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# Thermal Plasticity of Diving Behavior, Aquatic Respiration, and Locomotor Performance in the Mary River Turtle

## *Elusor macrurus*

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### ABSTRACT

Locomotion is a common measure of performance used in studies of thermal acclimation because of its correlation with predator escape and prey capture. However, for sedentary animals such as freshwater turtles, we propose that diving behavior may be a more ecologically relevant measure of performance. Increasing dive duration in hatchling turtles reduces predator exposure and therefore functions as an ecological benefit. Diving behavior is thermally dependent, and in some species of freshwater turtles, it is also reliant on aquatic respiration. This study examined the influence of thermal acclimation on diving behavior, aquatic respiration, and locomotor performance in the endangered, bimodally respiring Mary River turtle *Elusor macrurus*. Diving behavior was found to partially acclimate at 17°C, with turtles acclimated to a cold temperature (17°C) having a significantly longer dive duration than hatchlings acclimated to a warm temperature (28°C). This increase in dive duration at 17°C was not a result of physiological alterations in metabolic rate but was due instead to an increase in aquatic oxygen consumption. Increasing aquatic oxygen consumption permitted cold-acclimated hatchlings to remain submerged for significantly longer periods, with one turtle undertaking a dive of over 2.5 d. When burst-swimming speed was used as the measure of performance, thermal acclimation was not detected. Overall, *E. macrurus* demonstrated a partial ability to acclimate to changes in environmental temperature.

### Introduction

Temperature influences the rates of biochemical reactions that underlie animal function and as such directly affects the physiology and behavior of ectotherms (Huey 1982; Haynie 2001; Angilletta et al. 2002). Organisms can compensate for these fluctuations through the process of acclimation (laboratory based) or acclimatization (field based), which is the reversible change in physiological processes in response to environmental variability (Prosser 1991; Wilson and Franklin 2002; Seebacher 2005; Angilletta et al. 2006). The beneficial acclimation hypothesis suggests that these acclimatory responses benefit the organism by increasing individual fitness (Leroi et al. 1994; Wilson and Franklin 2002; Seebacher 2005; Angilletta et al. 2006).

Locomotion is one of the primary performance measures used in studies of thermal acclimation because of its correlation with predator escape and prey capture (Bennett 1990; Bennett and Huey 1990; Johnson and Bennett 1995; Domenici and Blake 1997; Johnston and Temple 2002; O'Steen and Bennett 2003; Wilson 2005). While locomotion is an ideal performance measure for active species such as fish, an alternative measure may be required for sedentary animals such as freshwater turtles. Hatchling turtles spend the majority of their time sheltering on the river bottom, with surfacing events for aerial respiration increasing the hatchlings' exposure to predation both in the water column and at the water's surface (Kramer et al. 1983; Kramer 1988; Heithaus and Frid 2003). Rather than maximizing burst-swimming speed, hatchling turtles are thought to reduce predator exposure by maximizing their dive duration and hence reducing surfacing frequency. Therefore, we propose that diving behavior is a more ecologically relevant measure of performance than locomotion for hatchling chelonians.

Diving behavior in freshwater turtles is known to be thermally dependent (Herbert and Jackson 1985; Prassack et al. 2001; Priest and Franklin 2002; Gordos et al. 2003a, 2003b). For example, a 15°C increase in temperature resulted in a five-fold decrease in dive duration of the short-necked turtle (*Emydura macquarii*; Priest and Franklin 2002). Temperature-dependent changes in diving behavior can be attributed to the physiological processes underlying the aerobic dive limit (Kooyman 1989; Schreer and Kovacs 1997). As temperature increases, metabolic rate also increases while oxygen storage capacity decreases, thereby resulting in shorter dive durations for chelonians (Kooyman 1989; Fuster et al. 1997). Diving behavior in freshwater turtles may also be dependent on aquatic respiration

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(Gordos and Franklin 2002; Mathie and Franklin 2006). Certain freshwater turtle species display the ability to respire aquatically, which allows them to undertake extended dives compared to those of primarily air-breathing species (Belkin 1968; Stone et al. 1992; King and Heatwole 1994a, 1994b; Bagatto et al. 1997; Bagatto and Henry 1999; Prassack et al. 2001; Maina 2002). For the Fitzroy River turtle *Rheodytes leukops*, aquatic respiration supports up to 70% of total  $\dot{V}O_2$ , which translates into extended dives of several days (Franklin and Priest 1997; Gordos and Franklin 2002). However, aquatic respiration in freshwater turtles is also thermally dependent. As temperature increases, aquatic respiration cannot fulfill the increased metabolic demands of the turtle, thus resulting in an elevated reliance on aerial respiration (Herbert and Jackson 1985; Yu and Woo 1985; Prassack et al. 2001).

