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Water Transport by Nesting Painted Turtles (*Chrysemys picta marginata*) in Michigan

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ABSTRACT. – **Gravid female midland painted turtles (*Chrysemys picta marginata*) transport water to nests and void the water during nest construction and oviposition. We estimated water transported by subtracting clutch mass from the difference of gravid and spent body masses of individual females. Clutch mass was calculated by multiplying clutch size by egg mass estimates derived from the relationship between egg width (measured from X-rays) and egg mass. Females exiting marshes to nest transported an average of 44.7 g (range 24.4–79.1) of water to nests, corresponding to 14% of spent body mass, 11% of gravid body mass, and exceeding mean clutch mass ($\bar{x} = 37.7$ g; range 21.5–61.2). The amount of water transported was positively correlated with female carapace length ($r^2 = 0.36, p < 0.001$). Females producing two clutches in one year had similar body masses prior to depositing each clutch, and clutch mass was not different between clutches, suggesting that more water is transported with second clutches than with first clutches.**

KEY WORDS. – **Reptilia; Testudines; Emydidae; *Chrysemys picta marginata*; turtle; eggs; nesting; reproduction; behavior; water transport; water storage; radiography; Michigan; USA**

In general, the vulnerability of turtle eggs to predation, desiccation, and overheating, combined with the lack of behavioral parental care, has made covering or burial of eggs essential for successful embryonic development. Typically, turtles buffer their eggs from heat and water stress during incubation by depositing them in flask-shaped cavities. A common scenario of aquatic turtle nesting behavior includes the following: 1) movement to nesting area, 2) nest site selection, 3) nest excavation, 4) egg deposition, 5) nest covering and concealment, and 6) return to water.

Another commonly observed component of nesting is the discharge of water stored in the urinary bladder and/or cloacal bursae into the nest. Females of many turtle species have been observed voiding water during nest excavation and into the nest cavity before egg deposition (Ehrenfeld, 1979). Observations of three species (midland painted turtles, *Chrysemys picta marginata*; snapping turtles, *Chelydra serpentina*; and Blanding's turtles, *Emydoidea blandingii*) made during the past 23 years on the E.S. George Reserve (ESGR) in Michigan indicate females that void water when captured do not continue nesting excursions without first returning to water. Despite its apparent importance to nesting, the amount of water transported during nesting movements has not been quantified for any turtle species. The lack of quantitative information on water transport is due, in part, to the difficulty of quantifying this parameter.

We made indirect estimates of the amount of water transported to nests by *C. picta* at the ESGR. Data were used to test four working hypotheses ($H_w1 - H_w4$) which were based on two general underlying assumptions: 1) females maximize the amount of water that is taken to nests and 2) all transported water is voided at the nest site (i.e., females leaving nests are empty of transported water). Assumption 1 is supported by data from this study. Assumption 2 is supported by the observation that, in contrast to gravid females which almost always void water upon capture, spent females never void water during capture and handling.

H_w1. – The amount of water transported to nests increases with female body size. Assumption: Larger females have larger body cavities with larger storage organs that allow them to transport greater amounts of water.

H_w2. – The amount of water transported is inversely related to the mass of eggs transported to nests. Assumption: Space for water and egg storage is limited by available body cavity volume and size of storage organs, leading to a trade-off between water and clutch volume.

H_w3. – Females that will produce a second clutch per season carry less water to their first clutch nests than do females that produce only one clutch in a given reproductive season. Assumption: Females with large follicles for second clutches have less space available for transporting water (equal to the space occupied by second clutch follicles) compared to females producing only one clutch of eggs per season.

H_w4. – Females that produce two clutches of similar mass within a season transport more water to second clutch nests than to first clutch nests. Assumption: The absence of large follicles during the second clutch allows more water to be transported.

MATERIALS AND METHODS

Our study is part of an ongoing long-term (23-yr) investigation of the nesting ecology (Congdon and Gatten, 1989) and demography (Tinkle et al., 1981; Congdon and Gibbons, 1996) of painted turtles conducted on the University of Michigan's E.S. George Reserve in Livingston County, Michigan. Since 1975, the ESGR study has resulted in 17,430 recaptures of 4490 painted turtles and 1650 documented nests. Painted turtles on the ESGR may fail to reproduce in some years, or may produce one or two clutches in a single nesting season. Hatching occurs in late August or September, but hatchlings usually overwinter in the nest and emerge the following spring (Breitenbach et al., 1984).

