
Influence of Water Availability during Incubation on Hatchling Size, Body Composition, Desiccation Tolerance, and Terrestrial Locomotor Performance in the Snapping Turtle *Chelydra serpentina*

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ABSTRACT

The effects of water availability during incubation on the water contents of neonatal snapping turtles at hatching were examined, along with the influence of hatchling water content on desiccation tolerance and terrestrial locomotor performance. The water contents of hatchlings from eggs incubated on wet substrates were both absolutely and proportionally greater than were those of hatchlings from eggs incubated on dry substrates. Hatchlings with greater water contents at hatching were able to survive longer and to lose more water before physiological performance was adversely affected by desiccation. Increased water contents in hatchlings with greater water availability during incubation may enhance survival by increasing the amount of water the animal can afford to lose before dehydration begins to adversely affect whole animal performance.

Introduction

The influence of water availability on the growth of embryonic turtles during incubation has been examined extensively, especially in the common snapping turtle, *Chelydra serpentina*. Increased water availability during incubation appears to increase the rate of mobilization of nutrients from the yolk and their subsequent assimilation into tissue (Packard et al. 1987, 1988; Packard 1991), to increase the amount of water contained within the body of the embryo (Packard et al. 1988; Finkler

1997), and to increase the duration of incubation such that more of the egg contents are used by the embryo (Morris et al. 1983; Miller and Packard 1992). Increased water availability during incubation thus tends to lead to the production of larger and presumably higher-quality hatchlings with more water contained within their bodies, greater dry carcass masses, and reduced residual yolk mass.

Although many suggestions have been made regarding the importance of these differences in hatchling size and body composition to the performance and survival of the hatchlings, whether or not these resultant differences in body size and body content do, in fact, lead to differences in fitness is unclear. Increased locomotor performance in hatchlings from eggs with increased water availability during incubation has been noted in some studies (Miller et al. 1987; Miller 1993) but not others (Janzen 1993; Finkler 1997). Most studies of hatchling performance have used forced velocity as their sole assessment of physiological and ecological performance, a measure that may not appreciably influence the survivorship of these organisms, which arguably cannot rely on speedy retreats as their major defense (Brooks et al. 1991). Suggestions that larger hatchlings may be able to capture prey more readily than smaller hatchlings have not been supported by laboratory observation (Finkler 1997). Larger hatchlings can effectively monopolize single stationary food sources against smaller hatchlings (Froese and Burghardt 1974), but whether differences in mass brought about by differential water availability during incubation can provide such competitive advantages, or even if such situations occur frequently enough in the wild to have an appreciable influence on the fitness of these animals, has not been determined. Whereas size differences among hatchlings from eggs incubated under different hydric conditions are sustained through the neonatal period (Miller 1993), it is unclear whether hatchlings from wet incubation conditions actually grow faster (i.e., show greater increases in size per unit time) than their dry-incubated counterparts (Brooks et al. 1991; Bobyn and Brooks 1994). It is thus questionable that the availability of water during incubation appreciably influences neonatal fitness once the hatchling has reached the water.

The time period in which differences in body mass and content derived from increased water availability during incubation would most likely influence the survival of hatchlings is during

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the migration of the hatchling from the nest site to the water. *C. serpentina* nests may be located several hundred meters from the nearest permanent water (Ernst and Barbour 1989). Robinson (1989) found that the percentage of hatchlings that successfully completed the nest-to-water migration decreased with increasing distance from nest site to water. A release-recapture study conducted by Janzen (1993) indicated that larger hatchlings have a greater probability of surviving the nest-to-water migration. However, as the study did not track the animals as they migrated from the nest site, the factors suggested as those upon which selection might act (size-selective predation, behavioral differences, and/or susceptibility to ambient environmental conditions) cannot be separated.

Despite the paucity of information on factors influencing the survival of freshwater turtle hatchlings as they migrate from nest site to water, it is plausible that differences in the amount of water available to a developing embryo might influence the resultant hatchling's ability to complete the nest-to-water migration successfully. During the nest-exodus period, resources available to the hatchling are likely restricted to those derived from the contents of the egg. Thus, the hatchling must complete its journey with a limited amount of water and nutrients. The stored energy reserves carried by the hatchling (e.g., yolk sac, body fat) probably would suffice for most migrations, as much of the original energy content of the egg is stored in the hatchling for posthatching activities (Wilhoft 1986). The amount of water carried by a snapping turtle hatchling, however, may be a more limiting factor during long migrations, as *C. serpentina* have relatively high rates of evaporative water loss and may be particularly prone to desiccation (Ernst 1968). The observation by Ernst et al. (1994) that hatchling snapping turtles typically drink almost immediately upon reaching water lends further credibility to the notion that dehydration may be a considerable problem. Dehydration by itself might potentially lead to mortality if a hatchling is not provisioned with enough water in its tissues to complete the migration. In addition, the degree of desiccation may determine how long that animal must spend on land before it can reach the water, as decreasing body water content may lead to decreased locomotor performance (Feder and Londos 1984), thus leading to a longer duration of migration for a set distance and consequently increased vulnerability to predation. Moreover, the increased time required to complete the migration that is incurred with loss of locomotor performance would lead to an even greater amount of water loss, resulting in a further decrease in performance. Despite this potential importance to the survival of hatchling turtles during the nest-to-water migration, the influence of variation in water availability on hatchling water content and its subsequent effects on hatchling performance and survival have heretofore received little attention (Miller et al. 1987; Miller 1993).