Despite the high dependence of dive duration on temperature, there have been no studies that investigated whether the diving behavior of turtles can be thermally acclimated. We hypothesize that it is beneficial for hatchling turtles to maximize dive duration in order to reduce predator exposure. Acclimation to a high temperature will therefore result in the turtles increasing their dive duration at that temperature, through a reduction in metabolic rate and an increase in aquatic respiration. Acclimation to a cold temperature, however, may actually result in a decrease in dive duration as a trade-off occurs between performance and metabolic rate. Acute exposure to cold temperatures has a depressive effect on metabolism, and as a result, the animals may increase their energy expenditure in order to maintain metabolic capacity (Wood et al. 1978; Evans 1990; Seebacher et al. 2003, 2004; Glanville and Seebacher 2006). For example, in winter, the metabolic enzymes of the Australian freshwater turtle (*Chelodina longicollis*) acclimatized so that activity levels could be maintained despite the drop in body temperature (Seebacher et al. 2004). We hypothesize that the metabolic rate of cold-acclimated *Elusor macrurus* turtles may also increase at cold temperatures and that as a result, dive duration will decrease. The aim of this study was to examine the influence of thermal acclimation on diving behavior, aquatic respiration, and swimming performance in the Mary River turtle *E. macrurus*.

## Material and Methods

*Elusor macrurus* eggs were collected from nesting sites along the Mary River near the town of Tiaro (25.72606°S, 152.58265°E) and transported to the University of Queensland, where they were incubated. Once hatched, the turtles were housed in a large holding tank (1,000 L) that contained basking platforms and shelters. The holding tanks were maintained at a constant temperature of 23°C with a photoperiod of 12L : 12D. At 10 mo of age, the hatchling turtles were randomly divided into two groups and placed into either a cold (17°C,  $N = 6$ ,  $29.88 \pm 1.70$  g) or warm (28°C,  $N = 7$ ,  $30.04 \pm 2.32$  g) acclimation treatment. These temperatures were selected as representatives of winter and summer water temperatures in

the Mary River (Pusey et al. 1993). The acclimation tank setup (140 L) was identical between treatments, consisting of basking platforms, shelters, aerators, and a 12L : 12D photoperiod. The hatchlings were acclimated for a minimum of 8 wk, at which time diving behavior, aquatic respiration, and swimming performance of both acclimation groups were examined at the two test temperatures, 17° and 28°C. This research was approved by Queensland Parks and Wildlife Service (SPP-WISP-01477903) and supported by the University of Queensland Ethics Committee (AEC-ZOO/ENT/595/04/URG and ZOO/ENT/731/05/URG).

## Diving Behavior

The diving behavior of the cold- and warm-acclimated turtles was examined at 17° and 28°C test temperatures. The behavioral experiments were conducted in a large glass aquarium measuring 150 cm × 60 cm × 65 cm (length × width × height). A Perspex sheet was placed down the middle of the aquarium to divide the tank into two halves, allowing for two groups of turtles to be recorded simultaneously. The aquarium contained a pebble substrate and benthic shelters, and the water was constantly filtered (Aqua One hang-on filter). The photoperiod was set at 12L : 12D, with red lights used during the dark period to facilitate recording. Turtles were placed into each side of the tank in groups of three and given 24 h to become accustomed to the new environment. Diving behavior was then recorded using a closed-circuit video camera and a time-lapse VCR. Recording time of diving behavior ranged between 12 and 86 h, depending on the activity levels of turtles within a group. At 17°C, a longer recording period was required so that an adequate number of dives were recorded, while less time was required at 28°C because of the short dive lengths. Turtles were given a minimum of 1 wk to rest before being tested at the remaining experimental temperature. Videotapes were analyzed for resting dive durations. A resting dive was defined as a dive in which the turtle sat relatively still on the bottom of the tank for a period greater than 1 min.

