



Demography of a painted turtle intergrade (*Chrysemys picta picta* X *C. p. marginata*) population from an altered wetland

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The demography of a painted turtle *Chrysemys picta picta* X *C. p. marginata* population from a eutrophic habitat was examined at a wetland site in south-central Pennsylvania (USA) during 2011–2019. Males reached sexual maturity at 90 mm carapace length (CL) in half the time taken, but at the same size, as painted turtles studied elsewhere in the north-eastern portion of the United States. Females matured at 130 mm CL at our site, which was larger and began at an earlier age than conspecifics. Our data corroborate findings of faster growth in *C. picta* juveniles resulting in earlier maturity at body sizes equal to or larger than slower growing juveniles. Our results also conform to previous findings linking wetlands altered by added nutrient input to increased growth patterns of their resident painted turtle population. Rapid growth rates for aquatic turtles are likely to become more common globally as urbanisation continues to expand and alter wetland habitats.

Keywords: Growth, population size, population structure, survivorship, urban

INTRODUCTION

The painted turtle *Chrysemys picta* Schneider 1783, is a polytypic aquatic species found across central and eastern North America (Powell et al., 2016) with three recognised subspecies (Uetz et al., 2021). In Pennsylvania, the range of the midland painted turtle, *C. p. marginata* Agassiz 1857, extends through much of the western and extreme northern portions of the state. Intergradation by *C. p. marginata* with the eastern painted turtle *C. p. picta* occurs throughout the eastern and south-eastern portion of the state (Ernst & Ernst, 1971). The lower sub basin of the Susquehanna River is the centre of the intergradation zone in the state (Hulse et al., 2001). Within this watershed is Wildwood Park in Harrisburg, Dauphin County, where intergrades of *C. p. picta* X *C. p. marginata* are abundant in a eutrophic canal and an artificial lake (Wingert & Meshaka, 2021).

Demographic studies of *C. picta* are common (e.g. Gibbons, 1968; Mitchell, 1988; Zweifel, 1989; Frazer et al., 1991; Congdon & Gibbons, 1996), and two studies have examined demographic patterns in Pennsylvania populations (Ernst, 1971a,b; Hughes & Meshaka, 2020). Studies by Ernst (1971a,b) were conducted on an intergrade population in south-eastern Pennsylvania, and a study by Hughes & Meshaka (2020) was conducted on *C. p. marginata* in an artificial wetland complex in south-western Pennsylvania. Nutrient levels within the aquatic

habitats occupied by this species can affect demographic traits within populations (Ernst & Lovich, 2009). Although neither of the wetland habitats in the two Pennsylvania studies were described as altered, three studies, one on *C. p. bellii* in Iowa (Quinn & Christiansen, 1972) and in Michigan (Gibbons, 1968), and one on *C. p. picta* in Maryland (Ernst & McDonald, 1989), explicitly examined growth in habitats altered by eutrophic conditions. Rapid growth was common to turtles of all three studies, larger adult body sizes was found in two studies (Quinn & Christiansen, 1972; Gibbons, 1968), and early maturity with an effect on minimum body size was detected by one study (Ernst & McDonald, 1989). More broadly, Congdon et al. (2018) identified a connection between fast growth of juveniles and early maturity at larger or similar sizes compared to slower-growing juveniles of three turtle species, including *C. picta*.

Altered aquatic habitats are highly influential in shaping variation in several important life-history traits and such demographic responses are likely common among urban populations of aquatic turtles worldwide. Within this context, we recognised the opportunity to comprehensively evaluate responses in multiple demographic traits by a single population of *C. p. picta* X *C. p. marginata* over a 9-year period to an artificially eutrophic and human-made wetland imbedded within a city in south-central Pennsylvania. Our research approach, in turn, provides findings that are not only globally relevant but also becoming increasingly common.

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MATERIALS & METHODS

Study area

Our study was conducted at Wildwood Park, a 93.5 ha county park located in Harrisburg, Dauphin County, Pennsylvania (40.310, -76.883). Approximately 60 % of the park is comprised of a shallow artificial lake that is fed by Paxton Creek (Fig. 1). An accumulation of detritus has resulted in a gradual filling-in of the lake with much of it converting to a marsh dominated by cattail *Typha* sp. During the time of this study, only a section of Paxton Creek (0.34 ha) at the south end, the spillway area (0.29 ha), a channel (0.99 ha) running more or less parallel to the tow path on the west end, and another channel (1.91 ha) running along the eastern edge of the lake, were deep enough to be habitable by *C. picta*. A section of the Pennsylvania Canal ran along the western boundary of the park adjacent to the lake and was separated by a tow path (Fig. 1). The canal measured 1,934.65 m in length, had an average width of 23.8 m, and an area of 26,467.6 m² (2.65 ha). The canal depth changed significantly from one to two metres from the west side of the towpath into the canal (Russell et al., 2014). A cleared utility right-of-way averaging 16.3 m borders the west side of the canal and separates it from a two-lane paved road. The main water lily found in the canal was spatterdock *Nuphar advena* L., and the dominant submergent aquatic macrophyte was coontail *Ceratophyllum demersum* L. Captured turtles frequently passed spatterdock seeds. Duckweed *Lemna* sp. was the common floating plant. Small painted turtle juveniles were seen feeding on duckweed at the surface. There are also algae species in the water which have not yet been identified (Russell et al., 2014).

The canal received extensive runoff from the adjoining road and industrial warehouses that run parallel and west of it, to the extent that much of the lake has converted to cattail marsh. The eutrophic condition of our site is quantified by water quality data recorded by the Susquehanna River Basin Commission's Paxton Creek monitoring station (ID 01571005, coordinates 40.306, -76.856) located upstream from Wildwood Park, its period of record having encompassed the duration of our study. The extent of eutrophication in Paxton Creek expressed in normalised concentration (mg/L) was available for total Nitrogen (0.676), dissolved Nitrogen (0.833), total Phosphorus (0.598), dissolved Phosphorus (0.618), total Ammonia (0.833), dissolved Ammonia (0.539), and total Suspended Solids (0.578). The topic of the watershed's impairment was addressed at both the state level by the Pennsylvania Department of Environmental Protection (DEP) and at the federal level by the Environmental Protection Agency. The DEP listed Paxton Creek in Harrisburg, Dauphin County, as impaired after studies in 2004, 2005, and 2006 based on siltation and the source as urban runoff/storm sewers, primarily phosphorus. In 2010, the DEP delisted the watershed that includes Paxton Creek (Shearer, 2012), but the EPA later determined that delisting of Paxton Creek for nutrient impairment was not appropriate (Sauro, 2019; DeJesus,



Figure 1. A section of the Pennsylvania Canal and Wildwood Lake at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania. Photograph taken 3 October 2018 by W.E. Meshaka, Jr.

