Experimental analysis of body size and shape during critical life-history events of hatchling slider turtles, *Trachemys scripta elegans*

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Summary

1. A fundamental goal of examining life-histories is to identify those traits that enable organisms to move from one stage of life to another; however, traits that are important in one stage or event may not be important in subsequent cases. For long-lived taxa like turtles, studies of early life stages might be especially revealing because mortality is high during those times.

2. In this study, we examined several morphological characters in hatchling turtles to assess their relationships with hatchling performance and survival. We assessed hatchling plastron shape and body size during a release–recapture field experiment and in subsequent swimming performance trials in the laboratory.

3. Hatchling mass and plastron shape were correlated. Heavier turtles were relatively shorter and wider than lighter turtles.

4. Hatchling mass had a significant positive correlation with both recapture rate, a proxy measure of survivorship, and with swimming speed.

5. Plastron shape and recapture probability were not significantly correlated, but shape was a significant predictor of swimming performance. Shorter, wider turtles swam faster than longer, skinnier individuals. We hypothesize that this may be advantageous for quick-start swimming to escape predation, a function of longer legs, or improved range of motion.

6. These data support previous studies that demonstrated the importance of hatchling size for survival in the critical overland migration from nests to the water and also document the impact of body shape on basic life-history traits for neonatal turtles.

Introduction

Life-history analyses provide insights into traits or time periods that are important for individual survival and reproduction. The traits and stages that are most important vary across species, with some species having critical stages early, middle or late in life. A thorough knowledge of the traits that help individuals live, grow, reproduce and survive through future breeding seasons is essential for developing a complete understanding of population biology (Roff 1992). However, few studies follow individuals throughout their entire life to completely quantify the effects of various traits on components of, and lifetime, fitness (e.g. Campbell & Waser 2007). Individual life stages or events may yield disparate predictions about the importance of various traits or may exemplify selection acting in opposite directions (Grant 1985; Gomez 2004).

For those species having a type III survivorship curve, with an initially high mortality rate followed by high survivorship throughout adulthood, understanding the proximate causes of, and influences on, early survivorship is important because this initial period of strong selection has the most influence on determining which individuals in a population will reproduce (Pearl 1928; Begon, Mortimer & Thompson 1996). As such, identifying traits that set surviving neonates apart from the rest of their cohort is critical. In turtles, the hatchling stage is characterized by high mortality that can approach 70%–100% in a given cohort (Janzen, Tucker & Paukstis 2000a; Feinberg & Burke 2003; Horne *et al.* 2003; Moll & Moll 2004). Therefore, this

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stage is of special interest in understanding survivorship to adulthood and the traits that influence this transition. Hatchling turtles face several critical tests of survival. In particular, hatchlings of aquatic turtles must navigate from the terrestrial nest site across land to their aquatic habitat (river, pond or ocean; reviewed in Moll & Moll 2004). This migration is fraught with difficulties, including desiccation and mortality due to avian predation associated with extended travel time (Janzen *et al*. 2000a; 2007). Once in the water, neonates still face substantial challenges. Young turtles must be able to swim well in bursts to escape predators, as well as potentially swim over longer distances to forage effectively for food (Bodie & Semlitsch 2000). Individuals that maximize their performance in these early stages are more likely to survive to adulthood, where mortality is much lower, and to subsequently reproduce (Moll & Moll 2004).

Previous research on survivorship and performance in turtles (Janzen *et al*. 2000a,b; 2007; Tucker 2000a), as well as other species (Jayne & Bennett 1990; Blomberg & Shine 2000; Alcobendas, Buckley & Tejedo 2004), has focused mainly on size during these early life-history events. In general, larger hatchlings are more likely to survive the overland migration and to have enhanced locomotor ability (Janzen *et al*. 2000a,b; Janzen *et al*. 2007; Tucker 2000a). Studies examining swimming performance have similarly focused on body size or have focused on kinematics of limb movement (Mullins & Janzen 2006; Rivera *et al*. 2006) rather than the effects of body shape. While body size is important for hatchling survival and performance, body shape may also be important either directly or by influencing locomotor ability. Standard measurements of body length and widths cannot separate hatchling morphology into its size and shape components. Analyses that can consider independently both shape and size would be advantageous to dissect the relative importance of each component to hatchling fitness. Research in lizards, for example, has shown that hindlimb span, not body size, as measured by mass, is crucial for maximal running speed (Bonine & Garland 1999).