A 1.3 km drift fence encircling East Marsh on the ESGR was walked every 20–40 min during daylight hours from 17 May to 3 July 1996 and from 1 May to 4 July 1997 to intercept gravid females on nesting forays. A portable electronic balance was used to weigh all females (± 1.0 g) captured at the fence. Body mass was not recorded if a female voided water prior to weighing or if she refused to remain on the balance long enough to be weighed (a factor particularly true of second clutch females). Females were taken to the laboratory where we measured straight-line plastron and carapace length (CL) and confirmed individual identification. X-rays of all females were taken (Gibbons and Greene, 1979; Graham and Petokas, 1989; Hinton et al., 1997) to determine reproductive condition, clutch size, clutch frequency, and X-ray egg width (XREW). Stick-on reflective numbers were then attached to the carapace of gravid females to allow identification of nesting turtles from a distance. After processing, all turtles were returned to the marsh directly inside their point of capture on the drift fence. When numbered females returned to the fence (1 hr to several days later) they were re-weighed and placed on the other side of the fence to allow continuation of their nesting foray. After nesting, turtles were recaptured near the nest site or at the drift fence and weighed again.

Because the present research was part of a long-term demographic study, we did not disturb nests at the ESGR to obtain clutch mass. Instead, we determined clutch mass and the mass of water carried to nests indirectly using the following procedure. Gravid female painted turtles ($n = 34$) were captured from sites near the ESGR, X-rays were taken, and oxytocin was administered to induce egg laying (Ewert and Legler, 1978). All eggs were weighed (± 0.01 g) and average egg mass was determined for each of the 34 clutches. We then established the relationship between mean egg width (measured from X-rays; XREW) and actual mean egg mass per clutch (Fig. 1). For the ESGR females, mean egg width was calculated from X-rays of each individual. Egg mass estimates were obtained using the XREW – egg mass regression (Fig. 1), and clutch mass was calculated by multiplying estimated egg mass by clutch size (also obtained from X-rays). Water transported to nests was determined for each female by subtracting the calculated clutch mass from the body mass loss that occurred between pre-nesting (gravid body mass) and post-nesting (spent body mass).

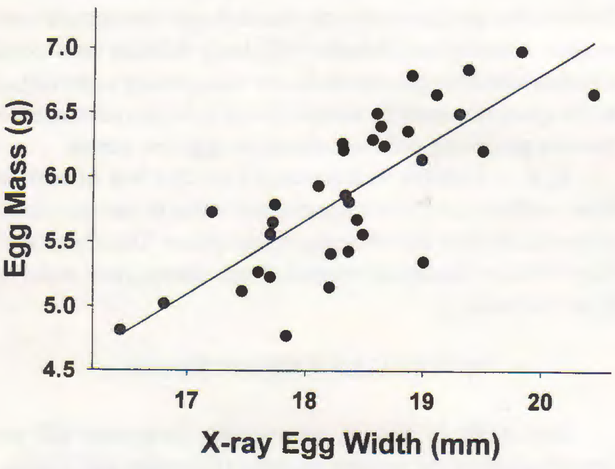

Figure 1. Relationship of mean egg mass (g) per clutch to mean X-ray egg width (mm) per clutch of 34 non-ESGR *C. picta*. The regression equation ($y = -4.63 + 0.57x$) is significant ($F = 49.18$; $r^2 = 0.61$; $p < 0.001$).

The assumption that females maximize the amount of water carried was tested by comparing water estimates from initial and subsequent drift fence captures of individual females with a given clutch of eggs. Two water mass estimates, obtained from gravid body masses taken at initial fence capture (before X-ray) and as females were lifted over the fence, were compared for 25 females. If water is indeed important to nesting, then females might be expected to transport as much water as possible on sequential nesting excursions with the same clutch of eggs.

Because the East Marsh drift fence was monitored for the entire nesting season, we were able to determine the number of females nesting each day and the reproductive status of each female with confidence. At the end of the nesting season, females were assigned to three reproductive categories: 1) single clutch per year, 2) first of two clutches, and 3) second of two clutches. The reproductive categories allowed us to examine whether reproductive materials (eggs or follicles) influence the amount of water transported to nests. However, to minimize the effect of enlarged follicles, examination of the trade-off between eggs and water (H_w2) was restricted to those turtles that produced only one clutch (reproductive category 1).

