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A 21-YEAR STUDY OF SEASONAL AND INTERSPECIFIC VARIATION OF HATCHLING EMERGENCE IN A NEARCTIC FRESHWATER TURTLE COMMUNITY: TO OVERWINTER OR NOT TO OVERWINTER?

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Abstract: Hatchling emergence patterns were studied in a community of six species of freshwater turtles in Lancaster County, Pennsylvania, USA, including: *Chelydra serpentina*, *Chrysemys picta*, *Clemmys guttata*, *Glyptemys insculpta*, *Glyptemys muhlenbergii*, and *Sternotherus odoratus*. Data were collected every year from 1965–1985 on estimated date of emergence, carapace length, April–May precipitation, August–September precipitation, annual precipitation, and low temperature and occurrence of precipitation during the 24 h prior to the time of each hatchling detection (n = 806). *Chelydra serpentina*, *Ch. picta*, and *Cl. guttata* hatchlings have a facultative delayed emergence strategy. The other species (*G. insculpta*, *G. muhlenbergii*, and *S. odoratus*) appear to be obligate early emergers, with the exception of one hatchling *G. muhlenbergii* that delayed emergence. Early emergence occurred in some species every year. However, the majority of hatchlings delayed emergence until the year following oviposition, except in 1973, the year following intense flooding and nest destruction associated with a major hurricane. Mean estimated calendar day of emergence varied annually in *C. serpentina* and *Ch. picta*. The same variable also differed among species for comparisons of both early and delayed emergence. *Chelydra serpentina* hatchlings emerged earlier than all other species whether they used an early or delayed strategy. Carapace length of *Ch. picta* hatchlings varied significantly among years, and *C. serpentina* hatchlings that delayed emergence were significantly larger in carapace length than those that emerged early. Seasonal and previous 24-h precipitation had varying effects on the number of emerging hatchlings, but August–September precipitation in one year had a strong correlation with the number of hatchlings that delayed emergence until the following spring. The number of hatchlings detected peaked at a previous 24-h air temperature of about 12°C for both early and late emergence. Small species like *G. muhlenbergii* and *S. odoratus* may emerge early to limit potential hatchling competition in diverse communities of freshwater turtles with primarily delayed emergence.

Résumé: Le motif d'émergence d'une communauté de 6 espèces de tortue d'eau douce a été étudié, dont *Chelydra serpentina*, *Chrysemys picta*, *Clemmys guttata*, *Glyptemys insculpta*, *Glyptemys muhlenbergii*, et *Sternotherus odoratus*, dans le comté de Lancaster, en Pennsylvanie, É.-U. Les données telles que l'estimé de date d'éclosion, la longueur de la carapace, les précipitation aux mois d'avril et mai et ensuite août et septembre, les précipitations annuelles, et la présence de basses températures et de pluie pendant les 24 h avant la détection d'éclosion de tortues (n = 806) ont été mesurées annuellement de 1965–1985. Les jeunes tortues des espèces *C. serpentina*, *Ch. picta*, and *Cl. guttata* semblent pratiquer une stratégie d'émergence tardive facultative, leur permettant d'émerger plus tard dans la saison si nécessaire. Les autres espèces (*G. insculpta, G. muhlenbergii*, et *S. odoratus*) semblent plutôt contraintes à émerger tôt dans la saison, sauf dans le cas d'une tortue *G. muhlenbergii* qui a été observé en émergence tardive. Au moins une espèce de tortue a été observée à émerger hâtivement à chaque année, à l'exception de 1973, année précédée d'un sévère ouragan causant l'inondation et la destruction de plusieurs nids. Par contre, la majorité des jeunes tortues ont repoussé leur émergence à l'année suivant l'oviposition. Le jour hebdomadaire moyen d'émergence a varié annuellement pour *C. serpentina* et *Ch. picta*. La même variable varie entre espèces lors de comparaisons entre l'émergence hâtive et tardive. Les jeunes *C. serpentina* émergeaient plus tôt que toutes les autres espèces dans notre étude, peu importe leur stratégie d'émergence. La longueur de la carapace des jeunes *Ch. picta* a fait preuve de beaucoup de variations à travers les ans, tandis que les jeunes *C. serpentina* qui ont émergé tardivement avaient une longueur de carapace significativement plus grande que ceux qui ont émergé plus tôt. Les précipitations annuelles et celles reues dans les 24-h précédant l'émergence avaient des effets variables en termes de nombre de tortues émergentes, mais nos observations semblent indiqués une forte relation entre les précipitations d'août et septembre au nombre de jeunes tortues restants dans le nid jusqu'au printemps suivant. Le nombre maximal de tortues en émergence a été observé quand la température de l'air était de 12°C pendant les 24-h précédentes, observation pour les tortues pratiquant une émergence

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hâtive ou tardive. Finalement, les espèces de petite taille, comme *G. muhlenbergii* et *S. odoratus,* peuvent parfois employer la stratégie d'émergence hâtive afin d'alléger la compétition entre elles et les autres espèces de tortue d'eau douces qui pratiquent principalement la stratégie d'émergence tardive.

Key words: Delayed emergence; Early emergence; Environmental determinants; Hatching; Nest; Overwintering; Turtles

Delayed emergence of hatchling turtles from the nest in the temperate zone, sometimes referred to in the literature as "overwintering in the nest" (Gibbons and Nelson, 1978; Gibbons, 2013), was once considered to be exceptional and limited to only a few species or unusual circumstances. We now know that delayed emergence is widespread both globally and taxonomically (reviewed by Gibbons, 2013), occurring in eight of 14 turtle families. For many years before Gibbon's reviews, the paradigm for turtle life history was that females nested in the late spring or early summer and hatchlings "normally" emerged from the nest in the late summer or early fall of the same year. However, although more commonplace than initially thought, and not unusual in turtle species that have received adequate study, delayed emergence is not universal either. Thus, turtles have a diversity of hatchling emergence strategies or patterns (fall, spring, or both) that can vary within and among species, locations, and years (Ewert, 1991). Explanations for this variation remain elusive due to the sometimes unpredictable and inconsistent expression of emergence strategies. Some species appear to have an obligate emergence strategy whereas others appear to be facultative. Identification of the most-influential environmental, genetic, or phylogenetic factors that elicit delayed emergence or a facultative strategy has received some attention but remains an important question to be addressed in turtle biology and conservation (Gibbons, 2013). Long-term field studies can contribute to understanding the temporal factors that influence turtle emergence strategies.

Two competing hypotheses have been advanced to explain delayed emergence of hatchling turtles as reviewed by Gibbons (2013). The first is that the strategy occurs in situations where the climate (or date of nesting) does not allow incubation to be completed prior to the arrival of cold temperatures preceding winter for temperate species. The second assumes that hatchlings are trapped in the nest by hard, dry soil conditions late in the summer or fall and can only emerge when the soils are wetted by spring rains. Studies by Gibbons and Nelson (1978) and Gibbons (2013) in South Carolina largely refuted these hypotheses for some species, but not all research supports that conclusion (e.g., DePari, 1996) and additional research is necessary. The working hypothesis of Gibbons (2013) is that delayed emergence of freshwater turtle hatchlings "is a genetically controlled, variable trait upon which natural selection operates," varying among species under different ecological conditions. As Gibbons further noted, natural selection favors hatchling turtles that "enter the aquatic habitat at the most propitious season for survival and subsequent growth."

