THE EFFECTS OF TEMPERATURE, BODY SIZE, AND GROWTH ON THE LOCOMOTOR PERFORMANCE OF JUVENILE TURTLES

By Michael A. Elnitsky

This study investigated the effects of temperature on the aquatic and terrestrial locomotor performance and growth effects on the scaling relationship between measures of performance and body mass in western painted turtles, *Chrysemys picta bellii*. Measures of locomotor performance and righting performance increased as temperature increased. Locomotor performance measures were highly correlated with one another and repeatable over time. The righting response was not correlated with any other measure of performance. Initially, measures of locomotor performance of hatchling turtles displayed positive scaling with body mass. However, the scaling of aquatic and terrestrial burst speed with body mass declined at each measurement interval over the 30-week period as a result of ontogenetic changes associated with growth. This suggests that if locomotor performance is under strong selection, larger hatchlings may have distinct advantages over smaller conspecifics; however, if smaller hatchlings do survive, such advantages may be reduced or lost over time.
THE EFFECTS OF TEMPERATURE, BODY SIZE, AND GROWTH ON THE
LOCOMOTOR PERFORMANCE OF JUVENILE TURTLES

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dedication</td>
<td>ii</td>
</tr>
<tr>
<td>Acknowledgements</td>
<td>iii</td>
</tr>
<tr>
<td>Table of Contents</td>
<td>iv</td>
</tr>
<tr>
<td>List of Tables</td>
<td>v</td>
</tr>
<tr>
<td>List of Figures</td>
<td>vi</td>
</tr>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Materials and Methods</td>
<td>3</td>
</tr>
<tr>
<td>Results</td>
<td>7</td>
</tr>
<tr>
<td>Discussion</td>
<td>9</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>15</td>
</tr>
<tr>
<td>Tables</td>
<td>23</td>
</tr>
<tr>
<td>Figure Legends</td>
<td>27</td>
</tr>
<tr>
<td>Figures</td>
<td>29</td>
</tr>
</tbody>
</table>
## List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Results of ANCOVAs testing the effects of temperature on measures of performance with body mass as a covariate.</td>
<td>23</td>
</tr>
<tr>
<td>2</td>
<td>Temperature coefficients ($Q_{10}$ values) for measures of aquatic and terrestrial locomotor performance trials.</td>
<td>24</td>
</tr>
<tr>
<td>4</td>
<td>Results of ANCOVAs testing the effects of growth (i.e., week) at six-week intervals over 30-weeks on measures of performance with body mass as a covariate.</td>
<td>26</td>
</tr>
<tr>
<td>5</td>
<td>Repeatability of performance measured at six-week intervals over a 30-week period for <em>Chrysemys picta bellii</em>.</td>
<td>27</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------------------------------------------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>1</td>
<td>Effects of temperature on aquatic and terrestrial burst speed and size-relative burst speed of juvenile <em>Chrysemys picta bellii</em>.</td>
<td>29</td>
</tr>
<tr>
<td>2</td>
<td>Effects of temperature on aquatic and terrestrial distance capacity measured at 0.10 m·s(^{-1}) and righting response</td>
<td>30</td>
</tr>
<tr>
<td>3</td>
<td>Aquatic and terrestrial burst speed and size-relative burst speed measured at 30 C at six-week intervals over a 30 week period</td>
<td>31</td>
</tr>
<tr>
<td>4</td>
<td>Initial and 30-week measurement of the relationship between body mass and aquatic and terrestrial burst speed</td>
<td>32</td>
</tr>
<tr>
<td>5</td>
<td>The power function scaling exponents describing the relationship between body mass and absolute aquatic and terrestrial burst speed as a function of week of measurement</td>
<td>33</td>
</tr>
<tr>
<td>6</td>
<td>Initial and 30-week measurement of the relationship between body mass and aquatic and terrestrial size-relative burst speed</td>
<td>34</td>
</tr>
<tr>
<td>7</td>
<td>The power function scaling exponents describing the relationship between body mass and size-relative aquatic and terrestrial burst speed as a function of week of measurement</td>
<td>35</td>
</tr>
<tr>
<td>8</td>
<td>The relationship between body mass and aquatic and terrestrial distance capacity</td>
<td>36</td>
</tr>
</tbody>
</table>
DEDICATION

This thesis is dedicated to my parents, Dennis and Deborah Elnitsky, who have provided me constant support and encouragement throughout my journey.
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INTRODUCTION

Performance capabilities (i.e., the maximal effort of which an animal is capable) set the ultimate limits to animal behavior (Bennett, 1989). More specifically, locomotor performance influences an array of behavioral interactions between organisms and their environment, including dispersal or migratory movements, escape from predators, and the acquisition of food. Effective locomotion across a range of environmental conditions is extremely important for the survival and/or reproduction of essentially all animals. Therefore, locomotor performance may significantly influence the lifetime fitness of individuals and may be subject to pressures of natural selection (Bennett, 1990; Jayne and Bennett, 1990).

Temperature is perhaps the greatest abiotic limiting factor affecting the locomotor performance of ectothermic animals. Body temperature limits the behavioral capabilities of animals by influencing the rate at which physiological processes operate (Cossins and Bowler, 1987; Bennett, 1990). Performance measures, including locomotion, typically increase as temperature rises above the lower critical temperature with temperature coefficients (Q_{10} values) of ~ 1.5 – 3.0, reach some maximal level at an “optimal” temperature, often corresponding with the animals preferred body temperature, and then decline as temperatures approach the critical thermal maximum (Bennett, 1990). For this reason, ectothermic animals may rely on behavioral thermoregulation in an attempt to maintain preferred body temperatures, thereby optimizing physiological and performance functions, which, in turn, may influence survivorship.

