RESEARCH ARTICLE

The Herpetological Bulletin 141, 2017: 16-22

Nesting characteristics of three turtle species along a wetland matrix in western Pennsylvania, USA

DANIEL F. HUGHES[1,*], KATRINA JOHNSTON[2] & WALTER E. MESHAKA, JR.[3]

[1]Department of Biology, University of Texas at El Paso, El Paso, Texas 79968, USA
[2]Powdermill Nature Reserve, Carnegie Museum of Natural History, 1847 Route 381, Rector, Pennsylvania 15677, USA
[3]Section of Zoology and Botany, State Museum of Pennsylvania, 300 North Street, Harrisburg, Pennsylvania 17120, USA
[*]Corresponding author Email: dfhughes@miners.utep.edu

ABSTRACT - We studied nesting activities and measured afternoon nest-temperatures of the midland painted turtle (*Chrysemys picta marginata*), common snapping turtle (*Chelydra serpentina serpentina*), and eastern box turtle (*Terrapene carolina carolina*) from a wetland matrix during May–November 2013 at the Powdermill Nature Reserve in western Pennsylvania, USA. Nesting turtles were encountered during a 36-day period (2 June–8 July). The aquatic turtle species nesting season spanned 17 days (2–18 June). In general, nests were located in areas lacking extensive vegetation and near wetlands. Across all species, successful nests constituted 15% (n = 5), abandoned nests 53% (n = 18), and depredated nests 32% (n = 11). Nest losses to predation were highest for *C. s. serpentina* at 75% (6/8 nests). Mean nest temperatures were lowest for *C. p. marginata* and *T. c. carolina*. Nest successes were highest for *C. s. serpentina* at 42% (19/45 eggs) and hatchlings emerged from these nests by late August. By the first freeze in November, 40% (4/10 eggs) of *T. c. carolina* eggs hatched and hatchlings remained in the nest to overwinter, whereas none of the eight *C. p. marginata* eggs had hatched by then. Our results from a single site are comparable to findings from other regions and for Pennsylvania generally. Our findings also provide the basis for examining responses in nesting phenology to environmental perturbations, most relevant being climate change.

INTRODUCTION

Reports documenting the nesting ecology of individual turtle species in North America are common (e.g., Congdon et al., 1987). However, reports on the nesting characteristics of turtle communities are more rare (Ernst & Lovich, 2009). Studies on nesting in turtle communities can provide insights into the local factors that influence interspecific variation in hatchling emergence, and in turn can lead to a better understanding of broad patterns underlying nesting ecology across the ranges of various turtle species (Lovich et al., 2014).

Six turtle species occur in Westmoreland County, Pennsylvania, USA (Hulse et al., 2001; McCoy, 1982; Russell et al., 2014). Four of these have been documented from the Powdermill Nature Reserve (PNR) in south-eastern Westmoreland County: midland painted turtle (*Chrysemys picta marginata*), common snapping turtle (*Chelydra serpentina serpentina*), eastern box turtle (*Terrapene carolina carolina*), and North American wood turtle (*Glyptemys insculpta*) (Meshaka et al., 2008). At PNR, the aquatic species (*C. p. marginata* and *C. s. serpentina*) have held the focus of a long-term demographic study from hoop-net trapping (Hughes et al., 2016), and the primarily terrestrial species (*T. c. carolina* and *G. insculpta*) have been monitored for over 50 years to ascertain long-term trends in population ecology (Miller, 2004). However, the nesting ecology of turtles at PNR, which is located near the north-eastern edge in the geographic ranges for these species in the US (Ernst & Lovich, 2009), has not been studied.

We set out to ascertain various nesting characteristics for three turtle species (*C. p. marginata*, *C. s. serpentina*, and *T. c. carolina*) including nesting activities, hatching success, and diel-nest temperatures from June–October 2013 from a wetland matrix at PNR. Our primary aim was to document the phenology and associated abiotic variables of nesting in a turtle community during a single season at PNR. Our findings not only offer a useful comparison to studies on nesting in these species from different localities (e.g., Christens & Bider, 1987), but also will serve as baseline information on turtle nesting to understand the effects from future environmental perturbations in the northern Allegheny Mountains of western Pennsylvania.

