ARTICLES

Overwintering in the Nest Chamber by Hatchling Painted Turtles, *Chrysemys picta*, in Northern New Jersey

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ABSTRACT. – Hatchling painted turtles (*Chrysemys picta picta* x *marginata* intergrades) overwinter in the nest chamber in northern New Jersey (40°42'N, 74°28'W), USA. During a four-year study (1983–1987), hatchlings in 86% (38/44) of monitored nests delayed emergence until the spring of the year following oviposition. Natural emergence from overwintered nests occurred an average of 314 days following nesting. Hatchlings in 14% (6/44) of monitored nests emerged in the fall of the same year, averaging 106 days from nesting to emergence. Substrate was found to be a significant factor influencing nest status, with proportionately more hatchlings in soil nests overwintering and more hatchlings in sand nests emerging in the fall. Nests constructed in the laboratory paralleled the relationship of substrate to emergence. Direct association of precipitation with hatchling emergence was observed in natural nests in both fall and spring. Minimum recorded natural nest temperature was -10.5°C. Hatchling mortality attributed to winter kill and spring flooding was low, accounting for only 4.3% of total mortality.

KEY WORDS. – Reptilia; Testudines; Emydidae; *Chrysemys picta*; turtle; hatchlings; nests; overwintering; emergence; nesting substrate; hibernation; ecology; USA

Overwintering is a form of delayed emergence from the nest chamber by developmentally complete hatchling turtles. Gibbons and Nelson (1978) documented delayed emergence from the nest in 13 species of turtles from five families. The majority of reports of overwintering by hatchling turtles involve the painted turtle, *Chrysemys picta* (Table 1). Painted turtle eggs oviposited in the early summer complete development and hatchlings emerge in the fall of the same year or delay emergence until the spring of the following year. Overwintering hatchlings are therefore exposed to, and able to survive, terrestrial freezing environmental conditions characteristic of temperate zone winters (Woolverton, 1961, 1963; Breitenbach et al., 1984; Storey et al., 1988; Packard et al., 1989). Hatchlings that overwinter are full term (embryonic stage 23 of Mahmoud et al., 1973), have internally absorbed yolk not used for embryogenesis, and are usually fully emerged from the eggshell. Unpipped eggs and embryos that are developmentally incomplete invariably fail to survive winter nest conditions (MacCulloch and Secoy, 1983; Storey et al., 1988; St. Clair and Gregory, 1990; Lindeman, 1991). Overwintering as a form of delayed emergence must therefore be considered distinct from diapause and embryonic estivation in turtle eggs as described by Ewert (1985).

Various hypotheses have been advanced to explain the occurrence of overwintering behavior. Gibbons and Nelson (1978) suggested that delayed emergence confers ultimate evolutionary advantage on overwintering hatchlings through avoidance of proximate factors, such as fall predation and

declining fall temperatures and resources. Carr (1952) also speculated that spring temperatures are more propitious for emerging hatchlings. Ernst and Barbour (1972) noted that in some species with a broad latitudinal distribution within the USA hatchlings of northern populations may overwinter in the nest chamber. Graham (1971) suggested that the ability to overwinter successfully may serve to extend the northern distribution of a species. Conversely, the inability to overwinter may be a factor limiting the northern distribution of some species (Obbard and Brooks, 1981). *Pseudemys scripta* hatchlings from late-season clutches in Louisiana were found to overwinter often (Cagle, 1950), and Newman (1906) reported overwintering of the map turtle, *Graptemys geographica*, in Indiana from a late July, possible second clutch nesting. Gibbons and Nelson (1978) also suggested that second and subsequent clutches should overwinter, implying that there is insufficient time at necessary incubation temperatures for clutches other than the first to complete development in time for fall emergence. Various authors (Obbard and Brooks, 1981; Breitenbach et al., 1984; Graham, 1987) have suggested that low temperatures during incubation may retard embryogenesis sufficiently to preclude fall emergence of hatchlings. Cagle (1944), Hartweg (1944), Carr (1952), and Ernst (1966) suggested that overwintering may be a passive response to adverse substrate conditions. Hatchlings may be unable to penetrate the roof of the nest which has been hardened by the summer sun during the incubation period, and spring rains may be necessary to soften the soil sufficiently to allow hatchling

emergence. Hartweg (1944) and Bleakney (1963) suggested that fall rains fail to stimulate emergence due to adverse temperature conditions which inhibit hatchling activity.

Little empirical evidence exists to address or support hypotheses involving costs, benefits, and ultimate evolutionary advantages of overwintering behavior. A review by Ultsch (1989) addresses various aspects of the hypotheses detailed above. This study reports on the occurrence of overwintering by *Chrysemys picta* hatchlings in New Jersey, USA, and on proximate environmental factors that appear to influence overwintering in, and emergence from, the nest chamber.

MATERIALS AND METHODS

Subspecific Designation of the Population.— Classification of the study population is *Chrysemys picta picta* x *marginata* intergrades, tending toward *picta*. Subspecific intergradation in *C. picta* does not appear to influence overwintering behavior as hatchlings of all subspecies have been shown to overwinter in the nest chamber (Table 1).

Study Site.— This study was conducted at the Great Swamp National Wildlife Refuge, Morris County, New Jersey (40°42'N, 74°28'W) from May 1983 – May 1987, a period encompassing four field seasons. The 2781 ha refuge is located in Chatham, Harding, and Passaic Townships and is 11 km south of Morristown, New Jersey. The swamp itself is 5 km wide and 11 km long and lies in a remnant of "Lake Passaic," a Pleistocene lake created by glacial withdrawal (U.S. Department of the Interior, 1987). The dominant soil types representing natural nesting substrates on the refuge are classified as Carlisle Muck and Parsippany Silt/Clay Loam. Substrates along roads (primarily Parsippany Silt/

Clay Loam) have been modified by the incorporation of gravel used to grade access roads within the management area, resulting in a mixture referred to as traprock/soil. A pile of sand used for refuge management activities represents the only substrate of this type available to nesting turtles in the study area and can be considered an artificial substrate condition.