Similarly, body size has profound influences on nearly all processes at the whole organism level throughout the life of an animal. Therefore, consideration of body size, often accomplished through scaling relationships, should be included in any investigation of performance. However, few studies have investigated how changes in body size (i.e., growth) influence overall locomotor performance. It has been suggested that developmental and ontogenetic changes place constraints or limitations on locomotion, or other measures of performance, as the process of growth may interfere with mature function (Ricklefs, 1979). On the other hand, some ectotherms undergo ontogenetic changes and possess phenotypic traits (i.e., relatively longer limbs, greater muscle contractile velocities, etc.) that allow juveniles to perform nearly as well as adults (Carrier, 1996). This may be especially important as young or
hatchling animals often face greater risk of predation. Such increased performance could greatly increase the probability of survival to maturity, and as a result selection may be especially strong for characteristics providing improved locomotor performance (Jayne and Bennett, 1990; Carrier, 1996).

Overall locomotor performance, including both burst speed (i.e., the maximum velocity an animal is able to attain under a given set of environmental conditions) and endurance, has been investigated extensively in a number of ectothermic vertebrates, including: fishes (e.g., see Webb, 1983; Domenici and Blake, 1993; Domenici, 2001) salamanders (e.g., see Feder, 1986; Else and Bennett, 1987; Shaffer et al., 1991; Austin and Shaffer, 1992), anurans (e.g., see Zug, 1985; Miller and Zoghby, 1986; Knowles and Weigl, 1990; Wilson et al., 2000), and lizards (e.g., see Bennett, 1980; John-Alder and Bennett, 1981; Hertz et al., 1983; Garland, 1999; Vanhooydonck et al., 2001). However, chelonians, as a group, have received relatively little attention. Nonetheless, a number of studies have focused on the effects of incubation conditions on the locomotor performance of hatchling turtles (Miller et al., 1987; Miller, 1993; Finkler, 1999; Du and Ji, 2003), as well as the energetics of locomotor activity (Gatten, 1974; Stockard and Gatten, 1983; Lowell, 1990; Baudinette et al., 2000).

A few investigators have also examined the effects of body size (Adams et al., 1987; Marvin and Lutterschmidt, 1997; Wren et al., 1998; Claussen et al., 2002) and temperature (Adams et al., 1987; Claussen et al., 2002) on either voluntary or forced locomotion in box turtles, *Terrapene* spp.. Zani and Claussen (1994) examined the influence of body size on the locomotor performance of painted turtles, *Chrysemys picta*, but did not consider temperature or how changes in body size associated with growth affect locomotor performance. Likewise, little attention has been given to the righting response behavior, or the ability of a turtle to return to the upright position after placement on the carapace, a behavior that may be ecologically relevant to survival (Steyermark and Spotila, 2001).

As yet no study has provided a complete picture of the effects of temperature and body size, especially during a period of relatively rapid growth, on the locomotor performance of semi-aquatic turtles. Therefore, the purpose of the present study was to investigate (1) the effects of temperature on aquatic and terrestrial locomotor performance, including burst speed (i.e., sprint speed) and endurance, as well as righting response, and (2) growth effects over a 30-week period on the scaling relationship between measures of locomotor performance and
body mass, along with the temporal repeatability of measures of performance in juvenile western painted turtles, *Chrysemys picta bellii* (Gray). I predicted that measures of performance would increase with increasing temperature (e.g., Bennett, 1990); that growth and changes in body size would result in a reduction of the power function scaling exponent describing the relationship between measures of performance and body mass as suggested by Zani and Claussen (1994); and that measures of performance would be highly repeatable over time (see Austin and Shaffer, 1992).

**MATERIALS AND METHODS**

*Experimental animals and thermal regime*

Eggs of *Chrysemys picta bellii* (Gray) were collected in late May and June 2002 near Gimlet Lake on the Crescent Lake National Wildlife Refuge (41°N, 102°W) in west-central Nebraska, from freshly laid nests (< 24 h) and from gravid females administered synthetic oxytocin (Etchberger et al., 1992). Eggs were subsequently transported to Miami University and incubated at 29 C in moist vermiculite (1.0g water · g vermiculite⁻¹; water potential approximately -150 kPa) until hatching in early August. Following hatching, turtles were maintained in complete darkness and progressively acclimated to temperatures corresponding to those in naturally occurring nests during the remainder of summer, autumn, and winter (see Costanzo et al., 1995). Hatchlings were maintained at 22 C until 1 October when the temperature was reduced to 15 C and then further reduced to 10 C on 1 November. On 1 December, turtles were exposed to 4 C and thereafter held at this temperature through the remainder of the over-wintering. This acclimation procedure is common when studying laboratory incubated *C. picta*, as naturally occurring hatchlings typically over-winter within the natal nest. The vermiculite substratum was periodically remoistened to prevent desiccation.

Successfully over-wintered hatchlings were gradually warmed to room temperature and brushed free of adherent vermiculite during early April 2003. Thereafter, turtles were maintained within a temperature controlled environmental chamber at 25±0.5 C on a 12L:12D photoperiod of full-spectrum lighting. Turtles were housed in groups of 5-10 in aerated aquaria filled with dechlorinated water to a depth of approximately 15 cm. Dry basking areas
were provided and animals were fed commercial aquatic turtle food (Zoo Med Laboratories Inc., San Luis Obispo, CA) ad libitum 2-3 times weekly.

Experimental conditions and testing schedule

All tests of locomotor performance were conducted within an adjacent environmental chamber under artificial lighting (i.e., fluorescent and incandescent) at 10, 20, and 30 C. Testing order of both individuals and temperatures were randomly determined; order of testing temperature was 30, 10, 20 C. Measures of endurance (see below) were also assessed at 15 C. Turtles were fasted two days prior to experimental testing, as food consumption and digestion may affect aerobic metabolism and/or locomotor performance (e.g., Alsop and Wood, 1997). Experimental animals were placed at test temperature approximately two hours prior to testing to allow equilibration of body temperature. Only one measure of locomotor performance (see below) was assessed per day per individual. Measurements were made of body weight (to the nearest 0.01g) on an electronic balance and of carapace length and carapace height (to the nearest 0.1mm), with vernier calipers following all performance assessments in order to minimize possible effects of handling stress. Following locomotor performance measurements, animals were returned to the aquaria, provided with food, and allowed a minimum of three days prior to subsequent testing.

