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Implications of extreme sexual size dimorphism for thermoregulation in a freshwater turtle

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Abstract Sexual size dimorphism (SSD) is a common phenomenon in animals. In many species females are substantially larger than males. Because body size plays a central role in modulating the body temperature (T_b) of ectotherms, intersexual differences in body size may lead to important intersexual differences in thermoregulation. In addition, because SSD is realized by differences in growth rate and because growth rate is strongly temperature dependent in ectotherms, a conflict between male reproductive behaviour and thermoregulation may affect the expression of SSD. In this study, we investigated the thermal implications of SSD in a reptile exhibiting spectacular female-biased SSD: the northern map turtle (*Graptemys geographica*). Over three seasons, we collected >150,000 measurements of T_b in free-ranging adult and juvenile northern map turtles using surgically implanted miniature temperature loggers. Northern map turtles exhibited seasonal patterns of thermoregulation typical of reptiles in northern latitudes, but we found that large adult females experienced a lower daily maximum T_b and a narrower daily range of T_b than adult males and small juvenile females. In addition, despite more time spent basking, large adult females were not able to thermoregulate as accurately as small turtles. Our findings strongly suggest that body size limits the ability to thermoregulate accurately in large females. By comparing thermoregulatory patterns between adult males and juvenile females of similar body size, we found no evidence that male reproductive behaviours are an impediment to thermoregulation. We also quantified the thermal significance of basking behaviour. We found, contrary to previous findings, that aerial basking allows northern map turtles to raise their T_b substantially above water temperature, indicating that basking behaviour likely plays an important role in thermoregulation.

Keywords Body size · Thermoregulation · Aerial basking · Ectotherm · Northern map turtle

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Introduction

Body size is often the most conspicuous trait differing between males and females. Understanding the causes and consequences of this widespread phenomenon has thus been an important quest in evolutionary biology. The most extreme cases of sexual size dimorphism (SSD) are found in ectothermic animals. In reptiles, for instance, females can be 1 order of magnitude heavier than males (Fitch 1981; Gibbons and Lovich 1990). Ectotherms, by definition, have limited capacity for metabolic heat production and must rely on behavioural thermoregulation to buffer the ubiquitous effects of body temperature (T_b) on physiological performance (Huey and Kingsolver 1989). Because body size and T_b interact in many ways (Fig. 1), we expect extreme SSD to have important consequences for thermoregulation in ectotherms.

The T_b of an ectotherm is the result of interactions between abiotic factors (e.g. ambient temperature, solar radiation) and the ability of the animal to use behavioural and physiological processes to control the fluctuations in T_b. Body size affects both behavioural and physiological thermoregulation. Larger animals heat and cool more

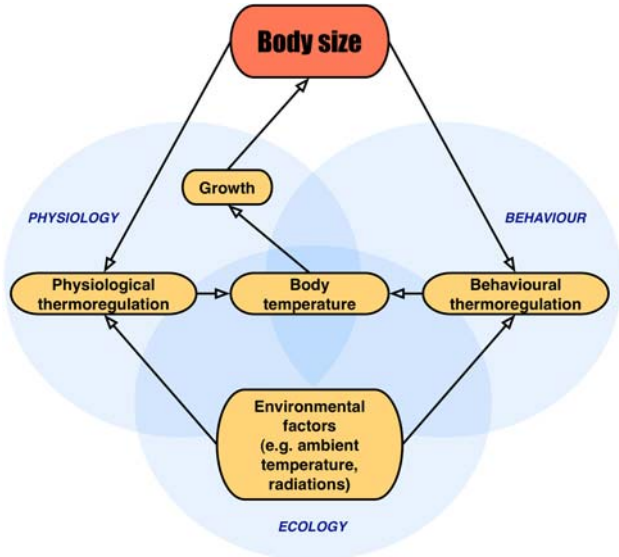

Fig. 1 Conceptual diagram illustrating possible interactions between body size and body temperature

Fig. 2 Adult male (*left*) and adult female (*right*) northern map turtles displaying typical aerial basking behaviour in Lake Opinicon, Ontario, Canada. Note the extreme sexual size dimorphism

slowly (Grigg et al. 1979), leading to more stable T_b (Stevenson 1985). In very large ectotherms, homeothermy even becomes possible (Paladino et al. 1990). In smaller ectotherms that do need to thermoregulate behaviourally, however, body size should have an important influence on thermoregulatory decisions, such as the frequency of shuttling required to maintain a stable T_b. Moreover, larger ectotherms are better able to exploit physiological processes to maintain their T_b within a desired range (Dzialowski and O'Connor 2004). Hence, we expect intersexual differences in field T_b or in thermoregulatory behaviour in ectotherms with pronounced SSD. On the other hand, intersexual differences in T_b or in behavioural thermoregulation may also act as a mechanism promoting the development of SSD.

