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Maryland Department of Transportation

**Maryland Department of Transportation
STATE HIGHWAY ADMINISTRATION**

RESEARCH REPORT

**Effectiveness of Nest Site Restoration for the Endangered
Northern Map Turtle**

**Report 2: Use of Artificial Nesting Sites and Wildlife
Exclusion Fence to Enhance Nesting Success**

Research Team

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TOWSON UNIVERSITY

**FINAL REPORT
October 2016**

The contents of this report reflect the views of the author who is responsible for the facts and the accuracy of the data presented herein. The contents do not necessarily reflect the official views or policies of the Maryland Department of Transportation's State Highway Administration. This report does not constitute a standard, specification, or regulation.

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<p>16. Abstract</p> <p>The Northern Map Turtle, <i>Graptemys geographica</i>, is a Maryland state endangered species, found only in the lower Susquehanna River in Maryland. The only area where nests of this species are not heavily impacted by predators occurs in the town of Port Deposit. However, the Port Deposit nesting site is the location for a new environmental education center dedicated to the Susquehanna River and its animal and plant life, including the Northern Map Turtle. The plans for the environmental education center call for establishment of a secured nesting area for Map Turtles that will be surrounded by a wildlife exclusion fence that will both prevent disturbance of female Map Turtles while they are nesting and which will prevent turtles from reaching areas where they may be killed by traffic or harassed by humans. How Map Turtles will react to such a restriction to their nesting sites is unknown. Turtles could seek to evade the fence or abandon the area entirely. The objectives of this project were to (a) test how female Map Turtles reacted to a wildlife exclusion fence, (b) whether females would make use of a series of artificial nesting mounds to improve soil conditions, and (c) whether confining females to a limited areas resulted in higher levels of human disturbance.</p> <p>Although some females evaded the fence early in the nesting season, most nests were dug within the fence perimeter and disturbance by visitors was minimal. Nest success was not quite as high as in previous years, possibly a result of poor drainage conditions around the fence used. The first known predation event within the town limits was documented, as was the attitude of the public towards the turtle. Specific recommendations are made for improving the nesting area and working with the public to reduce disturbance to the turtles while nesting.</p>			
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EXECUTIVE SUMMARY

The Northern Map Turtle, *Graptemys geographica*, is a Maryland state endangered species, found only in the lower Susquehanna River in Maryland. Like many riverine turtle species, populations of map turtles in the US are threatened by commercial harvesting for the pet trade and by human recreational activities. Impacts from habitat modification and human recreation are of special concern for Northern Map Turtles in Maryland; flows of the lower Susquehanna River are influenced by generation from the Conowingo Hydroelectric Dam and the river below the dam is heavily used for recreational activities such as hiking, fishing, and boating during the spring, summer, and fall.

Studies funded by the Maryland Department of Natural Resources and Exelon Corporation from 2008-2012 showed that (1) there is a reproductively-active population of Northern Map Turtles in the lower Susquehanna River, both below and above the Conowingo Hydroelectric Dam, with most turtles concentrated in a 1.9 km linear area from the upriver end of Roberts Island to the downriver end of Spencer Island across from Susquehanna State Park; and (2) nesting occurs along relatively open areas on both in-river islands, along the banks of Octoraro Creek and Deer Creek, and in the town of Port Deposit from May-July, but most nesting areas are heavily disturbed by humans and most nests (up to 100% in some years) are destroyed by predators.

The 2008-2012 studies indicated that the only known site with consistently successful nesting in Maryland is in the town of Port Deposit, especially in the area surrounding Tomes Landing Marina. However, the Tomes Landing nesting site is far from optimal; turtles nesting at this site must often cross through a gravel parking lot with constant vehicular traffic to reach the actual nesting sites, and adult and hatchling turtles may become disoriented by human disturbance and move away from the river, towards Maryland Route 222. In addition, the soil in which the turtles are nesting is heavily compacted and turtles often abandon nest sites after unsuccessful nesting attempts.

Because of the high importance of the Tomes Landing nesting sites to the viability of Northern Map Turtles in Maryland, the Maryland Department of Transportation's State Highway Administration (SHA), the town of Port Deposit, the Maryland Department of Natural Resources, and Towson University (TU) formed a joint effort in 2011 to seek funding to rehabilitate the current nesting sites with more appropriate soil and an exclusion barrier to keep turtles away from areas with high foot and vehicular traffic. In addition, these agencies collaborated on the development of a plan to renovate the historic Gas House in Port Deposit as a combined research station and environmental education center.

The approved plans for the environmental education center call for establishment of a secured nesting area for Map Turtles in front of and along the side of the center. This rehabilitated nesting area will be surrounded by a wildlife exclusion fence that will both prevent disturbance of female Map Turtles while they are nesting and which will prevent turtles from reaching areas such as the Tome's Marina parking lot and MD Rte. 222, where turtles may be killed by traffic or harassed by humans.

How Map Turtles will react to these rehabilitated sites and to restriction to their nesting sites is unknown. Turtles could seek to evade the wildlife fence, ignore the better soil types, or abandon

the area entirely. Thus, the objectives of this project were to (a) test how female Map Turtles reacted to a wildlife exclusion fence, (b) whether females would make use of a series of artificial nesting mounds to improve soil conditions, and (c) whether confining females to a limited area resulted in higher levels of human disturbance. These data will be useful in establishing a set of “Best Practices” for future management of areas where human visitation via foot traffic impact threatened or endangered species.

Research Findings

As in past years, nesting of Northern Map Turtles in Port Deposit occurred in May, June, and July, with most nesting occurring between early June and early July. A total of 12 females were found attempting to nest during 2015, of which four nested successfully. One female successfully completed two nests, and one nest by an unknown female was identified by a town resident. Three additional nests, two laid by unknown females, were found with the help of local residents near the developed condominiums upstream of the Gas House site. The total of eight nests at Port Deposit in 2015 was comparable to the numbers seen in 2013 (eight nests) and 2014 (seven nests).

Of the eight nests in 2015, four had at least some hatching success. One of the five nests at the Gas House site was attacked and destroyed by an unknown predator (possibly a dog or a coyote) on September 24, 2015. This was the first recorded instance of a predator destroying a nest at Port Deposit. Of the remaining four nests at the Gas House site, two had high hatching success, producing 8 and 11 hatchlings, respectively. Hatchlings from the third nest evaded the protective cage that was placed on the nest. The fourth nest produced only a single viable hatchling. Of the three nests at the condominiums, two produced hatchlings (7 and 13, respectively) and one nest was unsuccessful. A total of 30 hatchlings were captured emerging from nests during this study year. Mean sizes of these hatchlings were not different from those seen in 2014, but were smaller than those seen in 2013.

Observations from a wildlife blind (i.e. a concealed shelter for viewing wildlife) located adjacent to the wildlife fence indicated that some turtles attempted nesting outside the fence perimeter, especially early in the nesting season. Some females were observed entering the enclosed site and abandoning their attempt after walking along the perimeter of the fence and not being able to move beyond it. However, the only documented nesting at this site did take place within the area enclosed by the wildlife fence. Of the five nests constructed within the fence perimeter, three were built on or just adjacent to the nesting mounds that were placed to encourage females to nest in better soil conditions. However, two nests were built along the fence barrier itself. In addition, it became apparent that the current grade of the terrain does not sufficiently shed rainwater from the area surrounded by the temporary exclusion fence. Pooling of water from large storms could lead to inundation of nests within the site. It is recommended that the final site be graded or that the necessary steps be taken to ensure proper drainage of the site before final construction is completed.

