

**A test of the thermal coadaptation hypothesis in the common map turtle
(*Graptemys geographica*)**

by

Elad Ben-Ezra

Supervisor: Dr. Gabriel Blouin-Demers

**Thesis submitted to the Department of Biology in partial fulfillment of
the requirements for the B.Sc. Honours degree, specialization Biology**

University of Ottawa

Ottawa, Ontario

April 30, 2006

Abstract

According to the thermal coadaptation hypothesis, the preferred body temperature (T_{set}) of ectotherms should match their optimal temperature (T_o) for performance. The first objective of this study was to test this prediction with male common map turtles (*Graptemys geographica*) by determining T_{set} and T_o for swimming speed and righting time. The second objective was to compare T_{set} measured by two different methods: a dry thermal gradient and an aquatic basking arena. The third objective was to determine if there are any ontogenetic changes in performance by comparing hatchling and adult male turtles. Given that map turtles are highly aquatic, we contend that the T_{set} determined in the basking arena (22.5°C – 31.8°C) better represents T_o . In the dry gradient, T_{set} (23.5°C – 25.9°C) was likely affected by the unnatural environment in which moisture may have been a limiting factor. The optimal temperatures for swimming (28.6°C) and righting (31.6°C) were within the T_{set} range determined from the basking arena but not from the dry gradient. Performance curves were shifted to colder temperatures for hatchling turtles compared to adults, though the difference was non-significant for righting. Overall, our study has provided evidence in support of the thermal coadaptation hypothesis for two locomotory performances and demonstrated a new, more effective method for determining preferred body temperatures of turtles.

Introduction

Body temperature (T_b) of ectotherms has a profound effect on many ecologically relevant physiological systems (Huey and Stevenson 1979; Huey 1982; Angilletta *et al.* 2002; Blouin-Demers *et al.* 2003; Zhang and Xi 2004). Since ectotherms do not generally produce a significant amount of metabolic heat, they regulate their T_b primarily by heat absorption from their surrounding environment (Pough and Gans 1982). Thus, despite some physiological control of T_b (Bartholomew 1982), ectotherms must thermoregulate behaviourally (Huey 1982). The close link between behavioural 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 2006). As Huey and Bennett (1987) reason, the T_b s behaviourally selected by ectotherms should influence fitness via their direct effects on physiological performance, thereby promoting coadaptation. If selection of preferred temperature (T_{set}) is driven away from the optimal temperature for physiological performance (T_o), coadaptation pressures should favour a parallel shift in T_o (Huey and Bennett 1987). Although the concept of thermal coadaptation has been appreciated for over 20 years (Angilletta *et al.* 2006) there is limited empirical evidence in support of it. Kingsolver (1987) showed that in *Pieris* butterflies, thermoregulatory posture, wing pigment, and melanization pattern were coadapted traits that can affect fitness via their influence on flight performance. There is evidence of thermal coadaptation in lizards in both interspecific (Bauwens *et al.* 1995) and intraspecific (Angilletta *et al.* 2002) studies. Blouin-Demers *et al.* (2003) also provided support for the thermal coadaptation hypothesis in their intraspecific study of black rat and water snakes. Dorcas *et al.* (1997) found evidence that suggested that

passage rate, but not digestive rate, was coadapted with thermoregulatory behaviour of rubber boas. However, no studies to date have explicitly examined thermal coadaptation in turtles. In their review on the subject, Angilletta *et al.* (2006) contended that coadaptation is a unifying principal of thermal biology because it emphasises the simultaneous evolution of thermoregulation and thermal sensitivities. The challenge for biologists studying thermal coadaptation is, thus, to elucidate the intricate relationships between behavioural thermoregulation, thermal sensitivity of performance, and ultimately, fitness.

The first objective of this study was to test one of the most prominent intraspecific predictions of the thermal coadaptation hypothesis: that the optimal temperature for performance (T_o) should match the preferred body temperature (T_{set}) of a species. The common map turtle (*Graptemys geographica*) was selected as the study species, since very little is known about the thermal sensitivity or thermal preference of this turtle.

Two measures of locomotory performance – swimming speed and righting time, were scored, and compared with two measures of preferred temperature for adult male map turtles. Both swimming speed and righting time are important performances that are intimately linked to fitness. Male map turtles must find and mate with females that are much larger than themselves. Thus, the faster a male turtle swims the higher his chances are of mating successfully. Righting time is also ecologically relevant, as a turtle that cannot right quickly when on its carapace is subject to increased risk of predation (particularly for hatchlings) and desiccation.

Preferred temperature is most appropriately determined experimentally in the laboratory, and the most common method of determining T_{set} for reptiles is a thermal

gradient (Crawshaw 1980; Bennett and John-Adler 1986; Blouin-Demers and Weatherhead 2001). In addition, we used a second, novel method of determining T_{set} : an aquatic basking arena (or “shuttle box”). The shuttle box was a more natural environment that allowed the turtles to thermoregulate by basking under a heat lamp and cooling in water. The second objective of this study was to compare these two methods of determining T_{set} . We predicted that T_{set} determined in the basking arena would more accurately reflect the species’ preferred temperature and show evidence of coadaptation with performance.