Burst speed measurement

Terrestrial burst speed was measured using a 1.0 m long x 8.0 cm wide x 8.0 cm deep linear racetrack constructed of plastic rain gutter and lined with a layer of moist, coarse-grained sand. Infrared photocells positioned at each 0.25 m increment along the track and connected to an electronic stopwatch, allowed precise timing of the animal to the nearest 0.1 sec. Individual animals were placed at the beginning of the track and gentle tapping near the tail or to the rear of the carapace was used to elicit maximum speed over the length of the racetrack. Each measurement period consisted of three trials, allowing approximately 60 min between successive trials. Absolute burst speed was determined from the fastest 0.25 m traversal over all three trials. Size-relative burst speed (body lengths·s⁻¹) was determined by dividing absolute burst speed by carapace length.
Aquatic burst speed was measured by filling the racetrack with approximately 5 cm of dechlorinated water and following the procedures described above. Aquatic burst speed was likewise described in both absolute and size-relative terms. Any trial in which an animal failed to sustain locomotion over the entire length of the track was omitted from further analysis.

*Endurance measurement*

Terrestrial endurance was assessed using a 1040 ml respirometry chamber containing a 28 cm long x 6 cm wide motorized treadmill controlled via a rheostat. Individual animals were coaxed to locomote on the treadmill through gentle taps or prods to the tail and carapace. Once moving, animals usually sustained locomotion until they could no longer keep pace with the treadmill. Endurance was measured at 0.10 m·s⁻¹, and endurance capacity, defined as the maximum amount of time the animal could sustain a given locomotor speed, of individual turtles was timed to the nearest second using a digital stopwatch. Turtles were considered to be fatigued and the trial concluded following three successive failures to maintain speed and subsequent contact with the rear of the treadmill. Distance capacity, the maximum distance an animal could travel at a given locomotor speed, was calculated by multiplying exercise duration by treadmill speed. Trials in which an animal failed to maintain continuous locomotion throughout the trial were omitted from further analysis.

Aquatic endurance was assessed using a recirculating flow tank as described in Vogel and LaBarbera (1978), with a 50 cm long x 10 cm wide x 10 cm deep testing chamber which allowed constant access to air. Upon placement into the water current, turtles usually sustained swimming near the front of the testing chamber. Endurance was measured at 0.10 m·s⁻¹, and endurance capacity of individual turtles timed to the nearest second using a digital stopwatch. Timing continued until the turtle contacted a metal screen positioned at the rear of the testing chamber within the flow tank. An animal was deemed fatigued and a trial concluded following three successive failures to maintain position within the water current. Distance capacity was determined as above. Trials in which animals failed to maintain continuous swimming throughout the trial were omitted from further analysis.

*Righting Response*
Righting response was assessed by measuring the time it took an individual to turn over onto its plastron after being placed on its carapace. All righting response trials were video recorded, via a Videolabs Flexcam (Videolabs, Inc., Minneapolis, MN) linked to a Panasonic VHS system, from above the testing arena for subsequent analysis. Turtles were placed into a circular container, 20 cm in diameter and 5 cm deep, containing approximately 2 cm of moist, coarse-grained sand. Following placement of an individual onto its carapace attempted righting was observed, out of the animal’s view, via a monitor connected to the video recording system. Three successive trials were conducted per individual, with the fastest righting time used for all analysis. Each trial was terminated after 15 min if a turtle failed to right itself.

Righting response trials were analyzed as in Steyermark and Spotila (2001). Total righting response time, measured to the nearest 0.1 s, consisted of two distinct stages, the lag phase, or time between placement onto the carapace and initiation of righting, and the mechanical righting time, hereafter referred to as righting response, or the time between the first contact of the head or an appendage with the substrate and return to the upright position. Once initiated, the physical act of righting usually required only a few seconds.

Repeatability and Growth Effects

The temporal repeatability of aquatic and terrestrial burst speed was measured at 30 C over six-week intervals for 30 weeks. Similarly, six-week repeatability of righting response was also assessed. All experimental trials were conducted as described above. Following initial performance measurements, turtles were individually marked by clipping a unique combination of marginal scutes (Cagle, 1939) for subsequent identification. Between measurements, animals were maintained in aquaria at 25 C, as previously described, and provided aquatic turtle food 2-3 times weekly. Growth was evaluated from the measurements of body weight, carapace length and height taken after each series of performance tests.

Statistical analysis

Temperature effects on measures of performance were analyzed using repeated-measures analysis of covariance (ANCOVA) with body mass as the covariate. Multiple comparisons were made using least-squared means tests with Bonferroni adjusted probabilities
to examine differences in performance between pairs of test temperatures. Data not meeting the assumptions for ANCOVA testing were log transformed.

The relationships between logarithmically transformed measures of performance and body size (i.e., mass) were examined using power function regressions (performance = a(body mass)^b, where a is the scaling constant and b is the scaling exponent). Data were analyzed for significance using the coefficient of determination, R^2, and the F-statistic of the regression. Pearson product-moment correlation coefficients were used to test whether individual differences in performance were related and whether measures of performance were repeatable with time.

Growth effects over the 30-week period were analyzed using repeated-measures ANCOVA, with body mass as a covariate, to assess the effects of changes in size. Data not meeting the assumptions of ANCOVA were log transformed.

All data were analyzed using Statistical Analysis Systems (SAS Institute, Cary, NC) and results considered significant at \( P < 0.05 \) unless otherwise noted.

