Geographic variation in snapping turtle (*Chelydra serpentina serpentina*) egg components across a longitudinal transect

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Abstract: Common snapping turtles (*Chelydra serpentina serpentina*) have an extensive range across North America, inhabiting aquatic habitats in diverse thermal and hydric climates. Although geographic variation in reproductive characters such as female size, clutch size, and egg mass have been investigated, little is known about geographic variation in egg components. In this study, we examined variation in the water content, solid content, and shell mass of snapping turtle eggs from four populations dispersed along a longitudinal geographic transect (Pennsylvania, Michigan, Minnesota, and Nebraska). Initial egg mass and dry shell mass were similar among these four populations. However, water contents of eggs correlated positively with longitude, whereas dry content mass correlated negatively with longitude. Moreover, water content of eggs correlated negatively with the average number of days per year where average air temperatures exceeded 15 °C in a particular region (an indicator of regional thermal climate), and dry content of eggs correlated positively with both the number of days per year where average air temperatures exceeded 15 °C and the average total precipitation for the months of May through September (an indicator of regional hydric climate). These findings suggest that egg content (and perhaps egg quality) in this wide-ranging species of turtle varies in a manner reflecting differences in climate.

Résumé : La tortue serpentine commune (*Chelydra serpentina serpentina*) possède une vaste répartition en Amérique du Nord et habite les milieux aquatiques sous divers climats thermiques et hydriques. Bien qu'il y ait eu des études de la variation de ses caractéristiques reproductives, telles que la taille des femelles, la taille des couvées, et la masse des oeufs, on connaît mal la variation géographique des composantes de l'oeuf. Notre étude examine les variations du contenu hydrique, du contenu en solides et de la masse de la coquille dans quatre populations de tortues serpentines réparties le long d'un gradient longitudinal (Pennsylvanie, Michigan, Minnesota et Nebraska). La masse initiale des oeufs et la masse sèche des coquilles sont semblables chez les quatre populations. Cependant, il y a une corrélation positive entre le contenu hydrique et la longitude et une corrélation négative entre la masse sèche du contenu et la longitude. De plus, le contenu hydrique est en corrélation négative avec le nombre moyen de jours par année durant lesquels la température moyenne de l'air dépasse 15 °C dans la région (c'est un indicateur du climat thermique régional); le contenu sec des oeufs est en corrélation positive avec le nombre de jours par année durant lesquels la température moyenne de l'air dépasse 15 °C, mais aussi avec le total moyen des précipitations du mois de mai à la fin de septembre (c'est un indicateur du climat hydrique régional). Ces résultats laissent croire que, chez cette espèce de tortue à large répartition, le contenu des oeufs, et peut-être aussi la qualité des oeufs, varient en fonction des différences de climat.

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Introduction

The common snapping turtle (*Chelydra serpentina serpentina*) is found throughout much of the eastern and central United States. Because this is a wide-ranging species that inhabits regions with diverse thermal and hydric climates, this species may exhibit geographic variation in various phenotypic characters among populations, including reproductive characters (Iverson et al. 1993, 1997; Ewert et al. 1994). Iverson et al. (1997) reported that size of snapping turtle eggs tends to decrease with increased latitude but did not find any evidence that egg size varied longitudinally. However, it is unclear whether the components of similarly sized eggs (and hence the amount of energy invested by the female in each propagule) remain constant across the species' range. Moreover, it is unclear if geographical variation in egg size and (or) egg quality correlates with climatic variation across the range of the species. Such information may be important for evaluating differences in maternal investment in individual propagules among populations of snapping turtles and may have implications for the life history and demography of this species.

Turtles show no postoviposition parental care and, as such, females invest in their offspring fully within the con-

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fines of the egg and the environment in which the eggs are laid. The egg itself contains two resources to which considerable attention has been devoted in the last three decades: nutrients, primarily in the form of yolk (Congdon and Gibbons 1985), and water within the albumen and yolk (reviewed in Packard 1999). Because of the importance of both of these resources in embryonic development and hatchling survival (Congdon et al. 1999; Packard 1999; Janzen et al. 2000; Packard and Packard 2001), composition in terms of these two main components for an egg of a given size must strike a balance between the proportions of total water and yolk: more water may be necessary in dry incubation environments but might produce smaller neonates or leave them with fewer energy reserves relative to an egg with more yolk but less water. On the other hand, such an egg with less water may be more susceptible to desiccation, and embryonic development may be adversely affected if too little water is available.