We also scored swimming speed and righting time for hatchling map turtles that were captured for a concurrent study and transferred to the laboratory. The third objective of this study was to compare performance curves of adult and hatchling turtles to determine if there are any ontogenetic changes in performance. It is not known if the thermal ecology of hatchling map turtles matches those of adults. However, assuming that the thermal ecologies of both groups are similar, and given that hatchlings should experience a similar thermal environment than adults upon emergence, we did not predict a significant ontogenetic change in performance.

Methods

Study site

This study was primarily conducted in July and August 2005 at the Queen’s University Biological Station. Thirty-two male map turtles were captured from Lake Opinicon by snorkelling and using basking traps. The turtles were housed in groups of 2-3 in large (80 cm x 80 cm x 80 cm) tanks in the laboratory for two to three weeks during the trials. The laboratory received natural light and the tanks were filled with lake water,

which was changed every two days. The turtles were provided with rocks for basking and were fed 4-5 mealworms every other day. Turtles were released at their point of capture in Lake Opinicon as soon as they were finished performance trials and measures of preferred temperature.

Testing Procedures: Preferred Temperature

Preferred body temperature (T_{set}) of adult male turtles was measured using custom-made temperature-sensitive radio transmitters (AVM Inc., 6.0 g). The transmitter was attached to the carapace of the turtle with a probe inserted 5 cm into its cloaca. Transmitters were only placed on turtles large enough so that it was not an impediment to movement and did not exceed 5% of their mass in air. Of the 32 turtles sampled, 24 satisfied this condition. In order to calculate temperature from the pulse rate of the transmitters, we determined calibration curves for each transmitter using water baths and a digital thermometer. Pulse rates were measured at ten degree intervals between 0°C and 40°C and polynomial regression was used to derive an equation to predict temperature based on transmitter pulse rate. The calibration equations provided a very high degree of fit ($R^2 \geq 0.9996$ in all cases). In addition, we tested for any drift in the calibration curves throughout the study, but there was never any observed.

We used a radiotelemetry data logger (SRX 400, Lotek Engineering, Newmarket, Ontario, Canada) to record the pulse rate once the transmitters were placed on the turtles. The logger was programmed to record the mean duration between ten pulse intervals, along with the standard deviation of the mean, transmitter frequency, date, and time of each event. The data was subsequently downloaded onto a desktop computer and imported into Microsoft Excel, where the calibration equations were used to determine

T_b . By programming the logger to scan and record each frequency every minute, we were able to determine essentially continuous T_b of the turtles.

Two methods of measuring preferred body temperature (T_{set}) were used in this study: a dry thermal gradient and an aquatic basking arena. The experimental design for the thermal gradient follows that of Blouin-Demers and Weatherhead (2001). The gradient consisted of a plywood box (200 x 60 x 60 cm) divided along its length into two sections. A coil of tubing in which cold (10°C) water was constantly circulating under one end of the box and three heating pads under the other end produced a continuous thermal gradient between 18°C and 40°C. Turtles were placed individually in one of the two divisions of the gradient in the early evening, between 1800h and 1900h, and were given 24 hours to adjust to the environment before recording their T_b over the next 24 hours. In order to provide some moisture, 0.5 L of 25°C water was added to the gradient immediately before the turtle was placed in it, and another 0.5 L was added 1 hour before starting to record their T_b .

The experimental design for the aquatic basking arena is a modified version of the “shuttlebox” proposed by Kingsbury (1999). The aquatic basking arena, henceforth referred to as a shuttle box, consisted of a wooden basking platform (50 x 50 cm) with a heat lamp attached. The shuttle box was placed in a tank (150 x 60 x 60 cm) where cold (10°C) water constantly circulated. The heat lamp was adjusted to a height above the basking platform (60 cm) so that it reached 40°C on the surface. The turtles therefore had to shuttle between two environments that were obviously outside their preferred temperature range, and were constantly heating or cooling. This process enabled us to determine the set points, the temperature at which the turtle switched from heating to

cooling and vice versa, for each individual. Turtles were placed individually in the shuttle box in the early evening, between 1800h and 1900h, and were given 24 hours to adjust to the environment before recording their T_b over the next 24 hours.

