

Experimental Analysis of an Early Life-History Stage: Water Loss and Migrating Hatchling Turtles

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The effect of water dynamics is well known for some aspects of turtle biology, particularly for egg incubation. The role water plays during migration from the nest to the aquatic environment, however, is not well understood. To evaluate water loss and movement patterns of hatchling turtles during migration, we conducted an experimental release of 463 hatchling snapping turtles, *Chelydra serpentina*, under ecologically relevant field conditions. We recaptured 62.9% of hatchlings released, and 90% of these were caught during the first four days following release. Hatchlings migrating for less time lost more water than those migrating for a longer time; changes in water content ranged from +1.2% to -4.7%. Mean air temperature during the recapture interval was positively correlated with water loss. Furthermore, hatchlings lost significantly more water when recaptured during periods with no rainfall compared to intervals with rainfall (14.5% and 8.3% water loss, respectively). Additionally, more hatchlings were recaptured during precipitation events and intervals with intermediate mean air temperatures. Alternative strategies for migration may exist such that some hatchlings move quickly to the water, minimizing exposure to predators, but increasing water loss and risk of desiccation. Other hatchlings may wait for optimal weather conditions (i.e., moderate air temperatures and precipitation), increasing exposure to predators, but limiting water loss. Further studies are needed to elucidate the relative risks and benefits associated with each strategy.

WATER plays an important role in all stages of the life-history of aquatic turtles from eggs to hatchlings to adults. Moisture content of the incubation environment is important for hatching success and strongly influences hatchling phenotypes (Packard, 1999; Tucker and Paukstis, 2000). The hydric environment during incubation affects many hatchling traits including size (Packard, 1991, 1999), growth (Morris et al., 1983), locomotor speed (Miller, 1993), and desiccation tolerance (Finkler, 1999). Adult aquatic turtles live almost entirely in water except for brief trips onto land for egg laying and occasional terrestrial forays (Ernst et al., 1994). Water relations for hatchlings during their migration, after hatching from a protective egg and before reaching the aquatic habitat, are poorly understood. Aquatic turtles may be particularly vulnerable to water loss during migration to aquatic habitats.

Migration from the nest to water represents a crucial phase in the early life-history of hatchling aquatic turtles. Mortality during this time likely results from predation or desiccation (Janzen, 1993; Janzen et al., 2000a,b). However, little is known about water loss during migration and its implications for hatchling survival and behavior. Hatchlings generally lose mass during migration to the water (Janzen et al., 2000a,b; Tucker, 2000), but the effects of hatchling behavior, microhabitat, and weather conditions on

change in mass are poorly understood. It is possible that hatchlings employ different migration strategies depending on their hydration level, the amount of vegetation surrounding nest sites, temperature, precipitation, relative humidity, or risk of predation. Additionally, patterns of hatchling movement during migration may be influenced by unpredictable weather conditions during the hours to weeks they are on land (Filoromo and Janzen, 2002), and may be associated with temperature and precipitation conditions that minimize water loss (Tucker, 2000).

To investigate water dynamics and patterns of hatchling movement during migration from nest to water, we conducted an experimental release of hatchling snapping turtles, *Chelydra serpentina*, at a sand prairie along the eastern bank of the Mississippi River in Illinois. We were interested in the effects of hatchling behavior, microhabitat characteristics of the nest site, air temperature, and precipitation on water loss and the number of hatchlings recaptured. Little is known about water loss by hatchlings during migration or about the effect of air temperature and precipitation on the pattern of movement to the water (but see Tucker, 1997, 1999, 2000).

MATERIALS AND METHODS

For detailed methods on egg collection, egg incubation, and hatchling release see Kolbe and

Janzen (2001). In May 1998, 12 clutches of snapping turtle eggs were collected from sand prairie habitat along the Mississippi River in Whiteside and Carroll Counties, Illinois. All eggs were incubated in the laboratory at a moist water potential of -150 kPa and fluctuating temperatures of 28 C and 31 C for 12 h each. Turtles used in the experimental release hatched in late July and early August 1998 and were housed individually in plastic cups with a moistened paper towel at the same temperature regime as incubation. Hatchlings were weighed to the nearest 0.01 g and individually marked for future identification by a combination of marginal scute notching and photocopying of plastrons (Janzen et al., 2000b).

