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DIFFERENTIAL USE OF PONDS AND MOVEMENTS BY TWO SPECIES OF AQUATIC TURTLES (*CHRYSEMYS PICTA MARGINATA* AND *CHELYDRA SERPENTINA SERPENTINA*) AND THEIR ROLE IN COLONIZATION

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***Abstract*.—We examined turtle populations occupying eight artificial ponds in Westmoreland County, southwestern Pennsylvania, USA. Beginning in 2005, we used sardine-baited hoop-nets to trap turtles for eight consecutive years at one pond. In 2013, we expanded sampling to include seven additional ponds near the primary study pond. We deployed and checked traps during two 5-d periods at all eight ponds, once in June and again in July 2013. Two of the 12 turtle species native to Pennsylvania were detected, Common Snapping Turtle (*Chelydra serpentina serpentina*; n = 53) and Midland Painted Turtle (*Chrysemys picta marginata*; n = 70). We found the Common Snapping Turtle at all surveyed ponds and its abundance was associated with larger, sparsely vegetated ponds. We found the Midland Painted Turtle at six of the eight surveyed ponds and its abundance was associated with smaller, heavily vegetated, ponds. Juveniles of both species were distributed differently than adults and were most common in shallow, heavily vegetated ponds with low visibility and were absent or nearly so from deep ponds with little emergent vegetation favored by adults. Across eight years, the number of juveniles was low or they were absent from the primary study pond, yet recruitment was likely maintained through a nearby nursery pond favored by juveniles. In this heterogeneous pond matrix, turtle population structures were strongly influenced by certain physical features of the ponds to the benefit of one life stage over another. Species composition was influenced in a likewise manner. Inter-pond movements were likely encouraged by local habitats and resident population structures. We suggest that ponds can be constructed or modified to accommodate one or more life stages of these turtle species, and enhance opportunity for pond colonization and gene flow among ponds.**

Key Words.—Common Snapping Turtle; dispersal; Midland Painted Turtle; Pennsylvania; pond; Powdermill Nature Reserve

INTRODUCTION

Population dynamics and movement patterns have been well studied for many major vertebrate groups, such as fish (Krkosek et al. 2011), birds (Fasola et al. 2010), and mammals (Luis et al. 2010), but reptiles, especially turtles, have been unevenly examined (Ernst and Lovich 2009). Insufficient information and incomplete data sets are contributing factors to the decline of many turtle species (Klemens 2000; Bonin et al. 2006). Long-term studies are necessary to provide enough data to ascertain movement patterns by individuals belonging to different demographic groups (Gibbons 1986) and to accurately assess population trends over time (Riedle et al. 2009), particularly in long-lived vertebrates such as turtles (Gibbons 1987). To understand these phenomena and establish effective conservation measures (Gibbons 2003), it is critical to gather data on local population structures and sizes (Buhlmann 1995; Jones 1996).

Some species of freshwater turtles have been documented to move up to 5.83 km in streams (Pluto and Bellis 1988) and up to 0.29 km in pond habitats (Hall and Steidl 2007), and traverse terrestrial landscapes, thereby colonizing new aquatic habitats (Bennett et al. 1970; Tuberville et al. 1996; Bowne et al. 2006). Dispersal events of freshwater species may be stimulated innately (e.g., attainment of sexual maturity, search for mates by males, or nesting by females) or by stochastic events (e.g., rainfall, flooding, drought, or seasonal changes) (Sexton 1959; Gibbons 1970; Brown and Brooks 1993; Bodie et al. 2000). Turtles that occur in isolated ponds are excellent models for studies of movement patterns (Parker 1984) and for comparing assemblage-level responses to habitat features; first, because travel between ponds may be restricted as it requires traversing unfavorable terrain (Kiester et al. 1982) or may have costs in terms of increased exposure to predators and desiccation; and second, because each pond will undoubtedly possess a unique suite of physical characteristics to examine (Scott 1976).

Pennsylvania has 12 native turtle species (Meshaka and Collins 2012), yet studies relating to the population ecology of turtles in the state are generally uncommon,

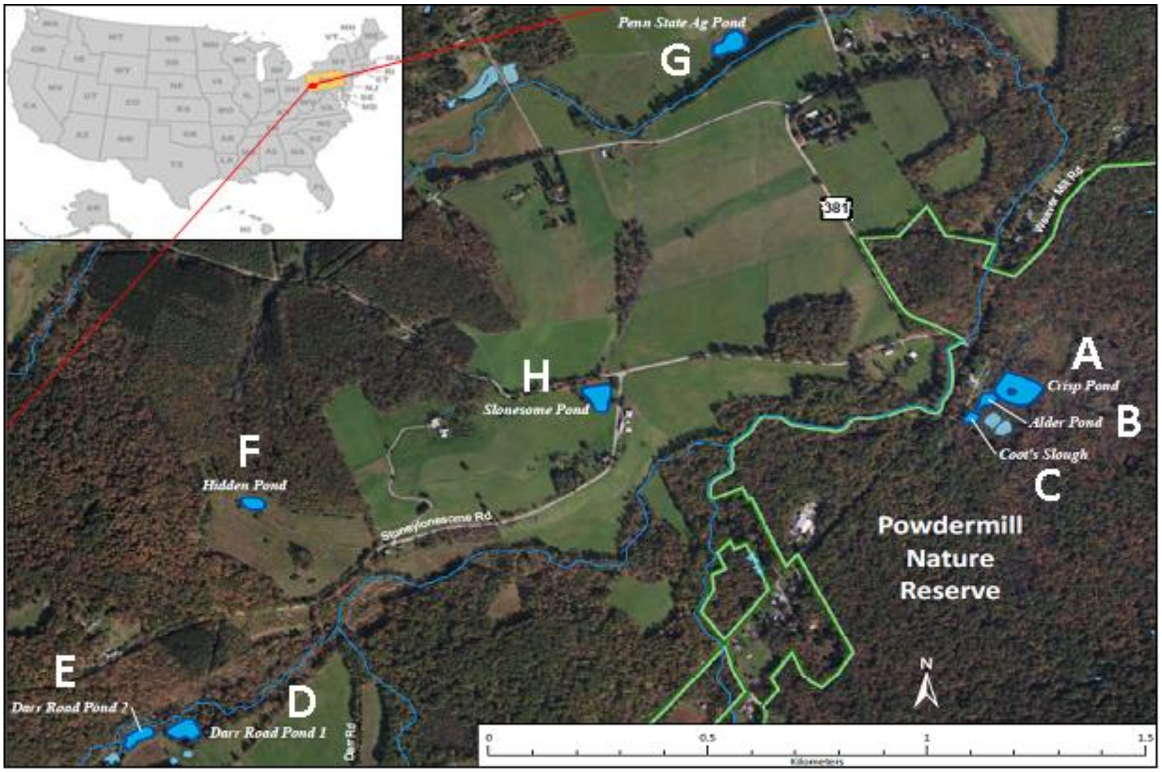

FIGURE 1. The study area in Westmoreland County, Rector, Pennsylvania, USA, depicting the eight artificial ponds (A-H) and other major landmarks. Powdermill Nature Reserve denoted by green boundary.

with notable exceptions (e.g., Ernst 1971, 1971a, 1971b, 1971c; Ernst and Ernst 1971). Here, we investigated the population dynamics and movements of the Midland Painted Turtle *Chrysemys picta marginata* (Agassiz 1857), and the Common Snapping Turtle *Chelydra serpentina serpentina* (Linnaeus 1758), as they relate to structural aspects of eight artificial ponds in Westmoreland County, southwestern Pennsylvania, USA, during 2005–2013. To explain differences in population size and structure of both species among ponds, we compared the effects of pond characteristics and dispersal phenomena. We set out to answer the following questions: How have species in aquatic turtle assemblages in southwestern Pennsylvania responded to local habitat features, as observed in certain demographic features of pond residents, and, in turn, how did these responses affect patterns of inter-pond movements in relation to colonization?