Testing Procedures: Performance

The two locomotory performances measured for adult turtles were swimming speed and righting time. Turtles were tested at T_b s of $11.0 \pm 0.1^\circ\text{C}$, $15.0 \pm 0.0^\circ\text{C}$, $20.0 \pm 0.0^\circ\text{C}$, $25.0 \pm 0.0^\circ\text{C}$, $30.0 \pm 0.1^\circ\text{C}$, and $35.0 \pm 0.1^\circ\text{C}$ for swimming and $11.4 \pm 0.1^\circ\text{C}$, $15.0 \pm 0.0^\circ\text{C}$, $20.0 \pm 0.0^\circ\text{C}$, $25.0 \pm 0.0^\circ\text{C}$, $30.2 \pm 0.1^\circ\text{C}$, and $35.1 \pm 0.1^\circ\text{C}$ for righting. The order of treatments were randomized, and once all trials were completed they were repeated to ensure that both maximal performance was obtained and that no individuals showed reduced performance throughout the study due to illness or injury. We did not test more than two temperatures in a day, and the turtles were given at least 5 hours rest before being tested again. All trials took place between 0900h and 1730h. The turtles were equilibrated in a tank filled with water at the experimental temperature for 30 minutes prior to testing. The turtles' T_b was measured immediately before and after each performance using a digital thermometer by inserting its thermocouple probe 5 cm into their cloaca. The mean of the two temperatures was taken as the T_b for each replicate.

Swimming trials were conducted in a plywood raceway lined with plastic that was 4.93 m long, 0.6 m high, and 0.4 m wide. We placed markers 0.5 m from each end of the raceway to mark the central swimming distance (3.93 m). An additional marker was placed at the halfway point of the central swimming distance for the 10°C trial, as the turtles swam at a very low speed at this temperature and a swimming distance of 1.97 m was more appropriate. For each trial, the temperature of the water in the raceway was

equal to that of the experimental temperature, and was filled to an approximate height of 0.3 m. Turtles were encouraged to swim by gently tapping their tail and the end of their carapace and the time it took their head to cross the two markers was recorded with a stopwatch. Once an individual reached the end of the raceway, it was immediately turned around and swam the length of the raceway for a second time. Thus, each trial consisted of two swimming replicates, and since all trials were repeated each turtle swam a total of four replicates per temperature. The fastest time (maximum speed) for each individual at each temperature was subsequently used for analysis. Once a turtle had completed a swimming trial, we immediately placed it back into the holding tank used for equilibration. After all turtles had completed a swimming trial at a particular temperature, we scored their righting time at the same temperature, using the same order in which they were tested individually for the swimming performance.

Righting trials were conducted in an open plywood box (70 x 50 x 50 cm) lined with Astroturf. The turtle was placed on its carapace in the box, and the time for it to right itself was recorded with a stopwatch. To separate “reaction time” from “righting time”, the time from when the individual was placed on its carapace until its first movement was recorded and excluded from analysis. Once the turtle had righted itself, we immediately placed it back in the holding tank. Five righting times for each turtle were measured per trial, for a total of ten replicates per temperature. The fastest time (maximum performance) for each individual at each temperature was subsequently used for analysis.

The hatchling map turtles tested for performance were reared in the laboratory for a concurrent study. Thirty-four gravid female map turtles were captured during the 2005

nesting season (June – July) and induced to lay eggs with an intramuscular injection of oxytocin (20 USP units/ml, 0.5 ml/kg). All clutches were incubated in moist vermiculite (1:1 vermiculite mass: water mass) at 29°C and emerged 55-65 days after oviposition (August 3 – 28, 2005). Six of the thirty-four clutches (36 out of 338 turtles) were randomly selected for performance analysis and were transferred to the laboratory at the University of Ottawa in September 2005. The hatchlings were housed individually in small (20 cm x 30 cm) plastic containers in an environmental chamber (Constant Temperature Control) and fed a diet of mealworms and bloodworms. The temperature of the chamber was set between 22°C and 25°C from September 2005 until they were tested for performance in March 2006. Thus, the hatchlings would likely have acclimated to this temperature range.

Hatchling turtles were tested for performance using the same general procedures that were used for adults. Both swimming and righting performances were conducted in the environmental chamber in which they were housed, where we were able to carefully manipulate temperature for the trials. Turtles were tested at T_{bs} of $12.6 \pm 0.1^\circ\text{C}$, $17.8 \pm 0.1^\circ\text{C}$, $21.9 \pm 0.1^\circ\text{C}$, $26.5 \pm 0.1^\circ\text{C}$, and $33.2 \pm 0.2^\circ\text{C}$ for swimming, and $12.6 \pm 0.1^\circ\text{C}$, $17.4 \pm 0.1^\circ\text{C}$, $21.8 \pm 0.1^\circ\text{C}$, $26.4 \pm 0.1^\circ\text{C}$, and $33.2 \pm 0.1^\circ\text{C}$ for righting. Hatchlings were placed in plastic containers filled with water at the experimental temperature for an hour before testing and the same procedure used for males was followed to record swimming speed and righting time. Two replicates of both swimming and righting performance were measured for each temperature trial. We did not repeat the trials, as this portion of the study was completed within a short period (eight days) and no turtles showed any sign of reduced performance, illness, or injury. The turtles swam in a plastic raceway (1.8

m long, 0.1 m wide, 0.15 m high), with a central swimming distance of 0.69 m for all trial except the lowest temperature, which had a central swimming distance of 0.28 m.

