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Dispersal of Hatchling Ouachita Map Turtles (*Graptemys ouachitensis*) from Natural Nests on the Lower Wisconsin River, Wisconsin

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ABSTRACT. – Despite its importance to individual fitness and population dynamics, the dispersal behaviors of most neonate freshwater turtles after nest emergence are poorly known. We studied the initial dispersal tendencies of neonate Ouachita map turtles (*Graptemys ouachitensis*) exiting natural nests during 2015–2017 along the Wisconsin River, Wisconsin. Overall, dispersal was nonrandom, and hatchlings largely oriented toward the nearest substantial vegetative cover, a woodland north of the nesting area. However, variation sometimes occurred in routes taken among hatchlings within a clutch. Directional changes within an individual's dispersal track, including route reversals, were also observed. As our work appears to be the first to use stand-alone trail cameras as a primary data-gathering tool for a hatchling dispersal study, it highlights the potential benefits and limitations of this technique for similar research.

KEY WORDS. – Reptilia; Testudines: Cheloniidae; *Graptemys ouachitensis*; dispersal; hatchling dispersal; hatchling turtle; monitoring; Ouachita map turtle; trail camera

Various proximate physiological and behavioral factors combine to directly influence the survivorship and fitness of freshwater turtle hatchlings (reviewed in Baker et al. 2013). In turn, these impacts exert ultimate effects on turtle population structure and thus are of considerable importance in species persistence and in conservation management efforts (e.g., Doody et al. 2001; Nagle et al. 2004; Congdon et al. 2011; Gibbons 2013).

Among these factors are postemergence dispersal behaviors, which influence both predation risk and the likelihood of finding suitable transitional microhabitats soon after nest exit (e.g., Tuttle and Carroll 2005; Congdon et al. 2011; Pappas et al. 2017). Failure to locate and disperse toward microhabitats that ameliorate temperature extremes and desiccation risks increases the risk of hatchling mortality (e.g., Kolbe and Janzen 2002). Similarly, the amount of time spent dispersing from nests and the directness of routes to vegetative or aquatic dispersal targets have implications for terrestrial predation risks (Janzen et al. 2007). Studies of hatchling emergence can inform land management decisions by identifying important microhabitats used by newly dispersing turtles to ensure they are maintained and managed.

Despite its biological importance, however, our knowledge of hatchling dispersal patterns for freshwater turtles in natural settings is limited and often anecdotal, mostly because of the historical difficulty of collecting data in field settings (e.g., Doody et al. 2001; Plummer 2007; Muldoon and Burke 2012). For example, the current potential for radiotelemetry in hatchling dispersal studies is limited by the large mass of transmitters relative to that

of turtle hatchlings (e.g., often over the 10% mass limit; Muldoon and Burke 2012). Further, many study designs impose restraints on natural hatchling behavior (e.g., dispersal hindered by drift fences or collection barriers) or yield imprecise data due to incomplete site visitation or monitoring schedules (Lovich et al. 2014).

As a novel way to gather these otherwise difficult-to-obtain data, the present study employed stand-alone, modern trail cameras as primary data collection tools, building on previous research on turtle hatchling emergence that used earlier camera technology (Doody et al. 2001; Plummer 2007). This camera-based approach yielded unique observational data on the initial dispersal tendencies of newly emerged Ouachita map turtle (*Graptemys ouachitensis*, Cagle 1953) hatchlings from natural nests. Study results complement recent experimental findings for this species (Pappas et al. 2017) and provide useful points of reference for comparisons with sympatric congeners, including the commonly overwintering hatchlings of *Graptemys geographica*, and other emydids. Finally, the present study demonstrates some of the advantages and limitations of using current trail camera technologies in elucidating details of hatchling emergence in field settings.

METHODS

Study Site and Time Lines. — This study is part of a larger investigation of hatchling emergence ecology conducted at a *G. ouachitensis* nesting site along the lower Wisconsin River within 10 km of Spring Green,

Wisconsin, from 2015 to 2017 (Geller et al. 2020). The site is an area of glacial outwash sand approximately 132 m² ($\sim 22 \times 6$ m) in size, oriented on a northeast-to-southwest longitudinal axis ~ 52 m west of the riverbank. The western half slopes downward to the north and south at approximately 1° – 10° on either side of a gently rounded apex, while the eastern half is a variably graded southward slope of approximately 1° – 6° . The overall east-to-west topography ranges downslope from 0° – 3° . Usually, dry drainage sloughs, approximately 0.5–1.0 m lower than the nesting substrate, surround much of the nesting area.

The site is bordered on the north and west sides by dry-mesic hardwoods (primarily river birch [*Betula nigra*] and maple [*Acer* spp.]) with dense understories of shrubs (especially *Rhus radicans* and *Rhamnus cathartica*) and on the east and south sides by drier, more open habitats with scattered trees (primarily oak [*Quercus* spp.] and ash [*Fraxinus* spp.]). The woodland to the north is the nearest, approximately 9 m from the edge of the nesting area. The nesting habitat is composed of various xerophytic herbaceous vegetation covering approximately 20% of the surface, predominantly common ragweed (*Ambrosia artemisiifolia*), with the remainder being open sand.

Newly constructed *G. ouachitensis* nests were located during late May to early July of each study year by daily, mid-afternoon, on-site review of data from 2 digital trail cameras (RECONYX,™ Inc., Holmen, WI) monitoring the nesting area using a laptop computer. Cameras were angled downward 30° within sheltering boxes mounted on poles at each end of the nesting area at heights of approximately 2.5 m, yielding a combined field of view (FOV) large enough to survey the entire site. Cameras were programmed to take continuous time-lapse (TL) images at 1-min intervals and provided multiple images of all nesting events. Thereafter, nests were protected from aboveground predators by capped, cylindrical screen cages (56-cm diameter, 31 cm high) made of 14-gauge, 5×10 -cm wire mesh; this lattice is large enough to minimally obstruct views of the surface by the overhead cameras (see below). To further limit nest depredation, nest cage sides were wrapped with 2.5-cm chicken wire, which had a mesh size large enough to allow hatchling dispersal. Half-meter-wide lengths of $\frac{1}{2}$ -inch hardware cloth were also secured to the substrate under the peripheries of the nest cages to prevent predators from digging under them. A plastic tag labeled with a unique identification code was affixed to the top of each nest cage to ensure correct nest identity. To facilitate interpretations of initial hatchling dispersal bearings within the camera FOV, each nest identification tag was attached at due north, and each nest cage was positioned such that the wire mesh forming the top was aligned with cardinal compass bearings.