MATERIALS AND METHODS

Study area.—Powdermill Nature Reserve (PNR), established as a field station in 1956 for the Carnegie Museum of Natural History, is an 856.2 ha preserve located along the western flank of Laurel Hill in eastern Westmoreland County, Pennsylvania, USA. Westmoreland County receives average precipitation of approximately 119 cm annually (Morton and Speedy 2012). The major habitat of PNR is primarily mixed mesophytic forest, dominated by tree types such as oaks (*Quercus* sp.), maples (*Acer* sp.), and beeches (*Fagus* sp.; Utech 1999). Previously farmed tracts of land within PNR have since succeeded to a current condition of mixed forest, such that < 5% of the property is now primary or secondary grassland. The principal natural water feature of PNR is Powdermill Run and its associated tributaries. Artificial ponds of various sizes and depths were created near the northern boundary of the reserve in the 1960s, in part to attract migratory birds for the banding program of the station (Powdermill Avian Research Center). The reserve, founded in 1956 by M. Graham Netting, has launched several long-term ecological programs to monitor the resident fauna, including birds (e.g., Marra et al. 2005) and snakes (e.g., Meshaka 2010).

Study ponds.—We trapped turtles at eight artificial ponds; three were located on the northern periphery of PNR, and the remaining five ponds were scattered across the adjacent agricultural property (Fig. 1). The eight ponds are Crisp Pond (Fig. 2A), Alder Pond (Fig. 2B), Coot's Slough (Fig. 2C), Darr Road Pond 1 (Fig. 2D),

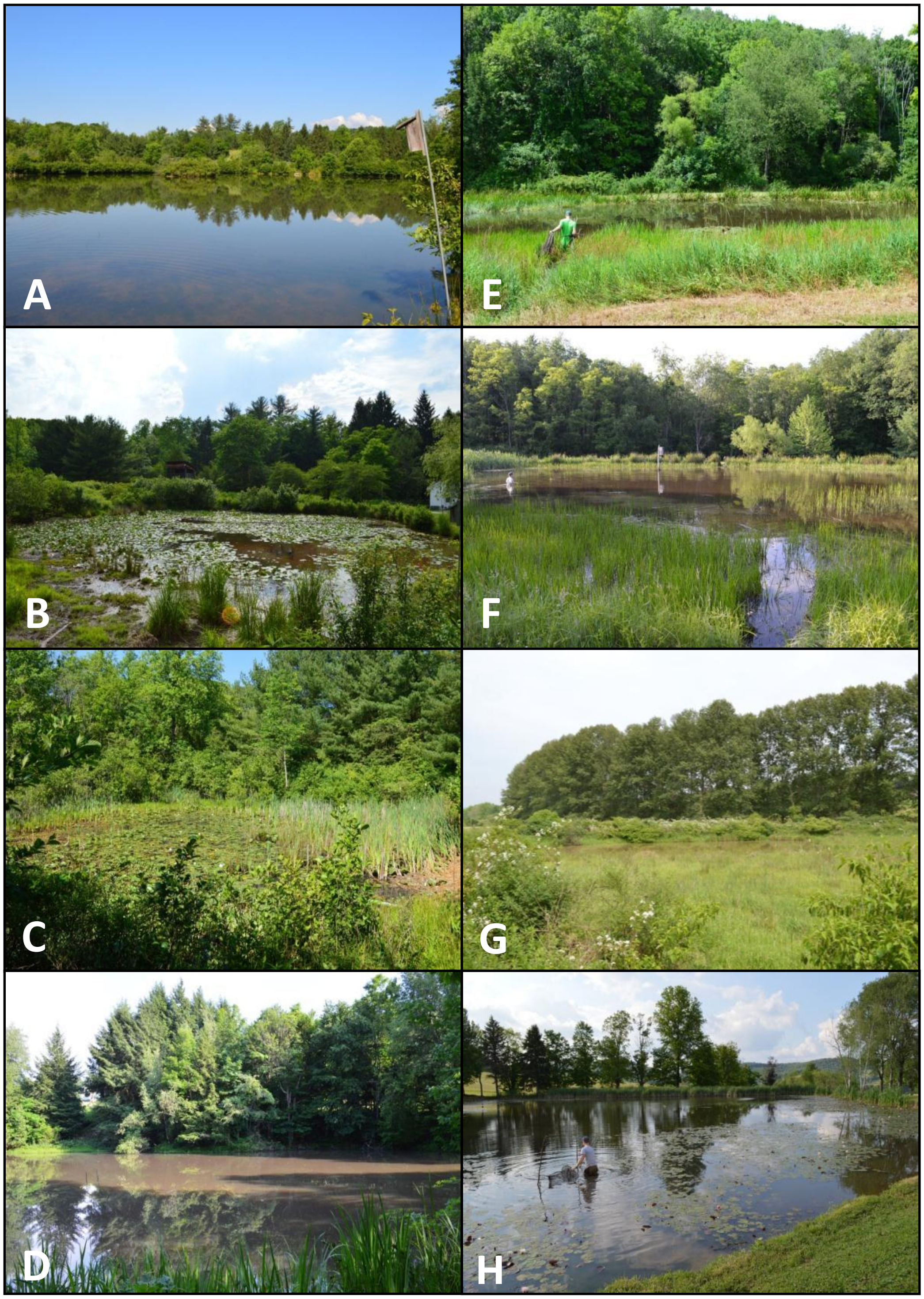

FIGURE 2. Habitat pictures of eight artificial ponds in Westmoreland County, Rector, Pennsylvania, USA. **A:** Crisp Pond, Powdermill Nature Reserve. (Photographed by Daniel F. Hughes). **B:** Alder Pond, Powdermill Nature Reserve. (Photographed by Daniel F. Hughes). **C:** Coot's Slough, Powdermill Nature Reserve. (Photographed by Daniel F. Hughes). **D:** Darr Road Pond 1. (Photographed by Daniel F. Hughes). **E:** Darr Road Pond 2. (Photographed by Jaclyn M. Adams). **F:** Hidden Pond. (Photographed by Jaclyn M. Adams). **G:** Penn State Pond. (Photographed by Daniel F. Hughes). **H:** Slonesome Pond. (Photographed by Jaclyn M. Adams).

TABLE 1. Pond characteristics of eight artificial ponds from this study located in Westmoreland County, southwestern Pennsylvania, USA.

Pond	Max Depth (m)	Littoral Zone	Dominant Vegetation (genus)	Open Water	Fish	Visibility	Year Created	Perimeter (m)	Area (m^2)
Alder Pond	< 1.5	> 90 %	*Typha/Nymphaea*	< 10%	N	Low	1977	145.7	1198.8
Coot's Slough	< 1	> 90 %	*Typha/Nymphaea/ Menyanthes*	< 10%	N	Low	1977–1980	109.1	872.0
Crisp Pond	4–5	< 25 %	*Typha*	> 90%	Y	High	1961	293.7	5989.3
Darr Rd Pond 1	3–4	< 25 %	*Cyperaceae*	> 90%	Y	High	1957	207.1	2784.9
Darr Rd Pond 2	2.5–3	50 %	*Typha*	75%	Y	Low	1957	196.0	1975.2
Hidden Pond	2.5–3	50 %	*Typha/Nymphaea*	75%	Y	High	ca. 1957–1967	141.7	1411.3
Penn State Pond	1.5–2	> 90 %	*Typha*	> 90%	N	Low	ca. 1970	215.6	2856.6
Slonesome Pond	4–5	< 25 %	*Typha/Nymphaea*	> 90%	Y	High	ca. 1957–1967	227.1	3117.8

Darr Road Pond 2 (Fig. 2E), Hidden Pond (Fig. 2F), Penn State Pond (Fig. 2G), and Slonesome Pond (Fig. 2H). Crisp Pond was the initial focus of a mark-recapture study that began in 2005. Crisp Pond was established in 1961 and its intended purpose, in addition to serving as a dike, was to attract migratory birds. Although the Common Snapping Turtle was first recorded at this pond in 1964, 3 y after its creation, and the Midland Painted Turtle in 1977, 16 y after its creation, the sampling methods for these captures were not consistent. Thus, we do not include these captures in the standardized results; however, we do incorporate some of these historic capture data into the population estimates at Crisp Pond and the discussion for comparative purposes. Standardized trapping occurred at Crisp Pond since 2005. In 2013, we expanded sampling to include seven additional ponds both on PNR and in the nearby vicinity (Fig. 1). We initiated the expansion of the study area with the expectation that marked turtles previously captured at Crisp Pond would be detected if they completed a movement to one of the newly included ponds.