MATERIALS AND METHODS

Study site

Powdermill Nature Reserve is an 856.2 ha field station located in the Ligonier Valley along the western flank of Laurel Hill in the northern Allegheny Mountains of south-eastern Westmoreland County, western Pennsylvania, USA (40°10'N, 79°16'W; 400 m elevation). Established as a field station in 1956 for the Carnegie Museum of Natural History by Dr. M. Graham Netting, PNR habitats consist of mixed forests, open fields, artificial ponds, natural wetlands, and mountain streams (Morton & Speedy, 2012). The mesophytic forests on PNR are dominated by oaks (*Quercus*), maples (*Acer*), and beeches (*Fagus*) (Utech, 1999). Several long-term ecological studies of the resident fauna of PNR are ongoing and include birds (e.g., McDermott & DeGroote, 2016), snakes (e.g., Meshaka, 2010; Dahlin et al., 2016), turtles (e.g., Hughes et al., 2016), and amphibians (e.g., Meshaka, 2009; Meshaka & Hughes, 2014). To attract migratory birds for PNR's banding program (Powdermill Avian Research Center), artificial ponds were created near the northern boundary of PNR in the 1960s and active management of these ponds continues today. Associated with this wetland matrix is an extensive network of mist-net lanes for the bird-banding program. Net lanes have been utilised in the morning for 3–6 days/week April–August from 1961 - present. Three turtle species (*C. p. marginata*, *C. s. serpentina*, and *T. c. carolina*) have been regularly encountered digging nests and laying eggs in the net lanes by members of the bird-banding staff over at least the last three decades (Robert C. Leberman, pers. comm.). We chose this area to study the nesting ecology of these turtle species because the trails have exposed soils amenable for digging and the consistent observations of turtles nesting along the trails.

Nesting ecology

The first author walked an approximately 1.4 km transect throughout the lanes of the wetland matrix and an adjacent field twice daily, once in the morning (0700–1000 hr) and another in the evening (1800–2100 hr), during the primary nesting season (late-May to late-June) for these turtle species in Pennsylvania (Hulse et al., 2001). During transects, the first author looked for signs of recent nesting activity (e.g., scratching or digging in soil, abandoned nests, etc.). The status of nests was categorised as active with eggs, depredated with eggshell remnants, or abandoned before eggs were deposited. If the turtle species was not directly observed, we assigned species to depredated and active nests based on proximity of the nest to wetlands and the amount and shape of eggs or shells, which varies among species (Hulse et al., 2001). Nests near wetlands (< 5 m) with numerous (> 10 eggs) spherical eggs were assigned to *C. s. serpentina*; nests near wetlands (< 5 m) with few (< 10 eggs) elliptical eggs were assigned to *C. p. marginata*; and nests away (> 5 m) from wetlands with few (< 8 eggs) elliptical eggs were assigned to *T. c. carolina*. Other types of nesting events (e.g., abandoned nests) could not be reliably assigned to species.

When nests or nesting turtles were encountered, we recorded the time, date, GPS coordinates, general canopy cover, and a qualitative assessment of the microhabitat within a 2-m circle of the site. Turtles found digging or laying were monitored from a safe distance until all eggs were laid and the nest was filled by the turtle. Turtles were then captured and given individual identities (see Hughes et al., 2016). We recorded body measurements of females, including weight to the nearest 1 g, carapace length and width, and plastron length to the nearest 1 mm of turtles.

Active nests were gently excavated, and the eggs were carefully removed. We measured various features of the nest chamber, including the depth to first egg, depth to last egg, chamber width, and size of chamber opening. We determined clutch size to be the number of eggs in the nest. We measured clutch mass to the nearest 1 g by placing eggs in a tared container attached to a digital spring scale. Each egg was measured for width and length to the nearest 0.1 mm with Vernier calipers. Eggs were carefully placed back into the nest in the order that they were removed and nests were covered with dirt.

To monitor nests for thermal profiles throughout the season, we placed a plastic fence (ca. 1 m high) around active nests to deter predators and to avoid being trampled by the banding staff. We measured temperatures of active nests from initial nest discovery until all nests were excavated on 4 November 2013. Approximately once a week at midday, we measured the temperature (˚C) inside the nest at two depths, one near the middle and another at the bottom of the nest using the probe of a quick-reading Fluke 51II thermometer. The depths varied based on the overall depth of each nest. We also recorded soil-surface temperature directly above the nest with a Pro-Exotics PE-2 infrared temperature gun and monthly average air temperatures were downloaded for Laurel Summit (https://www.ncdc.noaa.gov/), which is ca. 10 km from our site.