Overall substrate slope and topographic orientation of each nest was determined using a circular inclinometer (model AVF100/5; Level Developments Ltd, Surrey, UK) and compass placed on an elevated, 1.0-m-diameter wood disk centered over the nest location. The single slope



Figure 1. Example of dedicated carrying plate and attached monitoring camera in position over nest cage. Photo by G. Geller.

vector yielded in this manner reflected the immediate-proximity topographic environment presented to newly emerged hatchlings.

Camera Monitoring and Data Collection During Hatchling Emergence Period. — Observational data on hatchling emergence were collected from mid-August to early October via laterally movable dedicated cameras (RECONYX models with either low-glow or no-glow infrared emissions, programmed to take continuous TL images at 1-min intervals) suspended over each nest (Fig. 1). Each camera was affixed to the underside of a $\frac{1}{2}$ -inch exterior plywood carrying plate (15.2×16.5 cm) and held at a height of approximately 1 m above the substrate by tightly strung support wires attached to metal rails at the periphery of the nesting area. Cameras were pulled by attached strings to the nest site perimeter for data card and battery change-outs (every 10 d), thereby avoiding trampling vegetation and eliminating the need to install camera support structures near nests.

Initial dispersal bearings (azimuth from north) taken by hatchlings within and sometimes just beyond (~ 0.3 m) nest cage boundaries were assessed by placing a transparency of a 360° demarcated circle directly on the computer screen, centered and directionally aligned over the exit hole during image review. Only those bearings produced by hatchlings moving in relatively linear, nonvarying paths were used in analyses of dispersal tendencies. Additional cameras were positioned more remotely to survey the overall nesting site and nearby areas in an attempt to better delineate hatchling dispersal outside of nest cages. We have also incorporated observations of *G. ouachitensis* hatchling dispersal gained during past research on this and another nearby nesting site into our analyses.

Although nest emergence is a process first evidenced by cracks appearing in the substrate surface, we used the time stamp on the first 1-min TL camera image showing complete hatchling exit from the nest hole to designate the time of hatchling emergence. Hatchling emergence was

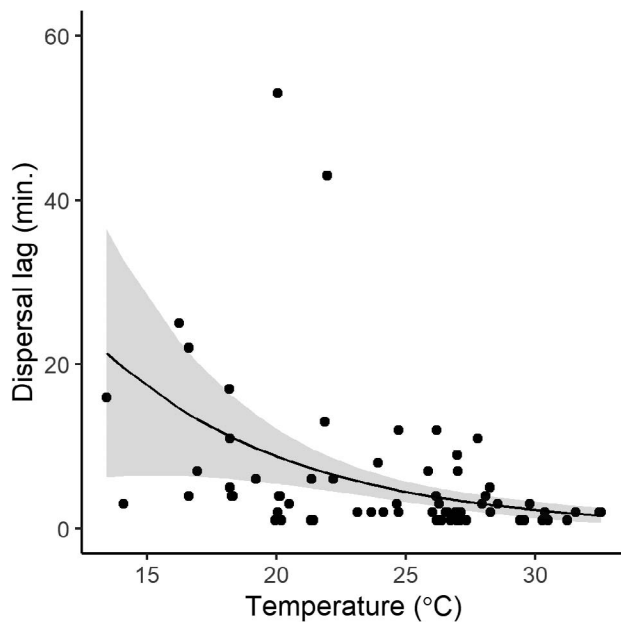


Figure 2. Relationship between temperature and time between emergence and dispersal for hatchlings that exhibited a lag ($n = 63$). The line represents fitted values from a gamma regression model; the gray shaded area is the 95% confidence interval.

considered to be diurnal if it occurred in the daytime, including dawn and dusk twilight periods, and nocturnal if it occurred in the nighttime between the hours of evening and morning astronomical twilight (i.e., astronomical night, when the sky is no longer illuminated by the sun).

Statistical Analysis. — We used several statistical methods to examine the dispersal ecology of emerging hatchlings. We examined the probability that hatchlings would wait to disperse after first appearing at the surface and the relationship between the lag to dispersal (when it occurred) as a function of temperature using binomial regression with a logit-link function and gamma regression with a log-link function, respectively. We used binomial regression with a logit-link function and circular predictor variable (cosine and sine of pre-dispersal orientation) to examine whether initial orientation affected the probability that a hatchling would change orientation between emergence and dispersal. We summarized pre-exit orientation (camera-visible, hatchling body position before emergence onto the surface) and dispersal direction (within overhead camera FOV) data using trigonometric moments (mean $[\mu]$ and mean resultant length $[\rho]$) and the circular standard deviation and tested for deviation from a uniform circular distribution with Watson's U^2 (Pewsey et al. 2013). We also used Watson's U^2 for analysis of dispersal toward dominant features on the landscape by binning diurnal emergences by nesting area (eastern and west-central) and to examine directionality of nocturnal hatchling emergences. We set statistical significance at $\alpha < 0.05$ for all tests. Reported sample sizes reflect varying numbers of camera records available for analysis,

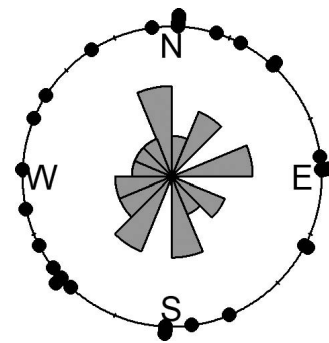


Figure 3. Distribution of initial pre-exit body orientations of first-of-the-day Ouachita map turtle hatchlings (*Graptemys ouachitensis*) on the lower Wisconsin River, Wisconsin, 2015–2017 ($n = 31$).

as influenced by camera position, intervening vegetation, and other variables.

