

Are Locomotor Performances Coadapted to Preferred Basking Temperature in the Northern Map Turtle (*Graptemys geographica*)?

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ABSTRACT.—We tested a common prediction of the thermal coadaptation hypothesis in the Northern Map Turtle (*Graptemys geographica*), an aquatic emydid with pronounced aerial basking. We measured the effect of body temperature on two locomotor performances (swimming and righting) to determine optimal temperature of performance (T_o) for each trait. According to the thermal coadaptation hypothesis, the preferred body temperature range (T_{set}) of ectotherms should match T_o of thermally sensitive traits that influence fitness. However, we predicted that preferred basking temperature and locomotor performance of Northern Map Turtles would not be coadapted, given that basking occurs on land and locomotion in water. We also tested for an ontogenetic shift in performance curves. We found that adult Northern Map Turtles have a wide T_{set} (19–30°C), both hatchlings and adults can achieve near-maximum performance over a wide range of temperatures, and an ontogenetic shift is present for swimming but not for righting. Although T_o for the two locomotor performances of adult turtles were within T_{set} , the large range of T_{set} coupled with the wide breadth in locomotor performance makes falsifying or supporting the coadaptation hypothesis difficult for these traits in Northern Map Turtles. Other metabolic and physiological processes need to be considered to understand more fully thermal coadaptation in aquatic emydids.

Body temperature (T_b) is the most important limiting factor of physiological processes in ectotherms (Angilletta et al., 2002b). Thus, despite some physiological control of T_b (Weathers and White, 1971; Seebacher and Franklin, 2005), most ectotherms must also thermoregulate behaviorally to maintain their T_b within a range that permits activity (Avery, 1982; Huey, 1982). The close link between behavioral thermoregulation and thermal sensitivity of physiological performance has led to the hypothesis that these two traits have evolved together, a process known as coadaptation (Huey and Bennett, 1987; Angilletta et al., 2006). As Huey and Bennett (1987) reasoned, the T_b s behaviorally selected by ectotherms should influence fitness via their direct effects on physiological performance. If the optimal temperature for physiological performance (T_o) is driven away from the preferred body temperature (T_{set}), coadaptation pressures should favor a corresponding shift in T_{set} (Huey and Bennett, 1987).

Locomotor performances have often been used to test for coadaptation between preferred and optimal temperature. Locomotor performances are thought to have a pervasive effect on fitness because for many species they determine the rate at which critical processes such as foraging, mating, and predator avoidance occur (Huey, 1982; Irschick and Garland,

2001). Evidence for coadaptation between T_{set} and T_o for locomotion has been found in insects (Kingsolver, 1987), lizards (Bauwens et al., 1995; Angilletta et al., 2002a), and snakes (Stevenson et al., 1985; Blouin-Demers et al., 2003). In chelonians, the thermal dependency of various processes including digestive rate (Avery et al., 1993), locomotion (Elnitsky and Claussen, 2006), growth (Williamson et al., 1989), and selected body temperature (Jarling et al., 1984, 1989; Nutting and Graham, 1993; Nebeker and Bury, 2000, 2001) have been examined independently. However, no study to date has explicitly examined thermal coadaptation in turtles.

Some turtles, such as aquatic emydids, present an interesting locomotory-coadaptation problem because aerial basking is the dominant thermoregulatory behavior (Boyer, 1965; Crawford et al., 1983; Krawchuk and Brooks, 1998). Therefore, thermoregulation occurs in microhabitats with different thermal properties than the water in which other activities (i.e., foraging and mating) occur. It has recently been shown that free-ranging emydids can reach and maintain substantially higher T_b s while basking than while in water (Edwards and Blouin-Demers, 2007). However, it is doubtful that the elevated T_b s achieved by basking on land can significantly improve locomotor performance for aquatic emydids during critical activities. Because of the high thermal conductivity of water, turtle T_b rapidly reaches thermal equilibrium with the water after basking has ceased. Because a turtle must remain in the aquatic environment

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for extended periods when foraging or attempting to mate, the locomotor potential of elevated T_b achieved by basking would rapidly be lost. This suggests T_{set} and T_o for locomotor performances may not be coadapted in turtles with pronounced aerial basking behavior.