The shell of the turtle may play an important role in determining which hatchlings are successful and which are not. Both the carapace (dorsal shell) and plastron (ventral shell) provide protection to the turtle. However, hatchlings found dead following avian predation were typically eviscerated via the plastron, suggesting that shape differences here might influence handling ability by predators (Janzen *et al*. 2000b). Additionally, research has shown that the majority of movement in turning and swimming of hatchling turtles occurs in the horizontal plane, level with the plastron (Rivera *et al*. 2006). Finally, examining the plastron may give insight as well into limb span and position, which may similarly be important in overland migration and/or swimming by restricting or influencing range of motion more than the carapace. In aquatic species, several morphological attributes, including body shape, limb/fin position and mobility, as well as body flexibility, have been shown to be related to turning performance and may similarly be related to overall swimming ability (Rivera *et al*. 2006). In examining body shape using basic fluid dynamic equations, one would predict that longer, thinner turtles would have a reduced drag coefficient relative to shorter, wider turtles holding a vertical component equal (White 1999, p. 458). Subsequently, we would predict that longer, thinner turtles, with a lower coefficient, would have faster swimming speeds than shorter, wider turtles with a higher coefficient.

In selecting the plastron, we recognize that not all aspects of body shape and movement for terrestrial or aquatic locomotion will be captured. In particular, drag can be broken into components contributed by shape in the horizontal plane (friction drag) and in the vertical plane (pressure drag); the relationship between the height : length ratio of a moving body and the relative contribution of each component to overall drag has been estimated empirically (White 1999). In this study, we assume that hatchlings have equal carapace height and thus contributions to the pressure drag component should be similar across hatchlings. Based on the ratio of carapace height to plastron length (data not shown), we estimate that *c*. 40% of turtles' overall drag, if completely submerged, would be a function of friction drag, and this percentage would be even higher (50%–80%) if turtles did not swim completely submerged (White 1999, fig. 7·12a). Non-submerged turtles may face additional wave-making drag (White 1999); however, friction drag based on plastron shape remains a main factor. Subsequent analyses may examine the amount of variability in carapace height and its relative contribution to drag forces compared to those in horizontal plane. Finally, the plastron should play an important role in both terrestrial and aquatic activities and is thus an ideal trait to examine for a first look at the importance of body shape.

The slider turtle is ideally suited for this type of evaluation of the relationship between body shape, performance and early life-stage survivorship. The ecology of hatchling sliders has been well studied in the field (Tucker 1997, 1999, 2000a, 2000b; Janzen *et al*. 2000a, 2007), and avian predation is one of the main selective forces on hatchling turtles (Janzen *et al*. 2000a). In a pivotal experiment, size-dependent hatchling performance accounted for two-thirds of the selective fitness advantage of larger turtles, whereas hatchling size *per se* accounted for about one-third of the advantage (Janzen *et al*. 2007). Additional research also examined plastron shape in the context of quantitative genetics within and between populations, estimating that plastron shape, independent of body size, was highly heritable ($h^2 \approx 0.57$) and thus could exert a substantial micro-evolutionary impact on early life-history stages (Myers *et al*. 2006).

In this study, we assessed the micro-evolutionary significance of body size and shape for two critical survival components during an early life-history stage

of *Trachemys scripta*. In particular, we aimed to determine whether plastron shape influences hatchling survival and performance independently of plastron size. To evaluate aspects of fitness, we quantified the importance of hatchling shape and size for: (i) escaping predation during simulated terrestrial migration from nest to water during a field experiment; and (ii) swimming performance of surviving turtles in the laboratory. We hypothesized that performance measures of survival and swimming ability in relation to hatchling size would be comparable to prior studies in this species (Janzen *et al*. 2000a,b; 2007) and others (Pluto & Bellis 1986). Additionally, we hypothesized that shape might be a significant factor in hatchling survivorship and swimming speed. Specifically, we predicted that, according to fluid dynamic principles, longer, thinner individuals would perform better than shorter, wider individuals in the water. Terrestrially, we hypothesized that wider turtles may have an advantage in being able to run more quickly to evade predators, similar to experiments in lizards (Bonine & Garland 1999) Additionally, wider body shapes may be advantageous by increasing the difficulty of handling and processing hatchlings by avian predators. While others have examined shape at or across various life-history stages (e.g. Grant 1985; Badyaev & Martin 2000), this study is the first, to our knowledge, to explicitly examine the relative roles of body shape and body size in offspring survival and performance during key life-history events.

