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Hatchling Emergence From Naturally Incubated Alligator Snapping Turtle (*Macrochelys temminckii*) Nests in Northern Louisiana

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ABSTRACT. – **We report emergence dates for 38 alligator snapping turtle (*Macrochelys temminckii*) hatchlings from 6 naturally incubated nests laid during the 2008 and 2009 nesting seasons in northeastern Louisiana. Per capita emergence success for 2008 and 2009 combined was 19.5%. Hatchling emergence occurred from 28 August to 25 September and was asynchronous for 80% of nests that had multiple hatchlings emerge, with emergence duration as long as 12 days. We found no evidence of delayed emergence; some hatchlings may remain in the nest for up to 3 weeks before successfully emerging.**

Although more than 30 years have passed since Gibbons and Nelson (1978) pointed out that dates of hatchling emergence were well known for relatively few species of turtles, there are still significant gaps in our knowledge of hatchling emergence phenology in many north temperate species. In some cases, it is not even clear whether particular species are more commonly characterized by fall emergence or spring emergence, i.e., delayed emergence after overwintering in the nest. Even for species for which there is a relative abundance of information on emergence phenology, such information is often available for only a portion of the species' range. Furthermore, it is not clear for some species whether hatchling emergence is synchronous (emergence occurs over a single day) or asynchronous (emergence occurs over multiple days).

One North American species largely lacking data on emergence phenology is the alligator snapping turtle, *Macrochelys temminckii*. The little information published regarding this aspect of the life history of *M. temminckii* is anecdotal and scattered. Information on this basic life history trait is particularly important since *M. temminckii* is a species of conservation concern throughout its range (Buhlmann and Gibbons 1997).

Allen and Neill (1950) first mentioned hatchling emergence in *M. temminckii*, reporting observations of 29 hatchlings emerging from a single nest laid on 3 June 1942 by a captive individual in Florida. Eleven hatchlings emerged from this nest on 11 September, with 2 or 3 additional hatchlings emerging each day until the final hatchlings emerged on 19 September. Powders (1978) reported emergence of *M. temminckii* hatchlings from a naturally incubated nest laid by a wild female in Georgia wherein 3 hatchlings emerged sometime between 25 September and 22 October, the time period between when the author previously checked the nest and when he discovered the escape tunnel. Ewert and Jackson (1994) indicated that fall emergence was normal for *M. temminckii* along the Apalachicola River in Florida, but no specific observations of natural emergence were recorded. Later, Ewert et al. (2006) reported that 137 of 139 hatchlings from 5 nests along the Apalachicola emerged before 6 October and stated that hatchlings of *M. temminckii* probably never overwintered in the nest. The discovery of a single hatchling basking in August by Shelby and Jensen (2002) provides additional evidence for fall emergence in *M. temminckii.* The only indication in the literature that *M. temminckii* might exhibit delayed emergence is from nests laid in captivity in an outdoor enclosure at the Tulsa Zoological Park (Grimpe 1987). In two instances, hatchlings had not emerged by mid-October, by which time fall emergence has usually been recorded in this and other species. One nest was excavated on 16 October, at which time one egg was found to be hatching, followed by additional eggs hatching in subsequent days. The other nest was not excavated and was allowed to incubate through the winter. Although Grimpe (1987) removed 2 live hatchlings from this nest in mid-February and another 7 were alive when excavated in mid-May, none emerged from the nest on their own and the author felt that few, if any, of the hatchlings would have successfully emerged from the nest without intervention.

More is known concerning the emergence phenology of *Chelydra serpentina*, the closest living relative of *M. temminckii.* Hammer (1969) observed hatchlings emerging from 8 of 22 nests in the fall and found no instances of successful overwintering in the South Dakota population he studied. Gibbons and Nelson (1978) reported finding one *C. serpentina* hatchling in the fall and no evidence of delayed emergence for the species in South Carolina. Obbard and Brooks (1981) found that only 1 of 129 monitored *C. serpentina* clutches successfully overwintered in the nest in Ontario and that 42 nests had hatchlings emerge in September or October. Other Canadian studies have reported overwintering in the nest based on small samples (Toner 1933, 1940; Bleakney 1963). In a Michigan population of *C. serpentina*, hatchling emergence was documented from late August to early October, with the majority emerging in

