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Natal Philopatry in a Long-Lived Species: The Return of Reproductive River Turtles Marked and Released as Hatchlings

Roy D. Nagle [1,*], Travis J. Russell [2], Christopher J. Grant [2], Melissa Innerst [3] and Seth J. Strawser [1]

[1] Environmental Science and Studies, Juniata College, Huntingdon, PA 16652, USA
[2] Department of Biology, Juniata College, Huntingdon, PA 16652, USA
[3] Department of Mathematics, Juniata College, Huntingdon, PA 16652, USA
* Correspondence: nagle@juniata.edu

Abstract: Natal philopatry—the return of an animal to its place of birth to reproduce—can shape population genetics and link essential habitats across generations, yet examples from long-term mark-recapture studies are rare. In this study, we observed 136 nests of Northern Map Turtles at Mount Union, Pennsylvania, between 2000 and 2008 and then individually marked and released 691 hatchling turtles into the Juniata River. During a recent six-year period (from 2017 to 2022), 46 of the hatchling-marked turtles (6.7%) returned to Mount Union as adult females to nest. The ages of these turtles ranged from 11–22 years at first recapture, and their mean age was 17 years. Forty-one hatchling-marked females came from observed nests with known mothers, and remarkably, just four (of 52) mothers produced over half of the returning females. The minimum ages of the oldest female turtles were estimated at 39 years, with reproductive lifetimes of at least 23 years. Our results indicate that a few long-lived Super Moms have made extraordinary contributions to hatchling recruitment and population viability of Northern Map Turtles of the Juniata River. The timing of release also had a significant influence on the probability of a turtle returning, with hatchlings released in May returning at a higher rate than those released earlier in the spring. In addition, morphological characteristics of hatchling-marked females suggest that factors causing shell shape abnormalities in adult turtles have not abated over the past two decades as previously theorized and likely involve exposure of juveniles to contaminants in the Juniata River rather than any maternal influence.

Keywords: hatchling; *Graptemys*; mark-recapture; natal philopatry; nesting; reproduction; turtle

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1. Introduction

The ability to mark individual animals and later recapture them can provide essential information about how individuals age, grow, reproduce, and move. Thus, in addition to their well-known use to estimate populations, mark-recapture techniques allow for studies of aging, demography, life histories, reproduction, and spatial ecology. Moreover, long-term field studies using mark-recapture are required to understand factors that shape the ecology and life histories of long-lived species [1–3].

Physical and logistical challenges limit the ability to mark neonates of many vertebrate species, including many reptiles [4]. While passively integrated transponders can provide reliable monitoring of adult turtles, transponder implants are not recommended for hatchlings due to their relative size and potential negative impacts on growth and development [5], and it can be costly to tag large numbers of animals with low recapture rates [6]. Visible implant elastomer has been employed for mark-recapture of hatchling turtles, yet evidence for mark retention is limited, and this method may be impermanent due to the breakdown and dispersion of the elastomer [7,8]. For long-term studies of turtle populations, the osseous shells of most species provide an excellent medium for assigning unique, permanent codes by marking the marginal scutes of the carapace [9]. Shells of hatchling turtles can be notched with iridectomy scissors or nail clippers, and such marks remain visible for many years following release [9].

Yet before they can be marked and released for ecological studies, hatchling turtles must be obtained in sufficient numbers, a substantial challenge given the relatively low abundance of many neonates and their often cryptic nature. Two methods used to obtain hatchling turtles for research include collecting eggs and incubating them at appropriate temperatures in the laboratory or protecting natural nests from predators in the field. Laboratory incubation allows for controlled incubation conditions, such as sex ratio manipulation for species with temperature-dependent sex determination, although constant temperature regimes typical of laboratory environments may produce hatchlings with lower fitness than fluctuating temperatures typical of natural nests [10–13]. Nest protection programs allow developing embryos to experience the natural environmental conditions selected by females at maternal nesting sites, are relatively inexpensive, and may increase hatchling recruitment to benefit species of conservation concern [14–16].

Northern Map Turtles (*Graptemys geographica*) are highly aquatic river turtles with a limited distribution in Pennsylvania [17]. The largest known nesting area in the Commonwealth is located along the Juniata River at Mount Union, where, from 2000 to 2008, 535 females were individually marked to investigate their reproductive ecology [18]. Nesting season varies with spring temperatures and occurs from late May through July. Females exhibit fidelity to specific nesting sites within and among years [19]. Minimum age at maturity for females is nine years; clutch size averages 10 eggs and increases with female body size [18]. Most hatchlings spend 8–9 months in the nest post-hatch and often emerge early in the morning on warm spring days before migrating to the river [20].