Although much attention has focused on the amount of yolk packaged within eggs, it has typically been directed towards the question of “optimal offspring size” (Kaplan and Cooper 1984; Parker and Begon 1986; Congdon and Gibbons 1990), which seeks to balance optimal offspring size for survival with the number of offspring produced. However, while a large proportion of yolk nutrients is indeed directed towards somatic growth and metabolic needs during embryonic development, there is also a portion of yolk remaining at the end of incubation available for posthatching use (Congdon and Gibbons 1990). For example, snapping turtle neonates commonly hatch in the laboratory with yolk still present in the yolk sac (Wilhoft 1986; Packard et al. 1987, 2000; Finkler 1999; Packard 1999; Rhen and Lang 1999) that can provide a significant amount of energy to fuel metabolism during the posthatching period. While the low energy demands of ectotherm neonates may allow for prolonged usage of such a resource, there is still a limit as to how long that energy can sustain a neonate under conditions of low or no food intake for an extended period of time. Thus, the amount of yolk packaged in an ectotherm egg may be important not only for its contribution to somatic growth, and thus body size at hatching, but also for its contribution to energy stores, and thus the neonates’ ability to survive an extended period of time.

The second major resource contained in the eggs is the water contained within the yolk and albumen. The importance of egg water balance on reptilian embryonic survival and phenotypic variation has been extensively examined over the last three decades (reviewed in Packard 1999). Water packaged in the egg and the ability of the egg to exchange water with its surroundings affect embryonic growth and incubation duration (e.g., Morris et al. 1983; Packard 1991), hatching success (e.g., Morris et al. 1983), hatchling size and body composition (e.g., Packard et al. 1988; Finkler 1999), and locomotor performance and desiccation tolerance of the hatchlings (Miller et al. 1987; Miller 1993; Finkler 1999).

Climates that different populations experience may affect ectotherm egg components because such differences in climate may affect both neonate energy expenditure and egg water balance. For example, neonate turtles that hatch in warmer climates may have higher energy expenditures relative to turtles that hatch in colder climates. Therefore, it may be advantageous for turtles from warmer climates to package more nutrients in the egg for postnatal use. Similarly, differences in hydric climate across the range of turtles may also influence variation in the components of their eggs, as eggs from drier climates may have denser shells to reduce water loss during embryonic development, greater water contents, or both.

In the present study, we examined variation in snapping turtle egg components among four populations distributed along a longitudinal transect (with little latitudinal variation) centered at approximately 42°N and answered three consecutive questions in our analyses. First, do egg mass and (or) egg components vary among the populations of snapping turtles represented in our sample? Second, if egg mass and (or) components vary among these populations, does this variation correlate with spatial position of the population within the species’ range (i.e., do mass or components correlate with longitude)? Third, if egg mass and (or) components correlate with longitude, do similar correlations exist with differences in thermal and hydric climate across the longitudinal transect?

Methods

The experimental procedures used in this study are in accord with the guidelines set forward by the Canadian Council on Animal Care and were conducted with the approval of the Institutional Animal Care and Use Committees of Drexel University (Philadelphia, Pennsylvania), Miami University (Oxford, Ohio), and Indiana University at Kokomo, where examinations of egg content took place.

The eggs used in this study were from populations located in southeast Pennsylvania, southeast Michigan, southeast Minnesota, and north-central Nebraska. The four populations were distributed at roughly 8° intervals longitudinally between 40° and 44°N latitude (Table 1). We collected eggs from freshly laid snapping turtle nests and weighed them within a few hours of collection. We then randomly selected three to eight eggs from each clutch for egg component analysis.