Righting trials were conducted in a plastic container lined with Duct Tape. Due to their small size, we could not measure cloacal temperature for hatchlings, and used the temperature of the water that they were equilibrated in as the measure of their T_b . Given the small thermal inertia of hatchlings, and considering that the T_b of adult male turtles generally equilibrated to water temperature within 20 minutes (Ben-Ezra, personal observation), it is reasonable to assume the T_b of the hatchlings equalled that of the water. Since the turtles were always in water for the swimming trials (either in plastic containers or the raceway), it is unlikely any change in T_b occurred while scoring this performance. The turtles were only out of the water during the righting trials. However, since the temperature of the environmental chamber was always within 3°C of the water, the potential for the hatchlings' T_b to change during the short amount of time while measuring righting (between a few seconds and three minutes) was low.

Sample Size – Preferred temperature

All 24 adult turtles that were large enough to have a radiotransmitter attached to their carapace were placed in the dry gradient. However, in one case the transmitter's probe slipped from the cloaca of a turtle, and its data was excluded from analysis. Twelve of the twenty-four turtles that were placed in the dry gradient were also placed in the shuttle box. However, due to complications regarding the radiotransmitters, data for two of the turtles were unmanageable and were excluded from analysis.

Sample Size - Performance

All 32 adult turtles sampled were tested for swimming performance. Six of the adults, however, would consistently refuse to right at all temperatures, and were therefore excluded from analysis of righting performance. Of the 36 hatchling turtles sampled, several showed signs of reduced capacities between September 2005 and March 2006. Thus, only 24 were tested for swimming performance and 23 for righting performance (as one consistently refused to right).

Analysis: Preferred Temperature.

Preferred temperature data was analyzed using JMP Version 5.0 (SAS Institute, 2002). For the dry gradient, T_{set} for each individual was taken as the central 50% of the distribution of T_b . While this is arbitrary, the central 50% distribution is commonly used as the measure of T_{set} from an experimental gradient (Hertz *et al.* 1993; Christian and Weavers 1996; Blouin-Demers and Weatherhead 2001). The mean T_{set} for all individuals was subsequently calculated. For the shuttle box, T_{set} for each individual was taken as temperature between the mean of the upper set point and the mean of the lower set point (Kingsbury 1999). The pooled mean T_{set} for all individuals was subsequently calculated.

Analysis: Performance.

Performance data was also analyzed using JMP Version 5.0. We fitted performance data to a logistic-exponential curve using non-linear curve fitting and the following equation: $Performance = S (1 / (1 + k_1 e^{-k_2 (T_b - CT_{min})})) (1 - e^{k_3 (T_b - CT_{max})})$ (Stevenson *et al.* 1985; Bulté and Blouin-Demers 2006). Hutchinson *et al.* (1966) reported that false map turtles (*Graptemys pseudogeographica*) lost their righting response between 38.5°C and 39.5°C. While map turtles begin to lose muscle tone below

10°C (Ben-Ezra, personal observation), they hibernate under ice in water at 4°C, where movement is extremely limited, and even for cold-acclimated turtles, locomotory performance is essentially zero. Thus, the critical thermal minimum (CT_{min}) and maximum (CT_{max}), where performance equals zero, were set at 4°C and 39°C, respectively. When fitting the curve, the experimental data points were given a weight of 1 and the CT_{min} and CT_{max} were given a weight of 10. For each individual, relative performance was calculated by dividing the speed (for swimming) or time (for righting) at all temperatures by the maximum. By using relative performance instead of absolute, we accounted for any consistently good or consistently poor performers in our sample. The fit of each curve was inspected using the error sum of squares, as non-linear curve fitting can be sensitive to starting parameter values. The equations for the performance curves for each turtle were subsequently inputted into a graphing calculator on a desktop computer to determine (1) the optimal temperature for performance (T_o), the temperature at which the performance was maximized, and (2) the 80% performance breadth (B_{80}), the temperature range at which the turtle could perform at least 80% of its maximum. All performance data was examined for the assumptions normality and homoscedasticity. When comparing means, two-tailed t-tests were used if these assumptions were upheld, and Welch ANOVA F-tests were used if they were violated. Results were considered significant at $\alpha = 0.05$ and all means reported are ± 1 SE.

Results

Preferred temperature.

The two measures of T_{set} from the dry gradient and shuttle box are presented in Table 1. The range of T_{set} determined in the shuttle box was much broader than that from the dry gradient, spanning almost ten degrees.

Performance.