Two methods were used to assess the effects of enlarged follicles on water storage capabilities. Because the slopes of the relationships between the amount of water voided by females and CL in reproductive categories 1 and 2 were different, the first method compared the residuals from these relationships between categories (H_w3). The second method was based on comparisons of first and second clutch gravid body masses and clutch masses of individual females (H_w4). The comparison of body masses was necessary because first clutch/second clutch pairs of water estimates for individual turtles were not available. The lack of paired measurements was due to the small percentage of females producing two clutches (17%, 21/124) and the tendency for second clutch females to be uncooperative during weighing. The first clutch gravid body mass is the sum of the component masses of: 1) female soma, 2) eggs, 3) developed follicles for a second clutch, and 4) water transported to the nest. Second clutch gravid body mass includes the sum of components 1, 2, and 4 (i.e., the mass of fully developed follicles in the ovaries present with the first clutch is absent with the second clutch).

Table 1. Summary of data for female painted turtles (n = 28) captured prior to and after nesting. Clutch mass calculated from X-ray egg widths, water mass calculated from body mass lost during nesting minus clutch mass. SE = standard error.

	Mean	Range	SE
Carapace Length (mm)	136.3	119–149	1.67
Clutch Size	6.8	4–10	0.26
Gravid Body Mass (g)	397.4	262–526	15.05
Spent Body Mass (g)	315.1	208–420	12.08
Body Mass Lost During Nesting (g)	82.4	54–120	3.71
Clutch Mass (g)	37.7	21.5–61.2	1.71
Water Mass (g)	44.7	24.4–79.1	2.81

Data analyses were performed using SAS 6.10 for Windows (SAS Institute, 1988). Gravid body masses measured during sequential nesting migrations for the same clutch and gravid body masses for the first and second clutches were compared using paired t-tests. Relative rates of increase of reproductive material (log-transformed water and clutch mass) with increasing female size were examined using linear models. Comparisons of water and clutch mass (and their residuals) between reproductive categories were conducted with ANCOVA using CL as a covariate. Significance was accepted at $\alpha \leq 0.05$.

RESULTS

On average, female painted turtles lost approximately twice the mass during nesting than could be accounted for by the loss of clutch mass alone (Table 1). We estimated that females transported an average of 44.7 g of water to the nest (range 24.4–79.1; SE = 2.81), which comprised approximately 14% of mean spent body mass of females ($\bar{x}$ = 315.1 g; range 208–420; SE = 12.1) and 11% of mean gravid body mass ($\bar{x}$ = 397.4 g; range 262–526; SE = 15.1). Mean mass of transported water exceeded mean clutch mass ($\bar{x}$ = 37.7; range 21.5–61.2; SE = 1.71).

Gravid body masses of individual females captured on sequential nesting excursions with the same clutch were similar; the mean absolute difference between two gravid body masses was 0.04 g (SE = 2.16; n = 25; t = - 0.02; p = 0.98). By inference the amount of water transported was also similar (since clutch and soma mass would not have changed). The similarities in gravid masses indicated that weights taken during initial excursions could be used to calculate the amount of water transported when spent body mass was obtained at the end of subsequent nesting movements.

Masses of materials transported to nests were positively related to female body size (H_w1). Log-transformed estimates of water and clutch mass were positively correlated with CL (Fig. 2A, water mass, $F_{1,27}$ = 14.48; r^2 = 0.36; $p < 0.001$; Fig. 2B, clutch mass, $F_{1,27}$ = 33.70; r^2 = 0.56; $p < 0.001$). Female CL explained 67% of the variation in the combined mass of voided water and clutch (Fig. 3; $F_{1,27}$ = 52.81; r^2 = 0.67; $p < 0.001$). As the total mass (water and clutch) transported to nests increased, the