Part of the challenge in determining the hatchling emergence strategy of particular turtles relates to the difficulty of identifying the actual dates that hatchlings leave the nest. Unequivocal evidence of emergence date requires the use of drift fences to intercept nesting females and newly emerged hatchlings (Gibbons and Semlitsch, 1981; Gibbons, 2013) or nest cages checked at daily intervals (Wilson and Ernst, 2005, 2008; Ennen et al., 2012a), but such studies are rare. As a result, most records of delayed emergence are anecdotal. Despite the need for additional studies, the widespread occurrence of delayed emergence led Gibbons (2013) to conclude that it should be considered the normal strategy for turtles unless research demonstrates otherwise.

Detailed studies that compare the extent of delayed emergence from the nest in communities of freshwater turtles are limited to only a few including Gibbons and Nelson (1978) for a population of five freshwater species in South Carolina, Congdon et al. (1983, 1987, 2011) for two species in southeastern Michigan, Costanzo et al. (1995) for five species in Nebraska, and Baker et al. (2010) for three species in Indiana. The scarcity of such

studies makes comparative research on delayed emergence in freshwater turtle communities a high priority for further investigation (Gibbons, 2013). A fundamental unanswered question is why the extent of delayed emergence differs within and among a community of turtle species that occupy the same general locality.

The objectives of this paper are threefold. First, we compare the incidence of intraspecific and interspecific delayed hatchling emergence in a community of six sympatric freshwater turtle species in Lancaster County, Pennsylvania, USA. Second, we examine the environmental correlates of delayed emergence, especially as related to annual and seasonal variation in temperature and precipitation. Third and finally, we examine how body size of hatchlings varies between the two strategies. Body size has been suggested as an important determinant of hatchling survival, with larger hatchlings having higher survivorship than those that are smaller (Janzen, 1993; Janzen et al., 2000a,b: but see Congdon et al., 1999). Data collection spanned three decades (1965–1985) of a study of freshwater turtle ecology (see citations below).

Materials and Methods

Research began in May 1965 on the autecology and behavior of six sympatric, freshwater turtle species including the Snapping Turtle (*Chelydra serpentina*), Painted Turtle (*Chrysemys picta*), Spotted Turtle (*Clemmys guttata*), Wood Turtle (*Glyptemys insculpta*), Bog Turtle (*Glyptemys muhlenbergii*), and Eastern Musk Turtle or Stinkpot (*Sternotherus odoratus*). The study continued for 21 yr through November 1985. The research effort was not initially designed to examine nest emergence patterns of hatchling turtles, but the accumulation of these data over more than 2 decades allows for such an analysis. As noted by Gibbons (2013), regardless of the original intent of studies that last longer than a researcher planned, they often provide the empirical evidence needed to address important biological questions.

Description of Study Site

The research took place in Lancaster County, Pennsylvania, in the White Oak area, approximately 2 km north of Manheim. The area included a 2.5-ha soft-bottomed mill pond bounded by 10 ha of mixed marsh, boggy pastures, and woodland habitat formed by the damming of Big Chickies Creek, a tributary of the Susquehanna River. The site is described in detail by Ernst (1971a) and Ernst et al. (2014). Numerous other publications resulting from research at this site are summarized in Ernst and Lovich (2009) under chapters for each of the species listed above. All research and collection of turtles at White Oak during 1965–1985 was covered by annual permits from the Pennsylvania Fish and Boat Commission.

Data Collection

A total of 1927 collecting trips were made to White Oak during the 21 yr: 1154 in the spring and 773 in the fall. Hatchlings were not found on all trips. Most collection of hatchlings (n = 806: 277 in the fall and 529 in the spring) occurred during the spring season (March–early June) of emergence from the nest by overwintering hatchlings. Fall collecting efforts (August–October) of hatchlings from that year's nesting activity in late May–early July were about 67% of that in the spring, as measured by days in the field. Had collecting efforts of the two seasons been equal, it is conceivable that an additional 23%-more hatchlings might have been collected in the fall at White Oak. Some of our spring–fall comparisons were adjusted in an attempt to partially compensate for the spring collecting bias (Table 1). Adjusted values were calculated as:

$$\left(\text{Actual number of August} - \text{October hatchlings} \times 100\right)/67.$$

Hatchling turtles were collected opportunistically on land or in shallow water by hand or with a dip net or seine as they were encountered; very few were found emerging from nests. Recently emerged young were identified by the presence of a caruncle, or egg tooth (both spring and fall); unretracted yolk masses, or unhealed, abdominal yolk scars (spring and fall; Ernst, 1971b); and by the absence of new areas of growth on their shells (in the fall; Ernst, 1971c), usually in

TABLE 1.—Nest emergence times for hatchling turtles encountered near Lancaster, Pennsylvania 1965–1985 based on early emergence (August–October) or delayed emergence (March–May) dates of encounter. Estimates are rounded to the nearest whole number. Percentages (rounded to a whole number) of early vs. delayed emergence are shown in parentheses for each species. Estimated percentages for delayed emergence are not shown but are equal to 100% minus the percentage shown under the estimated emergence column for each species.

	Emergence time			Total	
	Early (August–October)		Delayed (March–May)		
Species	Actual	Estimated	Actual	Actual	Estimated early + actual delayed
Chelydra serpentina	70 (27%)	104 (35%)	194 (73%)	264	298
Chrysemys picta	90 (22%)	134 (30%)	312 (78%)	402	446
Clemmys guttata	57 (72%)	85 (79%)	22 (28%)	79	107
Glyptemys insculpta	8 (100%)	12 (100%)	0	8	12
Glyptemys muhlenbergii	33 (97%)	49 (98%)	1 (3%)	34	50
Sternotherus odoratus	19 (100%)	28 (100%)	0	19	28
Total	277	413	529	806	942

aggregate. Small turtles that did not meet these criteria were not included in our analyses. These first encounters are our best estimates of the day of nest emergence for each hatchling, hence we refer to the day of encounter as "estimated day of emergence" or "estimated calendar day of emergence," in full recognition that they are not known with full precision but instead are approximations of the real date of emergence. Few studies are available to calibrate our estimates. Mitrus (2001) studied the retention time of caruncles in hatchling *Emys orbicularis* and noted that they fell off during a period of several weeks after hatching. If hatchlings overwintered and delayed emergence until the following spring, the caruncle was often still present. In contrast, Hamilton (1940) noted that the caruncle of *C. serpentina* is usually "absorbed" within 24 h but may persist up to 3 days in captivity. Given the ephemeral retention of caruncles, yolk masses (see Filoramo and Janzen, 1999), and absence of growth on the shell (Ernst and Lovich, 2009), our estimates may be off by several weeks from the actual date of emergence, but that would not significantly affect our assessments of whether hatchings emerged early or delayed emergence.

