Egg Component Comparisons within and among Clutches of the Diamondback Terrapin, *Malaclemys terrapin*

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The relationship between egg size and composition (relative amounts of lipid, protein, and water) can play an important role in determining neonate size, quality, or the amount of post-hatching care observed in many reptiles. We evaluated the relationship among egg wet mass, non-polar lipid mass, water content, shell dry mass, and lean dry mass within and among seven clutches of the Diamondback Terrapin, *Malaclemys terrapin*, from Chesapeake Bay. Egg size varied considerably among clutches, but was relatively uniform within clutches. Non-polar lipid mass, lean dry mass, and water content correlated positively with egg wet mass indicating that larger eggs contain a proportionally greater amount of these components. There was no relationship between egg wet mass and shell dry mass. Clutches had similar, positive slopes but different intercepts in the relationships between lean dry mass and lipid mass and between water content and total dry mass. Thus, clutches differed in the relative proportions of resources but had similar allocation patterns of egg components. Our data cannot resolve whether these effects are due to differences in resource availability or differences in the physiological mechanisms involved in egg provisioning.

EGG size and composition can be the target of natural selection when they affect offspring quality. A common assumption of hypotheses concerning egg size is that larger eggs contain more resources that can either result in larger offspring or better provisioning of the hatchling (bigger is better). However, females may not always make the largest eggs possible because natural selection should optimize the product of offspring fitness and offspring number when there is a tradeoff between egg size and number (Smith and Fretwell, 1974; Brockelman, 1975). Because resources allocated to offspring can vary, examination of resource components as a function of propagule size is important in ascertaining the fitness consequences of egg size (Congdon et al., 1983; Nagle et al., 1998). In viviparous organisms, offspring size, performance, or other fitness surrogates can be measured at parturition. For oviparous organisms, resources within the egg (Sinervo and Huey, 1990) and the environment where it incubates (reviewed in Packard, 1991, 1999) can influence offspring size and fitness. Egg size and composition in turtles is interesting because parental investment in care (PIC, Congdon, 1989; Congdon and Gibbons, 1990) through post-natal lecithotrophy (Lance and Morafaka, 2001) relies on the substantial energetic resources that remain after hatching that may affect post-hatching growth and survivorship.

Egg size in turtles can vary as a function of egg shape (Iverson and Ewert, 1991) and the water content, lipids, or proteins provisioned within the egg (Congdon and Gibbons, 1990). When increases in egg size occur without a concomitant increase in lipids, protein, or water, offspring size and quality may be affected. For example, experimental yolk reduction resulted in reduced yolk sac size in near term bird embryos (Finkler et al., 1998) and smaller neonates in lizards (Sinervo and Huey, 1990). These results imply that an increase in egg size without a concomitant increase in yolk could result in proportionally smaller hatchlings or reduced PIC, although similar effects remain to be demonstrated in turtles as they have been in birds (Finkler et al., 1998) and lizards (Sinervo and Huey, 1990). Similarly, experimental removal of albumen (primarily water) from bird eggs reduced the hydration state of the embryo (Finkler et al., 1998). Additionally, water permeable turtle eggs in dry incubation environments result in smaller hatchlings compared to similar sized eggs on wetter substrates (Packard, 1991) implying that reduced water content in turtle eggs could result in smaller hatchlings. Determining the covariation between the frequently measured traits of egg size and egg components within and among clutches may identify resource allocation patterns or "rules" (Dunham et al., 1989) and potentially provide insight into the relationship between egg size and offspring size and quality.

