

# Winter severity and phenology of spring emergence from the nest in freshwater turtles

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**Abstract** Although many species of freshwater turtles emigrate to water soon after hatching, the offspring of some species overwinter on land and move to aquatic habitats in the following spring. Timing of emigration can affect the hatchlings' fitness, but the factors underlying phenology of nest emergence are incompletely understood. We tested the supposition that cold stress imposed during hibernation can influence the timing of nest emergence in three species of turtles in the central USA. In each year of the 6-year study, *Chrysemys picta* emerged in late March and early April and, on average, these hatchlings left their nests 2 weeks earlier than those of *Graptemys geographica* and 4 weeks earlier than those of *Trachemys scripta*. Emergence of conspecific hatchlings from different nests usually occurred over 3–7 weeks, but in some years lasted several additional weeks. Relatively few nests had siblings that emerged on the same day (i.e., synchronously); complete emergence of the typical sibling group required 1 to 2 weeks. In winter, subzero cold occurred with regularity in the nests of all species, though *C. picta* experienced the lowest temperatures owing to their shallower nests. However, for no species did emergence date or length of the emergence period correlate with winter

minimum temperature and, at the level of the individual nest, neither did emergence synchrony or duration. Despite encountering lower temperatures, hatchlings of *C. picta* emigrated from their nests before those of sympatric species, suggesting that the fitness benefits of early emergence may lead to the improvement of cold-hardiness adaptations in northern populations of turtles.

**Keywords** Synchrony · Cold hardiness · Hatchling · Hibernation

## Introduction

Turtles have evolved diverse strategies for timing the hatching and emigration of their offspring to coincide with favorable environmental conditions (Ewert 1985). Although many temperate species produce young that leave the nest within days or weeks of hatching, the young of some species defer emigration until the following spring. The ecological significance of this behavior remains equivocal, but it is possible that overwintering in situ confers a survival advantage over conspecifics that emigrate in late summer or autumn (Costanzo et al. 2008; Gibbons and Nelson 1978).

After hatching, freshwater turtles ultimately must leave the natal nest and move to water. Timing of this transition seemingly is an important aspect of their natural history, because earlier-arriving individuals may benefit from a longer growing season (Warner and Shine 2007). However, because hatchlings making the overland trek to water might be exposed to predators and adverse environmental conditions, there is likely a strong selection pressure to optimize emigration timing to avoid such perils (Tucker et al. 2008). In addition, synchronizing emigration may reduce

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mortality by swamping predators with a multitude of prey (Brännäs 1995; Carr and Hirth 1961; Spencer et al. 2001). Therefore, a survival advantage may be gained by hatchlings that emigrate contemporaneously from a given nesting area, and also by siblings that coordinate emergence from their nest.

Despite the potential benefits, some field observations indicate that clutch mates commonly emerge in small groups or individually over an extended period (Butler and Graham 1995; Diaz-Paniagua et al. 1997; Houghton and Hays 2001; Pike and Seigel 2006). The cause(s) of emergence asynchrony is unknown, but speculation suggests that environmental heterogeneity within the nest (and across the nesting landscape) could differentially expose hatchlings to emergence cues or, on the other hand, to stressors that hamper escape from the nest (see Glen et al. 2005). Sublethal exposure to extreme cold can transiently perturb neurobehavioral function (Attaway et al. 1998; Costanzo et al. 2006; Costanzo et al. 1999; Muir et al. 2010), perhaps delaying (or preventing) nest emergence. Accordingly, we hypothesize that cold stress manifested during winter alters the timing and pattern of hatchling emigration, and that the effect is more pronounced in species that are less cold hardy.

Our primary objective in this study was to examine the phenology of nest emergence in three species of emydid turtles that share a common nesting area and are known to vary in their cold hardiness. By compiling data over six consecutive winters that varied in severity, we addressed the question of whether or not cold exposure influences the timing, duration, and synchrony of emergence of hatchlings at both the nest and landscape levels.

## Materials and methods

### Study area and study species

This investigation was carried out at Mount Zion Mill Pond (41°N, 86°W), Fulton County, Indiana, USA, during 2000–2006. Nesting at this site occurs on a 1.2-ha area encompassing a residence and surrounding mowed lawn adjacent to the pond. The local climate is characterized by cold, wet winters; cool, wet springs; hot, humid summers; and cool, damp autumns. Snowfall can be heavy, and snow cover may persist for long periods. For a more detailed description of the study site, see Costanzo et al. (2004).