**RESULTS**

Temperature affected both aquatic and terrestrial measures of locomotor performance, as well as righting response, in juvenile *C. picta bellii* (Table 1). Aquatic and terrestrial burst speed increased significantly \( (P < 0.0001) \) with increases in temperature (Fig. 1A). Similarly, size-relative burst speed increased with increasing temperature for both aquatic and terrestrial modes of locomotion (Fig. 1B; \( P < 0.0001 \)). Terrestrial locomotion tended to be faster than aquatic locomotion at all test temperatures, although significant differences \( (P < 0.05) \) were found only at 30°C for both absolute and size-relative burst speed.

Distance capacity measured at 0.10 m·s\(^{-1}\) was affected by temperature (Table 1). Both aquatic and terrestrial distance capacity increased significantly \( (P < 0.0001) \) with increasing temperature (Fig. 2A). Unlike the case for burst speed, aquatic distance capacity was significantly \( (P < 0.05) \) greater than terrestrial distance capacity at all test temperatures. Turtles were unable to sustain either aquatic or terrestrial locomotion at 10°C, therefore these data were excluded from the analysis.

The righting response time was also influenced by test temperature (Table 1). Righting response time was significantly \( (P < 0.0001) \) greater at 10°C than at 20 or 30°C (Fig. 2B). No
difference was found between the 20 and 30 C righting time. Total righting time, as result of large variations in lag time, was not influenced by temperature and was excluded from further analysis.

Temperature coefficients ($Q_{10}$ values) were significantly ($P < 0.05$) higher for the 10 – 20 C, or 15 – 20 C in the case of distance capacity, range than for the 20 – 30 C range for all measures of performance except righting response (Table 2). $Q_{10}$ values for aquatic and terrestrial distance capacity were significantly ($P < 0.0001$) higher than for any other performance measure. The $Q_{10}$ for righting response, being less than one, signifies that righting time decreased with increasing temperature (Fig. 2B).

In general, aquatic and terrestrial measures of locomotor performance were positively correlated at 30 C (Table 3). However, no significant correlation ($P > 0.05$) was found between aquatic size-relative burst speed and either aquatic or terrestrial endurance capacity. Righting response was not significantly correlated ($P > 0.05$) with any other measure of performance.

Measures of locomotor performance differed significantly over the 30-week measurement period (Table 4). Aquatic and terrestrial burst speed increased significantly with time (Fig. 3A). Terrestrial locomotion was significantly ($P < 0.0001$) faster than aquatic locomotion at all measurement periods. Similarly, both aquatic and terrestrial size-relative burst speed varied significantly over the 30-week period (Table 4). However, while absolute burst speed increased over the course of the study, size-relative burst speed increased significantly only between weeks 6 and 12 (Fig. 3B). Terrestrial size-relative burst speed was significantly ($P < 0.0001$) faster than aquatic size-relative burst speed at all measurement periods. The righting response did not differ over the 6-week measurement period (Table 4).

Aquatic and terrestrial burst speed were positively correlated ($P < 0.05$) with body mass at 30 C throughout the 30-week measurement period (Fig. 4; only the initial and 30 week measurement are shown for sake of clarity). However, the power function scaling exponents describing the relationship between burst speed and body mass decreased at each six-week measurement interval for both aquatic and terrestrial locomotion, resulting in a significantly ($P < 0.05$) lower scaling of performance with body mass following the 30-week period (Fig. 5). Size-relative aquatic and terrestrial burst speed initially were positively correlated ($P < 0.05$) with body mass, but were independent of body mass following the 30-week measurement.
period (Fig. 6). Similar to absolute burst speed, the scaling exponents describing the relationship between aquatic and terrestrial size-relative burst speed with body mass decreased at each measurement interval, resulting in a significantly ($P < 0.05$) lower scaling exponent following the 30-week measurement period (Fig. 7).

Distance capacity was positively correlated ($P < 0.05$) with body mass for both aquatic and terrestrial endurance (Fig. 8) with power function scaling exponents significantly ($P < 0.05$) higher than those observed for burst speed or size-relative burst speed. Righting response did not scale significantly ($P > 0.05$) with body mass.

Generally, measures of performance were repeatable over time (Table 5). The repeatability of aquatic locomotor performance tended to decrease over time and was significantly ($P < 0.05$) repeatable only through the 12-week measurement period, whereas both absolute and size-relative terrestrial burst speed were repeatable over the entire 30-week period. There was no apparent pattern to the repeatability of these latter responses over time. Righting response was significantly ($P < 0.05$) repeatable over a 6-week measurement period.

**DISCUSSION**

Both temperature and body size influence measures of performance in ectothermic animals through their pervasive effects on underlying physiological processes. The present study provides further support for these observations by demonstrating that both locomotor performance and righting performance increase with increasing temperature, that measures of performance are highly correlated and repeatable through time, and that ontogenetic changes in body size associated with growth significantly influence the performance and scaling of performance with body mass of juvenile *Chrysemys picta bellii*.

As predicted, locomotor performance increased with increasing temperature. Temperature coefficients for aquatic and terrestrial performance were greater between 10 and 20 C, than between 20 and 30 C, as is commonly observed for ectothermic animals (Bennett, 1980, 1990). Although the characteristic decline in performance at higher temperatures (e.g., Bennett, 1990) was not found, this would be expected to occur at temperatures more closely approaching the critical thermal maximum, 40 – 41 C (Kosh and Hutchison, 1968). The observed $Q_{10}$ values for aquatic and terrestrial burst speed were similar to the 1.35 value
reported for forced terrestrial locomotion in *Terrapene ornata* between 25 and 30 C (Claussen et al., 2002). However, Adams et al. (1989) reported a Q_{10} of 3.3 for voluntary terrestrial locomotion in *Terrapene carolina* between 10 and 32 C. This discrepancy may simply reflect motivational differences between forced and voluntary locomotion or species specific behavior, rather than differences in the operant physiological processes. Similarly, observed Q_{10} values for aquatic and terrestrial burst speed between 10 and 20 C, are lower than is typically reported for lizards, often 2 – 3 (Bennett, 1980, 1990), and for the snakes *Nerodia sipedon* and *Regina septemvittata*, ~ 2.4 and 3.1 for aquatic and terrestrial locomotion respectively (Finkler and Claussen, 1999).