In this study, we examined the effect of temperature on locomotor performance of adult male and hatchling Northern Map Turtles (*Graptemys geographica* LeSueur). Our first objective was to test for evidence of coadaptation between preferred basking temperature and optimal temperature for locomotion in adult male turtles. Two locomotor performances, righting and swimming, were measured and compared with T_{set} . Although righting behavior occurs on land, this performance is worth examining because it has been recently shown that righting and swimming performance are uncorrelated in turtles (Elnitsky and Claussen, 2006) and, thus, likely represent two distinct locomotor traits. In addition, righting has been examined in a variety of species and shows a strong thermal dependency (Steyermark and Spotila, 2001; Freedberg et al., 2004; Elnitsky and Claussen, 2006) and is an indicator of fitness in freshwater turtles (Delmas et al., 2007). Its relationship with T_{set} and the extent to which its thermal performance curve matches those of other locomotor traits, however, have not been examined.

Graptemys species are active aerial baskers (Lindeman, 1999) and dedicate a large portion of their time budget to this activity. Northern Map Turtles also inhabit large water bodies, such as lakes and rivers, that are generally cooler than the characteristic marsh and pond habitats of most other aquatic emydid species (Ernst et al., 1994). Therefore, the Northern Map Turtle is an interesting candidate to compare T_o for locomotion to T_{set} during basking.

Our second objective was to compare thermal performance curves of adult and hatchling turtles to determine the presence of ontogenetic changes in performance. Such ontogenetic shifts have been found in other ectotherms (Lillywhite et al., 1973; Blouin-Demers et al., 2003), but we are unaware of any comparison in turtles. Adult and juvenile turtles share the same thermal environment and hatchling emydids are also known to be active aerial baskers (Janzen et al., 1992; Lindeman, 1993). Hatchlings experience their thermal environment differently, however, because of their small heat capacity that keeps them close to equilibrium with the environment (Janzen et al., 1992) and may limit their ability to physiologically thermoregulate (Dzialowski and O'Connor, 2001, 2004). Therefore, differences in performance curves may be expected between adult and hatchling turtles.

MATERIALS AND METHODS

Study Site and Study Animals.—We conducted this study in 2005 and 2006 at the Queen's University Biological Station, approximately 100 km south of Ottawa, Ontario, Canada. Adult male Northern Map Turtles ($N = 44$) were obtained by snorkeling and from basking traps in Lake Opinicon. Males used in this study ranged from 87–135 mm in carapace length and from 72–244 g in mass. Turtles were housed in groups of 2–3 in a field laboratory in large ($80 \times 80 \times 80$ cm) basins filled with lake water ($24\text{--}27^\circ\text{C}$). We placed rocks in the basins to allow turtles to leave the water, and, although no radiant heat source was provided, turtles regularly exhibited typical basking behavior. The lab received natural sunlight from windows, and the ambient temperature was maintained at $24\text{--}26^\circ\text{C}$. Turtles were fed mealworms every other day and were released at their point of capture immediately after their trial was completed. Different individuals were used for the measurement of locomotor performance (2005) and the measurement of T_{set} (2006), but locomotor performance and T_{set} were measured in the same month (August) to ensure that individuals from each year had experienced a comparable thermal history.

The hatchlings used in this experiment were obtained from the same population as the adult turtles. Gravid female Northern Map Turtles were captured during the 2005 nesting season (May to July) and induced to lay eggs with an intramuscular injection of oxytocin (20 USP units/ml, 0.5 ml/kg; Ewert and Legler, 1978). All clutches were incubated in moist vermiculite (1:1 ratio by mass of water:vermiculite) at 29°C . Twenty-four hatchlings from eight clutches were randomly selected for performance trials and were transferred to the laboratory at the University of Ottawa in September. Hatchling turtles used in this study ranged from 29.4–34.2 mm in carapace length and from 6.7–9.1 g in mass. The hatchlings were housed individually in small ($20 \times 30 \times 15$ cm) plastic containers in an environmental chamber (Constant Temperature Control, Inc., Aurora, ON, Canada) and fed a diet of mealworms and bloodworms. The temperature of the chamber was set between 22°C and 25°C from September until the hatchlings were tested for performance in March. We selected this temperature such that the hatchlings would be acclimated (sensu Lagerspetz, 2006) to the same temperature as the adults (lake temperature during testing $21\text{--}26^\circ\text{C}$), even though most of the evidence suggests that ectotherms acclimate poorly for locomotor performance (reviewed in Bennett, 1990; but see Glanville and Seebacher, 2006). All

procedures were approved by the Animal Care Committee at the University of Ottawa (protocol BL-179).