2021). As of 2013, DEP listed Paxton Creek as impaired for sediment but not for nutrients. During the latter 20th century, the lake depth significantly decreased with sediment deposition. It originally averaged four to 152.4 cm in depth and as of 2015 Wildwood Lake averaged approximately 15.2 cm (Herbert et al., 2015). From 2003 through 2018, the lake depth diminished from shallow open water to mudflat and cattail marsh (Fig. 2).

Trapping and Processing Method

Six baited hoop-nets were set for five consecutive days in spring, summer, and autumn during 2011–2014 and opportunistically in 2015 (54 trap days), 2016 (30 trap days), and 2019 (30 trap days). The traps (Memphis Net and Twine Co., Memphis, TN) were 2.0 m x 1.0 m with 2.54 cm mesh. The traps were set at fixed locations near the shoreline of the canal, and the sites remained constant for the duration of the study. Traps were baited with a partially opened sardine can or with chicken gizzards which were changed daily after traps were checked.

We used a 61 cm aluminum sliding caliper, accurate to 0.5 mm, to measure straight-line carapace length (CL) and plastron length (PL). The sex for adult turtles was determined by foreclaw length (longer in males relative to CL) and by the location of the cloaca relative to the carapace (i.e. the cloaca extends beyond the carapace in males; Ernst & Lovich, 2009). New turtles were individually marked using two methods. Each new

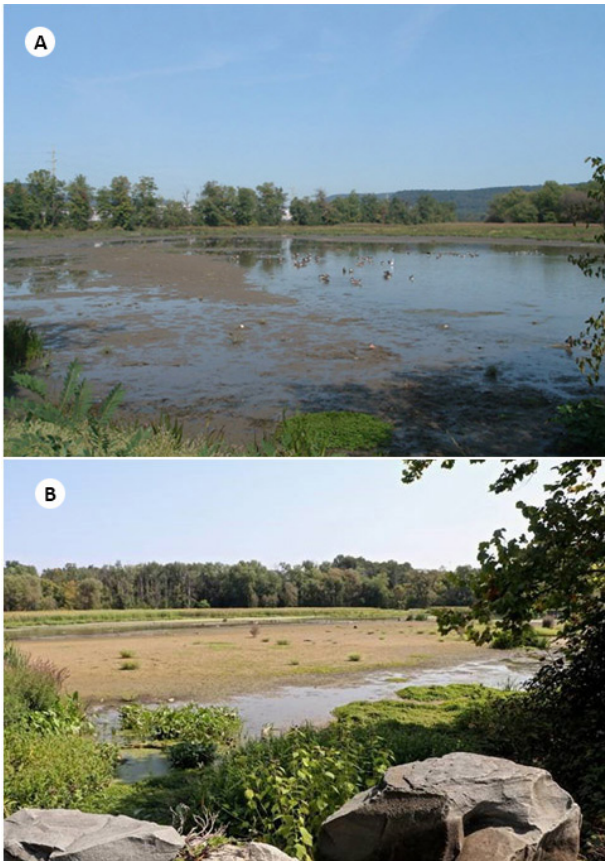


Figure 2. Wildwood Lake in 2003 **(A)** with open water and visited by wading birds and dabbling ducks, and in 2018 **(B)** having succeeded to mudflats and cattail marsh. Property of Wildwood Lake Nature Center Archives.

turtle was permanently marked using the Proximate Binary Coded Decimal (PBCD) scute-notching system of Buhlmann et al. (2008). The notches which displayed a unique number were made with a Dremel tool. Each new turtle was also given a Passive Integrated Transponder (PIT) tag inserted through the left thigh along the bridge of the carapace. The tags were HPT12 preloaded sterile tags from BioMark (Boise, Idaho), inserted using a BioMark MK-25 Rapid Implant Gun. Recaptured turtles were measured, scanned for the PIT tag, and carapacial notches were renewed as needed before releasing turtles on the same day of their capture.

Our study site supported three other turtle species, which were captured in the traps during this study. eastern musk turtles *Sternotherus odoratus* ($n = 2$) and snapping turtles *Chelydra serpentina serpentina* ($n = 62$), were individually marked using the same methods applied to painted turtles and released. Exotic red-eared sliders *Trachemys scripta elegans* also established at Wildwood, were captured ($n = 22$) and euthanised, and a sample of them was deposited in the State Museum of Pennsylvania, Harrisburg, Pennsylvania (Russell et al., 2014).

Determination of Sexual Maturity

Long foreclaws are associated with mature males in this species (Ernst & Lovich, 2009). Foreclaws of at least 7

mm were common in males ranging 93.0–121.3 mm CL. Foreclaws of at least 8 mm were common in males ranging 93.5–141.8 mm CL. Foreclaws of at least 9 mm were common in males ranging 90–140.5 mm CL. Among four males larger than 90 mm CL, one had foreclaws of 6 mm, and three had foreclaws of 5 mm. No foreclaws were larger than 6 mm among the five males smaller than 90 mm CL. Thus, we concluded that males of at least 90 mm CL evidenced clear sign of sexual maturity in this secondary sexual characteristic (Fig. 3).

We used body size of dissected and nesting females during 2011–2021, as the criterion of female shell length at sexual maturity. During 2016–2017, seven females (132.9–154.2 mm CL) were removed from the population to ascertain minimum shell length at sexual maturity. Specimens were deposited in the section of Zoology and Botany of the State Museum of Pennsylvania. Opportunistic observations of 15 nesting females during 2011–2014 (143–155 mm CL) and 2018, 2019, and 2021 (130–165.1 mm CL) provided additional data to determine shell length of the smallest mature female. The smallest sexually mature female measured 130 mm CL (124 mm PL) and was seen nesting on 2 July 2018. A female (SMP-H-9230) measuring 132.9 mm CL (124.6 mm PL) captured on the tow path on 8 July 2016 was found to contain luteal scars and yolking ovarian follicles. Based upon this sample, 130 mm CL was accepted as the cut-off for smallest sexually mature female in this study.