On 11 August 1998, a total of 463 hatchlings was released from eight release points that varied in microhabitat characteristics such as distance from the water, amount of ground vegetation, slope, and aspect. We constructed a 200 m \times 75 m drift fence enclosure with pitfall traps to recapture hatchlings migrating down slope to the Mississippi River and to insure that no hatchlings left the study area (see fig. 2 in Kolbe and Janzen, 2001). Pitfall traps were checked at 0700, 1300, and 1900 h for the 12 days of the experiment, from 1300 h on 11 August to 0700 h on 23 August 1998.

At recapture, hatchlings were identified and weighed. The change in mass from release to recapture was converted to the percent change in mass and arcsine transformed for statistical analyses. The majority of the change in mass from release to recapture likely reflects water loss during migration. A small percentage of change in mass may represent yolk metabolism (Tucker et al., 1998; Finkler, 1999, 2001), but less than 1% of live mass was dry yolk solids in hatchling red-eared slider turtles (Tucker et al., 1998). Moreover, dry yolk solids for snapping turtles incubated at the same water potential used in this study (i.e., -150 kPa) represented only 1.7% to 2.9% of hatchling mass (Finkler, 1999). Therefore, if some yolk metabolism occurred while hatchlings were migrating, it likely represents a negligible amount of the change in mass of hatchlings compared to water loss. For the purposes of this study, we considered the change in mass of hatchlings from release to recapture to be water loss and refer to it as such throughout this study. We recorded time from release to recapture (h), dispersal distance (the minimum straight-line distance from release point to recapture pitfall trap; m), and total number of recaptures per interval. Air temperatures at ground level over the entire period of the release were recorded with a HOBO® XT

temperature logger (Onset Computer Corporation, Pocasset, MA) placed under a shrub near the drift fence and rainfall was monitored with a rain gauge.

We determined whether there was a significant difference in mean air temperature among the three recapture intervals (AM: 0700–1300; PM: 1300–1900; Overnight: 1900–0700) using ANOVA. The influences of hatchling behavior and microhabitat characteristics of the release points on percent water loss of hatchlings were evaluated with linear regression. Independent variables for these analyses were time from release to recapture, dispersal distance, distance of the release point from the recapture fence, amount of ground vegetation, slope, and aspect. To determine the effect of air temperature and precipitation on percent water loss, we also used linear regression models. We used the mean air temperature and the amount of precipitation for the interval during which a hatchling was recaptured as the independent variables. The difference in percent water loss of individuals recaptured during intervals with and without precipitation was compared using a *t*-test.

We used a chi-square test to determine whether the number of hatchlings recaptured during intervals with precipitation and those without precipitation were different from a uniform distribution of hatchling recaptures. The effect of air temperature on the number of recaptures was addressed by comparing the number of recaptures in the three recapture intervals (i.e., AM, PM, and overnight) to the number expected from a uniform distribution using a chi-square test (Sokal and Rohlf, 1995).

RESULTS

Over the 12 days of the experimental release, 291 of the 463 (62.9%) hatchlings released were recaptured. Almost 90% of recaptures occurred during the first four days of the experiment (Fig. 1). We collected water loss data on 289 of the recaptured hatchlings, and all 291 hatchlings were included in analyses of the number of recaptures. Only one hatchling gained water. The difference in percent water ranged from a gain of 1.2% to a loss of 24.7% (Fig. 2, Table 1). Mean air temperatures differed significantly among the three recapture intervals ($F_{2,32} = 48.09$, $P < 0.0001$) with a mean air temperature of 19.7 C for the overnight, 23.3 C for the AM, and 27.9 C for the PM intervals (Fig. 1). During the experimental release, 131 snapping turtle and 19 Blanding's turtle, *Emydoidea blandingii*, hatchlings from naturally incubated nests were caught in either our pitfall traps or in the vicin-