In this experiment, I examined the influence of variation in water availability (from both maternal and environmental

sources) during incubation on hatchling mass and composition, subsequent effects on an endpoint for ecological death by dehydration, and locomotor performance after moderate dehydration of the body tissues. I hypothesized that eggs with greater water availability would yield hatchlings with greater water contents in their bodies. These hatchlings, in turn, would be able to survive longer periods of exposure to dehydrating conditions and would show less decrease in performance after experiencing a moderate amount of water loss than would hatchlings from eggs with less water availability.

Material and Methods

Fourteen *Chelydra serpentina* clutches were collected within 12 h of oviposition from sites in and adjacent to the Valentine National Wildlife Refuge, Cherry County, Nebraska, on June 13 and 14, 1996 (eight clutches), and on June 14 and 15, 1997 (six clutches). In 1996, eggs were marked for identification and weighed to the nearest milligram within 2 h of collection, then placed in a moistened vermiculite and kept cool with ice blocks until the eggs could be transported to Miami University on June 16. Eggs collected in 1997 were immediately placed in a similar vermiculite substrate and kept cool in a refrigerator until they could be transported to Miami University on June 20, whereupon the eggs were weighed and marked.

Eggs within each clutch were randomly assigned to either a dry-incubation treatment or a wet-incubation treatment upon arrival at the laboratory. Dry-treatment eggs from each clutch were randomly placed into one of four aluminum baking pans containing a vermiculite substrate composed of 0.18 g of water per gram of dry, sterilized vermiculite, with an estimated water potential of -850 kPa (Morris et al. 1983). Wet-treatment eggs were similarly allocated into four aluminum pans holding a vermiculite substrate containing 1.11 g of water per gram of vermiculite, with an estimated water potential of -150 kPa (Morris et al. 1983). Eggs were half buried in the vermiculite. One pan of each treatment was placed into each of four separate GQF Hova Bator 2362N incubators and the eggs were incubated at 29°C . Once every week, the eggs were weighed, the water content of the vermiculite substrate was restored by adding enough distilled water to replace the mass lost, and the pans holding the eggs were rotated among the four incubators.

Hatchlings were weighed upon hatching and then transferred to individual 100-mL beakers lined with moist paper tissue during the first 2 d after hatching to allow the yolk sac to be drawn through the umbilical fontanel into the body cavity. All hatchlings were weighed on day 2 posthatching. After this weighing, a subset of hatchlings from each clutch in each water-potential treatment ($N = 5-8$ hatchlings, depending on availability) was randomly selected, anesthetized with tricaine methanesulfonate, and killed by decapitation. In 1996, the animals were immediately placed in a 60°C drying oven and dried to a constant mass. In 1997, the hatchlings were dissected, the

yolk sacs removed from the carcasses, weighed, then dried separately from the carcasses. Wet and dry carcass and yolk sac masses for the 1997 hatchlings, as well as total water and solid contents of hatchlings for both years, were determined. Linear regression equations of total water and solid contents of the hatchlings as a function of day 2 hatchling mass were formulated within clutch and incubation substrate, and from these equations, estimates of the water and solid contents of the remaining hatchlings were derived. Further changes in the mass of the hatchlings after day 2 were assumed to be due solely to changes in the water content of the hatchlings.

To assess the desiccation tolerance of hatchling turtles, randomly selected day-3 hatchlings from each incubation treatment in the 1997 cohort ($N = 8$ for the dry treatment, $N = 6$ for the wet treatment) were placed into a still-air desiccator containing CaSO_4 desiccant (mean relative humidity [RH] = 12%) at 25°C until the animals began showing overt signs of dehydration stress (e.g., sunken eyes, reduced activity, etc.). Animals were then removed from the desiccator and placed upon their backs. Upon righting themselves, the animals were returned to the desiccators and the procedure was repeated after 2 h of additional desiccation. Animals that could not right themselves within a 10-min period (not counting individuals withdrawn into their shells as a defensive response to being handled) were weighed, anesthetized, and killed. Yolk sacs were removed from the carcasses, and both were dried separately in a 60°C drying oven to a constant mass.

