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Abstract

Environmental conditions during embryonic development affect morphology, behavior, and survival in turtles. Nest temperature also could affect posthatching traits of offspring, such as emergence behaviors. We monitored thermal conditions in painted turtle (*Chrysemys picta*) nests along the Mississippi River in Illinois to examine their influence on offspring survival and nest emergence. We recorded hourly temperatures within nest cavities during embryonic development in summer 2016 ($n = 34$) and after hatching through the following January ($n = 15-20$). Hatching success and posthatching survival appeared to be largely unaffected by thermal conditions recorded in nests. Emergence of neonates from nests was observed from 19 March through 12 May 2017. Onset of offspring emergence occurred later in the spring for nests with greater exposure to subzero temperatures in winter. For nearly all nests with live offspring, siblings did not emerge en masse, but instead departed the nest across multiple days. Nests with higher mean temperatures during incubation exhibited earlier mean emergence dates in spring, yet emergence duration was positively correlated with thermal maxima experienced in nests in fall and winter. Thus, thermal environments in nests at different times of year apparently elicited variation in spring emergence timing of *C. picta* hatchlings.

Keywords

Chrysemys picta, hatchlings, nest emergence, nest temperature, overwintering, painted turtle, synchrony

Disciplines

Behavior and Ethology | Climate | Ecology and Evolutionary Biology | Population Biology

Comments

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Nest Temperatures Predict Nest Emergence of Painted Turtle (*Chrysemys picta*) Offspring

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ABSTRACT. – Environmental conditions during embryonic development affect morphology, behavior, and survival in turtles. Nest temperature also could affect posthatching traits of offspring, such as emergence behaviors. We monitored thermal conditions in painted turtle (*Chrysemys picta*) nests along the Mississippi River in Illinois to examine their influence on offspring survival and nest emergence. We recorded hourly temperatures within nest cavities during embryonic development in summer 2016 ($n = 34$) and after hatching through the following January ($n = 15–20$). Hatching success and posthatching survival appeared to be largely unaffected by thermal conditions recorded in nests. Emergence of neonates from nests was observed from 19 March through 12 May 2017. Onset of offspring emergence occurred later in the spring for nests with greater exposure to subzero temperatures in winter. For nearly all nests with live offspring, siblings did not emerge en masse, but instead departed the nest across multiple days. Nests with higher mean temperatures during incubation exhibited earlier mean emergence dates in spring, yet emergence duration was positively correlated with thermal maxima experienced in nests in fall and winter. Thus, thermal environments in nests at different times of year apparently elicited variation in spring emergence timing of *C. picta* hatchlings.

KEY WORDS. – *Chrysemys picta*; hatchlings; nest emergence; nest temperature; overwintering; painted turtle; synchrony

Abiotic conditions in nests influence myriad embryonic and offspring traits in reptiles (Deeming and Ferguson 1991; Birchard 2004; While et al. 2018). Emergence from the egg also relies on external cues. Such ontogenetic transitions can be determined by a variety of abiotic and biotic factors (Spencer and Janzen 2011; Warkentin 2011). For example, pig-nosed turtle (*Carettochelys insculpta*) embryos expedite emergence when nests are flooded (Doody et al. 2001). Still other turtle embryos appear to communicate via sound late in development, possibly to coordinate the timing of hatching within nests (e.g., Ferrara et al. 2014). Timing of hatching further may be affected by longer-term factors, such as thermal conditions throughout development (Doody 2011). Indeed, temperature is crucial in embryonic development and is historically recognized as the primary agent affecting incubation length in oviparous species lacking parental care (Packard et al. 1987; Deeming and Ferguson 1991; Birchard 2004).

