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REPRODUCTIVE ECOLOGY OF *GRAPTEMYS GEOGRAPHICA* OF THE JUNIATA RIVER IN CENTRAL PENNSYLVANIA, WITH RECOMMENDATIONS FOR CONSERVATION

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***Abstract.*—From 2000–2008, we examined the reproductive and nesting ecology of Northern Map Turtles (*Graptemys geographica*) in central Pennsylvania, USA, at a mitigated nesting area associated with construction of a new highway and at an adjacent area of coal tailings. The first day of nesting varied by 29 d among years and was correlated with the number of heating degree days in May (i.e., colder springs were associated with later start dates). Substantial variation in body size was found among reproductive females, with a range of carapace lengths (CL) of 79 mm and a 3.8-fold difference in body mass. Larger females showed a weak but significant tendency to nest earlier than smaller females each year. Females captured on coal tailings had significantly higher body temperatures than females in the mitigated area. We estimated minimum female age at maturity at 9 y and the median age at 14 y from counts of scute annuli. Population age structure was probably much broader (and older) than that indicated by our age estimates, however, because more than a quarter of all adult females appeared to be too old to accurately age. Clutch size averaged 10.3 eggs and increased with female body size. Larger and heavier females also produced larger and heavier hatchlings. We estimate that 12–21% of females produced two clutches annually, and 0.5% of females produced three clutches. Our primary goals of protecting adult females and documenting reproductive ecology were achieved, yet additional work is needed to ensure long-term success of the mitigated nesting area. Several conservation challenges threaten the Mount Union site that may impact future population viability of Northern Map Turtles of the Juniata River.**

Key Words.—body temperature; clutch size; coal tailings; *Graptemys geographica*; map turtle; mitigation; nesting; offspring size; reproductive frequency

INTRODUCTION

Turtles are long-lived, with life histories characterized by high nest and hatchling mortality, delayed maturity, high juvenile and adult survivorship, and low annual fecundity (Congdon et al. 1993, 1994). The co-evolved life-history traits common among turtles result in populations of many species being sensitive to increased mortality of the oldest juveniles and adult females (Brooks et al. 1991; Congdon et al. 1993, 1994; Heppell 1998). Increased mortality of adult females during nesting activities reduces the duration of reproductive lifetimes and results in lowering hatchling numbers and subsequent juvenile recruitment into the adult population (Gibbs and Shriver 2002; Steen et al. 2006). Studies of nesting activities and nest-site characteristics can inform efforts to improve nesting areas, evaluate mitigation efforts, and provide an understanding of the risks at a particular site (Ashley and Robinson 1996; Gibbs and Shriver 2002; Aresco 2005; Steen et al. 2012).

Map turtles, genus *Graptemys*, are ornately-patterned river turtles of the eastern and central United States and Canada (Ernst and Lovich 2009; Lindeman 2013). Throughout their range, map turtles are noted for their heliothermy, molluscivory by females of some species, and female-biased sexual size dimorphism (Lindeman 2013). Populations of several *Graptemys* species have suffered substantial declines as a result of anthropogenic impacts to their riverine habitats (Lovich 1995; Moll and Moll 2004; Moore and Seigel 2006; Lindeman 2013), with two species (*G. flavimaculata* and *G. oculifera*) federally listed as Threatened in the USA (U.S. Fish and Wildlife Service 1986, 1991). The Northern Map Turtle (*Graptemys geographica*), the most northerly occurring *Graptemys* species, ranges into northwestern Vermont and southern Québec, Canada. It is listed as a Species of Special Concern in Canada (COSEWIC 2012), a state Endangered Species in Maryland (Lindeman 2013), and is of conservation concern in Pennsylvania (Nagle 2010).

Graptemys geographica of the Juniata and Susquehanna Rivers in Pennsylvania, USA are geographically isolated from the largest area of the distribution of the species (Ernst and Lovich 2009; Lindeman 2013). Nesting habitat along many sections of the Juniata River is limited to open-canopy areas that provide the soil temperatures necessary to support successful egg incubation. Nest depths average about 14

FIGURE 1. Map of study site for Northern Map Turtles (*Graptemys geographica*) in central Pennsylvania, USA. Blue line shows turtle fence; purple line at bottom encircles remnant coal tailings pile.

cm in substrates that include disturbed soils, fill materials, and coal tailings (Nagle et al. 2004). After pipping and emerging from eggs, most *G. geographica* hatchlings remain in natal nests through winter and disperse during the following spring (Nagle et al. 2004). Nesting migrations of female *G. geographica* can exceed 5 km within the river course itself (Pluto and Bellis 1988) and, although subsequent terrestrial movements to nest sites may involve shorter distances, the risks of overland travel to aquatic turtles may be substantial.

Our study began in an effort to monitor turtle nesting along a new highway that was constructed in 1998 near Mount Union, Pennsylvania, USA (Fig. 1), as the project appeared to threaten local turtle populations. More than 290,000 m^3 of coal tailings (a substrate used by nesting turtles) had been removed from the area to construct the highway. During the spring of 1999, the first year that the highway was used, at least 50 turtles were found dead on the road; most were *G. geographica*, but Wood Turtles (*Glyptemys insculpta*) and Snapping Turtles (*Chelydra serpentina*) were also found. The majority of turtles killed were gravid females attempting to cross the road to nest. In addition to the potential impact on turtle populations, the Pennsylvania Department of Transportation considered the large number of turtles on the roadway a safety concern for motorists.