From 2000 to 2008, we observed 136 nests of Northern Map Turtles at Mount Union and then individually marked and released 691 hatchling turtles into the Juniata River. During a recent six-year period (2017 to 2022), we monitored the Mount Union nesting area to determine current habitat use by turtles and whether any of the hatchlings marked and released more than a decade ago would return to the site as adult females to nest. The return of adult females marked as hatchlings to nest at Mount Union would provide evidence of natal philopatry—returning to their place of birth to reproduce—a behavior that can shape population genetics and link habitats across generations [21,22]. The implications of extensive natal philopatry are that females within shared nesting areas are closely related and that major communal nesting habitats are rare and ecologically essential.

Here, we report the extraordinary influence of maternal identity and release timing on the reemergence of female Northern Map Turtles marked as hatchlings. We also documented the longevity and reproductive characteristics of females marked more than 20 years ago, including long-lived grandmothers of recent hatchlings, and described how changes in habitat have altered turtle nesting behavior over decades. Lastly, we evaluated the morphology of hatchling-marked females to determine if previously reported shell abnormalities continue to occur as well as the relationship of abnormalities to natal incubation substrate and maternal identity.

2. Materials and Methods

2.1. Study Site

Our study is part of a long-term investigation of the ecology of Northern Map Turtles at Mount Union [18–20,23]. The Mount Union site consists of two very distinct areas of turtle nesting habitat: (1) ~500 m long by 40–70 m wide pile of coal tailings; and (2) ~1000 m^3 area of sand and shale within a 1150 m chain-link-fenced area, constructed by the Pennsylvania Department of Transportation to mitigate road mortality of female turtles along the adjacent highway (Figure 1).

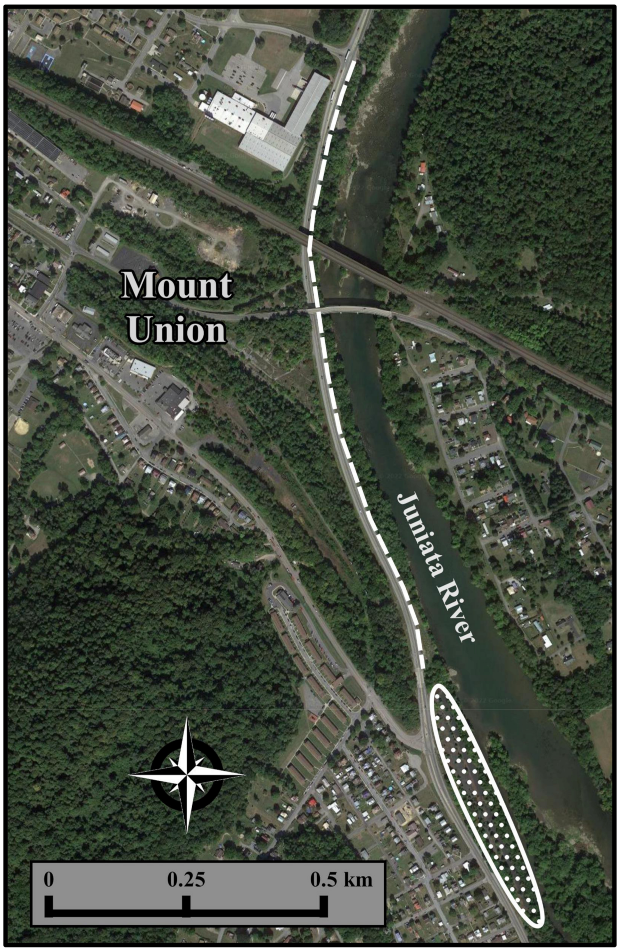

Figure 1. Map of our study site for Northern Map Turtles along the Juniata River at Mount Union, Pennsylvania. The white dashed line indicates the turtle exclusion fence adjacent to the highway, which forms the western border of the linear mitigation area of nesting habitat. The area to the south with a dotted interior is the coal tailings pile.

2.2. Adult Females

From 2000–2008 at Mount Union on the coal pile and within the mitigation area, we captured and monitored adult female Northern Map Turtles to examine their reproductive ecology, protect nests, and release hatchlings into the river to help mitigate turtle road mortality. Upon first capture, adult female turtles were measured with modified tree calipers (straight line plastron and carapace lengths = PL and CL, respectively), weighed on an electronic balance, and individually marked with 4-letter codes by notching or drilling marginal scutes of the carapace [9]. Ages were determined by counting growth annuli on carapace scutes [18,24], and females were palpated for the presence of oviductal eggs. We also recorded general locations of turtle captures and nest sites (coal pile or fenced mitigation area), GPS coordinates of nests on the coal pile in 2006 and 2007, as well as specific grid locations of captures and nests along the turtle fence within the mitigation area [19]. As the grid markings remain in place, during 2022 we obtained GPS coordinates of the locations of all nests constructed along the turtle fence from 2000–2008 [19].