Both absolute and size-relative terrestrial burst speeds were similar to those previously reported for juvenile *Chrysemys picta* at 26 C (Zani and Claussen, 1994). Terrestrial speeds in the present study were greater than forced terrestrial locomotor speeds reported for juvenile or adult *T. carolina* (Marvin and Lutterschmidt, 1997) and hatchling *Chelydra serpentina* (Miller et al., 1987) and similar to the voluntary speed of 0.11 m·s^{-1} of *Caretta caretta* hatchlings during the nest exodus (Dial, 1987). Relatively few data exist on chelonian aquatic burst speed. Janzen (1993a) reports values similar to those in the present study ranging from 0.05 to 0.095 m·s^{-1}, dependent upon incubation conditions, for forced aquatic locomotion of hatchling *Apalone mutica* tested at room temperature. Aquatic burst speeds for *C. picta bellii* were greater than those reported for hatchling *C. serpentina* (Miller et al., 1987), but slower than the voluntary swimming speeds of 0.30 (O’Hara, 1980) and 0.38 m·s^{-1} (Salmon and Wyneken, 1987) reported for *Caretta caretta* hatchlings. In general, chelonian burst speed appears somewhat slower than that reported for other reptilian groups (see Adams et al., 1989 for review) and most anurans (Putnam and Bennett, 1981).

Temperature coefficients for distance capacity were significantly higher than those observed for burst speed. While burst speed demonstrates temperature dependence similar to that for anaerobiosis (Bennett, 1980, 1990; Putnam and Bennett, 1981), endurance is largely a function of maximal oxygen consumption with both displaying similar temperature dependence (John-Alder and Bennett, 1981; Bennett, 1982; Bennett and John-Alder, 1984). Along these lines, the observed Q_{10}s for distance capacity in the present study closely match those reported for the active metabolic rate of *Trachemys scripta* (Gatten, 1974), a closely related species of the family Emydidae (Ernst et al., 1994).
While terrestrial burst speed slightly exceeded aquatic burst speed, aquatic distance capacity was significantly greater than its terrestrial counterpart at all test temperatures. The observed differences in burst speed may reflect differences in the drag of the medium and/or difference in the duty factor (e.g., Baudinette et al., 2000), or the proportion of the total stride over which a limb provides forward thrust. On the other hand, differences in distance capacity may largely be due to differences in the cost of transport. It is well known that the cost of transport, in terms of the energy required to move a given mass a unit distance, is greater for terrestrial than for aquatic locomotion (Schmidt-Nielsen, 1972). In Murray short-necked turtles, *Emydura macquarii*, the cost of transports is 2.6 times greater for terrestrial than aquatic locomotion (Baudinette et al., 2000).

The righting response behavior has been commonly used as an indicator or measure of stress (e.g., Finkler, 1999) or to assess recovery from stress, however, few data exist detailing the temperature dependence of the behavior. The present study supports previous findings that righting performance increases with increasing temperature (i.e., righting time decreases with temperature), as was reported for *C. serpentina* (Steyermark and Spotila, 2001). However, while the lag phase was independent of temperature in *C. picta bellii*, this phase was significantly affected by temperature in *C. serpentina* (Steyermark and Spotila, 2001). Again this discrepancy may simply reflect species specific behavior or motivational differences. Further studies of righting response should be undertaken utilizing other species in order to ascertain the generality of this result.

Burst speed and endurance capacity may well represent two opposing performance functions. Optimization of these functions may pose conflicting demands on the morphological and physiological design (e.g., limb lengths, muscle fiber composition, etc.) of the organism and foreseeably lead to a compromised phenotype and/or performance of one or both functions (Losos, 1990; Losos et al., 1993; Garland and Losos, 1994; Miles, 1994). Following this idea, a trade-off between endurance and burst speed has been documented in mice (Dohm et al., 1996), Atlantic cod (Reidy et al., 2000), and lacertid lizards (Vanhooydonck et al., 2001). On the other hand, the majority of studies have found no correlation (Bennett, 1980; Garland and Else, 1987) or a positive correlation (Bennett, 1980; Garland, 1988; Huey et al., 1990; Jayne and Bennett, 1990) between endurance and burst speed. The present study was in accord with the majority in demonstrating a high degree of
correlation between measures of burst speed and endurance, as well as between aquatic and terrestrial locomotor performance, for juvenile turtles. This result was not unexpected as measures of locomotor performance often correlate positively with body size (see below). On the other hand, righting response was not correlated with any other measure of performance. Further study should be conducted to assess the ecological significance of the righting response and its influence, if any, on survival.

Repeatability is an important concept in quantifying the stability of a trait within individuals, relative to differences among individuals (van Berkum et al., 1989). Repeatability is also useful in assessing the upper bound on heritability of a functional character (e.g., locomotor performance) (Garland et al., 1990). The present study is the first quantification of repeatability of locomotor performance measures for chelonians. Terrestrial performance, being highly repeatable throughout the 30-week measurement period, was in accord with most repeatability investigations of anurans, lizards, and snakes (reviewed in Austin and Shaffer, 1992). However, aquatic performance was only repeatable through the 12-week measurement interval. Differences between the two locomotor modes are unknown, but may reflect motivational differences.