We describe nesting habitat mitigation efforts, the reproductive traits of females, and the ecology and phenology of nesting in *G. geographica*. Initial monitoring of the site was conducted from 2000 to 2002 to establish the temporal and spatial aspects of nesting area use by females and hatchlings (Nagle et al. 2004). We continued the study from 2003 to 2008 to determine the effectiveness of mitigation activities and to collect additional information on reproductive traits and nesting ecology. Studies of nesting area mitigation for freshwater turtles are uncommon, as are field studies of *Graptemys* reproductive ecology.

MATERIALS AND METHODS

Study site.—The Juniata River meanders east from headwaters along the Allegheny Front through the Appalachian Mountains of central Pennsylvania and joins the Susquehanna River north of Harrisburg, Pennsylvania, USA. The Juniata undergoes substantial seasonal changes in flow rate and water temperature (Durlin and Schaffstall 2001). Much of the drainage basin is forested, with banks and floodplains bordered by Silver Maple (*Acer saccharinum*), Sycamore (*Platanus occidentalis*), and Black Willow (*Salix nigra*). The river channel is dominated by large rocks and emergent vegetation, predominantly Lizard's Tail (*Saururus cernuus*) and American Water-willow (*Justicia americana*; Pluto and Bellis 1986). Access to scarce open potential nesting areas is often obstructed by highways, railroad tracks, and rock rip-rap (Nagle 2010).

At our study site, the mitigation activities performed by the Pennsylvania Department of Transportation (PennDOT) during 2000 and 2001 were intended to reduce mortality of turtles and replace lost nesting habitat. After turtle road mortality was observed, PennDOT installed a 1-m high, 1,150-m long chain-link fence on the river side of the new highway to prevent turtles from moving onto the road to reach part of their previous nesting area (Fig. 1). U.S. Silica Corporation (Mapleton, Pennsylvania, USA) donated approximately 800 m^3 of sand, which was placed on the river side of the highway inside the fenced area to provide nesting substrate. Eight mounds of sand were created with dimensions that varied from approximately 0.50–0.75 m in height, 1–2 m in width, and 20–80 m in length (Fig. 2).

Following one year of monitoring, PennDOT moved large portions of the sand closer to the turtle fence and added crushed shale to reduce vegetation, control erosion, and provide a darker-colored nesting substrate. Immediately south of the mitigated area and between the old highway and the Juniata River, an undisturbed 500 × 40 m coal tailings pile (Fig. 1, purple line) provided us with the opportunity to compare turtle nesting in the mitigated area with nesting conditions similar to those

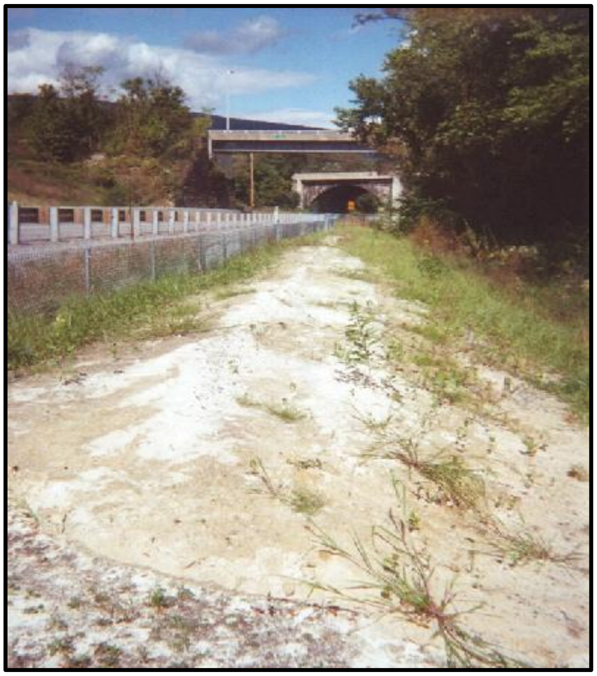

FIGURE 2. Sand mounds in the mitigated portion of the Mount Union turtle nesting area. Chain-link turtle fence is between the guardrail and the sand mounds. View faces north toward the two bridges in the center of Fig. 1. (Photographed by Roy Nagle).

present prior to construction of the new highway, when a large coal tailings pile covered most of the study area (Fig. 3). The coal had been mined 30 km south on Broad Top Mountain and the tailings were discarded in the early 20th Century by a coal-cleaning plant along the river at the junction of the East Broad Top Railroad and the mainline of the Pennsylvania Railroad at the town of Mount Union.

Methods.—We searched terrestrial areas along the Juniata River at Mount Union for reproductive female map turtles from 15 May to 20 July in 2000–2003 and 2005–2007. Surveys of shorter duration were conducted during 2008, and we had limited access to the coal tailings area in 2005. During all nesting seasons, we captured turtles during terrestrial movements or immediately after they had completed nesting. We measured cloacal temperatures of females to the nearest 0.1° C using Fisher Isotemp or Schultheis thermometers. We measured straight-line plastron and carapace lengths to the nearest 1.0 mm using calipers and determined the mass of turtles to the nearest 1.0 g on an electronic balance. We estimated ages by counting annuli on epithelial tissues of the carapace (Congdon et al. 2001, 2003). Individual turtles were given permanent marks by notching or drilling unique sets of marginal scutes on the carapace (Cagle 1939). We palpated females in the inguinal region to determine the presence or absence of oviductal eggs. Gravid females were also marked with

FIGURE 3. A female Northern Map Turtle (*Graptemys geographica*) at Mount Union, Pennsylvania, USA, nesting in coal tailings. (Photographed by John Matter).

small paint numbers on the carapace to allow individuals to be identified from a distance using binoculars. We released all turtles into the river near their points of capture.