Growth and Age Estimation

In most species of turtles, age can be reasonably estimated in young individuals using growth annuli on epidermal scutes (Spencer, 2002). However, counting growth rings has been found to be unreliable in providing accurate age estimates in adult turtles (Wilson & Tracy, 2003), especially for estimating ages in adult *C. picta* (Brooks et al., 1997). Lindeman (1996), in particular, showed that counting growth rings for individuals of *C. picta* becomes inaccurate around age 7 (i.e. counts of scute annuli are useful in age determination only among juveniles, and unreliable, if even readable, thereafter). Alternatively, we set out to establish sex-specific, length-at-age relationships for our samples based on repeated records of age and length from known-age individuals that had a more conservative value of 5 or fewer estimated growth rings when first captured (37 females captured 58 times; 60 males captured 94 times). We used a multi-model approach to compare three well established growth models (von Bertalanffy, Gompertz, and Logistic) using the ‘AquaticLifeHistory’ package (Smart, 2019a) in R (version 4.0.5; R Core Team, 2021). We rooted the models using the carapace length of a hatchling found at the site (24.8 mm). We assessed the best fitting models using an information theoretic approach (Akaike Information Criterion AIC; Burnham & Anderson, 2002). The best fitting model for each sex was then used as input to build length-at-age curves using a Bayesian Markov chain Monte Carlo process with the ‘BayesGrowth’ package in R running for 5,000 iterations (Smart, 2019b). Growth was also calculated as the difference in carapace

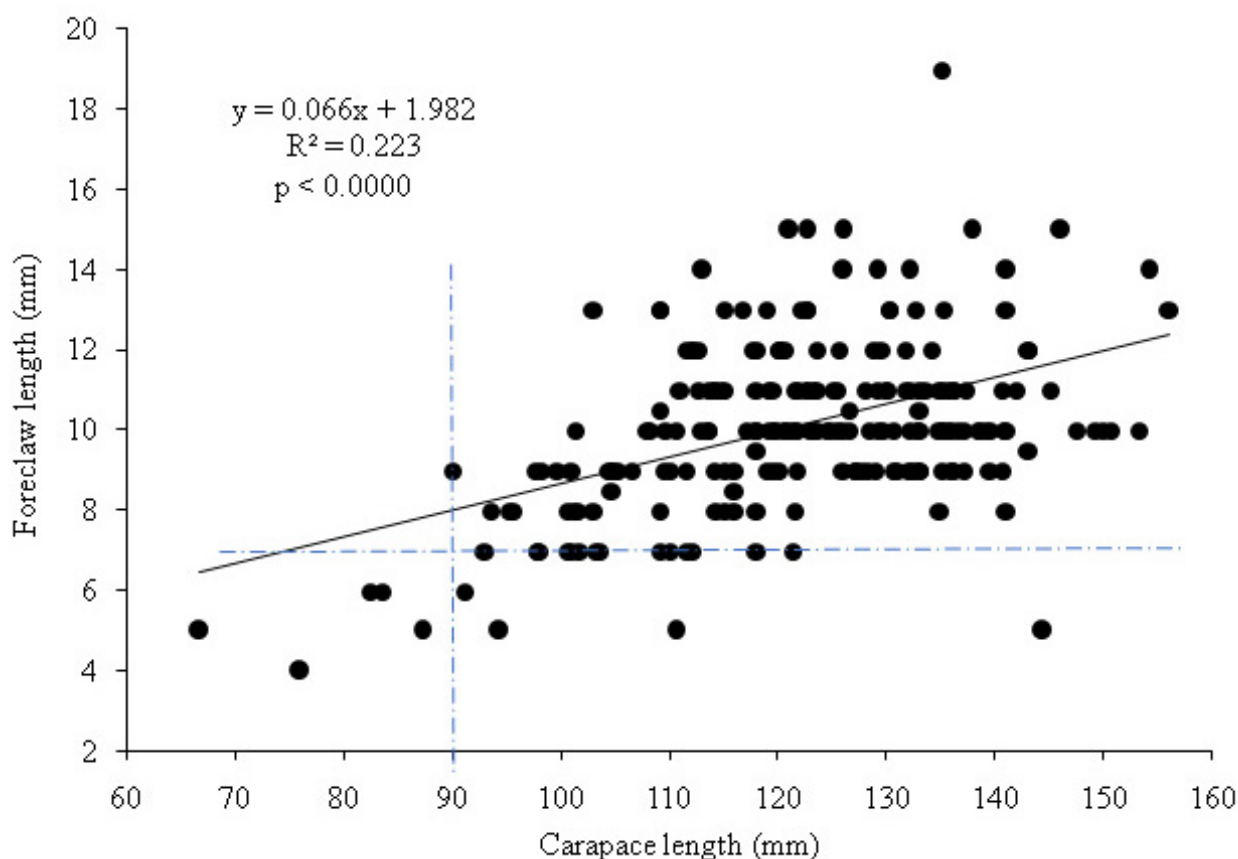


Figure 3. Relationship between foreclaw length and carapace length (CL) in 215 male painted turtles *C. picta picta* X *C. p. marginata* at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2011–2019. Blue crosshairs indicate thresholds associated with minimum foreclaw length associated with sexual maturity.

length between captures divided by the interval in years between captures, which we plotted against carapace length at first capture. Carapace size intervals in the bar histogram of body size distribution were determined using the equation of Sturges (1926). Summary statistics of body size were performed using Microsoft Excel 365 (Microsoft Inc., Redmond, Washington, USA).

Population Size and Survivorship

We calculated apparent annual survival (Φ) and recapture rates (p) using open population Cormack-Jolly-Seber models (CJS; Lebreton et al., 1992) in the program MARK (White & Burnham, 1999). To test for differences in Φ and p between sexes, we generated CJS models to examine whether Φ or p differed based on sex, time, or a sex-time interaction. We based model selection for all analyses on AICc (corrected AIC for small sample sizes) values, with lower values denoting greater parsimony (Burnham & Anderson, 2002). We calculated population abundance for adults using POPAN parameterisation of Jolly-Seber models (Jolly, 1965; Seber, 1965) in MARK (White & Burnham, 1999).

Encounter histories to calculate demographic traits estimate the probability that an individual will leave a population. With encounter rates reversed, the probability of an individual entering the population was estimated (Pradel, 1996), whereby λ = rate of individuals entering a population. Pradel's λ differs from traditional

estimates of λ as no fecundity values are included in its calculation, so is not necessarily equivalent to a true population growth rate. Pradel's λ was estimated in Program MARK in conjunction with the CJS models described above. Measure of central tendency was expressed as mean and standard deviation unless otherwise noted. Statistical significance was recognised at a p value of < 0.05 .