Pond features.—To explain turtle assemblage dynamics, we characterized nine habitat features of the eight ponds from a combination of GIS measurements, qualitative observations, personal accounts, and direct measurements. We determined pond size (i.e., area and perimeter) from PNR land-cover layers generated in ArcGIS (v. 10.0, ESRI, Redlands, California, USA). The dates of pond construction were provided by Robert C. Leberman (pers. comm.), one of the charter employees of PNR. We measured pond depth in meters with a tape measure. We identified dominant vegetation present at each pond to genus and we recorded fish (i.e., species and abundance), when captured in the turtle traps. We assigned percentages of extent of open water, littoral zone, and turbidity (i.e., visibility) based on repeated observations and photographic comparisons (Table 1).

We pooled turtle capture data from ponds that exhibited a common suite of habitat features for statistical analyses. For example, shallow ponds generally possessed a small size, large littoral zone, no fish found in traps, highly turbid water, and dense vegetation; whereas, deep ponds generally possessed a large size, small littoral zone, fish found in traps, less turbid water, and sparse vegetation. We compared observed capture numbers of each turtle species found in particular pond types to expected capture numbers.

Trapping and marking.—We trapped turtles in mesh hoop-nets (length = 2.1 m, diameter = 1.1 m, square mesh size = 5.5 cm) baited with canned sardines in olive oil. The number of traps we set was dependent upon the size of the pond. We used two traps in most ponds. We deployed hoop-nets for two 5-d periods at all eight ponds in 2013. The two trap periods were carried out once in each of June and July 2013. We checked traps for turtles and re-baited daily within each 5-d period. At the end of the 5-d trap period, we removed all nets from each pond. We used the two consecutive trapping sessions to ascertain an accurate measure of population sizes and structures by maximizing the total number of captures. Trapping intensity and frequency varied in the years prior to 2013, but were otherwise similar in methodology to the approach outlined above.

The two trap periods in 2013 did not cover the extent of seasonal activity for turtle species in Pennsylvania and may not have been sufficient to detect inter-pond overwintering movement patterns. However, June and July represent typical peaks in activity for several turtle species in the northeastern United States, such as the Midland Painted Turtle (Ernst 1971, 1971b), the

Common Snapping Turtle (Brown and Brooks 1993), the Common Musk Turtle, *Sternotherus odoratus* (Ernst 1986), and the Bog Turtle, *Glyptemys muhlenbergii* (Pittman and Dorcas 2009). Consequently, we feel that our two trap periods in 2013 provide reliable temporally constrained snapshots of the capacity of a pond to support turtles at that time and offer general patterns of pond occupancy.

We individually marked all turtles by notching marginal scutes with a metal file. We marked hatchlings and small juveniles by cutting a notch in marginal scutes with a sharp knife. We measured each turtle to the nearest 1 mm for maximum straight-line carapace length (CL), maximum carapace width (CW), and maximum plastron length (PL) with large or small Vernier calipers depending upon the size of the turtle. Weight (WT) was measured to the nearest 1 g by placing an individual turtle in a tared plastic bucket attached to a digital scale. We weighed smaller turtles in a plastic bag attached to a digital scale. Additional data we recorded for each individual turtle included the presence of ectoparasites, algal growth on the shell (scored as absent, light, or heavy growth), injuries, and abnormalities. We handled and photographed turtles on shore near their site of capture and released them back into the water immediately after processing.

We identified male Midland Painted Turtles by the presence of elongated claws on the forelimbs, longer thicker tails, and smaller adult body size, compared to females. We identified male Common Snapping Turtles by the presence of the cloacal opening extending well past the distal end of the carapace and larger adult body size, compared to females. Also, we used the technique demonstrated by Dustman (2013), which involved inverted Snapping Turtles for sex determination. When possible, we estimated age by counting the growth annuli on the second vertebral scute of the carapace. We assigned minimum size at sexual maturity in Midland Painted Turtles based on general sizes provided for the species by Ernst and Lovich (2009); males exceeding 90 mm CL, and females exceeding 145 mm CL. We assigned Midland Painted Turtles exceeding 90 mm CL that did not possess the secondary sexual characteristics detailed above as females, yet were not considered to be sexually mature for analyses. We assigned minimum size at sexual maturity in Common Snapping Turtles based on general sizes provided for the species by Ernst and Lovich (2009), males exceeding 250 mm CL, and females exceeding 200 mm CL. These assigned body sizes for the attainment of sexual maturity are conservative in comparison to other populations because both the age and size of these species at maturity increase with increasing latitude, and Pennsylvania is in the northerly range for both species (Ernst and Lovich 2009).

Statistical analyses.—We calculated population estimates with a mark-recapture Lincoln-Petersen Index to compare the ratio of marked turtles to the total number of turtles captured. We calculated population size (N) by the equation: $N = Mn/m$, where M was the number of marked turtles, n was the total caught during the period, and m was the number of marked turtles recaptured. We restricted capture periods to events of uninterrupted days of trapping; thus, capture periods occurred once per year in the sampling seasons prior to 2013 and twice in 2013 because we considered June and July as separate continuous capture events.

We used two-sample *t*-tests to compare mean values between samples. We used Chi-square goodness-of-fit tests to determine whether specific age-classes of turtle populations were associated with particular habitat features shared across ponds. We used contingency tables to determine if turtle abundance was evenly distributed across ponds. Statistical differences were deemed significant at $P < 0.05$.

We assessed a large number of habitat and population variables; therefore, we cannot exclude the possibility of a false-positive finding. However, we chose not to correct for multiple testing, based on the arguments of Rothman (1990), which he contends that not making data adjustments for multiple comparisons will lead to fewer errors of interpretation: when the data under evaluation are not random numbers but actual observations on nature; and chance alone is not the explanation for the observed phenomena because nature follows regular laws. Nevertheless, for readers who wish to know which results would and would not be statistically significant if we did adjust for multiple testing, we note that we conducted seven contingency table tests and 21 chi-square goodness-of-fit tests on the same data set. Therefore, to maintain a family-wise type I error rate of 0.05 using a Bonferroni-correction, P values would need to be $0.05/7 = 0.007$ and $0.05/21 = 0.002$, respectively.

RESULTS

Crisp pond from 2005 to 2013.—The population structure of the turtle assemblage captured at Crisp Pond was comprised primarily of sexually mature, large adults (Tables 2 and 3). For all captures of the Midland Painted Turtle at Crisp Pond (n = 79), 6.3% were juveniles (n = 5) and for all captures of the Common Snapping Turtle at Crisp Pond (n = 96), 3.1% were juveniles (n = 3). The largest population estimate for the Midland Painted Turtle at Crisp Pond was 13.9 turtles in 2005 and the density derived from this estimate was 23.4 turtles/ha. Likewise, the largest population size estimate for the Common Snapping Turtle at Crisp Pond was 15.9 turtles in 2005 and the density derived from this estimate was 26.7 turtles/ha. For the Midland Painted Turtle,

TABLE 2. Distribution of each species expressed as the number of new individuals followed by the number of recaptured individuals in parentheses and an estimate of abundance for each species from eight artificial ponds in Westmoreland County, southwestern Pennsylvania, USA, during 2005-2013. Asterisk (*) indicates that abundance estimates are not included in species totals.

		Species							
		Chrysemys picta marginata				*Chelydra serpentina serpentina*			
Year	Pond	Male	Female	Juvenile	Abundance	Male	Female	Juvenile	Abundance
2005	Crisp Pond	-	7 (3)	-	13.9	2 (0)	-	2 (0)	15.9
2006	Crisp Pond	-	5 (5)	-	9.8	2 (1)	1 (0)	-	5.8
2007	Crisp Pond	1 (0)	2 (3)	-	4.5	2 (3)	1 (0)	-	2.9
2008	Crisp Pond	-	1 (2)	-	2.2	0 (1)	-	-	1.4
2009	Crisp Pond	2 (1)	5 (5)	-	13.4	2 (5)	-	-	2.8
2010	Crisp Pond	4 (3)	4 (7)	2 (1)	11.8	5 (12)	-	-	6.3
2011	Crisp Pond	1 (3)	0 (2)	-	1.7	2 (15)	1 (0)	1 (0)	4.6
2012	Crisp Pond	0 (1)	1 (2)	1 (0)	3.5	0 (20)	3 (0)	-	3.8
2013	Crisp Pond	1 (1)	1 (3)	1 (0)	3.9	2 (11)	1 (1)	-	2.9
	Alder Pond	2 (1)	0 (2)	6 (13)	11.7	0 (2)	1 (0)	3 (1)	7.7
	Coot's Slough	-	-	1 (0)	1.0	-	-	1 (0)	1.0
	Darr Rd Pond 1	-	-	-	-	1 (0)	2 (5)	-	2.8
	Darr Rd Pond 2	2 (2)	-	1 (0)	2.8	2 (0)	1 (1)	-	2.8
	Hidden Pond	-	-	-	-	1 (0)	-	-	1.0
	Penn State Pond	6 (1)	4 (3)	8 (3)	19.8	3 (0)	-	3 (1)	9.8
	Slonesome Pond	1 (1)	-	-	2.9	4 (0)	1 (0)	2 (0)	6.7
	Column Totals	20 (14)	30 (37)	20 (17)	102.9*	29 (70)	12 (7)	12 (2)	78.2*
	Species Totals		70 (68)				53 (79)		

adult females (n = 26) outnumbered adult males (n = 9) and juveniles (n = 4). For the Common Snapping Turtle, adult males (n = 17) outnumbered adult females (n = 7) and juveniles (n = 3). The Midland Painted Turtle made up 45.7% of captures and the Common Snapping Turtle made up 54.3% of captures from Crisp Pond.