We suggest that egg components can vary in three ways and that analysis of covariance (ANCOVA) can be a useful tool to detect and un-

derstand resource allocation in eggs. First, egg components can vary independently among females resulting in heterogeneous slopes among clutches (e.g., analysis of egg lipid mass using egg lean dry mass as the covariate). The variation in allocation strategies among females suggests two interpretations that require additional study. Extrinsic factors such as incubation environments may have a greater effect on hatchling survivorship than egg resource levels; or variation in propagule composition may ensure that some offspring receive a suitable proportion of resources for a particular set of environmental conditions, a.k.a. adaptive coin-flipping (Kaplan and Cooper, 1984). In the second possible ANCOVA result, egg resources covary similarly (homogeneous slopes) among clutches, but clutches differ (intercepts) in the relative proportion of egg components. This scenario would suggest that the production or allocation of egg components is coupled, but there is variation among females in the composition of their eggs. The differences among clutches could reflect variation in resource availability or variation among females in the physiological pathways that construct egg components or regulate egg allocation. For example, there may be differences among females in the lipoproteins that make up the yolk or how it is sequestered within the eggs. In the third possible ANCOVA result, similar component levels both within (homogeneous slopes) and among clutches (same intercept) would suggest a conserved allocation strategy. The differences in egg size among clutches would most likely reflect differences in the resources available to the female during oogenesis. Both the second and third ANCOVA results suggest that the relative amount of two or more resources may be more important than a single resource during development or that these two resources are constrained because of coupled metabolic pathways involved in egg provisioning. The second ANCOVA result is more interesting because the variation among females would suggest that allocation patterns could evolve. One caveat about using ANCOVA to understand allocation patterns is that the use of a covariate that includes the dependent variable (e.g., analyzing egg dry mass using egg total mass as a covariate) is confounded because the covariate may affect the variable of interest thus limiting the scope of interpretation.

Incubation environments also can affect offspring size in reptiles whose eggshells are highly permeable to water. In general, dry incubation environments produce smaller hatchlings than do wetter incubation environments; and at the same moisture condition, cooler incubation temperatures produce slightly larger hatchlings (reviewed in Packard, 1991, 1999). Hatchlings from wetter incubation environments have a higher percentage of water, can tolerate greater water loss, and locomote faster, but have a higher body water content threshold than hatchlings from dry environments (Finkler, 1999). However, dry weights among different incubation environments are similar (Finkler, 1999) and the performance capability can vary from population to population (Finkler et al., 2000). Snapping Turtle hatchlings recover the difference in mass attributable to soil moisture shortly after entering aquatic habitats, however, length differences can persist for at least eight months (Finkler et al., 2002). Additionally, wetter incubation environments result in the use of more energy during embryogenesis contributing to lower energy reserves at hatching (Finkler et al., 2002). Lower energy reserves reduce the amount of parental investment in care (Congdon, 1989) for post-hatching lecithotrophy (Lance and Morafka, 2001). Because offspring size typically covaries with egg size in turtles (Roosenburg and Kelley, 1996), studies that investigate incubation environment effects on hatchlings typically use ANCOVA to focus on environmental effects independent of size.

We investigated egg size and composition in the Diamondback Terrapin, *Malaclemys terrapin*, to understand how allocation of egg resources varies with egg size. Terrapin egg size varies more among than within clutches, is independent of female size, and can vary from one clutch to the next within individual females (Roosenburg and Dunham, 1997). Egg size in terrapins does not appear to be constrained by the female's pelvic aperture or other morphological factors (Congdon and Gibbons, 1985, 1987; Roosenburg and Dunham, 1997) thus the production of larger eggs is possible. Finally, egg size is the primary determinant of hatchling size at constant soil moisture levels (Roosenburg and Kelley, 1996). We investigated the relationship among egg wet mass, dry mass, nonpolar lipids, lean dry mass, and water content to understand how maternal provisioning can vary among clutches.

MATERIALS AND METHODS

On 8 and 15 July 1999, we collected Diamondback Terrapin eggs within 12 hours of oviposition from the shores of the Patuxent River, a tributary of Chesapeake Bay and the site of a long-term terrapin demographic study (Roosenburg, 1991, 1996; Roosenburg and Dunham,