We opened each egg and separated the contents from the shell with small amounts of distilled water to remove adhering albumen from the shell. We dried the shell and egg contents separately to a constant mass using either lyophilization (Pennsylvania eggs collected in 1997) or 60 °C drying ovens (all others). Dry shell mass and dry content mass were then subtracted from initial egg mass to determine the egg’s water content. Preliminary analyses of egg size and egg components between Pennsylvania eggs collected in 1997 (lyophilized) and those in 2001 (dried at 60 °C) showed no significant differences between the two years; therefore, we combined eggs from both years to represent the population in subsequent statistical analyses.

We analyzed populational differences in egg size and components using the MIXED procedure (SAS Institute Inc. 1996) of SAS 8.2. We conducted three consecutive sets of ANOVAs (egg mass) and ANCOVAs (egg component mass) that all incorporated clutch as a random effect and, for the ANCOVAs, egg mass as a covariate. In the first set of analyses (Model I), population was included as a nominal variable

Table 1. Characteristics of snapping turtle (*Chelydra serpentina serpentina*) populations investigated in this study.

Location	Latitude and longitude	1 May – 30 September precipitation (cm)[a]	No. of days per year ≥15 °C[a]	Years eggs sampled	No. of clutches	Clutch size (mean)	No. of eggs sampled per clutch	Total no. of eggs
John Heinz National Wildlife Refuge, Pennsylvania	40°N, 75°W	54.9	163	1997[b], 2001	21	20–63 (40.4)	3–8	111
Washtenaw and Livingston counties, Michigan	42°N, 84°W	38.7	133	1997, 2001	17	16–40 (27.8)	5	105
Weaver Dunes Scientific and Natural Area, Minnesota	44°N, 92°W	50.6	126	2001	10	26–47 (36.3)	6	60
Valentine National Wildlife Refuge, Nebraska	42°N, 100°W	38.4	136	1993[c], 1995–1997	27	23–71 (47.5)	5–8	135

[a] Climate data are averages based on summed daily values obtained from the following National Oceanic and Atmospheric Administration weather stations: 366889 (Philadelphia, Pennsylvania, 1926–1999, 73 years per average), 200230 (Ann Arbor, Michigan, 1931–1997, 61–65 years per average), 218227 (Thielman, Minnesota, 1948–2003, 35–38 years per average), and 258775 (Valentine Lakes Game Refuge, Nebraska, 1948–2003, 35–38 years per average).

[b] Data from Steyermark and Spotila (2001*b*).

[c] Data from Finkler and Claussen (1997).

to determine whether there was any variation in egg mass or egg component mass among the populations. In the second set of analyses (Model II), we incorporated longitude as a covariate to determine whether variation in egg mass was linearly associated with longitude, and we also used egg mass as a covariate to determine if egg component mass was linearly associated with longitude. In the final set of analyses (Model III), average number of days per year with average temperatures ≥15 °C (determined by averaging reported minimum and maximum temperatures) and average total precipitation (rainfall) between 1 May and 30 September reported by the National Oceanic and Atmospheric Administration National Climate Data Center (U.S.A.) climate stations <65 km from each site (Table 1) were employed as covariates to ascertain whether variation in egg mass or egg components corresponded to differences in climatic conditions among the populations.

We chose the average number of days per year with average temperatures above 15 °C as a means of expressing differences in thermal climate based on observations that 15 °C is the lowest temperature at which snapping turtles feed and are otherwise highly active (Obbard and Brooks 1981; Williamson et al. 1989). This measure thus should reflect the amount of time that a hatchling may be able to feed after hatching, emergence from the nest, and migration to the water (assuming that hatching periods among the populations are comparable) and (indirectly) the amount of time that the hatchling may need to rely on stored energy reserves during winter before temperatures climb high enough to commence feeding again in the spring. These values are based on air temperatures and may not directly reflect water temperatures in specific microhabitats occupied by hatchling snapping turtles, but should adequately reflect regional differences in thermal climate. Preliminary analyses that used other measures of thermal climate, such as base 15 °C growing degree-days, provided similar results.