SSD develops because each sex follows a different growth trajectory, leading to intersexual differences in growth rates and in age and size at maturity (Shine 1990; Stamps 1993; Stamps and Krishnan 1997). In ectotherms, growth rate is largely temperature dependent (Avery et al. 1993; Steyermark and Spotila 2001). Thus, if intersexual differences in thermoregulatory behaviour are present, intersexual differences in growth are expected so long as food is not limited. In reptiles where males are smaller, energetically expensive behavioural and physiological processes tied to male reproductive effort are triggered by an increase in plasma testosterone at the onset of sexual maturity (Cox et al. 2005; John-Alder et al. 2007). These processes appear to take away most of the energy available for growth in males, thus leading to a steep decrease in growth rates after the attainment of sexual maturity (Cox et al. 2005; John-Alder et al. 2007). Therefore, the onset of reproductive activities in males could create a conflict between reproduction and behavioural thermoregulation. Such a conflict may have important effects on growth and on the development of SSD because reptiles, especially in temperate areas, rely on behavioural adjustments to regulate their T_b within their preferred range (Blouin-Demers and Weatherhead 2002; Huey et al. 1989; Quirt et al. 2006; Row and Blouin-Demers 2006), a process that is presumed to maximize energy acquisition (Huey and Slatkin 1976).

To understand better the interactions between thermoregulation, body size, and SSD, we investigated patterns of thermoregulation in an extremely size dimorphic reptile: the northern map turtle (*Graptemys geographica*). In this species, the largest females are 8–10 times the mass of the largest males (Fig. 2). We compared patterns of thermoregulation between adult males, immature females overlapping in size with adult males, and adult females to test predictions regarding the effect of SSD on thermoregulation. We first predicted that, because of their smaller size, males and immature females would be able to raise their T_b higher than adult females. In addition, we predicted that large adult females would experience a narrower range of daily T_b than males and small females because of their larger thermal inertia. We also investigated whether the conflict between reproduction and thermoregulation in males could be the proximate cause for the decrease in male growth rates following maturity and, thus, the mechanism underlying the development of SSD. A potential conflict between thermoregulation and reproduction should be most apparent when comparing mature, non-growing males to immature fast-growing females because these groups correspond to life stages at which the difference in allocation to growth versus reproduction is the most extreme and where the confounding effect of body size on T_b is absent.

Most aquatic emydid turtles regularly and conspicuously bask out of the water (Lindeman 1999). Basking behaviour is often presumed to function in thermoregulation (Boyer 1965; Crawford et al. 1983). However, there are very few measurements of internal T_b in free-ranging turtles (Edwards and Blouin-Demers 2007; Manning and Grigg 1997) and the thermal significance of the frequent basking bouts remains largely unknown. The only study we are aware of that addressed this question found that basking had no thermoregulatory function in the Australian turtle *Emydura signata* (Manning and Grigg 1997). Therefore, our secondary objective was to investigate the thermal significance of basking behaviour in northern map turtles. We wanted to quantify the thermoregulation benefits accrued through basking in a temperate emydid living in a thermally challenging environment.

Materials and methods

Study species and study site

The northern map turtle is a widely distributed freshwater turtle in eastern and central North America. It is characterized by an extreme SSD with females being more than twice the length of males and no overlap in size at maturity (Bulté and Blouin-Demers 2009). We conducted this study between 2004 and 2006 in Lake Opinicon, a small mesotrophic lake at the Queen's University Biological Station, 100 km south of Ottawa, Ontario, Canada.

Biologging and radio-telemetry

In late April and early May, we captured map turtles while snorkelling at a communal hibernation site. We surgically implanted temperature loggers (Thermochron iButton DS 2422 and DS1921; Dallas Semiconductor, Sunnyvale, Calif.) in the abdominal cavity of 14 juvenile females (mean carapace length 140 mm; SE = 1.67; range = 130–151 mm), 19 adult males (mean carapace length = 136 mm; SE = 1.33; range = 127–148), and 18 adult females (mean carapace length = 238 mm; SE = 3; range = 217–260). Details of the anaesthetic and surgical procedures for the logger implantation can be found in Edwards and Blouin-Demers (2007). The loggers could hold 2,048 (DS 1921) or 8,192 (DS 2422) temperature readings. Some adult females were implanted with two loggers (model DS 1921). Using these loggers, we obtained T_b readings every 110 min (single DS 1921), 55 min (two DS 1921), or 25 min (single DS 2422) between May and September. Each turtle implanted with a logger was also equipped with a radio-transmitter (SI-2FT and SB-2FT; Holohil Systems, Carp, ON, Canada) bolted to the outside edge of the carapace. We located each individual every 2–3 days. When tracking turtles, we applied special care not to disrupt normal basking behaviour. We recaptured the turtles to remove the transmitters and the loggers the fall or spring following implantation.

Effects of SSD of daily patterns of T_b

Body size has the potential to affect greatly the daily range of T_b (Stevenson 1985). To test if SSD affects the daily patterns of T_b, we calculated the daily maximum T_b (T_{max}), the daily minimum T_b (T_{min}), and the daily range of T_b (T_{range}). Because smaller animals warm up faster than larger ones, we expected males and juvenile females to reach higher daily T_{max} than adult females. Larger animals also cool down more slowly, however, so we expected adult females to experience higher daily T_{min}. Water has a higher specific heat than air, so the rate of heat exchange is higher in water than in air. Because cooling occurs in water while warming occurs largely on land in aquatic turtles, body size should have a larger effect on daily T_{max} than on daily T_{min}. Thus, we expected small turtles to experience a wider daily T_{range} mainly as a consequence of differences in daily T_{max}.

