

Effects of Hydric Conditions during Incubation on Body Size and Triglyceride Reserves of Overwintering Hatchling Snapping Turtles (*Chelydra serpentina*)

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Many studies have suggested that incubating eggs under wet conditions may lead to increased fitness in snapping turtles immediately following emergence from the nest, but little is known of the consequences of associated elevated embryonic yolk use on the energetic reserves of the hatchlings during the first winter. In this experiment, we measured the size, dry mass, and triglyceride contents of the carcasses and yolk sacs of hatchlings from eggs incubated under wet (–50 kPa) and dry (–300 kPa) conditions at three time intervals: at one week posthatching (late August); at the onset of an overwintering period following 10 weeks of ad libitum feeding (early November); and at the end of overwintering (late March). Although initially smaller, dry hatchlings demonstrated greater increases in live mass during the autumn than did wet hatchlings, eliminating differences in live mass by early November. Dry carcass masses were greater in wet-treatment hatchlings at one week posthatching but not in either November or March. Dry yolk sac mass was greater in dry hatchlings only at one week posthatching. Total triglyceride contents were higher in dry hatchlings than in wet hatchlings at all intervals. These findings suggest that possible preliminary survival advantages of hatchlings emerging from wet nests ultimately may be tempered by decreased energy reserves during the first winter.

DIFFERENCES in water availability during incubation have a pronounced influence on the size and body composition of hatchling turtles that develop in flexible-shelled eggs. Increased water availability from the nest substratum appears to increase the rate of metabolism of yolk by the embryo (reviewed in Packard, 1999). Larger hatchlings with greater dry carcass masses, greater water contents, and reduced yolk sac contents are produced from wetter nest environments.

Hatchlings of aquatic species that emerge from relatively moist nests have certain attributes that may enhance their chances of survival during dispersion from the nest. A number of studies have asserted this notion based largely upon laboratory observations of increased body size at hatching, increased locomotor performance, and greater body hydration (e.g., Miller et al., 1987; Finkler, 1999), with a handful of field-based observations providing some support (Janzen, 1993; Finkler et al., 2000; but see Congdon et al., 1999). However, if there are indeed preliminary survival advantages associated with increased growth during embryonic development, these advantages may be offset in the long term by associated decreases in amounts of residual yolk and body fat that help support the hatchling during the neonatal period (Congdon and Gibbons, 1990; Bobyn and

Brooks, 1994; Tucker et al., 1998). In northern regions, the hatchlings of many species of aquatic turtle (e.g., *Chrysemys picta*, *Trachemys scripta*, *Kinosternon flavescens*) overwinter either in the nest or terrestrial hibernacula and, therefore, must rely solely on stored energy reserves for maintenance metabolism during this period (Congdon et al., 1983; Costanzo et al., 1995; Tucker et al., 1998). Moreover, hatchlings of northern species that do emerge from the nest before winter (e.g., *Chelydra serpentina*, *Apalone spinifer*) may have only limited opportunity to feed prior to entering hibernation (Gibbons and Nelson, 1978; Obbard, 1983). Thus, the impact of water availability during incubation on the amount of energy stored in the body of the hatchlings could have considerable influence on hatchling survivorship during overwintering (Nagle et al., 1998). Although a handful of recent studies have examined this influence in the terrestrially overwintering hatchlings of *T. scripta* (Tucker et al., 1998; Filoramo and Janzen, 1999; Tucker and Paukstis, 1999), a similar examination in species that migrate to the water prior to winter (and thus may have a limited opportunity to feed prior to entering hibernation) has not been conducted.

In the present study, we examined the influence of nest substrate moisture during incubation on body size, body composition, and total

triglyceride content of hatchling snapping turtles (*C. serpentina*) from a population in southeast Michigan during the first autumn and winter of life. Almost all hatchlings in this region emerge from their nests during the period from late August to early October (Congdon et al., 1987) and, thus, may be able to supplement their energy reserves through feeding prior to hibernation. We tested two alternate hypotheses: (1) that larger hatchlings from wet incubation conditions would be able to maintain their greater size relative to hatchlings from dry incubation conditions through the winter by feeding prior to overwintering; and (2) that the difference in size between wet-incubated and dry-incubated hatchlings would not be sustained during overwintering because of increased metabolic cost associated with larger size and reduced energy reserves.