## Respiration

Resting metabolic rate, mean aerial and aquatic respiration, and percent aquatic respiration of acclimated animals were measured using closed-box respirometry. Respiration experiments were conducted in controlled-temperature rooms set at 17° or 28°C, with red lights used to simulate darkness to ensure that measures were of resting metabolic rate. Each respirometer consisted of a 900-mL circular container with an airtight lid that was filled with 500 mL of water to create an aquatic base chamber. The remaining 400 mL of the respirometer functioned as an aerial chamber into which the turtles could surface to breathe. Two-way taps fitted to the aquatic and aerial chambers permitted water and air sampling, respectively.

Before the beginning of experiments, the turtles were weighed and wiped down with a 70% ethanol solution to re-

move oxygen-consuming bacteria. Turtles were given 18 h to adjust to the respirometers and recover from handling stress before measurements began. The water in the respirometer was aerated continuously to maintain normoxia before respiratory measurements. At the beginning of the experimental trial, the aerators were switched off and mineral oil was added to the surface of the water to prevent diffusion of gas across phases. The respirometers were then sealed, and initial samples of water (5 mL) and air (20 mL) were taken from the sampling ports via a syringe to establish baseline levels of  $O_2$ . Turtles were then left for either 1 h (28°C) or 2 h (17°C) before the final aquatic and aerial gas samples were taken. Each turtle underwent a total of four trials, with a minimum 1-h period allowed between each trial. The hatchlings were given a minimum of 3 d rest before being tested at the other experimental temperature.

For gas analysis, water samples were injected into a water jacket that housed a Cameron oxygen electrode. The oxygen electrode was connected to a Cameron oxygen meter (Cameron Instrument OM200) that measured the aquatic  $PO_2$ . The aerial sample was passed through  $H_2O$ -absorbing Drierite before entering a gas analyzer (ADInstruments ML205), which measured percent oxygen. The Cameron oxygen meter and gas analyzer were connected to a PowerLab/4s, and the data were recorded on Chart software (ver. 4.2). Controls were conducted to account for consumption of oxygen by the electrode and to confirm the effectiveness of the mineral oil as a barrier to gas diffusion.

The rate of aerial oxygen consumption ( $\dot{V}O_{2a}$ ; mL  $O_2$  h<sup>-1</sup>) was determined using the standard equations of Vleck (1987):

$$\dot{V}O_{2a} = \frac{[(V - V_{H_2O})(F_1'' - F_c'') - F_c''(V_{CO_2})]/(1 - F_c'')}{t},$$

where  $V$  = volume of air in chamber (mL),  $V_{H_2O}$  = initial volume of water vapor in the chamber (mL),  $V_{CO_2}$  = volume of  $CO_2$  produced during the experiment (mL),  $F_1''$  = fractional concentration of  $O_2$  at the start of the experiment,  $F_c''$  = fractional concentration of  $O_2$  at the end of the experiment, and  $t$  = length of trial (h).

The rate of aquatic oxygen consumption ( $\dot{V}O_{2a}$ ; mL  $O_2$  h<sup>-1</sup>) was determined using the following equation, modified from an article by King and Heatwole (1994b):

$$\dot{V}O_{2a} = \frac{\Delta DO_2 \times \beta \times V_{H_2O}}{t},$$

where  $\Delta DO_2$  = change in dissolved  $O_2$  over trial (mmHg),  $\beta$  = oxygen coefficient of capacitance (mL  $O_2$  L<sup>-1</sup> mmHg),  $V_{H_2O}$  = volume of water in respirometer (L), and  $t$  = length of trial (h). For analysis, mean  $\dot{V}O_{2a}$  aerial and  $\dot{V}O_{2a}$  aquatic were standardized to a 35-g turtle and then presented on a per-gram basis (i.e.,  $\dot{V}O_{2a}$  in mL  $O_2$  h<sup>-1</sup> g<sup>-1</sup>). Total  $\dot{V}O_{2a}$  (metabolic rate; mL  $O_2$  h<sup>-1</sup> g<sup>-1</sup>) equaled the sum of minimum aerial and min-

imum aquatic  $\dot{V}O_{2a}$ , while percent aquatic respiration was estimated by expressing maximum aquatic  $\dot{V}O_{2a}$  as a proportion of total  $\dot{V}O_{2a}$ .

#### Swimming Performance

Swimming performance was examined in a 30 × 31 × 14.5-cm (length × width × height) temperature-controlled tank. Pilot studies revealed that the burst-swimming response of the turtles was to push off with their hind legs and swim along the bottom of the tank rather than to swim within the water column. To provide the gripping surface that is needed for this type of locomotion, a layer of plastic mesh was glued to the bottom of the tank.