2.3. Nest Protection

We protected 132 nests using wire mesh cages [20] and collected eggs from four other nests to incubate them in the laboratory for a study of hatching success in coal vs. sand substrates. During the first year of our study, turtle nests were encircled with rings of aluminum flashing and monitored daily to determine patterns of hatchling emergence [20].

During all subsequent years of study, nests were excavated to assess survivorship and collect hatchlings. Most nests were excavated in April and May during the period that hatchlings typically emerge, although eight nests (5.3%) were excavated in the fall (5% of natural nests emerged during the fall when we examined emergence patterns early in our study [20]).

2.4. Hatchling Mark and Release

Throughout our study, all hatchlings were measured with digital calipers (straight line PL and CL), weighed on an electronic balance, and marked by notching unique marginal scutes with iridectomy scissors or nail clippers (Figure 2). Six hundred fifty hatchlings were individually marked using 3-letter codes, and 41 hatchlings were individually marked using 4-letter codes. Hatchlings were collected from nests, marked, and released into the Juniata River, typically when ambient air temperatures exceeded 18 °C.

Figure 2. Hatchling Northern Map Turtle marked AIJ by notching three marginal scutes with iridectomy scissors. The first right marginal scute is always "A", following Nagle et al. [9].

2.5. Recent Monitoring and Recaptures

From 2017–2022, we monitored the Mount Union site to collect additional nesting data, evaluate recent habitat use, and determine if map turtles marked and released into the Juniata River as hatchlings returned to Mount Union as adult females to nest. Adult females marked as hatchlings were identified by their unique shell codes, and the notches of hatchling-marked females were often curved or irregularly shaped (Figure 3), which made them distinguishable from the sharper V-shaped notches typical of females marked as adults.

Figure 3. Adult female Northern Map Turtle AKO marked as a hatchling in 2007 and recaptured at age 14 on the coal pile. Curved notches are characteristic of adult turtles marked as hatchlings.

We captured and measured adult female turtles with modified tree calipers (PL and CL), weighed them on an electronic balance, obtained GPS coordinates of capture and nest locations, and examined turtles for shell shape abnormalities following Nagle et al. [23]. To calculate distances between recapture locations of returning adult females and their natal nest locations and make comparisons among habitats, we used one capture location per year (usually the last capture) so that individuals captured on successive days or within short time frames did not bias our analysis, unless captures were ≥13 d apart, representing distinct clutches [18].

2.6. Data Analysis

Minitab Statistical Software (version 21.1.3; Minitab LLC, 2022, State College, PA, USA) and R Statistical Software (v4.2.2; R Core Team, 2022, Vienna, Austria) were used to analyze data. We utilized a mixed-effects logistic regression to examine the probability of whether a hatchling-marked turtle would return based on two predictor variables: clutch (a "random effect") and Julian Day of release (a "fixed effect" numerical predictor). Only Julian Day releases during spring were included in the logistic regression analysis since the number of hatchling-marked turtles that returned from fall releases was very small ($n = 2$), and because fall and spring releases differ biologically, the combined dates would not be a linear predictor variable. For the random effect in the mixed-effects logistic regression, we tested for significance using a likelihood ratio test.

We also compared the body sizes of hatchlings that returned to those that did not, examined the relationship between body size of hatchling-marked females and their mothers, and compared the proportion of returning females with shell abnormalities to their mothers and to a much larger sample from an earlier study. We used a mixed-effects logistic regression model to address the question of whether, within each clutch, PL, CL, or mass influenced return (i.e., did the largest or heaviest hatchlings from each clutch have a survival advantage?). For more general comparisons, we used t-tests to compare the mean body sizes of hatchlings that returned as adults versus those that did not return, as well as to compare the sizes of hatchlings from the four females that produced the majority of returning hatchlings ("Super Moms") to hatchlings from all other females. We also used t-tests to compare mean distances between recapture locations and natal nests on the coal pile to those of natal nests in the fenced mitigation area. Linear regression was used to examine the relationship between hatchling-marked female carapace length and maternal carapace length. Two-proportion Z-tests were used to compare the proportion of hatchling-marked females with shell abnormalities to that of their mothers and to the larger sample reported in Nagle et al. [23]. Levels of significance for all analyses were set at $\alpha = 0.05$.