Varying strategies corresponding with the most favorable environmental conditions for timing of nest emergence have evolved in many turtle species (Ewert

1985; Costanzo et al. 2008; Gibbons 2013), such that neonates depart from nests shortly after hatching in some species yet often overwinter within nests in others. Even so, in situ environmental cues, both abiotic and biotic, presumably stimulate emergence from nests (DePari 1996; Nagle et al. 2004; Santos et al. 2016). In sea turtles, for example, hatchling emergence seems to be governed by temperatures at the nest's surface (Moran et al. 1999). Similarly, thermal conditions of nests in spring may affect nest emergence of hatchling freshwater turtles (e.g., Tucker 1999). Cold stress during winter also has been hypothesized to alter timing and pattern of emergence (Baker et al. 2010). If thermal environments at or near the date of emergence affect emergence timing from nests, even earlier temperatures within nests also may play a role in stimulation and synchrony of emergence.

Synchrony is defined as the departure of all neonates from a nest on the same day (Baker et al. 2010). Hatchling vulnerability is putatively decreased during such events, as the advantage of grouping dilutes individual predatory risk (Spencer et al. 2001; Tucker et al. 2008; Santos et al.

2016). Group environments, specifically within nests, are predicted to drive the evolution of environmentally cued emergence due to sibling–sibling communication (Doody et al. 2001; Spencer and Janzen 2011; Aubret et al. 2016). Whether thermal conditions during incubation influence emergence synchrony is unknown, but minimum winter nest temperatures for painted turtles (*Chrysemys picta*) in Indiana were not linked to emergence synchrony (Baker et al. 2010).

We monitored thermal profiles of painted turtle nests from oviposition into early winter. We first evaluated the impact of temperature on embryonic hatching success and then on posthatching survival in the nests. We predicted hatching success to be optimized by moderate thermal conditions (e.g., Birchard 2004) and overwinter survival to be maximized by absence of exposure to extreme subzero temperatures (e.g., Weisrock and Janzen 1999). Finally, given the putative advantages of group emergence, we predicted emergence synchrony for a preponderance of nests and for the onset of emergence to be accelerated by warm, but not extreme, nest conditions. For asynchronous emergence of hatchlings, we predicted duration of the emergence period for a given nest to be reduced by warm, but not extreme, nest conditions.

METHODS

Study Site. – We studied thermal characteristics of *C. picta* nests at the Thomson Causeway Recreation Area along the Mississippi River in Illinois, USA (lat 41°57'N, long 90°07'W). Painted turtles at this site nest annually from late May until the end of June, with some females nesting multiple times per year (Schwanz et al. 2010) and offspring almost invariably emerging from nests the following spring (Weisrock and Janzen 1999). Diverse canopy vegetation and soils in this area allow for potential variability in nest abiotic profiles (Schwanz et al. 2010; Mitchell and Janzen 2019). The local climate at the field site is distinguished by hot, humid summers and variable snowfall in winter (Warner et al. 2010; Bodensteiner et al. 2015).

Nest Protocols. – An initial set of 54 nests was located by visually searching for nesting turtles between 28 May and 23 June 2016. Data loggers (Thermochron iButtons, DS1921G-F5, Dallas Semiconductor, Dallas, TX; 2003–2006) were implanted at 8 cm (typical nest depth at this site; Morjan 2003) immediately adjacent to each nest cavity to record soil temperatures hourly without disturbing eggs (sensu Baker et al. 2010). This standardization was adopted because variation in depth among nests at this site has not been linked to detectable differences in thermal conditions (Mitchell et al. 2013; Refsnider et al. 2013). Due to storage needs required for recording hourly data, loggers were exchanged in a fraction of the nests when memory reached capacity. Insufficient memory capacity rendered the temperature data set incomplete for many nests during fall and winter and for all nests in the spring.

Overall, thermal data were available for 34 nests in summer (10 July through 31 August), 20 nests in fall (19 September through 14 December; 16 of which were also monitored in summer), and 15 nests in winter (5 November 2016 through 29 January 2017; 10 of which were also monitored in summer). No nests were monitored in both fall and winter.

Nest cavities were protected with 30 × 30-cm sections of 1-cm mesh aluminum hardware cloth fastened to the ground with metal stakes (Mitchell et al. 2013; Bodensteiner et al. 2015). Nonetheless, predators or people destroyed 8 nests. In March 2017, the wire mesh over intact nests was replaced with aboveground arenas constructed from cross sections of 20-cm-diameter polyvinyl chloride pipe overlain with 1.5-cm rigid plastic mesh. These arenas retained emerged neonates until we checked nests and they also prevented postemergence predation.