While some females abandoned nesting attempts, observations made from the wildlife blind at the Gas House showed little evidence that turtles could not complete nesting due to human disturbance. Although some visitors did ignore them, the majority obeyed the signs posted along

the fence perimeter asking that people avoid entering the site. In addition, although some local residents who were aware of the project avoided disturbing the site, there were some visitors that admitted to purposefully visiting in hopes of viewing the turtles up close. Discussions with visitors indicated that while the majority were aware of the presence of the Map Turtle and were supportive of conservation efforts, a minority of residents were either neutral regarding the turtle project or were outwardly antagonist to the monitoring and conservation programs. Reaching out to this minority will be an important challenge as the environmental education center is developed.

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List of Acronyms and Abbreviations

- 1) **CITES**: The Convention on International Trade in Endangered Species of Wild Fauna and Flora
- 2) **GPS**: Global Positioning System
- 3) **JMP**: Statistical software used for data analysis
- 4) **MD-DNR**: Maryland Department of Natural Resources
- 5) **R**: Statistical software used for data analysis
- 6) **SHA**: Maryland Department of Transportation's State Highway Administration
- 7) **SYSTAT**: Statistical software used for data analysis
- 8) **TU**: Towson University

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CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

The Northern Map Turtle, *Graptemys geographica*, is a state endangered species, found only in the lower Susquehanna River in Maryland. Like many riverine turtle species, populations of map turtles in the US are threatened by commercial harvesting for the pet trade (Klemens and Thorbjarnarson, 1995; Schlaepfer et al., 2005), habitat modifications (Moll, 1980; Pluto and Bellis, 1986; Jones, 1996; Mitchell and Klemens, 2000; Moll and Moll 2004, Bennett et al., 2009), by-catch from commercial harvesting (Midwood et al., 2015), and by human recreational activities (Moore and Seigel, 2006; Bulte et al., 2010). All populations in the US are listed under Appendix II of CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora). Impacts from habitat modification and human recreation are of special concern for Northern Map Turtles in Maryland. Flows of the lower Susquehanna River are influenced by generation from the Conowingo Hydroelectric Dam and the river below the dam is heavily used for recreational activities such as hiking, fishing, and boating during the spring, summer, and fall (summarized in Smith et al., 2008, 2009, 2010).

Given the potential impacts of the Conowingo Hydroelectric Dam and associated human recreational use of the river, the Maryland Department of Natural Resources (hereafter, MD-DNR) and Exelon Corporation funded a study by Towson University (TU) on the status and ecology of Northern Map Turtles in Maryland starting in 2008. These data showed that (1) there is a reproductively-active population of Northern Map Turtles in the lower Susquehanna River, both below and above the Conowingo Hydroelectric Dam, with most turtles concentrated in a 1.9 km linear area from the upriver end of Roberts Island to the downriver end of Spencer Island across from Susquehanna State Park; (2) that the diet of turtles in the river is highly gender and size-specific (Richards-Dimitrie et al, 2013), and (3) nesting occurs along relatively open areas on both in-river islands, along the banks of Octoraro Creek and Deer Creek, and in the town of Port Deposit from May-July, but most nesting areas are heavily disturbed by humans and most nests (up to 100% in some years) are destroyed by predators.

The 2008-2012 study indicated that the only known site with consistently successful nesting in Maryland is in the town of Port Deposit, especially in the area surrounding Tomes Landing Marina. All five nests found in this area in 2011 were successful, compared with a virtual 100% predation or failure rate for nests found at Octoraro Creek and on islands in the river (Seigel et al., 2011). However, the Tomes Landing nesting site is far from optimal; turtles nesting at this site must often cross through a gravel parking lot with constant vehicular traffic to reach the actual nesting sites, and adult and hatchling turtles may become disoriented by human disturbance and move away from the river, towards the roadway, Maryland Route 222. In addition, the soil in which the turtles are nesting is heavily compacted and turtles often abandon nest sites after unsuccessful nesting attempts.

Because of the high importance of the Tomes Landing nesting sites, SHA, the town of Port Deposit, the MD-DNR, and TU formed a joint effort in 2011 to seek funding to rehabilitate the current nesting sites with more appropriate soil and an exclusion barrier to keep turtles away from areas with high foot and vehicular traffic. In addition, these agencies collaborated on the

development of a plan to renovate the historic Gas House in Port Deposit as a combined research station and environmental education center.

To better study the rehabilitation project and increase its chances for success, Towson University conducted detailed studies of the nesting ecology of Northern Map Turtles in the vicinity of Port Deposit from 2013-2014. The primary objective of this project was to determine whether rehabilitation of the historic nesting areas in the immediate vicinity of the Tomes Landing Marina will result in enhanced utilization by nesting Northern Map Turtles and whether the nesting success of these turtles is also increased as a result of the rehabilitation project. Initially, the research plan called for one year of data before the establishment of the environmental education center and one year of data after the center was constructed. However, delays in obtaining funding and permits required modifications to this research plan. After consultation with SHA, the data collected from 2013-2014 focused on pre-construction nesting ecology (Seigel et al. 2015). Although construction of the environmental center is not expected until July 2016, research in 2015 used an experimental approach to (a) construct a facsimile of the permanent wildlife exclusion fence¹, (b) modify the existing available nesting sites by adding multiple nesting mounds made of sand or soil, and (c) make detailed observations of nesting behavior and how Map Turtle react to the presence of humans in the vicinity of the Gas House. These data were useful in establishing a set of “best practices” for future management of areas where road or foot traffic impact threatened or endangered species.

¹ Wildlife Exclusion Fence: Highway “silt” fence erected along perimeter of Tome Gas House property that served to prevent nesting female Map Turtles from leaving the nesting area established for that purpose

CHAPTER 2: RESEARCH OBJECTIVES AND METHODOLOGY

2.1 Establish temporary wildlife exclusion fence and artificial nesting mounds

The design for the environmental education center calls for (a) rehabilitation of the highly compacted soils available for nesting and (b) a permanent wildlife exclusion fence established along the perimeter of the Tome Gas House that will preclude nesting Map Turtles from leaving the primary nesting grounds. How turtles will react to this barrier and modified soil types is not known. By installing a temporary exclusion fence and a series of nesting “mounds”, the researchers were able to collect data on the behaviors of nesting female Map Turtles relative to this modified nesting environment and made predications on how Map Turtles will react to the permanent modifications in 2017. To begin the process of installing the temporary exclusion fence and creating improved the nesting area, the research team first created a series of discrete mounds (each 4’ high x 4’ diameter [30 cm x 150 cm]) within the area that will eventually be inside the permanent wildlife fence. The concept for using raised areas is based on observations of Map Turtles elsewhere which suggest that elevated areas are preferred for nesting (unpublished observations). Two of the mounds were made of sand and two of organic-rich soil (see Fig. 2-1). This allowed us to both compare nesting effort between the mounds and other sites within the enclosed nesting grounds and between soil types.



Figure 2.1. Close-up photograph of nesting mounds

Instead of a permanent wildlife fence, the research team installed a temporary fence made of highway-grade “silt” fencing. A powered trencher was used to dig a 6” deep trench and the research team then laid 36” high silt fencing into the trench, with wooden stakes at 5’ intervals (see Fig. 2-2).



Figure 2.2. Photograph of installation for trench for wildlife exclusion fence

The completed temporary fence with enclosed nesting mounds is shown below in Figure 2-3.