Capture trends in 2013.—The highest numbers of Midland Painted Turtles were found at Alder Pond (n = 11) and Penn State Pond (n = 18) and the highest numbers of Common Snapping Turtles were found at Crisp Pond (n = 8) and Slonesome Pond (n = 7). When both species were present in a pond, uneven assemblage structures existed. For example, the Midland Painted Turtle constituted > 70% of captures at Penn State Pond and Alder Pond and the Common Snapping Turtle constituted > 65% of captures at Slonesome Pond, Crisp Pond, and Darr Road Pond 1. The two species differed in numbers of new individuals across the eight ponds (2 × 8 Contingency Table, χ^2 = 15.4, df = 7, P = 0.031). The abundance of adult Common Snapping Turtles did not differ from adult Midland Painted Turtles (2 × 7 Contingency Table, χ^2 = 11.1, df = 6, P = 0.086; Coot's Slough was excluded from this analysis because no adult turtles were captured from this pond). Similarly, the abundance of juvenile Common Snapping Turtles did not differ from juvenile Midland Painted Turtles (2 × 6 Contingency Table, χ^2 = 5.31, df = 5, P = 0.379; Darr Road Pond 1 and Hidden Pond were excluded from this analysis because no juvenile turtles were captured from these ponds). The abundance of all juvenile turtles (both species) differed from all adult turtles (both species) across the eight ponds (2 × 8 Contingency Table, χ^2 = 15.3, df = 7, P = 0.033). Yet, juvenile turtle abundance did not differ from conspecific adults for both species across the eight ponds (Common Snapping Turtle: 2 × 8 Contingency Table, χ^2 = 11.1, df = 7, P = 0.133; Midland Painted Turtle: 2 × 6 Contingency Table, χ^2 = 4.89, df = 5, P = 0.430, with Darr Road Pond 1 and Hidden Pond excluded from this analysis because no Midland Painted Turtles were captured from these ponds). Lastly, the abundance of juvenile Midland Painted Turtles differed from adult Common Snapping Turtles across the eight ponds (2 × 8 Contingency Table; χ^2 = 17.8, df = 7, P = 0.001).

Chrysemys picta marginata*: *population size.—The Midland Painted Turtle (Fig. 3) was present at six sites, where it ranged in estimated abundance from 1.0 turtles at Coot's Slough to 19.8 turtles at Penn State Pond during the 2013 sampling period (Table 2). Earlier trapping effort at Crisp Pond yielded a range of estimated abundances for the Midland Painted Turtle from 1.7 turtles in 2011 to 13.9 turtles in 2005 (Table 2). In total, the Midland Painted Turtle represented 70 captures of new individuals and comprised 138 overall captures (Table 2). For all captured individuals across all sites and years, the sex-ratio slightly favored females at a ratio of 1.55:1.00, although this ratio was not

TABLE 3. Mean carapace length (mm) of adult males, adult females, and juveniles of the Midland Painted Turtle, *Chrysemys picta marginata*, and the Common Snapping Turtle, *Chelydra serpentina serpentina*, analyzed from captured individuals from eight artificial ponds in Westmoreland County, southwestern Pennsylvania, USA, during the 2013 sampling session. Mean carapace length is followed by ± 1 standard deviation. Sample sizes and ranges are displayed in parentheses.

	Carapace lengths (mm)					
	Chrysemys picta marginata			*Chelydra serpentina serpentina*		
Pond	Males	Females	Juveniles	Males	Females	Juveniles
Crisp Pond	94 (1)	152.7 ± 4.5 (3) (148–157)	79 (1)	315.3 ± 32.9 (6) (271–359)	253 ± 38.2 (2) (226–280)	-
Alder Pond	117 ± 19.4 (4) (96–135)	161 ± 5.7 (2) (157–165)	69.2 ± 1.7 (6) (66–71)	346 (1)	228 (1)	128.7 ± 27.5 (3) (97–147)
Coot's Slough	-	-	96 (1)	-	-	187 (1)
Penn State Pond	129.8 ± 15.9 (6) (107–145)	157.3 ± 4.1 (4) (152–162)	83.9 ± 14.8 (8) (61–107)	290.3 ± 12.6 (3) (277–302)	-	143.3 ± 50.1 (3) (111–201)
Slonesome Pond	162 (1)	-	-	283.3 ± 20.8 (3) (265–306)	229 (1)	180 ± 8.5 (2) (174–186)
Hidden Pond	-	-	-	300 (1)	-	-
Darr Rd Pond 1	-	-	-	353 (1)	297.5 ± 9.2 (2) (291–304)	-
Darr Rd Pond 2	126 ± 4.2 (2) (123–129)	-	84 (1)	313.5 ± 47.4 (2) (280–347)	245 ± 2.8 (2) (243–247)	-
Overall Average	125.4 ± 19.9 (14) (94–162)	156.5 ± 5.1 (9) (148–165)	79.1 ± 12.9 (17) (61–107)	308.2 ± 31 (17) (265–359)	257.3 ± 31 (8) (226–304)	151.4 ± 37.5 (9) (97–201)

significantly different than 1:1 (χ^2 = 2.0, df = 1, P = 0.157).

The abundance of the Midland Painted Turtle was unevenly distributed across the ponds in 2013 (χ^2 = 67.33, df = 7, P < 0.001). The associations between Midland Painted Turtles and pond features were non-random (Table 1). Overall, Midland Painted Turtles were found in greater abundance than expected at ponds with small maximum depth ≤ 2 m (χ^2 = 13.71, df = 1, P < 0.001), large littoral zone ≥ 90% (χ^2 = 13.71, df = 1, P < 0.001), no fish found in traps (x^2 = 13.71, df = 1, P < 0.001), creation of pond after 1970 (χ^2 = 13.71, df = 1, P < 0.001), and low visibility (χ^2 = 21.43, df = 1, P < 0.001). Although it was captured in larger and deeper ponds, this species was found to be less strongly associated with ponds that did not possess the characteristics described above.

FIGURE 3. Two juvenile Midland Painted Turtles (*Chrysemys picta marginata*) found in the same trap at Alder Pond, Powdermill Nature Reserve, Rector, Pennsylvania, USA. (Photographed by Daniel F. Hughes).

Population structure.—The percentage of male Midland Painted Turtles ranged from 25% at Alder Pond to 100% at Slonesome Pond during the 2013 sampling period (Table 2). The percentage of female Midland Painted Turtles ranged from 22% at Penn State Pond to 33% at Crisp Pond and juveniles ranged from 33% at Darr Road Pond 2 to 100% at Coot's Slough during the 2013 sampling period (Table 2). Earlier trapping efforts at Crisp Pond yielded 28% males in 2009 to 100% in 2011, 40% females in 2010 to 100% in 2005, 2006, 2008, and 20% juveniles in 2009 to 50% in 2011 (Table 2).