Materials and methods

ORGANISM

The experiments were conducted with hatchling red-eared slider turtles (*Trachemys scripta elegans*; Weid 1838), an aquatic turtle found throughout much of the southern, central USA. Unlike most turtles, neonatal sliders generally remain in the nest over the winter before emerging the following spring at our study site (reviewed in Gibbons & Nelson 1978; Tucker 1999). Emergence occurs from mid-April to mid-May (Tucker 1997, 2000a). Hatchlings are uniquely patterned on their plastrons, making it possible to re-identify individuals through visual inspection following a recapture event (Janzen *et al*. 2000a,b; Tucker 2000b).

FIELD SITE

The study area is a 13-ha agricultural field on the Mississippi River State Fish and Wildlife Refuge located 4·6 km north of Pere Marquette State Park, Jersey County, Illinois. The field is on the eastern edge of the Illinois River floodplain and has a 3% slope to the west. The study area is used extensively by *T. s. elegans* as a nesting area (Tucker 1997) and has been the focus of previous release experiments (Janzen *et al*. 2000a,b; Tucker 2000b).

EXPERIMENTAL METHODS

Collection and incubation of eggs

In May and June of 2004, 116 adult female *T. s. elegans* were captured on their nesting migrations. These turtles were returned to the laboratory where oviposition was induced with oxytocin within 48 h of capture (Ewert & Legler 1978). Eggs were tamped dry and mass of eggs was determined to the nearest 0·01 g with a Sartorius electronic balance. Following oviposition, females were returned to their original sites of capture.

Eggs were placed on moist vermiculite (about –150 kPa, equal amounts of vermiculite and water by mass) contained in covered, plastic boxes and were incubated at fluctuating temperatures (25–30 °C) to approximate thermal conditions likely to be encountered by turtle eggs in natural nests (Packard *et al*. 1985; Ratterman & Ackerman 1989; Cagle *et al*. 1993; Plummer, Shadrix & Cox 1994). Boxes were rehydrated *c.* once weekly to maintain the initial level of substrate moisture. Incubation period ranged from 60 to 87 days.

Hatchling measurement and maintenance

Following emergence from the egg, neonates were weighed to the nearest 0·01 g and their plastrons were scanned on a Hewlett-Packard Scan Jet 3970. The scans were used to measure shape vectors and identify recaptured hatchlings. Overall, 890 hatchlings were maintained in the laboratory for over-wintering and release in the following spring. During the winter, these turtles were housed in plastic blanket boxes containing moist vermiculite (–150 kPa) in a room kept dark except when entered to examine boxes and unheated except when necessary to prevent freezing temperatures (methods follow Janzen *et al*. 2000a,b; Tucker 2000a).

FIELD METHODS

Release

On 10 May 2005, 890 hatchling turtles were released at the field site in a single group at 06·00 central daylight time. The release point was 50 m east of the drift fence (see below) and aligned with the midpoint of the fence at pit 10. Release of the hatchlings was conducted by carefully depositing turtles onto the ground. Turtles were righted if overturned and smoothed into a single layer, but were not oriented in any specific direction. After the turtles were released, the investigator left the release area immediately.

Recapture of hatchlings

Hatchlings were recaptured on land using a drift fence. The drift fence was initially constructed in spring 1996 and repaired annually as part of an ongoing study of