We protected observed nests from predators using cylindrical wire-mesh cages (Nagle et al. 2004). During 2001, we outfitted nest cages with rings of aluminum flashing to restrain emerged hatchlings and inspected nests daily to determine patterns of hatchling emergence. We excavated and inspected samples of nests in the spring of all years of study to determine clutch size, embryo and hatchling survivorship, and morphological characteristics of hatchlings.

Statistical analyses.—We obtained climate data for March to May from the National Climate Center for Altoona, Pennsylvania (located approximately 45 km NW of the study site). We calculated summary statistics, *t*-tests, linear regression, and nonparametric Spearman's rank correlations using Minitab Statistical Software version 16.1.0 (Minitab Inc., State College, Pennsylvania, USA) with $\alpha = 0.05$.

RESULTS

Nesting ecology.—We captured 535 adult female *G. geographica* 2,255 times on land. Over eight years, we captured females as early as 22 May and as late as 1 August (Table 1). The first day of the nesting season varied by 29 d and was correlated with the number of heating degree days in May (i.e., the cooler the spring the later in the year the nesting season began; Spearman's $r_s = 0.81$; $P < 0.001$; n = 8). The last day of nesting varied by 31 d and the length of the nesting season varied from 24 to 53 d (Table 1). Start and end dates for eight nesting seasons were not correlated (i.e.,

TABLE 1. Summary of nesting seasons for reproductive female Northern Map Turtles (*Graptemys geographica*) at Mount Union, Pennsylvania, USA (no sampling took place in 2004, and sampling was limited in 2005 and 2008).

Year	Date of First Capture	Date of Last Capture	Nesting Season Duration (days)	Number Killed on Road
2000	22 May	14 July	53	10
2001	26 May	10 July	45	3
2002	1 June	19 July	48	1
2003	20 June	1 August	42	3
2005	7 June	1 July	24	5
2006	30 May	20 July	51	4
2007	29 May	6 July	38	3
2008	9 June	11 July	32	0

seasons with early start dates did not necessarily end early; $P = 0.498$). There was a weak negative relationship between body size of females and day of the nesting season (i.e., larger females nested earlier in the season compared to smaller females; Spearman's $r_s = -0.212$; $P < 0.001$; n = 1,432; Fig. 4).

We observed female map turtles nesting between 0725 and 1743, with peak nesting activity during mid-morning (Fig. 5). Nesting duration for nine females observed from the beginning of excavation until departure averaged 82.4 min (min-max = 61–143 min; SD = 25.7 min). During the first year, only two of 50 nests were constructed in sand. That first year, most females walked over or around the sand mounds and nested near the turtle fence, with an average distance from nest to the turtle fence of only 0.46 m (min-max = 0.15–2.25 m). In the mitigated area, straight-line distances of nests to the river averaged 29.5 m (min-max = 11.6–76.2 m). In an attempt to provide better habitat, much of the sand was moved closer to the turtle fence and mixed with soil, gravel, and shale prior to our second year of study, after which time we were unable to distinguish individual substrate materials within the mitigated area.

Body temperatures of all reproductive female *G. geographica* captured on land during the nesting season averaged 25.5° C (Table 2, Fig. 5c). Females captured on coal tailings had significantly higher body temperatures (mean = 26.7° C; min-max = 17.0–37.4° C; n = 299) than females captured in the area of the fence (mean = 24.7° C; min-max = 15.4–35.6° C; n = 490; $t = 7.37$; df = 787, $P < 0.001$). The fenced area contained a mixture of sand, soil and rock substrates. We observed some females with body temperatures above 34° C

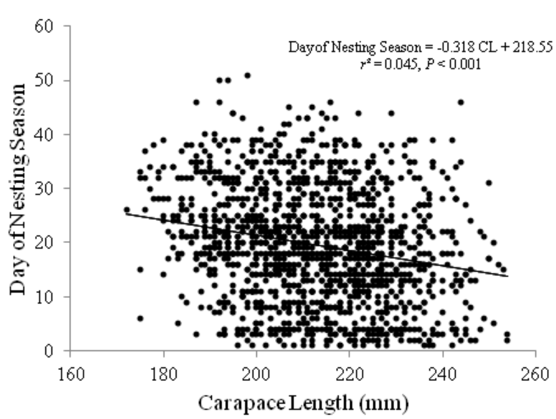

FIGURE 4. Linear relationship of day of nesting season with female Northern Map Turtle (*Graptemys geographica*) carapace length at Mount Union, Pennsylvania, USA.