RESULTS

Population Structure

Juveniles comprised 14.1 % of 375 new captures, outnumbered by adults at 6.08:1.00. The adult male:female sex ratio of this sample was 2.93:1.00. Adult male body size averaged 121.4 mm CL (std. dev. = ± 14.1 ; min-max = 90.0–156.0; $n = 240$) and 111.6 mm PL (std. dev. ± 12.8 ; min-max = 84.0–142.2; $n = 240$). Adult female body size averaged 147.8 mm CL (std. dev. ± 8.7 ; min-max = 129.7–171.0; $n = 82$) and 138.3 mm PL (std. dev. ± 8.4 ; min-max = 120.1–165.0; $n = 82$). Many of the 240 males (40 %) fell in the 111.0–126.0 mm CL range, and most of the 82 females (59.8 %) fell into the 143.0–158.0 mm CL range (Fig. 4). Plastron length was strongly related to CL in adults of both males ($r^2 = 0.95$, $F = 4357$, $p < 0.001$; mm PL = 0.8857 (mm CL) + 4.1118) and females ($r^2 = 0.89$, $F = 627.69$, $p < 0.001$; mm PL = 0.906 (mm CL) + 4.4546).

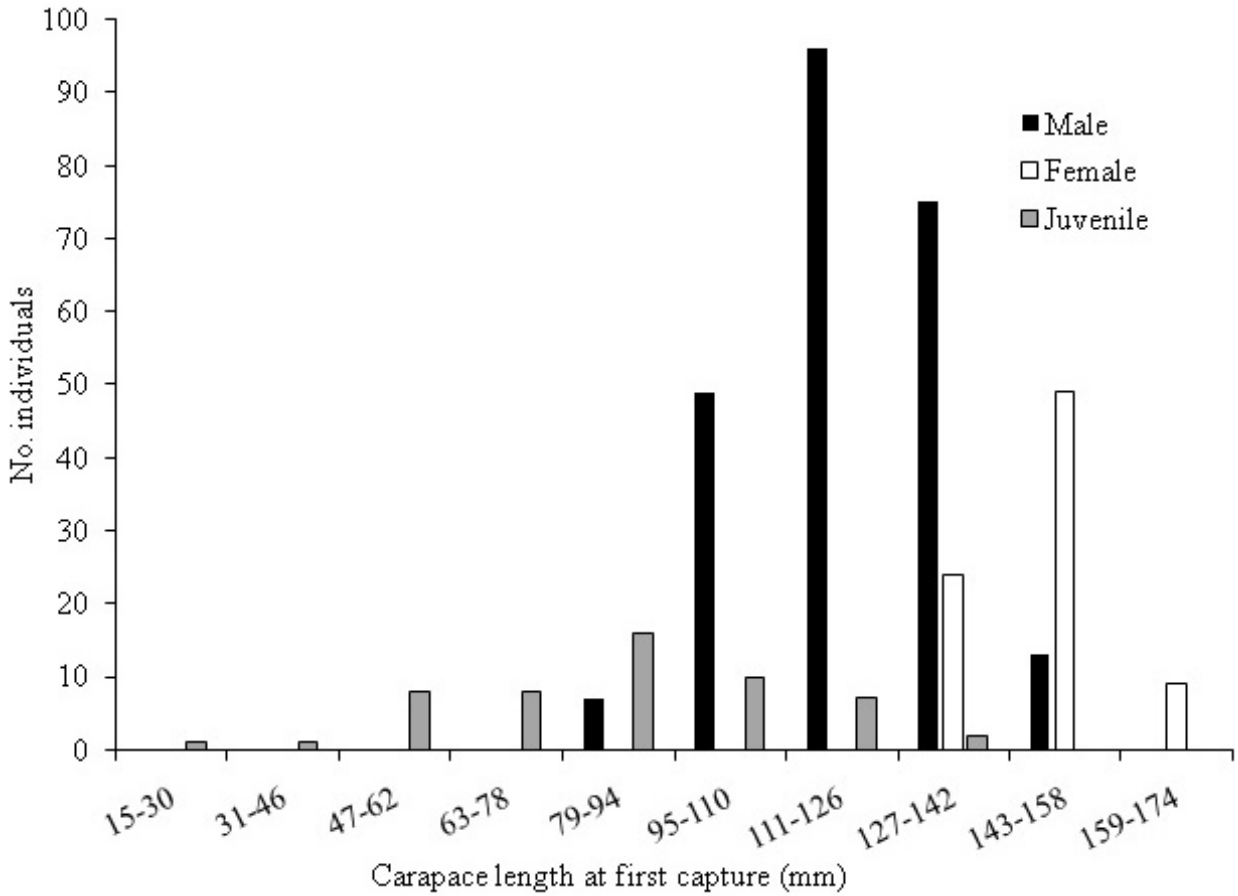


Figure 4. Body size distributions of 240 adult male, 82 adult female, and 53 juvenile painted turtles *C. picta picta* X *C. p. marginata* at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2011–2019.