emergence of natural hatchlings at the site. The fence ran north to south, parallel to the nearest aquatic habitat (see Tucker 2000a), and consisted of 0·3-m-high aluminum flashing. The fence was 285 m long with 20 evenly spaced 5-gallon plastic buckets buried 15 m apart. Just prior to the experimental release, vegetation in direct contact with the aluminum flashing was removed by hand so that turtles could not climb over the fence. No other alterations were made to vegetation near the fence to avoid creation of an ecotonal area adjacent to the fence. The drift fence was monitored twice daily at 06.00 and 18.00 CDT, beginning at 18.00 CDT on 10 May to check for recaptured hatchlings. For each recaptured turtle, the pitfall trap or nearest pit for turtles at the fence was recorded. Animals were returned to the laboratory for identification, scored as recaptured, and were then weighed to the nearest 0·01 g to assess weight loss. The last hatchling was recaptured on 12 June. The drift fence was checked for 20 days subsequent to 12 June and following each additional rain event; however, no additional hatchlings were recaptured. Most hatchlings were recaptured within the first 2 weeks of the experiment. Turtles not recaptured were considered predated, as previous work has found only decapitated or eviscerated individuals at the completion of a release (Janzen *et al*. 2000b, 2007). All recaptured hatchlings were subsequently transferred to Iowa State University for swimming performance testing. Turtles were not fed during this time or during their time at Iowa State University to simulate as closely as possible the natural order of life-history events, where neonates do not eat after egg emergence until their entry into the water. Following performance testing, animals were returned to Illinois and released at the water's edge of the site at which their mothers were collected.

PERFORMANCE TRIALS

Hatchling turtles were housed in plastic shoe boxes with a thin layer of tap water (*c.* 4 mm deep) at room temperature (*c.* 25 °C) at Iowa State University for 3–14 days before swimming and were kept in the dark, except when trials were occurring (*c.* 8 h:16 h photoperiod). Turtles were given a minimum of 3 days to acclimate to laboratory conditions. Subsequent handling times varied due to timing in the number of recaptured individuals and the number of swim trials performed in a given day. Prior to a swimming performance trial, each turtle was re-identified using the plastron markings.

A swim track was created in a standard 10-gallon (45·45 L) aquarium. The track was 50 cm in length and was 9 cm wide at the top, tapering inward to discourage settling on bottom of the tank. The water in the aquarium was allowed to reach room temperature before trials occurred.

Swimming performance of a turtle was measured as swim time (nearest 0·01 s) over 45 cm of swim distance.

To encourage performance, an observer tapped the posterior end of the carapace with a pencil to simulate avian predation attempts (similar to Mullins & Janzen 2006). Poking occurred strictly in a vertical motion so as not to impart additional forward momentum to the hatchling. Hatchlings were tested three times with 10–15 min rest between each test. For each test, a hatchling was given three chances to perform the swim trial. If, after three attempts, the hatchling could not be coaxed to swim, it was considered a non-performer and excluded from subsequent analyses. For all swimming analyses, the fastest swim time across all tests was used. In cases when a turtle only swam for one test, this time was used. Best times were then converted to swimming speed (cm s^{-1}).

MORPHOLOGICAL DATA COLLECTION

Plastron shape was quantified using landmark-based geometric morphometric methods (Rohlf & Marcus 1993). These methods quantify shape after the effects of non-shape variation have been mathematically held constant (Adams, Slice & Rohlf 2004). First, images of the plastron of each specimen were obtained by using digital scans of hatchling plastrons. From each image, the *x, y* coordinates of 12 anatomical landmarks (Fig. 1a) were then recorded using TpsDig (Rohlf 2002a). Only one side of the plastron was used to avoid potential singularity in the data set resulting from near or perfect symmetry between the plastron halves (Bookstein 1996a; Klingenberg, Barluenga & Meyer 2002). It is assumed that both sides of the plastron are the same, and interpretation of the results would apply equally to either side. Landmarks were chosen to match those of a previous study of plastron shape in this population (Myers *et al*. 2006) and included the intersections of the lines delineating the gular, humeral, pectoral, abdominal, femoral and anal scutes. Using the set of *x, y* coordinates, a Generalized Procrustes Analysis was performed to superimpose the specimens to a common coordinate system and mathematically eliminate the effects of digitizing position, orientation and scale (Rohlf & Slice 1990). Following alignment of specimens, an average specimen was calculated (Fig. 1b), and shape variables were then generated as partial warp scores from the thin-plate spline (Bookstein 1989, 1991) and the two standard uniform components (Bookstein 1996b; Rohlf & Bookstein 2003). Together, these variables (the weight matrix) capture both uniform and non-uniform aspects of shape variation, and can be used to test hypotheses of shape variation and covariation using standard multivariate statistics (see Adams & Rohlf 2000; Myers *et al*. 2006). Twenty shape variables were generated from the 12 landmarks used, creating a size-free measure of shape. All superimposition and thin-plate spline computations for generating morphometric shape variables were performed in TpsRelw (Rohlf 2002b).
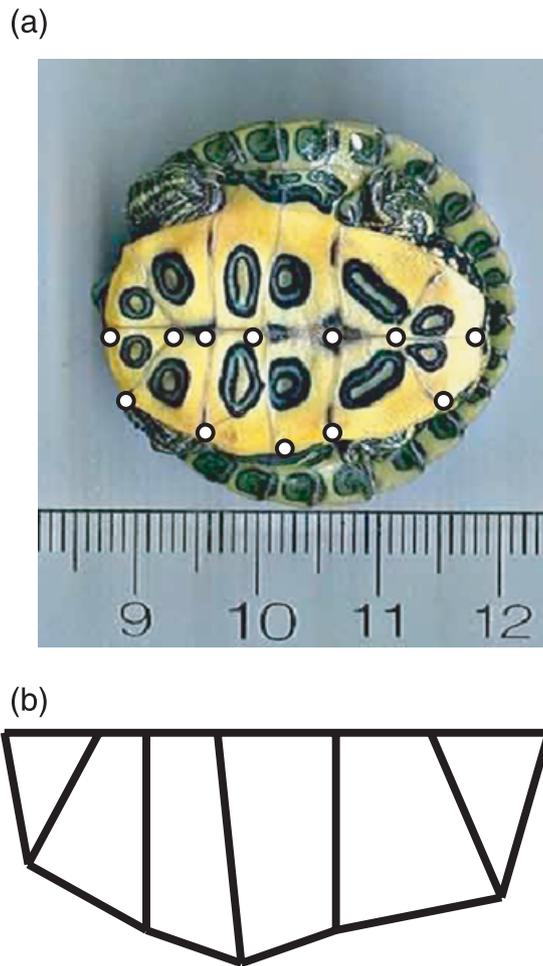
(a)