For each hatchling encountered, the date and time of first capture were recorded, and carapace length (CL) was measured with dial calipers read to 0.1 mm. The turtles were then marked with coded notches for future identification (Ernst et al., 1974) and released. Nesting in all six species occurred in June. All nests found (n = 190 from 1965–1985; Table 2) while being excavated by female turtles or afterwards were marked and visited frequently until the approximate date of emergence was determined. Those nests that did not produce hatchlings during the late summer or fall hatching period were monitored again the next spring for delayed emergence. From 1965–1993, CHE made 1927 research trips to White Oak during the nesting seasons for all six species.

TABLE 2.—Numbers of hatchlings encountered per month in Lancaster County, Pennsylvania. The numerals in parentheses after each species represent the total number of nests found (including those in the process of excavation–oviposition and those that were predated) on 1927 site visits during all years of the study.

	Month of emergence from nest						
Species (n nests)	March	April	May	August	September	October	Total
Chelydra serpentina (50)	0	48	146	29	41	0	264
Chrysemys picta (62)	1	79	232	15	72	3	402
Clemmys guttata (54)	0	7	15	0	57	0	79
Glyptemys insculpta (10)	0	0	0	0	4	4	8
Glyptemys muhlenbergii (6)	0	0	1	4	23	6	34
Sternotherus odoratus (8)	0	0	0	0	17	2	19
Total	1	134	394	48	214	15	806

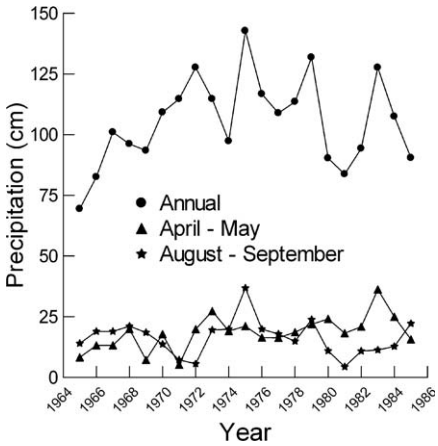

FIG. 1.—Annual and seasonal precipitation totals for Landisville, Pennsylvania during the period of study.

Weather data were obtained from the National Weather Service (2012) for Landisville, Pennsylvania (National Weather Station I.D. LDVP1; latitude 40.1167°N, longitude, 76.433°W; datum = NAD 27; elevation = 109.728 m), approximately 7 km southwest from the White Oak study area. Precipitation data collected included yearly total precipitation and precipitation for April–May and August–September (Fig. 1). In addition, the occurrence of rain during the 24 h prior to hatchling captures was recorded at the time of data collection, as some of these events were different than those at the Landisville recording station. Rain events were scored qualitatively from field notes as either "rain" or "no rain." The responses of hatchling numbers detected to 24-h prior rainfall were tested with Chi-square analyses. Low temperatures recorded in the 24 h prior to locating a hatchling turtle were also analyzed.

Defining Early vs. Delayed Emergence

We used essentially the same definitions of "early" and "delayed" emergence (relative to assumed time of hatching) given by Gibbons (2013). Early emergence was defined as leaving the nest at the end of incubation in the same year as oviposition, followed shortly by presumed entry into aquatic habitats. In contrast, delayed emergence was defined as departure from the nest and entry into aquatic habitat weeks or months after hatching; for our purposes, in the year following oviposition. In his definition of delayed emergence, Gibbons included hatchlings that delayed entering the aquatic habitat after hatching. Emergence strategies differ within and among species and there are three possibilities: (1) Emerge from the nest and hibernate on land (e.g., *Terrapene carolina* in New York fide Burke and Capitano, 2011) until entering aquatic habitats in the spring (e.g., *Malaclemys terrapin* in New York fide Muldoon and Burke, 2012); (2) emerge from the nest and hibernate in the water until becoming active in the spring (e.g., *C. serpentina* in Nebraska fide Costanzo et al., 1995); or (3) hibernate in the nest and emerge and enter aquatic habitats in the spring (e.g., *Ch. picta* in Nebraska fide Costanzo et al., 1995). The choice of strategies has potentially important demographic consequences for free-living hatchlings. For example, survival of *C. serpentina* hatchlings is higher in water than on land under simulated overwintering conditions in the laboratory (Sims et al., 2001), which may or may not adequately reflect natural conditions.

From the preceding discussion it can be seen that opportunistic encounters of hatchling turtles in the spring could theoretically represent recent emergence from nests oviposited the previous spring–summer with immediate entry into aquatic habitats. It is also possible that hatchlings found in the spring emerged from nests the previous fall and spent the winter on land before entering aquatic habitats in the spring, or they were in aquatic habitats the entire time following emergence. However, it is unlikely that hatchlings would have a caruncle, yolk sac, or fresh yolk scar so long after hatching (Hamilton, 1940; Mitrus, 2001; Ernst and Lovich, 2009). Gibbons' (2013) definition of delayed emergence does not require disentangling these overwintering strategies.

Data Analysis and Hypotheses

To examine if CL was different between hatchlings of a given species that emerged early or delayed emergence, we used analysis of variance (ANOVA). The tests were performed for each species with a dual emergence strategy and adequate sample sizes of

TABLE 3.—Possible effects (both positive and negative) of how seasonal and annual precipitation in consecutive years affect hatchling emergence strategies of turtles.

	Emergence strategy	
Precipitation	Early	Delayed
April–May	Spring precipitation affects both emergence and hatchling survival in the spring and fall. Floods or droughts may cause nest mortality.	Spring precipitation in year X is not expected to dramatically affect delayed (spring) emergence in year X + 1, unless flooding or drought causes nest failure.
August–September	Fall precipitation affects both emergence and hatchling survival in the fall. Floods or droughts may cause nest mortality.	Fall precipitation in year X affects both emergence and hatchling survival in the spring of year X + 1.
Annual	Spring and fall precipitation affect both emergence and hatchling survival in the spring and fall. Floods or droughts may cause nest mortality.	Annual precipitation in year X affects delayed emergence and hatchling survivorship in year X + 1, primarily through the contribution of August–September precipitation.

hatchlings (*C. serpentina, Ch. picta*, and *Cl. guttata*) to examine these relationships thoroughly. We did this because DePari (1996) and Riley et al. (in press) found that various measures of body size were significantly different between hatchling *Ch. picta* that emerged early or delayed emergence in New Jersey and Canada, respectively. In the former study, hatchlings that emerged early were significantly smaller in plastron length than those that delayed emergence, even though mean hatchling weight and yolk sac size did not differ. In the latter study, mean CL of hatchlings that emerged early was significantly larger than hatchlings that delayed emergence.