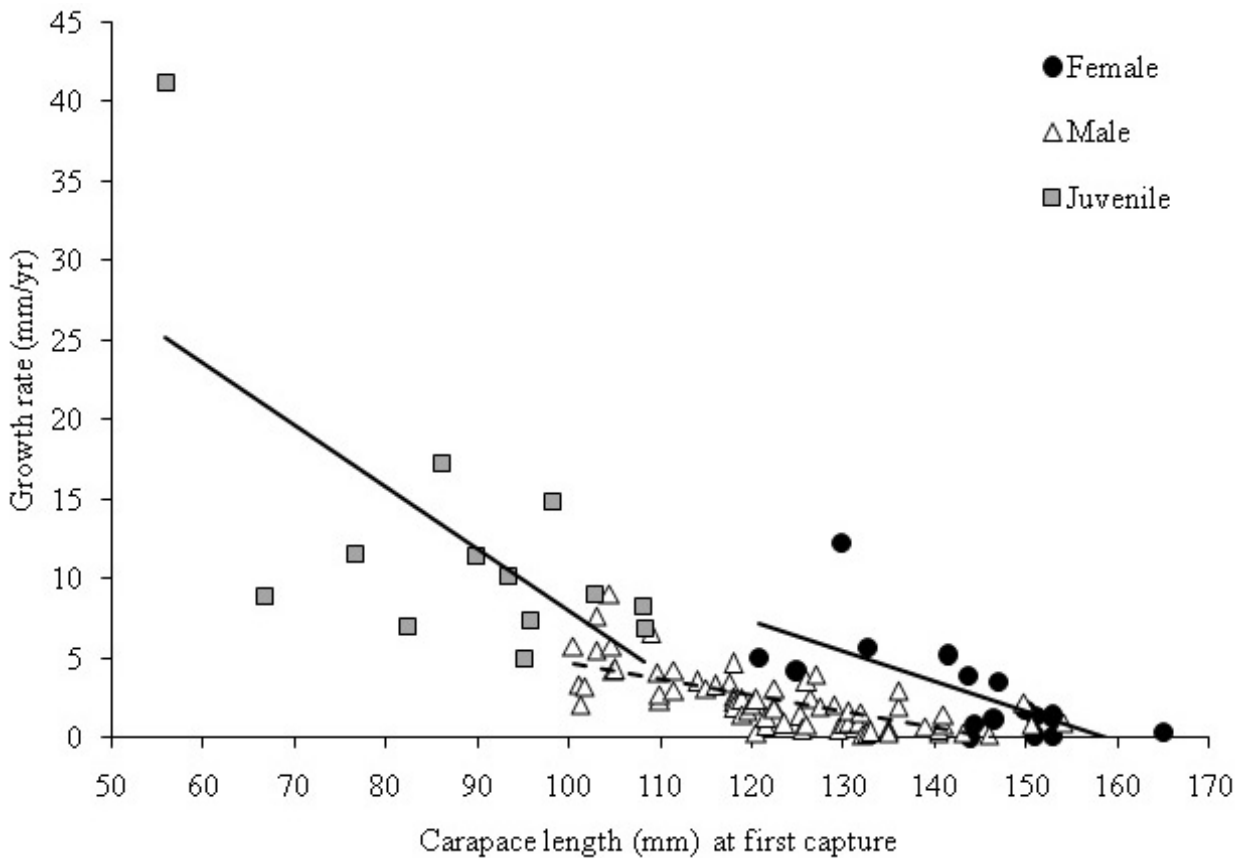


Figure 5. Annual growth rate plotted against carapace length at first capture for males, females, and juveniles of the painted turtle *C. picta picta* X *C. p. marginata* at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2011–2019.

Table 1. Multi-model comparisons for determining sex-specific, best-fitting growth curves for *Chrysemys picta* at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2011–2019. Asymptotic body size (A) and characteristic growth constant (k) \pm 1 standard error.

	Model	AICc	Δ AIC	AICc Weights	A	k
Males	von Bertalanffy	645.77	0	0.77	116.4 \pm 1.75	0.6 \pm 0.055
	Gompertz	648.48	2.71	0.20	114.8 \pm 1.53	0.97 \pm 0.105
	Logistic	652.25	6.47	0.03	113.9 \pm 1.44	0.79 \pm 0.079
Females	Gompertz	482.46	0	0.44	142.7 \pm 6.04	0.59 \pm 0.107
	Logistic	482.84	0.38	0.36	138.8 \pm 5.07	0.81 \pm 0.143
	von Bertalanffy	484.11	1.65	0.19	152.9 \pm 8.86	0.34 \pm 0.065

Growth and Age Estimation

Growth rates decreased with increasing carapace length (Fig. 5). The average growth rate was highest for juveniles (12.2 mm/yr, min-max = 4.9–41.2 mm/yr, n = 13) and much lower for females (2.8 mm/yr, min-max = 0–12.2 mm/yr, n = 17) and males (2.3 mm/yr, min-max = 0.2–9.1 mm/yr, n = 68). Based on AICc values, the top models for growth differed between the sexes: von Bertalanffy for males and Gompertz for females (Table 1). Estimates of asymptotic body size (A) and characteristic growth constant (k) returned the following values based on the top models for each sex: males (A = 116.4; k = 0.6) and females (A = 142.7; k = 0.59). The growth trajectory of males rose more rapidly than females, such that males reached maturity faster, at two years of age, but males exhibited almost no noticeable growth beyond an estimated age of four years (Fig. 6). Males were also smaller at their asymptotic body size compared to females. Females, in contrast, appeared to grow at a steadier pace until reaching maturity. Based on visual inspection of the growth curve and female body sizes (Fig. 6), a few females reached maturity at three years of age, many at four years, and by five years of age all females were mature. Thereafter, growth continued, albeit very slowly.

Survivorship, Detection, and Population Size

Female survivorship (0.80 \pm 0.04) was lower than that of males (0.89 \pm 0.02), although recapture probabilities were similar (Table 2). For the most parsimonious model, Φ differed between sexes and p was time dependent (Table 3). As expected, recapture probabilities increased with sampling intervals and numbers of individuals marked. Pradel's λ was stable to slightly increasing for females and stable to slightly decreasing for males. Since Pradel's λ values are based on probability of new animals entering the population, these values are indicative of the probability of capturing an unmarked individual entering the population. The population was male biased at roughly 2.1:1 among initial captures, which is reflected in the population estimates (Table 2). Population density

Table 2. Population dynamics of the painted turtle *Chrysemys picta* at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2011–2019. Parameters include apparent survivorship (Φ), recapture probability (p), Pradel's Lambda (λ), and population size (n) \pm one standard error and 95 % confidence intervals.

	Φ	p	λ	n
Female	0.80 \pm 0.04 (0.74, 0.93)	0.13 \pm 0.03 (0.08, 0.19)	1.02 \pm 0.02 (0.97, 1.06)	96 \pm 13 (73, 128)
Male	0.89 \pm 0.02 (0.84, 0.93)	0.17 \pm 0.02 (0.14, 0.21)	0.98 \pm 0.01 (0.95, 1.01)	227 \pm 24 (185, 283)

in the canal (2.65 ha) and the lake (3.53 ha) combined was 52.3 turtles/ha. Trends in recapture rates between sampling intervals increased over time (Fig. 7).