Field Nests.— Natural nests of *C. picta* were located following direct observation of nesting females. Completed nests were covered with 1.3 cm mesh wire screening to prevent egg predation (Wilhoft et al., 1979) and escape of hatchlings following emergence. Substrate type was noted for each nest and classified as soil (Carlisle Muck and Parsippany Silt/Clay Loam), traprock/soil (primarily Parsippany Silt/Clay Loam mixed with gravel), or sand. Temperature conditions were monitored in selected nests with Tempscribe™ continuous chart recorders, with a range of -34.4 to 48.9°C (Bacharach, Inc.). Tempscribes were calibrated to the nearest 0.1°C with a digital microprobe thermometer (Sensortek Model BAT-12) and a mercury thermometer (range 0 to 50°C). Tempscribe charts were changed at 7–day intervals, and nest conditions were noted at these times. All nests were checked regularly during periods of suspected hatchling emergence (August–October and March–May). Air temperature and precipitation data were obtained from records of the refuge. Hatchlings were obtained by excavating selected nests prior to emergence or following natural emergence from the nest chamber. Hatchlings were measured with vernier dial calipers to the nearest 0.1 mm along the midline of the carapace and plastron and weighed to the nearest 0.001 g. Hatchlings were sacrificed following anesthesia via cold exposure (-20°C). The internal yolk sac, containing yolk not used for embryogenesis, was dissected out and weighed to the nearest 0.001 g. Hatchlings were sexed based on gross morphology of reproductive structures as described by Wilhoft et al. (1983).

Laboratory Nests.— Laboratory nests were constructed during 1984 to test the hypothesis that overwintering may be influenced by substrate, moisture, and temperature conditions of nests. Eggs were obtained by hormonal induction of gravid females utilizing synthetic oxytocin (Sigma Chemical Co.) (Ewert and Legler, 1978). Laboratory nests were constructed in 1.9 liter covered plastic containers utilizing three substrates (soil, sand, or vermiculite) and two moisture levels (wet: estimated water potential approximately -150 kPa; or dry: for soil and vermiculite, estimated water potential approximately -600 kPa; for sand, estimated water potential approximately -1100 kPa). The eggs were incubated in low temperature incubators (Precision™ or Fisher Scientific™) under three temperature regimes (low: 24°C constant; fluctuating: 12 hrs 30°C, 12 hrs 20°C; and high: 30°C constant). Thirty-six nests were constructed allowing 18 possible combinations of substrate/moisture/temperature to be tested by two nests each. Four cm of substrate was placed in the bottom of each container. A 100 ml beaker was placed on top of this substrate in the center of the container.

Table 1. Reports of overwintering in the nest chamber by hatchling painted turtles, *Chrysemys picta*.

Location	°N Lat.	Subspecies	Source
Saskatchewan	49°37'	*bellii*	MacCulloch and Secoy, 1983
British Columbia	49°15'	*bellii*	St. Clair and Gregory, 1990
Minnesota	47°50'	*bellii*	Woolverton, 1961, 1963
Idaho	46°45'	*bellii*	Lindeman, 1991
Ontario	45°34'	*marginata*	Storey et al., 1988
Quebec	45°24'	*marginata*	Christens and Bider, 1987
Minnesota	44°20'	*bellii*	Legler, 1954
Nova Scotia	44°20'	*picta*	Bleakney, 1963
Michigan	42°30'	*marginata*	Breitenbach et al., 1984
Michigan	42°30'	*marginata*	Tinkle et al., 1981
Nebraska	42°30'	*bellii*	Packard et al., 1989
Nebraska	42°30'	*bellii*	Paukstis et al., 1989
Michigan	42°25'	*marginata*	Sexton, 1957
Michigan	42°20'	*marginata*	Hartweg, 1944, 1946
Connecticut	41°15'	*picta*	Finneran, 1948
Indiana	41°15'	*marginata*	Newman, 1906
New York	40°45'	*picta*	Nichols, 1933
New Jersey	40°42'	*picta* x *marginata*	Present study
Illinois	40°10'	*marginata* x *bellii*	Williams, 1957
Kansas	37–40°	*bellii*	Smith, 1956
Illinois	ca. 39°	*marginata*	Cagle, 1954
Kentucky	ca. 38°	*marginata*	Barbour, 1971
Tennessee	36°30'	*dorsalis*	Cagle, 1954
Louisiana	29–33°	*dorsalis*	Cagle, 1954

Figure 1. *Chrysemys picta* hatchlings in nest chamber in September, 1983, in Great Swamp, New Jersey, after removing overlying hard-packed soil.

An additional 5 cm of substrate was placed around the beaker, which was then removed, creating a nest cavity. Eggs were placed within this cavity and covered with 2–3 cm of substrate. To further approximate natural nest conditions, the cavities of nests constructed in wet soil were sealed with plugs of muddy soil. Nesting *C. picta* void fluid during nest construction which results in a plug of mud which hardens after exposure to the sun during incubation. Formation of plugs in sand, vermiculite, or dry soil nests was not possible due to the consistency of the substrate or the moisture level. Damp soil nests ($n = 6$) therefore most closely approximated natural nest conditions. Soil and sand used for laboratory nests were obtained at the refuge from areas utilized for nesting by *C. picta*. Completed nests were incubated and monitored until excavation or emergence. After 1 November incubation temperature was decreased by 4°C weekly until an ambient temperature of 0°C was reached. Nests were maintained at 0°C until 1 March 1985, when temperature was increased by 4°C weekly until an ambient temperature of 20°C was reached. Nests were monitored for hatchling emergence, and those failing to emerge by 10 May 1985 were opened.