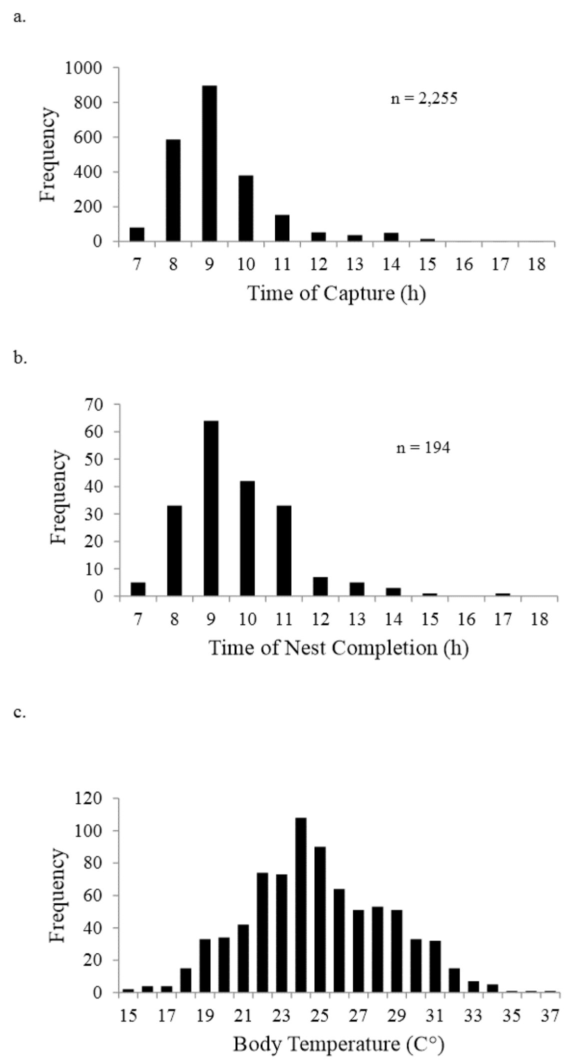

FIGURE 5. Distributions of (a) time of capture, (b) time of nest completion, and (c) body temperatures of female Northern Map Turtles (*Graptemys geographica*) in nesting areas at Mount Union, Pennsylvania, USA. Time depictions are based on the nominal hour of observation.

TABLE 2. Sample size (n), mean, standard deviation (Std Dev), and minimum and maximum (Min-Max) of various characteristics of reproductive female Northern Map Turtles (*Graptemys geographica*) at Mount Union, Pennsylvania, USA.

Variable	n	Mean	Std Dev	Min-Max
Plastron Length (mm)	535	179	11.7	150–227
Carapace Length (mm)	535	206	16.1	172–251
Body Mass (g)	535	1,194	289.8	660–2,500
Clutch Size	69	10.3	2.2	6–15
Body Temperature (° C)	794	25.5	3.7	15.4–37.4

abandon their uncovered nests and move quickly to shade.

During the first year of the study (2000), 10 turtles were killed on the road (Table 1). No map turtles were seen climbing or attempting to climb the turtle fence, but some females moved around it. Following that first nesting season and our discovery that some turtles nested beyond the northern end of the turtle fence, we installed approximately 300 m of welded wire fencing along the guardrails in that area. The additional fencing, annual maintenance such as patching the fence and filling holes under the fence caused by erosion, and our field crew actively moving turtles off the road all combined to reduce subsequent mortality, with 19 additional turtles found dead during subsequent years (Table 1).

Reproductive ecology.—We estimated minimum female age at maturity at 9 y and the median age at 14 y from scute annulus counts at first capture (Fig. 6a, b). Clutch sizes of 69 females averaged 10.3 eggs (Table 2; Fig. 7a). The linear relationship between clutch size and female carapace length (CL) was significantly positive ($F_{1, 67}$ = 4.61; P = 0.030; Fig. 7b). Larger and heavier females also produced larger and heavier hatchlings (Fig. 8).

We found substantial variation in body size among all reproductive females, with a CL range of 79 mm and a 3.8-fold range in body mass (Table 2). Among 378 females with clearly discernible carapace scute annuli, body sizes (CL) of older females were larger than those of younger females (Fig. 6a), and there was a significant linear relationship between CL and annulus count (CL =

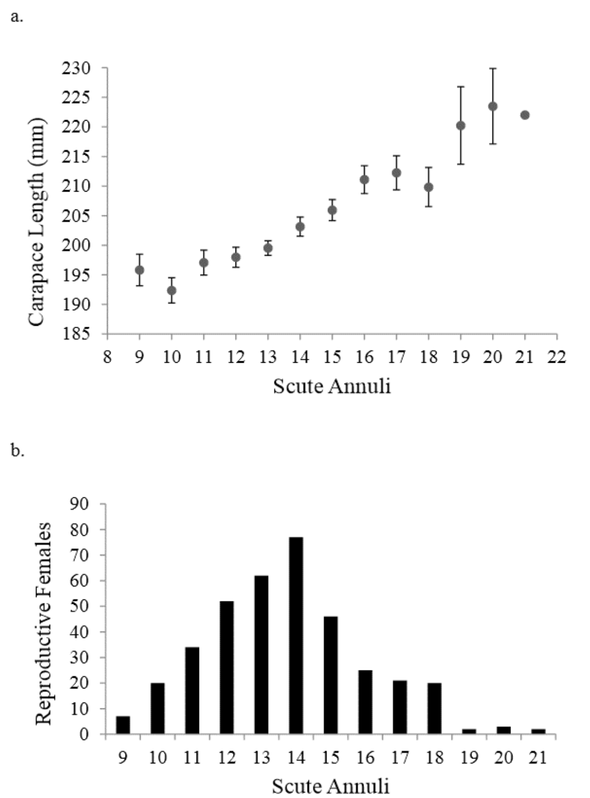

FIGURE 6. (a) Mean carapace length ± 1SE for each annuli count and (b) the distribution of reproductive female Northern Map Turtles (*Graptemys geographica*) with visible carapace scute annuli at first capture, Mount Union, Pennsylvania, USA.