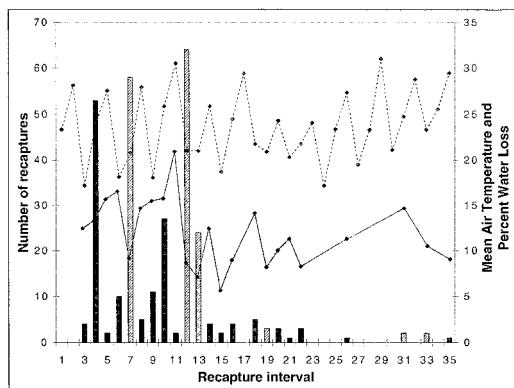


Fig. 1. Number of hatchlings recaptured during each of the 35 recapture intervals. Interval 1 was the 1300 h check on 11 August 1998, interval 2 was the 1900 h check on 11 August 1998, interval 3 was the 0700 h check on 12 August 1998, and so on. This pattern was continued for all 35 intervals. Note that every 0700 h check was a 12-h interval, whereas 1300 and 1900 h checks were 6-h intervals. Hatched bars indicate intervals when precipitation events occurred and solid bars indicate no precipitation. Precipitation amounts for the intervals when it rained are as follows: Interval 7 = 5 mm, Interval 12 = 10 mm, Interval 13 = 2 mm, Interval 19 = 12 mm, Interval 31 = 9 mm, and Interval 33 = 8.5 mm. The dashed line indicates the mean air temperature for each recapture interval and the solid line indicates the mean percent water loss for hatchlings recaptured in each recapture interval.

ity of our release site. Additionally, the emergence of snapping turtle hatchlings was monitored for three natural nests. Hatchlings from two nests emerged asynchronously, one from 13–23 August 1998 and the other from 15–20 August 1998, and hatchlings from one nest emerged synchronously on 20 August 1998. Thus, the timing of our experimental release (11–23 August) was ecologically relevant for the summer of 1998.

Time from release to recapture had a significant inverse effect on percent water loss ($r = -0.22, P = 0.0002$), but dispersal distance had

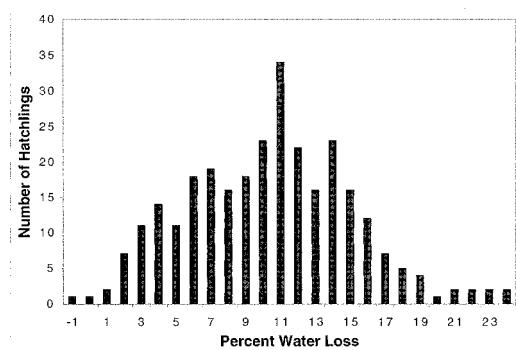


Fig. 2. Number of hatchlings recaptured in each water loss category ranging from -1% to 24%.

no effect ($r = 0.04, P = 0.47$). Hatchlings that took less time to reach the drift fence lost more water than hatchlings that were migrating for a longer time. Hatchlings that dispersed farther distances, however, did not show greater water loss than hatchlings that traveled shorter distances. None of the microhabitat characteristics that described release points had an effect on percent water loss of hatchlings: distance from the water ($r = 0.03, P = 0.64$), amount of ground vegetation ($r = 0.05, P = 0.39$), slope ($r = 0.01, P = 0.87$), or aspect ($r = 0.10, P = 0.15$). Time spent migrating to the drift fence was the only behavioral factor that influenced water loss in hatchlings.

The mean air temperature during the interval in which a hatchling was recaptured was significantly correlated with percent water loss ($r = 0.33, P < 0.0001$). Hatchlings lost more water when recaptured during an interval with a higher mean temperature. Precipitation also had a significant effect on water loss ($r = -0.45, P < 0.0001$) such that hatchlings lost less water if recaptured during heavier precipitation events (Fig. 1, Table 1). During the first four days of the experiment (intervals 1–13 in Fig. 1), when most hatchlings were recaptured, there was a significant difference in the mean percent water loss of hatchlings for intervals with and without

TABLE 1. MEAN (SD) AND RANGE FOR RELEASE MASS, RECAPTURE MASS, AND PERCENT WATER LOSS OF THE SNAPPING TURTLE HATCHLINGS IN THE EXPERIMENTAL RELEASE. The three categories are all hatchlings, those recaptured during intervals with precipitation, and those recaptured during intervals with no precipitation.

	All hatchlings	Precipitation	No precipitation
Release mass (g)	10.60 (1.53)/6.15–13.52	10.58 (1.52)/6.15–13.52	10.62 (1.54)/6.25–13.45
Recapture mass (g)	9.45 (1.46)/5.21–13.17	9.70 (1.49)/5.56–13.17	9.16 (1.39)/5.21–12.50
Water loss (%)	10.92 (4.72)/–1.20–24.72	8.41 (3.91)/–1.20–23.54	13.74 (3.87)/4.05–24.72
Number of hatchlings	289	153	136
Number of intervals	35	6	29

precipitation ($t = 12.95$, df = 255, $P < 0.0001$). Hatchlings recaptured during intervals without precipitation had a mean percent water loss of 14.5%, whereas recaptures during a precipitation event had only 8.3% water loss (Fig. 1, Table 1).