Beginning on 19 March 2017, the 46 nests were checked daily (0700 hrs). Once a nest yielded its first hatchling, the location was checked twice daily (0700 and 1900 hrs). Nest arenas also were checked for security at each visit so that no hatchlings had the opportunity to escape. After 2 wks passed without hatchling emergence from any nest, the 46 cavities were excavated by hand on 25 May (when the general public was permitted access to the site) to check for additional turtles (live or dead) and retrieve the data loggers. At this time, clutch size and winter survival were assessed by enumerating the unhatched eggs, dead hatchlings, and live/emerged offspring (sensu Baker et al. 2013). All live turtles from this study then were released in the nesting area adjacent to the river.

Statistical Analyses. – Analyses were conducted in JMP Pro 12.2.0 (SAS Institute Inc., Cary, NC). In sum, 54 nests were identified originally, 8 of which were destroyed by predators or people and one of which was unusable because field notes became illegible before transcription. Further, seasonal sample sizes were circumscribed because of iButton limitations. Thus, sample sizes and statistical power differ considerably among the analyses described below.

Exploratory general linear models were run to test whether oviposition date or clutch size were correlated with the dependent variables of hatching success (%), posthatching survival (%), date of first emergence (day of year), mean date of emergence (day of year), and emergence duration (d). Emergence duration was defined as the number of days between the first and last emergence from a nest. The 2 independent variables were almost uniformly unrelated to the 5 dependent variables ($p \geq 0.10$ in all but one case; see “Results”) and, thus, were excluded from subsequent analyses.

A series of linear regressions was run to test for relationships among nest thermal conditions and the dependent variables. Independent variables were the average, minimum, and maximum temperatures within

nests during summer, fall, and winter, as well as the number of hours a nest spent below 0°C during fall and winter. Because thermal data often were correlated within a season, and because summer, fall, and winter data sets consisted of different collections of nests, thermal models were run as separate regressions. Given the modest sample size of nests, statistical findings and data plots are presented where $p \leq 0.12$ and $|r| \geq 0.33$ to permit readers to judge the biological significance of the results (Gelman and Stern 2006; Wasserstein et al. 2019). Also, we report r , rather than r^2 , so that readers can immediately intuit the direction of the relationship between the 2 variables evaluated in a given linear regression analysis.

RESULTS

For the 45 nests, clutch sizes could be inferred for 41 (9.9 ± 2.3 SD, range = 5–16 eggs). Hatching success in these 41 nests averaged $82\% \pm 27\%$ SD, with nearly 89% producing ≥ 1 live offspring in fall 2016. No hatchlings emerged from any of the monitored nests prior to spring 2017. Mortality in the nest after hatching further reduced the number of neonates that could emerge in spring 2017 (mean survival, $74\% \pm 33\%$ SD). In the end, 37 nests contained ≥ 1 live hatchling in spring 2017 ($n = 233$ turtles).

Hatching success was largely unrelated to summer temperatures recorded in 34 nests ($p \geq 0.19$ for average, minimum, and maximum temperatures). Posthatching survival was nominally higher in relatively warm nests in all 3 seasons (summer minimum: $r = +0.33$, $p = 0.08$, $n = 30$; fall average: $r = +0.38$, $p = 0.12$, $n = 18$; winter maximum: $r = +0.43$, $p = 0.12$, $n = 14$).

Of the 15 nests monitored for winter temperatures, only 1 nest experienced thermal conditions below -8°C (and for 66 hrs), which is the lower limit of supercooling determined in the laboratory (Packard and Janzen 1996) and was linked to overwintering mortality in the field for hatchling *C. picta* from this population (Weisrock and Janzen 1999). Even so, all 7 hatchlings in this nest survived winter. Subzero nest temperatures were related to emergence timing. Of the 10 nests monitored for winter temperatures from which > 1 hatchling emerged, increasing time spent below 0°C varied positively with date of first emergence (Fig. 1). Neither nesting date nor any other temperature variable evaluated was important in predicting first emergence date ($p > 0.20$ in all cases). On the other hand, nests with smaller clutch sizes and higher mean temperatures in summer exhibited earlier mean emergence dates the following spring ($r = +0.45$, $p = 0.01$, $n = 31$ and $r = -0.47$, $p = 0.03$, $n = 22$, respectively).