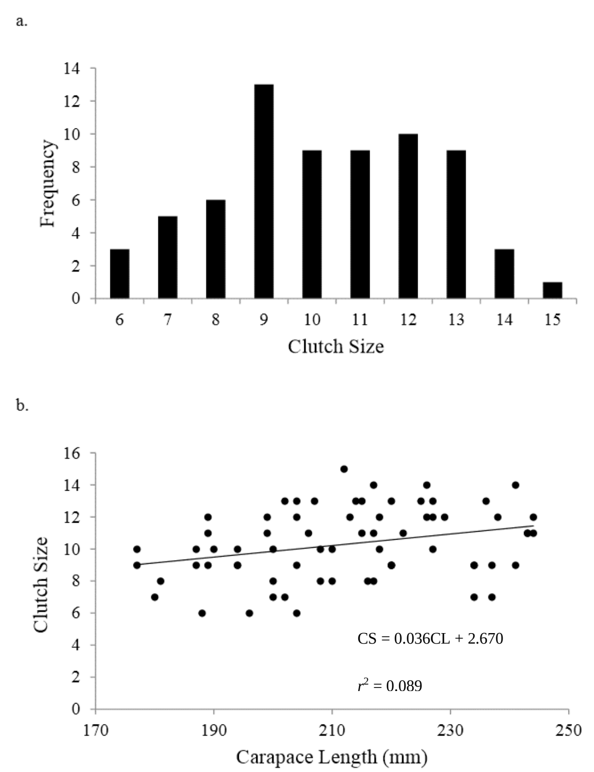

FIGURE 7. (a) Distribution of Northern Map Turtle (*Graptemys geographica*) clutch sizes (mean = 10.3 eggs), and (b) the linear relationship between clutch size and female carapace length at Mount Union, Pennsylvania, USA.

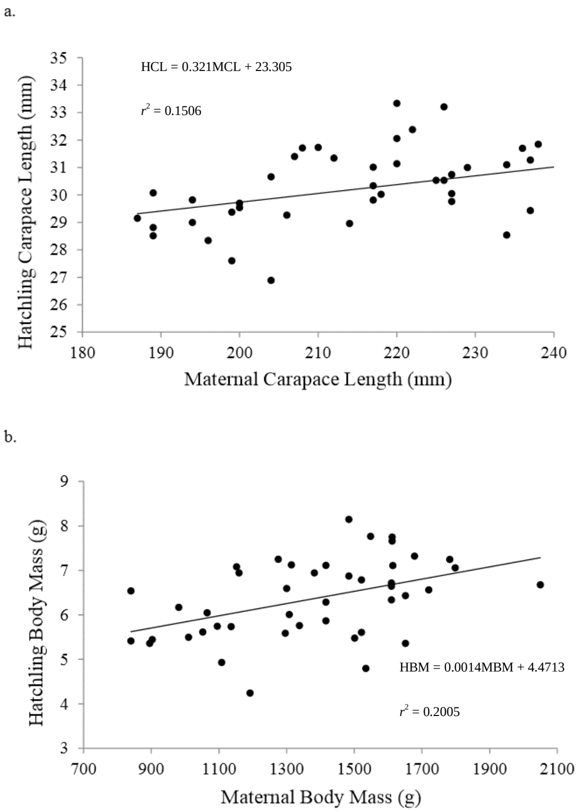

FIGURE 8. Linear relationships between (a) hatchling carapace length (mean per clutch) and maternal carapace length and (b) hatchling body mass (mean per clutch) and maternal body mass of Northern Map Turtles (*Graptemys geographica*) at Mount Union, Pennsylvania, USA.

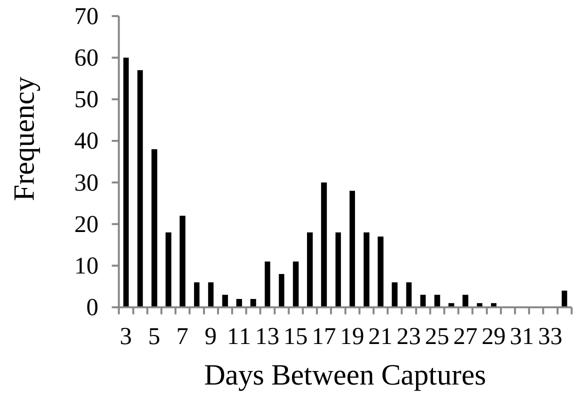

FIGURE 9. Frequency distribution for capture intervals > 2 d within each nesting season for reproductive female Northern Map Turtles (*Graptemys geographica*), Mount Union, Pennsylvania, USA.

166.4 + 2.65×annulus count; r^2 = 0.20, $F_{1, 367}$ = 94.05; P < 0.001). Average CL and body mass of the 27% of individuals for which we could not determine age (n = 157) were 214 mm CL and 1,339 g, respectively, values that were significantly larger than for turtles with discernable annuli (203 mm CL and 1,133 g body mass; n = 378; CL: t = 7.54, df = 533, P < 0.001; body mass: t = 7.90, df = 533, P < 0.001). During the 10 y following the estimated age of first reproduction, female *G. geographica* grew an average of 25 mm (2.5 mm/year).