Over five times as many hatchlings per interval were recaptured in the six intervals with precipitation as opposed to the 29 intervals with no precipitation events (Table 1), which is many more than expected compared to a uniform distribution of recaptured hatchlings ($\chi^2 = 37.20$, df = 1, $P < 0.0001$). Indeed, 51.9% of hatchlings were recaptured during these six precipitation events (Fig. 1, Table 1). Significantly more hatchlings (59.8%) than expected were recaptured during the AM interval (i.e., 0700–1300; $\chi^2 = 146.8$, df = 2, $P < 0.0001$), which was characterized by intermediate mean air temperatures. Fewer hatchlings (6.2%) than expected were recaptured during the PM interval (i.e., 1300–1900), a period with high mean temperatures. Finally, the overnight (i.e., 1900–0700) interval had the expected number of hatchlings (34.0%) recaptured and had low mean temperatures. Thus, more hatchlings were recaptured during intermediate temperatures and precipitation events.

Almost 24% of the total number of recaptures occurred during Intervals 3–6, a period where recaptured hatchlings had increasing water loss (Fig. 1). Recaptures during Interval 7, which had 5 mm of rain, accounted for 20% of the total number of recaptures. Hatchlings recaptured during this rainfall event lost significantly less water (8.9%) than hatchlings recaptured before then (13.7%; $t = 7.08$, df = 121, $P < 0.0001$). This same pattern was repeated from intervals 8–13 (Fig. 1). Hatchlings recaptured during the rain (intervals 12–13) lost significantly less water ($t = 11.23$, df = 130, $P < 0.0001$) than those recaptured during periods with no precipitation (7.9% vs 15.7%, respectively). Hatchlings showed increasing water loss when recaptured before precipitation events and then a sharp decrease in water loss during intervals with precipitation (Fig. 1).

DISCUSSION

Two likely causes of mortality of hatchling turtles during migration from the nest to water are predation and desiccation (Finkler, 1999, 2001; Janzen et al., 2000a), although parasitism, disease, and insufficient energy may also contribute to hatchling mortality (Vogt, 1981; Congdon et al., 1983). Hatchling behavior, physiology, and morphology may all influence hatchling

mortality. Some experimental releases of hatchlings are beginning to disentangle the relationship between predation and hatchling phenotypes (Janzen et al., 2000b; Tucker, 2000; J. K. Tucker, G. L. Paukstis, and F. J. Janzen, unpubl.). Far less is known about water loss and risk of desiccation during the overland migration of a hatchling aquatic turtle. Patterns of hatchling water loss in this study were linked to air temperature, precipitation, and behavior, but not to microhabitat. Air temperature and precipitation influenced hatchling movement patterns as well. Documenting these patterns under ecologically relevant field conditions is necessary to understand the influence of water loss on hatchling mortality.

Hatchlings lost more water when they took a shorter time to reach the fence in this study. Higher temperatures and lack of precipitation also resulted in hatchlings with greater water loss. Time and weather conditions were confounded for the beginning of the experimental release (intervals 1–7 in Fig. 1). The repeated pattern of increasing water loss in the absence of precipitation and a marked decrease in water loss during precipitation events (intervals 8–13), however, suggests that precipitation and possibly air temperature have a stronger influence on water loss than time alone. These findings suggest that alternative strategies may exist for hatchling movement to the water. A trade-off between the amount of time exposed to predators and the increased risk of dehydration when moving under harsh meteorological conditions is one possibility. Hatchlings may endure some water loss to avoid prolonged exposure to potential predators. Alternatively, hatchlings may conserve water resources during times of unfavorable environmental conditions (i.e., high temperatures and no precipitation), possibly through microhabitat selection (Finkler et al., 2000) or burying behavior, and move toward the water during periods with moderate temperatures and some precipitation (Tucker, 2000). During periods of limited movement, hatchlings may also lose water at the same rate as migrating hatchlings, then take up water while moving toward the water during precipitation events. Although we did not detect an effect of microhabitat on water loss in this study, microhabitat influenced hatchling survival and behavior during migration (Kolbe and Janzen, 2001), and wet-incubated hatchlings from Nebraska tended to move more in low vegetation compared to their dry-incubated counterparts (Finkler et al., 2000). In a study of interspecific differences in hatchling migration, Tucker (2000) found that the smaller painted turtle,

Chrysemys picta, migrated significantly faster than the larger red-eared slider, *Trachemys scripta*. Hatchlings of both species lost similar amounts of absolute mass, but this represented a larger relative loss for painted turtles (10.3%) over red-eared sliders (3.8%). Additionally, red-eared slider movements increased during rainfalls (Tucker, 1997, 1999, 2000). Interestingly, both of these strategies were observed for snapping turtles in our study. Some hatchling snapping turtles migrated quickly and lost more water while others moved during precipitation events, mitigating water loss.