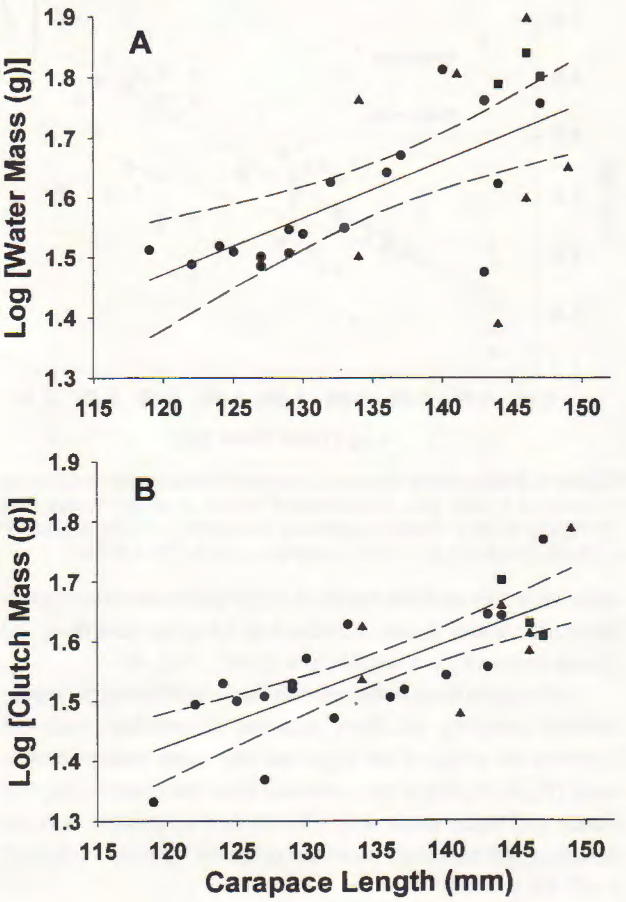

Figure 2. A. Relationship between voided water and female carapace length after logarithmic transformation of voided water. **B.** Relationship between clutch mass and female carapace length after logarithmic transformation of clutch mass. The regressions (solid lines) are significant for **A** ($F_{1,27}$ = 14.48; r^2 = 0.36; $p < 0.001$; equation: $y = 0.32 + 9.52x$) and for **B** ($F_{1,27}$ = 33.70; r^2 = 0.56; $p < 0.001$; equation: $y = 0.38 + 8.63x$). Circles indicate turtles laying their only clutch for the season. Triangles indicate estimates obtained from turtles laying their first of two clutches. Squares indicate estimates obtained from turtles prior to depositing their second clutch of eggs. Dashed lines represent 95% confidence intervals of the regression.

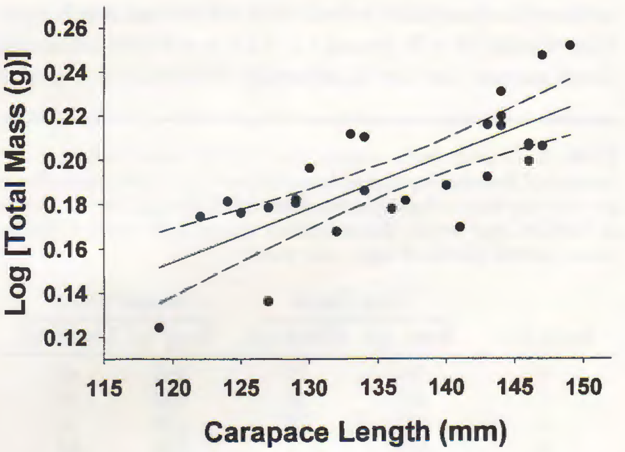

Figure 3. Relationship of total mass voided at nests (water plus clutch mass) with carapace length of females (F = 52.8; r^2 = 0.67; $p < 0.001$; equation: $y = 0.616 + 9.44x$). Dashed lines represent 95% confidence intervals of the regression.

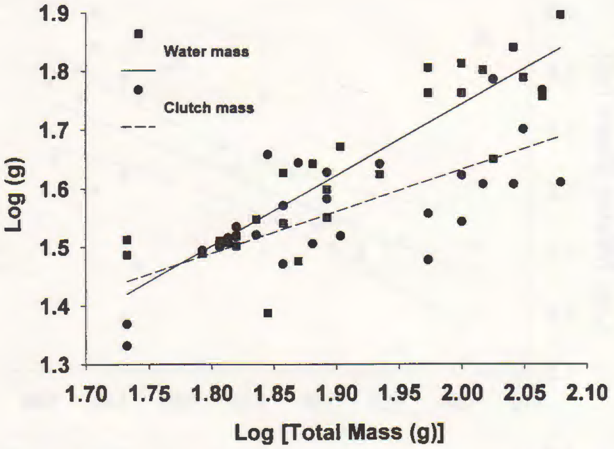

Figure 4. Relationship between component masses and total mass of material (water plus clutch mass) voided at nests (Water: F = 91.92; $r^2 = 0.78$; $p < 0.001$; equation: $y = -0.663 + 1.20x$; Clutch: F = 29.10; $r^2 = 0.53$; $p < 0.001$; equation: $y = 0.179 + 0.73x$).

mass of water and the mass of eggs increased disproportionately: water mass increased at a higher rate than did clutch mass ($F_{1,27} = 60.41$; $p = 0.001$; Fig. 4).