RESULTS

A total of 34 events associated with nesting were encountered, including 18 abandoned nests, 11 depredated nests, and five active nests with eggs (Fig. 1). Of the 11 depredated nests, six were assigned to *C. s. serpentina*, three to *T. c. carolina*, and two to *C. p. marginata*. Six turtles were encountered in the course of nesting over a 36-day period (2 June–8 July): *C. s. serpentina* on 2 June (n = 2) and 5 June (n = 1); *C. p. marginata* on 19 June (n = 1); and *T. c. carolina* on 10 June (n = 1) and 8 July (n = 1). An additional nest of *C. s. serpentina* with just five eggs was found on 5 June—a large root system at the base of the nest seemed to physically prohibit the presence of additional eggs—and depredated on 9 June. Across all species, nest sites were constructed along net lanes or a gravel road (Fig. 1). Nest-site selections for *C. p. marginata* and *T. c. carolina* were in areas with more extensive canopy cover or adjacent to taller vegetation than nests of *C. s. serpentina*.

Selected clutch and nest characteristics are presented in Table 1. For *C. s. serpentina*, 42% of the eggs hatched (19/45 eggs), and these hatchlings emerged naturally from the nests on 27 and 29 August. For *T. c. carolina*, 40% of the eggs hatched (4/10 eggs), which represented 100% of the eggs from one nest. All four hatchlings of *T. c. carolina* were still in the nest at the time of excavation and thus likely to overwinter in the nest. None of the eggs for *C. p. marginata* hatched (0/8 eggs) from a single nest by the excavation date. Mean carapace length for *T. c. carolina* from four hatchlings was 25.9 mm and from five *C. s. serpentina* hatchlings was 26.9 mm (Table 1).

Five active nests with eggs were monitored for thermal profiles: *C. s. serpentina* (n = 2 nests), *T. c. carolina* (n = 2 nests), and *C. p. marginata* (n = 1 nest). Mean temperature at the soil surface was higher than both depths, and mean temperatures closer to the center of the nests were higher than mean temperatures near the bottom of the nests (Tables 2-4). Mean nest temperatures at both depths and at the soil surface were generally highest among those of *C. s. serpentina* than for *T. c. carolina* and *C. p. marginata* (Tables 2-4).