We located nests by monitoring gravid turtles during their nesting forays. Spent females were captured and uniquely marked (by shell notching) so that we could recognize individual females during their subsequent nesting attempts. We covered each nest with a raised,

wire screen that deterred predators and retained emerged hatchlings. Nests were attended several times daily, from August until the following July, except that no visits were made from early November through late March because our prior experience indicated that turtles did not emerge during this period. We recorded the date that each hatchling was found outside its nest, and then released those individuals at the pond's edge. We replaced the screen over the nest in order to trap any additional turtles that emerged.

In early July, we carefully excavated all nests constructed in the previous year. We measured the depth (to 0.1 cm) from the soil surface to the floor of the chamber and enumerated any unhatched eggs and retained hatchlings. Of the dead turtles, we distinguished those that had died during winter from those dying soon after hatching from their relative state of decomposition (Costanzo et al. 2004). Summing the counts of unhatched eggs, dead hatchlings, and emerged hatchlings gave an estimate of clutch size for each nest.

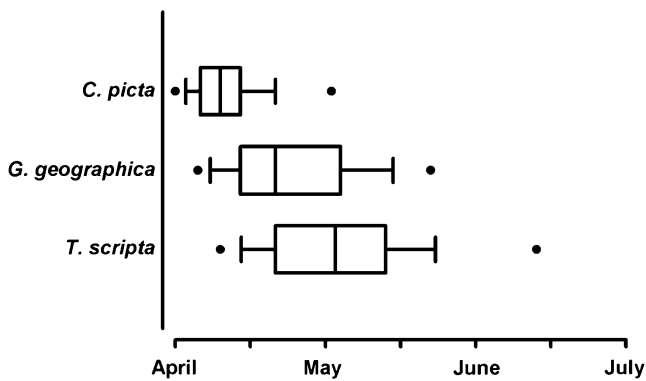
### Emergence parameters

We assigned to each nest an *emergence duration*, the interval (in days) between appearances of the earliest- and latest-emerging siblings, and an *emergence date*, taken as the median Julian date calculated from records of all emerging siblings. For each sibling group, we also characterized the emergence pattern as *synchronous* if emergence duration equaled 1 day and *asynchronous* if emergence duration exceeded 1 day. Averages of emergence dates and durations were used to represent all conspecific nests in each annual cohort. We defined *emergence period* as the interval (in days) between the first and last emergence dates recorded for each annual cohort.

### Environmental variables

Temperatures to which hatchlings were exposed during winter were recorded using automated loggers (TidBit®, Onset Computer Corp., Pocasset, MA). Shortly after a female left her completed nest, we placed a logger in the soil adjacent to the nest's chamber via a narrow excavation, which was then immediately backfilled. In doing so, we were careful to avoid disturbing the nest's chamber and plug. All loggers were programmed to record temperature to the nearest 0.1°C at 1-h intervals. After retrieving the data, we checked the accuracy of each logger by operating it in a stirred melting ice bath; data were discarded from any logger failing to record  $0.0 \pm 0.5^\circ\text{C}$  throughout the test.

We used either a Tidbit (before 2003) or wireless weather station (Davis Instruments, Davis, CA) to record



**Fig. 1** Timing of emergence from the natal nest by hatchling turtles at a nesting site in Fulton Co., Indiana, USA. Representation is a compilation of data for all nests from which at least three hatchlings emerged (*Chrysemys picta*,  $n=186$ ; *Graptemys geographica*,  $n=20$ ; *Trachemys scripta*,  $n=27$ ) during the 6-year study. Box ends demarcate 10th and 90th percentiles; vertical line inside box is 50th percentile (median). Filled circles represent extreme values

air temperature at ca. 2.5 m above grade in an area of concentrated nesting activity. Records of snowfall were obtained from a National Climatic Data Center weather station (Cooperative ID=127482, Rochester, IN) located within 10 km of the study site.