To examine the relationship between hatchling water content and whole-animal performance, remaining day-3 hatchlings

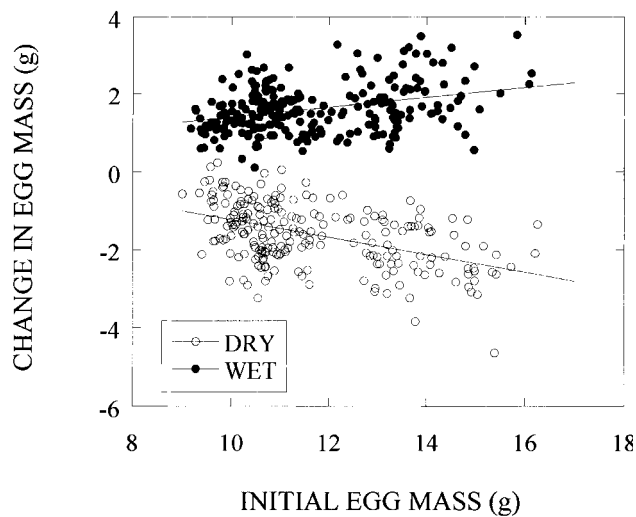


Figure 1. The relationship between the change in egg mass from the start of incubation to the seventh week of incubation and initial egg mass in wet- and dry-incubated eggs. Linear regressions are as follow: Dry-treatment eggs: $y = -0.207x + 0.803$, $R^2 = 0.203$, $P < 0.0001$; wet-treatment eggs: $y = 0.126x + 0.140$, $R^2 = 0.107$, $P < 0.0001$.

Table 1: Results from mixed-model ANCOVAs on change in egg mass from the onset of incubation to week 7, hatching mass, and hatchling component mass at posthatching day 2

Parameter and Source	df	F	P
Change in egg mass:			
Substrate	1, 50.3	.21	.64
Initial egg mass	1, 41.1	7.11	.01
Substrate × initial egg mass	1, 41.1	19.83	<.0001
Hatching mass:			
Substrate	1, 21.4	.08	.77
Initial egg mass	1, 229	245.51	<.0001
Substrate × initial egg mass	1, 17.4	6.67	.02
Total water content:			
Substrate	1, 42.3	1.89	.08
Initial egg mass	1, 42.1	197.8	<.0001
Substrate × initial egg mass	1, 42.1	11.32	.002
Total solid content:			
Substrate	1, 153	1.45	.23
Initial egg mass	1, 138	15.07	.0002
Dry carcass mass: ^a			
Substrate	1, 4.74	59.88	.0007
Initial egg mass	1, 5.23	23.55	.004
Dry yolk sac mass: ^a			
Substrate	1, 47	.22	.64
Initial egg mass	1, 6.98	.8	.4
Substrate × initial egg mass	1, 44.6	5.61	.02

^a1997 hatchlings only.

were individually placed onto a 1 × 0.1 × 0.1-m linear race-track lined with moistened sand in a 25°C environmental chamber. The length of the track was partitioned into 0.5-m intervals. I coaxed each turtle to traverse the track as quickly as possible with pinches to the tail by using a pair of forceps. When the animal reached the end of the track, it was immediately returned to the beginning of the track, and a second traversing of the track was elicited. Maximum crawling speed (cm/s) was determined from the fastest 0.5 m traversal.

Animals from clutches collected in 1996 were reweighed after this run, then placed individually into closed still-air desiccation chambers in which the hatchlings were suspended over a CaSO_4 desiccant at 25°C (mean RH = 20% during the study). Desiccation continued for approximately 30 h after this period, resulting in a 0.74–1.30-g (mean 0.94-g) loss of body mass (ca. 12% of the mean body mass for all hatchlings). Maximum crawling speed was retested after desiccation.

Because it was unclear from the 1996 testing whether potential ontogenetic changes in appendicular muscle performance during the first few days after hatching and/or changes in weight loading could also influence terrestrial locomotor performance, animals of both incubation treatments from clutches collected in 1997 were randomly divided into two desiccation treatments:

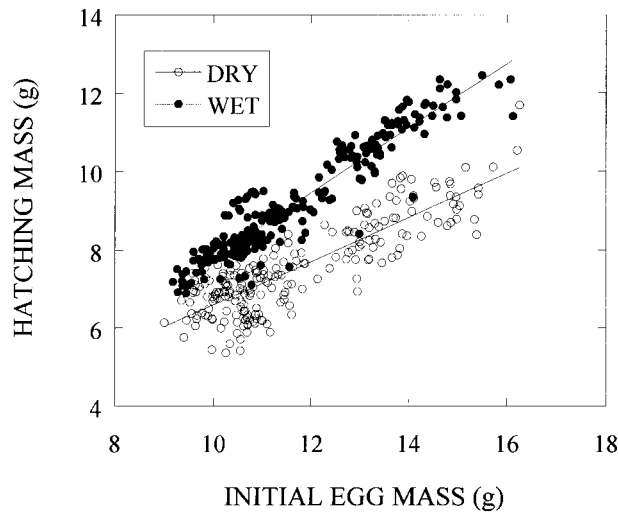


Figure 2. Variation in hatching mass (g) with initial egg mass (g) in wet- and dry-treatment hatchlings. Linear regressions are as follow: wet-treatment hatchlings: $y = 0.842x - 0.427$, $R^2 = 0.894$, $P < 0.0001$; dry-treatment hatchlings: $y = 0.560x + 0.991$, $R^2 = 0.715$, $P < 0.0001$.

a low-humidity treatment where the animals were suspended over CaSO_4 at 25°C (mean RH = 12% during the study) and a high-humidity treatment where the hatchlings were suspended over distilled water at 25°C (mean RH = 90% during the study). Animals remained in the desiccators for approximately 40 h until those in the low-humidity treatment had lost 0.99–1.78 g (mean 1.36 g, or about 16% of mean body mass) of body mass (animals in the high-humidity treatment lost from 0.03 to 0.38 g [mean 0.17 g, or about 2% of mean body mass] during this interval). Maximum crawling speed was retested after desiccation.