September; however, one hatchling was caught on land in April and was thought to have overwintered (Congdon et al. 1987). It was also reported that 35% of *C. serpentina* nests in Michigan exhibited asynchronous emergence (Congdon et al. 1987). Costanzo et al. (1995) reported that a few *C. serpentina* hatchlings were observed within nests around mid-October in Nebraska. It appeared that those hatchlings would have overwintered in the nest, but no monitoring was carried out. Despite these likely instances of delayed emergence, most hatchling *C. serpentina* emerged from nests in the Nebraska sandhills during late September (Costanzo et al. 1995). More recently, Parren and Rice (2004) reported the apparent overwintering of 3 hatchlings in Vermont but did not witness the emergence event. Carroll and Ultsch (2007) reported 14 dates of hatchling emergence for *C. serpentina* in New Hampshire, all in September. Therefore, it appears that although *C. serpentina* does exhibit delayed emergence to some extent, it is not nearly as common as fall emergence. Most of the available emergence data for *C. serpentina* are not from the southeastern United States, where its range overlaps that of *M. temminckii* and where behavioral similarities might reasonably be expected. However, Aresco et al. (2006) stated that overwintering does not occur in *Chelydra* populations in Florida.

Research into the nesting ecology of *M. temminckii* has been ongoing since 2002 at Black Bayou Lake National Wildlife Refuge (NWR), near Monroe, Louisiana. Nesting of *M. temminckii* at the refuge is concentrated primarily along a railroad causeway, where turtle nests have very high levels of depredation (Woosley 2005). Protection of nests from predators provided an opportunity to monitor nests with the objective of studying emergence phenology and related factors in *M. temminckii*.

METHODS

In order to find nests before they were destroyed by predators, we performed nest surveys daily during the nesting season in April and May of 2008 and 2009. Intact or partially intact nests were covered with a predator excluder cage made of 1.27 cm mesh hardware cloth that had one corner covered with shade cloth (Epperson and Heise 2003), and designed to contain any hatchlings that made it to the surface. When we located a *M. temminckii* nest, we excavated the nest, collected a soil sample, and divided the clutch in two. An Onset Hobo® Water Temp Pro v2 data logger programmed to record temperature every 15 minutes was placed at the bottom of the nest cavity along with half of the eggs and we took the other half of the clutch back to the lab for incubation. Particle size analysis (% sand, % silt, % clay) was performed on each soil sample by the ULM Soil and Plant Analysis Lab using the hydrometer method. We monitored all nests in the field but left the nests undisturbed until well after the estimated hatching date, based on incubation duration in the lab and from previous field seasons. We do not consider it likely that the handling of eggs necessitated by our methods had a negative impact on hatching success of the eggs left in the field, based on 85.8% hatching success of eggs incubated in the lab (which were handled more) and evidence from another study (Samson et al. 2007). When we found emerged hatchlings in the predator excluder cage, we removed and returned them to the lab for measurement, blood samples, and PIT-tagging (passive integrated transponder) before releasing the hatchlings into Black Bayou Lake. In 2009, we weighed emerged hatchlings, cleaned off all soil particles and other debris, and then reweighed them in order to calculate the substrate load for each hatchling.

We determined the interval between oviposition and nest emergence in days for each emerged hatchling, determined the emergence date (median date of emergence for all siblings) for each nest (Baker et al. 2010), and determined the interval from oviposition to emergence date (IE) for each nest for use in analyses. We followed Baker et al. (2010) in the use of the following terms: synchronous emergence, asynchronous emergence, emergence period (interval between first and last emergence dates for a nesting season), and emergence duration (interval between the first and last emergence events for siblings).