1997). July was the latter part of the nesting season, thus these nests were most likely second or third clutches (Roosenburg, 1994; Roosenburg and Dunham, 1997). We collected fifty eggs from seven clutches. Two clutches were represented by four eggs each and one by five eggs (remaining eggs of these clutches were used in another experiment) whereas all of the eggs were used from the remaining four clutches, consisting of 5, 8, 11, and 13 eggs (37 eggs). We measured wet mass to the nearest 0.01 g using an A&D FX–200 Electronic Balance and measured length and width to the nearest 0.1 mm using Mitutoyo CDN–P12 digital calipers. We also calculated egg volume using the ellipsoid formula [volume = $(\pi/6)$ (length) (width^2)] to correlate volume with other egg metrics (Iverson and Ewert, 1991). We stored eggs at -20 C and transported them back to Ohio University for lipid extraction. We removed the eggshells and separately dried the egg contents and shells at 50 C to a constant mass. Using a Mettler AG–245 analytical balance, we weighed dried egg contents and dried shells to the nearest 0.0001 g. Following drying, we ground the egg contents using a mortar and pestle and performed petroleum ether extraction in a SoxTec HT2 1045 extraction system to isolate non-polar lipids. All ground material was placed in an extraction thimble and the residues remaining in the pestle were rinsed into the thimble using petroleum ether. Samples refluxed for 60 minutes at 100 C, rinsed for 45 minutes, and the residual solvent was evaporated for an additional 45 minutes. We dried extracted lipids in a drying oven for 15 minutes at 50 C before weighing to the nearest 0.0001 g. Lean dry mass (including polar-lipids) was calculated as the dry mass–lipid mass because it was impossible to remove all remaining solids from the thimble. We repeated the extraction procedure for the solid material of three eggs and we were unable to recover additional non-polar lipids indicating that our extraction was complete. We extracted non-polar lipids because these reflect the energy available to the developing embryo and PIC. Polar-lipids also are important to embryo growth and may be limited (Congdon and Gibbons, 1990) but were not the focus of this study.

We analyzed all data using Statistical Analysis System SAS for PC (ver. 8.2, 1996. SAS Institute Inc., Cary, NC). Prior to analysis, we natural log transformed all data. To test if egg dry mass, lipid mass, and water content increased with egg wet mass, we used ANCOVA (PROC GLM) solely to test for homogeneity of slopes and identify similar proportional changes. We evaluated the relationship between various egg components (lipid mass, lean dry mass, water content, and shell dry mass) and egg wet mass using linear regression (PROC REG) of the mean for each clutch. We used ANCOVA to evaluate variation in non-polar lipids among clutches using lean dry mass as the covariate. We also analyzed water content among clutches using egg dry mass as the covariate. As part of the ANCOVA, we evaluated homogeneity of slopes by testing for a significant clutch by covariate interaction.

<div align="center">RESULTS</div>

Terrapin eggs had an average (mean) wet mass of 10.29 g (sd = 1.41, n = 50), length of 34.8 mm (sd = 1.68), width of 22.3 mm (sd = 1.18), and volume of 9.14 cc (sd = 1.18). Egg wet mass (ANOVA, $F_{6,43}$ = 26.65, $P < 0.0001$) and volume (ANOVA, $F_{6,43}$ = 23.28, $P < 0.0001$) differed among clutches. Interestingly, both wet mass and volume were more highly correlated with egg width (ρ = 0.874, P < 0.0001; ρ = 0.935, P < 0.0001) than with egg length (ρ = 0.727, P < 0.0001; ρ = 0.646, P < 0.0001), suggesting that egg size is influenced more by increasing egg width than length. Because wet mass was correlated with volume (ρ = 0.98, $P < 0.0001$) and volume was an estimated parameter, we restricted further analyses to mass measurements. Shell dry mass averaged 5.6% of egg wet mass (range 4.3%–6.3%). Lipids averaged 7.1% (range 5.6–11.8%) of egg wet mass and 29.7% (range 25.0–42.3%) of total dry mass without shell. Water content of eggs averaged 70.9% (range 66.5–73.5%) of egg wet mass. Figure 1 illustrates the relationship between various egg components and egg wet mass.