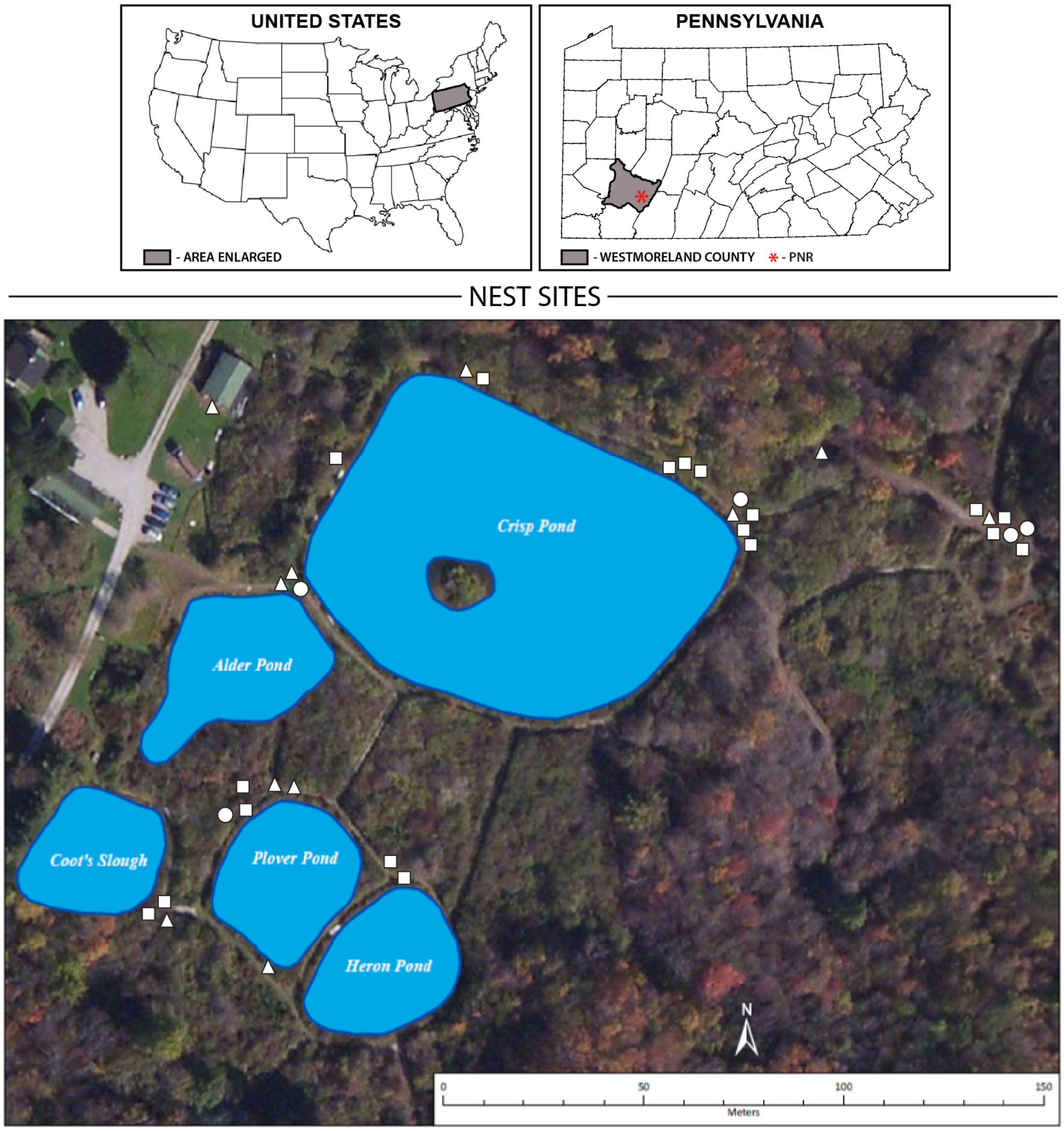

Figure 1. The study area at Powdermill Nature Reserve (PNR), Westmoreland County, western Pennsylvania, USA. Enlarged view of wetland matrix, mist-net lanes, and nest sites (bottom). Circles indicate nests with eggs that were monitored for thermal profiles, squares abandoned nests, and triangles depredated nests.

DISCUSSION

In general, the nesting characteristics (e.g., clutch size) of the three turtle species we examined at PNR were consistent with other studies on these species conducted in Pennsylvania (e.g., Bieber-Ham, 2011; Ernst, 1966, 1971; Hulse et al., 2001) and elsewhere (Ernst & Lovich, 2009). Afternoon nest temperatures of *C. s. serpentina* were higher than those of *T. c. carolina* and *C. p. marginata*. Our qualitative observations and quantitative temperatures indicate that *C. s. serpentina* nested in sparsely vegetated open areas, where exposure to direct sunlight was high. In contrast, *T. c. carolina* and *C. p. marginata* nests were adjacent to thick vegetation or near the edge of tree lines, where exposure to sunlight was comparatively lower. The deeper and generally south-facing nests of *C. s. serpentina* had consistently higher afternoon nest temperatures than the comparatively shallower nests of *T. c. carolina* and *C. p. marginata*. Our results are consistent with previous findings on the vital role that nest-site selection plays in regulating nest temperatures over other factors such as nest depth (Bodie et al., 1996). Differences in nest-site selection are an important source of intrapopulation variation in nest temperatures (Riley et al., 2014) and nest sites on south-facing slopes have been shown to increase hatching success (Schwarzkopf & Brooks, 1987). Moreover, overwintering in the nest with respect to hatchling survival has been shown to be a largely unsuccessful strategy in northern populations of *C. s. serpentina* (Obbard & Brooks, 1981), especially in comparison with other temperate freshwater species (e.g., *C. picta*: Costanzo et al., 1995), and thus the nest-site selections in areas of high sun exposure for *C. s. serpentina* likely promoted hatching and early emergence (Gibbons, 2013; Lovich et al., 2014).

The nesting season for the turtle community at PNR is within the range for these species in Pennsylvania (Hulse et

Table 1. Selected nest characteristics for three turtle species from Powdermill Nature Reserve, Westmoreland County, western Pennsylvania, USA. Means are presented ± one standard deviation with the ranges and sample sizes in parentheses.

	***Chelydra serpentina serpentina* (2 nests)**	***Terrapene carolina carolina* (2 nests)**	***Chrysemys picta marginata* (1 nest)**
Clutch size	22.5 ± 3.5 eggs (20–25 eggs)	5 ± 1.4 eggs (4–6 eggs)	8 eggs
Clutch weight	280 ± 42.4 g (250–310 g)	55 ± 7.1 g (50–60 g)	70 g
Egg weight	12.5 ± 0.1 g (12.4–12.5 g; n = 45)	11.3 ± 1.8 g (10–12.5 g; n = 10)	8.8 g
Egg dimensions	27.4 ± 0.9 mm (26–29 mm; n = 45)	L: 36 ± 2.2 mm (33–39 mm; n = 10) W: 21.7 ± 0.7 mm (21–23 mm; n = 10)	L: 31 ± 1.1 mm (29–32 mm; n = 8) W: 17.8 ± 0.5 mm (17–18 mm; n = 8)
Hatchling carapace length	26.9 ± 1.6 mm (25.2–28.6 mm; n = 5)	25.9 ± 0.4 mm (25.5–26.2 mm; n = 4)	-
Nest depth	110 ± 14.1 mm (100–120 mm)	65 ± 7.1 mm (60–70 mm)	55 mm
% nests depredated	75% (6/8 nests)	60% (3/5 nests)	66.6% (2/3 nests)
% hatching success	42% (19/45 eggs)	40% (4/10 eggs)	0% (0/8 eggs)
Overwintered in nest	No	Yes	-