Adult Midland Painted Turtle abundance was unevenly distributed across the ponds in 2013 (χ^2 = 36.18, df = 7, P = 0.001), but the associations between adult Midland Painted Turtles and pond features were random (Table 1). Whereas, juvenile Midland Painted Turtle abundance was unevenly distributed across the ponds in 2013 (χ^2 = 31.47, df = 7, P = 0.001), yet juvenile Midland Painted Turtles were non-randomly associated with certain pond features (Table 1). Overall, juveniles were found in greater abundance than expected at ponds with small maximum depth ≤ 2 m (χ^2 = 9.941, df = 1, P = 0.002), large littoral zone ≥ 90% (χ^2 = 9.941, df = 1, P = 0.002), no fish found in traps (χ^2 = 9.941, df = 1, P = 0.002), creation of pond after 1970 (χ^2 = 9.941, df = 1, P = 0.002), and low visibility (χ^2 = 13.24, df = 1, P < 0.001). In general, juvenile turtles had strong associations with the features listed above, whereas adults were also unevenly distributed yet lacked any associations with particular pond features. For example, we captured the most Midland Painted Turtles from Alder Pond and Penn State Pond in 2013 and many of these captures were juveniles, 87% (n = 6) and 44% (n = 8), respectively. The mean age of juveniles was estimated at 3.5 y (2–4 y) and the mean age of adults was estimated at 6.7 y (5–9 y).

Body size.—Earlier trapping effort at Crisp Pond yielded a range in mean CL of adult males from 119.3 mm (109.6–135.3 mm, n = 3) in 2009 to 131.3 mm (121.5–141 mm, n = 7) in 2010. Adult males weight averaged 234 g (± 83.9 g SD, range = 140–380 g, n = 14) in 2013. Mean adult male CL did not differ significantly ($F_{1,14}$ = 2.27, P = 0.138) among ponds in 2013. Earlier trapping effort at Crisp Pond yielded a range of mean CL of adult females from 152.3 mm (105–173 mm, n = 7) in 2005 to 155.7 mm (149–160.5 mm, n = 11) in 2010. Mean adult CL of females (156.5 ± 5.5 mm, range = 148–165 mm, n = 8) was significantly larger (t = 4.21, df = 19, P < 0.001) than that of males in 2013. Likewise, mean adult body weight of females (471.4 ± 66.2 g, range = 340–540 g, n = 8) was significantly greater (t = 6.23, df = 19, P < 0.001) than that of males in 2013. Mean adult female body size did not significantly differ ($F_{1,8}$ = 2.12, P = 0.195) among ponds in 2013.

Earlier trapping effort at Crisp Pond yielded a mean CL of juveniles of 89.8 mm (88.5–90 mm, n = 2) in 2010. Mean juvenile body size did not significantly differ ($F_{1,16}$ = 2.09, P = 0.135) among ponds in 2013. The mean CL of juvenile Midland Painted Turtles from Penn State Pond (83.9 ± 13.9 mm, range = 61–107 mm, n = 8) was significantly larger (t = -2.18, df = 12, P = 0.028) than that of juvenile Midland Painted Turtles from Alder Pond (69.2 ± 1.6 mm, range = 66–71 mm, n = 6). However, no significant difference was detected in mean weight (t = -1.53, df = 12, P = 0.147) between the two samples.

Inter-pond movements.—On 12 June 2013 at 1600, we captured an adult male Midland Painted Turtle (#47: CL = 139 mm, CW = 100 mm, PL = 125 mm, WT = 370 g) in good physical condition from Penn State Pond. The original capture of this turtle occurred 21 August 2010 at 0900 at Crisp Pond and we recaptured it on 8 June 2011 at the same site. The straight-line distance from Crisp Pond to Penn State Pond is 1,100 m. The physical characteristics and resident turtle assemblage of Crisp Pond differed greatly from those of Penn State Pond (Tables 1 and 2). Crisp Pond is deep with high visibility, a much reduced littoral zone, and fish present in traps, and these features were associated with a turtle assemblage of primarily large adult turtles, with relatively few juvenile turtles (Tables 2 and 3). The physical characterization of the Penn State Pond was shallow water with low visibility, an extensive littoral zone, and no fish in traps, and these features were associated with a turtle assemblage of mixed age and size-classes, and a large number of juvenile turtles (Tables 2 and 3).

On 17 July 2013 at 1500, we captured an adult male (#38: CL = 142 mm, CW = 99 mm, PL = 131 mm, WT = 330 g) in good physical condition from Slonesome Pond. We originally captured it 1 July 2010 at 1000 from Crisp Pond, and it was recaptured on multiple occasions at the same site (26 August 2010; 1 June 2011; 17 July 2011; 4 May 2013). The straight-line distance from Crisp Pond to Slonesome Pond is 907 m. The physical characteristics of Crisp Pond marginally differed from Slonesome Pond, except for the presence of lily pads (*Nymphaea* sp.) at the latter pond (Table 1). These ponds supported turtle assemblages comprised primarily of large adults and relatively few juveniles (Tables 2 and 3).

Chelydra serpentina serpentina*: *population size.—The Common Snapping Turtle (Fig. 4) was present at all sites, where it ranged in estimated abundance from 1.0 turtles at Hidden Pond to 9.8 turtles at Penn State Pond during the 2013 sampling period (Table 2). Earlier trapping effort at Crisp Pond yielded a range of estimated abundance for the Common Snapping Turtle from 1.4 turtles in 2008 to 15.9 turtles in 2005 (Table 2). In total, the Common Snapping Turtle represented 53 captures of new individuals and comprised 132 overall captures (Table 2). For all captured individuals across all sites and years, the sex-ratio favored males at a ratio of 2.42:1.00 (χ^2 = 7.05, df = 1, P = 0.007).

The abundance of the Common Snapping Turtle was unevenly distributed across the ponds in 2013 (χ^2 = 17.78, df = 7, P = 0.013). The associations between Common Snapping Turtles and pond features were non-random (Table 1). Overall, Common Snapping Turtles were found in greater abundance than expected at ponds with large amount of open water > 90% (χ^2 = 7.11, df =

FIGURE 4. Adult male Common Snapping Turtle (*Chelydra serpentina serpentina*) found opportunistically at Alder Pond, Powdermill Nature Reserve, Rector, Pennsylvania, USA. (Photographed by Daniel F. Hughes).

1, P = 0.008) and large perimeter > 150 m (χ^2 = 7.11, df = 1, P = 0.008). Although it was captured in smaller and heavily vegetated ponds, this species was found to be less strongly associated with ponds that did not possess the characteristics described above.

Population structure.—The percentage of male Common Snapping Turtles ranged from 33% at Darr Road Pond 1 to 100% at Hidden Pond during the 2013 sampling period and the percentage of females ranged from 14% at Penn State Pond to 33% at Crisp Pond and Darr Road Pond 2 during the same sampling period (Table 2). The percentage of juvenile Common Snapping Turtles ranged from 29% at Slonesome Pond to 100% at Coot's Slough during the 2013 sampling period (Table 2). Earlier trapping efforts at Crisp Pond yielded 50% males in 2005 and 2011 to 100% in 2009 and 2010, 25% females in 2011 to 100% in 2012, and 25% juveniles in 2011 to 50% in 2005 (Table 2).

Adult Common Snapping Turtle abundance was evenly distributed across the ponds in 2013 (χ^2 = 7.53, df = 7, P = 0.376), yet adults were found to be associated with certain pond features (Table 1). Overall, we found adults in greater abundance than expected at ponds with large maximum depth (> 2.5 m; χ^2 = 5.0, df = 1, P = 0.018), large amount of open water (≥ 75%; χ^2 = 5.0, df = 1, P = 0.018), and with fish found in traps (χ^2 = 5.0, df = 1, P = 0.018). Juvenile Common Snapping Turtle abundance was also evenly distributed across the ponds in 2013 (χ^2 = 11.4, df = 7, P = 0.117), but juveniles were not associated with any pond feature (Table 1). From a small sample, we found juveniles in greater abundance at shallow ponds with low visibility and in much less abundance than adults or entirely absent from ponds with adult-associated features listed above. For example, during the 2013 sampling period, 32% (n = 9) of the Common Snapping Turtles we captured were juveniles and 78% (n = 7) of these juveniles were from three littoral ponds with low visibility. Mean age of juveniles was estimated at 5.5 y (3–6 y) and the mean age of adults was estimated at 9.3 y (7–12 y).