Figure 2.3. Photograph of nesting beach at Port Deposit following establishment of nesting mounds and wildlife exclusion fence

2.2 Determine timing and duration of nesting season

These data indicated whether the installation of the wildlife exclusion fence and associated nesting mounds impacted the timing and duration of the nesting season. Understanding what changes in the behavior of the turtles might result from the installation of the fence and the nesting mounds is critical to appropriate management actions. For example, should turtles avoid the enclosed nesting areas and nest elsewhere in Port Deposit, this would be viewed as a negative impact.

In 2015, the research team made observations on timing and behaviors during nesting at the newly-enclosed nesting grounds via direct observation from a wildlife blind established at the downstream corner of the Gas House perimeter (see Fig. 2-4). Time of day, duration of the nesting foray, exact nest location, and environmental conditions (air temperature, relative humidity, cloud cover, wind speed and direction) were recorded for all turtles seen nesting. If a female was disturbed while nesting, the source and timing of the disturbance was recorded. Once nesting was completed, the female was captured, processed as indicated below, and released at the site of capture.



Figure 2.4. Photograph of wildlife blind (at red arrow) used to collect data on nesting Map Turtles in 2015. The blind can be seen in the front right corner of the Gas House. Vegetative growth on the nesting grounds can also be seen (inside red circles) in this photo.

All turtles were measured for carapace and plastron (i.e. top and underside of the shell) length using a tape measure or tree calipers, accurate to ± 5 millimeters (see Figure 2-5). Mass was recorded with a portable spring balance, accurate to ± 5 grams (see Figure 2-6).



Figure 2.5. Using calipers to measure carapace of hatchling



Figure 2.6. Measuring turtle's mass on portable spring balance

Gender was determined based on the size of the tail and the position of the vent (i.e. the opening on the underside of the tail) in relation to the rear edge of the plastron. (see Figures 2-7, 2-8 and 2-9)



Figure 2.7. The map turtle gets its name from the pattern on its shell that resembles the contour lines on a map. Hatchlings showing plastron with “map”.



Figure 2.8. Adult map turtle with a clear plastron.



Figure 2.9. Photograph of Adult Northern Map Turtles. Adult male turtle at top of photo. Adult female below.

All unmarked turtles were given an individual mark by notching or drilling marginal scutes (Ernst et al., 1974) (see Fig. 2-10). All adults were released at the site of capture within one hour. These procedures were approved by the Animal Care Committee at TU.

Carapace

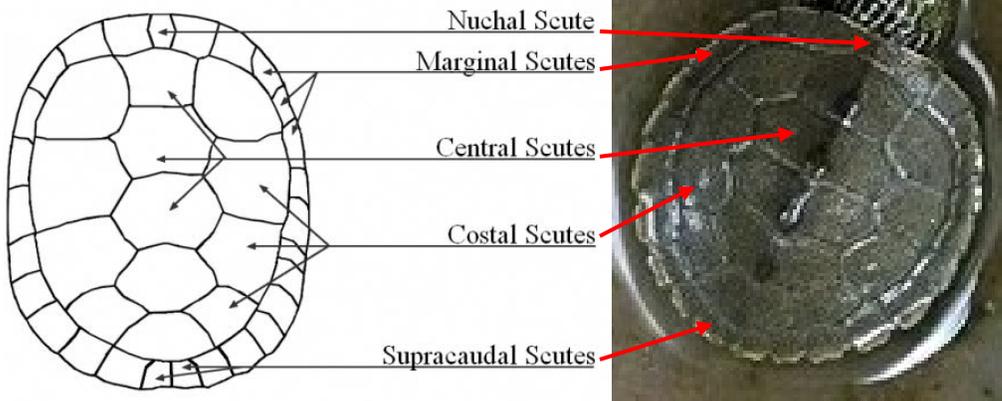


Figure 2.10. Northern Map Turtles scutes (scales)

2.3 Determine the spatial distribution of nests at the Tomes Landing site after the rehabilitation of the nesting areas

This objective was designed to compare site utilization between pre-rehabilitation and post-rehabilitation time periods. The nesting sites used by Map Turtles prior to the rehabilitation of the soils were generally along the chain link fence separating the Gas House from the adjacent railroad track, and some turtles moved to the opposite side of the chain link fence in order to nest (see Fig. 2-11). This exposed nesting turtles to possible human harassment and being run over by vehicular traffic. Testing whether the wildlife exclusion fence reduces the ability of the turtles to nest in such exposed areas is clearly critical to the appropriate management of this population.

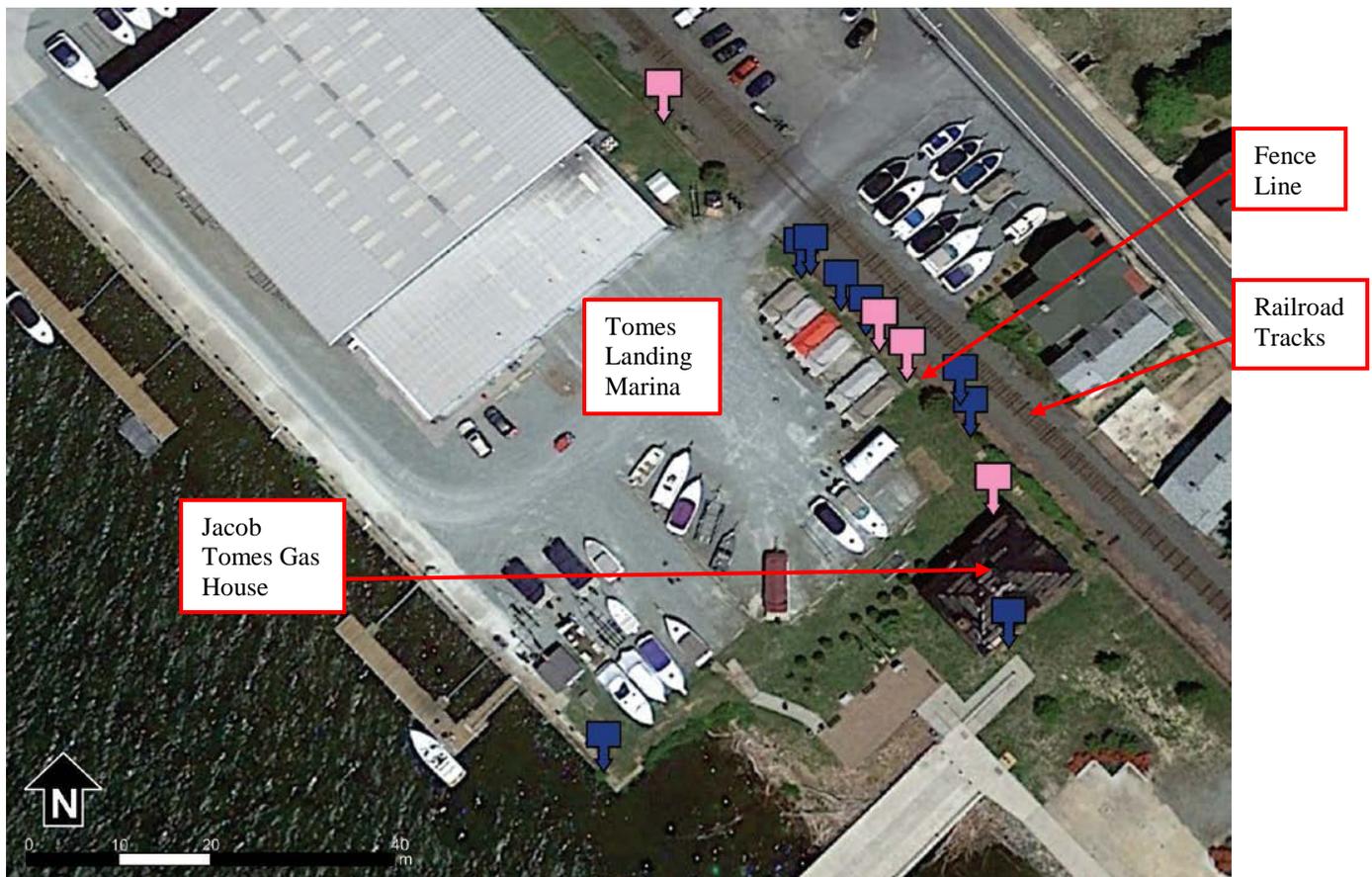


Figure 2.11. Original layout of turtle nesting sites (2013 – blue markers and 2014 – pink markers)