RESULTS

Overwintering in Field Nests.— A total of 58 nests were screened during the nesting seasons 1983–86 with the following results: 1983 — 8 nests (2 overwintered, 1 fall emerged, 4 excavated [3 in fall, 1 in spring], 1 failed); 1984 — 12 nests (11 overwintered, 1 excavated in fall); 1985 — 21 nests (11 overwintered, 4 fall emerged, 1 excavated in fall, 5 failed); 1986 — 17 nests (14 overwintered, 1 fall emerged, 2 failed). Table 2 summarizes the status of all nests. The apparent clutch size of 6 eggs/nest (347 hatchlings or eggs from 58 nests) is low due to escape of hatchlings — some screens failed to retain all hatchlings following emergence, and nests with an emergence hole were counted as overwintered even if no hatchlings were located ($n = 3$ nests). Estimated clutch size for natural nests ($n = 55$) is 7.1±1.63 eggs, (SE = 0.23, range 4–10). Thirty-eight nests

overwintered, producing 170 viable hatchlings (75.2% of 226 hatchlings, Table 2). Six nests emerged in the fall of the year of oviposition and accounted for 23 (10.2%) of the viable hatchlings produced in field nests. Three nests excavated in September (one each in 1983, 1984, and 1985) contained a total of 21 living hatchlings, 1 dead hatchling, and 1 dead egg. Two nests excavated on 30 November 1983 contained a total of 7 viable hatchlings and 5 dead eggs.

Mortality in Field Nests.— Of the 347 eggs known to have been incubated in natural nests, 98 (28.2%) failed to hatch and represent either infertility or mortality prior to overwintering. Hatchling mortality in field nests was low, with 23 dead hatchlings accounting for 6.6% of the 347 eggs in screened nests. Five nests failed due to 100% mortality in the egg stage and accounted for 32 of the 35 eggs contained in failed nests. One failed nest contained 3 eggs and 4 hatchlings, while the remaining two failed nests contained no eggs and a total of 12 hatchlings. Both of these nests suffered 100% mortality in the hatchling stage due to flooding, one in the fall ($n = 7$) and one in the spring ($n = 5$). Of the remaining 11 dead hatchlings, one was found in a nest excavated on 9 September 1984, indicating mortality prior to overwintering. Ten dead hatchlings (4 from a nest excavated on 17 February 1984 and 6 from 5 overwintered nests) may represent direct mortality due to overwintering (8.3% of all hatchling and egg mortality, 2.9% of the 347 eggs contained in field nests). However, one hatchling found dead in an overwintered nest was in an advanced state of decomposition and contained a large amount of yolk, suggesting that death occurred in the fall. No nest failed due to complete hatchling mortality with the exception of the two nests subjected to fall and spring flooding. Hatchling mortality attributed to winter kill (directly related to overwintering, $n = 10$) and spring flooding (indirectly related to overwintering, $n = 5$) represents 65.2% of all hatchling mortality (15 of 23 dead hatchlings), 12.4% of total (hatchling plus egg) mortality, and 4.3% of the 347 eggs in protected nests.

Duration of Incubation in Field Nests.— Excavation of field nests ($n = 3$) in September of 1983, 1984, and 1985 disclosed the presence of term hatchlings and eggs in the process of hatching (pipped). Excavation of a nest in extremely hard-packed soil on 21 September 1983 revealed 8 hatchlings in a well-formed nest chamber. The hatchlings immediately attempted to emerge from the nest when the overburden was removed (Fig. 1). All hatchlings retained the caruncle, and yolk not used for embryogenesis was completely absorbed and the umbilical scar healed. The carapace was completely unfolded and flattened, a process that is believed to aid in absorption of external yolk and to require 1–4 days after emergence from the eggshell (Ewert, 1979). Eggs containing hatchlings in late stage 21/early stage 22 of embryonic development (Mahmoud et al., 1973) were found in a nest opened on 15 July 1984, indicating that hatching can possibly occur as early as the end of July. After removal of 3 eggs for staging, this nest was resealed and 6 hatchlings representing the balance of the clutch of 9 eggs emerged about 15 March 1985.

Table 2. Field nest emergence results.

Nest Status (n; %)	Viable Hatchlings	%	Dead Hatchlings	%	Dead Eggs	%
Overwintered (38; 65.6%)	170	49.0%	6	1.7%	36	10.4%
Fall Emerged (6; 10.3%)	23	6.6%	0	0.0%	17	4.9%
Excavated (6; 10.3%)	33	9.5%	1	0.3%	10	2.9%
Failed (8; 13.8%)	0	0.0%	16	4.6%	35	10.0%
All Nests (58; 100.0%)	226	65.1%	23	6.6%	98	28.2%

Six nests naturally emerged in the fall, averaging 106 days from nesting to emergence (range 89–130 days). Of 38 overwintered nests, 27 emerged in the spring of the following year after an average of 314 days from nesting to emergence (range 288–346 days). Eleven overwintered nests were excavated prior to emergence, one on 27 March 1986 (304 days from nesting) and 10 during February, March, and April 1987 (averaging 273 days; range 244–332 days) to obtain hatchlings for laboratory analyses. Date of oviposition was not apparently related to time of emergence (fall vs. spring) of field nests (Fig. 2).

Environmental Conditions Affecting Field Nests.— SUBSTRATE: The average nest constructed in soil was 5.2 cm deep with an oval opening 3.8 cm wide x 4.6 cm long, capped with a plug of muddy soil approximately 2 cm thick. The majority of nests (93.1%, n = 54) were constructed in soil or traprock/soil. Three nests (5.2%) were constructed in sand, and one nest (1.7%) was oviposited in a pile of clippings of reed grass, *Phragmites communis*, overlying soil, which was mixed with the vegetation by the nesting female (this nest suffered 100% mortality in the egg stage). Thirty-seven (97.4%) of the nests which overwintered were constructed in

soil or traprock/soil. One overwintered nest (2.6%) was constructed in sand. Of fall emerged nests, 4 (66.7%) were soil or traprock/soil nests, and 2 (33.3%) were sand nests. The proportion of soil nests emerging in the fall was significantly less than the proportion of sand nests emerging in the fall (Fisher Exact Test, *P* = 0.04 [Zar, 1984]).