Table 2. Monthly mean nest and air temperatures for the common snapping turtle (*C. s. serpentina*) from Powdermill Nature Reserve, Westmoreland County, western Pennsylvania, USA. Hatchlings emerged naturally on 27 and 29 August 2013. Means are presented ± one standard deviation with the ranges in parentheses and sample sizes below.

	***C. s. serpentina* (2 nests)**			
Month	**Soil surface**	**Depth 1**	**Depth 2**	**Air**
June	30.6 ± 7.9 C° (21.4–40.6 C°) n = 8	27.8 ± 5.1 C° (23.2–36 C°) n = 8	26.7 ± 4.3 C° (22.8–33.8 C°) n = 8	16.7 C° (4.4–26.1 C°)
July	29.5 ± 3.6 C° (24.7–35.8 C°) n = 6	26.9 ± 2.8 C° (23.2–30.3 C°) n = 6	26.1 ± 2.6 C° (22.4–29.4 C°) n = 6	19.1 C° (8.3–27.8 C°)
August	32.3 ± 3.7 C° (27.3–36.1 C°) n = 4	28.4 ± 1.7 C° (27–30.8 C°) n = 4	27 ± 1.1 C° (26.1–28.5 C°) n = 4	17 C° (7.8–25 C°)
September	-	-	-	14.2 C° (3.3–26.7 C°)
October	-	-	-	
Overall	30.6 ± 5.6 C° (21.4–40.6 C°) n = 18	27.6 ± 3.7 C° (23.2–36 C°) n = 18	26.5 ± 3.2 C° (22.4–33.8 C°) n = 18	12.9 C° (-13.9–27.8 C°)

Table 3. Monthly mean nest and air temperatures for the eastern box turtle (*T. c. carolina*) from Powdermill Nature Reserve, Westmoreland County, western Pennsylvania, USA. Nests excavated on 4 November 2013. Means are presented ± one standard deviation with the ranges in parentheses and sample sizes below.

	***T. c. carolina* (2 nests)**			
Month	**Soil surface**	**Depth 1**	**Depth 2**	**Air**
June	27.3 ± 7.2 C° (21.2–37.3 C°) n = 4	26.6 ± 4.7 C° (22.6–32.6 C°) n = 4	26.2 ± 4.8 C° (22.2–32.4 C°) n = 4	16.7 C° (4.4–26.1 C°)
July	26.6 ± 1.7 C° (24.5–28.3 C°) n = 5	26.4 ± 1.4 C° (24.9–28.5 C°) n = 6	25.9 ± 1.7 C° (24.4–28.3 C°) n = 6	19.1 C° (8.3–27.8 C°)
August	26.1 ± 1.9 C° (23.1–28.5 C°) n = 6	25.2 ± 1 C° (23.5–26.3 C°) n = 6	23.9 ± 1.2 C° (22.4–25.8 C°) n = 6	17 C° (7.8–25 C°)
September	21.4 ± 1.5 C° (19.2–23.6 C°) n = 8	19.9 ± 1.4 C° (17.9–22.2 C°) n = 8	18.8 ± 1.8 C° (16–21.1 C°) n = 8	14.2 C° (3.3–26.7 C°)
October	15.4 ± 4.4 C° (8.5–21.6 C°) n = 10	14.3 ± 4.1 C° (8.2–20.5 C°) n = 10	13.8 ± 3.9 C° (8.2–19.1 C°) n = 10	9.8 C° (-2.8–26.1 C°)
Overall	21.9 ± 5.9 C° (8.5–37.3 C°) n = 33	20.9 ± 5.7 C° (8.2–32.6 C°) n = 33	20.1 ± 5.7 C° (8.2–32.4 C°) n = 33	12.9 C° (-13.9–27.8 C°)

al., 2001). For the aquatic species, the nesting season was shorter than the terrestrial species. A relatively extended nesting season is consistent with other populations of *T. c. carolina* (Wilson & Ernst, 2005), whereas *C. p. marginata* and *C. s. serpentina* typically exhibit a narrower nesting season lasting 2–3 weeks (Ernst & Lovich, 2009; Hulse et al., 2001). Incubation time for *C. s. serpentina* at PNR of 85–87 days is slightly less than the average in Pennsylvania of 90 days (Hulse et al., 2001), yet longer than eggs incubated at constant temperatures in the laboratory (Yntema, 1978).