DISCUSSION

We found that several demographic traits of the turtle population at our site were accelerated, and when examined in the context of other demographic studies in the mid-Atlantic region (Ernst & Lovich, 2009), it appears that differences in nutrient levels in the wetlands may be a likely factor. In Pennsylvania, for example, Ernst (1971a,b) provides a reasonable comparison to our results because he also studied a population of *C. p. picta* X *C. p. marginata* intergrades from a more natural wetland on Big Chickees Creek, which is only about 45 km south-east of our site. Our study site, on the other hand, was quantifiably eutrophic and subjected to continuous nutrient enrichment (see Methods). This apparent difference in resource availability, in turn, provided us with a variable to consider in the following discussion as an effect on comparative growth rates, body sizes, and ages at maturity between the populations. However, we note that meaningful interpopulation differences, possibly associated with hybrid vigour, cannot be ruled out, nor can other differences between the two

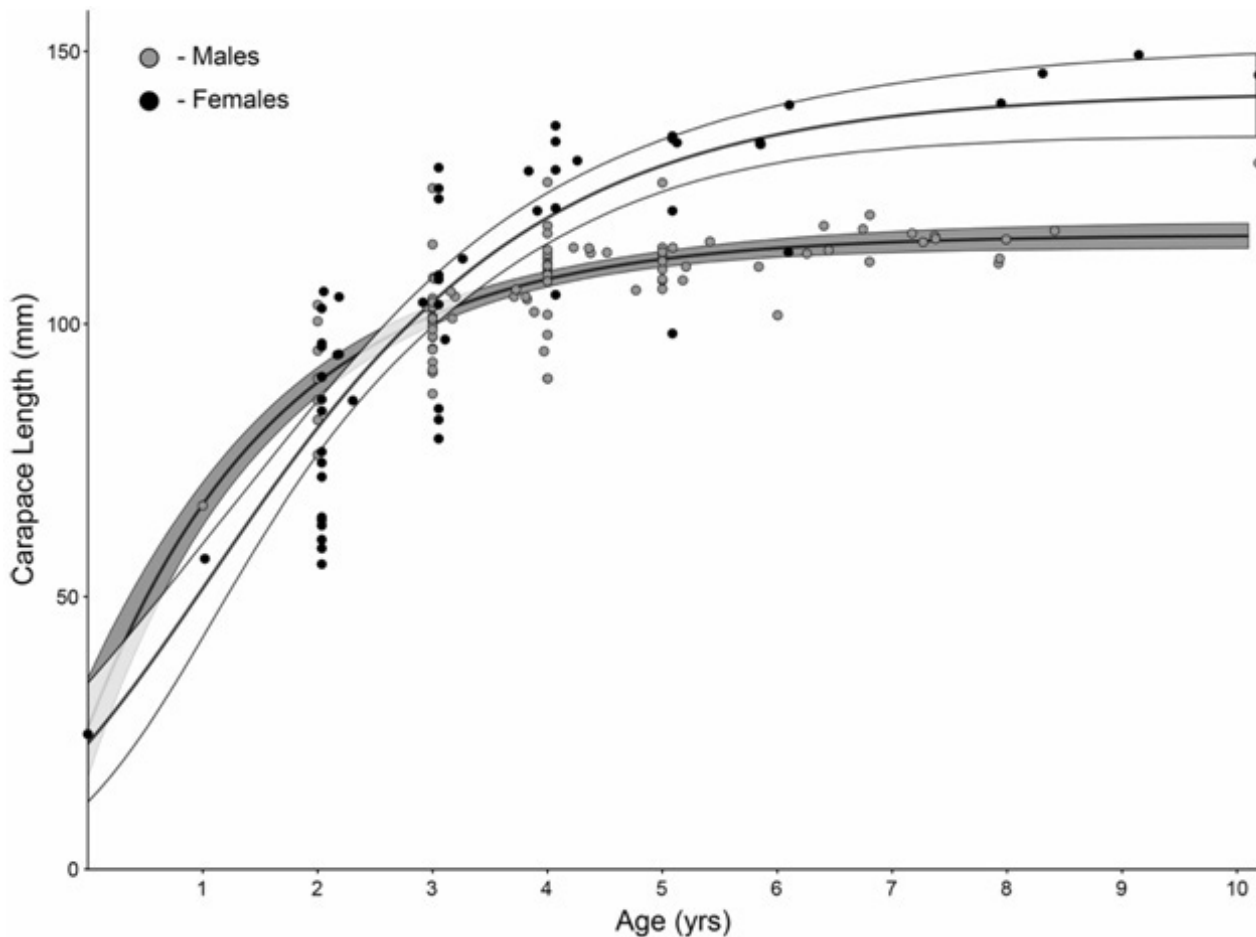


Figure 6. Best-fitting, sex-specific growth curves for the painted turtle *C. picta picta* X *C. p. marginata* using known length-at-age data collected from wild individuals at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2011–2019. Dark lines indicate age-length relationships and shaded areas confidence bands, generated by a Bayesian Markov chain MonteCarlo process.

habitats unrelated to nutrient levels, which may have accounted for the demographic differences we detail below.

Male painted turtles at Wildwood Park reached a larger minimum PL of 83.8 mm than the 70 mm PL reported by Ernst (1971a). Likewise, respective mean PL (111.6 mm, 96 mm) and maximum PL (142.2 mm, 121.0 mm) of adult males were larger at our eutrophic site than those reported by Ernst (1971a). Elsewhere in the mid-Atlantic region, sexual maturity in males of *C. p. picta* was reached at > 71 mm PL in Myrtle Grove Wildlife Management Area, a natural habitat in which turtles exhibited normal growth, Charles County, Maryland (Ernst & McDonald, 1989), and 71mm PL (77.7 mm CL) in a lake, creek and beaver ponds in Henrico County, Virginia (Mitchell, 1988). However, at a sewage treatment plant in Charles County, Maryland, the smallest mature male measured 87.1 mm PL (Ernst & McDonald, 1989). These comparisons between our study and more natural sites corroborate the conclusions by Ernst & McDonald (1989) that males exhibit plasticity in body length at sexual maturity. Our data and those of Ernst & McDonald (1989) on minimum PL at sexual maturity provide a PL range (83.8–87.1 mm) as a general response to eutrophic conditions in males of mid-Atlantic populations, such

that recently matured males from eutrophic systems are approximately 1.2 times the size of their counterparts from less altered systems.