MATERIALS AND METHODS

Five freshly laid clutches of snapping turtle eggs (clutch sizes 28–50 eggs, 184 eggs total) were collected from nests in Washtenaw County, Michigan (42°N, 84°W), on 31 May and 1 June 1998, and were transported to Miami University, Oxford, Ohio, on 1 June 1998. Eggs in each clutch were weighed, and randomly divided in equal numbers into two substrate moisture treatments: a wet incubation treatment and a dry incubation treatment. We chose to incubate the eggs half-buried in vermiculite substrates. Although some have argued that such incubation procedures do not effectively simulate natural incubation conditions (e.g., Ackerman, 1991), similar techniques have been used for the bulk of “wetter is better” studies, and, thus, our use of this technique will permit more direct comparison of our findings with those from prior research. Moreover, incubation in natural nests of varying degrees of wetness can lead to similar phenotypic variation in the hatchlings as that observed in eggs incubated in vermiculite (Packard et al., 1999; Packard and Packard, 2000).

Eggs from each clutch within each treatment were randomly divided between two nest boxes. Nest boxes contained vermiculite substrates of 1.11 ml water/g vermiculite in the wet treatment and 0.18 ml/g in the dry treatment. Water potentials were approximately -50 kPa and -300 kPa for the wet and dry treatments, respectively, based upon readings from a Wescor 33HT dew point microvoltmeter with a Wescor C-52 sample chamber. One nest box for each treatment was placed into each of a pair of Hova Bator 2362N incubators, and the eggs

were incubated at 25 C. Weekly, the eggs were weighed, enough water was added to the nest boxes to restore the weight of the substrate (to replace water lost by evaporation or water uptake by the eggs), and the nest boxes were rotated between the two incubators. Eggs and incubators were transported to Indiana University Kokomo, Kokomo, Indiana, on 1 August 1998 for the completion of incubation.

Hatchlings emerged from the eggs between 17 and 20 August 1998. The hatchlings were weighed to the nearest 0.001 g and placed in individual containers during the first week post-hatching until yolk sacs were absorbed. Hatching success was high for both treatments, with 81.4% and 85.2% hatching success in the wet and dry treatments, respectively (within clutch hatching success ranged from 58.3–93.8% in the wet treatment and 58.3–100.0% in the dry treatment). Most hatchlings were needed for use in other studies, limiting the number of animals available for this one. At day 7 posthatching, six hatchlings from each substrate treatment within each clutch were selected for inclusion in this study (i.e., 30 wet and 30 dry hatchlings). The hatchlings were weighed and their carapace lengths measured with vernier calipers to the nearest 0.1 mm, and two randomly selected hatchlings from each treatment within each clutch (10 wet and 10 dry hatchlings total) were anesthetized with tricaine methanesulfonate (MS-222) and sacrificed via decapitation followed by cranial pithing. The yolk sacs of the hatchlings were removed, and both they and the carcasses were dried in a 50 C drying oven to a constant mass. Dried yolk sacs and carcasses were homogenized in enough distilled water to produce 50 ml of carcass homogenate and 5 ml of yolk sac homogenate. A 1.0 ml sample of the homogenate was then added to 2.0 ml of chilled 0.6 N perchloric acid, and the mixture was shaken vigorously for 2 min to deproteinate the homogenate. After neutralization with 1 ml of 1.0 M KHCO_3 , the homogenate was analyzed for total triglyceride content using a glycerol kinase/glycerol phosphate oxidase/peroxidase colorimetric technique (Sigma 337).

Remaining hatchlings were placed individually into plastic shoeboxes filled with water and housed in an incubator with a 12:12 L:D photoperiod and a 25:20 C temperature cycle. Animals were offered commercial catfish feed ad libitum for a 24-h period three times per week beginning at Day 14 posthatching and ending on 28 October 1998. Beginning on 15 October 1998, the temperature was gradually reduced daily (by approximately 0.9 C day and 0.7 C night) until a constant temperature of 4 C was

obtained on 7 November 1998. Lighting was also gradually reduced until 1 November, after which the animals were housed entirely in the dark.