We tested six different hypotheses about the temporal effects of precipitation on hatchling emergence (Table 3). We assumed that precipitation effects are relatively short-lived (days to months) and that precipitation in one year has a greater effect on hatchling emergence and survivorship in the same year than it does in the following year. However, fall–winter precipitation in one year may have a lag effect on hatchling emergence and survivorship the following spring, especially due to accumulated snow melting in the spring at higher latitudes and elevations. Clearly, the effects of protracted droughts or wet periods confound this simplified overall hypothesis due to the interactions of climate with turtle clutch phenology, which affects timing of oviposition (Lovich et al., 2012a).

Recognizing that there is climatic variation among years (Ernst, 1974), especially for a study of this duration, we used ANOVA to compare differences in estimated mean calendar day of emergence for *C. serpentina* and *Ch. picta*, the two species with the largest sample sizes. We then used a hierarchical linear mixed model to compare mean estimated calendar day of emergence (estimated as the day of capture) with species as a fixed effect and year as a random effect. We conducted one analysis for early emergence (all six species) and another for delayed emergence (with *C. serpentina*, *Cl. guttata*, and *Ch. picta*). Calendar days were calculated from January 1 to the date of capture (of the estimated day of emergence year) for each hatchling following Lovich et al. (2012a). We used linear regression and correlation analyses to examine relationships between environmental variables (rainfall and air temperature) and the numbers of hatchlings encountered.

For all parametric statistical tests, we verified the assumptions of normality and homogeneity of variance by examination of normal probability and residual plots. When variance is reported, summary data are given as the mean ± 1 standard error. The significance level of $\alpha = 0.05$ was used for all statistical tests. Statistical analyses were performed using R (R Development Core Team, 2008) or SYSTAT® 12 or 13 for Windows (SYSTAT, 2008).

RESULTS

Some hatchlings emerged early in all 21 yr. However, they were greatly outnumbered in most years by hatchlings that delayed emergence until spring, except for 1973 (Fig. 2).

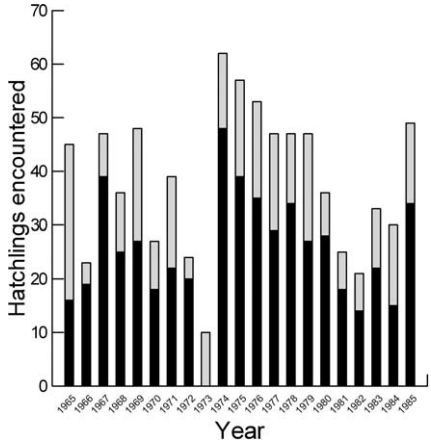

FIG. 2.—The number of hatchlings (n = 806) of six species of turtles encountered per year near White Oak, Lancaster County, Pennsylvania. Light portions of bars represent the number of early-emergence hatchlings (August–October) and dark portions represent delayed-emergence hatchlings (March–May).

Low numbers of hatchlings were found in 1966, a drought year, and in 1973, the year after Hurricane Agnes, a major storm that inundated the area during the June 1972 nesting season, destroying all *Ch. picta* nests except those situated on high ground (Ernst, 1974).

Table 2 presents the total number of hatchlings found by month for each species. Those with both early emergence and delayed emergence included *C. serpentina*, *Ch. picta*, *Cl. guttata*, and *G. muhlenbergii*. In the latter species, only a single hatchling out of 34 was found that delayed emergence. *Glyptemys insculpta* and *S. odoratus* appear to lack delayed emergence, although the sample sizes for both species were small. Because more emphasis was placed on spring collecting due to the abbreviated annual activity cycle of *Cl. guttata* during 1972–1980 (Ernst, 1976), the fall collection values in Table 1 were adjusted in an effort to compensate for this bias. The largest percentage (with or without adjustment for sampling bias in the fall) of both *C. serpentina* (73%) and *Ch. picta* (78%) hatchlings delayed emergence. In contrast, the largest percentage of *Cl. guttata* hatchlings emerged early.

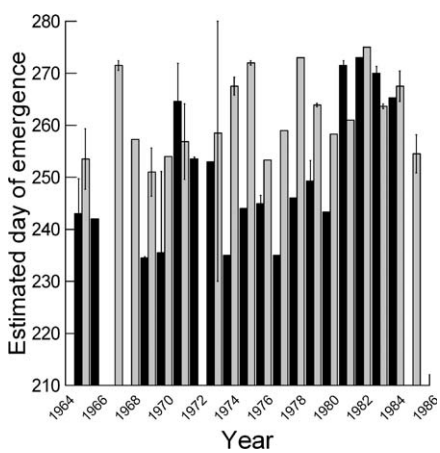

FIG. 3.—Annual variation in early emergence dates between *Chelydra serpentina* (black bars) and *Chrysemys picta* (gray bars). Standard error bars are shown.

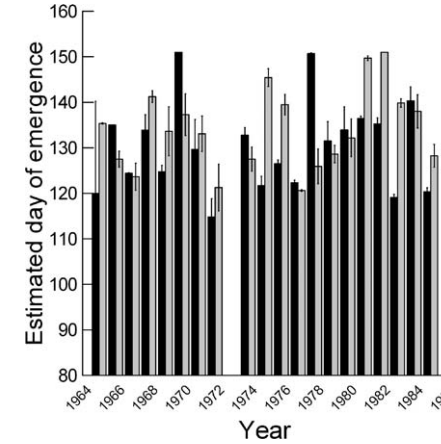

FIG. 4.—Annual variation in delayed emergence dates between *Chelydra serpentina* (black bars) and *Chrysemys picta* (gray bars). Standard error bars are shown.

Mean estimated calendar day of early (Fig. 3) and delayed emergence (Fig. 4) varied among years for the two species with the largest sample sizes (*C. serpentina and Ch. picta*). Annual variation in mean estimated calendar day was significant for *C. serpentina* for both early (ANOVA, $F_{17,52} = 6.02$, $P < 0.001$) and delayed emergence (ANOVA, $F_{19,174} = 12.67$, $P < 0.001$). The same was true for *Ch. picta* for early (ANOVA, $F_{18,71} = 2.54$, $P = 0.003$) and delayed emergence (ANOVA, $F_{19,292} = 8.02$, $P < 0.001$).

Mean estimated calendar day of early emergence varied among species. A hierarchical linear mixed model, comparing the mean day of emergence among species with

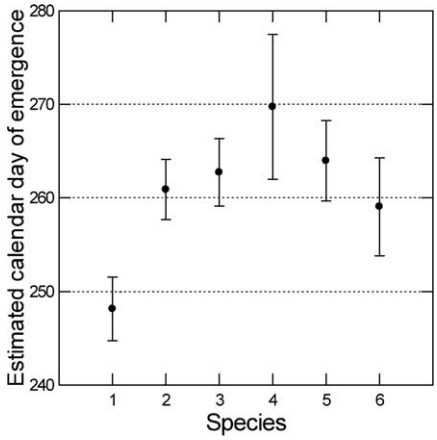

FIG. 5.—Estimated least squares mean calendar day of emergence for hatchling turtles in Lancaster, Pennsylvania from 1965–1985 that emerged early (August–October of the year of oviposition); 95% confidence intervals are shown. Species codes are as follows: 1 = *Chelydra serpentina*, 2 = *Chrysemys picta*, 3 = *Clemmys guttata*, 4 = *Glyptemys insculpta*, 5 = *Glyptemys muhlenbergii*, and 6 = *Sternotherus odoratus*.