The minimum PL associated with sexually mature females from our site (122.2 mm) was larger than the minimum (100.8 mm) reported by Ernst (1971a) from a natural setting. The same was true of respective mean PL (138.3 mm, 116.9 mm) and maximum PL (165.0 mm, 145.4 mm) of adult females (Ernst, 1971a). In Henrico County, Virginia, minimum size at sexual maturity in females of *C. p. picta* was reached at 97.2 mm PL (Mitchell, 1988). However, among four females collected at a sewage lagoon in Charles County, Maryland, two females measuring 127 mm and 129 mm PL were not yet mature, and 132 mm and 139 mm PL may or may not have been mature, but none of these females contained shelled eggs or corpora lutea, nor were collecting dates provided (Ernst & McDonald, 1989). An examination of the ovarian follicle size-classes and widest diameters indicated that the two largest females collected by Ernst & McDonald (1989) may have been developing their first clutch, or, if mature, their first clutch of the season. Our data and those of Ernst & McDonald (1989) suggest that females subjected to eutrophic conditions exhibit a larger body size at sexual maturity resulting in

Table 3. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture probability (p) between male and female painted turtles *Chrysemys p. picta* X *C. p. marginata* at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2011–2019. Models differ in whether Φ and p are assumed to be constant (.), fully time dependent (t), or differ between sexes (g), and whether there are interactions (*) among these factors.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par.	Deviance
$\Phi(g) p(t)$	1098.16	0	0.997	1	12	350.6368
$\Phi(g) p(g^*t)$	1110.135	11.975	0.0025	0.0025	22	340.9789
$\Phi(t) p(t)$	1113.476	15.3153	0.00047	0.0005	19	350.9133
$\Phi(t) p(g^*t)$	1119.644	21.4839	0.00002	0	29	334.7405
$\Phi(g^*t) p(t)$	1125.847	27.6863	0	0	29	340.9429
$\Phi(g^*t)p(g^*t)$	1136.363	38.2029	0	0	38	330.4361
$\Phi(t) p(g)$	1154.61	56.4493	0	0	12	407.0861
$\Phi(g^*t) p(g)$	1173.009	74.8488	0	0	22	403.8528
$\Phi(g) p(g)$	1177.345	79.1844	0	0	4	446.4368
$\Phi(.) p(.)$	1178.767	80.607	0	0	2	451.9216

a primiparous shell length at 1.3 times the size of their counterparts from more natural systems.

Mean values of shell dimensions can reflect differences in the environment, especially nutrient inputs. For example, in Virginia mean adult PL of males and females, respectively, were larger (103.1 mm and 124.1 mm) from a more eutrophic site (Mitchell, 1985a,b) than those in a less nutrient-rich site nearby (96.2 mm and 120.5 mm; Mitchell, 1988). To that end, we note that the mean PL of adult males (96.0 mm) and females (116.9 mm) from Ernst's (1971a) natural site were much smaller than those from our site (111.6 mm and 138.3 mm, respectively). Within a single study, Gibbons (1967) found decreasing size in longest shell lengths in both sexes from three sites in Michigan that varied in nutrient load: polluted river, eutrophic lake, and clean marsh. Carnivory in turtles from Gibbons (1967) also increased with increasing eutrophication, suggesting dietary differences may contribute to growth responses of individual males and females. Thus, rapid growth and overall larger body size is associated with more nutrient-rich sites, and larger body size at sexual maturity is more pronounced in females than in males.

We also wanted to know if growth rates and the minimum age at sexual maturity differed between eutrophic and natural sites. Quinn & Christiansen (1972) documented faster growth by western painted turtles *C. p. bellii* from Iowa in eutrophic systems than in those with demonstratively less organic matter in the substrate. Likewise, the nutrient level, adult body size, and carnivory of the turtles at Gibbons' (1967) sites were associated with differential growth rates in those in increasingly eutrophic

waterbodies. Ernst & McDonald (1989) corroborated faster growth in both sexes from a eutrophic site and determined that sexual maturity of males at a sewage treatment site was reached in two years, as was ours, instead of four years from natural sites in south-eastern Pennsylvania (Ernst, 1971a) and central Virginia (Mitchell, 1988), where all males had foreclaws of at least 8 mm. Sexual maturity of females was reached at 3–5 years of age at our site, but females from a sewage treatment plant in Maryland may have been mature at three years (Ernst & McDonald, 1989). Ernst & McDonald's (1989) uncertainty regarding a connection between enhanced growth and early maturity in females from the sewage lagoon is understandable considering their unavoidably small sample size of dissected turtles. However, because Ernst & McDonald's (1989) site was presumed to have been much more nutrient-rich than ours, we consider it probable that the large 3-yr old females at their site were mature. Comparatively, females from more natural sites in the mid-Atlantic region matured at an age of five (Ernst, 1971a) or eight years (Mitchell, 1988). Some females from our site reached the minimum body size at sexual maturity in three years, followed by many at four years, and all by five years. Whereas males and females consistently matured at larger sizes at our site, earlier age at sexual maturity varied more in females than in males. Fast growth in juvenile turtles in our study, linked to elevated nutrient input, results in earlier maturation at similar or larger body sizes compared to slower growing counterparts of *C. picta*, as well as blanding's turtle *Emydoidea blandingii* and *C. serpentina* (Congdon et al., 2018).