The burst-swimming performance of the cold- and warm-acclimated turtles was examined at 17° and 28°C. Turtles were allowed to adjust to the test temperature overnight and were then placed individually into the experimental tank and allowed to settle on the bottom. A burst-swimming response was generated by tapping the bottom of the tank behind the turtle. This action startled the turtle, resulting in two to three strokes of burst swimming. A mirror positioned above the tank at 90° reflected the movement of the turtle, which was captured by a high-speed camera at 100 frames s<sup>-1</sup> (Red Lake Imaging). The camera was connected to a computer that recorded the video on Motion Scope software. Maximum speed was calculated by documenting the ( $x$ ,  $y$ ) position of the turtle for each frame of movement, beginning from the first sign of locomotion. The distance between the frames was divided by time to produce speed (cm s<sup>-1</sup>). Four burst-swimming sequences were analyzed for each individual, and the maximum speed was recorded. To account for body size difference between acclimation groups, the maximum speed for each individual was divided by carapace length and then multiplied by 7 to standardize velocity to a 7-cm turtle.

#### Statistical Analysis

The effects of test temperature and acclimation temperature on diving behavior, respiration, and swimming performance were analyzed using a two-way, repeated-measures ANOVA. Where normality failed, data were log transformed before analysis. Significant differences were further analyzed using the Student-Newman-Keuls post hoc test. All results are presented as mean ± standard error unless otherwise stated, with statistical significant differences considered at the level  $P < 0.05$ .

## Results

#### Diving Behavior

There was a significant effect of thermal acclimation on mean and maximum dive durations of *Elusor macrurus* (mean  $F_{1,25} = 14.30$ ,  $P = 0.003$ ; maximum  $F_{1,25} = 41.26$ ,  $P < 0.001$ ; Fig. 1). However, the effect of thermal acclimation on dive durations was highly dependent on test temperature (mean

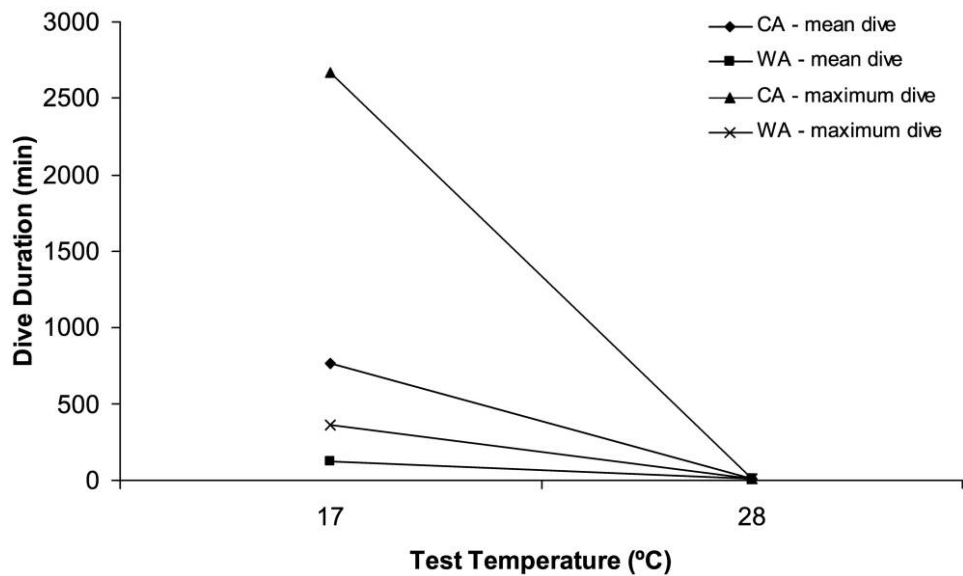


Figure 1. Effect of temperature on mean and maximum dive duration in cold- and warm-acclimated turtles (CA and WA, respectively). Mean and maximum dive durations were significantly longer at 17°C than at 28°C for both acclimation groups. There was a significant effect of acclimation group on mean and maximum dive duration at 17°C only.