The shape of the performance curves for adult male (Fig. 1) and hatchling (Fig. 2) turtles are, as expected, very similar. Performance increases with temperature from the critical thermal minimum, peaks close to the critical thermal maximum, and decreases sharply thereafter. Optimal temperatures (T_o) and 80% performance breadths (B_{80}) for the two performances are presented in Table 2. The T_o s for swimming and righting for adult males fall within the bounds of T_{set} for the shuttle box, but not for the dry gradient. The T_o for righting is significantly higher than the T_o for swimming for both adult males (Welch ANOVA: $F_{1,56} = 21.0$, $p < 0.0001$, $r = 0.54$) and hatchlings (Welch ANOVA: $F_{1,45} = 7.6$, $p < 0.01$, $r = 0.38$). The B_{80} for swimming is significantly larger than the B_{80} for righting for both adult males (Welch ANOVA: $F_{1,56} = 98.6$, $p < 0.0001$, $r = 0.82$) and hatchlings (two-tailed t-test: $t = -5.6$, $df = 45$, $p < 0.0001$). In terms of ontogenetic changes in performance, the hatchlings had a significantly lower T_o (Welch ANOVA: $F_{1,54} = 5.8$, $p = 0.02$, $r = 0.34$) and a significantly smaller B_{80} (Welch ANOVA: $F_{1,54} = 35.5$, $p < 0.0001$, $r = 0.66$) than adult males for the swimming performance. The hatchlings also had a lower T_o (Welch ANOVA: $F_{1,47} = 33.3$, $p = 0.37$, $r = 0.14$) and a smaller B_{80} (Two-tailed t-test: $t = 1.8$, $df = 47$, $p = 0.07$) than the males for righting, but the differences were not significant.

Discussion

In terms of the thermal coadaptation hypothesis, as predicted, the two optimal temperatures for performance for adult male map turtles matched their preferred temperature determined in the shuttle box, but not the dry gradient. The broad range of T_{set} determined in the shuttle box (Table 1) may have arisen from the opportunity to bask and attain higher T_{bs} while still having access to water. In the dry gradient, the turtles may have selected lower temperatures due to the unnatural environment in which moisture may have been a limiting factor. Since the T_{set} from the dry gradient fell within the lower end of the T_{set} from the shuttle box, the turtles may have been selecting for temperatures within their preferred temperature range that would also reduce water loss. Furthermore, the shuttle box method determined T_{set} based on the turtles' set points, which are measured directly, instead of relying on an arbitrary percentage of a distribution of T_{bs} . While the central 50% of the distribution of T_{bs} from a thermal gradient is commonly used as the measure of T_{set} (Hertz *et al.* 1993; Christian and Weavers 1996), any percentage (eg. central 30%, central 80%) could potentially be used. For example, if we assumed that the central 80% of the distribution was more appropriate than the central 50% for our study, our interpretation of T_{set} would have changed from 23.5°C - 25.9°C to 22.8°C – 27.2°C. By determining T_{set} based on the turtles set points, we relied on the choice the turtle, not the researcher, was making. Thus, we feel that the shuttle box more accurately reflects the true preferred temperature for map turtles, and should be used when determining T_{set} of turtles.

The four curves generated exhibited the same general form expected for locomotory performance, with their peak shifted toward the thermal maximum of the

species (Huey and Kingsolver 1989; Bennett 1990). Several trends are also evident when comparing performance curves between and within hatchling and male map turtles. First, swimming performance is optimized at a lower temperature than righting. Second, the turtles can perform “well” (at least 80% of their maximum) over a larger range of temperatures for swimming compared to righting. Third, the performance curves for hatchlings were shifted to slightly colder temperatures compared to adult males, although the differences in T_0 and B_{80} for righting were non-significant and marginally non-significant, respectively.

The differences between swimming and righting were not expected, as they are both measures of locomotory performance. While other studies have found that the thermal optima for different physiological systems within a species may be different (Stevenson et al. 1985), our results suggest that different thermal optima may exist even within a physiological system. Therefore, using one measure of performance, such as sprint speed (Huey and Bennett 1987), to estimate the physiological optimum for a species is inappropriate.

A key assumption in our study, however, is that the locomotory performances we measured in the laboratory accurately reflect performance under natural conditions. However, a study by Irschick *et al.* (2005) highlights the potential mismatch between laboratory measured sprint speed and natural escape speed in lizards. In some instances, intra- and interspecific classes of lizards that ran relatively slowly in the laboratory compensated by running close to their maximum speed in nature, whereas classes that were faster in the laboratory ran far below their maximum in nature (Irschick *et al.* 2005). While maximum sprint speed did correlate with escape speed for some classes, their

results provide a caution that laboratory measures of locomotory performance might not be representative of realized performance. Ideally, both measures of laboratory and field performance would be needed to eventually link variation in performance to variation in fitness (Irschick *et al.* 2005). Since we were unable to score swimming speed and righting time of map turtles in the field, we must acknowledge this weakness in our study.