In 2015, TU staff collected data on nest site selection after rehabilitation of the nesting area via installation of the nesting mounds. Once females completed nesting (see Figure 3-1A), the nest was located and marked with a flag about 0.5 meters from the nest site (to avoid predators using the flag as an indicator of the location). All predated and intact nest localities were recorded using a hand-held GPS with post-processing accuracy of 1-11 meters (> 90% localities at < 3 meter accuracy). The numbers and spatial distribution of nests in 2013-2014 (pre-rehabilitation) were compared with those in 2015 to determine how females responded to modification of the

nesting area. Because females had been marked in previous years, we were able to identify any females using the Jacob Tomes' Gas House that had not been previously captured at that site.

2.4 Responses to wildlife exclusion fence and habitat rehabilitation

The research team wanted to identify how nesting Map Turtles reacted to encountering the combination of the wildlife exclusion fence and new soil types. This reaction was an essential component to predicting whether the construction of the environmental education center will have any negative effects on Map Turtle reproductive success. Map turtles reacted in the following three ways: (1) reached the wildlife fence and returned to the water without nesting, (2) reached the wildlife fence and nested along the fence line, ignoring the nesting mounds, and (3) reached the wildlife fence and nested in one of the newly-established nesting mounds. If the females selected the first option, then the construction of the environmental education center could have negative impacts on this segment of the Map Turtle population.

Using a combination of direct visual observations from a wildlife blind and by using automated video cameras, the research team documented the behaviors of nesting Map Turtles when they encounter both the wildlife exclusion fences and the nesting mounds. Specific attention was paid to whether females (a) failed to nest – found one indication, (b) nested on the newly-established nesting mounds – found three nests, and (c) nested elsewhere within the perimeter of the wildlife fence – found two nests that were near the fence line.

2.5 Human disturbance and reactions of visitors

This objective was designed to determine if habitat modifications of existing nesting areas results in changes in nesting success and, consequently, population viability. Information from nesting after rehabilitation of the nest sites was collected.

The wildlife exclusion fence concentrated nesting activity in a much smaller area than has previously been the case in Port Deposit. This means that the foot traffic in the area may have a higher probability of disturbing turtles while they are nesting. The objective was designed to determine how commonly humans disturb nesting activities. Clearly, if nesting females are unable to complete nesting activities as a result of human interference, this would be viewed as a negative impact on the population and would negate the value of the exclusion fence. In addition, since the research team encountered members of the public frequently while using the wildlife blind adjacent to the nesting grounds, information on how the public reacted to the protection of the nesting area was recorded.

The research team calculated the percent of occurrences that nesting Map Turtles abandon their nesting attempts as a result of disturbance by humans and compared these rates to those seen in years when no wildlife fence has been installed. In addition, while observing the nesting beach from the wildlife blind, the researchers were sufficiently camouflaged from the view of the public to allow for recording of uncensored comments made about the project. The research team recorded the approximate age of the commenter, gender, the spoken comment(s), and the connotation with which the comment was made.

2.6 Determine the nesting success at the Tomes Landing after the rehabilitation of the nesting areas

This objective was designed to determine if habitat modifications of existing nesting areas resulted in changes in the nesting success and, consequently, population viability. Hatchlings were collected after the rehabilitation of the nesting site.

As with spatial distribution of nests, it was critical to understand whether the proposed rehabilitation of the nesting areas results in greater recruitment to the population, as measured by nest site success (the proportion of nests that hatch successfully). After recording the locations of nests as noted above, nests will be monitored 4-5 times per week for signs of predation (e.g., a dug up nest chamber with egg shells scattered at the nest site). After approximately 90 days, each intact nest was surrounded by a close-topped wire screen mesh cage that will allowed hatchlings to emerge but not leave the vicinity of the nest. The research team monitored the fate of each nest 1-2 times per week until late fall (early November) and then every two weeks from November through March, then twice weekly from April until hatching. If nests had not emerged by early June 2016, they were carefully excavated by hand to determine the fate of the eggs and release any hatchlings that had become entombed.

2.7 Determine the incubation period and timing of nest emergence both before and after the rehabilitation of the nesting areas

Baseline data from pre-rehabilitation nests was used to see if habitat modifications resulted in changes in incubation time, temperature, and timing of emergence of hatchlings. Information from nesting after rehabilitation of the nest sites was identified.

Most (but not all) nests of Northern Map Turtles “overwinter in the nest,” i.e., the hatchlings actually emerge from their eggs after about 60-80 days of incubation, then remain quiescent in the underground nest chamber until the following spring (Nagle et al., 2004). Data collected by the research team from 2009-2011 suggested that spring emergence is the rule in the Susquehanna River population, with most emergence occurring from late April through mid-May. The factors that determined how long hatchlings remain in the nest and what triggers hatchling emergence remains poorly understood. Since the timing of emergence may have important correlation with hatchling survival, a better understanding of the environmental factors regulating incubation periods and hatchling emergence is important to the viability of this population

Using the same nests monitored for survival noted above, the research team placed temperature-sensitive data loggers (‘iButtons²’) on selected nests to monitor incubation temperatures every 30 minutes from egg-laying through hatchling emergence (see Fig 2-12). These data were compared with data from nests constructed after rehabilitation of the nesting areas, to see if nests constructed in 2015 have a different thermal profile from nests constructed in prior years.

² iButtons: Miniature temperature-sensitive data loggers used to record nest temperatures of turtles



Figure 2.12. Photograph of “iButton” (left) used to monitor nest temperatures of Northern Map Turtles. A quarter is shown on the right to indicate scale.

2.8 Statistical Analysis.

The collected data were analyzed using JMP for Windows, SYSTAT (ver. 13) or R. Data for morphometric and distance comparisons. All data were first tested for assumptions of normality using a Kolmogorov-Smirnov one-sample test of the residuals of the analyzed data. Equality of variances was tested using a Levene’s test. If violations of assumptions were found, data were first transformed to natural logs and then re-tested. If violations were still found, a non-parametric test was used for further analysis. Frequency data were tested using a contingency table analysis.

CHAPTER 3: RESEARCH FINDINGS AND DISCUSSION

3.1 Establish temporary wildlife exclusion fence and artificial nesting mounds

Materials for the nesting mound were provided by two companies; York Buildings Products Company provided “cone sand” and Rob South Landscaping provided the same amount of friable (organic) soil. Each mound was 4 x 4’ in size and 3’ high for a total of about 48 cubic feet. The mounds were established in pairs near the rear edge of the available nesting site (see Fig. 3-3). Mound installation was completed by May 16, 2015, well before the onset of the nesting season

Establishing the wildlife exclusion fence proved to be more difficult than expected, due to the highly compacted and rocky nature of the soil types in the vicinity of the Gas House. Only the use of a gas-powered trencher allowed the research team to dig a trench of sufficient depth to install the silt fence (see Fig. 3-2). Once completed, the temporary fence was equipped with signs every 20’ indicating that this was an active nesting site for Map Turtles and requesting that the site not be disturbed. Fence installation was completed on May 22, 2015, just before the onset of the nesting season.