All analyses of data were conducted by using PROC MIXED on SAS 6.12 (SAS Institute 1996) unless otherwise noted. Random factors included in mixed models (i.e., clutch, interaction terms including clutch, and incubation pan nested within treatment) are not included in the summaries of the results.

Changes in egg mass between the start of incubation and week 7 of incubation, hatchling mass, total water content, total solid content, and wet- and dry-treatment carcass and yolk sac masses were analyzed by using ANCOVAs to examine the influence of substrate hydric condition (a fixed effect) and initial egg mass (the covariate) on hatchling mass and measures of body composition. Pan nested within treatment and clutch were included as random effects. To assess the overall relationship between changes in egg mass, body size, and body composition with initial egg mass, linear regressions of data for all individuals within a substrate moisture treatment were calculated.

The amount of water lost by the hatchlings during desiccation, the duration of desiccation, and the rate of water loss were analyzed with ANCOVAs, with incubation treatment as a

fixed effect, clutch and pan nested within treatment as random effects, and total solid content postdesiccation as a covariate. Water contents of the whole body, carcass, and yolk sacs of wet- and dry-incubated hatchlings used to assess desiccation tolerance were compared by using ANCOVAs with incubation treatment as a fixed effect, pan (nested within treatment) and clutch as random effects, and the corresponding wet mass (whole body, carcass, or yolk) as a covariate.

Because of differences in experimental design between the two study seasons, maximum crawling speed data for the 1996 and 1997 cohorts were analyzed separately in most cases. Changes in crawling speed due to dehydration effects were tested within each year with repeated-measures ANCOVAs. For the 1996 hatchlings, the analysis included incubation treatment as a fixed effect, interval as the repeated effect, and pan (nested within treatment) and clutch as random effects. For the 1997 hatchlings, incubation and desiccation treatments were tested as fixed effects, interval as the repeated effect, initial egg mass as a covariate, and clutch and pan as random effects. Where appropriate, pairwise comparisons between the least-squares means for the different treatment combinations were conducted with differences assessed at a significance level of $\alpha = 0.01$. Last, the crawling speed of all hatchlings after the desiccation period was plotted against the estimated relative water contents of the hatchlings after the desiccation period, and the data were an-

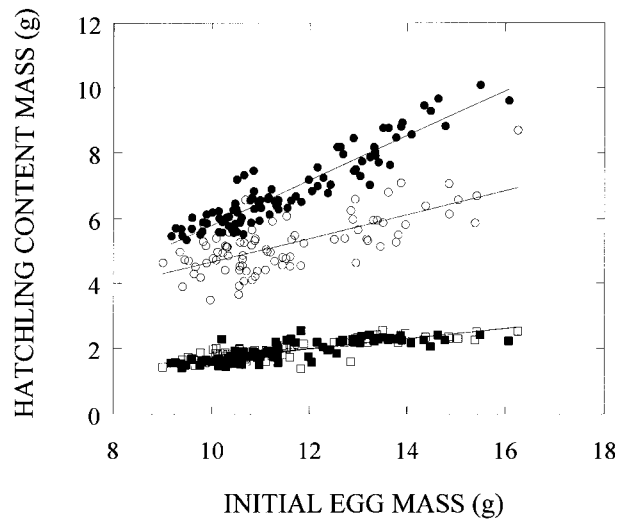


Figure 3. Variation in hatching total water and solid contents (g) with initial egg mass (g) in wet- and dry-treatment hatchlings. Filled circles denote water content of wet-treatment hatchlings ($y = 0.683x - 1.028$, $R^2 = 0.870$, $P < 0.0001$ for log-transformed data); open circles denote water content of dry-treatment hatchlings ($y = 0.364x + 1.028$, $R^2 = 0.500$, $P < 0.0001$); filled squares denote solid content of wet-treatment hatchlings ($y = 0.159x + 0.078$, $R^2 = 0.668$, $P < 0.0001$); open squares denote solid content of dry-treatment hatchlings ($y = 0.153x - 0.165$, $R^2 = 0.707$, $P < 0.0001$).