#### Statistical analyses

Analyses of emergence data using ANOVA included cohort (i.e., year of study) as a blocking factor. Where significant differences were found, the Bonferroni method was used in post hoc comparisons. We compared oviposition and emergence dates among species using Kruskal–Wallis tests. Spearman's rank correlation was used to examine relationships between air temperature or snowfall and mean minimum nest temperature; between mean minimum nest temperature and mean nest depth, emergence timing (average of nest emergence dates), mean emergence duration, and emergence period. A Chi-squared test for independence was used to determine whether the proportion of nests emerging synchronously varied by year. Data were analyzed with StatView (SAS Institute, Carey, NC). Values are presented as mean  $\pm$  SEM unless otherwise stated.

## Results

Generally, nesting began in the latter half of May and concluded by early July. Nesting periods of the three species strongly overlapped and there was no variation in mean dates of oviposition among species ( $H=0.59$ ;  $P=0.74$ ). Individual females constructed up to three separate nests during summer, but in order to simplify the analyses we treated all nests as independent elements of the data set. Estimated clutch size averaged 6 (range, 4–14) for *C. picta*, 9 (range, 6–14) for *G. geographica*, and 13 (range, 7–22) for *T. scripta*.

We monitored a total of 466 nests over the 6-year study. Majority ( $n=386$ ; 82.8%) of these nests were made by *C. picta*, the most populous of the indigenous turtle species. We did not compile data for nests that produced no viable offspring, could not be relocated, or were disturbed by researchers in the course of other investigations, and we omitted data for nests (*C. picta*,  $n=30$ ; *T. scripta*,  $n=1$ ) from which at least one hatchling emerged in fall. Mortality statistics, nest temperatures, and nest depth measurements were collected for all remaining nests. Analyses of emergence parameters were performed on this same sample after excluding all nests (*C. picta*,  $n=41$ ; *T. scripta*,  $n=5$ ) from which fewer than three hatchlings emerged in spring. Such analyses were based on results for 186 nests of *C. picta*, 20 nests of *G. geographica*, and 27 nests of *T. scripta* and the collective responses of 1,143, 161, and 320 hatchlings of the three species, respectively.

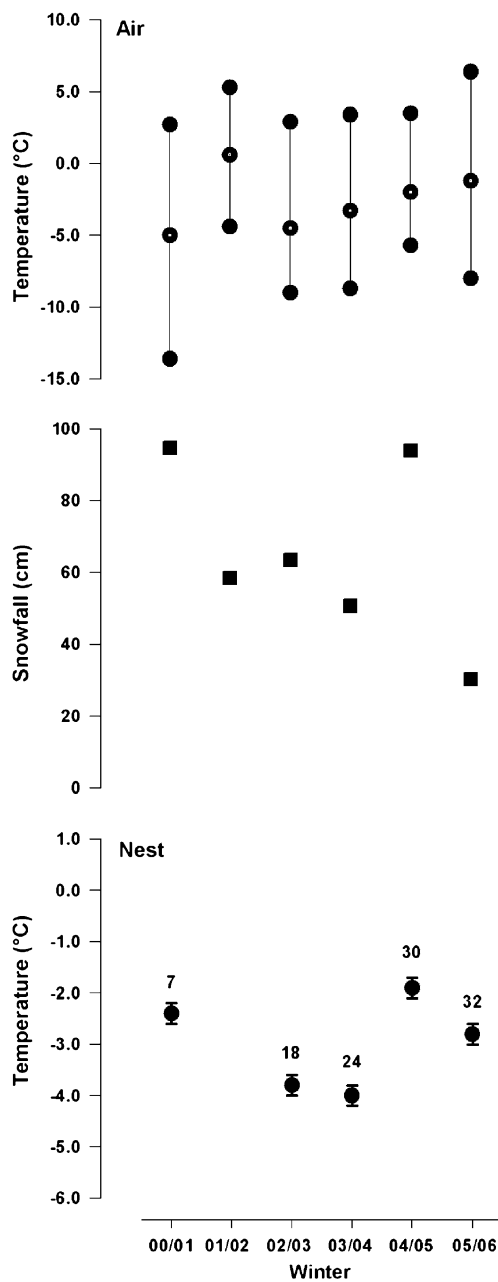
#### Timing and pattern of hatchling emergence