Two randomly selected hatchlings from each treatment within each clutch (10 Wet and 10 Dry total) were sacrificed on 7 November 1998 for determination of body composition and triglyceride content as above. Remaining hatchlings (10 wet and 10 dry) were maintained at 4 C until 27 March 1999, whereupon they were sacrificed for determination of body composition and triglyceride content.

Hatchling size, body component mass, and triglyceride contents were analyzed using mixed-model analyses of covariance conducted with the MIXED procedure on SAS 8.0 (Statistical Analysis Systems Institute, Inc., Cary, NC, 1996, unpubl.). In these analyses incubation treatment and sampling interval (month) were fixed effects, nest box and clutch were random effects, and initial egg mass was the covariate. The MIXED procedure correctly estimates covariance parameters for random effects but does not assess significance levels for this type of effect (Packard et al., 1999; Tucker and Paukstis, 1999). As such, differences among clutches and nest boxes are not evaluated below. Where appropriate, pairwise comparisons between least-squares means were evaluated based upon *t*-tests with Bonferroni-adjusted pairwise error rates of 0.017.

RESULTS

Changes in egg mass over the course of incubation were assessed by comparing initial egg mass with egg mass at the ninth week of incubation (approximately two weeks prior to hatching). There was no difference between the two treatments in the mass of viable eggs at the onset of incubation (dry treatment egg mass (least-squares mean \pm SEM) = 11.720 ± 0.428 g; Wet treatment egg mass = 11.616 ± 0.428 g; $t = 1.62$, $df = 177$, $P = 0.204$). However, mean mass of wet treatment eggs increased over the course of incubation, whereas dry treatment eggs lost mass by the ninth week of incubation (dry treatment egg mass = 10.044 ± 0.064 g; wet treatment egg mass = 12.833 ± 0.065 g; $t = 30.38$, $df = 179$, $P < 0.0001$).

Hatchlings from the wet incubation treatment were more massive and had greater carapace lengths at hatching than did hatchlings emerging from dry-incubated eggs (Tables 1–2). Although the difference in carapace length between the two treatments was sustained over the study period, differences in live mass between

the treatments disappeared by the beginning of overwintering, primarily because of a much greater increase in the body mass of dry-treatment hatchlings during this time period compared to that of their wet-treatment counterparts.

Changes in wet carcass mass over the course of the study reflected changes in live mass (Tables 1–2). However, the dry mass of the carcasses decreased during the study. Although the wet-treatment hatchlings had initially greater dry carcass masses than did dry-treatment hatchlings, greater decreases in dry mass in wet hatchlings led to no difference in dry mass between the two treatments by the beginning of hibernation. Both wet and dry yolk sac masses were greater in dry-treatment hatchlings at one week posthatching, but no difference was detected in these measures at later intervals.

Carcass triglyceride contents were greater in dry-incubated hatchlings than in wet incubated hatchlings at all time intervals (Tables 1–2). Yolk sac triglyceride contents were significantly higher in dry-treatment hatchlings than in wet-treatment hatchlings at one week posthatching, but there was no difference in yolk sac triglycerides between the two incubation treatments in either November or March. Total triglyceride content (carcass + yolk sac) was significantly higher in dry-treatment hatchlings than in wet treatment hatchlings at all intervals.

There was no evidence of food consumption by the hatchlings during the two months of ad libitum food availability prior to overwintering. No hatchlings were observed feeding, food pellets were typically whole when removed from the containers, and no solid feces were found during cleaning.

DISCUSSION

Chelydra serpentina has been one of the most extensively utilized species in research on the effects of hydric conditions on embryonic development in the flexible-shelled eggs of reptiles (see Packard, 1999). However, only a handful of studies have examined the effects of variable water availability during incubation on post-natal performance and survival beyond the first few weeks post-hatching (e.g., Brooks et al., 1991; McKnight and Gutzke, 1993; Bobyne and Brooks, 1994), and those that did typically reared the animals at higher temperatures (20 C or above) than the hatchlings would have experienced during overwintering in northern populations. Maintenance of such abnormally high temperatures would have a large influence on hatchling metabolism, energetics, and du-

TABLE 1. SIZE, COMPONENT MASSES, AND TRIGLYCERIDE CONTENTS OF HATCHLING SNAPPING TURTLES AT ONE WEEK POSTHATCHING, AT THE ONSET OF OVERWINTERING, AND AT THE END OF OVERWINTERING. Data are presented as least-squares means \pm SEM.