(b)

Fig. 1. (a) Location of landmarks along the plastron of slider turtles (*Trachemys scripta*) for morphometric analysis. (b) Consensus shape of the hatchling plastron.

STATISTICAL ANALYSIS

A multivariate analysis of variance (MANOVA) was performed in JMP (v. 5·0 & 6·0, SAS Institute Inc. 2002) to assess differences in shape between hatchlings recovered alive and those presumed dead. To quantify body condition, release mass was divided by plastron length cubed (WT × PL^{-3}; Laurie 1990). An analysis of variance (ANOVA) and a regression analysis were performed on body condition for recapture status and swimming speed for recaptured turtles, respectively, in JMP. A disparity analysis was performed in Excel (v. 2002 Microsoft) to assess differences in the dispersion of the hatchlings in shape space to test for stabilizing selection (Hollander *et al.* 2006). To test the difference between distributions, a Kolmogorov–Smirnov test (Sokal & Rohlf 1995) was used. Logistic regression was performed using SAS (SAS Institute 2002, v. 2001 for Windows) to examine the relationship between hatchling mass at release and recapture variables (e.g. pit number), as well as whether hatchlings were recovered alive or presumed dead. Additionally, a MANOVA was performed to examine shape differences between swimming performers and non-performers.

Regression of hatchling mass with best swim time was performed in JMP. Partial least-squares analysis (JMP v. 6·0) was used to test correlations among plastron shape, mass and swim time. A similar analysis was also performed to examine the relationship of plastron shape with recapture date, and significance was assessed using a permutation test with 999 random permutations in TpsPLS (v. 1·14, Rohlf 2002c). Summary statistics were generated in Excel (v. 2002, Microsoft).

Results

RELEASE EXPERIMENT

Of the 890 turtles released, 499 turtles were recaptured by June 12, the last day hatchlings were recaptured. There were no significant correlations between pit and date, pit and release mass, or pit and shape ($P > 0·2$); therefore, we conclude that there was no bias in the recapture of hatchlings in terms of pit affinity, a measure of spatial dispersion. Additionally, using standard statistical methods, we visually examined the shape data for any spurious outliers but detected no such individuals.