Hatchling *C. picta* began to appear above their nests in late March or early April. Emergence typically continued until mid-May, but in some years extended into early June. Hatchling *G. geographica* vacated their nests in April and May, and *T. scripta* did so primarily from April through early June. Thus, the records showed a species-specific pattern of emergence timing (Fig. 1). Emergence dates averaged over the entire study were 11 April for *C. picta*,

**Table 1** Parameters of emergence from the nest by hatchling turtles

	<i>C. picta</i>	<i>G. geographica</i>	<i>T. scripta</i>
Emergence period (day)	48 (24–77)	19 (1–37)	51 (18–85)
Emergence synchrony (%)	33 (24–50)	15 (0–100)	19 (0–33)
Emergence duration (day)	6 (3–9)	11 (1–18)	19 (5–25)

Mean values, followed by the range of values representing individual annual cohorts, in parentheses. Emergence period is the interval between the first and last emergence dates recorded for each annual cohort. Emergence synchrony is the percentage of nests in each annual cohort for which emergence duration equaled 1 day. Determined for individual nests, emergence duration is the interval between appearances of the earliest- and latest-emerging siblings



**Fig. 2** Environmental conditions at a turtle nesting area in Fulton Co., Indiana, USA, showing: (upper panel) maximum, mean, and minimum air temperature; total snowfall (middle panel); and mean ( $\pm$  SE) minimum temperature recorded December–February inside nests in which hatchling *Chrysemys picta* overwintered. Numbers of nests for each period are given above bars. Nest temperatures were not recorded during winter 2001–2002

25 April for *G. geographica*, and 9 May for *T. scripta* ( $H=66.7$ ;  $P<0.0001$ ). For each annual cohort, emergence period was typically 3–7 weeks (Table 1) and, averaged over the 6-year study, was 48 days for *C. picta*, 19 days for *G. geographica*, and 51 days for *T. scripta*. The apparent

variation among species in this metric approached statistical significance ( $H=5.8$ ;  $P=0.056$ ).

Sixty-one (33%) of the 186 *C. picta* nests examined in this study had hatchlings that emerged synchronously (i.e., on the same day). However, only three of the 20 (15%) *G. geographica* nests, and six of the 27 (22%) *T. scripta* nests, had hatchlings that emerged synchronously. Emergence duration varied by species ( $H=10.5$ ;  $P=0.005$ ) and, averaged over the 6-year period, was 6 days for *C. picta*, 11 days for *G. geographica*, and 16 days for *T. scripta* (Table 1). The longest recorded time taken by a sibling group to vacate its nest was 77 days (*C. picta*). Sufficient data were available to test for annual variation in emergence parameters only for *C. picta*. In this species, emergence duration varied by year ( $H=11.7$ ;  $P=0.040$ ), but the fraction of nests emerging synchronously did not ( $\chi^2=5.1$ ,  $P=0.40$ ).

#### Winter severity and cold exposure

Winters at the study site were cold, with the mean of all air temperatures recorded hourly from December to February being  $\leq 0^\circ\text{C}$  in each of the winters of record (Fig. 2). Annual snowfall ranged from 25 to 95 cm. Intermittent snow cover undoubtedly moderated the hibernaculum thermal environment, as the seasonal minimum temperatures occurring in the shallowest nests (constructed by *C. picta*) were not correlated with mean air temperature ( $\rho=0.10$ ;  $P=0.84$ ) nor minimum air temperature ( $\rho=0.30$ ;  $P=0.55$ ). Thermal conditions in nests to which hatchlings were exposed tended to be less severe in snowier years (Fig. 2), although the relationship between seasonal minimum nest temperature and total snowfall was not significant ( $\rho=0.60$ ;  $P=0.23$ ).

Subzero temperatures occurred inside most or all nests of each species in each year of record (Table 2), although the seasonal minimum temperature varied ( $F_{2,142}=4.0$ ,  $P=0.02$ ) among species. Post hoc comparisons revealed that thermal minima inside nests of *C. picta* ( $-2.9\pm 0.2^\circ\text{C}$ ,  $n=111$ ) were significantly lower than those within nests of *T. scripta* ( $-1.6\pm 0.3^\circ\text{C}$ ,  $n=17$ ); however, values for *G. geographica* nests ( $-2.9\pm 0.3^\circ\text{C}$ ,  $n=17$ ) were indistinguishable from those recorded in the nests of heterospecifics.