The frequency distribution of the number of days between captures of individual female *G. geographica* in nesting areas was strongly bimodal (Fig. 9). Based on the substantial interval increase at 13 d (Fig. 9), we determined that recapture intervals < 13 d represent repeated nesting attempts by females carrying the same clutch; whereas, intervals > 13 d represent turtles with distinct (typically first and second) clutches. Based on a 13-d minimum interval between clutches, the proportion of female *G. geographica* producing two clutches ranged from 12 to 21% annually (Table 3). Two gravid females were captured three times during single nesting seasons with capture intervals > 13 d, and four females were captured with 34-d intervals. Thus, our minimum estimate of production of third clutches in *G. geographica* is 0.5%, based on evidence of six of 1,324 females producing three clutches. Females that produced multiple clutches were significantly larger and heavier (means 210 mm CL and 1,271 g, respectively; n = 110) than females that produced only single clutches (means 205 mm CL and 1,173 g, respectively; n = 423; CL: t = −2.97, df = 533, P = 0.003; body mass: t = −3.21, df = 533, P = 0.001).

DISCUSSION

Nesting ecology.—Over eight years, the beginning of nesting for Juniata River map turtles varied by almost one month, from 22 May in 2000 to 20 June in 2003. During 2003, cool cloudy weather and elevated river levels during April and May reduced available basking sites and that apparently reduced rates of follicle development, delaying ovulation and the subsequent onset of nesting. Nesting seasons of other freshwater turtles at northern latitudes started earlier when there were more warm days during spring (Vogt 1980; Congdon et al. 1983, 1987; Obbard and Brooks 1987; Gibbons and Greene 1990; Geller 2012).

Among all years of our study, we found a significant but weak trend of larger females nesting earlier in the season compared to smaller females. Larger females may contain proportionally more energy reserves in the form of stored lipids, which allow them to allocate resources earlier during spring (Price et al. 1988). Larger females may be able to maintain preferred body temperatures over longer periods and more often during fall and spring, and thus be able allocate resources earlier each year (Congdon 1989). The late start of nesting during 2003 was associated with a very late end to the nesting season that year (1 August). We are not

TABLE 3. Number of reproductive female Northern Map Turtles (*Graptemys geographica*) and estimated proportion producing two clutches per year, based on a minimum 13-d inter-nesting interval.

Year	Total Number of Females	Capture Interval ≥ 13 d	Proportion with Two Clutches (%)
2000	141	29	21
2001	177	33	19
2002	234	27	12
2003	222	28	13
2005	114	18	16
2006	227	29	13
2007	209	24	12
Mean	189.1	26.9	14.2

aware of any other reports of turtles above 40° N latitude nesting during August, but some *Graptemys* species nest during August in the southern United States (Horne et al. 2003; Lovich et al. 2009).

Peak nesting activity of *G. geographica* occurred during mid-morning, with some activity through early afternoon, especially on rainy, overcast days with reduced mid-day temperatures (see also Vogt 1980). Female map turtles in Wisconsin (*Graptemys pseudogeographica* and *Graptemys ouachitensis*) nested from 0545 to 2030 and the majority of nests were completed before 1000 (Vogt 1980). Geller (2012) also found a predominance of morning nesting by *G. ouachitensis* in Wisconsin, and variation in daily and annual temperatures influenced the timing of nesting. Diurnal nesting reduces exposure of turtles to nocturnal or crepuscular predators, but may increase the risks of overheating and desiccation (Stone and Iverson 1999).

Temperatures and coal substrates.—Turtle body temperatures at the Mount Union nesting area varied by more than 20° C among reproductive females, ranging from 15.4 to 37.4° C. Body temperatures of a smaller sample of nesting *Graptemys* in Wisconsin ranged from 24.6 to 28.2° C (Vogt 1980). Preferred body temperatures of *G. geographica* under experimental and natural conditions are reported to range from about 20 to 30° C (Nutting and Graham 1993; Ben-Ezra et al. 2008; Bulté and Blouin-Demers 2010). Major influences on turtle body temperatures include levels of insolation energy (resulting in part from time of day and day of year), cloud cover, shading due to vegetation, and substrate color.

The coal tailings at Mount Union were uniformly black and contrasted with lighter-colored substrates of sand, soil, gravel, and shale found in the mitigated area (Nagle et al. 2004). Compared to females nesting on the lighter colored substrates, those nesting on the black coal tailings had elevated body temperatures. Some individual turtles with body temperatures above 34° C appeared overheated and physiologically impaired. Core body temperatures > 35° C are fatal to *G. geographica* (Akers and Damm 1963).

Vegetation on the coal tailings was sparse compared to the mitigated area, which has a substantial amount of early successional vegetation around the sand mounds that are partially shaded by dense forest canopy along areas closest to the river. In partially shaded areas along the turtle fence, female body temperatures were significantly lower than temperatures of females nesting in more open areas on coal tailings. Female turtles may select coal tailings for nesting because the substrate has reduced vegetation, is relatively easy to excavate, is well-drained, and has elevated nest temperatures (Roy Nagle, unpubl. data). Two potential problems for embryos incubating in coal tailings are low pH and elevated levels of heavy metals. In another emydid turtle, *Trachemys scripta*, eggshells and eggshell membranes provided an effective barrier to trace element uptake from coal fly ash that might otherwise have harmed developing embryos (Nagle et al. 2001). Whether or not membranes of *G. geographica* eggs are also barriers to trace elements has not been determined and nests in coal tailings may pose a conservation concern for developing embryos. Compared to nests in the mitigated area, temperatures of nests on the coal tailings are higher and, owing to temperature-dependent sex determination in *Graptemys* (Bull and Vogt 1979), may result in female-biased hatchling sex ratios (Roy Nagle, unpubl. data). If female-biased hatchling sex ratios from clutches of eggs incubated in coal tailings are the norm, then adult sex ratios in the population should also be female-biased because the coal tailings have been present at Mount Union for a century.