We chose average precipitation to serve as a surrogate for moisture availability for egg water exchange. While many factors influence the ability for water exchange to occur between the egg and soil (e.g., particulate size, humus content, and temperature), and soil water content and water potential can vary greatly from one location to another, the rate of infiltration of water into the soil via precipitation is a key determinant of overall soil water content and water potential (Hillel 1980) and may, in turn, influence the overall availability of adequate nesting sites. We specifically chose May through September because rainfalls may contribute to soil moisture for several months (Hillel 1980). Snapping turtles typically lay their eggs in late spring, and the eggs incubate throughout the summer. Therefore, precipitation accumulation in the interval preceding nesting as well as precipitation during egg incubation will contribute to soil water potential. Data are based on summed daily totals from 1 May to 30 September averaged over 55- to 73-year periods that were obtained from National Oceanic and Atmospheric Administration weather stations (Table 1).

The MIXED procedure correctly estimates covariance parameters for random effects (e.g., clutch) but does not calculate F statistics and associated probabilities for this type of effect (Packard et al. 1999; Tucker and Paukstis 1999). However, the significance of clutch as a source of variation was

Table 2. Statistical evalutions of the significance of clutch (a random effect) in the mixed models for variation in snapping turtle (*C. s. serpentina*) egg size and content with geographic location and climatic conditions.

Model design	Response variable	Clutch variance estimate[a]	χ^{2b}
Model I (population as a fixed effect)	Egg mass	2.306	568.4
	Dry shell mass	0.010	326.7
	Total water content	0.033	158.1
	Total solid content	0.022	130.3
Model II (longitude as a covariate)	Egg mass	2.324	576.3
	Dry shell mass	0.011	347.4
	Total water content	0.037	186.6
	Total solid content	0.033	205.0
Model III (precipitation and no. of days ≥15 °C as covariates)	Egg mass	2.261	576.3
	Dry shell mass	0.010	330.8
	Total water content	0.033	158.2
	Total solid content	0.022	131.2

[a] In Model I designs, clutch was nested within the nominal fixed effect population. In the other two model designs, clutch was not nested (as effects cannot be nested within continuous variables).

[b] The χ^2 statistic is the difference in –2 restricted log-likelihood values between models that included clutch as a random effect and otherwise identical models that did not include clutch; df = 74, $P < 0.001$ for all models.

Table 3. Results for ANOVA and ANCOVA testing differences in egg mass and egg component mass among four populations of *C. s. serpentina* (Model I).

Parameter	Factor	*F*	df	*P*
Egg mass	Population	1.16	3,72	0.332
Dry shell mass	Population	4.54	3,72	0.0057
	Egg mass	145.07	1,314	<0.0001
Water content	Population	8.47	3,72	<0.0001
	Egg mass	4867.04	1,314	<0.0001
Dry content mass	Population	23.69	3,72	<0.0001
	Egg mass	305.37	1,314	<0.0001

evaluated in each model by calculating the difference in –2 restricted log-likelihood values between models that included clutch as a random effect and otherwise identical models that omitted clutch. The associated probability for the resultant difference (a χ^2 statistic) was then used to assess the importance of clutch as a covariance parameter in the model (SAS Institute Inc. 1996).

Results

Clutch was found to be a significant source of variation in all models (Table 2). Therefore, results of all main effects reported here are derived from models that include clutch as a random effect.

ANOVAs (Table 3) indicated no significant variation in egg mass among the four populations but found significant differences among populations in the masses of all three egg components. These differences in egg components among populations correlated with longitude (Table 4, Fig. 1): egg water content increased and egg solid content mass decreased with increasing longitude (i.e., westward). Although shell mass varied significantly among populations, the linear correlation between dry shell mass and longitude was not significant: eggs from the Pennsylvania population had significantly lower dry shell masses, but dry shell mass of eggs did not vary significantly among the other three populations ($P < 0.01$, least-squares means test).

Neither egg mass nor dry shell mass correlated with either precipitation during the incubation season or the number of days with average temperatures at or above 15 °C (Table 5). Solid content was positively correlated with both the amount of precipitation and with temperature. Water content was positively correlated with the number of days with average temperatures at or above 15 °C but did not vary with precipitation.

Discussion

Our study attempted to answer three consecutive questions. The first question we asked was whether egg mass and (or) egg components varied among the populations of snapping turtles represented in our sample. Egg components, but not egg mass, varied among the four populations that we observed (Table 3). The mass of all three egg components that we examined (dry shell, water, and content solids) varied among populations.