However, it is not known if the model of locomotory compensation proposed by Irschick *et al.* (2005) holds for differences in temperature within a class, as all individuals were tested at the same temperature in their study.

A factor that was not explicitly considered in our study, but that nonetheless may have affected the results of our comparison of adult-hatchling performance, is thermal acclimation. Acclimation is the phenomenon of either reversible or irreversible plasticity of a physiological trait in response to an isolated environmental variable, such as temperature (Angilletta *et al.* 2006; Lagerspetz 2006). Developmental acclimation, involving reversible plasticity, and seasonal acclimation, involving reversible plasticity, are commonly observed in all types of organisms (Lagerspetz 2006). Since the hatchlings were incubated under identical conditions that also closely matched natural conditions, we can reasonably assume that developmental acclimation did not affect our results. In terms of seasonal acclimation, given that the male turtles tested for performance and preferred temperature were captured from Lake Opinicon and housed in tanks filled with lake water, we can assume that they acclimated to the temperature of the lake for July and August (approximately 23°C to 28°C). The hatchlings housed at the University of Ottawa, however, were kept at temperatures between 22°C and 25°C as we did not want to expose them to higher temperatures that would unnecessarily increase their metabolic

expenditure for several months. Thus, while most evidence suggests that ectotherms acclimate poorly for locomotory performance (Bennett 1990), it is possible that the hatchlings' performance curves were shifted to lower temperatures and less broad B_{80} s due to acclimation at a slightly lower and narrower temperature range. However, we are confident that the comparison of T_{set} and T_o for male turtles, as well as those for righting and swimming performance within classes, are appropriate and unbiased as all individuals sampled would have been acclimated at the same temperature. Seebacher (2005), in his review on acclimation, argued that coadaptation of preferred temperature and physiological performance must be considered only within clearly defined time periods. Since we sampled male map turtles during a period in which they are extremely active and had sufficient time to acclimate to the temperature of the lake throughout the summer, it is one of the most ecologically relevant times to test for thermal coadaptation.

While thermal acclimation may explain the differences between hatchlings and adults, the shifted performance curves may also be due to differences in their thermal ecologies. Since hatchlings emerge in August, they do not experience warm water temperatures for as long as adult males who have acclimated to summer water temperatures. Thus, it may be advantageous for hatchlings to optimize locomotory performance at lower temperatures. From the thermal coadaptation hypothesis, we would predict that the T_{set} of hatchlings would be lower than that of adult males. Continuing from our study, future work on T_{set} of hatchling map turtles would allow a further test of this prediction.

While our results provide support for the thermal coadaptation hypothesis, our study was limited to examining locomotory performance. Since the T_o s for both

swimming and righting were toward the upper end of T_{set} , it would be interesting to know where other thermal optima of performance fall. Testing such relevant behavioural and physiological measures of performance as appetite, gut passage time, and metabolic rate, would yield a more complete understanding of thermal coadaptation in map turtles.

Acknowledgements

This study would not have been possible without the tremendous conceptual and logistical help of Gregory Bulté. We would also like to thank Frank Phelan and the staff at the Queen's University Biological Station for logistical support. Financial support for this study was provided by NSERC, Parks Canada, and the University of Ottawa.

References

- Angilletta, M.J., Bennett A.F., Guderley, H., Navas, C.A., Seebacher, F., Wilson, R.S. 2006. Coadaptation: a unifying principal in evolutionary thermal biology. *Physiol. Biochem. Zool.* 79, 282-294.
- Angilletta, M.J., Hill T., Robson, M.A. 2002. Is physiological performance optimized by thermoregulatory behaviour?: a case study of the eastern fence lizard, *Sceloporus undulatus*. *J. Therm. Biol.* 27, 199-204.
- Bartholomew, G. A. 1982. Physiological control of body temperature. *In* C. Gans and F. H. Pough (Eds.), *Biology of the Reptilia*. Academic Press, London and New York, pp. 167-211.
- Bauwens, D., Garland Jr., T., Castilla, A.M., Van Damme, R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioural

- covariation. *Evolution* 49, 848-863.
- Bennett, A.F. 1990. Thermal dependence of locomotor capacity. *Am J Physiol. Regul. Comp. Physiol.* 259, 253-258.
- Bennett, A.F. and John-Adler, H. 1986. Thermal relations of some Australian skinks (*Sauria: Scinidae*). *Copeia* 1986, 57-64.
- Blouin-Demers, G., and Weatherhead, P.J. 2001. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82. 3025-3043.
- Blouin-Demers G., Weatherhead, P.J., McCracken, H.A. 2003. A test of the thermal coadaptation hypothesis with black rat snakes (*Elaphe obsoleta*) and northern water snakes (*Nerodia sipedon*). *J. Therm. Biol.* 28, 331-340.
- Bulté, G. and Bouin-Demers, G. 2006. Cautionary notes on the descriptive analysis of performance curves in reptiles. *J. Therm. Biol.* 31, 287-291.
- Christian, K.A. and Weavers, B.W. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecological Monographs* 66, 139-157.
- Crawshaw, L.I., Johnston, M.H., Lemons, D.E. 1980. Acclimation, temperature selection, and heat exchange in the turtle, *Chrysemys scripta*. *Am. J. Physiol. Integr. Comp. Physiol.* 238, 443-446.
- Dorcas, M.E., Peterson, C.R., Flint, M.E. 1997. The thermal biology of digestion in rubber boas (*Charina bottae*): physiology, behaviour, and environmental constraints. *Physiol. Zool.* 70, 292-300.
- Hertz, P.E., Huey, R.B., Stevenson, R.D. 1993. Evaluating temperature regulation by