Preferred T_b and accuracy of T_b

A widely used index to quantify the accuracy of T_b is the deviation of field T_b from preferred T_b (T_{set}; Hertz et al. 1993). T_{set} is the T_b selected in an environment without any costs associated with temperature selection, such as a laboratory thermal gradient. Dubois et al. (2008) recently demonstrated that the upper voluntary maximum (UVM) T_b selected in a thermal gradient matches the optimal temperature for energy assimilation in a freshwater turtle. Therefore, UVM offers a measure of T_{set} with an important functional significance for growth. We thus used UVM to determine T_{set} because we were mostly interested in testing if a conflict between thermoregulation and reproduction could affect growth rates.

We used a basking arena (Ben-Ezra et al. 2008) to measure UVM because aquatic or dry thermal gradients would be artificial environments for a species with pronounced aerial basking behaviour such as the northern map turtle. In the basking arena, turtles displayed typical basking behaviour, suggesting they were thermoregulating normally. The arena was composed of a basin with circulating cold water (10–14°C) and a basking platform heated with a heat lamp. To insure that turtles could reach their UVM, we adjusted the heat lamp so that turtles would eventually overheat by staying under the lamp (reach 50°C) and would thus be forced to return to the water to cool. We placed turtles individually in the basking arena and recorded their cloacal temperature every minute for 48 h using a 36-gauge copper-constantan thermocouple attached

to a temperature logger (HOBO H12-003; Onset Computer, Pocasset, Mass.).

Because energy assimilation is likely optimized within a narrow range of T_b rather than at a single T_b, we used the interval between the upper 75th and 95th quantiles of selected T_b in the basking arena as our measure of T_{set}. We verified that our measure of T_{set} approximated a range of T_b that is functionally important for growth by comparing it to the optimal temperature for food consumption in a closely related species, the red-ear slider (*Trachemys scripta*; Parmenter 1980). The 75th–95th quantile range corresponds to T_b where food consumption is ≥95% of the maximum. We then measured the accuracy of T_b (d_b) as the deviation of the field T_b from T_{set}, in absolute value (Hertz et al. 1993). Inspired by Christian and Weavers (1996), we also calculated the proportion of time T_b was within T_{set} as an alternate measure of thermoregulation.

Basking behaviour and thermal gain

To investigate the thermal significance of basking behaviour, we calculated the percentage of time spent basking as the percentage of time when T_b exceeded the maximum surface water temperature of the lake (S_{max}). Using temperature loggers (Thermochron iButton DL 1922; Dallas Semiconductor), we measured surface water temperatures at four locations in the lake. We calculated hourly S_{max} as the maximum surface temperature of the four locations. We determined if a turtle was basking by calculating the difference between T_b and S_{max} for each hour of the day. Positive values indicated that the turtle was basking and negative values indicated that the turtle was submerged. It is reasonable to assume that when T_b is below S_{max}, the turtle is submerged because turtles rapidly equilibrate with water temperature once submerged due to the high specific heat of water (Grigg et al. 1979). We then used the difference between T_b and S_{max} to calculate the thermal gain of basking (T_{gain}). For every positive difference between T_b and S_{max}, we calculated the difference between T_b and the mean surface temperature (S_{mean}) of the lake. This index provides a measure, in °C, of the thermal gain realized during basking.

Statistical analyses

To test for the effect of size on minimum daily T_b (T_{min}), maximum daily T_b (T_{max}), and the daily T_b range (T_{range}), we calculated the daily minimum T_b, the daily maximum T_b, and the daily range of T_b for each individual. We then calculated an overall mean T_{min}, T_{max}, and T_{range} for each individual and tested for group (adult male, adult female, juvenile female) effects using one-way ANOVAs. When the ANOVA was significant, we used a posteriori Tukey honest significant difference (HSD) pairwise comparisons to determine between which groups the difference lay.

We tested the effects of group (male, female, juvenile female) and month (May–September) on the mean T_b, d_b, T_{gain}, and the percentage of time spent basking with repeated measures ANOVAs. Because we were mostly interested in intergroup differences, when a significant group effect was found we conducted individual one-way ANOVAs for each month followed, when significant, by a posteriori Tukey HSD pairwise comparisons. We calculated mean hourly T_b for each individual and used these hourly means to calculate individual mean monthly T_b that we used in the repeated measures ANOVAs. We arcsin transformed the percentage of time spent basking and we log-transformed d_b to normalize the distributions. All tests were considered significant at $\alpha = 0.05$. Statistical analyses were conducted with JMP 5.01a (SAS Institute 2002).

Results

Preferred T_b

We measured T_{set} in 13 adult females, 11 juvenile females, and 12 adult males. There were no difference in the 75th quantile (ANOVA: $F_{2,33} = 2.00$, $P = 0.15$) or the 95th quantile (ANOVA: $F_{2,33} = 0.79$, $P = 0.46$) among the three groups. The overall mean 75th quantile was 28.7°C (±0.77) and the overall mean 95th quantile was 32.5°C (±0.40).

Accuracy of T_b

We obtained 156,646 mean hourly T_b measurements between May and September from the 51 turtles we implanted with temperature loggers. Overall, monthly mean T_b closely matched the monthly mean S_{max}, but was always higher than S_{mean} (Fig. 3a). Mean hourly T_b across the entire season was lower than S_{max}, but higher than S_{mean} between 1700 and 0700 hours (Fig. 3b). Between 0800 and 1600 hours, turtles maintained T_b above S_{max} (Fig. 3b). Season had a strong and significant effect on T_b, but group had a marginally non-significant effect (Table 1).