Hatchling emergence ($n = 218$) was recorded from 35 nests between 19 March and 12 May 2017 (Fig. 2). The largest pulse of hatchling emergence across nests (15 and 16 April) seemed to coincide with rapidly rising daily high and low temperatures above 0°C in spring, but not obviously as any function of occurrence or magnitude of

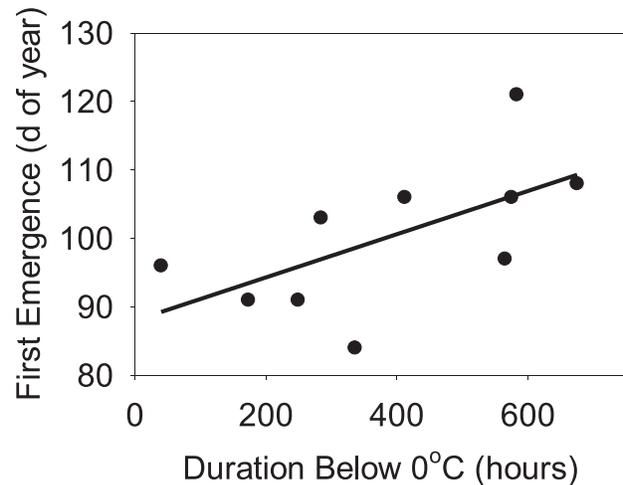


Figure 1. Day in 2017 when hatchling painted turtles (*Chrysemys picta*) first emerged from a nest as a function of time spent below 0°C in November–January in a nest cavity ($r = +0.61$, $p = 0.06$, $n = 10$).

precipitation events during spring (Fig. 2). Upon excavating all nests on 25 May, 6 yielded ≥ 1 live offspring, including 2 nests with the entire complement. Overall, only 26% of nests with > 1 live offspring emerging in the spring exhibited synchronous emergence. For the asynchronous nests that thus constituted the majority of the sample (even after excluding the 6 nests that still had ≥ 1 live hatchling on 25 May), emergence duration was positively, albeit modestly, influenced by the thermal maxima nests experienced in fall and winter (Fig. 3). That is, hatchlings emerged across a longer period for nests that encountered more extreme warmth in the cavities.

DISCUSSION

Although nest temperatures influence myriad embryonic and offspring traits in reptiles (Deeming and Ferguson 1991; Birchard 2004; While et al. 2018), factors responsible for the timing and duration of departure of hatchlings from the nests—especially in taxa with delayed emergence—remain largely obscure (Gibbons 2013). In our field study of the painted turtle, a species whose offspring generally exhibit delayed emergence, thermal conditions within nests minimally affected embryonic and posthatching survival. However, cooler summer temperatures and duration of freezing temperatures experienced in nest cavities appeared to delay hatchling emergence, which typically transpired over multiple days for a nest (i.e., asynchrony) as a positive function of prior thermal conditions.

Most of our findings are congruent with those of prior studies. That posthatching survival was elevated in nests with relatively warm conditions is entirely consistent with laboratory and field studies of this and other turtle species. For northern populations of turtles whose neonates spend extended periods in the nests before emerging, avoiding or tolerating protracted and extreme subzero temperatures is