3.2 Determine timing and duration of nesting season

Nesting activity in 2015 was recorded between May 22nd and July 16th, with a total duration of 56 days. In 2013-2014, nesting activity at this site was recorded as early as May 31st and as late as July 26th, with the duration of the season lasting between 46-54 days. Thus, there were no substantive differences in the timing of the nesting season between 2015 (after fence and nesting mound installation) and the dates seen in previous years.

A total of 12 females were found attempting to nest during 2015, of which four were known to nest successfully. One female successfully completed two nests and one nest by an unknown female was identified by a resident from town. Three additional nests, two laid by unknown females, were found with the help of local residents near the developed condominiums upstream of the Gas House site. Thus, the research team located a total of eight nests during 2015. The numbers of nests found in 2015 is consistent with the numbers seen in previous years at this site whereas the numbers of females found nesting in 2015 was somewhat higher compared with previous years (see Table 3.1). The higher number of females found in 2015 may reflect the level of effort focused on Port Deposit that year or an increase in the number of females using the site. Since the research team could not sample the nesting sites seven days a week, the differences in these values among years could represent a combination of sampling error and stochastic variation. Thus, no conclusion as to possible increases in nesting activity over time can be drawn from these data. However, they are a useful benchmark for long-term trends in nesting effort at Port Deposit.

Table 3-1: Numbers of Map Turtle females found nesting and number of nests located from 2013-2015 in Port Deposit.

Year	# of nesting females	# of nests
2013	10	8
2014	6	7
2015	13	8

3.3 Determine the spatial distribution of nests at the Tomes Landing site before and after the rehabilitation of the nesting areas.

Nesting occurred in two primary areas in Port Deposit with one in the immediate vicinity of the Gas House and another upstream of the Gas House near the developed condominiums (see Figures 3-1A and 3-1B, respectively).

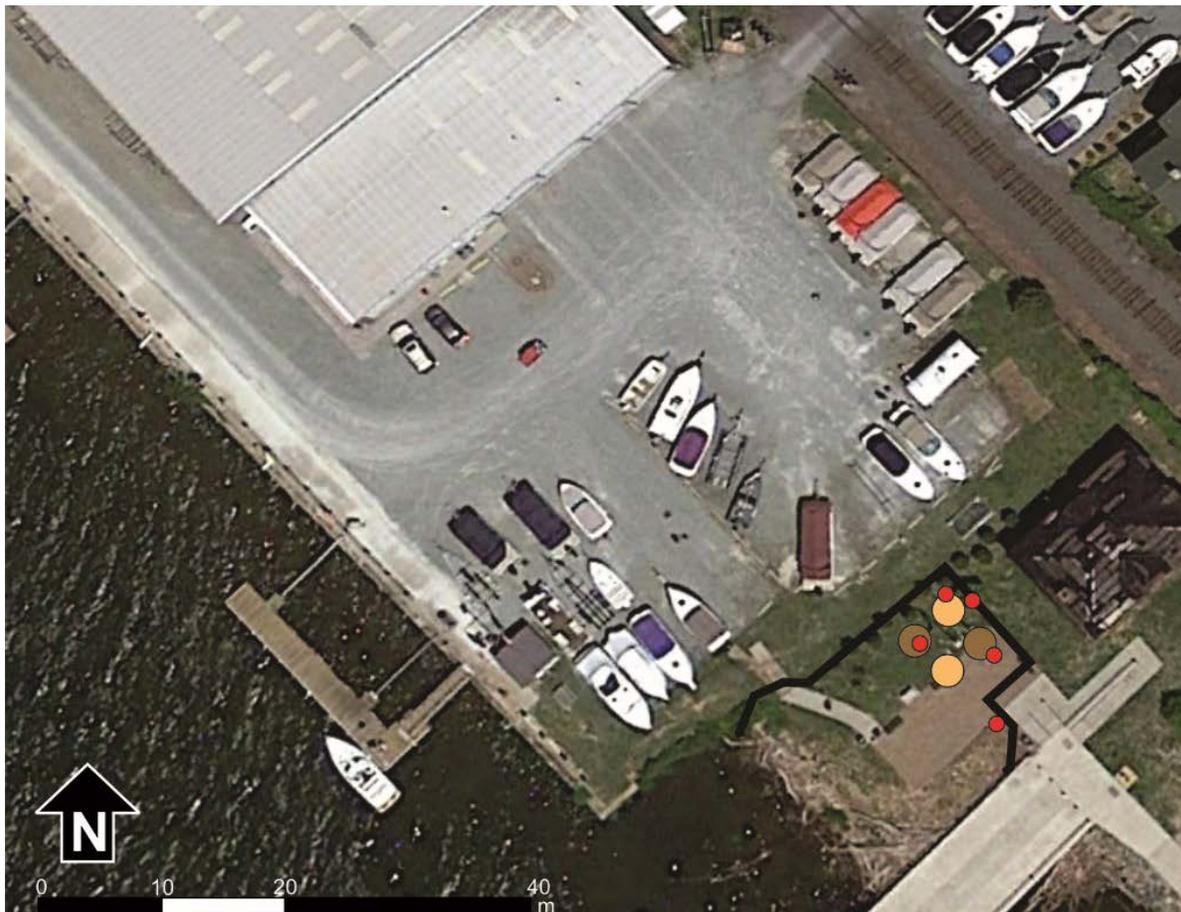


Figure 3.1A. Map showing locations of all Map Turtle nests in Port Deposit during 2015 (red circles) near the Gas House. The nesting mounds established at the Gas House site are shown by yellow and brown circles.