Body size—Earlier trapping effort at Crisp Pond yielded a range in mean CL of adult males from 283.3 mm (279.4–368 mm, n = 3) in 2006 to 347.5 mm (320–350 mm, n = 7) in 2009. Adult males weight averaged 7,031.7 g (± 2,168.5 g SD, range = 4,620–10,530 g, n = 16) in 2013. Mean adult male CL did not differ significantly ($F_{1,16}$ = 1.26, P = 0.358) among ponds in 2013. Earlier trapping effort at Crisp Pond yielded a range of mean CL of adult females from 256.3 mm (237–284 mm, n = 3) in 2012 to 263.8 mm (255–272.5 mm, n = 2) in 2007. Mean adult CL of females (257.3 ± 31 mm, range = 226–304 mm, n = 8) was significantly smaller (t = 3.57, df = 22, P = 0.001) than that of adult males in 2013. Likewise, mean adult body weight of females (4,610 ± 1,672.5 g, range = 3,020–6,750 g, n = 8) was significantly less (t = 2.67, df = 22, P = 0.015) than that of males in 2013. Mean adult female body size did not significantly differ ($F_{1,7}$ = 2.52, P = 0.239) among ponds in 2013. Earlier trapping effort at Crisp Pond yielded a mean CL of juveniles of 45.8 mm (31–75 mm, n = 2) in 2005. No significant difference was detected in mean CL of juveniles across the ponds in 2013 ($F_{1,16}$ = 2.09, P = 0.136).

Inter-pond movements.—On 24 June 2013 at 1400, we captured an adult female Common Snapping Turtle (# 40: CL = 243 mm, CW = 212 mm, PL = 193 mm, WT = 4,010 g) from Darr Road Pond 2. The original capture of this turtle occurred 24 May 2012 at 0900 at Crisp Pond. The straight-line distance from Crisp Pond to Darr Road Pond 2 is 2,033 m. The physical characteristics of Crisp Pond differed marginally from Darr Road Pond 2, except that the latter pond was smaller in size (Table 1). These ponds supported turtle assemblages comprised of large adults and relatively few juveniles (Tables 2 and 3).

DISCUSSION

Comparison to other populations.—The overall capture frequency of the Midland Painted Turtle (51.3%) in our study was comparable to other long-term studies. A 23-y study in southeastern Pennsylvania found that the Painted Turtle comprised 76% of all turtles captured (Ernst and Lovich 2009). A 20-y study in Michigan found that the Painted Turtle comprised 62% of all marked turtles (Congdon and Gibbons 1996). In large water bodies, Painted Turtles have been found in considerably lower numbers. From two water bodies in central Indiana (14.7 ha lake and 10-km long canal), the

Painted Turtle comprised 2.6% and 4% of all captures, respectively (Conner et al. 2005). This trend was also evident from a 30 ha pond in southeastern Illinois, in which Painted Turtles comprised 8.5% all turtles marked over 6 y (Dreslik et al. 2005). The estimated population density for Midland Painted Turtles from our study at Crisp Pond, which was nearly 0.6 ha in size, was relatively low compared to those reported from similar sized ponds elsewhere. For example, reported population densities have ranged from 137 turtles/ha at a 0.3 ha pond in New York (Zweifel 1989) to 149 turtles/ha at a 0.7 ha pond in Nebraska (Iverson et al. 2006). Yet, studies from larger bodies of water consistently reported low estimated densities of turtles: 25 turtles/ha from a 3 ha pond in New York (Bayless 1975), a yearly density of five turtles/ha from a 30 ha pond in Illinois (Dreslik et al. 2005) and 9.9 turtles/ha from several lakes in Minnesota for the Western Painted Turtle, *Chrysemys picta bellii* (Ernst and Ernst 1973). In general, our findings were similar to findings on the capture frequency of the Painted Turtle from long-term studies, yet our density estimates were much lower than like sized ponds. Accordingly, consideration to factors such as wetland productivity, sampling methods, and climate influencing these numbers, especially density estimates, is warranted.

The overall capture frequency of the Common Snapping Turtle (48.7%) in our study is comparable to other studies elsewhere, yet our capture numbers were inflated by one male who was captured disproportionately often (n = 44 captures). In the Ouachita Mountains, Arkansas, the Common Snapping Turtle comprised 62% of all captures (Phelps 2004). In Madison County, Kentucky, the Common Snapping Turtle comprised 32.6% of all captures (Ernst and Lovich 2009). However, in a review by Dreslik and Phillips (2005), the Common Snapping Turtle made up 3.1–12.03% of the turtle populations across the upper Midwest. Other findings of low relative abundance of Common Snapping Turtles have been recorded: 3.3% in western Illinois (Reehl et al. 2006), 8.6% in southern Illinois (Dreslik et al. 2005), 17% in southeastern Pennsylvania (Ernst and Lovich 2009), and 18.5% in central Oklahoma (Stone et al. 2005). High densities of the Common Snapping Turtle are typically concentrated in ponds and eutrophic systems; whereas, low density populations occur in lakes and oligotrophic systems (Galbraith et al. 1988). Our density findings at Crisp Pond adhere to this pattern, yet high variability in estimated densities has been reported from ponds of various sizes elsewhere: 1.2 turtles/ha from ponds at Lacreek Refuge, South Dakota (Hammer 1969), a range of 0.04–43 turtles/ha from four ponds in Leon County, Florida (Aresco et al. 2006), 60.5 turtles/ha from two 0.4 ha ponds in West Virginia (Major 1975), and 59 turtles/ha from a 0.8 ha pond in Tennessee (Froese and Burghardt 1975). In general, our findings are comparable to findings on the capture frequency of the Common Snapping Turtle across similarly sized ponds. Yet, the inconsistency of reported density estimates, in addition to discrepancies in density calculations for this species highlights the importance of other factors associated with these population parameters, not only pond size. Consequently, attention to pond productivity, capture method, and length of study are warranted when evaluating effects of habitat upon these numbers.

Artifactual biases in sex ratios can be obtained from samples depending on the sampling method chosen (Gibbons 1970a). Nevertheless, the adult sex-ratios for these two species found in most long-term population studies have been 1.00:1.00 (Gibbons 1968; Ernst 1971d; Mitchell 1988). Reported deviations have been most commonly skewed towards males for both the Painted Turtle (Sexton 1959; Bayless 1975; Zweifel 1989; Gibbons 1990; Congdon and Gibbons 1996) and the Common Snapping Turtle (Froese and Burghardt 1975; Brown and Brooks 1993; Anderson et al. 2002, Rizkalla and Swihart 2006; this study). A female biased sex-ratio for the Painted Turtle has also been reported (Anderson et al. 2002; Rizkalla and Swihart 2006; this study).

The adult to juvenile ratio in our study is consistent with other long-term studies, which have shown that age-classes of captures are skewed towards adults in both species (Browne and Hecnar 2007). The adult to juvenile ratio of Common Snapping Turtles was 3.42:1.00 in our study, 4.27:1.00 in Illinois (Dreslik et al. 2005), 8.71:1.00 in Minnesota (DonnerWright et al. 1999), and 13.89:1.00 in Ontario, Canada (Galbraith et al. 1988). The adult to juvenile ratio of Midland Painted Turtles was 2.50:1.00 in our study, 1.30:1.00 in Virginia (Mitchell 1988), 4.00:1.00 in southeastern Pennsylvania (Ernst 1971d), 5.00:1.00 in New York (Bayless 1975), and 1.00:0.00 in Minnesota (DonnerWright et al. 1999). Yet, juvenile Painted Turtles and juvenile Snapping Turtles may not be as rare as these findings suggest. From a 5 ha pond in Michigan, Gibbons (1968) recorded an adult to juvenile ratio for the Painted Turtle of 0.92:1.00. From a 0.81 ha pond in Tennessee, Froese and Burghardt (1975) recorded an adult to juvenile ratio for the Common Snapping Turtle of 0.75:1.00. The results presented by Gibbons (1968) were combined captures from five trapping methods (dip-netting from a rowboat, wire-mesh tapping, baited trapping, underwater diving, and muddling) and results presented by Froese and Burghardt (1975) were combined captures from two trapping methods (baited trapping and hand capture). To that end, Ream and Ream (1966) examined the effect of sampling methods on the estimated population structure of Painted Turtles in Wisconsin and each of their five trapping methods yielded a different size-class distribution. Therefore, with the goal of gathering a more complete dataset, future studies focused on population parameters of these two species and aquatic turtles in general, should consider a variety of trapping methods.