Nest depth, a factor that potentially can influence the thermal environment of hatchlings, ranged from ca. 7 to 15 cm and strongly varied by species ( $H=74.5$ ;  $P<0.0001$ ). Nests of *C. picta* were shallow and less variable in depth relative to those of *G. geographica* and *T. scripta* (Table 3). Combining the data from all species and all years of the project showed a trend for minimum nest temperature to be lower in shallower nests (Fig. 3);

**Table 2** Minimum temperature (°C) recorded during December–February inside nests harboring hatchling turtles during winter

Year	<i>C. picta</i>	<i>G. geographica</i>	<i>T. scripta</i>
2000–2001	–2.3 (–1.2 to –4.2; 7)	–2.4 (–1.4 to –3.5; 5)	–1.4 (–0.5 to –3.3; 7)
2001–2002	–	–4.7 (–3.6 to –5.4; 3)	–
2002–2003	–3.8 (0.7 to –7.7; 18)	–3.1 (–2.0 to –3.6; 6)	0.1 (n.a.; 1)
2003–2004	–4.0 (–0.5 to –7.7; 24)	–	–1.8 (–0.8 to –3.3; 5)
2004–2005	–1.9 (0.2 to –6.8; 30)	–1.9 (n.a.; 1)	–0.9 (–0.7 to –1.0; 2)
2005–2006	–2.7 (0.1 to –5.7; 32)	–0.9 (–0.9 to –1.7; 2)	–3.5 (–3.4 to –3.5; 2)
Overall	–2.9 (0.7 to –7.7; 111)	–2.9 (–0.9 to –5.4; 17)	–1.6 (0.1 to –3.5; 17)

Mean values, followed by the range of values for individual nests and the number of nests in the sample, in parentheses. Dashes indicate unavailable data. *n.a.*, not applicable

however, the relationship did not attain statistical significance ( $\rho=0.49$ ;  $P=0.08$ ).

### Winter mortality

When examined in early July, turtle nests typically contained only the fragmented shells of hatched eggs, although some contained unhatched eggs and/or hatchlings that had died before or during winter. Winter-killed hatchlings were recovered only from a few nests in certain years of the project. All three species incurred winter mortality, although *T. scripta* was the most impacted (Table 4). More hatchlings died in 2002–2003 than in any other winter of record; however, nest temperatures in that season were not significantly lower than winters (e.g., 2003–2004) with similar minimum temperatures (Table 2).

We refrained from excavating nests until early July in order to allow ample time for hatchlings to emerge. Nevertheless, inside 14 nests we found live hatchlings (*C. picta*,  $n=2$ ; *G. geographica*,  $n=4$ ; *T. scripta*,  $n=23$ ) that appeared healthy, albeit moderately dehydrated. One of the two *C. picta* nests and two of the ten *T. scripta* nests that harbored live hatchlings also contained at least one winter-killed sibling. Examining the physical structure of these nests offered no clues as to why the live hatchlings found within them had failed to emerge. There were no obvious barriers to egress and, in fact, half of these nests had earlier produced hatchlings; however, we are uncertain

whether or not these remaining turtles ultimately would have emerged.

### Cold exposure and hatchling emergence behavior

We tested the idea that timing and pattern of nest emergence were influenced by the degree of cold stress incurred by hatchlings during winter. There was no correlation between seasonal thermal minima within the nest and emergence date for any of the species under investigation (Table 5). To the contrary, the positive  $\rho$  values (and nearly significant  $P$  value for *C. picta*) suggested that, if anything, hatchlings experiencing lower temperatures during winter tended to emerge *earlier* than those subjected to milder conditions. Severity of the cold to which hatchlings were exposed had no bearing on emergence period in any species, and, at the level of the individual nest, seasonal thermal minimum was not linked to emergence synchronicity or the time required for sibling groups to vacate their nests (Table 5).