Measurements of Preferred Basking Temperature.—Aquatic gradients, in which turtles can settle at one temperature, have been used traditionally to measure selected temperature for aquatic turtles (Nutting and Graham, 1993; Nebeker and Bury, 2000, 2001). However, T_{set} determined in such gradients is not likely representative of preferred basking temperature because the turtle cannot leave the water, and aquatic emydids predominantly use shuttling between water and land to maintain their T_{set} in nature (Boyer, 1965). In addition, the upper and lower bounds of the T_{set} range determined with a gradient (e.g., central 50% or 80% of the T_b distribution) are arbitrary. To circumvent these limitations and to obtain a direct measure of preferred basking temperature, we used a basking arena similar to the "shuttle box" proposed by Kingsbury (1993).

In August 2006, we measured selected basking temperature with a basking arena. Our basking arena consisted of a wooden basking platform (50 × 50 cm) installed at the end of a large basin (150 × 60 × 60 cm). A heat lamp was adjusted above the basking platform so that a large male carcass (CL = 130 mm) would reach 50°C in less than 2 h. At our study site, physical models with the same reflectance and heat capacity as male Northern Map Turtles can reach a core temperature of 48°C when placed on known basking sites (unpubl. data). Therefore, the platform provided a thermal microclimate similar to one a turtle would experience on a warm sunny day. The lamp was programmed to turn on at 0800 h and turn off at 2200 h. Cold water (11–14°C) was circulated continuously in the basin and the water level was adjusted to be 5 mm lower than the edge of the platform. Therefore, turtles had to shuttle between cold water and a platform on which they would eventually overheat, such that shuttling was the only means for the turtles to maintain a T_b within their preferred range. By using a process that mimics the way Northern Map Turtles thermoregulate naturally, we were able to determine directly the set points (i.e., the temperatures at which the turtle switched from heating to cooling and vice versa) for each individual (Kingsbury, 1993).

Turtles were placed individually in the basking arena. T_b was recorded by inserting a 36-gauge copper-constantan thermocouple 5 cm inside the turtle's cloaca. The thermocouple was attached to a temperature logger (HOBO H12-003, 0.01°C precision, Onset Computer, Inc., Pocasset, MA) that recorded T_b every minute for 48 h. In small turtles (< 300 g), such as our male

Northern Map Turtles, there is no marked internal thermal gradient (Webb and Witten, 1973); thus, cloacal temperature is a good estimate of overall T_b .

Measurements of Locomotor Performances.—In August 2005, adult turtles were tested for swimming and righting velocity at 5° intervals between 10°C and 35°C. The order of treatments was randomized, and a maximum of two temperatures were tested in one day. The sequence of temperature trials for all individuals was 25, 20, 10, 30, 15, and 35°C. Once all temperature treatments had been completed, they were repeated in the same sequence. The turtles were equilibrated for 30 min in a tank filled with a combination of lake and well water at the experimental temperature prior to testing. Cloacal temperature was measured immediately before and after each performance using a digital thermometer to ensure T_b did not change over the course of a trial, and the mean was taken as T_b for each replicate.

Swimming trials were conducted in a plywood raceway (4.93 × 0.4 × 0.6 m) lined with plastic and filled with water. We placed markers 0.5 m from each end of the raceway to mark the central swimming distance (3.93 m). For each trial, the temperature of the water in the raceway equaled the experimental temperature. Turtles were encouraged to swim at maximum speed by gently tapping their tail and the end of their carapace. The time it took their head to cross the two markers was recorded with a stopwatch. Each trial consisted of two swimming replicates, which were measured back to back, and because all treatments were duplicated, a total of four replicates per temperature were recorded for each turtle. The fastest time (maximum speed) for each individual at each temperature was subsequently used for analysis. After a turtle had completed a swimming trial (two replicates) at a given temperature, we scored its righting time at the same temperature.