3. Results

3.1. Nest Success and Hatchlings

Among the 136 Northern Map Turtle nests observed from 2000–2008, 132 were protected in the field, and four were incubated in the laboratory. Eighty-four protected nests produced live hatchlings that were marked and released; hatchlings from all four nests incubated in the laboratory were also marked and released. Twenty protected nests failed entirely, containing evidence that all eggs, partially developed embryos, or fully developed hatchlings were dead, along with no indication that any hatchlings had emerged. Twenty-eight protected nests contained no live hatchlings but showed evidence that at least one hatchling had emerged in the fall or before nests were dug in the spring (e.g., emergence holes and eggshells but no live hatchlings).

3.2. Return of Hatchling-Marked Reproductive Females

From 2017 to 2022, 46 hatchling-marked turtles returned to Mount Union as adult females to nest (Table 1). The ages of these turtles ranged from 11–22 years at first recapture. The mean age of females at first recapture was 17 years, and the mean age among all recaptures was 18 years. All the returning females came from natural nests in 2000–2008 that were protected in the field; none were from laboratory-incubated clutches. Forty-four returning females were hatchlings released in the spring, and two were released during the fall. Forty-one hatchling marked females came from observed nests with known mothers, and five hatchling marked females came from nests found after completion without a female present, thus their mothers are unknown. Based on the total number of 691 hatchling turtles marked and released into the Juniata River from 2001 to 2008, the 46 females that returned represent an overall recapture rate of 6.7%.

Table 1. Characteristics at first recapture of reproductive female Northern Map Turtles marked as hatchlings that recently returned to Mount Union, Pennsylvania, as well as distances between recent recapture locations and their natal nests.

Variable	*n*	Mean	Std Dev	Range
Age (years)	46	17.0	2.9	11–22
Plastron Length (mm)	46	192.8	7.7	172–210
Carapace Length (mm)	46	226.1	9.7	207–249
Body Mass (g)	45	1568.4	219.3	1173–2016
Distance to natal nests on coal pile (m)	11	196.5	109.1	67.2–446.2
Distance to natal nests in fenced mitigation area (m)	61	665.3	381.3	39.1–1527.9

3.3. Influence of Maternal Identity and Timing of Release

The 46 hatchling-marked females that returned as reproductive adults came from 24 different nests, with 1–7 siblings returning per nest (Table 2; Figure 4). Maternal identity and timing of release each had a significant impact on the likelihood that hatchlings returned. Just four mothers of 52 known females whose nests we protected produced 21 hatchling-marked females; we refer to these four females below as "Super Moms" due to their substantial contribution of returning daughters. Clutch identity significantly influenced whether a hatchling-marked turtle returned ($\chi^2 = 18.147$, $p < 0.001$). Additionally, hatchlings released during May returned at a substantially higher rate than those released in other months (Table 3). Even after accounting for variability across nests, the Julian Day of release had a significant effect on the probability of a turtle returning ($\beta = 0.06995$, $p < 0.001$; a delay in a turtle's release by one day during spring increased the odds of returning by a factor of 1.07).

Table 2. The number of hatchling-marked sibling Northern Map Turtles per nest that returned to Mount Union as adult females during 2017–2022, from 24 nests protected during 2000–2008. Twenty nests were associated with known mothers, and four nests were found after completion; thus, their mothers are unknown. One female (ABDY) produced five hatchlings from one nest and two hatchlings from another nest—seven years apart—that returned as adult females.

Number of Female Siblings Returned Per Nest	Number of Nests	Product (Number of Females)
1	14	14
2	5	10
3	2	6
4	1	4
5	1	5
7	1	7
Total	**24**	**46**