RESULTS

Behavior and Initial Dispersal Bearings of Hatchling Turtles at Emergence. — A total of 48 *G. ouachitensis* nests were successfully protected from predation at our monitoring site (20 in 2015, 19 in 2016, and 9 in 2017), although some nests failed to produce emergent hatchlings due to flooding and other influences (see Geller et al. 2020). All hatchling emergence occurred during the fall. During diurnal periods, emerging hatchlings spent up to 53 min (mode = 2, SD = 8.59, $n = 79$) before exiting the nest, sometimes in bouts separated by withdrawals back into the exit hole. Although temperature did not affect the probability that hatchlings would wait to disperse (logistic regression $\beta_{\text{temp}} = -0.10$ (SE = 0.071, $z = -1.46$, $p = 0.15$), the lag between emergence and dispersal, when it occurred, was longer at colder temperatures (gamma regression with log link: $\beta_{\text{temp}} = -0.13$ [SE = 0.03], $t = -4.60$, $p = 2.2 \times 10^{-5}$; Fig. 2).

Body orientations immediately before nest exit of the first emergent hatchlings on a given day could not be distinguished from a uniform circular distribution ($\mu = 247^\circ$; $\rho = 0.022$; SD = 2.77; Watson's $U^2 = 0.040$, $p > 0.10$; Fig. 3) and were not reliable indicators of initial dispersal bearings within nest cage FOVs (using a 45° similarity criterion) because hatchlings often reoriented soon after emergence (53.6% of the time, $n = 84$). Hatchling body orientation at nest exit did not affect whether a hatchling changed orientation between emergence and dispersal (binomial regression with circular predictor variable: $\beta_{\cos(\text{initial orientation})} = 0.18$ [SE = 0.31], $z = 0.58$, $p = 0.56$; $\beta_{\sin(\text{initial orientation})} = -0.023$ [SE = 0.35], $z = -0.065$, $p = 0.95$); hatchlings were equally likely to change dispersal vectors regardless of which way they were initially facing at nest hole exit.

While variation was observed, diurnal hatchling dispersal bearings within the ~ 1 -m-diameter camera FOVs ($n = 81$) differed statistically from a uniform circular distribution (Watson's $U^2 = 0.56$, $p < 0.01$), with

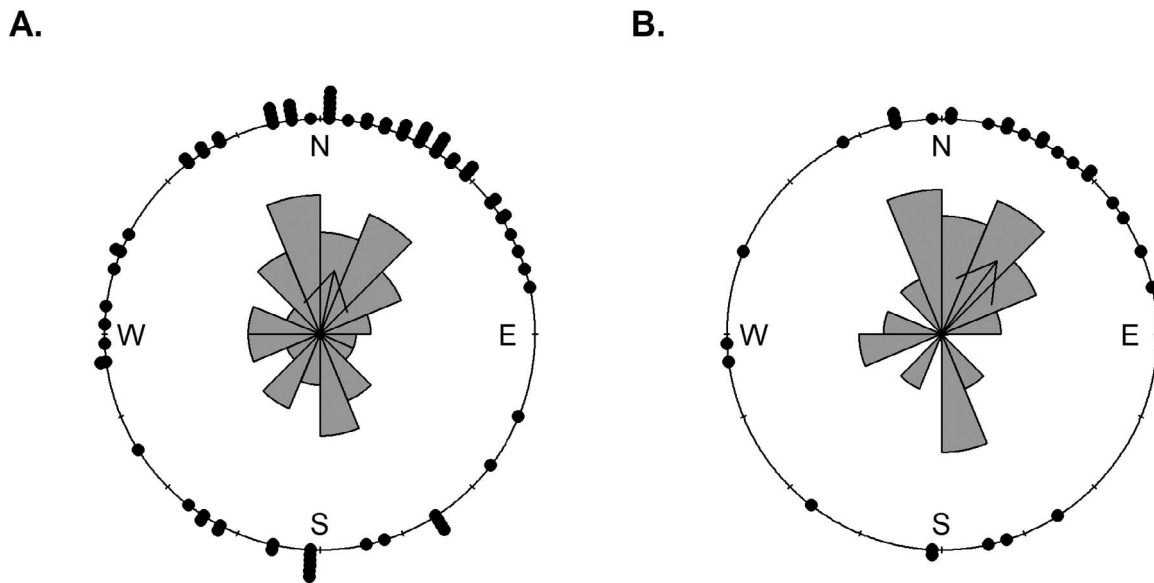


Figure 4. Distribution of initial dispersal bearings for (A) all diurnal ($n = 81$) and (B) diurnal first-of-the-day ($n = 30$) Ouachita map turtle hatchlings (*Graptemys ouachitensis*) on the lower Wisconsin River, Wisconsin, 2015–2017. Arrow direction represents mean dispersal orientation; length of arrow is equal to ρ , the mean resultant length (a measure of concentration about the mean).

a mean dispersal bearing of 12.6° ($\rho = 0.30$, $SD = 1.5$) and a mode of 360° (Fig. 4A). Dispersal bearings for first emergent hatchlings on a given day ($n = 30$) also differed from a uniform circular distribution ($U^2 = 0.38$, $p < 0.01$), with a mean dispersal bearing of 36.7° ($\rho = 0.42$, $SD = 1.3$) and a mode of 345° (Fig. 4B). This direction is slightly westward of the shortest route to water (52 m on a 60° bearing) and toward the dark horizon of the dry-mesic woodland north of the nesting area (see, e.g., Fig. 5A); the river is not visible to hatchlings due to intervening vegetation and topography.

