increase in energy gain, it should incur a cost that is expressed as a constraint on a turtle's time-activity budget and as predation risk while exposed on bare ground for basking (Pianka & Pianka 1970; Huey 1982; Shine & Madsen 1996).

As previously reported (Tuttle 1996; Arvisais 2000; Compton et al. 2002), we observed a strong link between habitat use and thermoregulation. Turtles selected open habitats that allow access to solar radiation. Turtles were more often in terrestrial habitats on sunny days than on cloudy days, suggesting that turtles took advantage of higher available $T_{\rm e}$ and greater basking opportunities offered by terrestrial habitats. The shuttling index indicated that basking was most pronounced in the morning as turtles sought to warm up, intermittent in early afternoon, and ceased in late afternoon, probably due to the scarcity of sun patches as the sun started to set. $T_{\rm b}$ profiles suggest that turtles regularly used the river as a thermal refuge at night, just as snakes and lizards use hot rocks or crevices (Huey & Porter 1989; Webb & Shine 1998; Blouin-Demers & Weatherhead 2001). This could explain why wood turtles staved within 250 m of the river during the summer active period in this and in another northern population (Arvisais et al. 2002). It appears that the requirements for thermoregulation impose constraints on the spatial distribution of these turtles.

We calculated how much thermoregulation would increase metabolic rate in turtles based on Dubois et al. (2008), excluding temperatures above T_{set} , which represented less than 2% of the recorded $T_{\rm b}$ and $T_{\rm e}$. We assume that habitats with $T_{\rm e} > T_{\rm set}$ did not impose a measurable cost or constraint on turtle movements and feel this is a reasonable assumption given the scarcity of spatial and temporal combinations that yield $T_{\rm b}$ above T_{set} in our study area. When we consider the complete and sunny days data sets, turtles exhibited a 20% and a 26% increase in metabolic rate compared with metabolic rates predicted for thermoconforming individuals. If we assume that turtles were generally absorptive when they selected higher $T_{\rm b}$, a 20% to 26% increase in metabolic rate will be accompanied by a substantial increase in net energy retention (see Appendix 1 in Dubois et al. 2008). Somewhat surprisingly, turtles did not exploit the benefits of thermoregulation to the maximum. A hypothetical turtle that maintained the highest possible $T_{\rm b}$ without exceeding $T_{\rm set}$ would have been able to increase its metabolic rate by 72% and 93%, respectively, for complete and sunny days.

Wood turtles are the only semi-terrestrial turtles at the latitude of our study. Using the same approach as above, we calculated the consequences of terrestriality for metabolic rate. For the complete and sunny days data sets respectively, a hypothetical fully aquatic turtle (i.e. one where T_b equals water temperature) would have a metabolic rate 21% and 4% greater than that of a thermoconforming fully terrestrial turtle. Because food processing rate is tightly tied to T_b and metabolic rate (Stevenson *et al.* 1985; Dorcas, Peterson & Flint 1997; Niu *et al.* 1999), we argue that even a semi-terrestrial lifestyle is only profitable in northern populations when it is

accompanied by thermoregulation. A completely terrestrial lifestyle is not as energetically profitable as a fully aquatic lifestyle at our high latitude because terrestrial temperatures fall below that of water bodies at night. By using the river as a thermal refuge at night, turtles were able to increase metabolic rate by 21 % compared with a turtle that remained terrestrial at night. Thus, there is a clear benefit for turtles to stay close to the river and to use it as a thermal refuge at night. Our analyses indicate that the spatial distribution, temporal activity patterns, and semi-terrestrial lifestyle of wood turtles are shaped by their thermal biology. We also note that advanced data loggers now allow a host of new information to be obtained about free-living animals, including activity patterns, foraging, and even metabolic rate (Wilson et al. 2006). This new generation of devices might shed more light on the links between thermoregulation and physiological ecology.

For all ectotherms, regulating $T_{\rm b}$ near $T_{\rm set}$ to increase net energy gain may be critical for fitness by increasing growth and reproductive rates, but this may be particularly true at northern latitudes due to the low T_a (Congdon 1989; Dunham, Grant & Overall 1989; Angilletta 2001). Because turtles forage continuously on small prey items (Harding & Bloomer 1979; Ernst et al. 1994), they may derive some benefit from higher $T_{\rm b}$ and enhanced processing rate almost continuously. The imprecise $T_{\rm b}$ regulation observed, however, suggests that the benefit of maintaining $T_{\rm b}$ close to the physiological optimum may be lower than the ecological cost, so that trade-offs are necessary to achieve the greatest net benefit (Huey & Slatkin 1976). Predation risk associated with thermoregulation (basking, movements; Pianka & Pianka 1970; Huey 1982) may represent one important ecological cost for turtles. For long-lived organisms with a high adult survival rate and low and variable reproductive success (Congdon et al. 1993; Congdon et al. 2003), selection may favour a risk-averse strategy aimed at increasing reproductive life span at the expense of high physiological performance and reproductive effort (Rollinson & Brooks 2007).

It is noteworthy that the thermal sensitivity of metabolism $(Q_{10} = 1.92 \pm 0.10;$ Dubois *et al.* 2008) over the 16 to 32 °C range where turtles are active (Ernst 1986; Tuttle 1996) is at the low end of the range reported for reptiles ($Q_{10} = 2$ to 3; Bennett & Dawson 1976). A low Q_{10} testifies to a comparatively low decline in metabolic rate (and we presume food processing capacity) as temperatures fall below the physiological optimum. If the limited opportunities for thermoregulation at high latitudes where climates are cool translate to high thermoregulatory costs, turtles with a low thermal sensitivity of metabolism may have greater overall fitness than those with a high thermal sensitivity. In other words, the former will maintain high physiological performance despite relatively $\operatorname{cool} T_{\rm b}$, while the latter will see their metabolic and processing rates fall sharply and for long periods when turtles are unable to regulate $T_{\rm b}$ close to $T_{\rm set}$. Measuring how thermal sensitivity of metabolic rate varies with latitude within a given species may shine light on the physiological adaptations that permit ectotherms to perform in climatically challenging high latitudes.

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