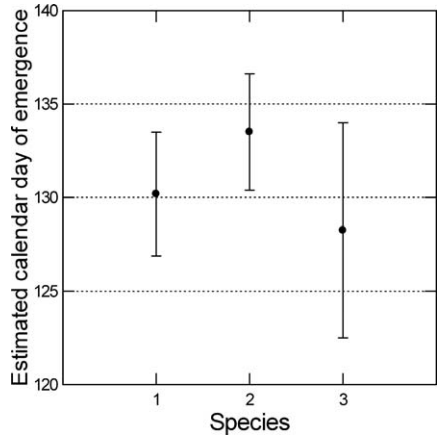

FIG. 6.—Estimated least squares mean calendar day of emergence for hatchling turtles in Lancaster, Pennsylvania from 1965–1985 that delayed emergence; 95% confidence intervals are shown. Species codes are as follows: 1 = *Chelydra serpentina*, 2 = *Chrysemys picta*, and 3 = *Clemmys guttata*.

species as a fixed effect and year as a random effect, was statistically significant (fixed effects, $F_{5,251} = 20.25$, $P < 0.0001$). Mean day of emergence for each species is shown in Fig. 5. Bonferroni tests of pairwise comparisons among species were statistically significant ($P < 0.05$) between *C. serpentina* and all other species but no other comparisons were significant. Using the same technique to compare mean estimated calendar day of emergence (Fig. 6) among those few species that delayed emergence was also significant (fixed effects, $F_{2,506} = 5.72$, $P < 0.003$). The only significant Bonferroni pairwise comparison was between *C. serpentina* and *Ch. picta* ($P = 0.009$).

For those three species with a dual emergence strategy (early and delayed) and adequate sample sizes of hatchlings (*C. serpentina*, *Ch. picta*, and *Cl. guttata*), only *C. serpentina* differed in CL between strategies ($F_{1,242} = 13.56$, $P < 0.001$). Hatchling *C. serpentina* that emerged early had a mean CL of 26.43 ± 0.28 mm ($n = 70$), and hatchlings that delayed emergence had a mean CL of 27.51 ± 0.15 mm ($n = 194$). Hatchling *C. serpentina* mean CL did not differ among years ($F_{20,242} = 1.17$, $P = 0.28$). *Chrysemys picta* CL was different among years ($F_{20,380} = 1.99$, $P = 0.01$) but CL of *Ch. picta* was not different between emergence strategies ($F_{1,380} = 1.53$, $P = 0.22$). Mean CL of *Ch. picta* hatchlings that emerged early was 25.57 ± 0.23 mm ($n = 90$) and mean CL of hatchlings that delayed emergence was 25.84 ± 0.10 mm ($n = 312$). For *Cl. guttata*, CL did not differ among years ($F_{20,57} = 1.93$, $P = 0.17$). Also, CL was not different between emergence strategies ($F_{1,57} = 1.12$, $P = 0.35$). Mean CL of *Cl. guttata* hatchlings that emerged early was 26.96 ± 0.11 mm ($n = 57$) while hatchlings that delayed emergence had a mean of 27.26 ± 0.19 mm ($n = 22$).

Yearly precipitation was not a significant determinant of total numbers of hatchlings detected annually, as shown by the results of linear regression analysis ($F_{1,19} = 0.27$, $R^2 = 0.01$, $P = 0.61$). The relationship between total numbers of hatchlings detected annually and April–May precipitation approached significance ($F_{1,18} = 3.50$, $R^2 = 0.16$, $P = 0.08$). August–September precipitation was regressed against the number of hatchlings that emerged early (in the fall of the same year), because fall precipitation would have no effect on hatchlings the previous spring, and again the relationship approached significance ($F_{1,18} = 4.20$, $R^2 = 0.19$, $P = 0.06$). Running the regression again, but excluding the outlier for 1965 (Fig. 7), the results were significant ($F_{1,17} = 9.53$, $R^2 = 0.36$, $P < 0.01$).

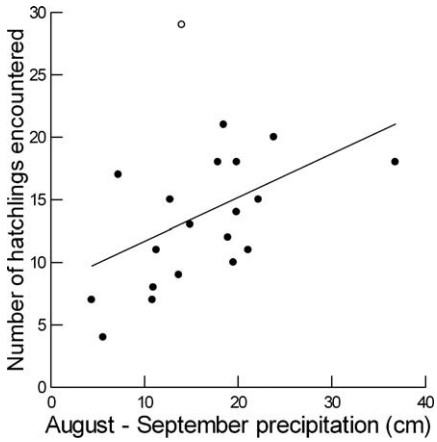

FIG. 7.—The relationship between August–September precipitation and the number of early emerging hatchling turtles of six species that were encountered in August–October of the same year from 1965–1985 near Lancaster, Pennsylvania. The outlier for the year 1965, referred to in the text, is shown as an open circle.

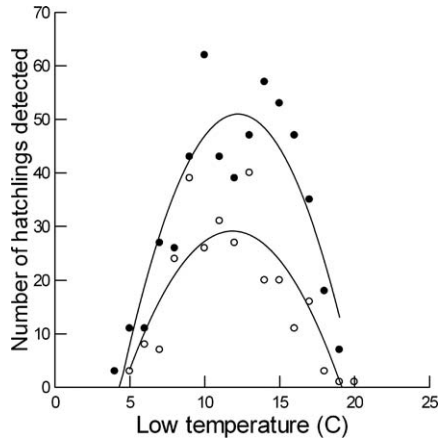

FIG. 9.—Relationship between number of hatchlings detected and low temperature values in the previous 24-h period before the hatchling was found. Dark circles are for data where hatchlings delayed emergence and open circles are for those that emerged early. Quadratic smoothers are fitted to the data to visualize trends.

Considering seasonal lag effects, we tested the relationship between August–September precipitation in each year against the number of hatchlings that delayed emergence until the spring of the following year (Fig. 8). Eliminating 1973, the year following Hurricane Agnes when no hatchlings were detected in the spring, the relationship was positive ($F_{1,17}$ = 10.16, R^2 = 0.37, P = 0.005). The relationship was still significantly positive if 1973 was included. In contrast, neither April–May nor annual precipitation in one year significantly affected the number of hatchlings that delayed emergence until the following year, whether 1973 was included or not. The number of hatchlings detected peaked (Fig. 9) when low temperature in the previous 24 h was about 12°C for both early (12.5°C) and delayed emergence (11.5°C).