Hatchlings recaptured before or between precipitation events lost significantly more water than hatchlings recaptured during rainfall (Fig. 1, Table 1). A similar pattern of recapturing hatchlings during rainfall events was detected in red-eared sliders (Tucker, 2000). When considering the first four days of this study (i.e., intervals 1–13), when 90% of recaptures occurred, half the total number of hatchlings ($n = 146$) migrated during the three precipitation events and lost less water than the 38% of hatchlings that moved during dry periods. Although precipitation and air temperatures significantly influenced hatchling movement patterns, several important questions still remain, including (1) how much water can hatchlings lose before performance is adversely affected or they die and (2) to what extent do hatchlings gain an advantage of avoiding predators by migrating faster? That is, what is riskier for a hatchling turtle, losing water or staying on land longer?

Evidence exists that well-hydrated snapping turtle hatchlings have increased locomotor performance over dehydrated hatchlings (Miller et al., 1987; Miller, 1993; Finkler, 1999). Hatchlings from eggs incubated on wet substrates were faster than hatchlings from dry substrates (Miller et al., 1987; Finkler, 1999), and hatchling performance dropped as water content (i.e., tissue hydration) decreased (Finkler, 1999). These studies manipulated water content through incubation conditions, whereas in our study hatchlings were incubated under only relatively wet conditions. Turtles in our study were wet-incubated (i.e., -150 kPa), and they lost a maximum of $\sim 8\%$ of their water content by body mass (estimated with data from Finkler, 1999). Loss in water content equivalent to 10% of body mass resulted in large differences in hatchling crawling speed for dry-incubated hatchlings (Finkler, 1999). It is unclear whether water losses experienced by the fairly well-hydrated hatchlings in our study affected locomotor performance. In general, however, water

losses observed in this study have the potential to adversely affect hatchling performance.

Several experimental releases of hatchlings have documented a relationship between body size and survival (Janzen, 1993; Tucker and Paukstis, 1999; Tucker, 2000), with larger hatchlings usually showing increased survival (but see Congdon et al., 1999). Avian predators differentially killed smaller red-eared slider hatchlings (Janzen et al., 2000a,b). Interestingly, predation on these hatchlings was stochastic with respect to body size when differences in locomotor behavior were controlled experimentally (J. K. Tucker, G. L. Paukstis, and F. J. Janzen, unpubl.). Thus, natural selection in previous studies was likely not acting directly on body size, but indirectly on the positively correlated trait of locomotor speed or propensity to move. That is, larger hatchlings moved faster and therefore reached the water (or drift fence) sooner, minimizing exposure to potential predators. In our study, hatchlings migrating during higher temperatures and no precipitation risked decreased performance resulting from water loss, but also minimized exposure to predation. Thus, our data provide some support for alternative strategies of hatchling migration but lack of knowledge of sources of mortality for migrating hatchlings makes this hypothesis tentative. Some evidence exists for species differences in hatchling migration behavior. Painted turtles (Tucker, 2000), and some snapping turtles (perhaps well-hydrated ones; this study; Finkler et al., 2000) may move quickly to the water suffering greater water loss, but decreasing predation risk. Alternatively, red-eared slider turtles (Tucker, 2000), some snapping turtles (perhaps poorly hydrated ones; Finkler et al., 2000), and Blanding's turtles (Butler and Graham, 1995; Standing et al., 1997) may wait for favorable conditions reducing water loss, but increasing predation risk. Conditions under which these alternative "fast" and "slow" migration strategies are observed need to be explored further.

Water relations are of central importance to the life-history of aquatic turtles (e.g., Packard, 1999). Water loss during migration has the potential to impair locomotor behavior (Finkler, 1999) and may result in desiccation mortality. Hatchling behavior (i.e., time from release to recapture) and especially weather conditions have the largest impact on water loss. Weather conditions also affect movement patterns, and, although weather cannot be predicted, monitoring such conditions during experimental releases is necessary to better understand the functional relationship between environmental

factors and hatchling migration and to account for abnormal conditions (Tucker and Paukstis, 1999; Filoromo and Janzen, 2002). Future studies should include within and among population or species comparisons to tease apart differences in water loss and migration patterns resulting from historical influences versus current environmental conditions (Finkler et al., 2000; Tucker, 2000).

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