NEST AND AIR TEMPERATURES: Partial records of temperature profiles were obtained for two nests. Both nests equipped with Tempscribe chart recorders exhibited 100% fertility, hatching, and overwintering success. In Nest 1-1985 (Fig. 3) minimum recorded nest temperature was -10.5°C during January 1986. Nest temperature did not exceed -2.7°C for a period of 86 days (15 December 1985 – 10 March 1986). Nest temperatures during the fall emergence period (August–October) were less variable than air temperature. Maximum air temperatures were higher and minimum air temperatures were lower than corresponding nest temperatures (Fig. 3). The period of fall emergence was marked by a steady decline in air and nest temperatures. Conversely, air and nest temperatures increased during the spring emergence period of overwintered nests (March–April, Fig. 3). Spring nest temperatures were substantially cooler than those of fall nests. In Nest 1-1985 neither nest nor air temperatures appear to have directly influenced hatchling emergence (Fig. 4).

PRECIPITATION: Bimonthly plots of emergence and rainfall suggest that hatchling emergence in both fall and spring is associated with precipitation (Fig. 5). Rainfall > 2.0 inches (> 5.0 cm) was associated with hatchling emergence during four bimonthly periods ranging from the latter half of August through the first half of October. Conversely, rainfall during the first half of August and the latter half of October failed to induce hatchling emergence. Spring precipitation was associated with emergence during five bimonthly periods ranging from 1 March through 16 May. In 1984 and 1986 all spring emergence occurred in April. Rainfall of 5.59 inches during 1–15 April 1984 was associated with emergence of all remaining field nests of the 1983–1984 season (Fig. 5A). In 1986 rainfall of 2.24 inches during 1–15 April was associated with emergence of 4 nests out of a total of 10 nests remaining in the field. Nest checks on 15 April confirmed that the remaining 6 nests were intact. A total of 3.55 inches of rain fell on 16 and 17 April. All six nests had emerged when checked on 18 April (Fig. 5C), including Nest 1-1985 equipped with a Tempscribe chart recorder (Fig. 4). Rainfall during March and April of 1985 averaged 2.75 and 2.99 inches, respectively, both below normal (Climatological Data, New Jersey). Emergence occurred over an extended period ranging from about 15 March through 6 May (Fig. 5B). Direct observation of hatchling emergence during rain was made on 19 April 1985 (0.49 inches total rainfall).

Hatchling Morphometrics.— Table 3 presents general morphometric parameters of fall emerged and overwintered hatchlings. Fall emerged hatchlings were significantly smaller than overwintered hatchlings using mean hatchling plastron length (t-test for independent groups, 1-tailed; *t* = 1.768; *P*
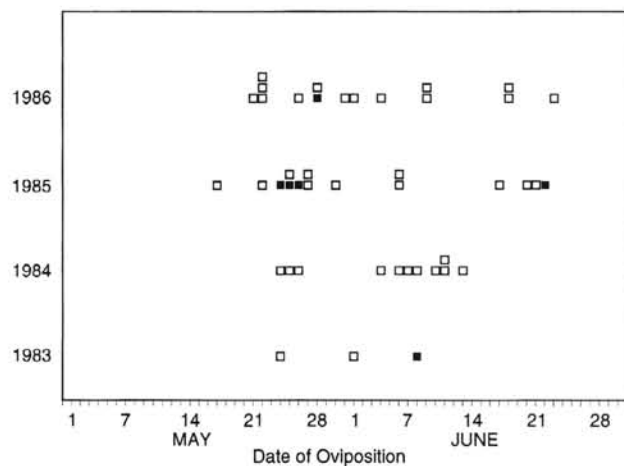

Figure 2. Relationship of date of oviposition to emergence status in natural nests. □ = overwintered, ■ = fall emerged.
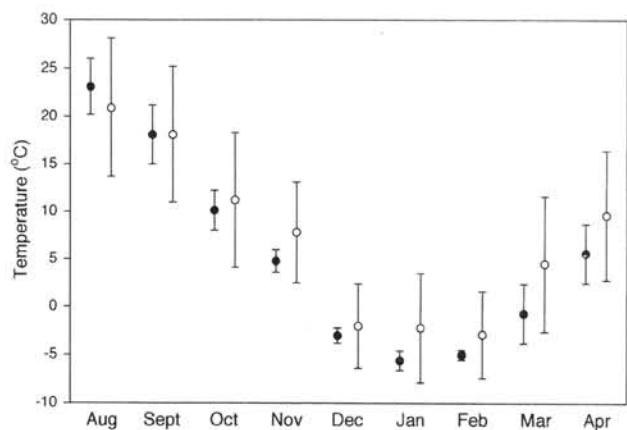
Figure 3. Nest temperatures and air temperatures for the 1985–86 season. ○ = air temperatures, ● = nest temperatures. Monthly average minimum, mean, and average maximum in °C. Nest temperatures from Nest 1-1985.

< 0.05; df = 38) and individual plastron length ($t = 2.935$; $P < 0.01$; df = 180). Mean hatchling weight did not differ between fall emerged and overwintered hatchlings ($t = 1.604$; $P > 0.05$; df = 38), while individual hatchling weight differed significantly ($t = 2.303$; $P < 0.05$; df = 180). All hatchlings contained residual yolk not used for embryogenesis as small internalized yolk sacs. Yolk sac size did not differ between fall emerged and overwintered hatchlings (t-test for independent groups, 2-tailed; $t = 1.102$; $P > 0.20$; df = 173).

Hatchlings from nests constructed in sand were significantly smaller than hatchlings from soil or traprock/soil nests. This relationship was demonstrated for both mean plastron length and mean weight (Analysis of Variance

followed by the Tukey Multiple Comparison Test; plastron length: $F_{2, 44} = 3.455$, $P < 0.05$; weight: $F_{2, 45} = 3.661$, $P < 0.05$). Elimination of sand nests from the analyses eliminated the significance in size difference between fall emerged and overwintered hatchlings.