Month of the year had a strong and significant effect on d_b (Table 1). d_b was highest in July and lowest in May (Fig. 4a). The effect of group was also marginally non-significant (Table 1). Overall, 9% of the T_b measured were within T_{set}. During the day (0700–1800 hours), however, 15.8% of T_b measured fell within T_{set}. The percentage of observations when T_b was within T_{set} was significantly affected by month, but also by group, and there was a nearly significant month by group interaction (Table 1). We found significant group effects in July ($F_{2,48} = 3.34$, $P = 0.043$),

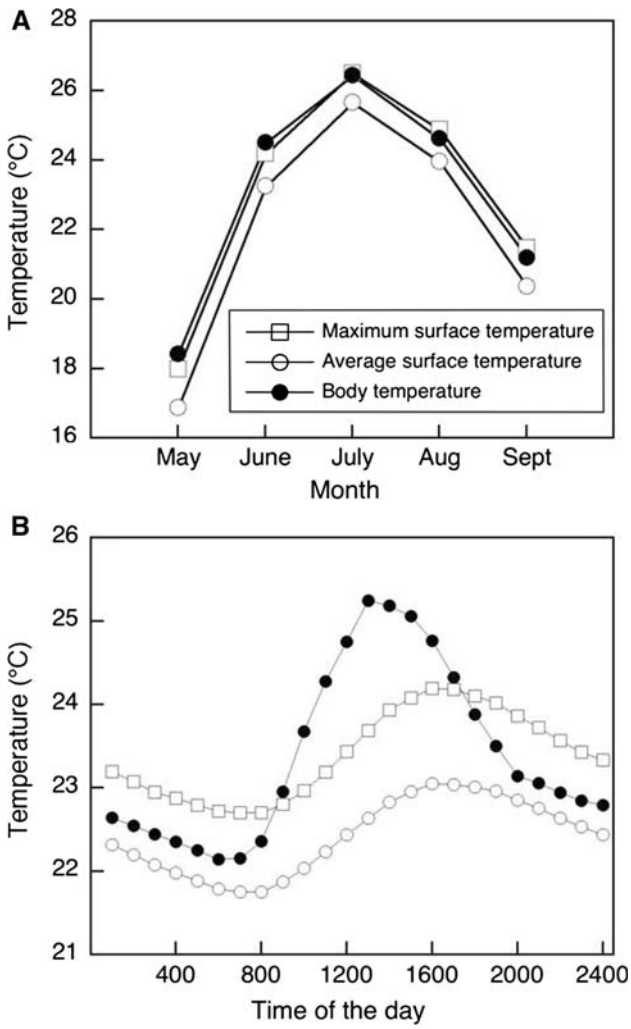

Fig. 3 **a** Monthly mean T_b of northern map turtles from Lake Opinicon compared to maximum and mean surface water temperatures. **b** Hourly mean T_b of northern map turtles from May to September compared to hourly maximum and mean water surface temperatures for the same period

Table 1 Summary of repeated measures ANOVAs testing for the effects of group and month on body temperature (T_b) and the accuracy of T_b (d_b) for adult male, juvenile female, and adult female northern map turtles from Lake Opinicon, Ontario, Canada

Response variables	Factors	*df*	*F*	*P*	R^2
T_b	Full model	62,185	28.98	<0.0001	0.88
	Group	2,185	3.05	0.056	
	Month	4,185	431.47	<0.0001	
	Group × Month	8,185	1.23	0.28	
d_b	Full model	62,185	31.08	<0.0001	0.89
	Group	2,185	2.63	0.082	
	Month	4,185	465.14	<0.0001	
	Group × Month	8,185	1.2	0.3	