## Discussion

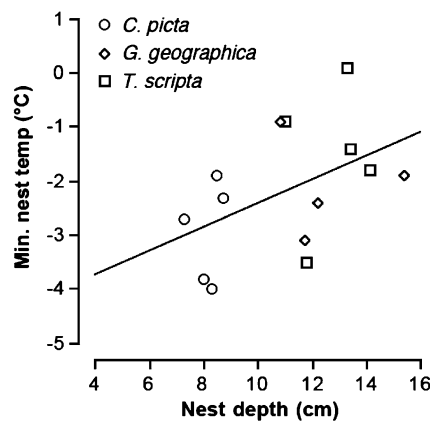
Timing of emigration from the natal nest has potentially important implications for the fitness of turtles inasmuch as it may affect predation risk and the quality and quantity of resources they require for growth. Few studies have been devoted to factors mediating emigration timing in freshwa-

**Table 3** Depth (cm) of nests harboring hatchling turtles during winter

Year	<i>C. picta</i>	<i>G. geographica</i>	<i>T. scripta</i>
2000–2001	8.7 (6.5–12.0; 22)	12.2 (11.0–14.0; 5)	13.4 (12.0–16.3; 10)
2001–2002	–	11.8 (9.0–14.0; 6)	–
2002–2003	8.0 (6.5–9.5; 26)	11.7 (9.0–13.5; 7)	12.7 (10.1–15.0; 5)
2003–2004	8.3 (4.8–12.5; 46)	10.9 (n.a.; 1)	14.1 (12.3–17.1; 7)
2004–2005	8.6 (4.5–12.2; 54)	14.2 (14.2–16.5; 2)	11.0 (6.2–14.8; 4)
2005–2006	7.4 (5.5–10.0; 59)	10.8 (8.0–13.5; 2)	11.8 (10.0–13.5; 5)
Overall	8.1 (4.5–12.5; 207)	12.1 (8.0–16.5; 23)	12.9 (6.2–17.1; 31)

Mean values, followed by the range of values for individual nests and the number of nests in the sample, in parentheses. Dashes indicate unavailable data. *n.a.*, not applicable





**Fig. 3** Relationship between nest depth and minimum temperature recorded during December–February inside nests in which turtle hatchlings overwintered. Each symbol represents the average of all values of nest depth ( $n=1-50$ ) and nest temperature ( $n=1-32$ ) collected for a separate annual cohort. Nest temperatures were not recorded during winter 2001–2002

ter turtles, particularly those whose hatchlings hibernate within the nest (Costanzo et al. 2008). Because hatchlings commonly are subjected to severe cold in hibernation, and because cold stress can transiently impair neurobehavioral function, we questioned whether winter severity influences emigration phenology. In the present study, we examined timing and pattern of nest emergence in hatchlings of three species of emydid turtles that vary in cold hardiness.

Hatchlings of the species under investigation commonly overwinter in the nest, even in the northern portion of their range, but a small percentage of the nests constructed by *C. picta* and *T. scripta* had hatchlings that emerged in fall, as has been reported previously (Costanzo et al. 2004; DePari 1996; Gibbons and Greene 1978). Fall emergence has also been reported for *G. geographica* (Baker et al. 2003; Nagle et al. 2004; Pappas et al. 2000), although this behavior was not observed in the present study. Instances of fall emergence in these species may be caused by adverse conditions within the nest (e.g., inundation or degradation of the nest plug; see

**Table 4** Winter mortality of hatchlings hibernating inside nests, showing for each year of the study the total number of nests examined/number of nests with  $\geq 1$  dead hatchling, followed by the total number of dead hatchlings in parentheses

Year	<i>C. picta</i>	<i>G. geographica</i>	<i>T. scripta</i>
2000–2001	24/0 (0)	5/0 (0)	10/1 (3)
2001–2002	37/0 (0)	6/1 (1)	7/0 (0)
2002–2003	26/2 (4)	7/0 (0)	4/1 (13)
2003–2004	46/0 (0)	1/0 (0)	7/0 (0)
2004–2005	51/2 (2)	2/1 (1)	4/1 (5)
2005–2006	49/0 (0)	2/0 (0)	5/0 (0)
Overall	232/4 (6)	23/2 (2)	37/4 (21)

Costanzo et al. 2008), although we discerned no difference in the integrity of those particular nests.