Sex ratio of hatchlings produced in natural nests was strongly biased in favor of males. Of 194 hatchlings from field nests, 53 (27.3%) were female and 141 (72.7%) were male, resulting in a female:male ratio of 1:2.6. Sex ratio of 12 fall emerged hatchlings (33.3% female, 66.7% male; female:male ratio 1:2.0) approximated that of the 194 hatchlings from all field nests.

Overwintering in Laboratory Nests.— The results of 36 individual nests constructed in the laboratory in 1984 are presented in Table 4 and summarized as follows: 16 (44.4%) emerged in the fall (August–October); 6 (16.7%) overwintered; 1 (2.8%) was excavated on 5 September; 13 (36.1%) exhibited 100% mortality. Duration of incubation in fall emerged nests was significantly different among the three temperature regimes used (Analysis of Variance followed by the Tukey Multiple Comparison Test for unequal sample sizes: $F_{2, 13} = 67.929$, $P < .001$; $q_{0.05, 3, 13} = 7.570$, 16.440, 9.601, $P < 0.01$). Nests incubated at high temperature (constant 30°C, $n = 5$) emerged after an average incubation period of 58 days, those at fluctuating temperature (12 hrs 30°C, 12 hrs 20°C, $n = 6$) averaged 74 days from nest construction to emergence, and low temperature nests (constant 24°C, $n = 5$) emerged after an average incubation period of 87 days. All viable sand, dry soil, and vermiculite nests ($n = 16$) emerged in the fall. All nests constructed in wet soil ($n = 6$), which most closely approximated conditions of natural field nests, overwintered and contained viable hatchlings
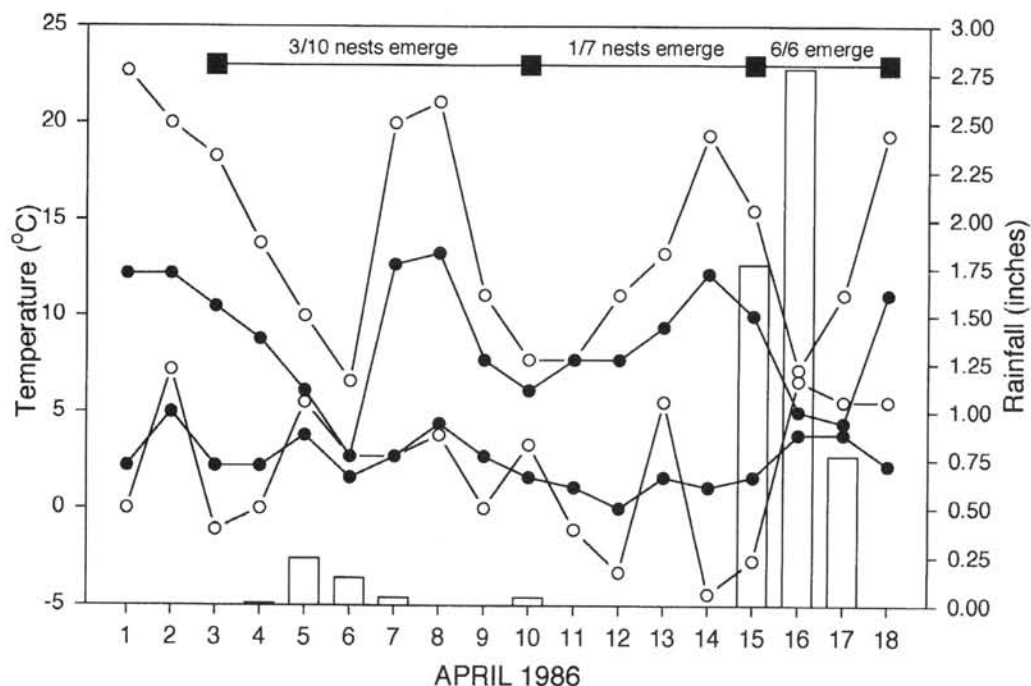

Figure 4. Nest temperatures, air temperatures, and precipitation during the April 1986 period of hatchling emergence. ○ = air temperatures, maximum and minimum, ● = nest temperatures, maximum and minimum, bars = precipitation, ■ = dates on which field nests were checked for emergence. Nest temperatures from Nest 1-1985.
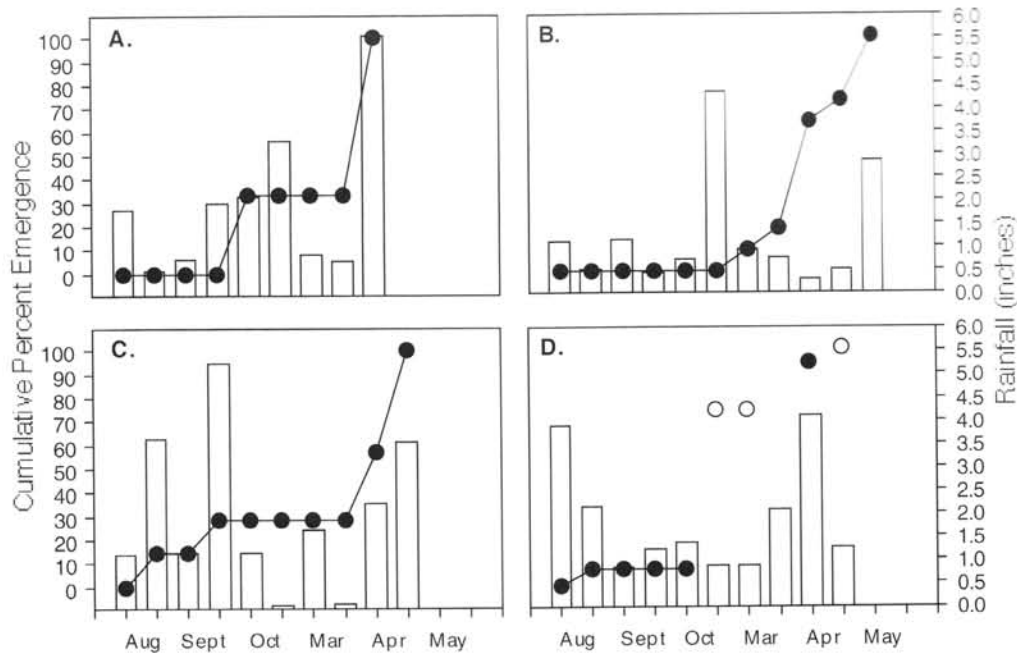
Figure 5. Cumulative percent nest emergence associated with rainfall for bimonthly periods during fall emergence (August–October) and spring emergence (March–May) periods for the 1983–87 field seasons. **A.** 1983–84, **B.** 1984–85, **C.** 1985–86, **D.** 1986–87. ● = hatchling emergence, ○ = nest excavation, nests/hatchlings used for laboratory analyses.