The second question we asked was whether the observed variation in egg components among populations correlated with spatial position of the populations within the species' range (i.e., do egg components correlate with longitude). Our data provide strong evidence that there is a correlation between egg components and longitude. From east to west, eggs had relatively more water and less solid content (Table 4, Fig. 1). Although shell mass did not correlate with longitude, eggs from the easternmost population examined (Pennsylvania) had proportionately smaller shell masses than did those of the other populations.

The third question we asked was whether the observed geographic variation in egg components correlated with a definable climatic variable. We chose to examine hydric and thermal conditions across the longitudinal transect as likely candidates for climatic variables that might affect egg components. We chose hydric conditions because egg – substrate water relationships during egg incubation can affect embryonic development, hatchability, and neonatal phenotypes

Table 4. Linear models for snapping turtle (*C. s. serpentina*) egg mass and egg component mass as functions of longitude and latitude (Model II).

Parameter	Factor	Estimate (SE)	*t*	df	*P*
Egg mass	Intercept	11.8010 (1.5042)	7.85	74	<0.0001
	Longitude	–0.0002 (0.0169)	–0.01	315	0.992
Dry shell mass	Intercept	–0.0197 (0.1222)	–0.16	74	0.872
	Longitude	0.0022 (0.0012)	1.86	314	0.064
	Egg mass	0.0599 (0.0050)	12.02	314	<0.0001
Water content	Intercept	–1.5832 (0.2444)	–6.48	74	<0.0001
	Longitude	0.0089 (0.0023)	3.87	314	0.0001
	Egg mass	0.7846 (0.0114)	68.35	314	<0.0001
Dry content mass	Intercept	1.6453 (0.2266)	7.26	74	<0.0001
	Longitude	–0.0112 (0.0022)	–5.19	314	<0.0001
	Egg mass	0.1521 (0.0103)	14.74	314	<0.0001

Fig. 1. Linear regressions of snapping turtle (*Chelydra s. serpentina*) egg mass and fractional component masses with longitude. See Table 4 for the appropriate statistical interpretation of these results.