We imported temperature readings from the data loggers into Excel (Microsoft 2006) and isolated the readings for the incubation period (based on a mean incubation time of 87 days in the laboratory). We then analyzed this information using PROC MEANS in SAS (SAS Institute 2003) to find the mean daily temperature for each nest for every day during incubation and then determined the grand mean of the daily mean temperatures for each nest using Excel (Microsoft 2006). We used the grand mean temperature to estimate the incubation period for each nest using the equation provided by Ewert and Jackson (1994; $y = -0.021539x^2 + 1.8995x - 25.498$). We calculated the difference between the estimated incubation period (to pipping) and the oviposition to emergence interval, yielding an estimate of the time spent in the nest by each hatchling prior to emergence. This estimate includes time spent emerging from the egg, absorbing the residual yolk, and digging out of the nest cavity. Finally, we performed linear regression in SAS (SAS Institute 2003) using PROC REG to examine the relationship between grand mean nest temperature and IE, as well as the relationship between ordinal date of oviposition and IE.

RESULTS

Hatchling emergence in 2008 was documented from 1 nest out of 5 monitored, with 2 hatchlings emerging from nest no. 2008-05. These 2 hatchlings were removed from the nest protector and returned to the lab, where they subsequently died. The other 4 nests did not produce any

Table 1. Emergence data for six naturally incubated *Macrochelys temminckii* nests from 2008 and 2009 at Black Bayou Lake NWR.

Nest ID	Date laid	No. eggs	No. emerged	Date(s) emerged	% emerged
2008-05	5 May 08	6	2	25 Sep	33.3
2009-09	11 May 09	15	8	2 Sep–14 Sep	53.3
			1	2 Sep	
			2	4 Sep	
			1	9 Sep	
			2	10 Sep	
			1	11 Sep	
			1	14 Sep	
2009-11	20 May 09	14	5	10 Sep–11 Sep	35.7
			4	10 Sep	
			1	11 Sep	
2009-12	21 May 09	11	9	10 Sep–14 Sep	81.8
			7	10 Sep	
			1	11 Sep	
			1	14 Sep	
2009-13	23 May 09	10	1	5 Sep	10.0
2009-14	25 May 09	14	13	28 Aug–31 Aug	92.9
			12	28 Aug	
			1	31 Aug	

hatchlings. On a per capita basis, emergence success for 2008 was 4.2%.

In 2009, we monitored 11 nests for hatchling emergence. We documented emergence from 5 of the nests, with a total of 36 hatchlings (Table 1). In 2009, per capita emergence success was 24.5%. For the 2 years of this study combined, we documented 19.5% per capita emergence success, with 6 of 16 nests (37.5%) producing at least 1 emerged hatchling. In 2009, emerged hatchlings had a substrate load that averaged 19.6% (± 14.5, $n = 35$) of their body weight, with individual hatchlings having substrate loads ranging from 1.5% to 85% (Fig. 1). Nests from which these hatchlings emerged averaged 14.1% clay (± 4.4, range = 7.2%–19.2%).

We found the emergence period for this population to be 28 August to 25 September for the 2 years combined. For 4 of the 5 nests with more than 1 emerged hatchling, emergence was asynchronous. Emergence duration was as long as 12 days, with 5 days being the longest interval between hatchling emergence events for an individual nest (Table 1). The IE ranged from 96.5 days to as long as 143 days (Table 2). A linear regression of the relationship between the 87-day grand mean nest temperature and IE can be seen in Fig. 2a ($y = -12.43x + 442.3$; $r^2 = 0.70$; $p = 0.077$). Although the relationship is not statistically significant, there does appear to be a strong relationship between nest temperature and IE, with IE decreasing as temperature increases. The relationship between ordinal date of oviposition and IE (Fig. 2b) was even stronger, with IE decreasing as ordinal date increased, and this relationship was statistically significant ($y = -1.99x + 389.3$; $r^2 = 0.88$; $p = 0.005$). The estimated incubation period for nests that had hatchling emergence ranged from 98 to 121 days, with shorter estimated incubation periods generally corresponding with shorter IE (Table 2). Based on these estimates, it appears that some hatchlings may have remained in the nest cavity for up to 3 weeks before emerging.

Figure 1. Hatchling *Macrochelys temminckii* photographed shortly after emerging from the nest. Note the heavy substrate load adhering to the hatchling. Photo by J.L. Carr.