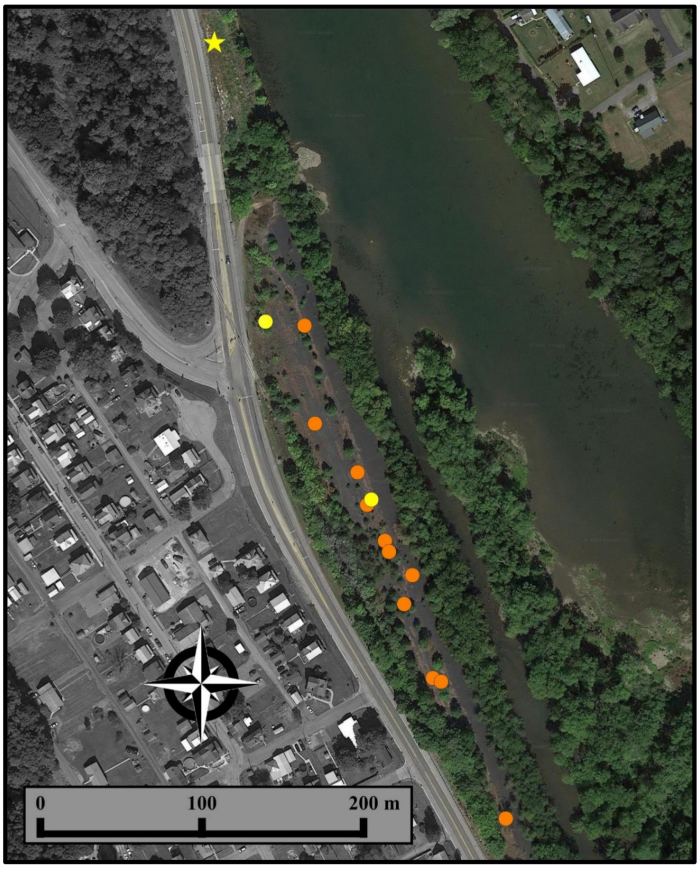

Figure 4. Map showing the nest and capture locations of a Northern Map Turtle mother and her returning adult daughters at Mount Union, Pennsylvania. A yellow star indicates the initial nesting location of female ABHP in 2000 along the turtle fence; yellow dots show recapture locations of ABHP in 2020 and 2022 on the coal pile; and orange dots show the recapture locations of her seven adult daughters that returned in 2017–2022 at ages 17–22 on the coal pile.

Table 3. Number of Northern Map Turtle hatchlings released into the Juniata River at Mount Union from 2001–2008, by month of release, and number that returned as reproductive adults from 2017–2022. Note: Of the 69 hatchlings released in August, 44 were incubated in the laboratory (rather than naturally incubated in the field), and none of those returned as adults.

Month Released	Number Released	Number Returned	Percent Returned
March	66	9	13.6
April	477	14	2.9
May	77	21	27.3
August	69	2	2.9
September	3	0	0
Total	**691**	**46**	**6.7**

Hatchling size did not influence the likelihood of return, and maternal size did not influence the size of hatchling-marked females at recapture. Using a mixed-effects logistic regression model with nest as a random effect, neither PL ($\beta = -0.1981$, $p = 0.42$), CL ($\beta = -0.1243$, $p = 0.54$), nor mass ($\beta = -0.0595$, $p = 0.89$) significantly influenced whether turtles returned (i.e., hatchling size within clutches did not affect return). No differences in PL, CL, or mass of hatchlings were observed between those from the four Super Moms ($n = 21$) compared to all other hatchling-marked females ($n = 25$; all p-values > 0.10), and no differences in PL, CL, or mass of hatchlings were observed between all hatchling-marked females that returned ($n = 46$) and those that did not return ($n = 645$; all p-values > 0.28). The linear regression model predicting offspring carapace length from maternal carapace length was also not significant ($F_{1,39} = 1.68$, $p = 0.2$, $R^2 = 0.02$).

3.4. Female Longevity and Reproductive Lifetime

The ages of female Northern Map Turtles were estimated at up to 39 years, with documented reproductive lifetimes of at least 23 years. Two reproductive females, ages 17 and 18 based on annuli counts in 2000, were captured again in 2022 and 2021, respectively, thus we estimate they were each 39 years old. Among all females in our study, 100 individuals were captured when gravid over a span of a decade or longer, and 23 of those females were captured when gravid over a span of 20 years or more. Ten females were captured when gravid between 2000 and 2022 (and often in between), exhibiting reproductive lifetimes that span at least 23 years.

Three mothers of hatchling-marked females who nested between 2000–2008 were recaptured again during 2020–2022. The first female had been assigned a minimum age of 17 in 2003 based on growth annuli; thus, we estimate the minimum age at 36 years in 2022; she had grown 9 mm CL over 19 years. The second and third females were not ageable at first captures (in 2000 and 2005) and were conservatively assigned minimum ages of 15 years. In 2022, these females were estimated to be at least 37 and 32 years old, and they had grown 12 mm CL in 22 years and 14 mm CL in 17 years, respectively.