Righting trials were conducted in an open plywood box (70 × 50 × 50 cm) lined with synthetic grass carpet. Each turtle was placed on its carapace in the box. The time for the turtle to right itself was recorded with a stopwatch. To separate righting time from reaction time, we considered the former to consist of the time from when the turtle initiated movement when on its carapace until it was on its plastron. For each individual, five replicates were measured per trial. The turtles were given 15 min to rest after each replicate. Because all treatments were duplicated, a total of 10 righting events per temperature were recorded for each turtle. The fastest time (maximum performance) for each individual at each temperature was subsequent-

ly used for analysis. Individuals that consistently failed to right at all temperatures (six of 32) were excluded from analysis.

Hatchling turtles were tested for performance using the same general procedures that were used for adults. Both swimming and righting performance trials were conducted in the environmental chamber in which they were housed, where we were able to manipulate temperature for the trials. Turtles were tested at each 5° interval between 13°C and 33°C for both performances. The sequence of temperature trials for all individuals was 18, 23, 13, 33, and 28°C. Hatchlings were equilibrated in water at the experimental temperature for an hour before testing and the same procedure used for adults was followed to record swimming speed and righting time. Two replicates of both swimming and righting performance were measured for each temperature treatment. The turtles swam in a plastic raceway (1.8 × 0.1 × 0.15 m) with a central swimming distance of 0.69 m. Because of the small size of the hatchlings, we could not measure cloacal temperature. We used the temperature of the equilibration water as the measure of hatchling T_b at the beginning of the trials. Given the small thermal inertia of hatchlings, and considering that the T_b of adult males equilibrated to water temperature within 20 min (EB-E, pers. obs.), we assumed that the T_b of the hatchlings equaled the temperature of the water.

Statistical Analyses.—We applied a series of rules in our analysis of preferred basking temperature to ensure consistency. (1) The first four hours after the turtle was placed in the basking arena were discarded, because preliminary observations showed that turtles required at most 4 h to initiate shuttling behavior. (2) T_b had to drop at least 2°C at a rate of at least 1°C/min to count as a “trough.” Because turtles sometimes shifted their position on the basking platform under the heat lamp, rule 2 ensured that we only counted troughs when the turtle moved from the basking platform to the water. (3) If a turtle remained at a relatively stable T_b for more than an hour, we considered it to be at a “plateau.” Plateaus were usually the result of the turtle remaining in the water. Because the turtle was not shuttling during a plateau phase, these periods were discarded, and we used only the time when the turtle was shuttling for our T_{set} analysis. We confirmed that the “peaks” and “troughs” we identified in the T_b profiles were indeed caused by shuttling between the basking platform and the water by videotaping the turtles. (4) We did not consider T_b s measured while the heat lamp was off (2200 h to 0800 h) because the turtles could not access the heat source during this period.

T_{set} for each individual was taken as the temperature range between the mean of the upper set point (peaks) and the mean of the lower set point (troughs; Kingsbury, 1999). The mean T_{set} for all individuals was subsequently calculated.

To determine whether there was any change in shuttling behavior over the 48-h testing period, we compared the set points and the number of peaks and troughs on day 1 and day 2. Differences in set points or in the number of peaks and troughs could indicate that shuttling in our arena was too demanding for the turtles.

To analyze the locomotor performance curves, we fitted the mean of the maximum performance of both hatchling and adult turtles to five functions and used Akaike’s information criterion (AIC) to select the best model for each performance; Table 1). All five functions used were left-skewed, as opposed to the symmetric functions favored by Angilletta (2006), because this is the natural shape of thermal performance curves (Huey and Kingsolver, 1989; Bennett, 1990). The function with the lowest AIC-value for each class was subsequently used to fit the data for each individual and determine two parameters: the optimal temperature for performance (T_o), and the 80% performance breadth (B_{80} : the range of temperatures at which the individual can perform $\geq 80\%$ of its maximum; Huey and Stevenson, 1979). The response to T_b of both swimming and righting performance were normalized per individual (i.e., expressed as a percentage of individual maximum) to control for factors systematically affecting absolute performance (e.g., size, carapace shape; Huey and Stevenson, 1979; Bulté and Blouin-Demers, 2006).

All statistical analyses were performed with JMP 5.0 (SAS Institute, Cary, NC). Data were tested for normality and homoscedasticity using the Shapiro-Wilk test and Levene’s test, respectively. When comparing means, two-tailed t -tests were used if these assumptions were upheld, and Welch ANOVA F -tests were used if the assumptions were violated. Results were considered significant at $P < 0.05$, and all means reported are ± 1 standard error.