$F_{1,25} = 21.19$ ,  $P < 0.001$ ; maximum  $F_{1,25} = 19.34$ ,  $P = 0.001$ ). Mean dive duration at 17°C was  $765 \pm 213$  min in the cold-acclimated turtles, compared with  $125 \pm 21$  min in the warm-acclimated group ( $P < 0.001$ ; Fig. 1). At 17°C, maximum dive duration of the cold-acclimated turtles was  $2,667 \pm 420$  min, which was significantly greater than the maximum value of  $366 \pm 71$  min recorded for the warm-acclimated turtles (Fig. 1). There was no effect of thermal acclimation on mean or maximum dive duration at the 28°C test temperature, where mean dive durations were  $8.36 \pm 0.58$  and  $6.78 \pm 0.96$  min for

the cold- and warm-acclimated groups, respectively (mean  $P = 0.346$ , maximum  $P = 0.323$ ). Mean and maximum dive durations were greater at 17°C than at 28°C for both the cold- and the warm-acclimated turtles (mean  $F_{1,25} = 655.45$ ,  $P < 0.001$ ; maximum  $F_{1,25} = 486.51$ ,  $P < 0.001$ ; Fig. 1).

#### Respiration

The resting metabolic rate of *E. macrurus* hatchlings did not thermally acclimate ( $F_{1,25} = 0.24$ ,  $P = 0.634$ ; Fig. 2). However,

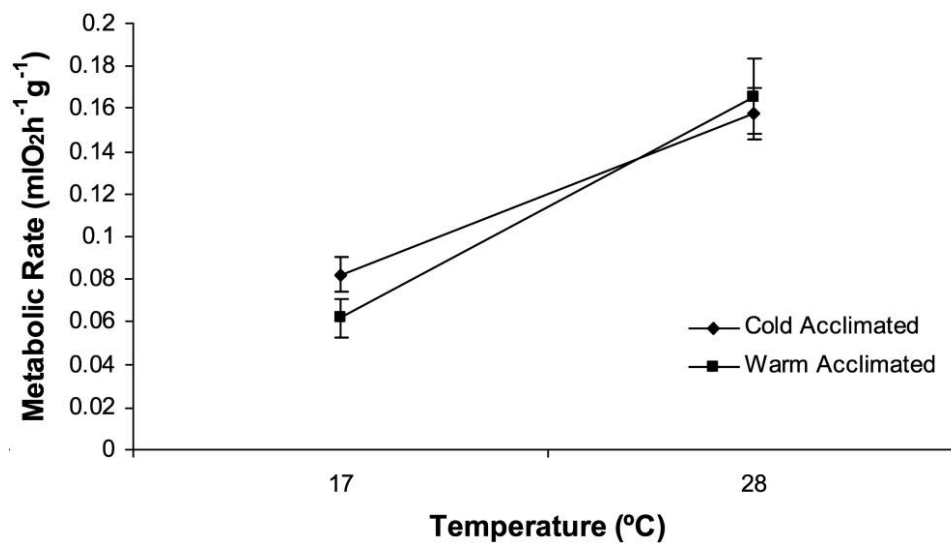


Figure 2. Effect of temperature on metabolic rate in cold- and warm-acclimated turtles. Metabolic rate was significantly higher at 28°C than at 17°C in both acclimation groups. There was no influence of acclimation temperature on metabolic rate at either test temperature.

the metabolic rate of both acclimation groups was influenced by test temperature ( $F_{1,25} = 50.84, P < 0.001$ ; Fig. 2). Metabolic rate increased from  $0.08 \pm 0.008$  to  $0.16 \pm 0.012$  mL O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup> in the cold-acclimated turtles and from  $0.06 \pm 0.009$  to  $0.17 \pm 0.017$  mL O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup> in the warm-acclimated turtles at 17° and 28°C, respectively. The Q<sub>10</sub> values for the cold- and warm-acclimated animals were 1.80 and 2.46, respectively.

The observed increase in metabolic rate at 28°C was a direct result of an increase in both aerial and aquatic oxygen consumption (aerial  $F_{1,25} = 54.15, P < 0.001$ ; aquatic  $F_{1,25} = 27.95, P < 0.001$ ; Fig. 3). Aerial oxygen consumption increased from  $0.08 \pm 0.006$  and  $0.065 \pm 0.008$  mL O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup> at 17°C to  $0.158 \pm 0.012$  and  $0.178 \pm 0.021$  mL O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup> at 28°C in the cold- and warm-acclimated turtles, respectively. As test temperature increased from 17° to 28°C, aquatic oxygen consumption of the cold-acclimated turtles increased from  $0.018 \pm 0.0008$  to  $0.023 \pm 0.002$  mL O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup>, while that of the warm-acclimated turtles increased from  $0.014 \pm 0.0008$  to  $0.018 \pm 0.001$  mL O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup>. There was no effect of acclimation temperature on aerial oxygen consumption at either 17° or 28°C ( $F_{1,25} = 0.013, P = 0.911$ ). However, aquatic oxygen consumption was significantly influenced by acclimation temperature, with consumption higher in the cold-acclimated turtles than in the warm-acclimated turtles at both test temperatures (17°C  $P = 0.036$ ; 28°C  $P = 0.020$ ).