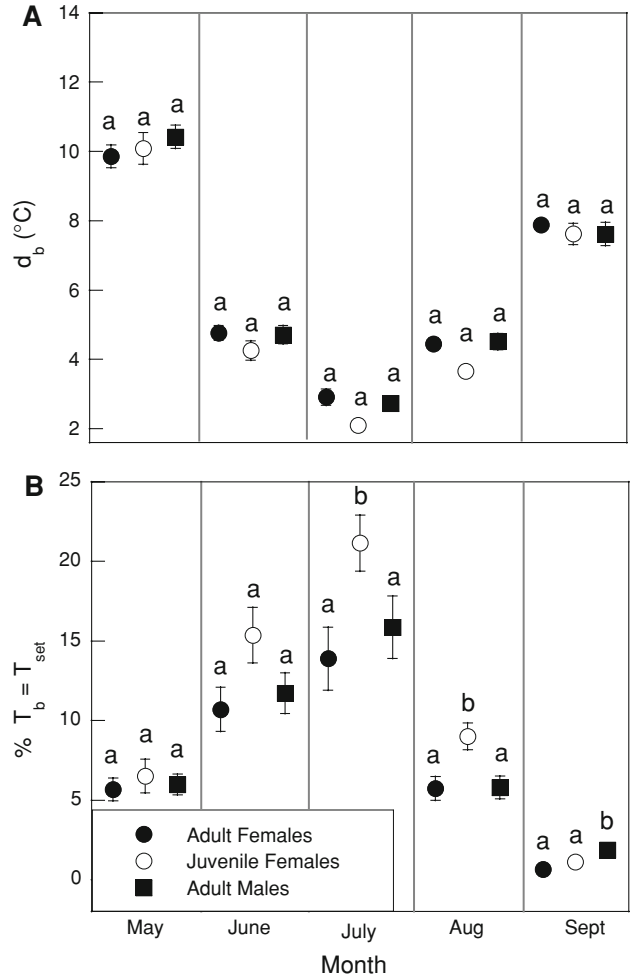

Fig. 4 Monthly mean accuracy of T_b (d_b; **a**) and the percentage of time when T_b is within the preferred range ($T_b = T_{set}$; **b**) for adult female, immature female, and adult male northern map turtles from Lake Opinicon. *Error bars* indicate 1 SE. Groups labelled with *different letters* within each month are statistically significantly different

August ($F_{2,48} = 5.33$, $P = 0.008$), and September ($F_{2,47} = 5.57$, $P = 0.007$). Juvenile females kept their T_b more often within T_{set} than adults of both sexes (Fig. 4b). In July and September, the percentage of $T_b = T_{set}$ observations was higher in juvenile females than in adult females, and males did not differ from either female group. In August, the percentage of $T_b = T_{set}$ observations was higher in juvenile females compared to both adult groups.

T_{min}, T_{max}, and T_{range}

Across all 5 months, mean daily T_{min} was 21.7°(SE = 0.09) and did not differ between groups ($F_{2,48} = 1.24$, $P = 0.298$). In contrast, males and juvenile females had higher T_{max} than adult females ($F_{2,48} = 8.75$, $P = 0.0006$; Fig. 5a). Consequently, adult females had a narrower T_{range} than males and juvenile females ($F_{2,48} = 5.32$, $P = 0.008$; Fig. 5b).

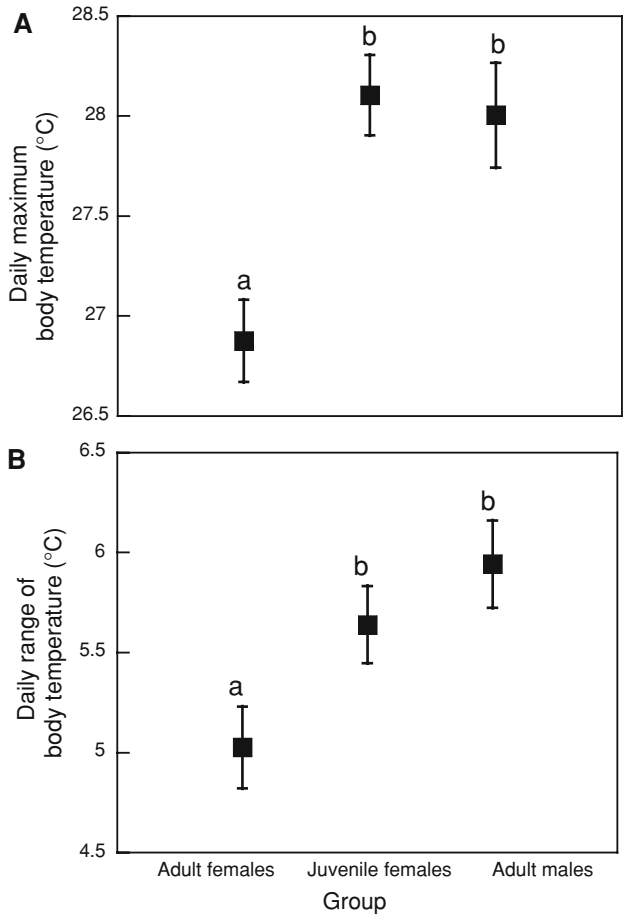

Fig. 5 Mean daily maximum T_b (**a**) and daily range of T_b (**b**) between May and September in northern map turtles from Lake Opinicon. *Error bars* indicate 1 SE. Groups labelled with *different letters* are statistically significantly different

Table 2 Summary of repeated measures ANOVAs testing for the effects of sex and month on the thermal gain of basking, the percentage of time that T_b is within the preferred range (% $T_b = T_{set}$), and the percentage of time spent basking (% $T_b > S_{max}$) for adult male, juvenile female, and adult female northern map turtles from Lake Opinicon

Response variables	Factors	*df*	*F*	*P*	R^2
Thermal gain of basking (log-transformed)	Full model	62,185	4.5	<0.0001	0.54
	Group	2,185	4.64	0.014	
	Month	4,185	58.45	<0.0001	
	Group × Month	8,185	1.93	0.057	
% $T_b = T_{set}$ (arcsin transformed)	Full model	62,185	7.95	<0.0001	0.68
	Group	2,185	4.65	0.014	
	Month	4,185	98.38	<0.0001	
	Group × Month	8,185	1.96	0.054	
% $T_b > S_{max}$ (arcsin transformed)	Full model	62,185	3.36	<0.0001	0.47
	Group	2,185	3.58	0.030	
	Month	4, 185	18.51	<0.0001	
	Group × Month	8,185	2.99	0.003	

Basking behaviour and thermal gain

Across the entire season, the mean percentage of T_b observations above S_{max} varied between 13 and 54% and month explained most of this variation (Table 2). Group also had a significant effect, however, and a significant month by group interaction was present (Table 2). Group differences in the percentage of T_b observations above S_{max} were found in May ($F_{2,42} = 6.28$, $P = 0.004$) and in August ($F_{2,48} = 5.8$, $P = 0.005$). In May, the T_b of adult females were more frequently above S_{max} than the T_b of juvenile females and adult males while in August the T_b of adult males were more frequently below S_{max} than the T_b of adult and juvenile females (Fig. 6a).