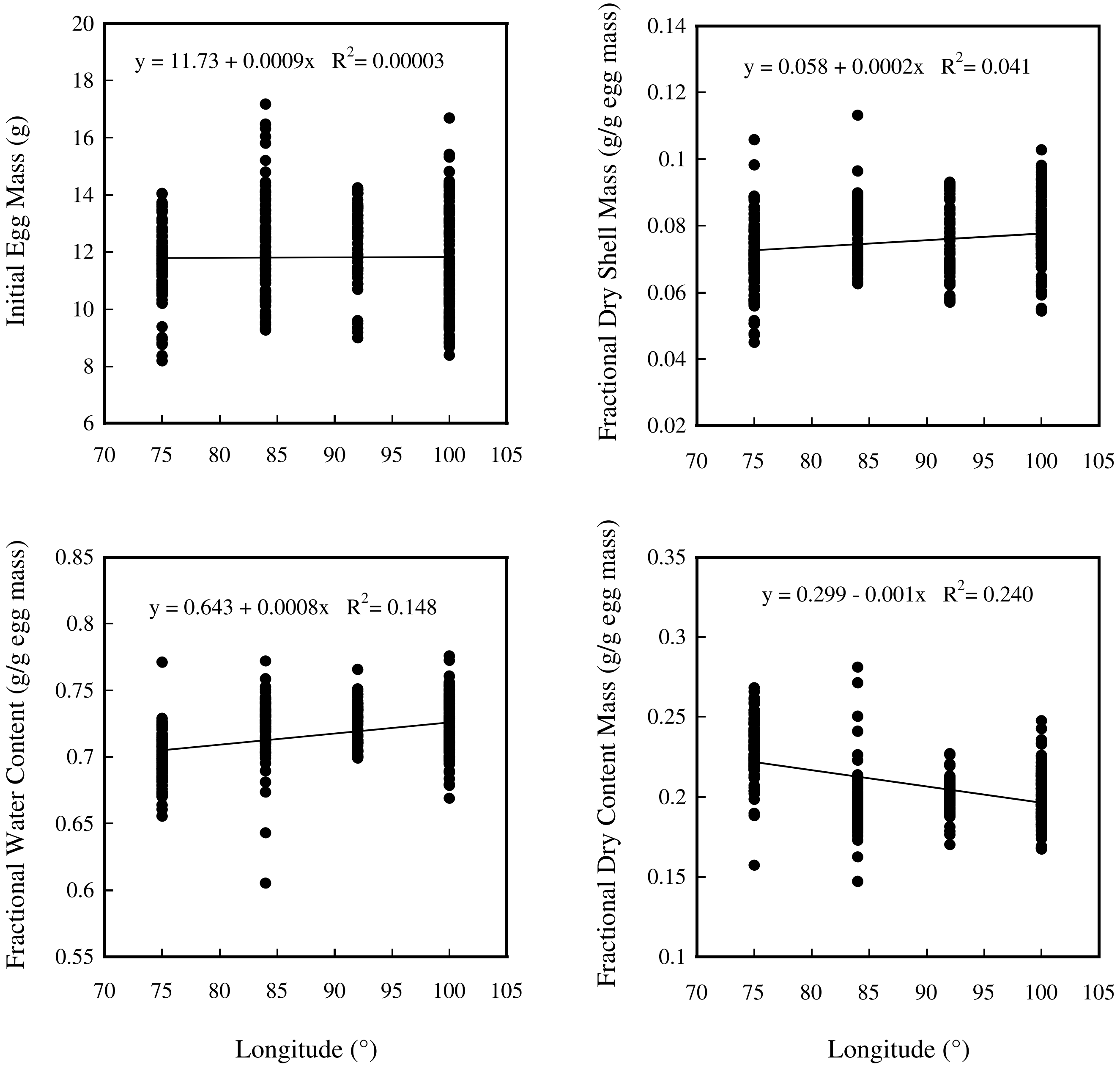

Table 5. Linear models for snapping turtle (*C. s. serpentina*) egg mass and egg component mass as functions of climatic variables (Model III).

Parameter	Factor	Estimate (SE)	*t*	df	*P*
Egg mass	Intercept	14.6644 (1.8507)	7.92	72	<0.0001
	Precipitation	0.0350 (0.0332)	1.06	316	0.292
	No. of days ≥15 °C	–0.0314 (0.0182)	–1.73	316	0.085
Dry shell mass	Intercept	0.5588 (0.1447)	3.86	72	0.0002
	Precipitation	–0.0032 (0.0023)	–1.42	315	0.2015
	No. of days ≥15 °C	–0.0016 (0.0012)	–1.30	315	0.3789
	Egg mass	0.0591 (0.0049)	11.99	315	<0.0001
Water content	Intercept	0.3161 (0.2868)	1.10	72	0.274
	Precipitation	–0.0065 (0.0042)	–1.53	315	0.128
	No. of days ≥15 °C	–0.0053 (0.0023)	–2.27	315	0.0241
	Egg mass	0.7781 (0.0112)	69.79	315	<0.0001
Dry content mass	Intercept	–0.8880 (0.2377)	–3.74	72	0.0004
	Precipitation	0.0096 (0.0035)	2.76	315	0.0061
	No. of days ≥15 °C	0.0069 (0.0019)	3.62	315	0.0003
	Egg mass	0.1638 (0.0094)	17.35	315	<0.0001

(e.g., Packard 1999; but see Rimkus et al. 2002) and thus may affect fitness (Janzen 1993; Janzen et al. 2000; but see Congdon et al. 1999). Geographical differences in rainfall, which may influence substrate water potential (Hillel 1980) and thus water availability during embryonic development (Packard 1991, 1999), may have acted as a selection agent on variation in egg components, with drier environments influencing the formation of eggs that have either more water, heavier egg shells (to prevent desiccation), or both relative to eggs from wetter environments.