Reproductive ecology.—We estimated the minimum age at sexual maturity for gravid female *G. geographica* as nine y (n = 7). Minimum sizes of reproductive females were carapace lengths > 171 mm and body masses of 700–800 g. Given the small number of turtles found with nine annuli, the large number of turtles first captured gravid with greater than nine annuli, and the wide ranges of age at maturity documented among other freshwater turtles (5–7 y: Congdon and van Loben Sels 1991; Congdon et al. 1994, McGuire et al. 2011), it seems likely that many female *G. geographica* mature beyond the minimum age. Based on growth rates, Iverson (1988) estimated that female *G. geographica* in Indiana require at least 9–10 y to reach maturity, and Bulté and Blouin-Demers (2009) estimated that females in Ontario require a minimum of 12 y. Vogt (1980) reported that some 10- and 12-y-old female *G. geographica* in Wisconsin had not yet reached sexual maturity. Male *G. geographica* mature at much smaller sizes and younger ages (Vogt 1980; Iverson 1988; Bulté and Blouin-Demers 2009; Lindeman 2013). For female *G. geographica*, the long delay in reaching sexual maturity suggests that average juvenile survivorship from age one to maturity must remain high to maintain a stable population (Congdon et al. 1993, 1994).

Clutch size typically increases with body size of female turtles, both within and among species (Congdon and Gibbons 1985). In our study, the relationship between clutch size and body size of female *G. geographica* was positive but weak, and a similar weak, positive relationship was found between log transformed plastron length and clutch size for the population at Presque Isle State Park, Erie, Pennsylvania (r = 0.35, P = 0.012; Ryan and Lindeman 2007). In the smaller Yellow-blotched Map Turtle (*Graptemys flavimaculata*) in Mississippi, USA, there was a much stronger positive relationship between clutch size and female body size (Horne et al. 2003).

The female *G. geographica* at Mount Union whose ages could not confidently be assessed (27%) were significantly larger and heavier than individuals with discernible annuli. The majority of females for which we could not determine age are likely to be at least as old as individuals with the maximum number of visible annuli (21). Although no long term mark-recapture studies have been conducted on natural populations that document maximum longevity of *G. geographica*, based on correlations between age at maturity and longevity among vertebrates (Charlesworth 1980; Charnov and Berrigan 1990; Prothero 1993), *G. geographica* is likely a relatively long-lived species.

The most rapid adult growth in female turtles usually occurs within 10 y following maturity (Bjorndal et al. 2012; Congdon et al. 2013). In our study, female *G. geographica* grew an average of 25 mm (2.5 mm/year) during the 10 y following the minimum age of first reproduction; growth that would, on average, confer an increase in clutch size of one egg. Much of the variation in body size of female map turtles likely results from variation in juvenile growth rate and age at maturity (Carr and Goodman 1970; Bjorndal et al. 2012; Congdon et al. 2013), as is the case in many other vertebrate ectotherms (Halliday and Verrell 1988).

Reproductive output is correlated with female body size in many reptiles, including turtles (Cox and Marion 1978; Ewert 1979; Iverson 1979; Gibbons 1982; Congdon and Gibbons 1985). Larger females produce larger offspring (Congdon and Gibbons 1985, 1987), more offspring (Smith and Fretwell 1974; Brockelman 1975), or both. Larger female *G. geographica* allocate energy to both larger clutches and larger individual offspring (Ryan and Lindeman 2007, our study). The reproductive pattern exhibited by *G. geographica* is consistent with a morphological constraint on offspring size hypothesis, where egg size, particularly among smaller females, increases proportionately with width of the pelvic aperture (Tucker et al. 1978; Congdon and Gibbons 1987; Ryan and Lindeman 2007).

Body sizes of female *G. geographica* captured on land near the Juniata River were larger than females from Indiana (Conner et al. 2005) and smaller on average than turtles from Wisconsin (Vogt 1980) and Lake Erie, Pennsylvania (Ryan and Lindeman 2007); however, maximum sizes in the Wisconsin and Pennsylvania populations were nearly identical. In accordance with smaller female body size, both clutch size and hatchling body size of Juniata River map turtles were slightly smaller than those in the Erie, Pennsylvania population (Ryan and Lindeman 2007). Because body sizes of female turtles and their hatchlings are positively associated in both populations, reproductive allocation in *G. geographica* represents a pattern of compromise between producing exclusively more offspring of optimal size (Smith and Fretwell 1974; Brockelman 1975) or larger offspring of a fixed clutch size.

Reproductive frequency is one of the largest contributors to variation in reproductive output of female turtles (Gibbons 1982; McGuire et al. 2014). Our estimate of a 13-d minimum inter-nesting interval of *G. geographica* is similar to that found in other studies, which described minimum inter-nesting intervals of about two weeks (Gibbons 1982; Gibbons and Greene 1990; Horne et al. 2003; Jones 2006; Ryan and Lindeman 2007). At Mount Union, the 110 female *G. geographica* that produced multiple clutches were larger than 423 females that produced single clutches, demonstrating yet another reproductive advantage for larger body size.