- field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142, 796-818.
- Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. In: Gans, C., Pough, F.C. (Eds.), *Biology of the Reptilia*. Academic Press, New York, pp. 25-74.
- Huey, R.B., and Bennett A.F. 1987. Phylogenetic studies of coadaptation – preferred Temperature versus optimal performance temperatures of lizards. *Evolution* 41, 1098-1115.
- Huey, R.B. and Kingsolver, J.G. 1989. Evolution of thermal sensitivity of ectotherm performance. *TREE* 4, 131-135.
- Huey, R.B., and Stevenson, R.D. 1979. Integrating thermal physiology and ecology of ectotherms – discussion of approaches. *Am. Zool.* 19, 357-366.
- Hutchinson, V.H., Vinegar, A., Kosh, R.J. 1966. Critical thermal maxima in turtles. *Herpetologica* 22, 32-41.
- Irschick, D.J., Herrel, A., Vanhooydonck, B., Huyghe, K., Van Damme, R. 2005. Locomotor compensation creates a mismatch between laboratory and field estimates of escape speed in lizards: a cautionary tale for performance-to-fitness studies. *Evolution* 59: 1579-1587.
- Kingsolver, J.G. 1987. Evolution and coadaptation of thermoregulatory behaviour and wing pigmentation pattern in pierid butterflies. *Evolution* 41, 472-490.
- Kingsbury, B.A. 1999. An experimental design for examining thermoregulatory set points in ectothermic animals. *The American Biology Teacher* 61, 448-452.
- Lagerspetz, K.Y.H. 2006. What is thermal acclimation? *J. Therm. Biol.* *In press*.

Pough, F.C., and Gans, C. 1982. The vocabulary of reptilian thermoregulation. In: Gans, C., Pough, F.C. (Eds.), *Biology of the Reptilia*. Academic Press, New York, pp. 17-23.

Seebacher, F. 2006. A review of thermoregulation and physiological performance in reptiles: what is the role of phenotypic flexibility? *J. Comp. Physiol. B.* 175, 453-461.

Stevenson, R.D., Peterson, C.R., Tsuji, J., 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Phys. Zool.* 58, 46-57.

Zhang, Y.P. and Ji, X.A. 2004. The thermal dependence of food assimilation and locomotor performance in southern grass lizards, *Takydromus sexlineatus* (Lacertidae). *J. Therm. Biol.* 29, 45-53.



Table 1.

Mean T_b ($^{\circ}\text{C} \pm \text{SE}$) for upper and lower bounds of T_{set} determined for adult male map turtles in the dry gradient and shuttle box. For the dry gradient, the upper and lower bounds represent the 75% and 25% quartile of the distribution, respectively. For the shuttle box, the upper and lower bounds represent the pooled mean of the upper and lower set points, respectively.

Method	Lower bound	Upper bound	N
Dry gradient	23.5 ± 0.4	25.9 ± 0.6	23
Shuttle box	22.5 ± 0.3	31.8 ± 0.3	10

Table 2.

Mean ($^{\circ}\text{C} \pm \text{SE}$) T_o and B_{80} for swimming and righting performances for adult male and hatchling map turtles.

Class	Performance	T_o	B_{80}	N
Adult male	Swimming	28.6 ± 0.3	20.2 ± 0.3	32
	Righting	31.6 ± 0.6	11.3 ± 0.8	26
Hatchling	Swimming	26.8 ± 0.7	15.5 ± 0.7	24
	Righting	30.4 ± 1.1	9.0 ± 0.9	23