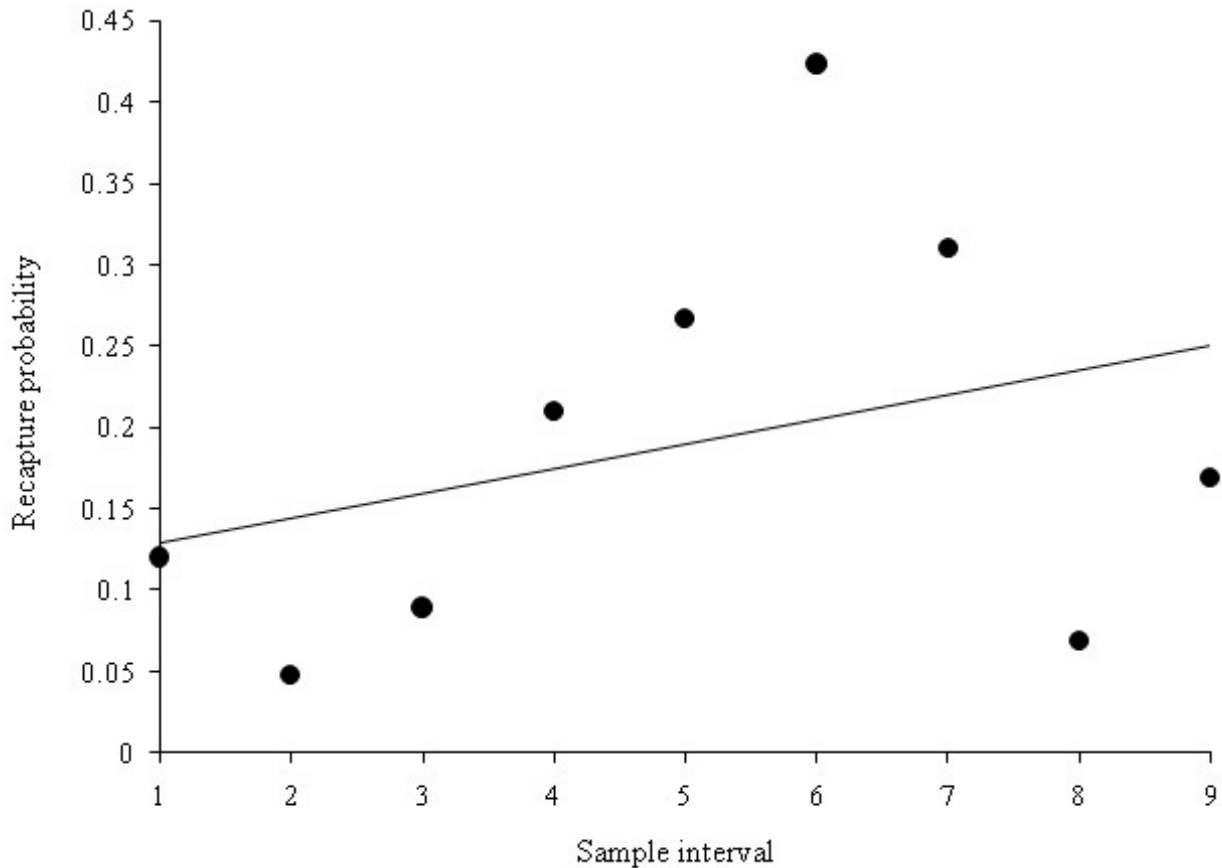


Figure 7. Trends in recapture rates between samples of the painted turtle, *C. picta picta* X *C. p. marginata*, at Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2011–2019.

Other demographic measures of our study population were in general agreement with those of other populations of *C. p. picta* and *C. p. picta* X *C. p. marginata* intergrades. Survivorship of both sexes was high at our site, a finding typical of *C. p. picta* (Mitchell, 1988; Zweifel, 1989) and *C. p. marginata* (Hughes & Meshaka, 2020) in the north-east and mid-Atlantic. Population density, however, can range widely across and within regions. Our estimate of 52.3/ha exceeded 25/ha of *C. p. picta* in a New York pond (Bayless, 1975) and 13.9/ha of *C. p. marginata* in a Pennsylvania pond (Hughes et al., 2016). In three Michigan ponds, population densities of *C. p. bellii* ranged from 39.9 to 89.5/ha (Congdon et al., 1986). Seasonal population density estimates range even more widely, including a published range of 137–248/ha for *C. p. picta* in New York ponds (Zweifel, 1989), and estimates as high as 590.4/ha for *C. p. picta* X *C. p. marginata* in a marsh and pond in south-eastern Pennsylvania (Ernst, 1971b) and 590/ha for *C. picta* in a Michigan pond (Gibbons, 1968).

The adult:juvenile ratio of a population also varies widely among populations, across habitats, and over time within a population. Our adult:juvenile ratio of first captures (6.08:1.00) was comparable to values of 5.0:1.0 from a pond (Bayless, 1975), and 4.20:1.00 from a marsh and pond (Ernst, 1971b). The ratio was much lower at a lake (1.1–1.3:1.00) studied by Mitchell (1988). On the other hand, an 18-year study in New York ponds yielded an average adult:juvenile ratio of 2.16:1.00 and range

0.45–6.30:1.00 (Zweifel, 1989). In general, hoop-net based population inferences tend to be skewed towards trapping larger species (Ennen et al., 2021) and mostly adults of smaller species (Tesche & Hodges, 2015). For example, it was recently shown that the average CL of 95 *C. picta* caught in hoop-nets with a mesh width size of 5.08 cm was significantly larger than the mean CL of 231 individuals caught in hoop-nets with a mesh size of 2.54 cm (Gulette et al., 2019). We suggest that future efforts employ a variety of turtle sampling methods to determine if the patterns we found reflect the size-class distribution of this turtle population (e.g. Ream and Ream, 1966).

Adult sex ratios of *C. picta* are often even (Bayless, 1975; Ernst, 1971b, Mitchell, 1988), however, they can vary over time (0.62–1.80:1.00) (Zweifel, 1989) and subjected to differences based on sampling technique used (Ream & Ream, 1966). To that end, our hoop-nets could have drawn males to a single female already in the traps resulting in a male bias. We also consider a potential combined effect of early sexual maturity in males and differential mortality in nesting females that may have influenced the sex ratio we found. Many of the well-known mesopredators of nesting females and their eggs (Ernst & Lovich, 2009) were regularly encountered at Wildwood Park: raccoons *Procyon lotor*, red foxes *Vulpes vulpes*, mink *Neogale vison*, striped skunks *Mephitis mephitis*, and long-tailed weasels *N. frenata* (W.E.M. and E.W., pers. obs.).

Fully comparable, systematic comparisons of physical and chemical parameters among sites, or data on temporal transitions within sites, as in comparisons with Ernst's (1971a,b) sites are lacking; therefore, we cannot rule out alternative explanations for the observed pattern. However, the population of *C. picta* at our site displayed demographic patterns consistent with those of populations in other eutrophic systems, suggesting a general effect of water quality that we suggest should be investigated experimentally. Both sexes grew faster and matured at longer shell lengths than conspecifics from less nutrient-rich habitats. Comparatively, males showed less plasticity in body size at sexual maturity and a narrower range in reduced age at maturity than females at our site. From a 33-yr study in Michigan, Congdon et al. (2018) demonstrated that the juvenile growth rate in *C. picta* females has a profound effect on age at sexual maturity, such that faster growing juveniles matured up to 6-yrns sooner than slower growing females and that post-maturity growth had very little effect on size-dependent reproductive traits, such as clutch size. Consequently, the earliest-maturing females, such as those that matured in 3-yrns at our site, can potentially have more lifetime egg output than the oldest-maturing individuals at Wildwood (5-yrns). Based on average clutch sizes of primiparous and older female *C. picta* in Congdon et al. (2018), the earliest-maturing females at Wildwood could produce 12 eggs over two years before the oldest-maturing females first laid eggs, and in turn, it would take these females decades until they caught up in lifetime egg output to the earliest-maturing females. One question that remains to be answered in life history theory for *C. picta* is whether there is a strong relationship between age at maturity and longevity, such that the turtles at Wildwood may mature earlier compared to elsewhere but die sooner, a phenomenon that could impact population dynamics in a long-lived, often abundant species that is ever more subjected to altered environments in expanding urban ecosystems across its geographic range. This last point, and the potential effects of human-altered habitats on chelonian demography in general, can by extension apply as testable hypotheses to aquatic turtle species worldwide, which are facing increasing contact with human impacts to their remaining aquatic habitats.

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