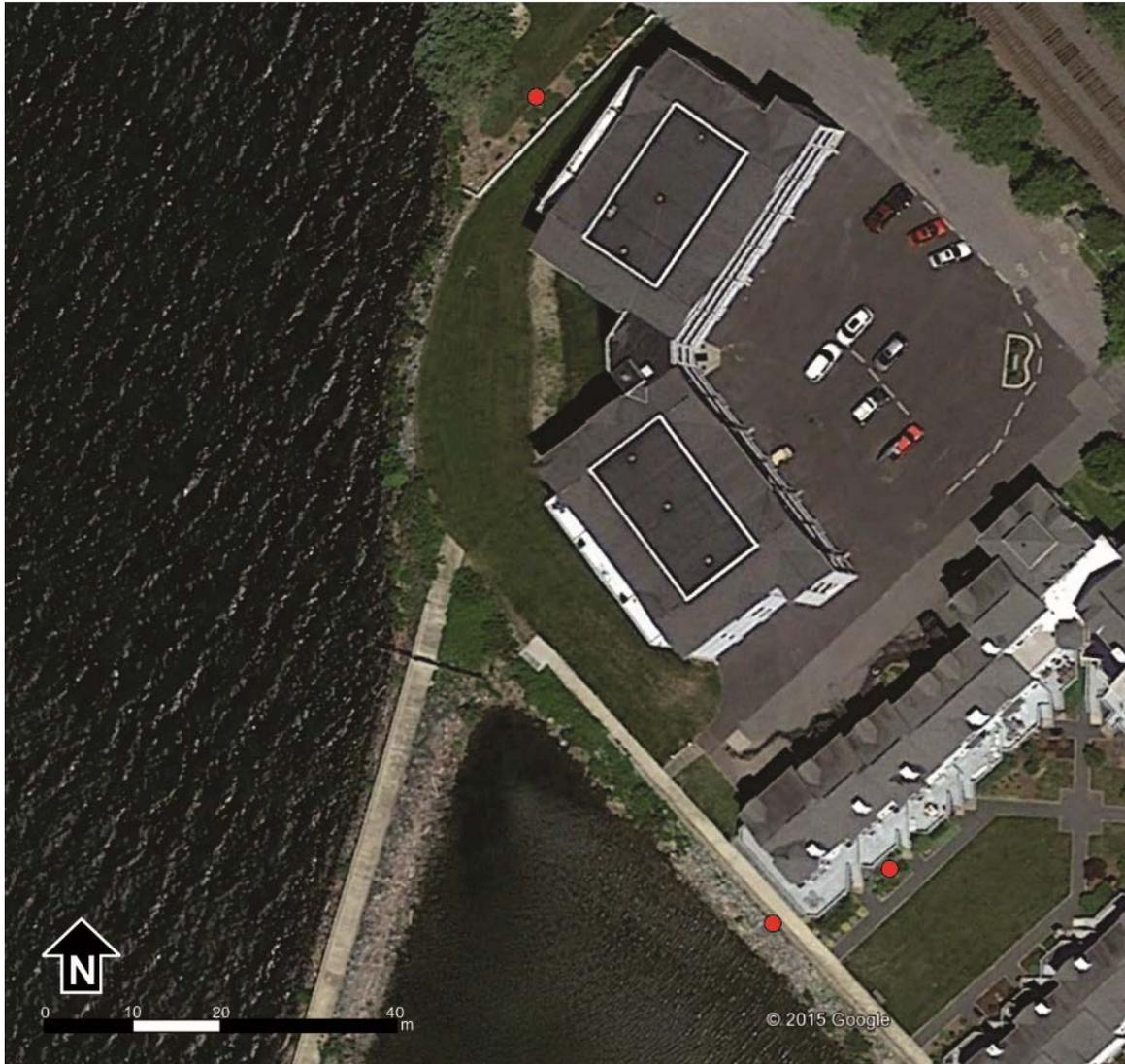


Figure 3.1B. Map showing locations of all Map Turtle nests in Port Deposit during 2015 (red circles) near the upstream condominiums.

Compared with 2013-2014, turtles nested much closer to the water, as nesting at the Gas House was constrained by the presence of the silt fence. As shown in Table 3.2, completed nests at the Gas House in 2015 were between 4.3-23.2 m from the river's edge, whereas nests in previous years were located as far as 60 m from the river.

Table 3-2: Distance (in meters) between nest sites and the closest entrance to the Susquehanna River for Northern Map Turtles at Port Deposit from 2013-2015.

2013	2014	2015
1.06	62.4	19.0
31.6	7.6	19.6
47.9	14.7	22.0
50.4	41.9	22.1
59.7	59.7	23.2
53.8	40.5	4.3
57.4	60.3	9.5
52.9		18.0
Mean = 44.3 ± 6.88 m	41.0 ± 8.43 m	17.2 ± 2.38 m

Means shown + 1 SE. There were significant differences among the three years, with 2015 having the shortest distances from the water (Kruskal-Wallis test = 6.35, P = 0.04)

3.4 Responses to wildlife exclusion fence and habitat rehabilitation

Both direct visual observations and the location of several incomplete nests outside the perimeter of the wildlife fence indicated that the initial behavioral response of the turtles was to avoid both the enclosed nesting ground and the associated soil mounds. Figure 3-2 shows a photograph of such a nest, one of eight attempts found in the mulched soils approximately 14 m downstream of the enclosed nesting grounds.



Figure 3.2. Photograph of incomplete nest (inside red circle) found outside the perimeter of the wildlife fence early in the season (May 27th 2016).

However, most of these incomplete nests (five of eight) were seen only in the early part of the nesting season, primarily in late May. The remaining three nesting attempts were found on a single day in late June. The first viable nests (those with eggs and which were completed) were built inside the perimeter of the wildlife fence starting on May 28th. Of the five complete nests located within the wildlife fence, two were dug in or partially in the soil mounds and one in the sand mound. One of the three nests was completely within the soil substrate of one of the mounds and two were in the underlying substrate but with the perimeter of the nest mound. Of the remaining two nests, one was built along the silt fence within 1 m of a soil mound and the other built along the silt fence well away from the mounds (see Fig. 3-1A).

Although these data are clearly limited, the available information suggests that Map Turtles will (a) utilize a nesting ground that is enclosed by a wildlife fence and (b) make at least some use of artificial nesting mounds for nest excavation. However, several cautionary points need to be made. First, the wildlife exclusion fence will not prevent nesting from occurring outside the fence perimeter, as turtles can evade the fence, especially just downstream of the Gas House. Second, although the placement of the soil and sand nesting mounds did indeed attract females to nest there, they covered only a very small portion of the possible nesting sites. Thus, true rehabilitation of the nesting grounds will require a substantial effort to place a larger number of nesting mounds within the fence perimeter. In addition, because 40% of the nests in 2015 were placed immediately along the fence line, soil conditions should be improved along the fence line as well. A specific recommendation would call for sandy soil to be placed along the fence line at a depth of at least 24" and extending at least 24" from the fence line into the interior of the

nesting grounds. This would allow females nesting along the fence line access to greatly improved soil condition compared with the current soil at the site.

3.5 Human disturbance and reactions of visitors

Of 15 nesting attempts seen in 2015 by the research team, five were affected by human disturbance. This disturbance rate can be compared to the 81% rate of disturbance seen by Moore and Seigel (2005) for the related species, *Graptemys flavimaculata*. Unfortunately, these data are based on a year in which two key elements for 2017 and beyond were not present; (a) the much higher levels of foot traffic expected to be attracted to the nesting areas by the presence of the completed environmental education station and (b) the permanent wildlife fence, which is projected to be 6' high and be equipped with a visual barrier to limit the ability of turtles and humans to see each other.

A total of 181 comments were collected that expressed the public's sentiment towards the turtles and the project being done. There were 51.4% positive comments, 42.5% neutral comments, and 6.1% negative comments. Many of the positive commenters expressed strong enthusiasm and interest in the turtles, the nesting site, and the planned renovation of the Gas House. The public was eager to ask about the habits of the turtles, when the hatchlings would emerge, and whether any turtles had been observed on a given day. Comments like "Any turtles today?", "Awesome," and "Cool" were frequently-repeated phrases, as well as wishing the researchers luck with the study and thanking them "for all that [they] do". In addition to the supportive nature of the town, people also expressed a general interest regarding what was being done. These comments did not express the enthusiasm of the positive comments so they have been described as neutral. The research team received many questions asking for information, as well as several instances of people sharing personal stories of the turtles they had seen in and out of town.

The negative comments that were noted were made indirectly 72.7% of the time, and directly to a researcher 27.3% of the time. One of the two direct negative comments came from a community member who was of the opinion the research should be done as volunteer work. The second direct and remaining indirect comments were of little content besides profanity or general dislike of turtles. In two instances the commenters who made negative indirect remarks about the project took notice of the wildlife blind, and, seemingly out of embarrassment of being overheard feigned an interest in the project.

The comments that were observed from the wildlife blind reflect a generally positive attitude from the community towards the Map Turtle's presence in Port Deposit and the steps being taken towards its conservation. Some members of the community expressed concern for the project suggesting larger signs so that people were more aware of the site, and one member suggested posting a bulletin for the condo residents to become more involved in sighting turtles attempting to nest. Additionally, there were 13 documented instances of community members reaching out to educate other members of the public about the turtles and the nesting beach, so far as to direct them to the wildlife blind if they wanted to learn more about what was going on. One man was even documented as commenting that he believes the turtle project is bringing the community closer together.