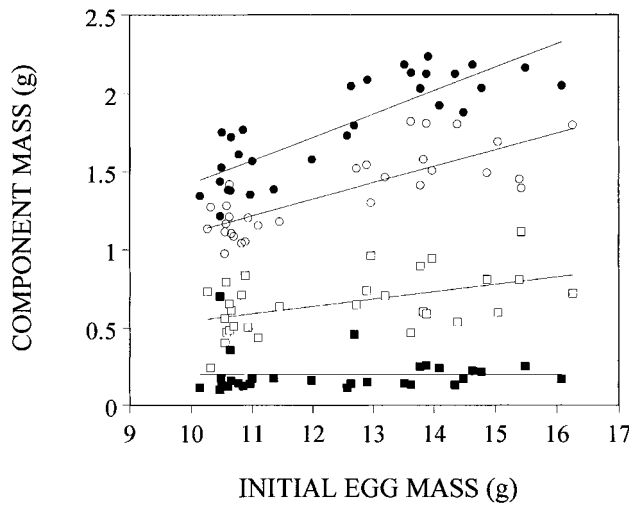


Figure 4. Variation in hatching dry carcass mass and dry yolk sac mass (g) with initial egg mass (g) in wet- and dry-treatment hatchlings. Filled circles denote dry carcass mass of wet-treatment hatchlings ($y = 0.149x - 0.065$, $R^2 = 0.710$, $P < 0.0001$); open circles denote dry carcass mass of dry-treatment hatchlings ($y = 0.107x + 0.037$, $R^2 = 0.642$, $P < 0.0001$); filled squares denote dry yolk sac mass of wet-treatment hatchlings ($y = -0.0005x + 0.205$, $R^2 = 0.00004$, $P = 0.485$); open squares denote dry yolk sac mass of dry-treatment hatchlings ($y = 0.047x - 0.080$, $R^2 = 0.225$, $P = 0.004$).

alyzed by using piecewise linear regression models (Mendenhall and Sincich 1989) formulated by using PROC GLM in SAS (SAS Institute 1989) to assess the influence of tissue hydration on locomotor performance.

Results

Egg mass changed considerably over the course of incubation (Fig. 1). Eggs in the wet substrate gained mass over the course of incubation, whereas those incubated on the dry substrate typically lost mass. A significant interaction between substrate and initial egg size also appeared to influence the degree to which egg mass changed over the course of incubation (Fig. 1; Table 1). Larger eggs tended to gain more mass in the wet substrate and lose more mass in the dry substrate than did smaller eggs.

Differences in the change in egg mass over the course of incubation between wet- and dry-incubated eggs were reflected in size differences among the hatchlings (Fig. 2; Table 1). Wet hatchlings tended to be larger than dry-treatment hatchlings for a given initial egg mass. Moreover, differences between the two treatments were observed in the scaling of hatching mass with initial egg mass. Hatching mass increased more acutely with increasing initial egg mass in the wet treatment than in the dry treatment (Fig. 2).

Substrate moisture and initial egg mass significantly influ-

enced day-2 body composition (Figs. 3, 4; Table 1). In hatchlings from both years, total water content was greater in wet-treatment hatchlings than in dry-treatment hatchlings, whereas total solid content did not differ between the two incubation conditions (Fig. 3; Table 1). In addition, the scaling of water content with initial egg mass differed between wet- and dry-treatment hatchlings. Water content increased more with increasing initial egg mass in the wet treatment than in the dry treatment. Although the total solid content of hatchlings did not differ between the two incubation conditions, the allocation of dry mass in day-2 hatchlings from the 1997 cohort was influenced by substrate moisture (Fig. 4; Table 1). Hatchlings from eggs incubated on the wet substrate had greater dry carcass masses and smaller dry yolk sac masses than did their dry-treatment counterparts.

The ability of the hatchlings to tolerate desiccating conditions differed between animals from the two incubation treatments (Tables 2, 3). With similar size-adjusted dehydration rates between the two treatments, wet hatchlings lost more water before loss of righting ability, and sustained their righting ability for a longer period of time, than did dry-treatment hatchlings. Curiously, the whole-body water contents of wet-treatment hatchlings were somewhat higher at loss of righting ability than were those of dry-treatment hatchlings, even after correction for differences in body size.

Forced crawling speeds for the 1996 cohort were not significantly influenced by initial egg mass ($F_{1,161} = 0.53$, $P = 0.47$). Consequently, the data were reanalyzed by using repeated-measures ANOVA (Table 4). Speeds were significantly higher in wet-treatment hatchlings than in their dry-treatment counterparts (Fig. 5A; Table 4), both before and after desiccation. The degree of desiccation itself did not appear to influence locomotor performance for this cohort, as velocity after desiccation did not differ from that before desiccation.

Table 2: Least-squares means (\pm SEM) for measures of desiccation tolerance, rate of water loss, and water content of hatchling components at loss of righting ability in wet- and dry-incubated hatchlings

Parameter	Wet	Dry
Water loss (g)	4.064 \pm .221	1.629 \pm .191
Time to loss of righting (h)	69.00 \pm 5.18	31.22 \pm 4.48
Rate of water loss (g/h)060 \pm .003	.052 \pm .003
Whole-body water content (g)	4.003 \pm .060	3.433 \pm .062
Carcass water content (g)	3.627 \pm .147	3.134 \pm .156
Yolk sac water content (g)288 \pm .146	.351 \pm .119

Table 3: Results from mixed-model ANCOVAs for measures of desiccation tolerance, rate of water loss, and water content of hatchling components at loss of righting ability in wet- and dry-incubated hatchlings

Parameter and Source	$F_{1,3}$	P
Water loss (g):		
Substrate	68.64	.004
Total solid content	11.28	.04
Time to loss of righting (h):		
Substrate	30.17	.01
Total solid content	2.04	.25
Rate of water loss (g/h):		
Substrate	3.82	.15
Total solid content	29.39	.01
Whole body water content (g):		
Substrate	46.37	.007
Total solid content	202.08	.0008
Carcass water content (g):		
Substrate	6.2	.09
Dry carcass mass	24.66	.02
Yolk sac water content (g):		
Substrate08	.8
Dry yolk sac mass	4.57	.12