Although sample sizes are small (11 hatchlings from 3 nests), initial diurnal dispersal bearings of hatchlings from the eastern part of the nesting area were largely toward the nearby vegetative cover both north and south of this location (45.5% for each), with little movement toward the more open areas to the east or west ($U^2 = 0.16$, $0.05 < p < 0.10$; $\mu = 236^\circ$, $\rho = 0.28$, $SD = 1.59$). Similarly, most diurnally emerging hatchlings originating from nests within the western and central parts of the nesting area dispersed toward the woodland vegetation north of these locations (51.7%, $n = 29$ hatchlings from 9 diurnally emerging nests, and 53.7%, $n = 41$ hatchlings from 11 diurnal nests, respectively), with relatively little movement toward other cardinal directions ($U^2 = 0.59$, $p < 0.01$; $\mu = 346^\circ$, $\rho = 0.34$, $SD = 1.47$). Overall, the lesser-vegetated eastern and western quadrants, with the most open vistas, were used least often for initial diurnal dispersal movements based on the area-restricted views provided by overhead nest cameras (12.4% each, total $n = 20$ hatchlings). The limited data available on initial dispersal of nocturnally emerging hatchlings indicate trajectories did not differ from a random uniform

distribution ($n = 8$ hatchlings; $U^2 = 0.07$, $p > 0.10$; $\mu = 136^\circ$, $\rho = 0.33$, $SD = 1.50$). Despite our attempts, we obtained few images of hatchling turtles from cameras monitoring relatively open pathways within the vegetated drainage sloughs north and east of the nesting area, which we had presumed might have been potential routes to the river.

Chance direct observations and data from peripheral cameras documented that 55.2% ($n = 29$) of dispersal routes were variable and nonlinear over the course of several meters and that 37.5% of the nonlinear routes incorporated course reversals. Further evidence of individual variation in hatchling dispersal tendencies, even when in clear view of nearby water, was gained via a field experiment of 4 September 2018, where 4 artificially incubated *G. ouachitensis* hatchlings were shallowly buried 3 m from the Wisconsin River on an open sand nesting site. The first hatchling to emerge moved 17 m upslope, away from the river to an open woodland area beyond the nesting area, and buried itself in sandy loam soil under leaf litter, while the other 3 individuals entered the river after traveling nonlinear routes for several minutes.

Slope, as a single factor, did not appear to strongly influence initial hatchling dispersal bearings, although slope grades on this site are modest: typically less than 3° . Dispersal bearings remained mostly northern (315° – 45°) when nests were on slopes $< 1^\circ$ (50.0%, $n = 20$ hatchlings), 1° – 3° (47.9%, $n = 48$ hatchlings), and $> 3^\circ$ (45.0%, $n = 20$ hatchlings) (Figs. 5–7). Similarly, most dispersal bearings were northerly under all weather conditions (52.6% while clear to partly cloudy, $n = 38$, and 57.9% while overcast, $n = 19$).

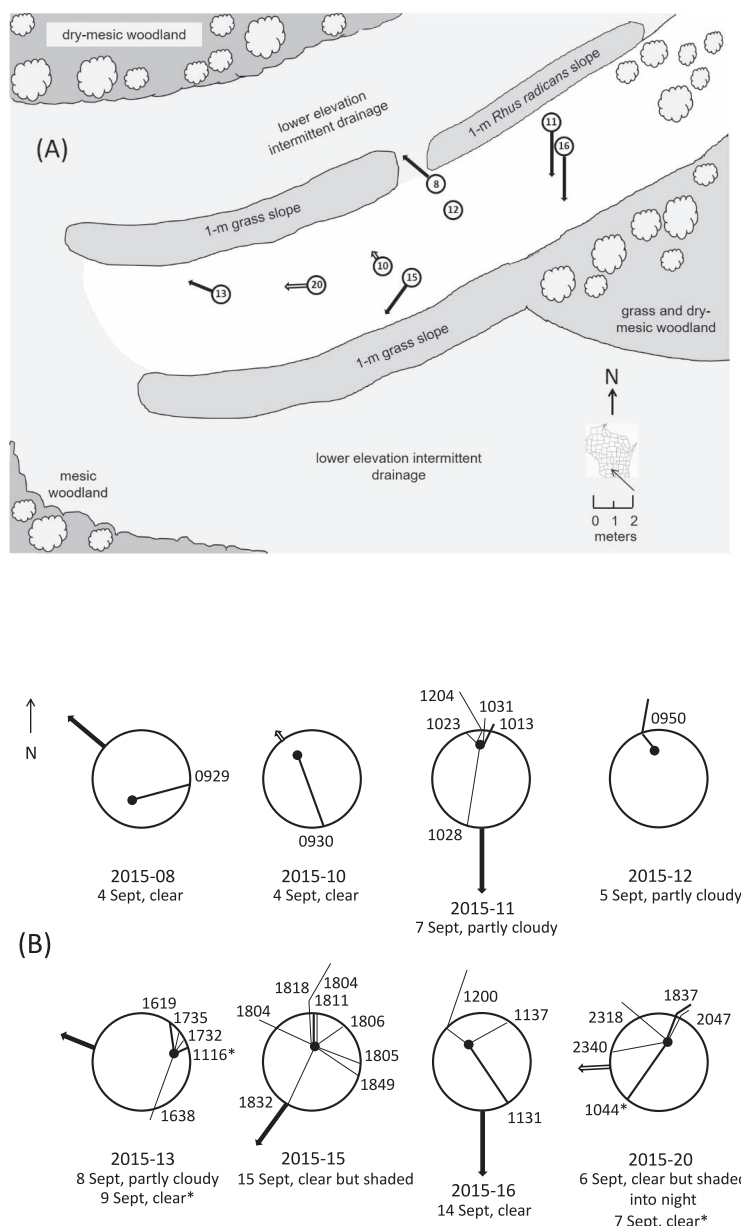


Figure 5. Location and slope map for successful nests with tracked hatchlings in 2015 (A) and initial hatchling dispersal bearings within camera fields of view, nest slope, time (hrs), and sky conditions for emergence events with adequate data (B). Arrows in both parts represent overall downslope vectors, with lengths proportionate to degree of slope; nests on slopes $\geq 3^\circ$ designated by solid black arrows. Bolded dispersal bearings in (B) represent trajectories for first or only hatchlings on a given day. For simplicity, dark dots within nest cages (open circles) in (B) may represent more than 1 exit hole.