Both aquatic and terrestrial absolute burst speed increased over the 30-week measurement period. Alternatively, when burst speed is expressed relative to body lengths per unit time, increases in speed were observed only between the 6 and 12 week measurements. The reason for this result is largely unknown; however, this may represent a critical period during the muscular and/or skeletal development of the animals. A number of ontogenetic changes associated with growth may have contributed to the increased burst speeds with time. First, muscular development associated with growth was likely involved in the observed increase in speed (Marsh, 1988). Development likely results in increased strength of muscular contraction resulting in increased force generation, increased stride length, and/or stride frequency. Second, developmental changes in the skeletal structure of the animals may have influenced burst speed. The skeletal structure of hatchling turtles is primarily cartilaginous with mineralization and stiffening of the skeleton acquired over time. A rigid skeletal structure has been shown to influence the efficiency with which muscle contraction is translated into locomotion (McHenry et al., 1995). Finally, ontogenetic changes in energy utilization and/or storage may have influenced burst speed.
Interspecific studies have revealed an apparent optimum body size for speed amongst mammals (Garland, 1983). Within orders of mammals and within many families of lizards, burst speed appears to be largely independent of body mass (Garland, 1982). Amongst the few turtle species investigated most studies have demonstrated an apparent, yet not significant, increase in terrestrial speed with body mass (Adams et al., 1989; Muegel and Claussen, 1994; Zani and Claussen, 1994; Marvin and Lutterschmidt, 1997; Wren et al., 1998; Claussen et al., 2002). In the only investigation focusing specifically on juveniles, Miller et al. (1987) reported a significant positive relationship (b = 0.54) between burst speed and body mass for hatchling *Chelydra serpentina*. Zani and Claussen (1994) report a scaling exponent of 0.288 for forced terrestrial locomotion with body mass for *Chrysemys picta*, but suggest maximum speeds may occur at some intermediate body size. Therefore, differential scaling of speed with body mass may be expected to occur between juvenile and adult animals.

The present study demonstrated that both aquatic and terrestrial burst speed and distance capacity of juvenile *C. picta bellii* scale positively with body mass. However, the scaling of locomotor performance with body mass declined with each measurement over a 30-week period, resulting in a significantly lower scaling of locomotor performance following the measurement period. To my knowledge, this is the first investigation to demonstrate differential scaling of locomotor performance associated with ontogenetic changes in body size over time. This result suggests that if locomotor performance is under strong selection, larger hatchlings may have a distinct advantage over smaller conspecifics initially after emergence; however, if smaller hatchlings do survive, such advantages may be greatly reduced or lost over time. Further, the changes in scaling of burst speed are in accord with the suggestion that maximum speeds occur at some intermediate body size (Zani and Claussen, 1994).

The cause of the reduction in scaling of locomotor performance with body mass over time is unknown. However, ontogenetic changes associated with muscular or skeletal development may again be implicated. For example, the shell makes up a larger percentage of the total wet weight of adult turtles than that of juveniles, 33.8% vs. 24.1% respectively in *Trachemys scripta* (Zani and Claussen, 1994). Therefore, as the animal grows a heavier shell may provide added protection, but also place limitations on further gains of locomotor performance. Improved performance may be more crucial to hatchlings, while the benefits of a
heavy, rigid shell may outweigh further gains of locomotor performance with time. Further research is needed to determine the cause(s) and implications of the present results.

A trade-off has been reported between growth rate and swimming speed in fathead minnows (Kolok and Oris, 1995), rainbow trout (Gregory and Wood, 1998, 1999), Atlantic silverside (Billerbeck et al., 2001), and tadpoles of two species of anurans (Arendt, 2003). The cause of this trade-off is unknown; however, it has been suggested that the allocation of energy to growth may limit the energy available for active metabolism, thereby reducing locomotor capacity (Billerbeck et al., 2001). As all turtles in the present study were of a common age, larger individuals necessarily had a higher growth rate than smaller individuals over the measurement period. If such a trade-off between growth rate and locomotor performance exists for all vertebrates, as has been suggested (Arendt, 2003), the observed increased growth rate of larger hatchlings may place limitations on their locomotor capabilities. The present study demonstrates that larger turtles with higher growth rates maintained superior absolute performance over smaller conspecifics throughout the measurement period. This result appears to contradict the general trade-off between growth rate and burst speed suggested by Arendt (2003). However, such a trade-off could have played a role in the observed reductions in the scaling of locomotor performance with body mass throughout the measurement period. Future investigation is needed to further assess the effects of growth rate on locomotor performance.

The predominant view of survivorship for neonatal reptiles is that ‘bigger is better’ (reviewed in Packard and Packard, 1988), and several studies have demonstrated that larger hatchling turtles have increased survivorship (Janzen, 1993b; Janzen et al., 2000a,b; Tucker and Paukstis, 1999; Tucker, 2000, but see Congdon et al., 1999). Increased locomotor performance of larger hatchlings, resulting in a reduction in the potential exposure time to predators during the migration from the nest site to water, has been suggested as a potential explanation for the increased survivorship of larger hatchlings (Janzen et al., 2000a,b). The present study demonstrating superior locomotor performance, both burst speed and endurance, of larger hatchlings is in accord with current hypotheses as to the size-selective survivorship. However, field studies of hatchling Chelydra serpentina have found little evidence to attribute first-year survivorship of larger hatchlings to improved locomotor performance (Janzen,
1993b; Janzen, 1995). Clearly, further field investigations, utilization other species, are needed to elucidate the importance of locomotor performance in hatchling turtle survivorship.

To date, the present study has provided the most complete investigation into the effects of temperature and body size on the locomotor performance of turtles. Several of the present results, including changes in the scaling of locomotor performance with body mass and the lack of a trade-off between growth and locomotor performance, have not previously been reported. However, further research is needed to fully assess the implications of these results. Likewise, further investigations of chelonian locomotor performance, utilizing an array of species, are sorely needed to provided context and assess the generality of the present results.

**LITERATURE CITED**


Table 1. Results of ANCOVAs testing the effects of temperature on measures of performance with body mass as a covariate.