In contrast to the relatively simple model derived for the 1996 hatchlings, a rather complex array of factors influenced maximum crawling speed of 1997 hatchlings (Fig. 5B; Table 4). As in the 1996 cohort, initial egg mass did not significantly influence crawling speed ($F_{1,66} = 0.06$, $P = 0.80$), thus the covariate was removed and the analysis reverted to an ANOVA design. Speed was significantly influenced by a substrate moisture \times humidity condition \times interval interaction. Whereas crawling speeds did not differ among the treatments before desiccation, dry-treatment hatchlings desiccated at low humidity were significantly slower than both dry-treatment hatchlings that were desiccated under high-humidity conditions and wet-treatment hatchlings desiccated at low humidity ($P < 0.01$, least-squares means test). A plot of crawling speed of all hatchlings after desiccation against their estimated post-desiccation relative water contents (Fig. 6) suggests that crawling speed is influenced by the level of tissue dehydration. Crawling speed after desiccation speed dropped precipitously as body water content decreased below 72.1% total body mass.

Discussion

The mass of eggs in the two substrate moisture levels changed in a manner consistent with changes observed for eggs incubated under similar thermal and hydric conditions in other studies (Packard et al. 1980; Morris et al. 1983). Wet-treatment eggs generally gained mass throughout the course of incubation,

whereas dry-treatment eggs showed marked decreases in mass by the end of incubation. Moreover, the degree to which egg mass changed during incubation was associated with the size of the eggs. Larger eggs tended to show greater variation in the amount of water gained or lost over the course of incubation than did smaller eggs.

The differences in the change in mass of the eggs associated with initial egg size and level of hydration during incubation resulted in pronounced differences in the scaling of hatchling mass and hatchling composition with initial egg mass between the two treatments. Not only did larger hatchlings emerge from eggs incubated on wet substrates, but greater increases in hatchling mass accompanied increases in initial egg mass in the wet-incubation treatment compared to those in the dry-incubation treatment. This, in turn, reflects differences in the scaling of the water contents of the hatchlings between the two treatments: not only did wet-treatment hatchlings typically have more water within their bodies than did dry-treatment hatchlings, but their water contents increased more acutely with initial egg mass than did those of dry-treatment hatchlings.

The greater proportion of water contents of wet-treatment hatchlings enhanced their ability to survive under desiccating conditions. Despite having slightly higher water contents at loss of righting ability, wet-treatment hatchlings were able to lose more water overall and withstood exposure to desiccating conditions longer before losing their ability to right themselves than their dry-treatment counterparts. Though the desiccating conditions used in this study were extreme, comparable relative humidities may be encountered for periods lasting several hours in more open areas traversed by hatchlings in the field (M. S. Finkler, D. L. Knickerbocker, and D. L. Claussen, unpublished data), suggesting greater water contents may enhance the ability of the hatchlings to survive prolonged exposure to dehydrating conditions under field conditions.

Table 4: Results from mixed-model repeated-measures ANOVAs on maximum crawling speed (cm/s)

Year and Source	F	P
1996:		
Substrate	8.46 ^a	.03
Interval57 ^b	.45
1997:		
Interval	1.29 ^c	.26
Substrate	6.68 ^a	.04
Humidity	2.29 ^c	.14
Substrate \times interval	1.75 ^c	.19
Humidity \times interval57 ^c	.45
Substrate \times humidity	1.96 ^c	.21
Substrate \times humidity \times interval	2.12 ^c	.006

^a $df = 1, 6$.

^b $df = 1, 162$.

^c $df = 1, 67$.

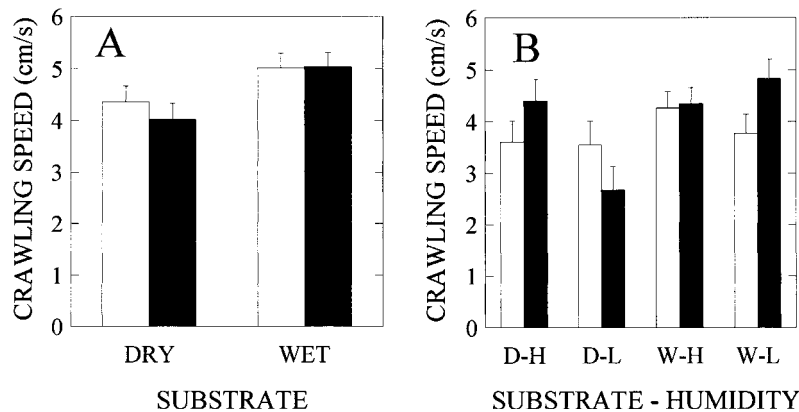


Figure 5. A, Crawling speed (cm/s) before and after desiccation for 1996 hatchlings from eggs incubated on wet and dry substrates. B, Crawling speed (cm/s) before and after the desiccation in either high or low humidity conditions of 1997 hatchlings from eggs incubated on wet or dry substrates. Data are presented as least-squares means + SEM. White columns represent velocity before desiccation; black columns represent velocity after desiccation. D-H = dry-incubation condition, high-humidity desiccation; D-L = dry-incubation condition, low-humidity desiccation; W-H = wet-incubation condition, high-humidity desiccation; W-L = wet-incubation condition, low-humidity desiccation.