Unlike aquatic oxygen consumption, percent aquatic respiration ([maximum aquatic oxygen consumption/total metabolic rate] × 100) was not affected by thermal acclimation at either test temperature ( $F_{1,25} = 0.007, P = 0.935$ ). However, there was a significant effect of temperature on percent aquatic respiration in the warm-acclimated *E. macrurus* but no effect

in the cold-acclimated turtles (warm  $P = 0.012$ ; cold  $P = 0.173$ ). At 17°C, aquatic respiration was 21.54% in cold-acclimated turtles and 24.20% in warm-acclimated turtles. When tested at 28°C, aquatic respiration in the cold- and warm-acclimated turtles was 16.07% and 13.73%, respectively.

#### Swimming Performance

Burst-swimming speed of *E. macrurus* was not affected by thermal acclimation ( $F_{1,25} = 0.03, P = 0.876$ ; Fig. 4). However, burst-swimming speed was significantly faster at 28°C than at 17°C in both cold- and warm-acclimated turtles ( $F_{1,25} = 33.52, P < 0.001$ ; Fig. 4). Maximum velocity of the cold-acclimated turtles increased from  $68.0 \pm 2.5$  cm s<sup>-1</sup> at 17°C to  $79.1 \pm 2.9$  cm s<sup>-1</sup> at 28°C. Maximum velocity of the warm-acclimated turtles increased from  $67.3 \pm 1.5$  to  $78.8 \pm 1.6$  cm s<sup>-1</sup> as temperature increased. The Q<sub>10</sub> value for this relationship was 1.15 for both acclimation groups.

#### Discussion

*Elusor macrurus* hatchlings displayed partial thermal acclimation with respect to their diving behavior; however, the turtles did not acclimate according to our hypothesis. At 28°C, dive duration was expected to increase after warm acclimation, due to a decrease in metabolic rate and an increase in aquatic respiration. However, neither of those parameters were affected by thermal acclimation in *E. macrurus* hatchlings maintained at a warm temperature. As a result, no difference in dive duration was observed between cold- and warm-acclimated turtles at 28°C. In contrast, hatchlings acclimated to a cold temperature

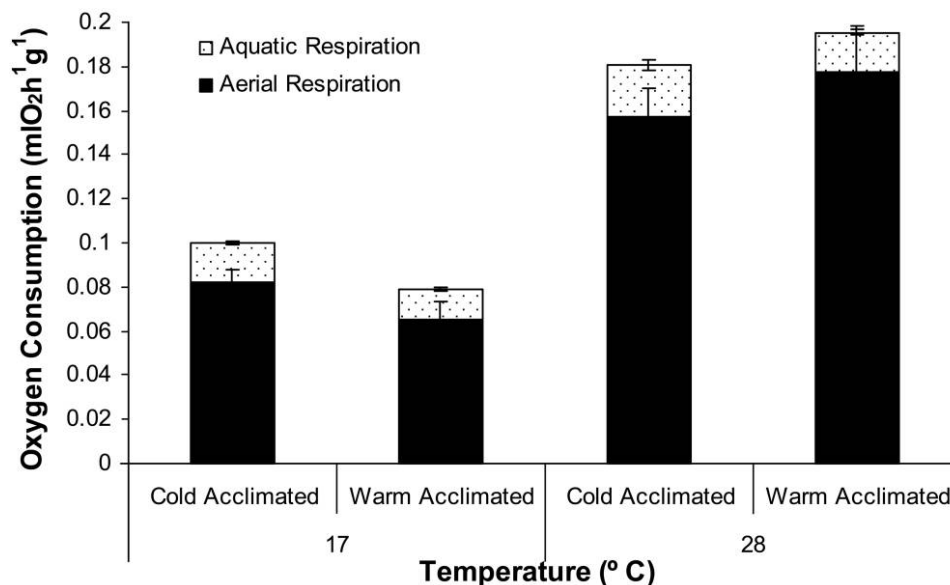


Figure 3. Influence of temperature on mean aerial and aquatic oxygen consumption in cold- and warm-acclimated Mary River turtles. Aerial and aquatic oxygen consumptions are significantly higher at 28°C than at 17°C. There is no influence of acclimation temperature on aerial oxygen consumption. Aquatic oxygen consumption is significantly higher in the cold-acclimated turtles than in the warm-acclimated turtles.