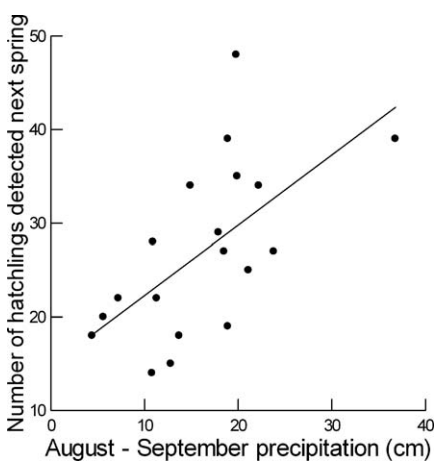

FIG. 8.—The relationship between August–September precipitation and the number of hatchling turtles of six species that delayed emergence until they were encountered in the spring of the following year, from 1966–1985 near Lancaster, Pennsylvania. Data do not include the outlier for 1973, the year following Hurricane Agnes, when no hatchlings were found that spring.

Rainfall (or the lack thereof) in the previous 24 h had the following effects. For *C. serpentina* hatchlings that delayed emergence, substantially more (84%) were found following rain (χ^2 = 87.11, df = 1, P < 0.001; Table 4). However, the reverse was true for *C. serpentina* hatchlings that emerged early; more (63%) were found if there was no rain in the previous 24 h (χ^2 = 4.63, df = 1, P = 0.03; Table 5). For *Ch. picta* hatchlings that delayed emergence, more were found (87%) following rain (χ^2 = 169.55, df = 1, P < 0.001; Table 4). No significant difference was observed for *Ch. picta* hatchlings that emerged early, as the percentages were nearly equal (χ^2 = 0.04, df = 1, P = 0.83; Table 5). When *Cl. guttata* delayed emergence, 21 of 22 hatchlings were detected within 24 h of rain (χ^2 = 18.18, df = 1, P < 0.001; Table 6). Small sample sizes limit our ability to draw conclu-

TABLE 4.—Number of *Chelydra serpentina* and *Chrysemys picta* turtle hatchlings in Lancaster County, Pennsylvania that delayed emergence from the nest and rainfall quality in the 24 h prior to detection.

	Rainfall previous 24 h?		
Species	No	Yes	Total
Chelydra serpentina	32	162	194
Chrysemys picta	41	271	312
Total	73	433	506

sions about the categorical effect of rainfall in the previous 24 h on the response of hatchling *G. insculpta*, *G. muhlenbergii*, and *S. odoratus* (Table 6).

DISCUSSION

Based on our long-term data, delayed emergence appears to be the most-common hatchling emergence strategy (Fig. 2). *Chelydra serpentina*, *Ch. picta*, and *Cl. guttata* hatchlings appear to have a facultative delayed emergence strategy, and *G. muhlenbergii* (with one exception), *G. insculpta*, and *S. odoratus* appear to be obligate early emergers—but these strategies vary geographically, as summarized in Table 7 and discussed in more detail below. For example, Parren and Rice (2004) reported a single record of a *G. insculpta* hatchling delaying emergence from the nest in southwestern Vermont, attributing the event to dry conditions and a mild winter. Female *G. insculpta* are quite terrestrial during the nesting season (Ernst, 1986) and may wander long distances from water before nesting, so their hatchlings may occur farther from the wetlands that are often the focus of aquatic and semi-aquatic turtle studies. Also, hatchling *G. insculpta* seek cover in ground vegetation and may even construct protective forms while migrating to water, making it more difficult to find them (Tuttle, 1996). Thus, the values in Table 2 may not present an accurate picture of delayed emergence in this species. J.H. Harding (unpublished data) found hatchling *G. insculpta* emerging in September in Michigan, but never in the spring, a pattern suggested for hatchling *G. insculpta* in Minnesota by Buech et al. (2004).

TABLE 5.—Number of *Chelydra serpentina* and *Chrysemys picta* turtle hatchlings in Lancaster County, Pennsylvania that emerged early from the nest and rainfall quality in the 24 h prior to detection.

	Rainfall previous 24 h?		
Species	No	Yes	Total
Chelydra serpentina	44	26	70
Chrysemys picta	46	44	90
Total	90	70	160

TABLE 6.—Number of turtle hatchlings of various turtle species in Lancaster County, Pennsylvania that emerged early from the nest and rainfall quality in the 24 h prior to detection.

	Rainfall previous 24 h?		
Species	No	Yes	Total
Clemmys guttata	32	25	57
Glyptemys insculpta	6	2	8
Glyptemys muhlenbergii	22	11	33
Sternotherus odoratus	9	10	19
Total	159	118	277

Considering geographic emergence patterns in *S. odoratus*, Cahn (1937) thought that Wisconsin hatchlings may overwinter in the nest, and Risley (1933) reported that the young in one nest were alive in the fall but dead when the nest was examined the next spring. Gibbons and Nelson (1978) reported hatchling *S. odoratus* from June through November and in February and March, concluding that the species had a variable emergence pattern.

The single observation of an overwintering hatchling *G. muhlenbergii* at our White Oak study site is the first documented record of delayed emergence. That hatchling, collected in May, 1985 still had a partially filled yolk sac (Ernst et al., 1994). Adult *G. muhlenbergii* are secretive animals that spend much time buried in mud, and their hatchlings are no exception. Most hatchlings have been found within stalks of *Carex*. Because the hatchlings are very small, finding them was often merely by chance. It is likely that our detection rates were underestimates for *G. muhlenbergii* at any time of the year.

Similarly, there are few records of delayed emergence in *Cl. guttata* and we are aware of only one (Conant, 1951) in Ohio. Data in Table 2 indicate that in Lancaster County, significantly more *Cl. guttata* hatchlings emerge in September than overwinter in the nest and emerge the next spring. However,

TABLE 7.—Selected references showing geographic variation in hatchling emergence strategies (facultative or obligate, early or delayed emergence) for the six species of freshwater turtles we studied near Lancaster, Pennsylvania. For a more-complete list of hatchling turtle emergence strategies, see Gibbons (2013).

Species	Location	Emergence strategy reported	Comments	Citation
Chelydra serpentina	Canada	Delayed		Logier, 1939; Toner, 1940; Bleakney, 1963; Obbard and Brooks, 1981
	Michigan	Delayed		Congdon et al., 1987
	New York	Delayed	Suggested	Hamilton, 1940
	Pennsylvania	Facultative		This study
Chrysemys picta	Canada	Facultative		Riley et al., in press
	Michigan	Delayed		Tinkle et al., 1981; Breitenbach et al., 1984;
	New York	Delayed		Nichols, 1933; R.G. Zweifel, personal communication
	Pennsylvania	Facultative		This study
Clemmys guttata	Ohio	Delayed		Conant, 1951
	Pennsylvania	Facultative		This study
Glyptemys insculpta	Minnesota	Delayed	Suggested	Buech et al., 2004
	Pennsylvania	Obligate early		This study
	Vermont	Delayed	One record	Parren and Rice, 2004
Glyptemys muhlenbergii	Pennsylvania	Obligate early	One exception	This study
Sternotherus odoratus	Pennsylvania	Obligate early		This study
	South Carolina	Facultative		Gibbons and Nelson, 1978
	Wisconsin	Delayed	Hatchlings dead in the spring	Risley, 1933

28% of our *Cl. guttata* hatchlings delayed emergence.