RESULTS

Preferred Basking Temperature.—The upper and lower bounds for T_{set} of adult male turtles were $29.9 \pm 0.7^\circ\text{C}$ and $19.4 \pm 0.9^\circ\text{C}$, respectively ($N = 12$). The turtles averaged 16 peaks and 15 troughs while in the basking arena (Fig. 1). There was no significant difference between the upper set points (paired t -test: $t_{11} = 2.12$, $P = 0.06$) or lower set points (paired t -test: $t_{11} = 1.39$, $P = 0.19$) on day 1 compared to day 2. There

TABLE 1. A comparison of functions used to describe the thermal performance curves of Northern Map Turtles from Lake Opinicon, Ontario, Canada, using Akaike's information criterion (AIC). The function with the lowest AIC is the one that best describes the data. K = number of parameters in the function, MSR = mean square of the residuals, w_i = Akaike weight. ¹Stevenson et al., 1985. ²Logan et al., 1976. Models in boldface were selected for analyses.

	Performance (N)	Function	AIC	K	MSR	w_i
Adult	Swimming (32)	Log-exponential¹	105.85	7	67.4	0.67
		Exponential-exponential ¹	108.74	6	104.8	0.16
		Sextic	108.77	8	65.0	0.16
		Quartic	113.00	6	143.0	0.02
		Logan ²	144.11	6	1334.8	0.00
	Righting (26)	Quartic	105.83	6	351.7	0.48
		Exponential-exponential ¹	106.43	6	365.7	0.36
		Log-exponential ¹	108.93	7	328.8	0.10
		Logan ²	110.43	6	526.0	0.05
		Sextic	112.88	8	325.3	0.01
Hatchling	Swimming (24)	Quartic	91.75	6	193.0	0.59
		Exponential-exponential ¹	92.97	6	212.7	0.32
		Log-exponential ¹	95.91	7	243.1	0.07
		Sextic	100.13	8	190.0	0.01
		Logan ²	108.77	6	634.4	0.00
	Righting (25)	Quartic	104.74	5	594.2	0.86
		Logan ²	109.50	6	758.1	0.08
		Log-exponential ¹	110.14	7	568.6	0.06
		Sextic	114.30	8	569.0	0.01

was also no significant difference in the number of peaks (paired *t*-test: $t_{11} = 0.69$, $P = 0.51$) or troughs (paired *t*-test: $t_{11} = 0.74$, $P = 0.47$) on day 1 compared to day 2.

Locomotor Performances.—According to AIC, the quartic function was the best model for both swimming and righting for hatchling and righting for adults, whereas the logistic-exponential function was the best model for swimming performance of adults (Table 1). T_o for

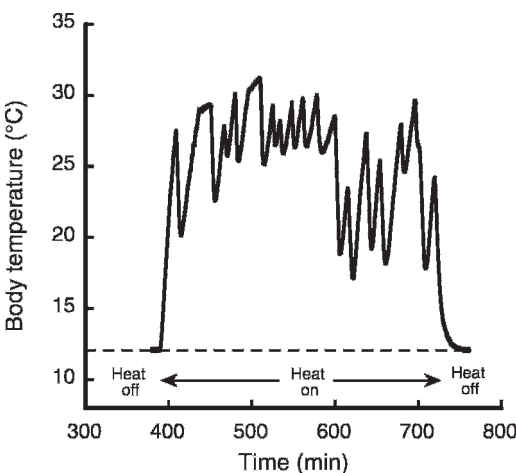


FIG. 1. Representative body temperature profile from an adult male Northern Map Turtle from Lake Opinicon, Ontario, Canada, placed in the basking arena showing the characteristic peaks and troughs.

both swimming and righting fell within T_{set} for adult turtles (Fig. 2). T_o for righting was significantly higher than T_o for swimming for both adult males (*t*-test: $t_{56} = 3.25$, $P = 0.002$) and hatchlings (Welch ANOVA: $F_{1,47} = 9.23$, $P = 0.004$, $R^2 = 0.16$). B_{80} for swimming was wider than B_{80} for righting for both adult males (*t*-test: $t_{56} = 26.91$, $P < 0.001$, Table 2) and hatchlings (*t*-test: $t_{47} = 7.34$, $P < 0.001$, Table 2).