Parameter	Month	Incubation treatment	
		Wet	Dry
Live mass (g) ^a	August	7.718 \pm 0.249	6.578 \pm 0.248
	November	8.172 \pm 0.249	7.717 \pm 0.249
	March	8.064 \pm 0.257	7.767 \pm 0.250
Carapace length (mm) ^a	August	28.0 \pm 0.2	27.3 \pm 0.2
	November	28.3 \pm 0.2	27.6 \pm 0.2
	March	28.3 \pm 0.2	27.6 \pm 0.2
Wet carcass mass (g)	August	7.560 \pm 0.241	6.339 \pm 0.240
	November	8.119 \pm 0.241	7.692 \pm 0.240
	March	8.045 \pm 0.248	7.750 \pm 0.242
Dry carcass mass (g)	August	1.672 \pm 0.048	1.549 \pm 0.048
	November	1.275 \pm 0.048	1.261 \pm 0.048
	March	1.179 \pm 0.049	1.206 \pm 0.048
Wet yolk sac mass (g)	August	0.156 \pm 0.166	0.238 \pm 0.166
	November	0.021 \pm 0.166	0.025 \pm 0.166
	March	0.014 \pm 0.173	0.022 \pm 0.167
Dry yolk sac mass (g)	August	0.054 \pm 0.006	0.098 \pm 0.006
	November	0.004 \pm 0.006	0.006 \pm 0.006
	March	0.002 \pm 0.007	0.004 \pm 0.006
Carcass triglycerides (mg)	August	95.03 \pm 5.77	118.41 \pm 5.77
	November	23.79 \pm 5.77	38.49 \pm 5.77
	March	10.67 \pm 6.08	27.74 \pm 5.79
Yolk sac triglycerides (mg)	August	9.07 \pm 0.98	14.55 \pm 0.97
	November	0.28 \pm 0.97	1.04 \pm 0.97
	March	0.11 \pm 1.03	0.53 \pm 0.98
Total triglycerides (mg)	August	104.10 \pm 6.06	132.96 \pm 6.06
	November	24.07 \pm 6.06	39.59 \pm 6.06
	March	10.77 \pm 6.39	28.27 \pm 6.08

^a Similar differences in live mass and carapace length between wet- and dry-treatment animals were observed in August and November for animals culled in March.

ration of feeding during the neonatal period (see Parmenter, 1980) that could limit the applicability of the results to these animals in their natural environment.

Under environmental conditions similar to those encountered by the hatchlings in nature, differences in body mass resulting from differences in hydric conditions during incubation were reduced by the onset of overwintering, likely because of increased water uptake by dry-incubated hatchlings. Initial differences in carapace length persisted through the first winter; hatchlings that were larger at nest emergence remained larger by the end of their first winter. However, it is unlikely that the relatively small difference in mean carapace length (\sim 0.7mm) would have an appreciable influence on survivorship based upon size (e.g., gape limited predation, etc.). The greater reduction in dry mass observed in wet-incubated hatchlings was likely because of increased use of energy substrates stored in their tissues, whereas dry-incubated

hatchlings had larger yolk sac contents from which to derive their metabolic fuel, thus decreasing reliance on energy sources stored in the carcass.

Changes in dry carcass mass observed in this study were consistent with those observed by Costanzo et al. (2000) for *C. serpentina* and *C. picta* from western Nebraska but contrary to changes observed in overwintering *T. scripta* from southern Illinois (Tucker et al., 1998; Filoramo and Janzen, 1999) in which dry carcass mass was higher in nestlings after overwintering than in newly hatched animals. Differences in changes of dry carcass mass over time between *C. serpentina* and *T. scripta* are likely because of differences in residual yolk content at hatching, with *T. scripta* hatchlings of comparable live masses to the *C. serpentina* hatchlings in this study having dry yolk sac masses four to seven times as large (Tucker et al., 1998; Filoramo and Janzen, 1999). Thus, although *T. scripta* hatchlings may have ample yolk to support not only main-

TABLE 2. RESULTS FROM MIXED-MODEL REPEATED-MEASURES ANCOVAs ON THE SIZE, COMPONENT MASS, AND TRIGLYCERIDE CONTENT OF HATCHLING SNAPPING TURTLES AT ONE WEEK POSTHATCHING, AT THE ONSET OF OVERWINTERING, AND AT THE END OF OVERWINTERING.