Data on nesting success and the factors influencing survivorship from the egg to hatchling are important to understanding reproductive strategies. Nest depredation among species in our study was comparable to other studies that have shown it can range from 0–94% in some years (Christens & Bider, 1987; Congdon et al., 1987; Congello, 1978; Petokas & Alexander, 1980). Predation is a major source of nest failures in turtles (Ernst & Lovich, 2009); however, several studies have shown that nests fail for other reasons unrelated to predators, such as environmental fluctuations (e.g., Tinkle et al., 1981). We found that none of the *C. p. marginata* eggs hatched before the first freeze in November, which is generally consistent with larger samples demonstrating that hatching success in this species can be very low (Christens & Bider, 1987). We suspect that inadequate temperatures were reached for the embryos to fully develop before the first freeze because this particular nest location was adjacent to tall vegetation. Four hatchling *T. c. carolina* were found in the nest upon excavation in November, suggesting that these individuals were likely to overwinter in the nest, which has been observed in *T. carolina* from New York (Madden, 1975). However, overwintering in the nest by *T. carolina* was not observed in Maryland by Kipp (2003) or from another site in New York by Burke & Capitano (2011). Gibbons & Nelson (1978) suggested that species with elevated levels of uncertainty in reproduction or habitat will be more likely to delay emergence (i.e., overwinter). This phenomenon has been recently considered to be normal of temperate zone turtle species (Gibbons, 2013) and can be common in populations throughout the ranges of *C. p. marginata* and *C. s. serpentina* (Lovich et al., 2014).

Aside from the small adult population sizes of these turtle species at PNR (Miller, 2004; Hughes et al., 2016), we note two salient factors adversely affecting the nesting ecology at this wetland matrix that the impacts of which may be mitigated through active management. First, a significant reduction in areas with adequate sun exposure for egg development due to overgrown vegetation could be cleared and returned to a more open habitat (Tesauro & Ehrenfeld, 2007). Second, the high number of nests lost to mesopredators may be mitigated through an annual harvest of small mammals, turtle nest screening (Ratnaswamy et al., 1997), or aversive conditioning (Conover, 1990).

Our findings provide a solid base for future studies aimed at examining the long-term dynamics of nesting ecology at PNR. The nest-temperature profiles and patterns in nest-site selection we found are not likely to remain stable in the face of predicted global climate changes (e.g., Mainwaring et al., in press). Consequently, our baseline data will allow us to test the extent to which the nesting ecology at PNR is affected by future environmental changes, for which climate-related phenological changes have already been documented in some of PNR's avian taxa (McDermott & DeGroote, 2017).

ACKNOWLEDGEMENTS

We extend our sincere gratitude to the staff of PNR and the Carnegie Museum of Natural History for support of this research project and countless others, especially John W. Wenzel, Robert C. Leberman, and Cokie Lindsay. We thank Carl H. Ernst for an insightful review of this manuscript. We acknowledge James Whitacre for his cartographical efforts to produce Figure 1. Lastly, we thank Pablo R. Delis for graciously lending us his personal equipment used in this project.

Table 4. Monthly mean nest and air temperatures for the midland painted turtle (*C. p. marginata*) from Powdermill Nature Reserve, Westmoreland County, western Pennsylvania, USA. Nest excavated on 4 November 2013. Means are presented ± one standard deviation with the ranges in parentheses and sample sizes below.

	***C. p. marginata* (1 nests)**			
Month	**Soil surface**	**Depth 1**	**Depth 2**	**Air**
June	30.9 ± 9.5 C° (24.2–37.6 C°) n = 2	27.6 C° n = 1	30.3 ± 4.1 C° (27.4–33.2 C°) n = 2	16.7 C° (4.4–26.1 C°)
July	24.6 ± 3.1 C° (21–26.5 C°) n = 3	26.5 ± 1.9 C° (24.3–28 C°) n = 3	26.1 ± 1.7 C° (24.4–27.8 C°) n = 3	19.1 C° (8.3–27.8 C°)
August	25.2 ± 4.1 C° (21.6–29.7 C°) n = 3	25.3 ± 2.6 C° (23.4–28.3 C°) n = 3	24.3 ± 1.6 C° (23.3–26.1 C°) n = 3	17 C° (7.8–25 C°
September	22.3 ± 1.5 C° (20.5–24.2 C°) n = 4	21.4 ± 1.6 C° (19.4–23.3 C°) n = 4	19.9 ± 1.5 C° (18.4–21.2 C°) n = 4	14.2 C° (3.3–26.7 C°)
October	16 ± 5.3 C° (8.5–22.7 C°) n = 5	15.3 ± 4.6 C° (8.7–20.9 C°) n = 5	14.5 ± 4 C° (8.8–19.1 C°) n = 5	9.8 C° (-2.8–26.1 C°)
Overall	22.4 ± 6.4 C° (8.5–37.6 C°) n = 17	21.6 ± 5.6 C° (8.7–28.3 C°) n = 16	21.3 ± 6.1 C° (8.8–33.2 C°) n = 17	12.9 C° (-13.9–27.8 C°)