DISCUSSION

Although this report is of a fairly small number of emerged hatchlings from a small number of nests, it greatly increases the amount of available information about emergence phenology in *M. temminckii* and is the first natural emergence data from west of the Mississippi River. It appears that, at least for this population, emergence occurs in the fall, as we found no evidence of delayed emergence. This is consistent with what has been reported from both Georgia (Powders 1978) and Florida (Ewert and Jackson 1994; Ewert et al. 2006). There is no indication that *M. temminckii* routinely delays emergence from the nest to the following spring in the wild. The only reported case of overwintering in *M.*

Table 2. Interval to emergence date (IE), incubation period estimated from incubation temperature, and estimated time between hatching and emergence (nest 2009-14 was not equipped with a temperature data logger, so incubation period was not estimated).

NEST ID	Interval to emergence date (d)	Estimated incubation period (d)	Estimated time spent in nest (d)
2008-05	143	121	22
2009-09	120	105	15
2009-11	113.5	113	0.5
2009-12	114	102	12
2009-13	105	98	7
2009-14	96.5	N/A[a]	N/A

[a] N/A = not available.

temminckii remains Grimpe's (1987) observations of 2 nests in captivity, which provided no evidence that successful emergence would have followed. Our observations also indicate that hatchling emergence in *M. temminckii* is largely asynchronous, as was indicated by Allen and Neill (1950) for the nest of a captive individual. This contrasts with a preponderance of synchrony (62%–65%) reported in *C. serpentina* in Michigan (Congdon et al. 1987, 2008); however, only 36% synchrony was recorded in a Quebec population (Robinson 1989). Furthermore, the predominance of fall emergence is consistent with what has been reported for *C. serpentina*, although *M. temminckii* may not exhibit the plasticity in emergence phenology found in northern populations of *C. serpentina*. Given the fact that hatchling emergence has been documented only in the fall within wild populations, it is important to release hatchling *M. temminckii* from headstart programs (e.g., in Oklahoma; Riedle et al. 2008) during the fall.

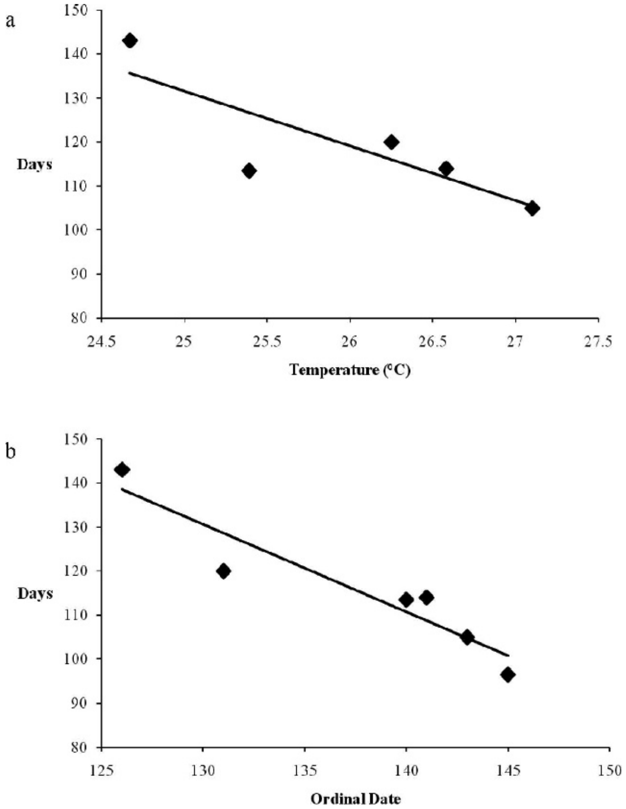

Figure 2. a) Relationship between interval to emergence date (IE), in days, and grand mean nest temperature during incubation. **b)** Relationship between interval to emergence date (IE), in days, and ordinal date of monitored nests.