The monthly mean T_{gain} across the entire season ranged from 0.3 to 2°C and was highest in May and lowest in September (Fig. 6b). In addition to the significant effect of month, the effect of group was also significant along with a nearly significant month by group interaction (Table 2). Individual one-way ANOVAs for each month indicated a significant effect of group in August only ($F_{2,48} = 7.99$, $P = 0.001$; Fig. 6b). In August, T_{gain} was on average 0.3°C higher in juvenile females compared to both adult groups and a posteriori Tukey HSD pairwise comparison indicated that this difference was statistically significant.

On a daily basis, T_{gain} varied considerably with the lowest values between 2000 and 0800 hours and the highest values between 1100 and 1400 hours (Fig. 7a). In May between these hours, mean T_{gain} could reach 6°C (Fig. 7a). Mean monthly maximum T_{gain}, however, could be substantially higher. For instance, mean maximum T_{gain} in May across all groups was 17°C and around 10°C in the remaining months (Fig. 7b).

Discussion

Thermal preference

The UVM temperature we measured on map turtles in a shuttle arena was similar to the value of approximately 30°C reported for other temperate reptiles (Dubois et al. 2008). UVM was demonstrated to match the optimal temperature for energy assimilation in emydid turtles (Dubois et al. 2008). This measure is thus particularly appropriate to investigate the interplay among thermoregulation, growth, and SSD.

General patterns in T_b and thermoregulation

We found important seasonal variation in T_b, d_b, and the percentage of time T_b is within T_{set}. These seasonal patterns

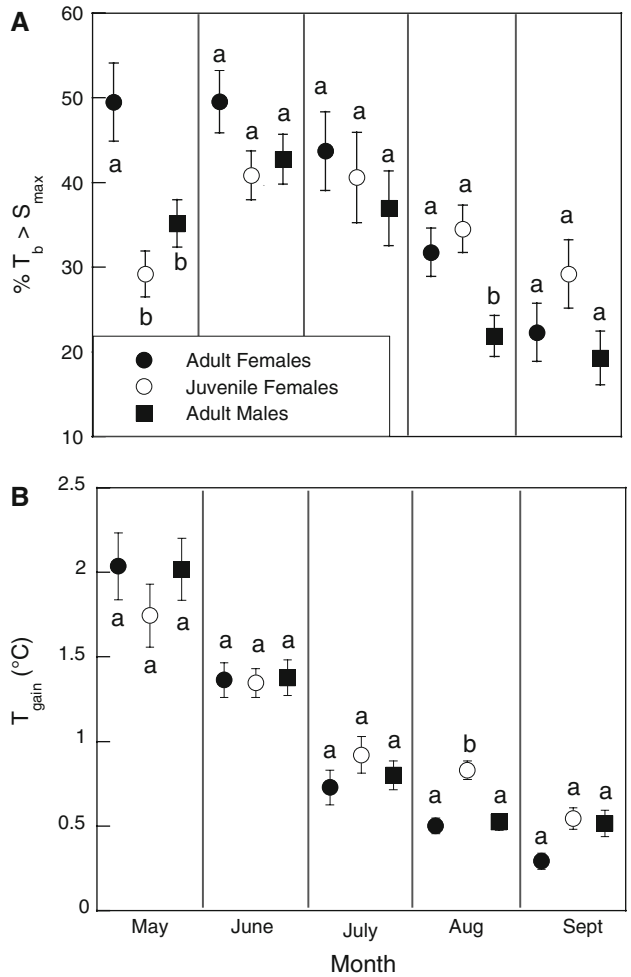

Fig. 6 Monthly mean percentage of time spent basking ($\%T_b > S_{max}$; **a**) and thermal gain of basking (T_{gain}; **b**) in adult female, immature female, and adult male northern map turtles from Lake Opinicon. *Error bars* indicate 1 SE. Groups labelled with *different letters* within each month are statistically significantly different