In this study, I examined maximum crawling speed as a measure of animal performance and an indicator of the influence of desiccation on the physiological capacity of the hatchlings. Miller et al. (1987) and Miller (1993) found that maximum crawling speed was higher in day 7 hatchlings from eggs incubated under wet conditions than in those from eggs incubated under dry conditions and suggested that the difference in velocity was primarily due to the dry-treatment animals suffering from the effects of dehydration. My findings confirm

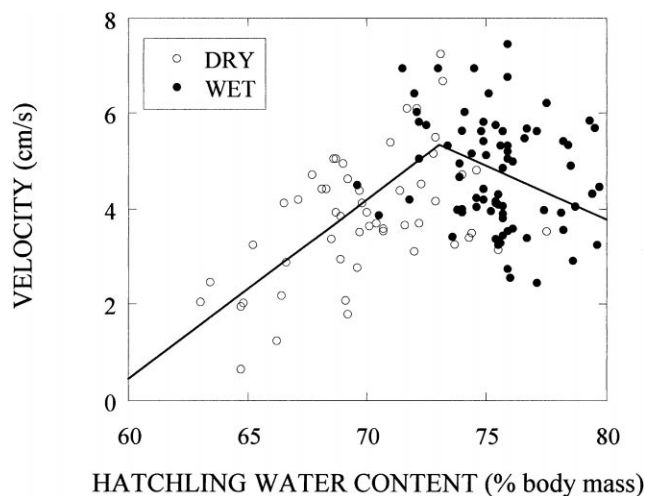


Figure 6. Variation in the forced crawling speed of wet- and dry-incubated hatchlings after desiccation with estimated postdesiccation water contents of the hatchlings. Line represents the following piecewise regression model: $y = -21.884 + 0.373x_1 - 0.481x_2$ (where $x_2 = x_1 - 72.1\%$ if $x_1 > 72.1\%$, 0 otherwise), $R^2 = 0.282$, $P < 0.0001$.

this assertion that tissue hydration has considerable influence on locomotor performance. Moreover, the findings of the present study show that there is a level of tissue hydration where performance is maximized. Hatchling performance dropped considerably as the tissues were desiccated below this optimal level, perhaps due to hyperosmolarity and hypovolemia inhibiting circulatory function (Shoemaker et al. 1992). In contrast to Miller et al. (1987) and Miller (1993), however, my data indicate that hatchlings from eggs incubated under wet conditions do not necessarily have greater locomotor performance than do hatchlings from eggs incubated under dry conditions. Hatchlings from both treatments appeared to perform equally well at equivalent body water contents. Under desiccating conditions, however, wet-treatment hatchlings were able to tolerate greater losses of water before performance levels began to drop from the effects of dehydration. Thus, hatchlings from eggs incubated under dry conditions are at a greater risk of dehydration than are their counterparts emerging from eggs incubated under wetter conditions.

The findings of this study suggest that differential water availability during incubation may influence the survival of neonatal snapping turtles under certain conditions, based upon their ability to withstand dehydration during the nest-to-water migration. Hatchlings from eggs incubated under dry conditions have less water within their bodies. Therefore, these hatchlings are more limited in the amount of water they can lose before the effects of dehydration begin to affect whole body performance adversely, and thus would succumb sooner to dehydrating conditions than would hatchlings from eggs incubated on wet substrates if such conditions are present. Hatchlings emerging from dry nests may offset this increased sensitivity of susceptibility to dehydration by restricting movement to areas that

may aid in conservation of water loss but may hinder rapid movement and/or restricting activity to time periods that allow movement without high rates of evaporative water loss (Knickerbocker 1997). Prolonging the nest-to-water migration, however, may increase the time the animals are exposed to the risk of discovery by terrestrial predators. Thus, either directly or indirectly, differences in the water contents of the hatchlings may influence the chance those hatchlings have of successfully reaching the water.

Caution must be taken in the application of these findings to the survival of hatchlings under natural conditions. For increased body water content to be advantageous to the neonate, water must be a potential limiting factor within the environment. Snapping turtles have the largest distribution of any freshwater turtle species in North America (Iverson 1992), and hydric climate may vary considerably among different regions within the species range (National Oceanic and Atmospheric Administration 1985). This variation in hydric conditions needs to be considered in assessing whether water availability during incubation has an appreciable influence on posthatching success in a given population. In addition, the distance from nest site to water is also an important consideration in evaluating the relationship of hatchling water content to hatchling survival, as dehydration is not likely to be a problem for the hatchlings if they can easily reach the water before dehydration adversely affects performance. Variation in hatchling water content may influence hatchling survival appreciably only during prolonged migrations under relatively dry conditions.