DISCUSSION

Newly emerged hatchling turtles, operating without parental assistance, are believed to rely on innate processes to evaluate environmental cues and disperse from nesting areas (Pappas et al. 2009). As such, our observations of hatchlings sometimes delaying exit for several minutes after appearing at the surface could represent initial landscape assessment and cue acquisition behaviors (see also Tuttle and Carroll 2005). Hatchlings also sometimes changed bearings after emergence, suggesting that dispersal cues continue to be evaluated and responded to for

some time after nest exit (see also Tucker 1997; Congdon et al. 2011).

Several potential cues to freshwater turtle hatchling dispersal orientation have been proposed and/or investigated (reviewed by Tuttle and Carroll 2005; Pappas et al. 2017), including response to slope, visible and polarized light, contrasting horizons, olfaction, audition, and geomagnetic/sun compass. Overall, visual cues seem to be the most important in determining initial dispersal routes of both hatchling freshwater turtles (e.g., Congdon et al. 2011; Pappas et al. 2017) and hatchling sea turtles (reviewed in Lohmann et al. 1996).

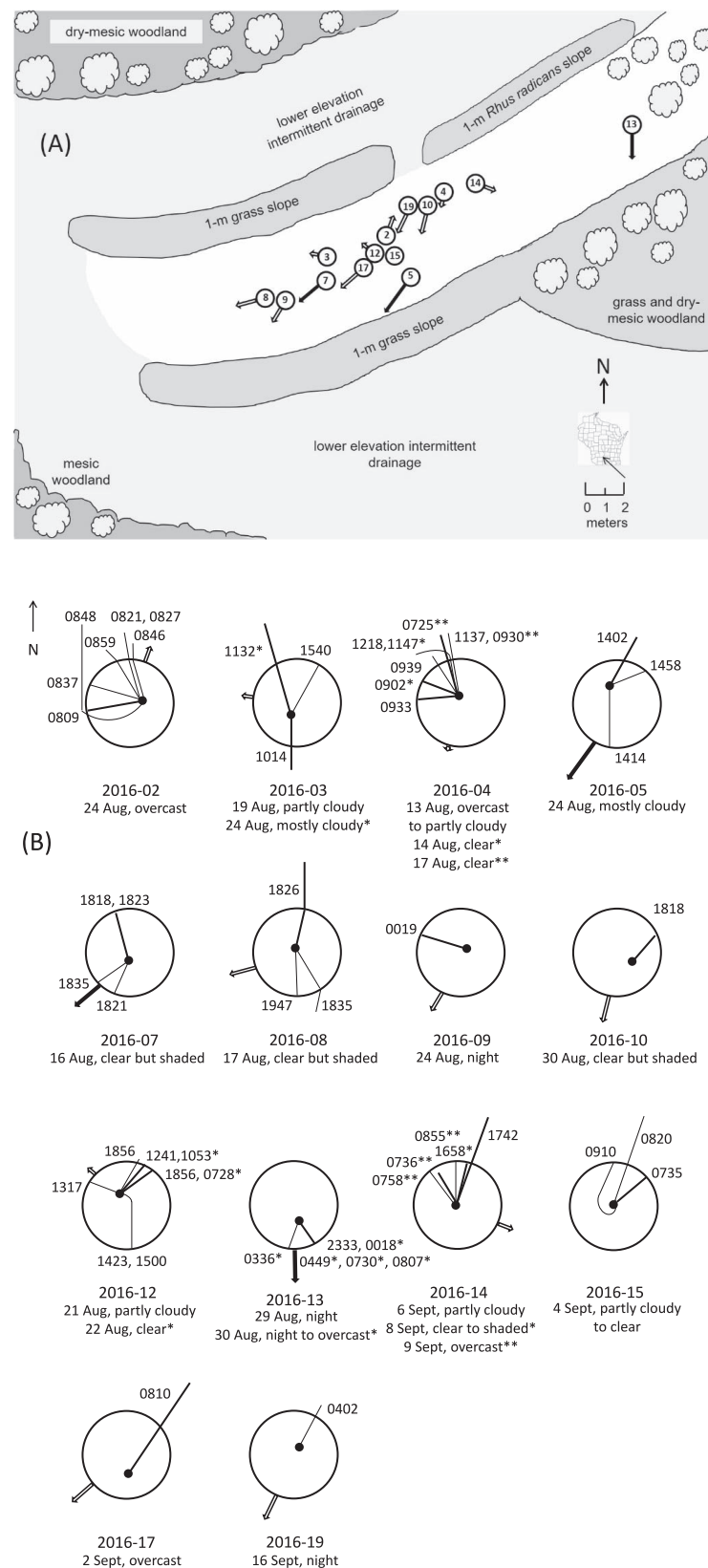


Figure 6. Location and slope map for successful nests with tracked hatchlings in 2016 (A) and initial hatchling dispersal bearings within camera fields of view, nest slope, time (hrs), and sky conditions for emergence events with adequate data (B). Arrows in both parts represent overall downslope vectors, with lengths proportionate to degree of slope; nests on slopes $\geq 3^\circ$ designated by solid black arrows. Bolded dispersal bearings in (B) represent trajectories for first or only hatchlings on a given day. For simplicity, dark dots within nest cages (open circles) in (B) may represent more than 1 exit hole.