REFERENCES

Bieber-Ham, L.M. (2011). Population and nesting ecology of painted turtles (*Chrysemys picta*) in Pennsylvania. Carlisle, Pennsylvania: Dickinson College Honors Theses No. 133. 37 pp.

Bodie, J.R., Smith, K.R. & Burke, V.J. (1996). A comparison of diel nest temperature and nest site selection for two sympatric species of freshwater turtles. *American Midland Naturalist* 136: 181-186.

Burke, R.L. & Capitano, W. (2011). Eastern box turtle, *Terrapene carolina*, neonate overwintering ecology on Long Island, New York. *Chelonian Conservation and Biology* 10: 256-259.

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

Congdon, J.D., Breitenbach, G.L., van Loben Sels, R.C. & Tinkle, D.W. (1987). Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in south-eastern Michigan. *Herpetologica* 43: 39-54.

Congello, K. (1978). Nesting and egg laying behavior in *Terrapene carolina*. *Proceedings of the Pennsylvania Academy of Science* 52: 51-56.

Conover, M.R. (1990). Reducing mammalian predation on eggs by using a conditioned taste aversion to deceive predators. *The Journal of Wildlife Management* 54: 360-365.

Costanzo, J.P., Iverson, J.B., Wright, M.F. & Lee, R.E. (1995). Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. *Ecology* 76: 1772-1785.

Dahlin, C.R., Hughes, D.F., Meshaka, W.E., Jr., Coleman, C. & Henning, J.D. (2016). Wild snakes harbor West Nile virus. *One Health* 2: 136-138.

Ernst, C.H. (1966). Overwintering of hatchling *Chelydra serpentina* in southeastern Pennsylvania. *Philadelphia Herpetological Society Bulletin* 14: 8-9.

Ernst, C.H. (1971). Observations on the egg and hatchling of the American turtle, *Chrysemys picta*. *British Journal of Herpetology* 4: 224-227.

Ernst, C.H. & Lovich, J.E. (2009). *Turtles of United States and Canada*. Baltimore, Maryland: John Hopkins University Press.

Gibbons, J.W. & Nelson, D.H. (1978). The evolutionary significance of delayed emergence from nest by hatchling turtles. *Evolution* 32: 297-303.

Gibbons, J.W. (2013). A long-term perspective of delayed emergence (aka overwintering) in hatchling turtles: Some they do and some they don't, and some you just can't tell. *Journal of Herpetology* 47: 203-214.

Hughes, D.F., Tegeler, A.K. & Meshaka, W.E., Jr. (2016). Differential use of ponds and movements by two species of aquatic turtles (*Chrysemys picta marginata* and *Chelydra serpentina serpentina*) and their role in colonization. *Herpetological Conservation and Biology* 11: 214-231.

Hulse, A.C., McCoy, C.J. & Censky, E.J. (2001). *Amphibians and Reptiles of Pennsylvania and the Northeast*. New York, New York: Cornell University Press.

Kipp, R.L. (2003). Nesting ecology of the eastern box turtle (*Terrapene carolina carolina*) in a fragmented landscape. Unpublished M.Sc. thesis, University of Delaware, Delaware.

Lovich, J.E., Ernst, C.H., Ernst, E.M. & Riley, J.L. (2014). A 21-year study of seasonal and interspecific variation of hatchling emergence in a Nearctic freshwater turtle community: To overwinter or not to overwinter? *Herpetological Monographs* 28: 93-109.

Madden, R. (1975). Home-range, movements, and orientation in the eastern box turtle, *Terrapene c. carolina*. Unpublished Ph.D. dissertation, City University of New York, New York.

Mainwaring, M.C., Barber, I., Deeming, D.C., Pike, D.A., Roznik, E.A. & Hartley, I.R. (In press). Climate change and nesting behaviour in vertebrates: A review of the ecological threats and potential for adaptive responses. *Biological Reviews* doi:10.1111/brv.12317.