Hatchlings of *C. serpentina* are known to overwinter in numerous locations (Gibbons, 2013) including eastern Canada, Maine, and Michigan (Logier, 1939; Hamilton, 1940; Toner, 1940; Bleakney, 1963; Obbard and Brooks, 1981; Congdon et al., 1987), but winter kill of both hatchlings and adults can be extensive at these northern localities (DeSolla et al., 2001). In a 4-yr study at Algonquin Park, Ontario, Obbard and Brooks (1981) found that 42 of 257 clutches of *Chelydra* emerged in the fall while only one clutch successfully overwintered. Congdon et al. (1987) reported only one hatchling that still had its caruncle in April at a site in Michigan, and they thought it probable that this turtle had spent the winter either in a nest or on land.

Hatchling *Ch. picta* also overwinter in many northern localities (see review in Gibbons, 2013). In addition, Tinkle et al. (1981) and Breitenbach et al. (1984) have reported that all hatchlings at the George Reserve, Michigan overwinter in the nest. Nichols (1933) and R.G. Zweifel (unpublished data) have both found overwintering hatchling *Chrysemys* on Long Island, New York but, surprisingly, Bayless (1975) found none at a more-northern site in New York. Seigel (in Breitenbach et al., 1984) stated that hatchling *Ch. picta* apparently do emerge from nests in the fall in New Jersey. In Algonquin Park in central Ontario, some clutches emerge in the fall and others delay emergence until the spring. In 2010–2011, out of 13 nests 23% emerged in the fall. In 2011–2012, out of 25 nests 48% emerged in the fall (Riley et al., in press). Fall emergence was associated with nests that were infested by sarcophagid fly larvae, a direct mortality threat to developing turtle eggs and embryos (Iverson and Perry, 1994; Riley et al., in press).

Similar to our results, the majority of hatchlings collected by Gibbons and Nelson (1978) in South Carolina delayed emergence because they were found from February–April: *Pseudemys floridana*, 97%; *Trachemys scripta*, 87%; *Deirochelys reticularia*, 96%; and *Kinosternon subrubrum*, 98%. The more-efficient collecting method (drift fences and pitfall traps) used by Gibbons and Nelson may help explain the higher overwintering percentages in South Carolina. The rate of overwintering of *Chelydra* and *Chrysemys* in Pennsylvania may possibly be closer to those

of the species from South Carolina. In contrast, Congdon et al. (1983) reported that delayed emergence of *Emydoidea blandingii* in southern Michigan occurs only rarely, in spite of records from other northern states reported by Ernst and Lovich (2009).

We did not observe significant differences in mean CL of hatchling *Ch. picta* between early and delayed emergers as did DePari (1996) for New Jersey, where hatchlings that delayed emergence were larger, or Riley et al. (in press) for Canada where hatchlings that delayed emergence were smaller. However, hatchling *C. serpentina* that emerged in the fall at our site were significantly smaller than those that delayed emergence. This is the same relationship reported by DePari (1996) for *Ch. picta* but opposite to the trend reported for *Ch. picta* by Riley et al. (in press). It is of interest to note that while comparisons of mean CL of early vs. delayed emergence hatchlings for *Ch. picta* and *Cl. guttata* were not statistically different, the mean values were still larger for delayed emergence hatchlings, as shown by DePari for *Ch. picta*.

The general accordance of our findings with those of DePari (1996) may be related to similarities in climate between Pennsylvania and his study site in adjacent New Jersey, and their collective difference in climate with Canada. On the west side of Algonquin Park, the elevations (370–570 m a.s.l.) are higher than the surrounding landscape and the area experiences a colder and wetter climate as a result (Ontario Ministry of Natural Resources, 1998). The climate is reflective of the northern range limits of *C. serpentina* and *Ch. picta*, and the winters are extremely cold and harsh. In Lancaster County, Pennsylvania and Morris County, New Jersey, both about 650 km to the south of Riley's study site in Canada, the climate is milder and warmer.

Filoramo and Janzen (1999) demonstrated that a substantial portion of *Trachemys scripta elegans* yolk mass is converted into hatchling carcass mass during overwintering, such that hatchling carcass mass increased during overwintering and hatchlings weighed more in the spring than in the fall. This may be reflected in the fact that hatchling *C. serpentina, Ch. picta*, and *Cl. guttata* from Lancaster County had a greater mean CL in the spring, even if the results were not significantly different. If larger hatchlings have higher survivorship than do smaller hatchlings, as has been suggested (Janzen, 1993; Janzen et al., 2000a,b), this could also explain the generally higher encounter rate we observed for hatchlings that delay emergence.

Environmental Factors

It appears that some turtle species regularly delay their emergence until the next spring, while others do not or do so only under certain conditions (Gibbons, 2013). Delayed emergence in the far north might be linked to a brief developmental period in the spring and summer for some species, but this would not explain the extent of overwintering observed in more-southern locales where the climate is milder. Nagle et al. (2004) suggested that early emergence is an adaptive response to nests that provide poor environments for successful overwintering. Two environmental factors have been suggested to play a role in delayed emergence by hatchling turtles; rainfall and cool temperatures, recognizing that there may be interactions between the two (Long, 1986; Nagle et al., 2004). Hartweg (1944) and Moll and Legler (1971) thought that rainfall was very important for softening the ground to allow hatchlings to dig their way to the surface. Moll and Legler (1971) observed that young *Trachemys* in Panama remained in the nest after hatching until the occurrence of heavy rains. The effects of precipitation and temperature on embryogenesis and eventual emergence of turtles are exemplified by those species with long periods of embryonic diapause such as *Chelodina rugosa* (Kennett et al., 1993), *Kinosternon sonoriense* (van Loben Sels et al., 1997), and *Kinosternon baurii*, where embryonic diapause is interrupted by immersion in water in the first and exposure to cold temperatures in the latter two species (Ewert, 1991; Ewert and Wilson, 1996; Lovich et al., 2012b).

In contrast, Sexton (1957) reported that hatchling *Chrysemys* from Michigan did not emerge during heavy fall rains even when the air was still warm, and Gibbons and Nelson (1978) found the dates of emergence in South Carolina uncorrelated with precipitation. The

above discussion on the effects of rainfall on emergence by hatchling turtles seems to indicate that rainfall is a more-important factor in late summer and fall and, as our results suggest, can affect emergence the following spring. Our data also suggest that rainfall in the prior 24 h was positively related to the number of hatchlings detected, especially for *C. serpentina*, *Ch. picta*, and *Cl. guttata*, but only in the spring. Similarly, most hatchlings of *Graptemys geographica* that delayed emergence at another site in Pennsylvania were found on mornings following rain (Nagle et al., 2004). In contrast, hatchlings we observed that emerged early showed no response to rainfall in the previous 24 h or were observed in greater numbers when there was no rain in the previous 24 h. In Pennsylvania, the lowest numbers of hatchlings found annually in August and September were in 1966 ($n = 4$), 1967 ($n = 8$), 1972 ($n = 4$), 1980 ($n = 8$), 1981 ($n = 7$), and 1982 ($n = 7$) when severe droughts made the soil extremely hard (Ernst, 1966). However, in the drought years 1983 and 1984, 11 and 15 hatchlings were collected during these months but only after rain storms. It appears that precipitation at least plays a role during drought years in late summer and fall emergence.