Using a MANOVA, we found no significant difference in shape between hatchlings that were recaptured (alive) and those that were not recaptured (considered dead) during the release ($F = 1·38$, d.f. = 19, 840, $P = 0·13$). Additionally, there was no significant correlation of plastron shape with recapture date ($r = 0·17$, $P = 0·21$). We found no significant difference in the disparity of the shape data between all turtles and those turtles recaptured. The average disparity from the mean was 0·041 in both data sets, thus stabilizing selection was not present. However, mass and recapture date varied inversely ($r = –0·26$, $P < 0·0001$), indicating that heavier turtles reached the drift fence more quickly. Accordingly, the alive and dead groups differed significantly in release mass ($F = 12·7$, $P = 0·004$). Mean hatchling mass for turtles recaptured alive was 6·00 ± 1·01 g ($n = 499$), while the mean mass for those not recaptured and presumed dead was 5·77 ± 1·08 g ($n = 391$). Logistic regression on mass and recapture status demonstrated that heavier turtles were more likely to be recaptured ($\chi^2 = 10·34$, $P = 0·001$). This selective event resulted in a shift of the mass distribution of recaptured hatchlings relative to the starting pool of individuals (Fig. 2), rather than a simple truncation event. The distributions of hatchling masses were marginally significantly different ($0·1 < \alpha < 0·13$) and were characterized by a larger percentage of heavy weight turtles in the alive group as compared to a larger percentage of lighter turtles in the all turtles group. Turtles recaptured later were significantly lighter than those recaptured earlier ($F = 21·10$, d.f. = 1, 422, $P < 0·0001$). Hatchlings lost an average of 11·45% ± 5·87% of body mass between release and recapture. Body condition was not significantly different between recaptured and non-recaptured hatchlings ($F = 0·23$, d.f. = 1, 886, $P = 0·64$).

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*Body size and
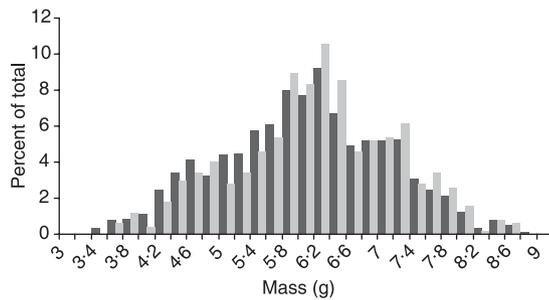plastron shape of
hatchling turtles*

Fig. 2. Frequency distribution of hatchling mass represented as a percentage of the total hatchlings in each group. Charcoal bars represent distribution for all hatchlings and light grey bars represent distribution of recaptured individuals. Recaptured hatchlings were significantly heavier than those presumed dead and not recaptured ($F = 12.7$, $P = 0.004$). The distributions were only marginally significantly different ($0.1 < \alpha < 0.13$).

SWIMMING TRIALS

In total, 424 turtles (85%) completed at least one test of swimming performance. There was no significant difference in shape between those turtles that performed the swim tests and those that did not ($F = 0.77$, d.f. = 19, 467, $P = 0.74$). There was, however, a significant difference between swimmers and non-swimmers according to recapture mass. Non-swimmers were significantly lighter than turtles that swam in the trials (non-swimmers 5.08 ± 0.11, swimmers 5.36 ± 0.05, $F = 5.40$, d.f. = 1, 496, $P = 0.02$). Turtles that were recaptured later swam significantly slower than turtles recaptured earlier ($F = 10.53$, d.f. = 1, 422, $P = 0.001$). Using a two-block partial least-squares analysis, swim speed was correlated to both plastron shape and recapture mass simultaneously ($r = 0.23$, $P < 0.0001$).
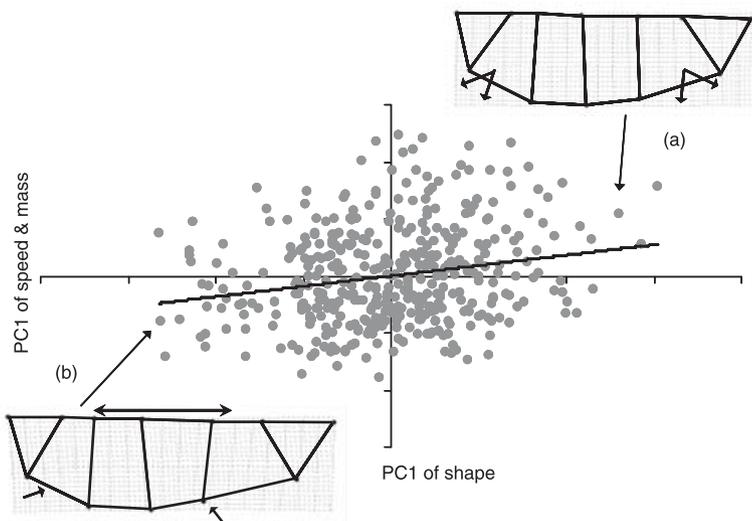
When this relationship was deconstructed into its individual components, swim speed was significantly correlated with mass and shape independently (mass: $r = 0.13$, $P = 0.008$; shape: $r = 0.21$, $P < 0.0001$, Fig. 3). Recapture mass and plastron shape were significantly correlated ($r = 0.37$, $P < 0.0001$). The correlation reveals a trend between lighter turtles that were longer, skinnier and slower swimmers vs. faster, heavier turtles that were shorter and wider. Much of the shape change is focused in the expansion and contraction of the humeral and femoral scutes with elongation also occurring along the mid-line of the plastron (Fig. 3). Body condition was not significantly correlated with swimming speed ($r = 0.03$, $P = 0.39$).