In summary, water availability during incubation influences the amount of water present within the bodies of the hatchlings. This water, in turn, likely influences the ability of hatchlings to survive prolonged nest-to-water migrations under dehydrating conditions. Thus, the amount of water available from maternal and environmental sources during incubation may have an appreciable influence on hatchling fitness for populations of *Chelydra serpentina* inhabiting more xeric regions of the species' range.

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Literature Cited

- Bobyne M.L. and R.J. Brooks. 1994. Interclutch and interpopulation variation in the effects of incubation conditions on sex, survival and growth of hatchling turtles (*Chelydra serpentina*). *J Zool (Lond)* 233:233–257.
- Brooks R.J., M.L. Bobyne, D.A. Galbraith, J.A. Layfield, and E.G. Nancekivell. 1991. Maternal and environmental influences on growth and survival of embryonic and hatchling snapping turtles (*Chelydra serpentina*). *Can J Zool* 69:2667–2676.
- Ernst C.H. 1968. Evaporative water loss relationships of turtles. *J Herpetol* 2:159–161.
- Ernst C.H. and R.W. Barbour. 1989. *Turtles of the World*. Smithsonian, Washington, D.C.
- Ernst C.H., J.E. Lovich, and R.W. Barbour. 1994. *Turtles of the United States and Canada*. Smithsonian, Washington, D.C.
- Feder M.E. and P.L. Londos. 1984. Hydric constraints upon foraging in a terrestrial salamander, *Desmognathus ochrophaeus* (Amphibia: Plethodontidae). *Oecologia* 64:413–418.
- Finkler M.S. 1997. Impact of egg content on post-hatching size, body composition, and performance in the common snapping turtle (*Chelydra serpentina*). *Chelonian Conserv Biol* 2: 452–455.
- Froese A.D. and G.M. Burghardt. 1974. Food competition in captive juvenile snapping turtles, *Chelydra serpentina*. *Anim Behav* 22:735–740
- Iverson J.B. 1992. A revised checklist with distribution maps of the turtles of the world. Privately published, Richmond, Ind.
- Janzen F.J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. *Ecology* 74:332–341.
- Knickerbocker D.L. 1997. Effects of hydric conditions during the incubation of common snapping turtle (*Chelydra serpentina serpentina*) eggs on hatchling evaporative water loss and microhabitat selection during a simulated nest exodus. BA diss. Kalamazoo College, Kalamazoo, Mich.
- Mendenhall W. and T. Sincich. 1989. *A Second Course in Business Statistics: Regression Analysis*. 3d ed. Dellen, San Francisco.
- Miller K. 1993. The improved performance of snapping turtles (*Chelydra serpentina*) hatched from eggs incubated on a wet substrate persists through the neonatal period. *J Herpetol* 27:233–236.
- Miller K. and G.C. Packard. 1992. The influence of substrate

- water potential during incubation on the metabolism of embryonic snapping turtles. *Physiol Zool* 65:172–187.
- Miller K., G.C. Packard, and M.J. Packard. 1987. Hydric conditions during incubation influence locomotor performance of hatchling snapping turtles. *J Exp Biol* 127:401–412.
- Morris K.A., G.C. Packard, T.J. Boardman, G.L. Paukstis, and M.J. Packard. 1983. Effect of the hydric environment on growth of embryonic snapping turtles (*Chelydra serpentina*). *Herpetologica* 39:272–285.
- National Oceanic and Atmospheric Administration. 1985. *Climate of the States*. 3d ed. Gale Research, Detroit.
- Packard G.C. 1991. Physiological and ecological importance of water to embryos of oviparous reptiles. Pp. 213–228 in D.C. Deeming and M.J.W. Ferguson, eds. *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles*. Cambridge University Press, New York.
- Packard G.C., M.J. Packard, K. Miller, and T.J. Boardman. 1987. Influence of moisture, temperature and substrate on snapping turtle eggs and embryos. *Ecology* 68:983–993.
- . 1988. Effects of temperature and moisture during incubation on carcass composition of hatchling snapping turtles. *J Comp Physiol B* 158:117–125.
- Packard G.C., T.L. Taigen, M.J. Packard, and T.J. Boardman. 1980. Water relations of pliable-shelled eggs of common snapping turtles (*Chelydra serpentina*). *Can J Zool* 58:1404–1411.
- Robinson C. 1989. Orientation and survival of hatchlings and reproductive ecology of the common snapping turtle (*Chelydra serpentina*) in southern Quebec. MSc diss. McGill University, Montreal.
- SAS Institute. 1989. *SAS/STAT User's Guide, Version 6*. SAS Institute, Cary, N.C.
- . 1996. *SAS/STAT Software: Changes and Enhancements through Release 6.11*. SAS Institute, Cary, N.C.
- Shoemaker V.H., S.S. Hillman, S.D. Hillyard, D.C. Jackson, L.L. McClanahan, P.C. Withers, and M.L. Wygoda. 1992. Exchange of water, ions and respiratory gases in terrestrial amphibians. Pp. 125–150 in M.E. Feder and W.W. Burggren, eds. *Environmental Physiology of the Amphibians*. University of Chicago Press, Chicago.
- Wilhoft D.C. 1986. Eggs and hatchling components of the snapping turtle (*Chelydra serpentina*). *Comp Biochem Physiol A* 84:483–486.