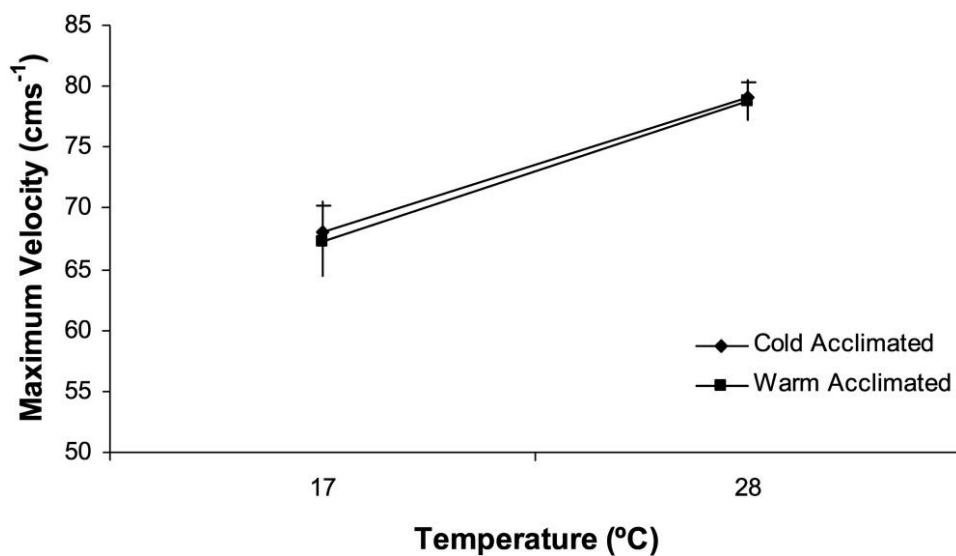


Figure 4. Effect of temperature on the swimming performance of cold- and warm-acclimated turtles. At 28°C, the swimming performance of the hatchlings was significantly faster than at 17°C in both acclimation groups. There was no influence of acclimation temperature on swimming performance at either test temperatures.

were expected to display a decreased dive duration at 17°C, as a result of an increased metabolic rate, yet acclimation to a cold temperature resulted in a sixfold increase in dive duration.

High costs associated with aquatic respiration at 28°C may explain why warm-acclimated turtles did not thermally acclimate dive duration. Aquatic respiration in *E. macrurus* can occur via diffusion across the skin or by active ventilation of the cloacal bursae. Tidal ventilation associated with the cloacal bursae requires a continual change in the kinetic energy of water, which compared to air is 60 times as viscous and contains 30 times less oxygen per volume (Dejours 1994). In accordance with the theory of optimal breathing, as metabolic rate increases with increasing temperature, turtles are likely to become more reliant on aerial respiration, which equates to shorter dive durations (Kramer 1988). For the softshell turtle *Apalone ferox*, reliance on aquatic respiration decreased from 44.1% to 17.4% as temperature increased from 15° to 25°C (Prassack et al. 2001). Additionally, surfacing frequency for the softshell turtle increased more than threefold with the associated temperature increase (Prassack et al. 2001). Aquatic respiration in the warm-acclimated *E. macrurus* hatchlings accounted for only 14%–16% of total oxygen consumption, suggesting that at 28°C hatchlings were primarily relying on pulmonary oxygen supplies.

At 17°C, the reduction in metabolic rate of both the cold- and warm-acclimated turtles resulted in an increased reliance on aquatic respiration. This increase in aquatic respiration permitted an increase in dive duration of both acclimation groups; however, the dive duration of the cold-acclimated turtles was six times longer than that of the warm-acclimated hatchlings. Some species of freshwater turtles are known to show an inverse compensatory response at low temperatures by entering a state

of dormancy (Guppy and Withers 1999). For example, snapping turtles *Chelydra serpentina* acclimated at 10°C showed a 13% reduction in metabolic rate at 25°C compared with that of turtles acclimated at 25°C (Gatten 1978). However, our results suggest that at 17°C, *E. macrurus* hatchlings do not enter a state of metabolic depression (i.e., metabolic rate did not differ between cold- and warm-acclimated animals at 17°C). Instead, the increase in dive duration observed in cold-acclimated turtles tested at 17°C may be due to an increased reliance on aquatic respiration, which was opposite to our original hypothesis.