3.6 Determine nest success at the Tomes Landing site after the rehabilitation of the nesting areas

Of the eight nests constructed in 2015 and were monitored through spring 2016, four had at least some hatchlings emerge. Of the five nests constructed within the perimeter of the wildlife fence, only three had successful emergence. One nest was depredated on September 24, 2015, possibly from a dog or a coyote. One other nest did not experience any natural emergence, and had to be dug up by the research team on June 11, 2015. This nest produced only a single live hatchling, which did not appear to be viable outside of the nest environment. Thus, only three of the five nests produced multiple live, viable hatchlings in 2015. This stands in contrast to findings from previous years, where the very large majority of nests produced multiple, viable hatchlings.

Given the small sample size and that the data are from a single year, it is difficult to attribute any biological significance to the relatively low hatching success in 2016. However, two issues are worth raising; first, direct observations at the site made it apparent that the current grade of the terrain does not sufficiently shed rainwater from the area surrounded by the temporary exclusion fence. Pooling of water from large storms led to inundation of some nests within the site, possibly reducing survival of eggs within such nests. It is recommended that the final site be graded or that the necessary steps be taken to ensure proper drainage of the site before final construction of the environmental education center is completed. Second, the fact that the research area experienced the first predation on a nest in Port Deposit shows the need to ensure the security of the wildlife exclusion fence during the nesting season in 2017 and beyond.

Table 3.3 shows that there were strong differences in four measurements of hatchling body size among years 2013-2016, with all measurements of body size being largest in 2013 and smallest in 2016. There has been a pattern for smaller hatchling sizes between 2013 and 2016, with each year after 2013 showing smaller sizes. This trend is puzzling and is difficult to explain. Possible causes include (a) smaller females laying eggs among later years, (b) females allocating less energy to egg size among years, or (c) changes in incubation conditions. Sufficient data to test these possibilities are lacking.

Table 3.3: Mean sizes of Northern Map Turtle hatchlings at Port Deposit from 2013-2016.

Year	Body Mass	Carapace Length	Min Plastron Length	Max Plastron Length
2013 N = 53	6.99 ± 0.232	32.22 ± 0.371	28.7 ± 0.271	29.48 ± 0.229
2014 N = 40	6.18 ± 0.192	30.49 ± 0.303	27.33 ± 0.288	27.93 ± 0.293
2015 N = 35	6.1 ± 0.118	29.8 ± 0.246	27.1 ± 0.184	27.6 ± 0.175
2016 N = 33	6.0 ± 0.115	29.7 ± 0.233	27.0 ± 0.173	27.5 ± 0.163
Kruskal-Wallis Test	16.4; P < 0.001	33.7; P < 0.001	30.2; P < 0.001	33.3; P < 0.001

Lengths in millimeters, mass in grams. Means are shown ± 1 SE. Differences between years tested using a non-parametric Kruskal-Wallis test due to severe non-normality of the data (uncorrected by log-transformations).

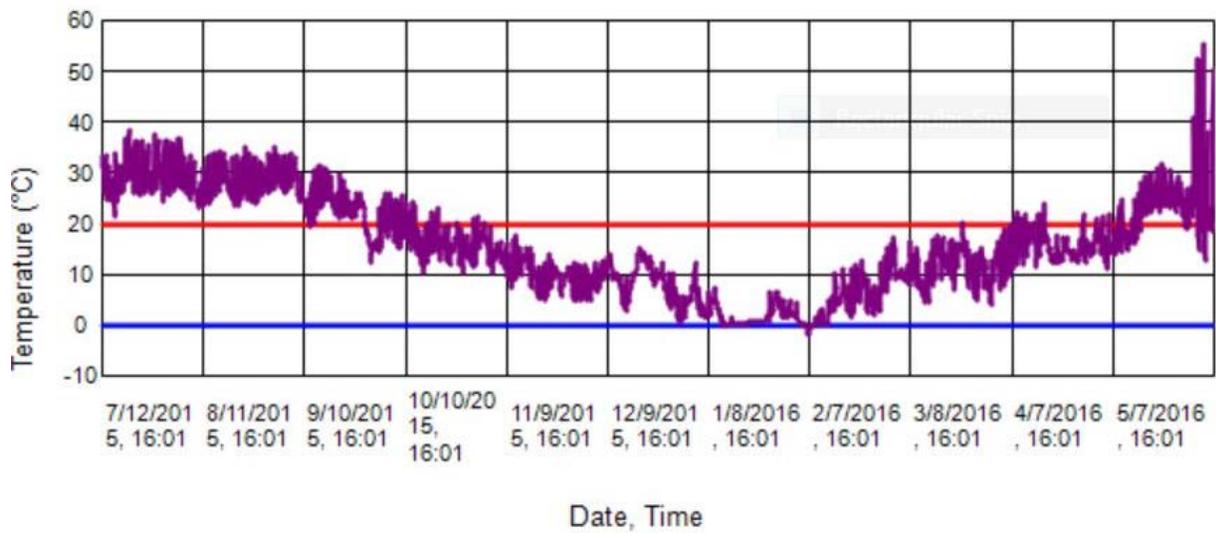
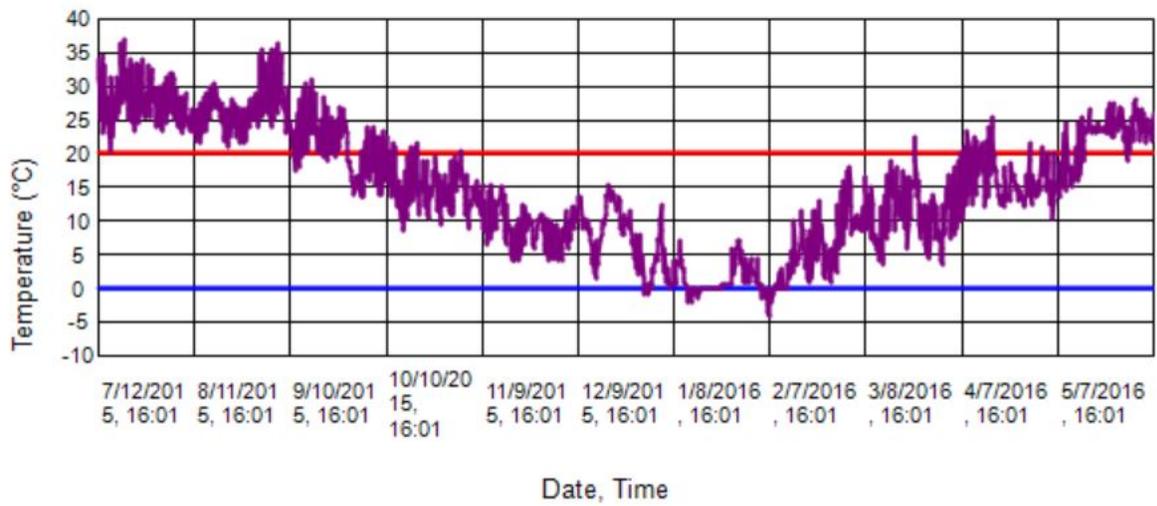
3.7 Determine the incubation period and timing of nest emergence both before and after the rehabilitation of the nesting areas

All nests of Northern Map Turtles in this population overwintered in the nest, i.e., hatchlings in nests constructed in summer 2015 emerged in spring 2016. Only one exception to this pattern has ever been seen at this site, when a clutch of eggs laid in June 2013 emerged in late August of the same year. The research team did not see a repeat of this event in 2015-2016.