when excavated on 10 May 1985. The proportion of wet soil nests emerging in the fall was significantly less than the proportion of sand, dry soil, and vermiculite nests emerging in the fall (Fisher Exact Test, $P = 0.00001$).

DISCUSSION

A scenario that explains the occurrence of both fall emergence and overwintering of *Chrysemys picta* hatchlings in nests is based on nest integrity and factors that serve to degrade it. Nest integrity is directly related to substrate selection and nest construction by the ovipositing female.

Table 3. Morphometric parameters of hatchlings from natural nests; lengths in mm, weights in g.

Parameter Status	*n*	Mean ± SD	SE	Range	*P*
Carapace length					
Fall Emerged	17	24.1 ± 1.96	.47	20.7–27.9	
					> .05
Overwintered	165	24.7 ± 1.45	.11	20.0–27.5	
Plastron length					
Fall Emerged	17	22.1 ± 2.20	.53	18.7–25.8	
					< .01
Overwintered	165	23.3 ± 1.45	.11	18.9–26.2	
Weight					
Fall Emerged	17	3.5 ± .76	.18	2.3–4.6	
					< .05
Overwintered	165	3.8 ± .55	.04	2.1–5.0	
Yolk sac weight					
Fall Emerged	15	.07 ± .039	.010	.01–.12	
					> .20
Overwintered	160	.05 ± .064	.005	.01–.58	

Integrity of the nest chamber is degraded by hatchling emergence activity, precipitation causing soil saturation, and freezing/thawing cycles. For some nests simple hatchling emergence activity may degrade the integrity of the nest chamber sufficiently to allow fall emergence. Fall precipitation in addition to hatchling activity may be required in other nests to allow sufficient degradation for fall emergence to occur. Ultsch (1989) reported that Ernst and Lovich (unpublished data) found a 59% correlation between fall precipitation and hatchling emergence in southeastern Pennsylvania. In the present study the roof of one nest was washed away by rain in October. The hatchlings were prevented from escaping from the nest chamber by the wire screening. Hammer (1969) noted that fall emergence of *Chelydra serpentina* hatchlings occurred shortly after rainfall softened the ground. Hartweg (1944) and Bleakney (1963) implied that fall rains fail to cause emergence due to low temperatures which inhibit hatchling activity. In the present study substantial precipitation during the latter half of October (Figs. 5A and 5B) failed to elicit hatchling emergence.

Reports suggesting that overwintering is a passive response by hatchlings unable to penetrate the roof of the nest chamber which has been hardened by the sun during the incubation period (Cagle, 1944; Hartweg, 1944, 1946; Carr, 1952; Legler, 1954; Ernst, 1966; Barbour, 1971; Tinkle et al., 1981) are supported by field and laboratory results of this study. The inhibition of emergence due to adverse substrate conditions may be the most parsimonious explanation for the widespread occurrence of overwintering behavior in *Chrysemys picta* as it can conceivably operate over the entire range of the observed phenomenon (Table 1). As shown by this study, hatchlings from field nests constructed in sand were more likely to emerge in the fall than hatchlings from

Table 4. Laboratory nest emergence results, 1984–85. All overwintered nests were excavated on 10 May 1985.

Nest	Moisture/Substrate/Temperature	Dates	Days to Emerge	Status
8	Wet/Soil/Low	22 Jun-10 May	322	Overwintered
35	Wet/Soil/Low	28 Jun-10 May	316	Overwintered
4	Wet/Soil/Fluctuating	21 Jun-10 May	323	Overwintered
21	Wet/Soil/Fluctuating	26 Jun-10 May	318	Overwintered
7	Wet/Soil/High	22 Jun-10 May	322	Overwintered
19	Wet/Soil/High	26 Jun-10 May	318	Overwintered
12	Wet/Sand/Low	22 Jun-17 Sep	87	Fall emerged
31	Wet/Sand/Low			Died
24	Wet/Sand/Fluctuating			Died
17	Wet/Sand/Fluctuating			Died
18	Wet/Sand/High	23 Jun-25 Aug	63	Fall emerged
26	Wet/Sand/High			Died
14	Wet/Vermiculite/Low			Died
29	Wet/Vermiculite/Low			Died
1	Wet/Vermiculite/Fluctuating	21 Jun-3 Sep	74	Fall emerged
28	Wet/Vermiculite/Fluctuating	27 Jun-9 Sep	74	Fall emerged
5	Wet/Vermiculite/High	21 Jun-20 Aug	60	Fall emerged
32	Wet/Vermiculite/High			Died
15	Dry/Soil/Low	23 Jun-14 Sep	83	Fall emerged
36	Dry/Soil/Low	28 Jun-21 Sep	85	Fall emerged
2	Dry/Soil/Fluctuating	21 Jun-5 Sep	76	Fall emerged
22	Dry/Soil/Fluctuating	26 Jun-12 Sep	78	Fall emerged
10	Dry/Soil/High	22 Jun-20 Aug	59	Fall emerged
27	Dry/Soil/High	27 Jun-5 Sep	70	Excavated
16	Dry/Sand/Low			Died
30	Dry/Sand/Low			Died
3	Dry/Sand/Fluctuating			Died
23	Dry/Sand/Fluctuating			Died
11	Dry/Sand/High			Died
25	Dry/Sand/High			Died
13	Dry/Vermiculite/Low	23 Jun-14 Sep	83	Fall emerged
34	Dry/Vermiculite/Low	28 Jun-1 Oct	95	Fall emerged
6	Dry/Vermiculite/Fluctuating	21 Jun-2 Sep	73	Fall emerged
20	Dry/Vermiculite/Fluctuating	26 Jun-4 Sep	70	Fall emerged
9	Dry/Vermiculite/High	22 Jun-14 Aug	53	Fall emerged
33	Dry/Vermiculite/High	27 Jun-23 Aug	57	Fall emerged

nests constructed in soil. Hatchlings from laboratory nests constructed in friable substrates (sand, vermiculite, or dry soil) were also more likely to emerge in the fall than hatchlings from nests constructed in damp soil, which most closely mimicked conditions of natural field nests.