Aquatic oxygen consumption of the cold-acclimated turtles was significantly greater than that of the warm-acclimated turtles at both test temperatures. This result suggests that the cold-acclimated turtles underwent a physiological and/or morphological adaptation that increased their efficiency in extracting aquatic oxygen. Obtaining accurate measures of percent aquatic respiration is generally difficult due to the turtle's ability to voluntarily change its reliance on aerial and aquatic oxygen consumption. In a shallow respirometry chamber, hatchlings are likely to increase their reliance on aerial oxygen consumption because of the costs associated with aquatic respiration under these conditions (Mathie and Franklin 2006). Measures of percent aquatic respiration are therefore likely to be underestimated. Percent aquatic respiration in *E. macrurus* did not differ between acclimation groups; however, the diving behavior data support the increase in aquatic oxygen consumption seen in the cold-acclimated turtles.

The dramatic increase in dives at 17°C indicates a greater reliance on aquatic oxygen consumption, as exemplified by one cold-acclimated hatchling that recorded a dive of more than 2.5 d. This extended dive duration marks one of the longest

submergences recorded for any freshwater turtle in captivity and was five times longer than the maximum dive duration of any warm-acclimated *E. macrurus* hatchling. Similarly, in a study on the natural diving behavior of *Rheodytes leukops*, dive durations of more than 3 wk were recorded during winter (16.5°C), compared with a maximum duration of only 2.39 d in summer (27.3°C; Gordos et al. 2003b). Based on these results, Gordos et al. (2003b) suggested that freshwater turtles can use aquatic respiration as an effective overwintering strategy at cooler temperatures.

Traditionally, studies of the beneficial acclimation hypothesis have used locomotion as the performance measure (Bennett 1990; Johnson and Bennett 1995; Wilson and Franklin 1999; O'Steen and Bennett 2003; Wilson 2005). In this study, the burst-swimming speed of *E. macrurus* hatchlings did not thermally acclimate. This result supports the hypothesis that thermal acclimation of locomotor performance in reptiles is minimal in its extent (Bennett 1990; Angilletta et al. 2002). However, research into this area is limited and generally restricted to terrestrial species. Instead, thermal acclimation is believed to apply more to aquatic species that are protected from large daily variations of temperature due to the thermal stability of water but that are exposed to marked changes in seasonal temperature (Seebacher 2005). This hypothesis is supported by a study on amphibians where the highly aquatic larval form of the striped marsh frog *Limnodynastes peronii* was found to thermally acclimate locomotor performance, while no difference was observed in swimming or jumping performance in adults (Wilson and Franklin 1999, 2000). Although *E. macrurus* fits into the category that is most likely to benefit from thermal acclimation (highly aquatic, no thermoregulation), no differences were observed in burst-locomotor performance. Burst-locomotor performance, however, is a measure of anaerobic capacity that is known to be less thermally dependent than aerobic metabolism (Bennett 1990; O'Steen and Bennett 2003). The effect of thermal acclimation on sustained swimming performance may differ from the effect on burst-swimming performance, and therefore, further research is required to support the lack of acclimation in *E. macrurus*.

This study has demonstrated that the respiratory physiology of the Mary River turtle is influenced by water temperature and that this has a significant effect on hatchling behavior. This dependence on aquatic respiration in this species raises concerns about the potential impact of river regulation on the species' survival. Water storage impoundments are known to significantly change the ecological properties of rivers by converting narrow, flowing systems into large, stagnant reservoirs (Ligon et al. 1995; Reese and Welsh 1998; Bodie 2001; Arthington 2003). Environmental costs of impoundments include loss of pool-riffle sequences, reduced water velocity, decreased aquatic oxygen levels, increased water depth, and increased temperature stratification (Ligon et al. 1995; Reese and Welsh 1998; Bodie 2001; Turner and Erskine 2005). Temperature stratification in impoundments results in the formation of a warmer-than-usual surface layer (Turner and Erskine 2005).

Hatchling turtles are likely to occur near the surface margins of reservoirs and hence will more likely inhabit this warmer stagnant water. This study has shown that at higher temperatures, the turtle's reliance on aerial respiration will increase, leading to a reduction in dive duration and an increase in surfacing frequency. Hatchlings that inhabit the warm surface layers of impoundments may therefore potentially increase their exposure to predators due to this change in respiratory physiology and diving behavior.

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