<table>
<thead>
<tr>
<th>Performance measure</th>
<th>df</th>
<th>Absolute F</th>
<th>Absolute P</th>
<th>Size-relative F</th>
<th>Size-relative P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aquatic burst speed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>2</td>
<td>128.21</td>
<td>&lt;0.0001</td>
<td>144.53</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Body mass</td>
<td>1</td>
<td>110.77</td>
<td>&lt;0.0001</td>
<td>26.45</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Temperature X body mass</td>
<td>2</td>
<td>6.28</td>
<td>0.0026</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td><strong>Aquatic distance capacity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>2</td>
<td>627.28</td>
<td>&lt;0.0001</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Body mass</td>
<td>1</td>
<td>1102.45</td>
<td>&lt;0.0001</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Temperature X body mass</td>
<td>2</td>
<td>186.90</td>
<td>&lt;0.0001</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td><strong>Terrestrial burst speed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
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<td>187.36</td>
<td>&lt;0.0001</td>
<td>221.93</td>
<td>&lt;0.0001</td>
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<td>Body mass</td>
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<td>145.21</td>
<td>&lt;0.0001</td>
<td>45.31</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Temperature X body mass</td>
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<td>16.67</td>
<td>&lt;0.0001</td>
<td>1.55</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Terrestrial distance capacity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>2</td>
<td>547.33</td>
<td>&lt;0.0001</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Body mass</td>
<td>1</td>
<td>525.81</td>
<td>&lt;0.0001</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Temperature X body mass</td>
<td>2</td>
<td>135.98</td>
<td>&lt;0.0001</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td><strong>Righting response</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>2</td>
<td>27.41</td>
<td>&lt;0.0001</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Body mass</td>
<td>1</td>
<td>0.31</td>
<td>0.5802</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Temperature X body mass</td>
<td>2</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>
Table 2. Temperature coefficients ($Q_{10}$ values) for measures of aquatic and terrestrial locomotor performance trials, as well as righting response, for *Chrysemys picta bellii* over the range of test temperatures. Data are mean ± SEM.

<table>
<thead>
<tr>
<th>Performance measure</th>
<th>Q$_{10}$</th>
<th>10 - 20 C</th>
<th>15 - 20 C</th>
<th>20 - 30 C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Aquatic</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burst speed (m/s)</td>
<td>1.98 ± 0.061</td>
<td>---</td>
<td>1.33 ± 0.062</td>
<td></td>
</tr>
<tr>
<td>Size-relative burst speed (BL/s)</td>
<td>1.78 ± 0.055</td>
<td>---</td>
<td>1.49 ± 0.061</td>
<td></td>
</tr>
<tr>
<td>Distance Capacity (m)</td>
<td>---</td>
<td>2.61 ± 0.054</td>
<td>2.28 ± 0.033</td>
<td></td>
</tr>
<tr>
<td><strong>Terrestrial</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burst speed (m/s)</td>
<td>1.83 ± 0.080</td>
<td>---</td>
<td>1.46 ± 0.051</td>
<td></td>
</tr>
<tr>
<td>Size-relative burst speed (BL/s)</td>
<td>1.74 ± 0.076</td>
<td>---</td>
<td>1.65 ± 0.053</td>
<td></td>
</tr>
<tr>
<td>Distance Capacity (m)</td>
<td>---</td>
<td>2.76 ± 0.10</td>
<td>2.40 ± 0.075</td>
<td></td>
</tr>
<tr>
<td>Righting Response (s)</td>
<td>0.56 ±0.062</td>
<td>---</td>
<td>0.70 ± 0.059</td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Pearson product-moment correlation coefficients between measures of performance at 30 C in _Chrysemys picta bellii_. *P < 0.05.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Performance measure</th>
<th>Aquatic Distance capacity</th>
<th>Aquatic Burst speed</th>
<th>Aquatic Size-relative burst speed</th>
<th>Terrestrial Distance capacity</th>
<th>Terrestrial Burst speed</th>
<th>Terrestrial Size-relative burst speed</th>
<th>Terrestrial Righting Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aquatic</td>
<td>Distance capacity</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Burst speed</td>
<td>0.426 *</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Size-relative burst speed</td>
<td>0.241</td>
<td>0.957 *</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terrestrial</td>
<td>Distance capacity</td>
<td>0.892 *</td>
<td>0.370 *</td>
<td>0.211</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Burst speed</td>
<td>0.625 *</td>
<td>0.598 *</td>
<td>0.469 *</td>
<td>0.487 *</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Size-relative burst speed</td>
<td>0.516 *</td>
<td>0.535 *</td>
<td>0.453 *</td>
<td>0.373 *</td>
<td>0.978 *</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Righting Response</td>
<td>-0.197</td>
<td>-0.058</td>
<td>-0.016</td>
<td>-0.353</td>
<td>-0.009</td>
<td>0.043</td>
<td>1.000</td>
</tr>
</tbody>
</table>
Table 4. Results of ANCOVAs testing the effects of growth (i.e., week) at six-week intervals over 30-weeks on measures of performance with body mass as a covariate. Righting response was measured only over a six-week period.

<table>
<thead>
<tr>
<th></th>
<th>df</th>
<th>Absolute</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td><strong>Aquatic burst speed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week</td>
<td>5</td>
<td>78.31</td>
<td>&lt;0.0001</td>
<td>8.16</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body mass</td>
<td>1</td>
<td>423.93</td>
<td>&lt;0.0001</td>
<td>11.54</td>
<td>0.0008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week X body mass</td>
<td>5</td>
<td>5.75</td>
<td>&lt;0.0001</td>
<td>3.75</td>
<td>0.0029</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Terrestrial burst speed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week</td>
<td>5</td>
<td>55.05</td>
<td>&lt;0.0001</td>
<td>8.47</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body mass</td>
<td>1</td>
<td>352.46</td>
<td>&lt;0.0001</td>
<td>18.96</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week X body mass</td>
<td>5</td>
<td>3.07</td>
<td>0.0110</td>
<td>4.04</td>
<td>0.0016</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Righting response</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week</td>
<td>1</td>
<td>0.00</td>
<td>0.9824</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body mass</td>
<td>1</td>
<td>6.06</td>
<td>0.0172</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week X body mass</td>
<td>1</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5. Repeatability of performance measured at six-week intervals at 30 C over a 30-week period for *Chrysemys picta bellii*. Values are the Pearson product-moment correlation coefficients of initial measured performance with performance at six-week intervals.
* $P < 0.05$. Sample size in parentheses.