McCoy, C.J. (1982). Amphibians and reptiles in Pennsylvania: Checklist, bibliography, and atlas of distribution. *Special Publication of the Carnegie Museum of Natural History* 6: 1-91 + 74 maps.

McDermott, M.E. & DeGroote, L.W. (2016). Long-term climate impacts on breeding bird phenology in Pennsylvania, USA. *Global Change Biology* 22: 3304-3319.

McDermott, M.E. & DeGroote, L.W. (2017). Linking phenological events in migratory passerines with a changing climate: 50 years in the Laurel Highlands of Pennsylvania. *PLoS ONE* 12: e0174247.

Meshaka, W.E., Jr., Huff, J.N. & Leberman, R.C. (2008). Amphibians and reptiles of Powdermill Nature Reserve in western Pennsylvania. *Journal of Kansas Herpetology* 25: 12-18.

Meshaka, W.E., Jr. (2009). The terrestrial ecology of an Allegheny amphibian community: Implications for land management. *The Maryland Naturalist* 50: 30-56.

Meshaka, W.E., Jr. (2010). Seasonal activity and breeding seasons of snakes from Powdermill Nature Reserve in western Pennsylvania: The importance of site-specific data in land management programs. *Herpetological Conservation and Biology* 5: 155-165.

Meshaka, W.E., Jr. & Hughes, D.F. (2014). Adult body size and reproductive characteristics of the Green Frog, *Lithobates clamitans melanotus* (Rafinesque, 1820), from a single site in the northern Allegheny Mountains. *Collinsorum: The Journal of Kansas Herpetology* 3: 13-16.

Miller, T. (2004). Report on wood turtles, box turtles and painted turtles. Unpublished report, Carnegie Museum of Natural History, Powdermill Nature Reserve, Pennsylvania. 27 pp.

Morton, C.M. & Speedy, L. (2012). Checklist of the vascular plants of Westmoreland County, Pennsylvania. *Journal of the Botanical Research Institute of Texas* 6: 681-705.

Obbard, M.E. & Brooks, R.J. (1981). Fate of overwintered clutches of the common snapping turtle (*Chelydra serpentina*) in Algonquin Park, Ontario. *The Canadian Field-Naturalist* 95: 350-352.

Petokas, P.J. & Alexander, M.M. (1980). The nesting of

Chelydra serpentina in northern New York. *Journal of Herpetology* 14: 239-244.

Ratnaswamy, M.J., Warren, R.J., Kramer, M.T. & Adam, M.D. (1997). Comparisons of lethal and nonlethal techniques to reduce raccoon depredation of sea turtle nests. *The Journal of Wildlife Management* 61: 368-376.

Riley, J.L., Tattersall, G.J. & Litzgus, J.D. (2014). Potential sources of intra-population variation in the overwintering strategy of painted turtle (*Chrysemys picta*) hatchlings. *The Journal of Experimental Biology* 217: 4174-4183.

Russell, J.L., Hughes, D.F. & Meshaka, W.E., Jr. (2014). The red-eared slider, *Trachemys scripta elegans* (Wied, 1838), found in Westmoreland County, Pennsylvania. *Collinsorum*: *The Journal of Kansas Herpetology* 2-4: 19.

Schwarzkopf, L. & Brooks, R.J. (1987). Nest-site selection and offspring sex ratio in painted turtles, *Chrysemys picta*. *Copeia* 1987: 53-61.

Tesauro, J. & Ehrenfeld, D. (2007). The effects of livestock grazing on the bog turtle [*Glyptemys* (= *Clemmys*) *muhlenbergii*]. *Herpetologica* 63: 293-300.

Tinkle, D.W., Congdon, J.D. & Rosen, P.C. (1981). Nesting frequency and success: Implications for the demography of painted turtles. *Ecology* 62: 1426-1432.

Utech, F.H. (1999). Checklist of the vascular plants of Powdermill Nature Reserve, Westmoreland County, Pennsylvania. *Carnegie Museum of Natural History Special Publication* No. 20. Carnegie Museum, Pittsburgh, Pennsylvania, USA.

Wilson, G.L. & Ernst, C.H. (2005). Reproductive ecology of the *Terrapene carolina carolina* (eastern box turtle) in central Virginia. *Southeastern Naturalist* 4: 689-702.

Yntema, C.L. (1978). Incubation times for eggs of the turtle *Chelydra serpentina* (Testudines: Chelydridae) at various temperatures. *Herpetologica* 34: 274-277.

Accepted: 23 August 2017