Clutch frequency has been a difficult reproductive parameter to determine in map turtles due to very low recapture rates of nesting females in field studies (Lindeman 2013). Based on dissections which indicate maximum reproductive potential, White and Moll (1991) estimated annual clutch frequency of 2.3 with a range of 2 to 3 clutches per year for *G. geographica* in Missouri. Our estimate that 12 to 21 % of *G. geographica* in the Juniata River produce two clutches and 0.5 % produce three clutches annually results in an estimated reproductive frequency of about 1.15 clutches per year. Similar estimates have been established for *G. oculifera* (1.1; Jones 2006) and *G. flavimaculata* (1.2; Horne et al. 2003) in the other mark-recapture field studies that examined reproductive frequency in map turtles.

Overview of conservation challenges and nesting area mitigation.—Across their range, map turtle populations are susceptible to declines due to very specific habitat requirements, limited distributions (Moll and Moll 2004; Ernst and Lovich 2009; Lindeman 2013), and the sensitivity of populations to road mortality (Gibbs and Shriver 2002) or nest-site disturbances (Moore and Seigel 2006). Additional ongoing conservation challenges in Pennsylvania include habitat loss and disturbance, water pollution, and invasive species (Nagle 2010; Lindeman 2013). The Juniata River provides all of the major habitat requirements for *G. geographica*, including heterogeneous aquatic areas with variable depths and flow rates (Pluto and Bellis 1986), numerous basking sites, adequate levels of invertebrate prey, and accessible terrestrial nesting habitat at Mount Union (Nagle et al. 2004; Nagle 2010).

During our study, installation of the turtle fence substantially reduced female road mortality on a newly constructed highway. Adding nesting substrate on the river side of the turtle fence resulted in extensive use of the area by many females, yet several challenges remain regarding the continued effectiveness of the mitigation protocols. Heavy equipment operations in the constructed nesting areas can cause negative impacts during much of the year, because either nesting females, embryos incubating in nests, or hatchlings delaying emergence from nests result in turtles being present at the site during every month. Vegetation in the mitigated area has rapidly undergone succession and has apparently caused a substantial decrease in nesting by turtles in recent years, yet use of the coal tailings nesting area by turtles appears to have increased (Roy Nagle, pers. obs.). The coal tailings area may be removed and used for fuel at modern cogeneration power plants. A more immediate problem is that the turtle fence requires continued maintenance to be effective in preventing female road mortality.

More than 100 female *G. geographica* migrate to Mount Union each summer seeking access to nesting habitat, making the site the largest riverine turtle nesting area known in central Pennsylvania. We recommend the following continued efforts to maximize the progress already obtained by mitigation: (1) maintenance of the turtle fence to reduce road mortality; (2) maintenance of open areas among the herbaceous vegetation, shrubs, and trees in the mitigated area (although use of herbicides in nesting areas may be problematic for developing embryos, Sparling et al. 2006; deSolla and Martin 2011); (3) nesting habitat replacement or restoration in the event that the coal tailings pile is removed; and (4) continued research of the risks, costs, and benefits incurred by turtles nesting both near the highway and in the coal tailings. Unless long-term issues that negatively impact conservation goals can be addressed, the combined threats to the nesting areas and to adult female *G. geographica* may reduce hatchling recruitment at what appears to be an important source population. Protection of adult females and continued management of the Mount Union nesting areas will help ensure long-term viability of *G. geographica* of the Juniata River.

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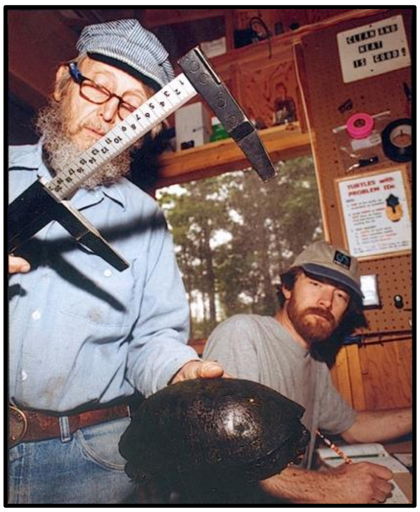

JUSTIN D. CONGDON (left) and **ROY D. NAGLE** (right) have been studying turtles together since 1987, and this is their 20th paper together. Roy Nagle is Director of Environmental Health and Safety and Instructor of Environmental Science and Studies at Juniata College in Huntingdon, Pennsylvania, USA. For 20 y Roy worked on a long-term life-history study of freshwater turtles on the E.S. George Reserve, Michigan. He was awarded a Pennsylvania Quality Initiative Environmental Award in 2001 for his work to conserve the Mount Union population of map turtles. His current research includes studies of box turtles, map turtles and wood turtles in central Pennsylvania. Justin Congdon is Professor Emeritus at the University of Georgia, Savannah River Ecology Laboratory where he conducted research on the physiological ecology and toxicology of vertebrates and invertebrates. He was PI on a 33-y study (1975-2007) of the life histories of three species of turtles on the University of Michigan's E. S. George Reserve near Hell, Michigan. Justin was the recipient of the *Prix Longevite* from Foundation Ipsen in 2001 for his research on aging in turtles. He currently studies Sonoran Mud Turtles in SE Arizona and hatchling orientation and dispersal from nests of freshwater turtles in Minnesota. (Photographed by Barry Yeoman).