In terms of ontogenetic changes in performance, the hatchlings had a narrower B_{80} (*t*-test: $t_{54} = 21.42$, $P < 0.001$, Table 2) than adult males for swimming and a lower T_o (*t*-test: $t_{54} = 1.80$, $P = 0.077$), although the difference for the latter was not significant. There was no difference in T_o (Welch ANOVA: $F_{1,49} = 0.08$, $P = 0.777$, $R^2 = 0.002$) or B_{80} (*t*-test: $t_{49} = 1.49$, $P = 0.143$) between adults and hatchlings for righting (Table 2).

DISCUSSION

Northern Map Turtles appear to be thermal generalists, exhibiting very wide T_{set} and performance breadths. Northern Map Turtle T_{set} which spans over 10° , is wider than those previously reported for other aquatic turtles, for which the central 50% of the temperatures selected in a gradient ranged from 2–6°C (Schuett and Gatten, 1980; Tamplin, 2006; Edwards and Blouin-Demers, 2007). However, this is the first study to measure preferred temperature for aquatic emydids using a bask-

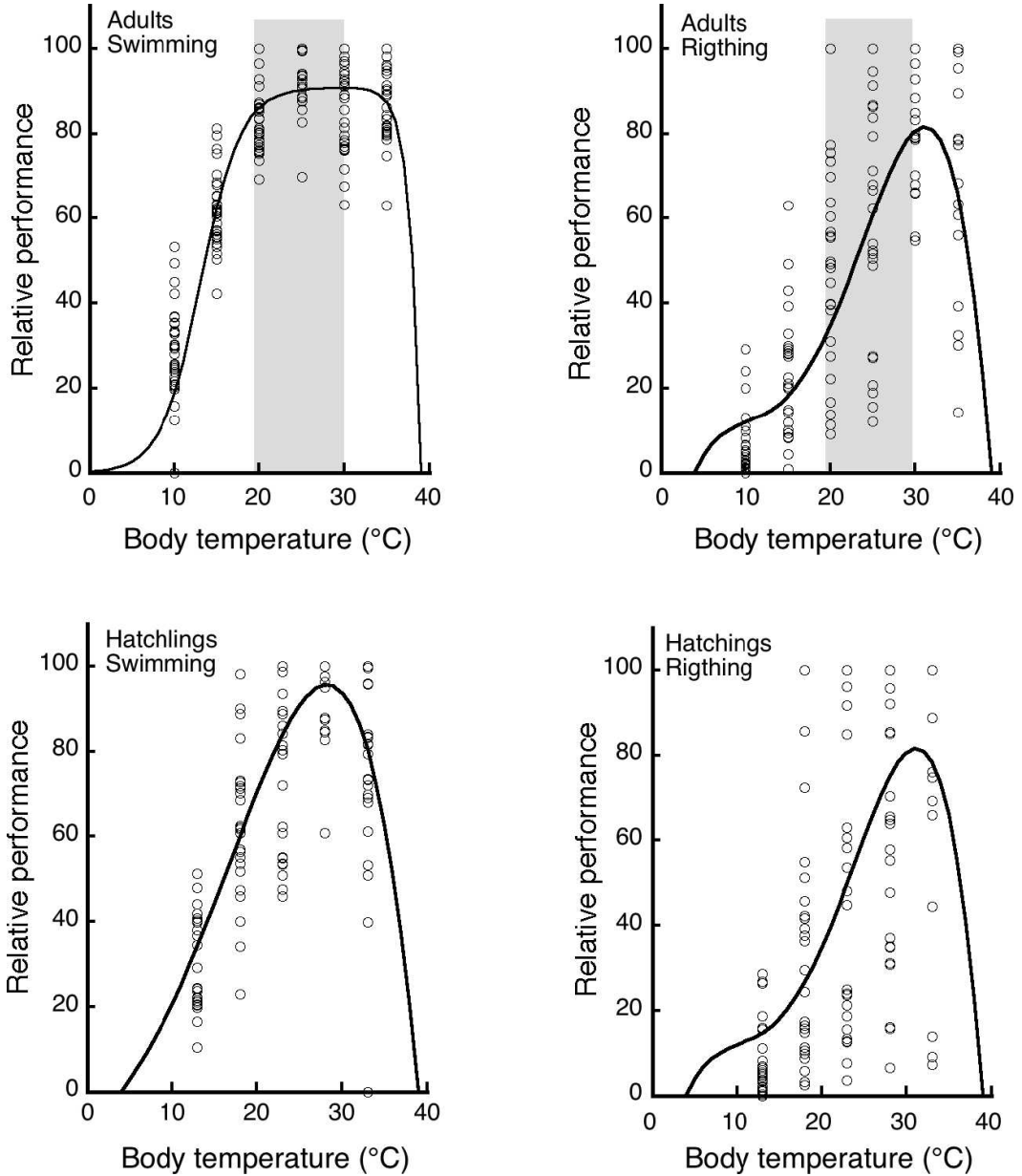


FIG. 2. Mean fitted thermal performance curves (lines) and individual responses (open symbols) of adult male and hatchling Northern Map Turtles. The grey boxes indicate the mean preferred temperature range in the basking arena.

TABLE 2. Mean ($^{\circ}\text{C} \pm \text{SE}$) T_o and B_{80} for swimming and righting performances for adult male and hatchling Northern Map Turtles from Lake Opinicon, Ontario, Canada. ¹Performance = $S \{1/[1 + k_1 e^{-k_2(T_b - CT_{\min})}]\} [1 - e^{k_3(T_b - CT_{\max})}]$. ²Performance = $aT^4 + bT^3 + cT^2 + xT + z$.

Class	Performance	T_o ($^{\circ}\text{C}$)	B_{80} ($^{\circ}\text{C}$)	N	Curve
Adult	Swimming	28.8 ± 0.3	20.3 ± 0.3	32	Log-exponential ¹
	Righting	30.5 ± 0.4	9.3 ± 0.3	26	Quartic ²
Hatchling	Swimming	27.9 ± 0.4	11.7 ± 0.3	24	Quartic ²
	Righting	30.3 ± 0.6	8.7 ± 0.3	25	Quartic ²

ing arena that allows shuttling between water and basking under a heat source. This approach fundamentally differs from that of an aquatic thermal gradient and, thus, may partially explain the wider T_{set} found in our study. There was no significant change in T_{set} or shuttling behavior during the two days the turtles were in the basking arena. This result indicates that neither fatigue nor learning affected the turtles' selection of T_b and that shuttling in a basking arena has a trivial cost. Therefore, we are confident that our estimation of T_{set} for male Northern Map Turtles accurately reflects the real T_{set} in our population.