3.5. Recapture Locations and Natal Philopatry

The 46 hatchling-marked females were captured a total of 98 times: 88 captures were made on the coal pile, and 10 were made along the turtle fence. The mean distance from recapture locations to natal nests on the coal pile (196.5 m, $n = 11$) was significantly smaller than the mean distance from recapture locations to natal nests in the fenced mitigation area (665.3 m, $n = 61$, $p < 0.001$). Among 35 hatchling-marked females from 17 nests along the turtle fence, 29 were recaptured only on the coal pile, and three were recaptured only along the turtle fence. Among the 11 hatchling-marked females from seven nests on the coal pile, nine were recaptured only on the coal pile, and one was recaptured only along the turtle fence.

3.6. Shell Shape Abnormalities

Ten of 46 (22%) female turtles that returned to nest at Mount Union exhibited an abnormal carapace shape. All ten hatchling-marked females with abnormal shell shapes were from nests incubated in the fenced mitigation (sand/shale) area rather than the coal pile. Of the 20 known mothers of the 41 hatchling-marked females, six (29%) exhibited abnormal shell shapes. The proportion of hatchling-marked females with abnormalities did not differ from the proportion of mothers with abnormalities ($z = -0.69$, $p = 0.49$); or from the proportion of the large sample of females with shell abnormalities reported in Nagle et al. [23] (156/535, 29%; $z = -1.16$, $p = 0.25$). There was no apparent relationship between the shell shapes of mothers and their returning daughters: abnormal-shaped females produced normal offspring, and normal females produced abnormal-shaped offspring. Three of the ten clutches with multiple returning hatchling-marked females included both normal and abnormal-shaped siblings.

4. Discussion

4.1. Return of Hatchling-Marked Females

Among the 691 hatchling Northern Map Turtles marked and released from 2001–2008, 46 returned to Mount Union as adult females to nest. The ages of hatchling-marked females that returned as reproductive adults ranged from 11–22 years. The minimum age at maturity of Northern Map Turtles is nine years, although most females probably reach maturity at 12–15 years, and some mature at older ages [18]. Although all the hatchlings marked and released in the early 2000s should have attained sexual maturity by the time of our recent sampling period (2017–2022), some turtles marked later in the decade may not yet have reached maturity, and these turtles may continue to reemerge at Mount Union as reproductive adults.

4.2. Super Moms

Maternal identity had a significant influence on the survival and return of hatchling-marked females to the Mount Union nesting area. Among the known mothers of the 41 returning turtles, just four mothers produced over half of the returning females. Differential fitness among female freshwater turtles can be driven primarily by nest predation [25], a factor we substantially reduced by protecting nests with wire cages. Beyond our nest protection program, turtles in our study may have influenced offspring fitness through genetic effects or a range of maternal effects, which in freshwater turtles can include provisioning of eggs, hatchling attributes that result from nest site selection, or parental care [26–28]. Across taxa, maternal effects can explain much of the phenotypic variation within populations and are especially pronounced among juveniles [29,30], including many neonate turtles [10,31,32].

As a long-lived species, year-to-year differences in fitness among female Northern Map Turtles may be compounded over decades of iteroparous reproduction. Our age estimates combined with reproductive data suggest minimum lifespans of 39 years with reproductive lifetimes of at least 23 years in Northern Map Turtles. Our results suggest that conservationists, wildlife rehabilitators, and ecological modelers should not underestimate the reproductive power of a few individual females, especially older females among long-lived, iteroparous animals, and the potential impact of their loss on population stability and viability. Over the 23 years of our study, the four most successful mothers with the greatest number of returning daughters produced a total of 58 offspring and 79 grand-offspring, all marked and released into the Juniata River.

4.3. Timing of Release

The phenomenon of overwintering in the nest by hatchling turtles is explained by the costs and benefits relative to the predictability of resources. Northern Map Turtles are the most northerly distributed *Graptemys* species and the only species in the genus known to exhibit delayed nest emergence [33]. In many regions inhabited by Northern Map Turtles resource levels can decline sharply during fall, and the timing of such declines may be unpredictable, especially for hatchlings from second or third clutches that emerge late in the year. Hence, selection favors turtles that remain in the "proven sanctuary" or relative safety of their nest during periods of unpredictable or low resource availability, particularly when risks are high [34,35]. Beyond the broadly defined benefits of delayed (spring) vs. immediate (fall) nest emergence, our results indicate that within spring, delaying emergence and migration to the river until late spring may provide an advantage compared to early spring emergence.

The timing of the release of Northern Map Turtle hatchlings had a significant influence on the likelihood that turtles returned years later to nest at Mount Union. The return rate of hatchlings released in May was approximately an order of magnitude greater than the return rate of those released in April, despite the natural emergence of hatchling Northern Map Turtles having been documented from 10 April through 25 May [20]. Across all years of our study, a one-day delay in a turtle's release during spring increased the odds of it returning by a factor of 1.07. Two non-exclusive explanations for the higher return rate of hatchlings released in late spring are increased survival or decreased displacement. Perhaps hatchlings released earlier in the spring travel farther downriver due to higher water levels and stronger currents, beyond the range of feasible nesting migrations upon reaching adulthood.