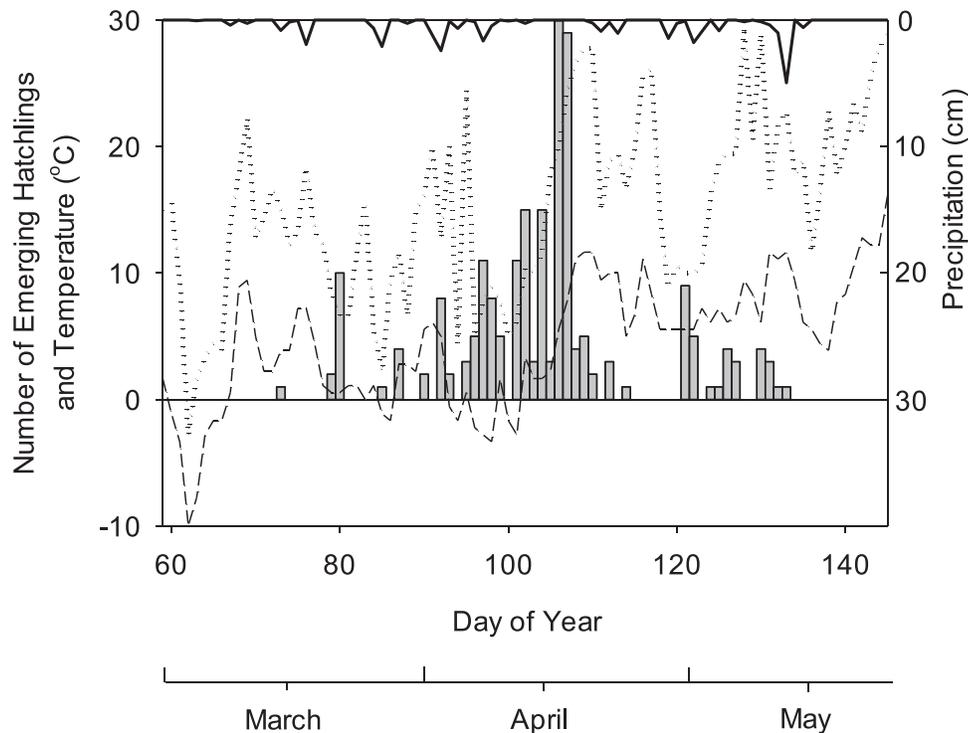


Figure 2. Time course of emerging hatchlings across 35 painted turtle (*Chrysemys picta*) nests in 2017 in relation to daily minimum air temperature ($^{\circ}\text{C}$, dashed line), daily maximum air temperature ($^{\circ}\text{C}$, dotted line), and daily precipitation (cm, black line) at the field site (data from www.ncdc.noaa.gov for Fulton Dam, ~ 8 km south of the nesting area).

imperative for survival (reviewed in Weisrock and Janzen 1999; Costanzo et al. 2008). Excessively warm ambient temperatures after hatching, which are presumably transmitted to nest cavities, can also have adverse fitness consequences (Willette et al. 2005; Muir et al. 2013).

We ascertained an inverse relationship between mean nest temperatures in summer and mean emergence dates of offspring the following spring. Warmer temperatures during embryogenesis in laboratory studies of reptiles yield hatchlings with smaller overall energy stores (carcass mass plus yolk mass; reviewed in Booth 2004). If true for our *C. picta* nests, this initial physiological impact might

promote earlier departure of offspring from nests to replenish these resources (sensu Willette et al. 2005; Muir et al. 2013).

We detected a positive relationship between how long a nest (and presumably the offspring) spent at $< 0^{\circ}\text{C}$ and the length of delay in emergence of the first hatchling from that nest. In contrast, Baker et al. (2010) found no relationship between the minimum temperature a nest experienced in winter and date of hatchling emergence for *C. picta*, *Trachemys scripta*, or *Graptemys geographica*. Why our results should differ so strikingly from those of Baker et al. (2010) is uncertain beyond being distinct