In females that produced only one clutch of eggs (reproductive category 1), there was no discernible trade-off between the mass of the eggs and the water transported to nests (H_w2). A plot of the residuals from the relationships of clutch and water mass with CL showed no pattern, and the means of the residuals were not different (paired $t = 0.000$; $p = 0.99$; $n = 18$).

Similar amounts of water were transported on nest excursions by females carrying their first and only clutch of the year and those carrying their first of two clutches (H_w3). Residuals of the relationship between the mass of water transported and CL of females in reproductive categories 1 (no enlarged follicles) and 2 (enlarged follicles) were not significantly different (ANOVA; $F_{1,23} = 0.00$; $p = 0.99$).

During 1996 and 1997, the size of first and second clutches were not different (paired $t = -1.29$; $p = 0.22$; $n = 13$). Gravid body masses of a sample of individual females captured on excursions to both first and second clutch nests were similar ($n = 7$; paired $t = 0.43$; $p = 0.68$); estimated clutch masses were not significantly different ($n = 5$; paired $t = -2.63$; $p = 0.06$; Table 2). The similarity between body masses occurred despite the additional mass of second clutch follicles in the first clutch gravid body mass (H_w4).

Table 2. Gravid body masses and clutch mass estimates for individual females depositing two clutches per season. First clutch gravid body mass = female soma, first clutch of eggs, second clutch of follicles, and water. Second clutch gravid body mass = female soma, second clutch of eggs, and water.

	First Clutch		Second Clutch	
Turtle No.	Body (g)	Clutch (g)	Body (g)	Clutch (g)
1	394	37	400	40
2	420	30	408	29
3	340	28	338	–
4	558	–	554	47
5	488	38	482	44
6	470	46	484	50
7	396	42	390	45
Means:	438.0	38.6	436.6	41.6

DISCUSSION

Observations of painted turtle nesting behavior on the ESGR indicate that transporting water to nests is an obligatory component of oviposition (i.e., all females that voided water upon capture during nesting excursions discontinued the nesting process). Results from the present study indicate that, on average, mass of water transported to nests exceeds clutch mass and is equivalent to approximately 14% of female spent body mass and 11% of gravid body mass. The consistency in the amount of water transported within clutches suggests that water estimates obtained are the upper limits of water storage capabilities and that females are maximizing the amount of water transported to nests. Transporting water to nests (in addition to eggs) probably represents a substantial energetic cost given the distance (up to 600 m from aquatic habitats) and the duration (approx. 1–4 hrs) of nesting forays (Christens and Bider, 1986; Congdon and Gatten, 1989; Lindeman, 1992).

Both clutch mass and mass of water transported to nests increased with female CL (Figs. 2A, B). Increased body cavity volume or possibly larger water storage organs (e.g., urinary bladder and cloacal bursae) appear to enable larger females to transport more water to nests than smaller females (H_w1). We found no evidence for the predicted volume trade-off between water and eggs (H_w2).

That similar amounts of water were transported by females laying one clutch per year and those carrying their first of two clutches leads to the conclusion that space available for water was not limited by the presence of second clutch follicles (H_w3). This conclusion assumes that component volume of the female soma (e.g., liver, fat bodies, and follicles) are not substantially different among individuals in reproductive categories 1 and 2. Therefore, in this specific case, the volume of enlarged follicles does not appear to limit the amount of water transported.

Given that masses of first and second clutches are not different, the similar body masses of individual turtles depositing their first and second clutches (Table 2) suggest that more water is carried to second clutch nests than to first clutch nests (H_w4). In addition, water estimates of second clutches females (reproductive category 3) fell above the predicted line derived from all water measurements (Fig. 2A), providing further support that absence of large follicles allows for increased water storage.

An alternative explanation for the similarity in gravid body masses between clutches is that females fed during the internesting period ($\bar{x} = 19$ days, range 10–21, SE = 0.56), contributing to an increase in second clutch gravid body mass. Trapping records from the ESGR indicate that gravid females rarely enter baited traps during the internesting period between clutches. That traps had been baited with a variety of vegetable and animal matter, and males and nongravid females were captured more frequently, suggests that gravid females feed infrequently during the internesting interval, and therefore, the contribution of gut contents to body mass is probably slight during this period.