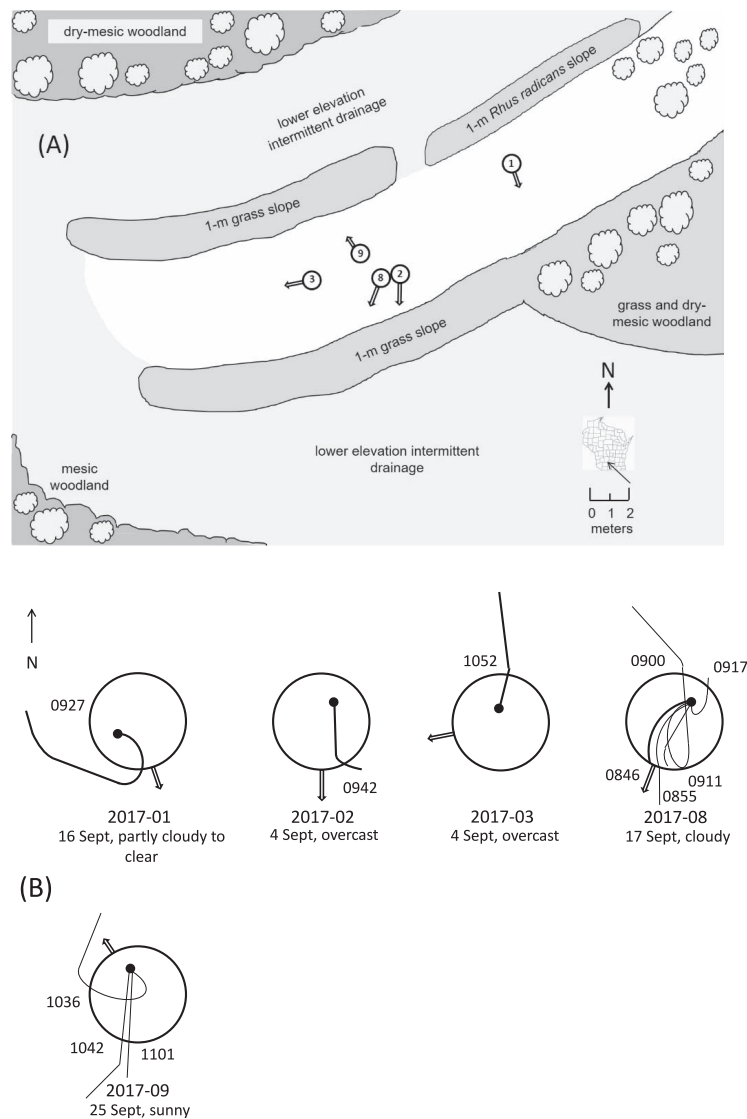


Figure 7. Location and slope map for successful nests with tracked hatchlings in 2017 (A) and initial hatchling dispersal bearings within camera fields of view, nest slope, time (hrs), and sky conditions for emergence events with adequate data (B). Arrows in both parts represent overall downslope vectors, with lengths proportionate to degree of slope; nests on slopes $\geq 3^\circ$ designated by solid black arrows. Bolded dispersal bearings in (B) represent trajectories for first or only hatchlings on a given day. For simplicity, dark dots within nest cages (open circles) in (B) may represent more than 1 exit hole.

Accordingly, in contrast to potential visual cues, this study found no apparent impact of nest slope (minimal on this site) or sky condition on initial dispersal bearings.

Hatchling *G. ouachitensis* dispersal in this study, while variable, was primarily toward the dense vegetation of the nearby woodland north of the nesting area during diurnal periods rather than the unobservable river over 50 m away, a tendency also documented by cameras in previous studies on this site ($n = 11$ records; G.A.G., pers. obs.). At another nearby site adjacent to an open sand beach, none of the dispersal routes taken by emerging *G. ouachitensis* hatchlings were toward the open horizon of the river only 15–30 m away but were typically in the opposite direction toward significant grass and tree cover ($n = 6$ records; G.A.G., pers. obs.).

These findings are in accord with recent observations of neonate *G. geographica*, *Graptemys pseudo-geographica*, and *G. ouachitensis* dispersing toward dark horizons of trees and away from open river horizons (Pappas et al. 2017) as well as observations of these species moving into dense vegetation on land after being placed in shallow river water (Pappas and Congdon 2003). Previously, Anderson (1958) also noted that hatchlings of *Graptemys pearlensis* (as *Graptemys pulchra*) and *Graptemys oculifera* turned around and moved toward shade or woodlands when experimentally placed near water under sunny conditions. Initial movement toward vegetative cover has also been noted for other turtle taxa (e.g., for *Pseudemys scripta*, Murphy 1971; for *Malaclemys terrapin*, Burger 1976; for *Emydoidea blandingii*, Butler and Graham 1995; Stand-

ing et al. 1997; McNeil et al. 2008; for *Glyptemys insculpta* and *Chrysemys picta*, Tuttle and Carroll 2005). These behaviors have been interpreted as possibly leading hatchlings to shelter from predators (Burger 1976) or to slower-moving water bodies with more food and cover resources (Pappas et al. 2017) or as a mechanism to reduce overheating and desiccation risks via ameliorating microclimates (Tuttle and Carroll 2005). The scarcity of camera images of hatchlings on open pathways leading to the river in this study further suggests that neonate *G. ouachitensis* may prefer vegetative cover to open dispersal microhabitats and may not initially move directly toward the nearest water. However, how long hatchlings remain in this vegetative cover is unknown and requires further study.