Movement of hatchlings as they emerge from the eggshell may displace substrate above the nest chamber, which falls to the bottom, essentially displacing the hatchlings toward the surface. Carr and Ogren (1959, 1960), Carr and Hirth (1961), and Carr (1967) have shown that such a phenomenon occurs in sea turtle nests, and that the effort of emergence from the nest chamber must be shared by siblings. A mechanism of social facilitation operates to insure a coordinated emergence effort. *Chrysemys picta* nests constructed in soil consist of a well-formed chamber sealed with a plug of muddy soil formed by the nesting female. The integrity of this chamber may not be compromised by the movement of hatchlings as they emerge from their eggs. Small clutch size (average number of hatchlings per nest = 7) may explain why some nests fail to emerge without the aid of additional factors that soften the soil sufficiently to allow emergence. Soil-softening may occur as a result of (1) freezing and thawing of the substrate from winter to spring and (2) precipitation. The activity of large numbers of

hatchlings in nests of snapping turtles, *Chelydra serpentina*, with an average clutch of 30 eggs (Wilhoft et al., 1983), may result in a coordinated emergence effort sufficient to breach the integrity of the nest chamber to allow fall emergence typical of this species.

Nest temperatures during spring emergence were lower than those in the fall (Fig. 3), suggesting that absolute temperature in the fall does not inhibit emergence. Hatchling emergence may be inhibited by declining fall temperatures that ultimately trigger a shift in hatchling activity from emergence behavior to acclimatization to winter nest conditions. Bleakney (1963) reported that a negative temperature gradient exists in nests from October to March, with the surface of the ground cooler than the soil at nest level, and speculated that hatchlings react to this negative gradient by remaining in the nest chamber until the following spring. Conversely, in April the surface of the ground is warmer than the soil at nest level, and hatchlings respond to this positive gradient by moving upward toward the warmer surface soil and out of the cooler nest chamber. Lindeman (1991) reported no hatchling emergence in the fall in natural nests of *Chrysemys picta* in northern Idaho. Hatching without emergence was noted to have occurred by 30 August in selected nests. Storey et al. (1988) also reported no hatchling emergence in the fall in Algonquin Park, Ontario, despite the presence of active hatchlings in nests examined from August to October.

It is likely that declining temperatures inhibit early fall emergence in northern populations of painted turtles (e.g., Storey et al., 1988) and late fall emergence in more southerly populations (present study). Overwintering that appears unrelated to substrate or precipitation conditions may be explained by temperature conditions that inhibit hatchling emergence activity. Conversely, rising spring temperatures result in resumption of hatchling emergence activity, following the reversal of physiological acclimatization to winter nest conditions. The integrity of some nests will have been sufficiently degraded by winter freezing, thawing, and soil moisture saturation to allow hatchling emergence immediately or shortly after the resumption of hatchling emergence activity, while other nests will require still further degradation by exposure to spring precipitation one or more times. In this study six monitored nests failed to emerge in April 1986 until 5.32 inches of rain fell during a three-day period, despite the occurrence of warmer air and nest temperatures and small amounts of rain earlier in the month (Nest 1-1985, Fig. 4). Inability to mimic natural precipitation patterns in laboratory nests may explain the ultimate failure of overwintered laboratory nests to emerge naturally.

Acknowledgments

LITERATURE CITED

BARBOUR, R.W. 1971. Amphibians and Reptiles of Kentucky, Kentucky Nature Studies: 2. Lexington: The University Press of Kentucky, 334 pp.

BLEAKNEY, J.S. 1963. Notes on the distribution and life histories of turtles in Nova Scotia. Canadian Field-Naturalist 77(2):67-76.

BREITENBACH, G.L., CONGDON, J.D., AND VAN LOBEN SELS, R.C. 1984. Winter temperatures of *Chrysemys picta* nests in Michigan: effects on hatchling survival. Herpetologica 40(1):76-81.

CAGLE, F.R. 1944. Activity and winter changes of hatchling *Pseudemys*. Copeia 1944(2):105-109.

CAGLE, F.R. 1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). Ecological Monographs 20(1):31-54.

CAGLE, F.R. 1954. Observations on the life cycles of painted turtles (genus *Chrysemys*). American Midland Naturalist 52(1):225-235.

CARR, A. 1952. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. Ithaca: Cornell University Press, 542 pp.

CARR, A. 1967. So Excellent A Fishe, A Natural History of Sea Turtles. Garden City, New York: Natural History Press, 249 pp.

CARR, A., AND HIRTH, H. 1961. Social facilitation in green turtle siblings. Anim. Behav. 9(1-2):68-70.

CARR, A., AND OGREN, L. 1959. The ecology and migrations of sea turtles. 3. *Dermochelys* in Costa Rica. Am. Mus. Novitates 1958:1-29.

CARR, A., AND OGREN, L. 1960. The ecology and migrations of sea turtles. 4. The green turtle in the Caribbean Sea. Bull. Am. Mus. Nat. Hist. 121:1-48.

CHRISTENS, E., AND BIDER, J.R. 1987. Nesting activity and hatching success of the painted turtle (*Chrysemys picta marginata*) in southwestern Quebec. Herpetologica 43(1):55-65.