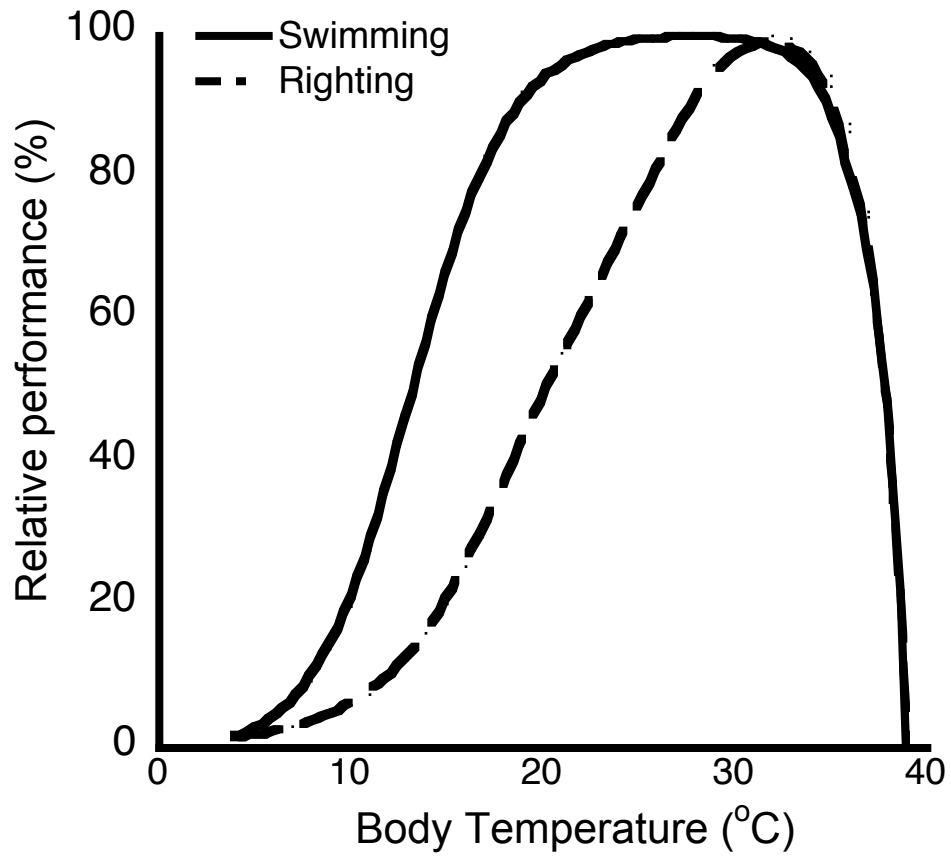


Fig. 1. Relative performance as a function of T_b for swimming and righting for adult male map turtles.

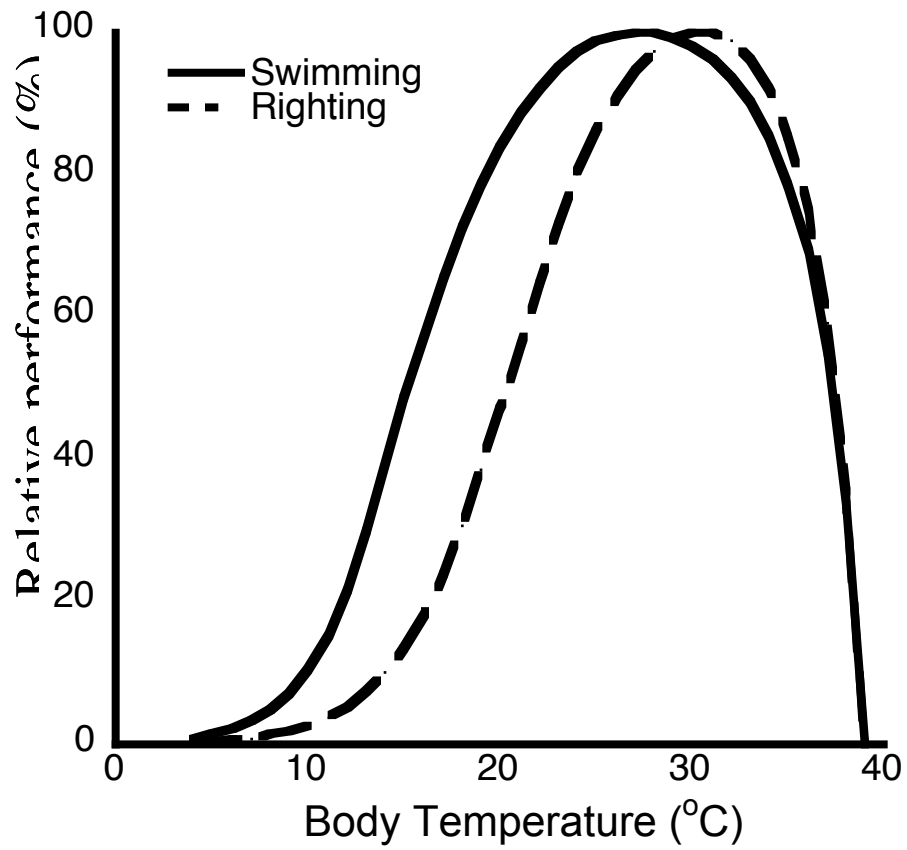


Fig. 2. Relative performance as a function of T_b for swimming and righting for hatchling map turtles.