For the three viable nests that were monitored in 2015-2016, the incubation period was 315-335 days, with an average of 324.7 ± 5.8 days. This compared to a mean of 327 ± 15.7 days seen in 2013-2015. Obviously, small sample sizes limit any statistical inferences, but no major differences seem apparent between pre and post-rehabilitation incubation periods.

A typical nest temperature profile, as measured by the iButtons, for two nests constructed in 2015 and which hatched in 2016 are shown in Figure 3-3. The temperature profile data collected for nests constructed in 2013-2014 are quite similar to nests constructed in 2015 and no substantial differences were seen between years, although sample sizes are small.

Figure 3.3. Graph of nest temperatures experienced by Map Turtles nesting in rehabilitated nest sites in 2015 at the Tome Gas House.



CHAPTER 4: CONCLUSIONS AND BEST PRACTICES

The basis of this study was to compare data on the nesting ecology of Northern Map Turtles from before and after rehabilitation of the nesting grounds. Although sample sizes for post-rehabilitation nesting are small, certain conclusions can be drawn at this time:

- 1) The nesting period for this population varies only slightly among years, commencing in late May or very early June and ending from mid to late July. A “safe” period when construction or other human activities should be curtailed or eliminated would be May 20th - July 25th.
- 2) The number of nests at Port Deposit also varies only slightly each year, from a low of four to a high of 10 nests per year. The total number of females attempting to nest at Port Deposit were higher in 2015 compared with previous years, but no conclusions can be drawn from such a limited sample.
- 3) Female Map Turtles did successfully complete five nests within the perimeter of the temporary wildlife fence, although use of the rehabilitated soil types was limited. More extensive soil rehabilitation will be useful once the environmental education center is completed.
- 4) Despite the limited area available for nesting and considerable foot traffic in the vicinity of the nesting site, the research team found limited examples of human disturbance of nesting females. The attitude of the public towards the Map Turtle was generally positive and supportive of the project and conservation of the Map Turtle, but there were a number of negative comments as well, especially regarding the cost of the project. Additional public education would clearly be valuable.
- 5) Unlike patterns seen in previous years, three nests at Port Deposit were unsuccessful in 2015-2016, with two proving to be non-viable and one nest depredated by a predator.

Recommendations of Best Practices

- 1) The total area of rehabilitated soils provided for nesting by female Map Turtles should represent a higher proportion of the total available nesting area than was provided in 2015. At least 25% of the total area available should consist of rehabilitated soils and such soils should be placed along the wildlife exclusion fence to a depth of at least 24” and extending at least 36” inside the fence line.
- 2) The nesting mounds provided in 2015 all were colonized by weeds during the 2015 nesting season. While some vegetative growth may be beneficial, control of this vegetation will be needed in 2016 and future years to prevent excessive shading of the nest sites and to prevent root masses from destroying viable nests

3) Careful attention needs to be paid to the drainage of water from storms at the nesting areas. Pooling of water at the wildlife exclusion fence could be responsible for destruction of nests by erosion or drowning of eggs.

4) Careful testing will need to be conducted in 2016 and future years to see if the materials used to prevent disturbance of nesting turtles are effective. Due to the nature of the temporary wildlife exclusion fence used in 2015, such testing has not been conducted yet.

REFERENCES

- Bennett A, M. Keevil, and J.D. Litzgus. 2009. Demographic differences among populations of Northern Map Turtles (*Graptemys geographica*) in intact and fragmented sites. *Canadian Journal of Zoology* 87: 1147-1157.
- Bulte, G., M. A. Carriere and G. Blouin-Demers. 2010. Impact of recreational power boating on two populations of northern map turtles (*Graptemys geographica*). *Aquatic Conservation: Marine and Freshwater Ecosystems* 20:31-38.
- Ernst, C. H., R. W. Barbour, and M. F. Hershey. 1974. A new coding system for hardshelled turtles. *Trans. Kentucky Acad. Sci.* 35:27-28.
- Jones, R. L. 1996. Home range and seasonal movements of the turtle *Graptemys flavimaculata*. *Journal of Herpetology* 30:376-385.
- Klemens, M. W., and J. B. Thorbjarnarson. 1995. Reptiles as a food resource. *Biodiversity and Conservation*. 4:281-298.
- Midwood, J.D., N.A. Cairns, L.J. Stoot, S.J. Cooke and G. Blouin-Demers. 2015. Bycatch mortality can cause extirpation in four freshwater turtle species. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25: 71-80. doi:10.1002/aqc.2475.
- Mitchell, J. C., and M. W. Klemens. 2000. Primary and secondary effects of habitat alteration. In: *Turtle Conservation*. M. W. Klemens (ed.), pp. 5-32. Smithsonian Institution Press Washington, D.C.
- Moll, D. 1980. Dirty River Turtles. *Natural History* 89:42-49.
- Moll, D., and E. O. Moll. 2004. Habitat alteration. In: *The ecology, exploitation and conservation of river turtles*, pp. 242-249. Oxford University Press, New York.
- Moore, M. J. C., and R. A. Seigel. 2006. No place to nest or bask: effects of human disturbance on yellow-blotched map turtles (*Graptemys flavimaculata*). *Biological Conservation* 130:386-393.
- Nagle, R. D., C. L. Lutz, and A. L. Pyle. 2004. Overwintering in the nest by hatchling map turtles (*Graptemys geographica*). *Canadian Journal of Zoology* 82:1211-1218.
- Pluto, T. G., and E. D. Bellis. 1986. Habitat utilization by the turtle, *Graptemys geographica*, along a river. *Journal of Herpetology* 20:22-31.
- Richards-Dimitrie, T., S.E. Gresens, S.A. Smith and R.A. Seigel. 2013. Diet of Northern Map Turtles (*Graptemys geographica*): Sexual differences and potential Impacts of an altered river system. *Copeia* 2013: 477-484.

- Schlaepfer, M.A., C. Hoover, and C. K. Dodd, Jr. 2005. Challenges in evaluating the impact of the trade in amphibians and reptiles on wild populations. *BioScience* 55: 256-264.
- Seigel, R. A., T. M. Richards, K. Anderson, and S. Badolato. 2011. Nesting and Basking Ecology of Northern Map Turtles in the Susquehanna River: Impacts of Human Disturbance and Effectiveness of Mitigation Measures. Unpublished Interim Report to Exelon, November 2011.
- Seigel, R. A., K. Anderson, B. Durkin, and T. Richards-Dimitrie. 2015. Effectiveness of Nest Site Restoration for The Endangered Northern Map Turtle. Report No. 1: Nest Site Selection and Nest Success From 2013-2014 and Establishment of Environmental Center. Report MD-15- SHA-TU-1-1.
- Smith, S. A., T. Richards, and R. A. Seigel. 2008. Distribution and habitat use of the common map turtle in the lower Susquehanna River. In: Maryland Department of Natural Resources State Wildlife Grants-Implementation Job Performance Report. Job No. 228.
- Smith, S. A., T. Richards, and R. A. Seigel. 2009. Distribution and habitat use of the common map turtle in the lower Susquehanna River. In: Maryland Department of Natural Resources State Wildlife Grants-Implementation Job Performance Report. Job No. 228.
- Smith, S. A., T. Richards-Dimitrie, and R. A. Seigel. 2010. Northern Map Turtle Distribution and Habitat Use in the Lower Susquehanna River. In: Maryland Department of Natural Resources State Wildlife Grants-Implementation Job Performance Report. Job No. 228.
- Ultsch, G. R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Review* 81:339–367.