All four performance curves exhibited the same general form expected for locomotion, with their peaks shifted toward the thermal maximum of the species (Huey and Kingsolver, 1989; Bennett, 1990). However, there are important differences between swimming and righting that are common to hatchlings and adults. First, swimming performance is maximized at a lower temperature than righting. Second, both adult and neonate turtles can perform well (at least 80% of their maximum) over a larger range of temperatures for swimming compared to righting. These results suggest that the thermal dependence of righting and swimming performance are not equal in aquatic emydids. In addition, unlike hatchlings, nearly 20% (six of 32) of adult turtles did not right, indicating that righting may not have a major influence on fitness for adult male Northern Map Turtles, whereas righting has been shown to be a good indicator of fitness in hatchlings of other freshwater turtles (Delmas et al., 2007).

Our first objective was to examine thermal coadaptation of locomotor performance and preferred basking temperature in the Northern Map Turtle. One of the most common predictions of the thermal coadaptation hypothesis is that the preferred body temperature of a species should match the thermal optimum for performance (Angilletta et al., 2006). We found that the optimal temperature for swimming and righting fell within T_{set} very close to the upper bound. Because T_{set} encompasses T_o for swimming and righting, one would conclude that both traits are coadapted with preferred basking temperature. However, for the Northern Map Turtle, this interpretation may be too simplistic. Because support for the coadaptation hypothesis depends partly on the breadth of T_{set} , a larger T_{set} will more likely lead to support for the hypothesis. However, this support would be weak because the prediction of the hypothesis would be very difficult to falsify. In a case such as the Northern Map Turtle, coadaptation may not reflect selective pressure for the convergence of T_o and T_{set} . The wide range of T_{set} may

be indicative of selective pressures to improve other physiological and metabolic processes in addition to locomotor performance.