At our study site in northern Indiana, emergence of hatchling turtles usually began in late March with the appearance of the first *C. picta* and ended in early June with the egress of the last *T. scripta*. The average date of emergence for *C. picta* (11 April) was 2 weeks earlier than that for *G. geographica* (25 April) and 4 weeks earlier than that for *T. scripta* (9 May). These dates and this general pattern are consistent with reports for other populations of *C. picta* (Breitenbach et al. 1984; DePari 1996), *G. geographica* (Nagle et al. 2004), and *T. scripta* (Tucker and Packard 1998; Willette et al. 2005) at similar latitudes.

Cues stimulating hatchling emigration are probably complex and remain poorly understood; although rainfall and temperature apparently are key stimuli (see review by Costanzo et al. 2008). Variability in timing of hatchling emergence can reflect variation in environmental conditions over the nesting landscape, although this probably was not an important factor in our study because the nesting area was small (<1 ha) and most nests were proximal to other nests. It is more likely that the species-specific pattern in emergence timing reflected phenological variation in appearance of emergence cues within their respective hibernacula, as for example, the late emergence of *T. scripta* could reflect delayed warming of their relatively deep nests. It is also possible that these species varied in ability to perceive and respond to emergence cues; however, the apparent similarity in annual emergence period argues against this being the case.

For all three species, annual emergence period usually lasted 3–7 weeks, but was even longer in some years. Such a protracted period of emigration could reflect latency in the materialization of emergence cues within different nests, perhaps owing to variation in the depth of hatchlings within the soil column (Costanzo et al. 2008). We surmised that a protracted emergence period would follow an especially harsh winter, assuming that hatchlings are differentially exposed to (or impaired by) severe cold during hibernation. However, we found no correlation between annual emergence period and minimum nest temperature.

#### Timing and pattern of nest emergence

Synchronization of life-stage transitions, such as emigration from the natal nest, is thought to be advantageous (Brännäs 1995; Carr and Hirth 1961; Spencer et al. 2001). By working cooperatively, turtle hatchlings can more efficiently tunnel to the ground surface and thereby conserve their endogenous energy reserves. In addition, emerging en masse could deluge predators with a surplus of prey, effectively minimizing per-capita mortality rate. Finally, remaining inside a nest that has been breached by one's

**Table 5** Results of correlation analyses testing relationships between cold stress, as represented by minimum temperature in the nest, and various parameters concerning nest emergence of hatchling turtles

	<i>C. picta</i>		<i>G. geographica</i>		<i>T. scripta</i>	
	$\rho$	<i>P</i>	$\rho$	<i>P</i>	$\rho$	<i>P</i>
Emergence date	0.05	0.92	0.18	0.73	0.30	0.55
Emergence period	0.30	0.55	−0.80	0.11	−0.10	0.86
Emergence synchrony	0.10	0.84	−0.28	0.58	−0.13	0.80
Emergence duration	0.20	0.69	0.30	0.55	0.00	0.99

Coordinates used in analyses are values (averages) representing all individual annual cohorts of the 6-year study

siblings carries a heightened risk of mortality from predation, parasitism, or exposure to environmental extremes (Baker et al. 2006; Christens and Bider 1987; Christiansen and Gallaway 1984; McGowan et al. 2001; Nagle et al. 2004). Therefore, clutch mates that coordinate nest emigration should have a survival advantage over those that do not. These points notwithstanding, in the present study, some nests contained hatchlings that emerged synchronously (i.e., on the same day), but most had hatchlings that emerged individually or in small groups over a period of days or weeks. Of the three species we investigated, *C. picta* showed the greatest propensity to emerge en masse, but this occurred in only about one third of their nests. Contrary to common belief, synchronous emergence of clutch mates is not a prevalent behavior, at least in the populations under investigation.

Clutch mates tended to emerge from their nest over the course of 1 to 2 weeks, although some took considerably longer (e.g., 11 weeks for one *C. picta* nest). Generally, emergence duration was longer for *G. geographica* and *T. scripta* than for *C. picta*, perhaps because in these species, additional time was needed for the entire complement of siblings to detect or respond to emergence cues. The time required for a sibling group to vacate its nest was not uniform over the 6-year study, suggesting that emergence duration was sensitive to some as yet unidentified environmental factor(s), albeit not minimum nest temperature.

#### Cold exposure and emergence phenology

Winters at the study site were cold, and temperature inside most nests repeatedly fell below 0°C. Seasonal minimum temperature tended to be lowest within nests of *C. picta*, which, usually being less than 10-cm deep were also the most superficial. However, owing to prevalent snow cover, these nests did not become as cold as do *C. picta* nests in more arid regions, such as the central Plains (Costanzo et al. 2004).