Discussion

The results of this study support the conclusions of other experiments showing improved survival for hatchlings of larger body size when migrating across land. The benefit of larger body size is largely due to improved speed in migration and consequent reduction in time exposed to predators rather than to an increase in physical size that reduces predation ability (Janzen *et al.* 2007). Whether this fitness advantage is the result of improved body condition or the result of longer legs leading to longer strides and faster movement is not completely known, as leg length was not measured. However, a preliminary assessment of body condition was not significantly different between recaptured and non-recaptured hatchlings, suggesting that this effect may be more likely driven by an increase in limb length rather than improved body condition in larger turtles. The difference in mass between the alive and dead groups was 0·23 g (3·8%), consistent with the mass typically lost over the duration of a recapture experiment (Tucker 2000b) and similar to *c.* 3 days of crawling (Clusella Trullas, Spotila & Paladino 2006). In our study, turtles lost 11% of their body weight on average due to extended travel times and dry conditions. Hatchlings recaptured earlier were heavier and consequently performed better at swimming, suggesting a better ability to escape predation while in the water, much as larger size improves migration speed and reduces predation terrestrially (Janzen *et al.* 2007). Similar to the terrestrial results, body condition was not significantly related to swimming speed, suggesting that increased limb length rather than improved body condition is advantageous for improved swimming performance.

This study also assessed the role of body shape, exclusive of size, in hatchling fitness and performance. Interestingly, although plastron shape and body mass were significantly correlated, shape was not significantly associated with hatchling survival during the overland migration. Body shape, however, was an important factor in swimming speed. Turtles that were long and skinny had relatively slower swimming times than those that were wider and shorter. Surprisingly,

Fig. 3. Principal components plot from partial least-squares analysis showing the relationship between the variables swimming speed and mass with plastron shape in hatchling slider turtles ($r = 0.21$, $P < 0.0001$). This shows a general trend between heavier turtles with short, wide shape that swim faster (a) and lighter, slower turtles, exhibiting a longer skinnier plastron (b). Arrowheads indicate the direction of shape change. For visual representation, only the first principal component of shape and variables are shown.

when shape and mass were combined in examining correlations of swimming time, mass added little to the result. This outcome suggests that plastron shape is a greater factor in relation to swimming speed than mass itself. Thus, the relative importance of size and shape may differ depending on the life-history trait or stage examined.