In fact, hatchlings of some species may spend prolonged periods on land before moving into nearby water bodies and may even overwinter in terrestrial habitats outside of the nest (e.g., *E. blandingii*, Paterson et al. 2012; *M. terrapin*, Muldoon and Burke 2012, Duncan and Burke 2016; and possibly for closely related *G. pseudogeographica*, M. Pappas, pers. obs. of terrestrial hatchlings in spring in Minnesota, 2012–2015, in Pappas et al. 2017). Our field experiment in the autumn of 2018 also suggests this possibility for at least some *G. ouachitensis* hatchlings, all of which emerged from nests in the fall. Successful terrestrial overwintering requires freeze tolerance or an ability to supercool, an attribute that *G. geographica* (which commonly overwinters within the nest) shares with the closely related sister taxon, *Malaclemys* (Duncan and Burke 2016). However, the degree to which *G. ouachitensis* tolerates extreme cold has not been explored. Additional investigations of the freeze tolerance and resistance to inoculative freezing in *Graptemys* would be of value in interpreting overwintering strategies both within that genus and in comparisons to *Malaclemys* (Duncan and Burke 2016).

Regardless, initial directed movement toward nearby water is common for Emydids; including for *G. pearlensis* and *G. oculifera* during nocturnal emergence (without supporting data; Anderson 1958) and for *Graptemys ernstii* (Shealy 1976). Other studies have noted *Graptemys* hatchlings finding water within short time lines even if initial dispersal movements were in other directions (e.g., most during the same night of emergence for *Graptemys nigrinoda*, Lahanas 1982). Further, some studies have demonstrated hatchling dispersal directed toward open, illuminated horizons, not dark horizons as in this study (e.g., for *Chelydra serpentina* and *C. picta*, Noble and Breslau 1938, Congdon et al. 2011; for *Apalone* spp., Pappas et al. 2017). Variance in dispersal tendencies may relate to differences in local site factors (e.g., habitat structure, nest-to-water distance, and presence/absence of an open horizon; e.g., Congdon et al. 2011), interspecific differences in hatchling desiccation risks and perception

distance abilities (Congdon et al. 2011; Figueras et al. 2018), or other life history variables, including propensity to overwinter on land (Muldoon and Burke 2012).

Camera records within and outside of nest cages, as well as occasional direct observations of emergence events, show that there can be considerable variation in initial trajectories taken by hatchlings; this includes within-clutch variation of siblings emerging within a few minutes of each other under the same environmental conditions. Dispersal patterns of individual hatchlings sometimes involved direction changes and other divergences from a straight course, including actual route reversals over several-meter distances. Multidirectional dispersal patterns have been widely noted elsewhere (reviewed in Congdon et al. 2011) and may represent a bet-hedging strategy (Cooper 1981; Cooper and Kaplan 1982) adaptive in promoting at least some hatchling survival from a given nest (e.g., Standing et al. 1997; Tuttle and Carroll 2005; however, see Pappas et al. 2009).

While trail cameras provided otherwise difficult-to-obtain observational data relevant to natural dispersal patterns and produced results in accord with similar research, the technique does have limitations. Close camera FOVs 1 m above nests were too limited to reliably describe dispersal routes over greater distances, as many instances of route changes were noted via peripheral cameras. Our attempts to document patterns of hatchling dispersal beyond the confines of nest cages via peripherally placed cameras were, in turn, limited by the seasonal increase in vegetation, which obscured camera views; however, this method would likely prove useful in elucidating dispersal routes at greater distances from nests at more open sites. In some cases, initial exit bearings may have been influenced by nest cage walls presenting as barriers to free travel, although this cage design did allow for unaided hatchling exit without requiring active researcher involvement and associated risk of influences on hatchling behavior; as in this study, researchers are encouraged to use only those dispersal routes that did not appear to be influenced by nest cage walls in analyses. Finally, the ½-inch hardware cloth screening used to prevent predator digging reduced the natural plant cover near some nests and may have influenced both initial exit bearings and first excursion distances undertaken by newly emerged hatchlings.

Despite these limitations, our methods provided enough observational data on hatchling turtle dispersal from in situ nests to both greatly increase our knowledge of this life history stage for *G. ouachitensis* and inform future land management goals on this site—namely, suggesting the retention of the vegetative cover provided by the nearby woodland. We thus anticipate that this unobtrusive methodology may prove useful as an adjunct to other data collection methods, such as the use of fluorescent powders, passive integrated transponder tags, or perhaps small radio transmitters in future studies. All of

these methods will help to resolve the questions that remain about hatchling turtle dispersal in natural settings.