Egg components increased with egg wet mass (Fig. 1), suggesting that larger eggs contain more resources. The slopes of the lines comparing lean dry mass, water content, and non-polar lipid mass to egg wet mass were similar and had a mean slope of 1.04 (SE = 0.27; ANCOVA, $F_{1,155}$= 0.32, $P = 0.573$; Fig. 1), indicating that egg components increased proportionally with egg size. Regression analyses of mean clutch values indicated that as egg wet mass increased, lean dry mass increased (ln lean dry mass = ln wet mass $(0.8269) - 1.3765$, r^2 = 0.83, $P < 0.005$, d. f. = 6), lipid mass increased (ln lipid mass = ln wet mass $(0.9522) - 2.5297$, r^2 = 0.86, $P < 0.001$, d. f. = 6), and egg water content increased (ln water mass = ln wet mass $(1.0430) - 0.3756$, r^2 = 0.99, $P < 0.0001$, d. f. = 6). Shell dry mass did not increase with egg wet mass ($P > 0.062$, d. f. = 6).

We detected a difference in the amount of non-polar lipids per unit lean dry mass among
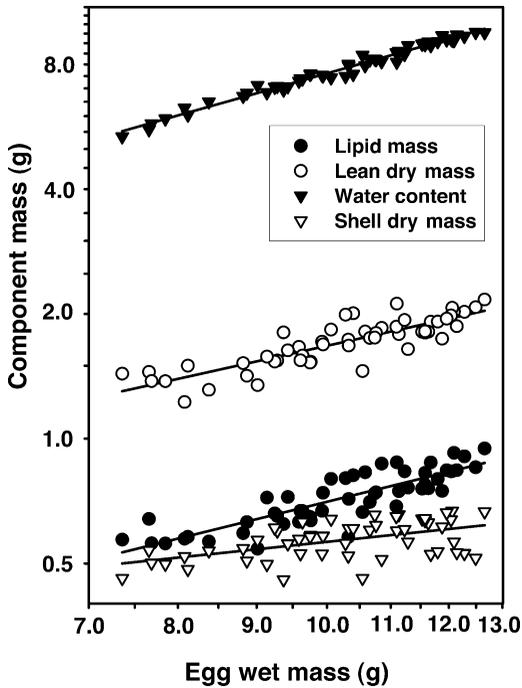
Fig. 1. The relationship between egg wet mass, dry shell mass, non-polar lipid mass, lean dry mass, and water content. Data are plotted on a log scale, slopes of the lines are similar (see text), indicating that increasing egg size results in proportional increases in egg components.
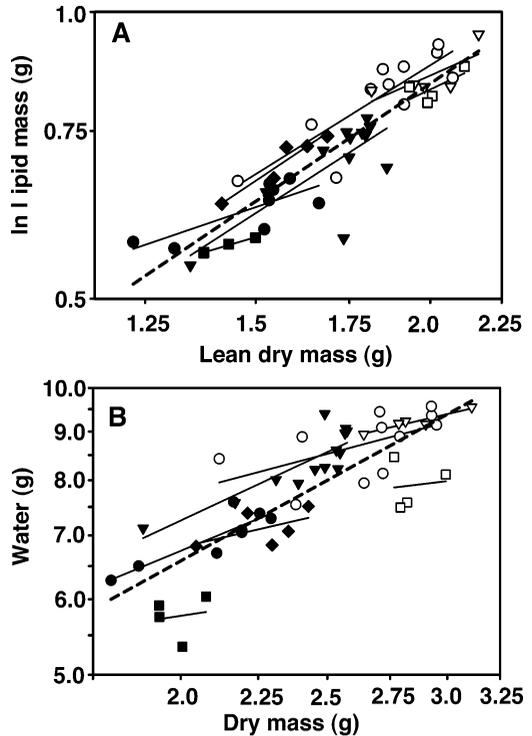

Fig. 2. (A) The relationship between egg lean dry mass and non-polar lipid mass for each clutch. There were differences among clutches (see text) in the amount of non-polar lipids. (B) The relationship between shell-free, total dry mass and water content. There were differences among clutches for water content (see text). For both graphs, the dotted line represents the population level relationship. Solid lines are the relationships within each clutch. All data are on a log scale.