Effects of pond features on populations.—Interspecific differences in pond use between Midland Painted Turtles and Common Snapping Turtles can be explained by species-specific habitat preferences. The abundance of the Common Snapping Turtle and the Midland Painted Turtle were not evenly distributed across the eight artificial ponds of our study. We detected species-specific associations with certain pond features that strongly influenced population sizes. Large population sizes of the Midland Painted Turtle were associated with ponds that had a small maximum depth, large littoral zone, no fish found in traps, low visibility, and ponds created after 1970. Whereas, large population sizes of the Common Snapping Turtle were associated with ponds that had a large perimeter and a large amount of open water. The disparate distribution in abundance of these two species reflected their basic known biological preferences. The Midland Painted Turtle prefers shallow water bodies with abundant aquatic vegetation, and the Common Snapping Turtle is more of a habitat generalist but is comparably better-suited for larger, deeper water bodies (Ernst and Lovich 2009). From the Saint Croix River in Minnesota and Wisconsin, high abundances of these two species were most strongly associated with the same features of the river (e.g., channel width), yet the Common Snapping Turtle differed in that it was most abundant in areas with deeper and faster moving water than the Painted Turtle (DonnerWright et al. 1999). In New Hampshire, Painted Turtle abundance was greater at ponds with ample shoreline vegetation than ponds without this feature (Marchand and Litvaitis 2004). In the Mississippi River, near Hamilton, Illinois, Painted Turtles were nearly absent from deep water and most common in the shallow (< 1 m) slough with abundant vegetation (Anderson et al. 2002). Similarly, in central Illinois, Painted Turtles were most commonly found in shallow marshes (Rizkalla and Swihart 2006). The Common Snapping Turtle was consistently found across a greater range of wetland types, appearing to be more of a generalist with fewer associations to particular habitat features, compared to the Painted Turtle (Anderson et al. 2002; Marchand and Litvaitis 2004; Rizkalla and Swihart 2006). To that end, from Will County, Illinois, Common Snapping Turtles were found to be habitat generalists, whereas Painted Turtles were more habitat specialists (Anthonysamy et al. 2014). Generally, our findings adhered to these associations, as the Common Snapping Turtle was found at all eight ponds and the Midland Painted Turtle at six ponds.

Ontogenetic differences in habitat preference were detected in the Midland Painted Turtle. Juveniles were unevenly distributed across the eight ponds and their non-random distribution was explained by certain physical features of the ponds (e.g., depth). Juvenile Midland Painted Turtles have been found in greater abundance and more frequently in shallower water than adults (Congdon et al. 1992). Differential use of ponds by adults, on the other hand, was not explained by any of the physical features of the ponds, perhaps either because pond features associated with adult pond-use were not measured in our study or perhaps because high inter-pond movements by adults obscured otherwise meaningful associations with one or more of the structural features examined in these ponds. To that end, more adult Midland Painted Turtles emigrated from and more juveniles remained in a southern Michigan pond than expected (Sexton 1959). In eastern Mississippi, juvenile Slider Turtles, *Trachemys scripta* (Thunberg in Schoepff 1792), were also more sedentary and over several years a higher proportion of juveniles remained in the same pond than adults (Parker 1984).

Ontogenetic differences in habitat preference were also detected in the Common Snapping Turtle. In this case, adults and juveniles were both evenly distributed across the eight ponds, yet adults were found to have strong associations with certain pond features while juveniles did not. That 78% of the juveniles were captured in similarly-specific pond conditions, leads us to suspect that biologically meaningful associations between juvenile Common Snapping Turtles and their habitat may have been statistically undetected because of the small sample size.

Separate analyses indicated that the abundance of adult or juvenile Midland Painted Turtles did not differ from the abundance of adult or juvenile Common Snapping Turtles, respectively. The similar distribution of age-classes for both species suggests that the effect of pond features on certain segments of these turtle populations (i.e., adults or juveniles) has a similar affect across species. In turn, the distribution of all juvenile turtles of both species differed from the distribution of all adults across the eight artificial ponds, such that juveniles were found in different numbers as adults in ponds of co-occurrence. Large population sizes of juvenile turtles of both species were strongly associated with ponds that had a small maximum depth, large littoral zone, no fish found in traps, low visibility, and ponds created after 1970. In sharp contrast, adults of both species were associated with ponds that had a large maximum depth, high visibility, and large area of open water, such that juveniles were either entirely absent or nearly so from ponds that were favored by adult turtles. The small percentage of juveniles captured of both species at Crisp Pond 2005–2013 may suggest low recruitment in that pond. Weekly surveys at Crisp Pond in 2013 also failed to detect either the presence of juvenile turtles at basking sites frequently used by adults (Midland Painted Turtle) or the occurrence of juvenile turtles breaking the surface of the water when adults were regularly observed (both species) (Daniel Hughes, pers. obs.). A lack of suitable nesting area and high rates of nest predation are often referred to as primary reasons for the absence of recruitment to a turtle population (Ernst and Lovich 2009). However, nests and nesting turtles of both species were observed around the banks of Crisp Pond in 2013 and in prior years (Amy Tegeler, pers. obs.). Therefore, a dearth of suitable nesting sites alone cannot explain why the pond was entirely devoid of juveniles in several sampling years and nearly so across all the years sampled. Yet, further research is warranted to understand the interannual variation of nest predation rates, which have been recorded to range from 20% (Tinkle et al. 1981) up to 100% (Congdon et al. 1987) for some turtle populations in some years.

The ability of small turtles to pass freely through aquatic traps can explain a lack of juvenile turtles in population studies (Congdon et al. 1994). Notwithstanding the smallest turtles that could pass through the trap mesh, juveniles (> 61 mm CL in Midland Painted Turtles and > 97 mm CL in Common Snapping Turtles) were readily caught and differentially so among ponds. For example, among Midland Painted Turtles, most captures were of juveniles in Alder Pond and Penn State Pond, and among Common Snapping Turtles, most captures were of juveniles in Alder Pond. Young aquatic turtles are considered philopatric, often not venturing far from their original nest site to remain in a nearby water body (Gibbons 1970). The high numbers of small turtles captured in our hoop-nets at ponds other than Crisp Pond and the presence of active nests around the banks of Crisp Pond, suggest that the low abundance of juveniles at this site over an eight year period cannot be explained by an artifact of sampling or absence of nesting sites. However, further research is warranted to understand the potential influence of seasonal variation of movement patterns on our occupancy findings, which spatial reorganization of population structures have been documented in response to seasonal changes associated with temperature and vegetation (Sexton 1959).

Rather, the physical structure of the pond itself seemed to play a significant role in the population structure of the two species. Crisp Pond was large and deep, with a high percentage of open water and little emergent aquatic vegetation. Centrarchid fish, including the Largemouth Bass (*Micropterus salmoides*), were consistently found in traps during the 2013 trapping period. This suite of habitat features can provide sufficient food sources and ample space for large adult turtles. Across an eight-year period at Crisp Pond, the majority of the individuals captured for both species were adults. Comparatively, Alder Pond was small and shallow, with a low percentage of open water with extensive emergent and submerged aquatic vegetation. In Alder Pond, fish were not found in any traps during the 2013 sampling period and the majority of turtles captured for both species were juveniles. This collection of habitat features could provide sufficient protection from aquatic and aerial predators and abundant food sources and microhabitats from vegetation productivity. In effect, a relatively safe nursery seemed to exist for turtles at Alder Pond, separated by a narrow levee from the nearly adult-only Crisp Pond. We speculate that nursery ponds could benefit smaller turtles by providing physical cover above and below water, in this case Lily Pads, for protection from aerial predators, as well as Largemouth Bass and visiting adult Common Snapping Turtles, while providing a richer source of food for small turtles. Ultimately, nursery ponds could be a refuge for small turtles and thereby increase recruitment to the local population. Further research is necessary to test the extent to which nursery ponds benefit certain size-classes of aquatic turtle populations (i.e., small turtles).

Isolated ponds tend to have lower turtle abundance, for example Painted Turtle abundance increased as distance to neighboring ponds decreased in a study by Marchand and Litvaitis (2004). However, we found that isolated ponds that possessed features capable of accommodating adult and juvenile life-history stages supported some of the largest population sizes in our study (e.g., Penn State Pond and Slonesome Pond). We also found that a series of ponds in close proximity offered a suite of features unique to each pond that were favored by certain species and/or certain age and size-classes, over others. Consequently, what appeared to us as separate ponds were in actuality traversable larger-scale versions of microhabitat for different life stages of both turtle species. Rather than a large lake or canal that might have all the habitat features for a sustainable population of Midland Painted Turtles and Common Snapping Turtles, these ponds, through accident of design, were suited primarily for either juveniles (shallow, weedy) or nearly exclusively for large adults (deep, little emergent vegetation). Therefore, the unique physical makeup of these ponds serves as a benefit to specific life-history stages of both species and is likely concomitant with predator-prey relationships in shaping the structures of the turtle communities occupying these ponds.