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LITERATURE CITED

- ANDERSON, P.K. 1958. The photic responses and water-approach behavior of hatchling turtles. *Copeia* 1958:211–215.
- BAKER, P.J., COSTANZO, J.P., IVERSON, J.B., AND LEE, R.E. 2013. Seasonality and interspecific and intraspecific asynchrony in emergence from the nest by hatchling freshwater turtles. *Canadian Journal of Zoology* 91:451–461.
- BURGER, J. 1976. Behavior of hatchling diamondback terrapins (*Malaclemys terrapin*) in the field. *Copeia* 1976:742–748.
- BUTLER, B.O. AND GRAHAM, T.E. 1995. Early post-emergent behavior and habitat selection in hatchling Blanding's turtles, *Emydoidea blandingii*, in Massachusetts. *Chelonian Conservation and Biology* 1:187–196.
- CONGDON, J.D., PAPPAS, M., BRECKE, B., AND CAPPS, J. 2011. Conservation implications of initial orientation of naïve hatchling snapping turtles (*Chelydra serpentina*) and painted turtles (*Chrysemys picta bellii*) dispersing from experimental nests. *Chelonian Conservation and Biology* 10:42–53.
- COOPER, W.S. 1981. Natural decision theory: a general formalism for the analysis of evolved characteristics. *Journal of Theoretical Biology* 92:401–415.
- COOPER, W.S. AND KAPLAN, R.H. 1982. Adaptive “coin-flipping”: a decision-theoretic examination of natural selection for random individual variation. *Journal of Theoretical Biology* 94:135–151.
- DOODY, J.S., GEORGES, A., YOUNG, J.E., PAUZA, M.D., PEPPER, A.L., ALDERMAN, R.L., AND WELSH, M.A. 2001. Embryonic aestivation and emergence behaviour in the pig-nosed turtle, *Carettochelys insculpta*. *Canadian Journal of Zoology* 79:1062–1072.
- DUNCAN, N.P. AND BURKE, R.L. 2016. Dispersal of newly emerged diamond-backed terrapin (*Malaclemys terrapin*) hatchlings at Jamaica Bay, New York. *Chelonian Conservation and Biology* 15:249–256.
- FIGUERAS, M.P., BASTARACHE, B.A., AND BURKE, R.L. 2018. Water exchange relationships predict overwintering behavior in hatchling turtles. *Canadian Journal of Zoology* 96:928–932.
- GELLER, G.A., CASPER, G.S., AND HALSTEAD, B.J. 2020. Hatchling emergence ecology of Ouachita map turtles (*Graptemys ouachitensis*) on the lower Wisconsin River, Wisconsin. *Chelonian Conservation and Biology* 19:217–235.
- GIBBONS, J.W. 2013. A long-term perspective of delayed emergence (aka overwintering) in hatchling turtles: some they do and some they don't, and some you just can't tell. *Journal of Herpetology* 47:203–214.
- JANZEN, F.J., TUCKER, J.K., AND PAUKSTIS, G.L. 2007. Experimental analysis of an early life-history stage: direct or indirect selection on body size of hatchling turtles? *Functional Ecology* 21:162–170.
- KOLBE, J.J., AND JANZEN, F.J. 2002. Experimental analysis of an early life-history stage: water loss and migrating hatchling turtles. *Copeia* 2002:220–226.
- LAHANAS, P.N. 1982. Aspects of the life history of the southern black-knobbed sawback, *Graptemys nigrinoda delticola* Folkerts and Mount. MS thesis, Auburn University, Auburn, AL.
- LOHMANN, K.J., WITHERINGTON, B.E., LOHMANN, C.M.F., AND SALMON, M. 1996. Orientation, navigation, and natal beach homing in sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). *The Biology of Sea Turtles*. New York: CRC Press, pp. 107–135.
- LOVICH, J.E., ERNST, C.H., ERNST, E.M., AND RILEY, J.L. 2014. A 21-year study of seasonal and interspecific variation of hatching emergence in a nearctic freshwater turtle community: to overwinter or not to overwinter? *Herpetological Monographs* 28:93–109.
- MCNEIL, J.A., HERMAN, T.B., AND STANDING, K.L. 2008. Movement of hatchling Blanding's Turtles (*Emydoidea blandingii*) in Nova Scotia in response to proximity to open water: a manipulative experiment. *Chelonian Conservation and Biology* 3:611–617.
- MULDON, K.A. AND BURKE, R.L. 2012. Movements, overwintering, and mortality of hatchling diamond-backed terrapins (*Malaclemys terrapin*) at Jamaica Bay, New York. *Canadian Journal of Zoology* 90:651–662.
- MURPHY, G.G. 1971. Orientation of adult and hatchling red-eared turtles, *Pseudemys scripta elegans*. PhD Dissertation, Mississippi State University, State College, 71 pp.
- NAGLE, R.D., LUTZ, C.L., AND PYLE, A.L. 2004. Overwintering in the nest by hatchling map turtles (*Graptemys geographica*). *Canadian Journal of Zoology* 82:1211–1218.
- NOBLE, G.K. AND BRESLAU, A.M. 1938. The senses involved in the migration of young fresh-water turtles after hatching. *Journal of Comparative Psychology* 25:175–193.
- PAPPAS, M.J. AND CONGDON, J.D. 2003. Weaver Bottoms 2001–2002 turtle surveys: management and conservation concerns. Minnesota Department of Natural Resources and US Fish and Wildlife Service.
- PAPPAS, M.J., CONGDON, J.D., AND BRECKE, B.J. 2017. Orientation in five species of hatchling turtles dispersing from artificial nests. *Chelonian Conservation and Biology* 16:3–11.
- PAPPAS, M.J., CONGDON, J.D., BRECKE, B.J., AND CAPPS, J.D. 2009. Orientation and dispersal of hatchling Blanding's turtles (*Emydoidea blandingii*) from experimental nests. *Canadian Journal of Zoology* 87:755–766.
- PATERSON, J.E., STEINBERG, B.D., AND LITZGUS, J.D. 2012. Revealing a cryptic life-history stage: differences in habitat selection and survivorship between hatchlings of two turtle species at risk (*Glyptemys insculpta* and *Emydoidea blandingii*). *Wildlife Research* 39:408–418.
- PEWSEY, A., NEUHÄUSER, M., AND RUXTON, G.D. 2013. *Circular Statistics in R*. Oxford: Oxford University Press, 198 pp.
- PLUMMER, M.V. 2007. Nest emergence of smooth softshell turtle (*Apalone mutica*) hatchlings. *Herpetological Conservation and Biology* 2:61–64.

- SHEALY, R.M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur, in Alabama. Bulletin of the Florida State Museum, Biological Sciences 21:47–111.
- STANDING, K.L., HERMAN, T.B., HURLBURT, D.D., AND MORRISON, I.P. 1997. Postemergence behaviour of neonates in a northern peripheral population of Blanding's turtle, *Emydoidea blandingii*, in Nova Scotia. Canadian Journal of Zoology 75:1387–1395.
- TUCKER, J.K. 1997. Natural history notes on nesting, nests, and hatchling emergence in the red-eared slider turtle, *Trachemys scripta elegans*, in west-central Illinois. Illinois Natural History Survey Biological Notes 140, 13 pp.
- TUTTLE, S.E. AND CARROLL, D.M. 2005. Movements and behavior of hatchling wood turtles (*Glyptemys insculpta*). Northeastern Naturalist 12:331–348.
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