Parameter	Source	df	F	P
Live mass	Substrate	1,50.3	16.74	0.0002
	Month	2,50.3	11.49	<0.0001
	Initial egg mass	1,25.1	5.26	0.03
Carapace length	Substrate	1,50.7	17.57	<0.0001
	Month	2,50.7	1.61	0.47
	Initial egg mass	1,26.3	5.14	0.03
Wet carcass mass	Substrate	1,48.3	18.43	<0.0001
	Month	2,48.4	17.91	<0.0001
	Substrate × month	2,48.1	3.72	0.03
	Initial egg mass	1,23.3	6.69	0.02
	Substrate × month	2,48.3	3.42	0.04
Wet yolk sac mass	Substrate	1,41.4	5.50	0.02
	Month	1,50.3	6.11	0.02
	Initial egg mass	2,50.4	84.97	<0.0001
Dry yolk sac mass	Substrate	1,9.78	0.00	0.99
	Month	1,48.4	10.22	0.002
	Substrate × month	2,48.5	94.34	<0.0001
	Initial egg mass	2,48.1	7.89	0.001
Carcass triglycerides	Substrate	1,7.2	0.20	0.67
	Interval	1,54	15.37	0.0003
	Initial egg mass	2,54	136.95	<0.0001
Yolk sac triglycerides	Substrate	1,54	2.49	0.12
	Month	1,49.1	7.74	0.008
	Substrate × month	2,49.2	90.07	<0.0001
	Initial egg mass	2,48.9	4.23	0.02
Total triglycerides	Substrate	1,6.0	2.91	0.14
	Month	1,54	17.28	<0.0001
	Initial egg mass	2,54	158.16	<0.0001

tenance metabolism but also soft tissue growth during the winter, *C. serpentina* hatchlings may need to rely more upon energy stored within their tissues (fat bodies, liver glycogen, etc.) to support them during overwintering. However, potentially greater thermal fluctuations in a terrestrial nest environment, coupled with possible desiccating conditions in the nest, may necessitate having a larger supply of yolk in species that overwinter on land than in species that overwinter in water, both for maintenance energy requirements and as a source of metabolic water (Costanzo et al., 2000).

With the caveats that food consumption was not directly monitored in this study and that the type of food presented to the hatchlings (e.g., inert vs moving) could have influenced feeding behavior, the observed decreases in dry carcass mass and yolk sac mass, coupled with the failure to observe direct feeding or other evidence of solid food consumption, suggest that hatchling snapping turtles from this population may not feed extensively prior to their first winter even

if food is available. Rather, the hatchlings relied considerably on stored nutrients both within the yolk sac and within their carcasses. Consequently, the lower triglyceride contents and higher metabolic rates of hatchlings from wet nests (Miller and Packard, 1992) may place them at greater risk of starvation during overwintering in comparison to their dry nest counterparts, given that the low metabolic rate of hibernating turtles (Gatten, 1980; Graham and Guimond, 1995) may mean that even small differences in triglyceride content could lead to large differences (weeks or possibly months) in the amount of time the turtle can sustain itself. Further investigation of the possible effects of the hydric environment during incubation on feeding behavior, as well as temperature effects on the metabolism and energy budgets of overwintering hatchling snapping turtles, is warranted.

Results from this study lend support to the second of the two alternate hypotheses proposed: that the difference in size between wet-

incubated and dry-incubated hatchlings is not sustained during overwintering and that larger size at hatching is associated with reduced energy reserves in the form of residual yolk and body fat at the start of overwintering. Thus, if indeed increased moisture during incubation bestows certain benefits on snapping turtle hatchlings during the immediate neonatal period, there may also be a cost associated with incubation under moist conditions in the reduction of stored energy available to the hatchling during the first winter posthatching. This cost could temper the proposed benefits for survival derived from wet incubation conditions and may ultimately attenuate any influence that size-based selection may have on the survivorship of juvenile snapping turtles (Congdon et al., 1999).

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