ERNST, C.H. 1966. Overwintering of hatchling *Chelydra serpentina* in southeastern Pennsylvania. Phil. Herp. Soc. Bull. 14(2):8-9.

ERNST, C.H., AND BARBOUR, R.W. 1972. Turtles of the United States. Lexington: University Press of Kentucky, 347 pp.

EWERT, M.A. 1979. The embryo and its egg: development and natural history. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research. New York: John Wiley and Sons, pp. 333-413.

EWERT, M.A. 1985. Embryology of turtles. In: Gans, C., Billett, F., and Maderson, P.F.A. (Eds.). Biology of the Reptilia, Vol. 14. New York: John Wiley and Sons, pp. 75-267.

EWERT, M.A., AND LEGLER, J.M. 1978. Hormonal induction of oviposition in turtles. Herpetologica 34(3):314-318.

FINNERAN, L.C. 1948. Reptiles at Branford, Connecticut. Herpetologica 4(4):123-126.

GIBBONS, J.W., AND NELSON, D.H. 1978. The evolutionary significance of delayed emergence from the nest by hatchling turtles. Evolution 32(2):297-303.

GRAHAM, T.E. 1971. Eggs and hatchlings of the red-bellied turtle, *Chrysemys rubriventris*, from Plymouth, Massachusetts. J. Herpetol. 5(1/2):59-60.

GRAHAM, T.E. 1987. Recovery in red: preservation of the Plymouth redbelly turtle. South Shore 1(2):24-26, 45.

HAMMER, D.A. 1969. Parameters of a marsh snapping turtle population, LaCreek Refuge, South Dakota. J. Wildl. Manag. 33(4):995-1005.

HARTWEG, N. 1944. Spring emergence of painted turtle hatchlings. Copeia 1944(1):20-22.

HARTWEG, N. 1946. Confirmation of overwintering in painted turtle hatchlings. Copeia 1946(4):255.

LEGLER, J.M. 1954. Nesting habits of the western painted turtle, *Chrysemys picta bellii* (Gray). Herpetologica 10(3):137-144.

LINDEMAN, P.V. 1991. Survivorship of overwintering hatchling painted turtles, *Chrysemys picta*, in northern Idaho. Canad. Field-Natur. 105(2):263-266.

MACCULLOCH, R.D., AND SECOY, D.M. 1983. Demography, growth, and food of western painted turtles, *Chrysemys picta bellii* (Gray), from southern Saskatchewan. Can. J. Zool. 61:1499-1509.

MAHMOUD, I.Y., HESS, G.L., AND KLICKA, J. 1973. Normal embryonic stages of the western painted turtle, *Chrysemys picta bellii*. J. Morphol. 141:269-279.

NEWMAN, H.H. 1906. The habits of certain tortoises. J. Comp. Neurol. Psychol. 16:126-152.

NICHOLS, J.T. 1933. Further notes on painted turtles. Copeia 1933:41-42.

OBBARD, M.E., AND BROOKS, R.J. 1981. Fate of overwintered clutches of the common snapping turtle (*Chelydra serpentina*) in Algonquin Park, Ontario. Canad. Field-Natur. 95(3):350-352.

PACKARD, G.C., PACKARD, M.J., McDANIEL, P.L., AND McDANIEL, L.L. 1989. Tolerance of hatchling painted turtles to subzero temperatures. Can. J. Zool. 67:828-830.

PAUKSTIS, G.L., SHUMAN, R.D., AND JANZEN, F.J. 1989. Supercooling and freeze tolerance in hatchling painted turtles (*Chrysemys picta*). Can. J. Zool. 67:1082-1084.

SEXTON, O. 1957. Notes concerning turtle hatchlings. Copeia 1957(3):229-230.

SMITH, H.M. 1956. Handbook of Amphibians and Reptiles of Kansas. University of Kansas, Museum of Natural History, Misc. Publ. No. 9, Second Edition. Lawrence: University of Kansas, 356 pp.

ST. CLAIR, R.C., AND GREGORY, P.T. 1990. Factors affecting the northern range limit of painted turtles (*Chrysemys picta*): winter acidosis or freezing? Copeia 1990(4):1083-1089.

STOREY, K.B., STOREY, J.M., BROOKS, S.P.J., CHURCHILL, T.A., AND BROOKS, R.J. 1988. Hatchling turtles survive freezing during winter hibernation. Proc. Nat. Acad. Sci. USA 85:8350-8354.

TINKLE, D.W., CONGDON, J.D., AND ROSEN, P.C. 1981. Nesting frequency and success: implications for the demography of painted turtles. Ecology 62(6):1426-1432.

ULTSCH, G.R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biol. Rev. 64:435-516.

U.S. DEPARTMENT OF THE INTERIOR. 1987. Final Environmental Impact Statement, Master Plan, Great Swamp National Wildlife Refuge, Morris County, New Jersey. U.S. Fish and Wildlife Service, Region 5, Newton Corner, Massachusetts, 202 pp.

WILHOFT, D.C., DEL BAGLIVO, M.G., AND DEL BAGLIVO, M. 1979. Observations on mammalian predation of snapping turtle nests (Reptilia, Testudines, Chelydridae). J. Herpetol. 13(4):435-438.

WILHOFT, D.C., HOTALING, E., AND FRANKS, P. 1983. Effects of temperature on sex determination in embryos of the snapping turtle, *Chelydra serpentina*. J. Herpetol. 17(1):38-42.

WILLIAMS, K.L. 1957. Possible overwintering of a turtle egg in east-central Illinois. Herpetologica 13:248.

WOOLVERTON, E. 1961. Winter survival of hatchling painted turtles in northern Minnesota. Copeia 1961(1):109.

WOOLVERTON, E. 1963. Winter survival of hatchling painted turtles in northern Minnesota. Copeia 1963(3):569-570.

ZAR, J.H. 1984. Biostatistical Analysis, Second Edition. Englewood Cliffs, New Jersey: Prentice-Hall, 718 pp.