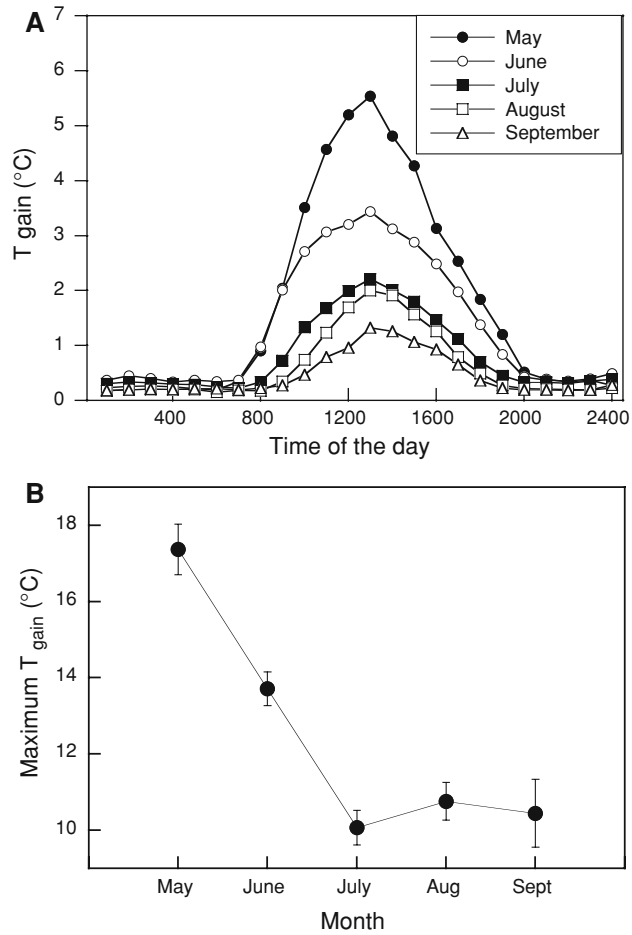

Fig. 7 **a** Daily mean T_{gain} for every month of the active season in northern map turtles from Lake Opinicon. **b** Mean daily maximum T_{gain} for every month of the active season

were concordant with those of other reptiles from the same latitudes (Blouin-Demers and Weatherhead 2001; Edwards and Blouin-Demers 2007; Row and Blouin-Demers 2006). This seasonal effect reflects the seasonal variation in environmental temperature as well as in the thermal quality of the environment. The highest air and water temperatures were in June and July. Thus, it is not surprising that it is during these months that the highest T_b are reached. In addition, it is also in June and July that the thermal quality of the environment is the highest in our study area (Blouin-Demers and Weatherhead 2001; Edwards and Blouin-Demers 2007). Thermal quality is usually measured by the deviation of the environmental temperature from T_{set} (Hertz et al. 1993). When thermal quality is high, d_b is typically low and the percentage of time T_b is within T_{set} is high (Blouin-Demers and Weatherhead 2001).

Effect of SSD on thermoregulation

Because thermal inertia increases with body size, larger ectotherms have a more restricted range of possible daily T_b (Stevenson 1985). Thus, we expected smaller turtles (i.e. adult males and juvenile females) to be able to achieve higher T_{max} and to experience wider T_{range} than larger turtles (i.e. adult females). However, because for freshwater turtles cooling occurs mainly in water, an environment with a high specific heat, we expected to find a weaker effect of size on daily T_{min}. Small turtles achieved higher daily T_{max} than large adult females, but the large females did not experience higher daily T_{min}. Consequently, daily T_{range} was wider in small turtles than in large females. Our results indicate that the factor limiting daily T_{max} and T_{range} is the rate of heating while basking in air rather than the rate of cooling while in water. Although we did not measure heating and cooling rates in a controlled environment in the present study, previous studies in aquatic turtles support

this notion. Indeed, a 2,454-g turtle (i.e. the size of an adult female map turtle) cooling in water between 30 and 20°C needs 23 min to reach thermal equilibrium with the water (Weathers and White 1971). In contrast, a 396-g turtle (i.e. the size of adult males and juvenile females) needs about 11 min to cool down by 10°C in water. In both cases, cooling is rapid. Thus, the larger size of adult females seems unlikely to allow them to maintain higher daily T_{min}. The effect of body size is more important for heating rate, however. For instance, the same 2,454-g turtle needs 111 min to elevate its T_b from 20 to 30°C in air, while a 349-g turtle needs only 47 min (Weathers and White 1971). Thus, body size does restrict the possible range of daily T_b by affecting heating rate and the daily T_{max}. Overall these results show that pronounced SSD does have implications for the thermal ecology of ectotherms by affecting potential daily patterns of T_b.

Despite smaller turtles being able to achieve higher T_{max} and experiencing wider T_{range}, however, the overall mean T_b was the same between small and large turtles. The daily window of time turtles have to reach T_{max} was limited to 2–3 h per day and the difference in mean T_{max} between large adult females and small turtles was only 1°C. Thus, the leverage of T_{max} was insufficient to affect the mean values.

Although larger reptiles experience restricted T_{range} compared to their smaller counterparts, being larger also permits them to maintain a more stable T_b (Grigg et al. 1979; Pearson et al. 2003). In addition, being larger appears to facilitate the effectiveness of physiological thermoregulation (Dzialowski and O'Connor 2004). Thus, large turtles could be predicted to thermoregulate more accurately than small turtles. We did not find appreciable differences in d_b, but we did find that, contrary to our prediction, T_b of adult females was less often within T_{set}. These results are surprising because it should be easier for adult females to maintain a stable T_b. In addition, reproductive females are expected to thermoregulate more accurately than males and non-reproductive females (Blouin-Demers and Weatherhead 2001). It was impossible in our study to account for the reproductive condition of females by using both reproductive and non-reproductive females (e.g. Blouin-Demers and Weatherhead 2001) because adult females in our population reproduce every year (G. Bulté, personal observation). We did find, however, that adult reproductive females maintained lower T_b and thermoregulated less accurately than males and juvenile females. Thus, even with the extra need to thermoregulate accurately to favour embryogenesis, reproductive females were still unable to thermoregulate as accurately as males and small females in some months.