DePari (1996) studied the emergence patterns of *Ch. picta* in New Jersey and found that both spring and fall rainfall were important determinants of hatchling emergence, but he did not measure the strength of the correlation explicitly. Field and laboratory experiments demonstrated that hatchlings were more likely to emerge from laboratory nests in the fall if they were placed in friable materials like sand, vermiculite, or dry soil than if they were placed in damp soil. Those in wet soil were more likely to emerge in the spring. DePari concluded that this provided support for the idea that hatchlings might be trapped in the nest chamber due to adverse substrate conditions until rains allowed emergence.

However, is the most-important effect of precipitation restricted only to those months when hatchlings emerge? This would include rainfall during the embryonic period as well as that during the period spent within the nest prior to emergence. This might appear to only include 3 or 4 mo if nesting is in June and emergence occurs in August or September; but the percentage of soil moisture at the time of oviposition may be very critical, and this moisture is from precipitation that fell during the previous winter and spring. The effects of substrate moisture on the development, growth, metabolism, and sex determination in turtle embryos has been previously discussed by other researchers (see Packard et al., 1981, 1984, 1985; Gettinger et al., 1984; Packard and Packard, 1984; Paukstis et al., 1984). For those hatchlings that delay their emergence until the next April or May, almost an entire year must pass during which they are dependent on soil moisture to either prevent their desiccation or not drown them.

Precipitation likely has lag effects that affect later seasons and years, as suggested in our six hypotheses in Table 3. For early emerging hatchlings, our predictions on the effects of April–May and August–September rainfall approached significance, but annual precipitation did not have a significant effect on the number of hatchlings found in a given year. For delayed emergence our hypotheses in Table 3 were confirmed for the previous year's April–May and August–September precipitation and partially confirmed for annual precipitation. Despite conflicting reports in the literature regarding the effects of precipitation on hatchling emergence, our data suggest a strong relationship between August–September precipitation in one year and the number of hatchlings that delay emergence in the next year. Collectively, these data support our contention that the effects of precipitation on the number of emerging hatchlings are strongest on a short temporal scale (including the 24 h prior to detection of a hatchling), with recognition that longer-term precipitation patterns (including El Niño–Southern Oscillation events) can also have lag effects on reproduction and activity of turtles beyond what our data suggest (Lovich et al., 1999, 2012a; Limpus and Nicholls, 2000; Ennen et al., 2012b).

Cold temperatures that delay development and prolong the incubation period have also been suggested as a major factor in the occurrence of overwintering for various species (Ernst and Lovich, 2009). Others suggest

that some species hatchlings, such as *E. blandingii*, cannot overwinter in the nest because of their vulnerability to freezing and drying (Packard et al., 2000; Packard and Packard, 2004). In all turtle species, a cooler than normal summer and fall may delay development of clutches laid early in the nesting season, while later clutches may not have the time to develop fully before the onset of cold fall weather. Both of these situations would be more critical at higher latitudes. No newly emerged hatchlings were found in the fall at Lancaster County after the minimum air temperature for the day dropped to 4°C. In contrast, no hatchlings were found in the spring until the minimum daily air temperature had risen to 5°C (Fig. 9). DePari (1996) found that nest temperatures during spring emergence were lower than those found during fall emergence, suggesting that temperature alone is not limiting early emergence. In fact, Baker et al. (2010) found that in a community of three turtle species in the central United States, emergence date did not correlate with minimum winter temperatures during a 6-yr study.

If cold temperatures have a strong effect on the occurrence and extent of delayed emergence, then why do hatchlings in South Carolina or even Florida (Jackson, 1994), which have more-moderate climates than Pennsylvania, delay emergence? Gibbons and Nelson (1978) suggested that hatchlings do not emerge in South Carolina in the fall, when temperatures are actually higher than those in the spring, because emergence from the nest is triggered by an appropriate cold cue such as is received during the winter. However, this does not fully explain why *S. odoratus* has such extended emergence periods (Feburary–March and June–November) in South Carolina. Gibbons and Nelson (1978) suggested that a cost–benefit relationship may help determine the season of emergence in temperate zone freshwater turtles. Gibbons (2013) further elaborated by stating that, "Seasonal timing of emergence from the nest and entry into the wetland has been favored by natural selection operating on hatchlings not only to arrive at times that are most likely to be productive for initial growth but also during times that provide the lowest relative risk of mortality in the nest."

Obviously the season of emergence can have a direct bearing on survivorship of the hatchling. If hatchlings leave the nest upon completion of development, the date of nesting will have some effect on the date of emergence (Lovich et al., 2012a). If the environment is variable for those young that leave the nest immediately after hatching, delayed emergence could overcome the rigors of capricious climate (if hatchling yolk reserves allow) and, possibly, also seasonally low food availability. This may be especially true in the case where female turtles lay multiple clutches throughout the nesting season, such as the five species from South Carolina. Some of those clutches may be oviposited too late in the season to achieve full embryonic development and allow hatchling emergence into environments supporting high survivorship.

The role of clutch order in determining timing of hatchling emergence deserves additional study. In Pennsylvania, *S. odoratus*, *Cl. guttata*, and *Ch. picta* lay more than one clutch per season, and it is tempting to speculate that, with the exception of *S. odoratus*, spring hatchlings may represent those from later clutches while fall hatchlings are those from the first clutch. Riley et al. (in press) explicitly tested if *Ch. picta* oviposition date or clutch order affected occurrence of early vs. delayed emergence. She observed that second clutches do not always delay emergence and first clutches do not always emerge early. Because no statistical effect was observed, she concluded that emergence strategy is not affected by clutch date or order. The lack of effect could be due to females selecting warmer locations, depending on clutch order, which could potentially equalize development. Second clutches have been shown to have shorter incubation periods in some turtles due to warmer environmental temperatures later in the nesting season (Ennen et al., 2012a), and this could affect emergence strategy by speeding up development.

For turtles laying a single clutch per season, such as *G. muhlenbergii*, it may be selectively advantageous to nest early in the season so that their young could emerge to warm temperatures, abundant food, and several suitable months in which to grow and store resources for the approaching winter. Also, by

emerging in August and September, competition with a great proportion of the hatchlings of overwintering species may be avoided. Early emergence could be of significance to small species, such as *G. muhlenbergii* and *S. odoratus*, which are sympatric with larger and more-fecund species with which they might compete as hatchlings. The obligate early emergence pattern for these smaller species suggests this possibility, but information on competitive interactions among sympatric hatchling turtles is not yet available.

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