The plastron shape of turtles whose swimming speeds were greatest was contrary to the predictions we made based on drag coefficients. In general, turtles with longer, narrower plastrons were expected to perform the best but actually performed slightly slower. While this result is unexpected, wider plastrons may be adaptive. In lizards, individuals with a larger span between the hindlimbs had enhanced running ability, although this was due in part to axial flexibility leading to increased stride length (Bonine & Garland 1999). This wider stance may be more advantageous to build up speed; however, turtles have a rigid body design. Interestingly, the scutes that showed the greatest amount of shape change, relative to the average turtle, were the humeral and femoral scutes, which are located at the insertion points for the fore- and hind-limbs (Fig. 3). The wider plastron shape would be indicative of a wider spread between the limbs of the hatchling, potentially influencing the range of motion for the fore- and hindlimbs where increased range of motion could lead to increased thrust potential (Pace, Blob & Westneat 2001) or confer a similar 'quick-start' advantage. Body mass and body condition results are suggestive that heavier turtles may have longer limbs which would lead to faster movements over land and in the water (Pace *et al.* 2001). Additional studies have speculated that the position of the turtle limbs equally spaced and near the centre of rotation enhances their overall manoeuvrability (Rivera *et al.* 2006) and thus could similarly influence straight line performance. Heavier turtles tended to have a wider plastron and thus there could be a relationship between shell shape and limb length, shape or movement. Direct measurements of limb length are beyond the scope of this present study but should be examined more thoroughly to have an accurate understanding of the relationship between body size, shape, limb length and performance. If the same hatchling turtles were tested over a longer distance, where endurance is measured rather than sprint speed, one might expect that the advantage would switch to the turtles with the shell shape predicted to have the least drag. Similar types of general body differences in morphology have been noted between groups of fish adapted for quick acceleration vs. long distance cruising (Domenici 2003). Predicted relationships between shape and performance are not always met because shape is based on a large number of factors and is linked not only to the swimming performance but also to activities such as feeding and escape behaviours (Domenici 2003).

While we did not measure all aspects of body shape that could influence drag, in particular carapace height, our data should nevertheless be relevant to the aquatic performance of hatchling turtles. Our assumption of equal height is supported by the observation that carapace height was relatively uniform over a range of hatchling sizes measured in a subsample of preserved turtles at a range of sizes similar to the present study (data not shown). Many of the hatchling turtles that participated in the swimming trials did not swim completely submerged below the surface (personal observation). These turtles swam with their limbs, heads and tails, and *c.* two-thirds of the shell submerged. Thus, the carapace height would have a relatively reduced influence on the overall drag experienced by the turtles.

Ontogenetic variation in the relative importance of shape and mass for performance in turtles highlights the significance of examining more than one trait in life-history analyses. In a study of finches, Grant (1985) assessed beak shape over several life-history stages and for several components of overall fitness. The tendency of beak shape to change in one direction was counteracted by selection in an opposite direction either through correlation with a different bill dimension, selection on the same dimension in the other sex or selection on the same dimension in a different life-history stage (Grant 1985). Similar forces could conceivably be operating in turtle populations. Earlier research has shown that hatchling plastron shape in this population is highly heritable (Myers *et al.* 2006). This finding suggests that plastron shape has the potential to respond evolutionarily to selection (Roff 1997). In examinations of standard body measurements, plastron measures and carapace measures are strongly correlated (data not shown); thus selection on different aspects of body shape may influence the shape of the plastron. While sex was not examined in this study, it is conceivable that selection could act differently on plastron shape between the sexes, potentially favouring a larger size of the anal scute regions for a wider pelvic aperture for oviposition. Finally, adult turtles spend considerably more time in faster flowing, deeper waters (Pluto & Bellis 1986; Bodie & Semlitsch 2000) where a more streamlined body shape (long and skinny) could be more advantageous for minimizing drag resistance. Consequently, it would be worthwhile to further examine plastron shape at other points in the turtle's life history to determine if selection acts more strongly in different directions or at different times.

Plastron shape may play a larger role in determining other fitness-related behavioural traits than previously thought, such as righting ability or swimming performance over longer distances. Hatchling righting ability, a trait commonly used to assess performance (Freedberg *et al.* 2004; Mullins & Janzen 2006), is an important behaviour in reducing exposure to predation and thermal stress (Burger 1976). In contrast, long-distance swimming may reflect performance in daily activities, such as finding basking sites and foraging for food (Bodie & Semlitsch 2000; Moll & Moll 2004). Future research should test the relationships of these

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*Body size and
plastron shape of
hatchling turtles*

additional performance traits with hatchling size and shape.

In conclusion, our results support those of other related studies on the importance of the relationship between body size (as measured by hatchling mass) and both survivorship and swimming performance. Plastron shape, though not important in overland migration and survival, may play a more essential role during aquatic challenges experienced by neonatal turtles. Neonates with a wider, shorter plastron performed better than longer, skinnier cohorts. These results suggest that mass and shape may vary in the timing of their importance, highlighting the benefit of examining more than one life-history trait and stage. We encourage other researchers to examine the effects of both size and shape during ontogeny in performance and life-history studies, as well as examine more than one life-history event to determine the importance of traits on fitness.

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