Despite the occurrence of subzero temperatures within many nests, winter mortality of hatchlings was relatively low. Species whose hatchlings overwinter terrestrially are capable of surviving exposure to subzero temperatures by remaining supercooled or by tolerating the freezing of their body fluids (Costanzo et al. 2008). However, cold hardiness is better developed in *C. picta* than in *G. geographica* and *T. scripta* (Baker et al. 2003; Costanzo et al. 2006; Dinkelacker et al. 2005) and, accordingly, *C. picta* can successfully overwinter in superficial nests where temperature fluctuations generally are more extreme, and thermal minima lower. By the same token, winter mortality was highest in *T. scripta* despite the increased thermal buffering afforded by its deeper nests.

Upon recovering from chilling in the supercooled or frozen states, turtle hatchlings commonly exhibit neuro-behavioral impairment that can persist for extended periods (Attaway et al. 1998; Baker et al. 2007; Muir et al. 2010). Thus, it is possible that relatively severe winters delay hatchling emigration and lengthen the nest emergence period, especially in less cold hardy species. However, this seemed not to be the case in our study, perhaps because emigration timing was more strongly influenced by other, as yet unknown, factors. Similarly, Willette et al. (2005) found no association between mean air temperature in winter and the date hatchling *T. scripta* emigrated from nests the following spring.

Despite having experienced the lowest recorded temperatures, *C. picta* emerged from their nests earlier than did *G. geographica* and *T. scripta*, possibly because, being highly cold tolerant and unimpaired, they could respond to thermal cues developing earlier in their more superficial nests. The later emergence of *G. geographica* and *T. scripta* may be a consequence of their comparatively lower cold tolerance and, presumably, greater susceptibility to cryoinjury. That *G. geographica* and *T. scripta* overwinter lower in the soil column (chiefly due to the deeper nests excavated by their larger mothers) may partly explain why they have not evolved a more extensive cold hardiness. The northerly

distribution of *T. scripta*, which only reaches northern Indiana and southern Michigan (Ernst et al. 1994), may be limited by this species' relatively poor tolerance for cold (Costanzo et al. 2006; Tucker and Packard 1998).

Clutch mates likely encounter a range of temperatures in winter owing to the strong thermal gradients occurring in their nests (Costanzo et al. 1995; Packard et al. 1997; Tucker 1999). Variable cold exposure (and resultant injury) leading to differential ability to emigrate from the nest could be manifested as a protracted and asynchronous emergence of the sibling group (Glen et al. 2005; see also Spencer et al. 2001). However, we found no evidence that minimum temperature in winter was associated with a delay in emergence, longer emergence duration, or reduced synchrony. To the contrary, there was a trend (albeit non-significant) for hatchlings overwintering in colder nests to emerge relatively early in spring (Table 5), although this pattern could simply reflect a more expeditious warming of the hatchlings in these shallower nests.

## Conclusion

Our findings did not support the idea that cold stress influences the timing and pattern of nest emergence of hatchling turtles. However, we used minimum nest temperature in hibernation as the predictive determinant of emergence behavior. Although the degree of cold stress incurred by turtles is obviously a function of body temperature, this variable may be too simplistic, given that other factors can strongly mediate the effect of temperature on hatchling physiology. For example, the moisture content and texture (particle size distribution) of nesting soil are key determinants of whether a hatchling exposed to a chilling excursion will remain supercooled or freeze (Costanzo et al. 2004), the latter outcome having the more severe and enduring effect on neurobehavioral function (Baker et al. 2007).

Our results reveal an intriguing relationship between the level of cold hardiness and the emigration timing of hatchling turtles. By virtue of their exceptional cold hardiness, *C. picta* can successfully hibernate in shallow nests, which tend to warm rapidly in spring. By arousing early, when ambient temperatures are relatively low, hatchlings may benefit from a reduced risk of desiccation during emigration from the nest. In addition, by emigrating to water earlier than sympatric species, *C. picta* can exploit unoccupied habitats and abundant resources. The fitness advantage of early emergence may lead to the improvement of cold-hardiness adaptations in northern populations.

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