<table>
<thead>
<tr>
<th>Performance measure</th>
<th>Week 6</th>
<th>Week 12</th>
<th>Week 18</th>
<th>Week 24</th>
<th>Week 30</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aquatic</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burst speed (35)</td>
<td>0.469 *</td>
<td>0.422 *</td>
<td>0.328</td>
<td>0.242</td>
<td>0.156</td>
</tr>
<tr>
<td>Size-relative burst speed (35)</td>
<td>0.368 *</td>
<td>0.369 *</td>
<td>0.299</td>
<td>0.143</td>
<td>0.072</td>
</tr>
<tr>
<td><strong>Terrestrial</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burst speed (35)</td>
<td>0.586 *</td>
<td>0.387 *</td>
<td>0.357 *</td>
<td>0.534 *</td>
<td>0.447 *</td>
</tr>
<tr>
<td>Size-relative burst speed (35)</td>
<td>0.475 *</td>
<td>0.393 *</td>
<td>0.436 *</td>
<td>0.487 *</td>
<td>0.496 *</td>
</tr>
<tr>
<td>Righting response (25)</td>
<td>0.473 *</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>

* P < 0.05. Sample size in parentheses.
FIGURE LEGENDS

Figure 1. Effect of temperature on aquatic (squares) and terrestrial (circles) burst speed (A) and size-relative burst speed (B) of juvenile Chrysemys picta bellii. Data presented as least squares means ± SEM, to account for changes in body mass between test temperatures. Within a locomotor type (i.e., aquatic or terrestrial), mean values sharing a common letter do not differ significantly ($P > 0.0167$, least-squares means test). * denotes significant difference ($P < 0.05$) between aquatic and terrestrial locomotion at a given temperature. Samples sizes 35-47 individuals per test temperature.

Figure 2. Effect of temperature on aquatic (squares) and terrestrial (circle) distance capacity (A) measured at 0.10 m·s$^{-1}$ and righting response (B) of juvenile Chrysemys picta bellii. Data presented as least squares means ± SEM, to account for changes in body mass between test temperatures. Within a locomotor type (i.e., aquatic or terrestrial), mean values sharing a common letter do not differ significantly ($P > 0.0167$, least-squares means test). * denotes significant difference ($P < 0.05$) between aquatic and terrestrial locomotion at a given temperature. Samples sizes 30-42 individuals per test temperature.

Figure 3. Aquatic (squares) and terrestrial (circles) burst speed (A) and size-relative burst speed (B) measured at 30 C at six-week intervals over a 30-week period in Chrysemys picta bellii. Data presented as means ± SEM. Within a locomotor type (i.e., aquatic or terrestrial), mean values sharing a common letter do not differ significantly (Bonferroni multiple comparisons). * denotes significant difference ($P < 0.05$) between aquatic and terrestrial locomotion at a given time. Sample size = 35 for all measurements.

Figure 4. The initial and 30-week measurement of the relationship between body mass and aquatic (A) and terrestrial (B) burst speed measured at 30 C at six-week intervals over a 30-week measurement period in Chrysemys picta bellii. The F-statistic was statically significant ($P < 0.05$) for all regressions.
Figure 5. The power function scaling exponents describing the relationship between body mass and absolute aquatic (A) and terrestrial (B) burst speed as a function of the week of measurement. All Measurements were taken at 30 C. Verttical lines represent 95% confidence intervals. * denotes a statistically significant ($P < 0.05$) difference relative to week 0.

Figure 6. The initial and 30-week measurement of the relationship between body mass and aquatic (A) and terrestrial (B) size-relative burst speed measured at 30 C at six-week intervals over a 30-week measurement period in *Chrysemys picta bellii*. The F-statistic was significant ($P < 0.05$) only for the initial measurement.

Figure 7. The power function scaling exponents describing the relationship between body mass and size-relative aquatic (A) and terrestrial (B) burst speed as a function of the week of measurement. All Measurements were taken at 30 C. Verttical lines represent 95% confidence intervals. * denotes a statistically significant ($P < 0.05$) difference relative to week 0.

Figure 8. The relationship between body mass and aquatic and terrestrial distance capacity measured at 30 C and a constant speed of 0.10 m·s$^{-1}$ in *Chrysemys picta bellii*. The F-statistic was significant ($P < 0.05$) for all regressions.
A

Aquatic burst speed (m s\(^{-1}\))

Body mass (g)

0wk -- \(y = 2.585 \times x^{0.723}\)  \(R^2 = 0.260\)

30wk -- \(y = 5.929 \times x^{0.365}\)  \(R^2 = 0.909\)

B

Terrestrial burst speed (m s\(^{-1}\))

Body mass (g)

0wk -- \(y = 1.7524 \times x^{0.995}\)  \(R^2 = 0.359\)

30wk -- \(y = 5.916 \times x^{0.448}\)  \(R^2 = 0.792\)
Aquatic size-relative burst speed (BL s\(^{-1}\))

Body mass (g)

0wk -- \(y = 1.593 \times x^{(0.387)}\)  \(R^2 = 0.0767\)

30wk -- \(y = 3.807 \times x^{(-0.006)}\)  \(R^2 = 0.001\)

Terrestrial size-relative burst speed (BL s\(^{-1}\))

Body mass (g)

0wk -- \(y = 1.020 \times x^{(0.700)}\)  \(R^2 = 0.213\)

30wk -- \(y = 3.862 \times x^{(0.074)}\)  \(R^2 = 0.111\)
Aquatic: $y = 0.568 \times x^{1.838}$  $R^2 = 0.887$

Terrestrial: $y = 0.449 \times x^{1.381}$  $R^2 = 0.897$