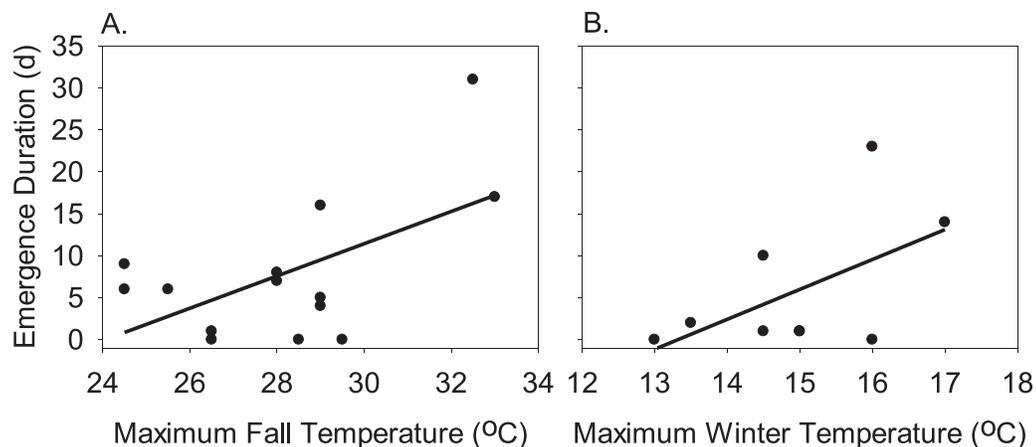


Figure 3. Emergence duration (d) of hatchling painted turtles (*Chrysemys picta*) from nests as a function of (A) maximum fall nest temperature ($r = +0.58$, $p = 0.03$, $n = 14$) and (B) maximum winter nest temperature ($r = +0.55$, $p = 0.12$, $n = 9$; 2 nests with winter maximum = 15°C had emergence durations of 1 d).

populations. Perhaps our focus on duration of subzero temperatures in nests and their emphasis on severity of the cold in nests is involved.

Our study supports the idea that synchronous emergence of siblings from a nest is uncommon in freshwater turtles. Roughly one-quarter of the *C. picta* nests we monitored experienced all neonates emerging within 24 hrs. Such synchronous emergence also was rare in a 6-yr study of a syntopic nesting assemblage of 7 turtle species in Indiana (Baker et al. 2010, 2013) and in other freshwater turtle studies throughout North America (Lindeman 1991; DePari 1996; Tucker 1999; Kolbe and Janzen 2002; Nagle et al. 2004; Holcomb and Carr 2011; but see Christens and Bider 1987; Congdon et al. 1987). Still, the high degree of emergence asynchrony is unexpected for several reasons. First, freshwater turtles have mechanisms that promote synchronous hatching (reviewed in Spencer and Janzen 2011). Second, emergence synchrony from nests occurs in some sea turtles (e.g., Santos et al. 2016). Third, abundant theory (e.g., Ims 1990) and field experimentation (e.g., Tucker et al. 2008) suggests that synchronous emergence from nests in turtles should reduce per-capita odds of depredation either via predator swamping or prey switching. Despite the putative advantages of emergence synchrony, its infrequent occurrence in freshwater turtle nests signals a mismatch between assumptions of the models and the biology of these systems. For instance, emergence asynchrony theoretically arises when predators are generalists rather than specialists (Ims 1990), which is almost certainly true for many predators of hatchling freshwater turtles (e.g., see predator list in Janzen et al. 2000).

The date on which a nest was laid had no discernible influence on the onset of hatchling emergence. Despite the possibility that declining energy stores might elicit hastier nest departure (sensu Willette et al. 2005; Muir et al. 2013), nests laid earlier did not correspondingly yield hatchlings that emerged in the fall (DePari 1996) or sooner the following spring. In fact, Baker et al. (2013) detected the opposite pattern for *C. picta*, *T. scripta*, and *G. geographica*: hatchlings from nests laid later the prior season actually emerged sooner the following spring. The severity of subzero temperatures in our nests might have been of overriding importance by inducing differential cryoinjury (Baker et al. 2010). Thermal conditions in nests—although not just in winter—also appeared to affect the duration of emergence. Nests that experienced higher thermal maxima were often characterized by extended emergence durations.

The causes and consequences of delayed emergence of offspring from a nest in so many turtle species remain enduring mysteries despite many decades of inquiry (Gibbons 2013). Our collective findings in the context of the literature suggest that the most beneficial future studies for clarifying the biological significance of this phenomenon might be those manipulating abiotic conditions in

nests or assessing differential fitness of fall- vs. spring-emerging offspring.

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