clutches (ANCOVA, $F_{6,42} = 4.46$, $P < 0.001$). However, the slopes were similar among clutches (mean slope = 0.945, SE = 0.067; ANCOVA, homogeneity of slopes test, $F_{6,36} = 0.61$, $P = 0.721$; Fig. 2A). The difference in non-polar lipids among clutches was 0.1094 g (least square means, range = 0.6576–0.7670 g). We also found differences in the water content per unit dry mass among clutches but again the slopes were similar (ANCOVA, $F_{6,42} = 17.39$, $P < 0.0001$; mean slope = 0.893, SE = 0.107; ANCOVA, homogeneity of slopes test, $F_{6,36} = 0.0013$, $P = 0.51$, $P = 0.7937$; Fig. 2B). The range of water content among clutches was 1.9839 g (least square means, range = 6.4430–8.4269 g).

DISCUSSION

Non-polar lipids, lean dry mass (primarily protein and structural lipids), and water content increased proportionally to increases in terrapin egg wet mass (Fig. 1). Shell dry mass, however, did not increase with egg size. The proportional increase in resources with egg size indicates that increasing egg size does not compromise the amount of energy for embryonic growth or post-natal lecithotrophy. We suggest that egg allocation patterns are similar among females because non-polar lipids increased relative to lean dry mass and water content increased relative to total dry mass in a similar manner among clutches. However, differences among females in non-polar lipids and water content allocated to eggs suggest that females vary in the relative allocation of egg components.

Maryland Diamondback Terrapin egg non-polar lipid content averaged 29.7% of shell-free dry mass and 24.0% of total dry mass. Ricklefs and Burger (1977) reported that New Jersey terrapin egg lipids averaged 26.4% of shell-free dry mass. Turtles can be separated into species with high and low lipid content eggs. In general, low lipid eggs (< 20% non-polar lipid) are characteristic of species that emerge following development, whereas high lipid eggs (> 20% non-

polar lipids) have either embryonic diapause or delayed hatchling emergence (e.g., nest over-wintering in temperate species [Congdon et al., 1983; Congdon and Gibbons, 1985]; however, some non-over-wintering species also have high lipid eggs [Nagle et al., 1998; Hewavisenthi and Parmenter, 2002]).

The terrapin eggs we and Ricklefs and Burger (1977) examined fell in the high lipid group. In the Patuxent population, over-wintering is facultative and characteristic of some late season nests laid at the time we collected our eggs (Roosenburg, pers. obs.). Over-wintering in the nest is more common for Diamondback Terrapins in northern parts of the range (Auger and Giovannone, 1979). Interestingly, terrapin egg size decreases with increasing latitude (Roosenburg, 1994). The clinal variation in egg size is usually attributed to the need to maintain a balance in the number of offspring among populations whose annual reproductive output varies due to environmental factors (Roff, 1992). Southern populations can reproduce more often in a longer nesting season than northern populations whose activity season is considerably reduced resulting in similar numbers of offspring but with dramatic differences in egg size (Roosenburg, 1994). We suggest that the egg size cline observed in terrapins and other species may be facilitated by reduced requirements for post-natal lecithotrophy (Lance and Morafka, 2001) in cooler environments that require less energy while over-wintering than warmer environments with extended activity seasons. If resource acquisition by hatchling turtles is limited, then the longer growing season of warmer climates may increase the temperature-dependent energy consumption and, thus, increase the dependency on lipid reserves for hatchling survival to the following spring (Congdon, 1989). When activity resumes in the following spring, the reduced energetic demands of cooler environments may result in similar energy levels compared to hatchlings in warmer environments that may have greater investment. Our interpretation suggests that there may be a cline in the optimal egg size in terrapins driven by PIC, however further studies are needed to confirm this. The lower lipid levels observed in New Jersey terrapin eggs (Ricklefs and Burger, 1977) are consistent with our suggestion. However, we lack an egg composition study along the Florida to Massachusetts cline to accurately describe and understand the egg size variation in *Malaclemys* and other turtles (Moll, 1979; Iverson et al., 1993).