The IE was highly variable among nests, ranging from 96.5 to 143 days (mean IE = 115.3 days). Congdon et al. (1987) reported the IE in their Michigan *C. serpentina* population as 73–117 days, with an average of 90–93 days (Congdon et al. 2008). The approximately 3 weeks longer IE in *M. temminckii* can be accounted for by factors of both geography and egg size. Ewert (1985) noted geographic variation in incubation period inversely related to latitude and a positive relationship with egg size in both intraspecific and interspecific comparisons. There was a strong relationship between the grand mean nest temperature during the total incubation period and the IE, and although the relationship was not statistically significant, this is likely due to the sample size. Nests with higher grand mean temperatures had a shorter IE and nests with lower grand mean temperatures had a longer IE. This likely reflects differences in developmental rates caused by different incubation temperatures since increases in temperature accelerate development of turtle embryos (Ewert 1979, 1985; Georges et al. 2005). Further support for the correlation between higher temperature and shorter IE is provided by the relationship between ordinal date and IE because ordinal date should indirectly reflect warmer weather and higher incubation temperatures as the nesting season progressed. Even within nests, there are likely to be differences in developmental rate between siblings due to within-nest temperature variation, which would result in faster-developing hatchlings emerging before slower-developing hatchlings, resulting in asynchronous emergence (Houghton and Hays 2001), as seen in this study.

We observed a relatively large amount of nest substrate adhering to emerged hatchlings, adding to the difficulty of emerging from the nest as well as adding a significant weight burden for the trip to water. Although there do not appear to be previous reports of such a weight burden added to hatchlings by their substrate, the additional weight we recorded in the 2009 hatchlings was 4–6 times the generally reported radio-tag load at which deleterious effects on animal locomotion have been observed (Kenward 2001). Janzen et al. (2007) found substantial support to show that the size-related fitness benefit of large size for an emerged hatchling freshwater turtle was mediated through the length of time a hatchling was exposed to predation, by virtue of traversing the nest-water distance more rapidly. The substrate load adherent to a hatchling would thus be predicted to incur a fitness cost by means of protracting both the time to emergence and the time to reach water. Conversely, the substrate coating might increase resistance to desiccation and assist in camouflaging the hatchling from predators. The possible consequences of substrate type and its propensity (or lack thereof) to adhere to hatchlings may be relevant much more so in *M. temminckii* than other turtles because of the extreme amount of texture associated with the natal scutes of the shell in this species.

It appears that some hatchlings in this population of *M. temminckii* are remaining in the nest cavity for extended periods of time before emerging, as long as 3 weeks in some cases. These lengthy intervals between hatching and emergence could be partially explained by the nest substrates along the railroad causeway, which may result in a protracted period of digging, as nests deposited in clay and gravel are known to pack down and become hard for hatchlings to dig through (Epperson and Heise 2003). This, along with asynchronous emergence, could serve to increase the vulnerability of hatchlings to predation by invertebrates, including the red imported fire ant, *Solenopsis invicta*. Parris et al. (2002) indicated that hatchling turtles may be especially vulnerable to attack by fire ants while in the nest cavity prior to emergence, so later emerging hatchlings from a given nest could be at the most risk. Moulis (1997) also observed that hatchlings were subject to fire ant attack while in the process of emerging from the nest. This appears to be true at Black Bayou Lake NWR as well, as emerged hatchlings from 2 nests in this study showed injuries due to *S. invicta* attack, including severely damaged limbs and tails. Long periods of time spent in the nest by hatchlings, coupled with asynchronous emergence, could prove extremely detrimental to emergence success in the presence of *S. invicta*. This has potential implications for the conservation of *M. temminckii*, given the overlap in range between this species and *S. invicta*.

Multiple factors in the natural nest environment appear to be depressing emergence success and thus recruitment in this population of *M. temminckii*. In order to successfully emerge and make it safely to water a hatchling must overcome the challenges to digging presented by the nest substrate, negotiate a gauntlet of *S. invicta* and phorid flies (Holcomb and Carr 2011), and potentially contend with a significant substrate burden once out of the nest cavity. These considerations, along with the discrepancy seen between hatching success in the lab and emergence success in the field, illustrate the potential utility of headstart programs because artificial incubation can result in far more hatchlings entering the population than natural incubation alone.

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