The lower accuracy of thermoregulation in adult females may reflect the cost-benefit balance of thermoregulation. If adult females experience higher costs than males and juvenile females when thermoregulating, they should thermoregulate less accurately (Huey and Slatkin 1976). We have, however, no reason to think that the costs of thermoregulation are higher in adult females than in males or juvenile females. On the contrary, accurate thermoregulation should have high reproductive benefits in adult females, such as speeding follicular development (Sarkar et al. 1996), which may be critical at northern latitudes where the active season is short (Rollinson and Brooks 2007). We found that adult females actually spend more time basking than males and juvenile females prior to and during the nesting season (May and June). Sex bias in basking behaviour was also observed in painted turtles (Carrière et al. 2008). Despite more time spent basking, large adult females were not able to thermoregulate as accurately as small turtles. Our findings suggest that body size limits the rate of heating and the maximum daily T_b, which in turn affect the ability of large females to reach T_{set}.

Thermoregulation: reproductive conflict and the expression of SSD

T_b is a central determinant of growth rate in reptiles and SSD is realized by intersexual differences in growth rate and maturation (Shine 1990). Thus, intersexual differences in thermoregulation may affect the expression of SSD. Reproductive activities including mate searching, courtship, and mating occur in water in northern map turtles. Thus, reproductive behaviours may impede thermoregulatory behaviours, especially aerial basking. This impediment may be especially pronounced in males since they invest more in courtship and mate searching than females. Thus, this impediment could contribute to the steep decrease in growth rate observed in males at the onset of sexual maturity (Bulté and Blouin-Demers 2009). We found that juvenile females kept their T_b within T_{set} more than males and adult females in June, July, and August, but not in May and September. The lower accuracy of thermoregulation of males during these months is unlikely to stem from a conflict between thermoregulation and reproduction because northern map turtles, like most temperate emydid turtles, mate in spring (April and May) and in autumn (September and October; Ernst et al. 1994). The difference in the accuracy of thermoregulation between males and juvenile females can be explained from a life history perspective. Immature females are expected to maximize growth to reach maturity early to decrease the probability of death before maturity (Congdon et al. 1993). Maintaining T_b within the range that optimizes energy assimilation (i.e. T_{set}) should promote faster growth. In contrast, mature males are not growing and, during summer, are not mating. Thus, the benefit of thermoregulation may not be as important in males during the summer. Contrary to our findings, we expected to find the most important discrepancy in the

accuracy of thermoregulation between mature males and immature females during the mating season. Spermatogenesis occurs in fall in temperate turtles (Gist et al. 2002; Meylan et al. 2002) and accurate thermoregulation during that period may accelerate spermatogenesis. Thus, the benefit of thermoregulation in terms of spermatogenesis may be higher than the potential cost in terms of lost mating opportunities.

Overall our results do not support the notion that male reproductive activities involve an important thermoregulatory cost contributing to the development of SSD. Our study is among the first to investigate the links between thermoregulation and SSD (but see also Brown and Weatherhead, 2000). Although comparing different sexes and age groups provided valuable insights into these links, an experimental approach such as manipulating steroid hormones levels via castration (e.g. Cox and John-Alder 2005) would provide a more direct test of the effect of reproductive behaviour on thermoregulation. Unfortunately, such manipulation is challenging on turtles with a hard carapace.

Thermal significance of basking

Aerial basking is a very conspicuous behaviour in many aquatic turtles (Boyer 1965) and is assumed to play an important thermoregulatory role. Very few studies, however, have investigated the thermoregulatory benefit of basking by directly measuring internal T_b in free-ranging freshwater turtles (Manning and Grigg 1997). The thermoregulatory role of basking is thus unclear. Manning and Grigg (1997) found that *Emydura signata*, a turtle exhibiting aerial basking behaviour, rarely raised its T_b above water temperature. Manning and Grigg (1997) thus concluded that basking behaviour has no thermoregulatory function in this species and argued that this may be the case in most small aquatic turtles. Our results contrast with these findings. Northern map turtles raise their T_b above S_{max} on a daily basis. For instance, in May map turtles kept their T_b on average 4–6°C above S_{max} for 6–7 h per day. The daily maximum T_{gain} during that period was on average 17°C and even during the warmest month the maximum daily T_{gain} were high (~10°C). Aerial basking is actually necessary for map turtles to reach their optimal temperature for energy assimilation (i.e. T_{set}) because water temperature is always lower than the optimal range for assimilation. Although we cannot say with confidence that the primary goal of basking is thermoregulatory, northern map turtles certainly derive a thermal benefit from this conspicuous behaviour. Interestingly, however, their overall mean T_b closely match S_{max}. Nonetheless, it would be erroneous to conclude that map turtles are thermoconformers because at night map turtle T_b were below S_{max} while during the day they were above S_{max}. Without aerial basking, the mean T_b of map turtles would be below S_{max}. Our findings support the idea that basking plays an important thermoregulatory role in northern map turtles, but more studies are necessary to confirm the generality of this phenomenon. Basking likely serves other purposes as well, such as enhancing vitamin metabolism (Ferguson et al. 2003), desiccating leeches (Ernst 1971), and creating fevers to fight infection (Monagas and Gatten 1983).

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