Why might hatchlings released into the river during May have a survival advantage compared to those released earlier? Hatchlings that delay emergence until May enter environments where water temperatures are as much as 10 °C warmer [36] and levels of sunlight and food are more conducive to growth and survival than conditions in March and April. Yet there may be tradeoffs between staying in nests as long as possible for safety and depletion of energy stores, as hatchlings that delay emergence have no access to food and rely on maternal provisioning of yolk [37,38]. Another possible benefit of late spring emergence could result from social interactions with adult females that return in May to areas in the river adjacent to nesting areas—places at which females congregate and hatchlings enter the river (Nagle and Russell, personal observations). Adult female *Podocnemis expansa* in the Amazon evidently respond to hatchling vocalizations before and after hatchlings enter the river and then lead them downstream to productive foraging grounds [28,39].

4.4. Recapture Rate

The 6.7% return rate of female Northern Map Turtles to their natal nesting area was higher than expected given the possibility that females might choose to nest outside of our study area, the decade-long interval between the time hatchlings first reach the river and the age at which they attain sexual maturity [18], as well as the highly variable juvenile survivorship reported among freshwater turtle species [40]. While it's certainly possible that some hatching-marked females nested elsewhere, our surveys along the Juniata River over the past 22 years suggest there are no other large-scale nesting areas like Mount Union, and our overall mark-recapture results indicate a general trend of natal philopatry in Northern Map Turtles.

The recapture rate observed in our study for female turtles with an average age of 17 years would require an annual juvenile survivorship of approximately 75% from age 1 through maturity combined with an annual post-maturity survivorship exceeding 80%. These levels of survivorship are like those documented in other relatively long-lived species [41–44]. Yet our survivorship estimates do not account for the likelihood that at least some hatchlings marked and released were male, which is more likely in nests along the turtle fence than those on the coal pile, where elevated nest temperatures are strongly female-biased [23]. Survival of a sizable portion of males would require even higher levels of juvenile and adult survivorship than the estimates above based solely on returning females. We have not recaptured any hatchling-marked male Northern Map Turtles, although our sample of males obtained by trapping in the river is small compared to our sample of reproductive females observed nesting on land. We also recognize that the difference between the relatively high offspring survivorship observed in our study and more moderate survivorship was driven by only a few highly successful mothers. Without hatchling turtles from these very successful Super Moms, our recapture rate would have been much lower.

An additional factor that may have contributed to the high survivorship of returning female turtles was releasing hatchling-marked turtles directly into the river. Hatchlings did not have to make the overland trek from their nest site to water, reducing their risks of desiccation and exposure to terrestrial predators [45–47]. Hatchling Northern Map Turtles are small (<10 g), relatively defenseless, and threatened by a wide variety of mammalian and avian predators. Furthermore, camera traps placed along our study site captured numerous predators (red foxes [*Vulpes vulpes*], bobcats [*Lynx rufus*], and raccoons [*Procyon lotor*]), with video of raccoons actively excavating nests. Results from other studies suggest that risks vary depending on species, season, and terrain and that hatchlings of several freshwater turtle species orient toward thick vegetational cover during dispersal to reduce risk [48–50].

4.5. Natal Philopatry and Recapture Locations

If first-year movement patterns influence long-term habitat use and reproductive females exhibit natal philopatry, there should be a general tendency for Northern Map Turtles to move upstream to nest. Hatchling turtles released into the river move downstream due to their small size and the strong river currents they encounter during spring, with movements as much as 5 km during their first year [51]. Although we do not know the full extent of riverine nesting migrations of adult females, our data using radiotelemetry indicate that females migrate from at least 6 km away to nest at Mount Union, and most monitored females migrate upstream ([19], and recent unpublished data). Carrière et al. [52] reported that Northern Map Turtles in the St. Lawrence River moved up to 5 km to reach nesting sites, and the researchers attributed significantly longer nesting migrations in lotic vs. lentic habitats to some combination of downstream dispersal caused by strong river currents, limited availability of nesting habitat along the river, and natal philopatry.