The stark contrast between the juvenile turtles at Crisp Pond and nearby Alder Pond perhaps reflects the difficulty of juveniles to successfully establish and then persist in a pond occupied by adult turtles, especially in the presence of the predatory Common Snapping Turtle. Musk Turtles, Blanding's Turtles (*Emydoidea blandingii*), and conspecifics were reported from the diet of Common Snapping Turtles in Michigan (Lagler

FIGURE 5. Juvenile Midland Painted Turtle (*Chrysemys picta marginata*) found in a trap exhibiting a serious wound to its plastron at Alder Pond, Powdermill Nature Reserve, Rector, Pennsylvania, USA. (Photographed by Daniel F. Hughes).

1943). We detected an incidence of attempted predation upon a juvenile Midland Painted Turtle (CL = 90 mm) at Alder Pond in 2013. The juvenile was captured on 15 July 2013 exhibiting an injury to its plastron; a deep laceration that occurred between two trapping days (no observable injury from first capture on 13 July 2013) (Fig. 5). The severity of the injury was likely caused by a failed attempt to consume the small turtle by a large predator. We speculate that this large predator was likely an adult Common Snapping Turtle. This isolated incident may also suggest a potential relationship between small turtles of both species and adult Common Snapping Turtles so abundant at these neighboring ponds.

From the Missouri River, in central Missouri, juvenile turtles were captured on average farther in the river from adults, likely reflecting habitats free of aquatic predators of adult turtles and fish (Bodie and Semlitsch 2000). Similarly, from the Juniata River, in central Pennsylvania, Pluto and Bellis (1986) found that larger turtles were more often captured from deeper water and areas that lacked emergent vegetation relative to smaller turtles, and these habitat association differences between size classes were attributed to differential predation risks (aquatic and terrestrial). Fish predation of hatchling turtles has been reported (Gyuris 1994) and at Crisp Pond, Largemouth Bass were detected. Largemouth Bass will consume dead hatchling Painted Turtles (Semlitsch and Gibbons 1989) and attack live hatchling Common Snapping Turtles (Britson 1998). We speculate that the abundance of potential predators at Crisp Pond (many adult Common Snapping Turtles and Largemouth Bass) and scarcity of juvenile refugia may enforce colonization of hatchlings and small turtles in the nearby Alder pond, which was nearly free of adult turtles and completely lacked fish.

The presence of submerged and emergent vegetation could provide an advantage to smaller turtles if it serves to protect them from aerial predators and provides habitat for food exploited by juvenile stages. Penn State Pond appeared to be exceptional in our study, such that pond features were present to accommodate adult and juvenile life-history stages of both species: high area of open water (adults), large littoral zone (juveniles), and no fish in traps (juveniles). The presence of juvenile turtles in the company of adult turtles will undoubtedly increase the amount of adult-juvenile interactions, likely having a negative impact upon the smallest turtles. The average body size of juvenile Midland Painted Turtles at Alder Pond was smaller than that of juveniles from Penn State Pond. We venture that the abundance of Lily Pads at Alder Pond provided additional protection and increased underwater microhabitats and in turn was responsible for the persistence of the smallest turtles in this pond. Aerial predators that rely heavily on visual cues, such as the Great Blue Heron (*Ardea herodias*), frequent wetlands across Pennsylvania and are known to consume hatchling turtles (Niemela and Bury 2012). The existence of this additional threat without concealment via emergent vegetation could negatively impact small turtles at ponds without this feature (e.g., Penn State Pond). Therefore, it is likely that the suite of pond features at Penn State Pond have reinforced selection against or modified the behavior of the smallest turtles through increased exposure to aerial (i.e., Great Blue Heron) and aquatic (i.e., Common Snapping Turtle) predators. Ultimately, the distribution of potential predators has likely been affected by the features of the ponds and concomitantly predator-prey interactions have possibly played a role in shaping the structures of the turtle assemblages at these neighboring ponds.

Inter-pond movements.—Ernst and Lovich (2009) state that dispersal events can be infrequent at isolated ponds because the terrestrial distance that a turtle must travel is too great or the pond is too remote. However, the inter-pond movements we detected did not reflect this, as some turtles traveled great distances. Although, movements are often initiated by innate changes or by stochastic events, we speculate that the inter-pond movements detected in our study were also influenced by the population structures at the pond the turtle left and pond it ultimately sought out. The detection of two sexually mature adult male Midland Painted Turtles completing long-distance dispersals is consistent with patterns of males dispersing in search of mates or potential mates (Sexton 1959; Bennett et al. 1970; Scott 1976; Parker 1984; Rowe 2003). No female Midland Painted Turtle movements were detected and this is generally consistent with males moving more often than females (Morreale et al. 1984). Both males left Crisp Pond that had a Midland Painted Turtle population composed of mostly older adults. The movement by larger males in our study was similar to the segment of the Slider population associated with overland movements in Mississippi ponds (Parker 1984). These generally large males from Crisp Pond moved long distances to ponds having populations comprised of a greater range of age- and size-classes than in Crisp Pond. Older females may be less receptive to mates than younger females because of factors associated with senescence and some reptilian species exhibit changes in selection differentials with age across a lifespan that may reduce reproductive output (Bronikowski 2008). However, female Painted Turtles have demonstrated a marked increase in reproductive output with age (Congdon et al. 2003), as well as Blanding's Turtles (Congdon et al. 2001), yet intersexual receptiveness over time has not been addressed. The detection of an adult female Common Snapping Turtle completing a long-distance inter-pond movement suggests that this individual was in search of either an optimal nesting site or overwintering site and then remained at the nearest pond. A female Common Snapping Turtle in Michigan traveled 1,625 m from a pond to a nesting site, yet eventually returned to the original pond (Congdon et al. 1987). The female from our study left Crisp Pond, composed of adults, and it remains possible that factors associated with the age of the resident population structure may have played a role in prompting this inter-pond movement. In what is on average a sedentary population of aquatic turtles where terrestrial movements between isolated ponds seem unfavorable, inter-pond movements by males in search of mates or females in search of nesting sites can dramatically increase gene flow (Kiester et al. 1982).

Wetland management implications.—Continued surveying and monitoring is necessary to record data sufficient enough to properly analyze growth, survivorship, and reproductive parameters of turtles associated with these ponds. This will help to assess the relative influence of these life-history traits on the population dynamics of the two species compared to the traits measured in this study. Many explanations exist for the creation and restoration of artificial wetlands (e.g., agriculture), often exclusive of providing suitable habitat for aquatic turtles. Yet, our findings suggest that the physical structure and extent of aquatic vegetation of the pond play a prominent, and to some extent, a predictable role in the structure of the resident turtle assemblage, dramatically affecting certain population parameters. We argue that this warrants serious attention to wetland management. Based on the general system we studied, it appears that smaller, well-vegetated, shallower ponds adjacent to larger, less-vegetated, deeper ponds function as nursery ponds to the benefit of small turtles, thereby increasing juvenile recruitment to the local population. In our opinion, this is a key factor to the health of the turtle communities in Westmoreland County ponds and pond systems elsewhere. Nursery ponds adjacent to ponds occupied by adult turtles can substantially promote recruitment of hatchlings and juveniles to the population by providing suitable habitat and protection for small turtles, ultimately promoting the continued survival of the population in the area. We suggest that ponds, or a series of ponds, can be constructed or modified to accommodate one or more life-history stages of these two species of turtles. Reasonable inter-pond distances for movements by breeding males or nesting females can serve to increase gene flow and accelerate the colonization process. Our study should serve to underscore the importance of adjusting pond features and inter-pond distance in creating or modifying ponds to find the best combination of characters for effective management of species such as the Midland Painted Turtle and the Common Snapping Turtle by private land owners and resource managers. These findings can be used by wetland management as a formula for creating nursery, adult, or mixed-age-class ponds of turtles. To that end, this approach can serve as a test as it might apply as a conservation tool for other pond-dwelling chelonian species.

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