Our results do not support the hypothesis that spring–summer precipitation affects either eggshell mass or water content (Table 5). The amount of precipitation for the months leading up to oviposition and during embryonic development (the periods most likely to affect egg – substrate water relationships) does not appear to affect snapping turtle fitness to the extent that differential fitness would result in phenotypic variation in egg components. This may be due to the high variability in soil water potential on a localized scale within a geographic region. Alternatively, it may indicate that the degree to which water potential varies in natural nests is not enough to affect embryonic or neonatal survival (Rimkus et al. 2002).

An alternative hypothesis to explain clinal variation in egg components centers around the effects of environmental temperature on neonatal nutrient consumption. We used the number of days per year with average air temperatures ≥15 °C as an index for thermal climate. This particular measure should correlate with the active season for these turtles and may be indicative of how long the hatchlings are active following nest emergence, assuming similar nest emergence periods among the populations. Although longer warm periods may enable the hatchling to forage before overwintering, the higher temperatures would also increase maintenance metabolism costs.

Our results support the hypothesis that temperatures experienced after nest emergence affect egg components (Table 5). Therefore, energetic factors may explain the longitudinal variation in egg components. Hatchlings acquire their posthatching energy reserves from lipids and protein in the egg (Wilhoft 1986; Janzen et al. 1990). In addition to nutrient stores in the bodies of the hatchlings (e.g., fat bodies, liver, etc.), snapping turtles commonly hatch in the laboratory with some residual yolk, ranging from about 0 to 2.2 g wet mass (Wilhoft 1986; Packard et al. 1987, 1988, 2000; Finkler 1999; Rhen and Lang 1999), providing approximately 0 to 4.95 kcal of total energy (as calculated from Wilhoft 1986). The amount of residual yolk may depend on incubation conditions such as temperature and soil moisture (Packard et al. 1987, 1988, 2000; Finkler 1999; Rhen and Lang 1999).

Snapping turtles in the laboratory typically do not feed for several days after hatching (M.S. Finkler, personal observation) and can survive for at least 30 days at approximately 26 °C without food (Steyermark and Spotila 2001*a*). Although it is not known if juvenile snapping turtles feed in the wild during their first few months post hatching, it is assumed by some that they do not (Sims et al. 2001), and in northern climates, where water temperatures may drop below the threshold temperature for activity (~15 °C) soon after nest emergence, the amount of time that can be spent foraging is likely quite limited.

If posthatching snapping turtles do not feed in the wild during their first fall, then their lipid, glycogen, and protein reserves must be enough to maintain at least standard metabolic function until the spring, when they commence feeding. During the winter months, all populations of snapping turtles considered here likely face similar low temperatures in aquatic overwintering sites (Ernst et al. 1994; Reese et al. 2002). The low environmental temperatures result in very low metabolic rates, and thus in very low energy expenditures (Gatten 1980; Finkler et al. 2002). Therefore, population differences in total metabolic rate energy expenditure from post hatching until the spring will likely come in the fall.

Because naturally incubated eggs from the various locations hatch at approximately the same time of year (typically from late August to mid-September: Congdon et al. 1987; M.S. Finkler and A.C. Steyermark, personal observation; G.C. Packard, personal communication), turtles in Pennsylvania generally face a longer period of warm temperatures when their metabolic rates would be increased relative to their counterparts at the other locations. Barring any strong population differences in temperature-specific metabolic rates, this would result in Pennsylvania turtles requiring more energy to make it through to the spring than would the more western populations. If turtles do not feed from hatching until the spring, or even if they feed minimally, then differences in energetic needs between the populations would be reflected in differences in egg components.

We have shown that snapping turtle eggs distributed longitudinally from the eastern mid-Atlantic region to the western Great Plains region of the United States have progressively more water and less solids. The increase in water content does not correlate with longitudinal differences in precipitation. However, the westward decrease in solids negatively correlates with the number of days with average temperatures ≥15 °C. Snapping turtle neonates spend more time at higher temperatures before hibernation in the eastern United States and thus may need greater energy reserves, relative to turtles that spend less time at high temperatures before hibernation in the western United States, and need less energy reserves. Potential differences in energy reserves may result from the progressively smaller solid content of eggs from east to west that we measured. We propose that the particular life-history trait of egg components is selected for by differences in climate that neonates experience upon hatching.

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