In our study, many hatchling-marked Northern Map Turtles returned to the turtle nesting habitat at Mount Union, with distances between natal nests and recapture locations ranging from 39–1528 m. Releasing hatchlings directly into the river may have promoted high survivorship, but it may also have obscured the ability of hatchlings to imprint on their specific terrestrial natal nest site, as hatchlings did not experience natural emergence and migration to the river. To our knowledge, the mechanisms by which hatchling freshwater turtles might imprint on natal nest sites remain undocumented, although sea turtles use geomagnetic imprinting and sensory cues to navigate oceans and return to their natal beaches [53–56]. Our study results are consistent with the premise that female Northern Map Turtles use natal homing to return to the general area of their natal nest or the area at which they first entered the river and then employ sensory cues or social facilitation to find specific nest sites [57–59].

Other studies have used genetic markers rather than mark-recapture to infer the existence of natal philopatry in turtles. These studies presume that closely related females nesting near one another are the result of siblings that imprint on natal nest sites and then return to those sites as reproductive adults [60]. Reinhold [61] hypothesized that selection should favor natal philopatry in species with environmental sex determination at rare, high-quality nesting habitats that tend to produce females. Byer and Reid [62] suggested that natal philopatry reduced risk and uncertainty in long-lived species such as turtles. Genetic support for natal philopatry has been reported for populations of *Emydoidea blandingii* [59], *Graptemys kohnii* [60], *Malaclemys terrapin* [63], and *Podocnemis expansa* [64], as well as most sea turtle species [65–69]. In contrast, no genetic evidence for natal philopatry was found within a population of *Chelydra serpentina* that nested in agricultural fields, in which shading from dense crops produced strongly male-biased sex ratios [70].

Habitat stability at Mount Union may have influenced the recapture locations of hatchling-marked females. Twenty-two years after our study began, forest succession and shading have eliminated much of the northern portion of nesting habitat along the turtle fence, and the majority of open-canopy nesting habitat remaining is located south on the coal pile. The average distance between the recapture locations of hatchling-marked females and natal nests on the coal pile was less than one-third of that distance in the fenced mitigation area. Overall, while only 22% of hatchling-marked turtles were produced in nests on the coal pile, 90% were recaptured there as adults. The coal tailings pile at Mount Union provides persistently stable, relatively rare nesting habitat that should favor natal philopatry as well as strong fidelity of adult females to nest sites [19,61] and perhaps fosters an enduringly female-biased population [71].

4.6. Shell Shape Abnormalities

Turtles with morphological abnormalities may be long-lived environmental indicators, and adult female Northern Map Turtles at Mount Union exhibit a high incidence of shell shape abnormalities [23]. We proposed that these abnormalities could reflect a delayed morphological response to characteristics of the nesting substrate, differential gene expression, or direct exposure to contaminants in the river as subadults, and we theorized that problems affecting turtles a generation ago may have abated [23]. Yet our recent finding of marked hatchlings returning as abnormally-shaped adults suggests that, unfortunately, the environmental assault on turtle shell development remains undiminished in the 21st century.

Ten of the 46 turtles (22%) that returned to the nest exhibited abnormal shell shape, and these abnormalities were unrelated to any maternal or clutch effects. As the abnormal-shaped females came from nests outside the coal pile area, the hypothesis that high temperatures or chemical insults from incubation in coal produce abnormalities in adult females was not supported. Further, abnormal-shaped mothers produced normal-shaped offspring, normal-shaped mothers produced abnormal-shaped offspring, and multiple clutches of hatchling-marked females that returned included both normal- and abnormal-shaped siblings. Consequently, rather than any maternally derived influence, it seems likely that direct exposure to contaminants in the Juniata River as sub-adults is responsible for the abnormal shell shapes observed in adult females [23]. Our ongoing research is focused on determining levels of contaminants in turtle prey items and turtle tissues, as well as using radiotelemetry to identify feeding areas of deformed female turtles.

5. Conclusions

Our system of marking hatchling turtles was effective in recapturing 46 individual female Northern Map Turtles after more than a decade. Maternal identity, timing of hatchling release, and changes in habitat influenced recapture and natal philopatry. Our study highlights the value of turtle nest protection as a research tool as well as a cost-effective method for increasing recruitment. Overall, a relatively small number of mothers produced all the hatchlings that returned to Mount Union years later as adult females to nest. Our results indicate that a few long-lived Super Moms have made extraordinary contributions to hatchling recruitment and population viability of Northern Map Turtles of the Juniata River. Additionally, morphological characteristics of hatchling-marked females suggest that factors causing shell shape abnormalities in adult turtles have not abated over the past two decades as previously theorized and likely involve exposure of juveniles to contaminants in the Juniata River rather than any maternal influence.

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Data Availability Statement: The data presented in this study are available from the corresponding author upon reasonable request.

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