The B_{80} for swimming was very wide, spanning over 20°C, meaning that adult Northern Map Turtles can swim well at virtually all ecologically relevant temperatures. Thus, the elevated temperatures associated with basking do not improve the turtles' swimming performance markedly. This finding is concordant with the species' ecology because Northern Map Turtles in our study area swim in water that varies from 10°C in spring to 28°C in summer. It is likely that, given the large variability in thermal quality of the aquatic environment, selective pressure may have favored a wide performance breadth for swimming. The wide T_{set} and B_{80} for swimming contrast with findings from other terrestrial reptiles, such as snakes and lizards, that tend to exhibit narrower T_{set} and B_{80} (Angilletta et al., 2002a; Blouin-Demers et al., 2003). Aquatic turtles at high latitudes, such as Northern Map Turtles, have to shuttle between two environments with very contrasting temperatures (i.e., water and land) to maintain their T_b within T_{set} . Thus, thermo-regulating may be much more challenging for semiaquatic riverine reptiles than for terrestrial snakes and lizards. Terrestrial habitats are generally characterized by finer-grained variation in thermal microclimates, facilitating the fine tuning of T_b . Thus, the wider T_{set} found in Northern Map Turtles may indicate that shuttling is more costly for aquatic emydids than for other terrestrial reptiles.

Righting, which occurs on land, had a much narrower B_{80} and a higher T_o . In turtles, the righting reflex is a response to the relatively rare and unpredictable event of being flipped over onto the carapace. Because righting only occurs on land, where temperatures are generally higher than in the water, selection may have favored a shift toward a higher T_o compared to swimming.

Our second objective was to determine the presence of an ontogenetic shift in locomotor performance in the Northern Map Turtle. There was no difference between hatchlings and adults for righting performance. However, a shift in the swimming curve was present between hatchling and adult turtles. Swimming T_o for hatchlings was 1°C lower than that of adults (Table 1), although this difference may not be ecologically meaningful given the wide plateau of both curves near T_o (Fig. 2). A more pronounced shift, however, was observed for the 80% performance breadth. Hatchlings (21–33°C) had a narrower B_{80} than did adults (16–37°C; Table 1). This pattern was also found in Northern Water Snakes, but not in Black Rat

Snakes, the only two species for which ontogenetic shifts in performance curves have been examined (Blouin-Demers et al., 2003). In Northern Water Snakes, the shift in B_{80} and T_o is associated with a shift in preferred body temperature. This suggests that hatchlings have a different thermal ecology than adults, perhaps because of different microhabitat selection in the aquatic environment.

The difference in the shape of the swimming performance curve between adults and hatchlings could also be caused by an ontogenetic shift in performance. Juvenile animals, including reptiles, often exhibit reduced performance compared to adults (Herrel and Gibb, 2006). This ontogenetic shift in performance could account for the lower performance of hatchlings at low temperatures (i.e., narrower B_{80}). However, how ontogenetic shifts in performance are affected by temperature is unknown. Alternatively, the lower performance of hatchlings at lower temperatures could be the result of their thermal history. The hatchlings used in our experiment were never exposed to temperatures below 18°C for extended periods of time, whereas the adults spend nearly five months of the year at temperatures near 0°C. Thus, perhaps exposure to low temperatures is necessary to perform well at those temperatures.

Data on the preferred body temperature of hatchling Northern Map Turtles are not available from this study because of the difficulty associated with continuously recording T_b of small turtles (<9 g) in an aquatic shuttling arena. Such data would help elucidate the ecological significance of the observed shift (for swimming) and lack thereof (for righting) in locomotor performance. The ecology of neonatal reptiles is poorly understood (Marafka et al., 2000), and the generality of our findings as well as their potential proximate causes deserve further investigation.

In conclusion, we found evidence that locomotor performance and preferred basking temperature were coadapted in the Northern Map Turtle. However, because of the wide range of T_{set} and the generally wide B_{80} of locomotor performance, the traditional prediction of the thermal coadaptation hypothesis may not be appropriate for the Northern Map Turtle. This study is the first to analyze both preferred basking temperatures and locomotor thermal performance curves in chelonians. Further studies on the thermal dependency of other physiological traits that affect fitness are now needed to gain a more complete understanding of thermal coadaptation in the Northern Map Turtle and other turtles. Traits that are directly affected by basking, such as gut passage and digestion rate, would be of particular interest

because they would help us gain a more complete understanding of the trade-offs that affect temperature selection in aquatic emydids.

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