Terrapin eggs averaged 70.9% water, which is within the range of emydid turtles with flexible shelled eggs (66.5%–74.4%; Congdon and Gibbons, 1985, 1990). Interestingly, the relationship between water content and total dry mass appears to be different within clutches compared to the population (Fig. 2B), suggesting that the among clutch allocation pattern may not reflect the within female strategy. Although our sample size of seven clutches is small, we believe that our results are robust and that increasing the number of clutches will only strengthen our results.

The relationship between lipid mass and lean dry mass was similar within and among clutches (Fig. 2A), suggesting that the within clutch allocation strategy was similar to the pattern observed for the population. The allocation of lipid and protein derives from the hepatic synthesis of vitellogenin that results in a lipoglyco-phosphoprotein that varies little in the ratio of lipid to protein (Kuchling, 1999) and likely maintains a strong lean dry weight to lipid content correspondence. In contrast, albumen and water are added in the oviduct after ovulation (Ewert, 1979); thus, the physiological processes that determine total dry mass and egg water content occur independently. In Snapping Turtles the relationship between total dry mass and total egg mass varied considerably within clutches whereas the general population trend was increasing dry mass with increasing total egg mass, suggesting different allocation patterns among females (Finkler and Claussen, 1997). However, water content varied in a similar manner within and among clutches. Nonetheless, in both Finkler and Claussen's (1997) and our study, egg wet mass was still a good predictor of total dry mass.

Interestingly, the differences in lipid and water content among clutches could have consequences for the hatchling's development and post-natal survivorship. The 0.11 g difference in non-polar lipid mass (9.3 kcal/g; Burton, 1994) is equal to 1.017 kcal or roughly equivalent to 10.5 days at 26 C (based on a CO_2 production of 0.60 ml/hr for an average hatchling, (Roosenburg and Freshwater, unpubl. data; RQ = 0.7, and 4.7 calories per ml O_2 consumed, Kleiber, 1961). The difference of 10 days is likely an underestimate because most of the over-wintering occurs at cooler temperatures that result in lower metabolic rates. This additional parental investment could increase hatchling body size or resources for post hatching lecithotrophy, extending the amount of time that an individual could be active at a higher temperature or allowing for growth before hatchlings learn to feed.

The 2 g water difference among clutches was

considerable given the effects that soil moisture can have on hatchling size (reviewed in Packard, 1991, 1999). However, the difference may have no affect on hatchling size if the egg is in relatively moist substrates where it readily can absorb water similar to other turtle eggs (reviewed in Packard, 1991, 1999). However, if the substrate dries, then the extra water could affect hatchling size, incubation duration, and lipid reserves (reviewed in Packard, 1991, 1999). Terrapins nest primarily in sand, which requires low water content to maintain high water potentials compared to the vermiculite traditionally used to investigate the effects of soil moisture on turtle hatchlings (reviewed in Ackerman, 1991). Therefore, in sand, the nest could remain hydrated, particularly when the water difference of a single egg (2 g) is multiplied over the entire clutch (26 g, mean clutch size = 13 eggs; Roosenburg and Dunham, 1997). Thus, the difference in both lipid and water that we have observed among clutches suggests that hatchling energy reserves and hydration state may vary because of the resources provided in the egg. How variation in egg components affects hatchling fitness in terrapins is a compelling question for further study.

Determining how the maternal effects of egg size, water content, and energy content are related will lead to understanding how egg size can evolve (Bernardo, 1996). The allocation strategy among females we describe here indicates egg size is coupled with energy and water content. Increasing egg size without a proportionate increase in lipids could result in hatchlings without sufficient energy reserves to ensure growth and survival (Congdon, 1989). Thus, the relative proportions of egg components may be more important for development and post-natal survivorship than egg size per se. Variation in egg components among females suggests that allocation strategies can evolve and that both the incubation and the hatchling environment may optimize the relationship between egg components and offspring size and energy reserves. Thus, within species comparisons across latitudinal and other gradients could be particularly informative in determining the importance of egg size and the amounts of egg components.

ACKNOWLEDGMENTS

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