Ambiguous test results for the effects of large follicles and eggs on water storage indicate the lack of a clear relationship among abdominal cavity volume, clutch contents, and stored water. Whereas comparisons of gravid body masses provide indirect evidence that individuals void more water with second clutches than with first clutches, the lack of a difference in the amount of water transported between females in reproductive categories 1 and 2 suggests no clutch volume – water volume trade-off. Given the small sample of second clutch females and the indirect nature of the water estimates, conclusions regarding the trade-off between reproductive material and water should be viewed as tentative. Moreover, an alternative explanation may be that size of the bladder and cloacal bursae, not body cavity volume, are the primary determinants of water volume carried to a nest.

The relative importance of water voided at nests to reproductive functions remains somewhat unclear. Reports of turtles voiding water onto the nest site prior to and during digging suggest that water facilitates nest excavation (Thoreau, 1884, cited in Babcock, 1919; Stromsten, 1923; Taylor, 1935; Cagle, 1937, 1950; Mahmoud, 1968; Ehrenfeld, 1979; this study). Voiding water probably enhances the ability of females to: 1) construct flask-shaped cavities in hard clay or dry sand substrates by softening the soil (Patterson, 1971), and 2) manage dry soil during construction of the nest (Thoreau, 1884). For example, turtles that nest in hard clay on the ESGR often void relatively large quantities of water into the nest hole during excavation, causing the hole to become filled with a viscous muddy liquid (see also Stromsten, 1923). In addition, moistened soil facilitates formation of nest plugs which help to maintain air space above the eggs during incubation (Cagle, 1950).

Additional evidence for the importance of moist soil to nest construction is the relationship between turtle nesting and rain. Peak nesting activity of *C. picta* appears to be associated with periods of rainfall (*pers. obs.*), as in other turtle species (Richmond, 1945; Ewert, 1985; Burke et al., 1996). Rain-moistened soil may facilitate nest construction, and possibly lessen risk of nest predation by obliterating visual and olfactory signs at nest sites. Yet, rain can be unpredictable or infrequent during the nesting season (Gibbons et al., 1983; Lindeman and Rabe, 1990), therefore, a dependence on rain could impose limits on reproductive opportunities. Water transport may allow turtles to deposit their eggs relatively independent of rainfall patterns.

Although water transport can broaden the range of environmental conditions conducive to nesting, the amount of transported water may not be adequate for nest construction during drought conditions. For example, during an unusually warm, dry nesting season (1987), water voided during excavation by several nesting females on the ESGR did not adequately condition the dry nesting substrate, resulting in the construction of funnel- instead of flask-shaped nest cavities. In turn, the collapsing sides of the funnel-shaped cavity caused some eggs to be broken by the females during covering and other eggs to be left partially exposed after nest completion (*pers. obs.*). The observations cited above suggest that the amount of water transported to nests can indeed influence nesting success and carrying less water on nesting excursions can potentially limit excavation under certain conditions.

Conant (1945) suggested that, in addition to facilitating nest construction, water discharged into the nest chamber may prevent egg desiccation. Given that water conductance levels of eggs are high early in incubation due to a moistened mineral layer in the eggshell (Ewert, 1985), eggs may desiccate quickly in nest cavities constructed in dry soils. Voiding water into the nest and/or nesting in association with rainfall may decrease the water potential gradient between soil and eggs, thereby reducing the probability of egg dehydration and providing water for immediate uptake. However, whether the amount of water voided in nests has a substantial effect on the water balance of eggs during early incubation remains unknown.

Water voided at nests has also been suggested to deter predators by providing a foul smell or taste at the nest site, although previous studies offer conflicting evidence. Other researchers have postulated that water discharged onto nests by turtles: 1) has a mild inhibitory effect on canine predators (Patterson, 1971), 2) attracts predators (Moll and Legler, 1971), and 3) neither attracts nor inhibits predators (Wilhoft et al., 1979). That the majority of nest predation on the ESGR occurs within a few hours of oviposition (Tinkle et al., 1981; Congdon et al., 1983, 1987) argues that the dominant predators (raccoons and foxes) are not substantially deterred by the presence of voided water on nests.

In conclusion, observations of painted turtles on the ESGR indicate that: 1) all females transport water from the marsh and void it during nest excavation, 2) the amount of water transported to nests increases with body size of females, 3) more water may be transported to second clutch nests than to first clutch nests, and 4) voided water functions to facilitate nest excavation and may reduce the dependence on rainfall for nesting opportunities. Overall, results from this study, as well as observations of water voiding in a diverse assemblage of other turtle species (Ehrenfeld, 1979), indicate that water voiding during nesting is an essential component of the nesting process.

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