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Do observed sex ratios in a turtle community in northern Indiana vary over 35 years (1979–2014)?

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***Abstract.*—Anthropogenic changes to the environment (e.g., climate change, roads, habitat alteration) can cause sex ratios in freshwater turtles to differ from the expected 1:1 ratio. We examined long-term trends in the sex ratios of five species of freshwater turtles in Dewart Lake in northern Indiana from 1979 to 2014. None of the species (*Chelydra serpentina*, *Chrysemys picta*, *Graptemys geographica*, *Trachemys scripta elegans*, and *Sternotherus odoratus*) showed significant temporal trends in sex ratio, and indeed they all showed remarkably consistent sex ratios (i.e., proportion of males). Overall, the mean proportion of males did not differ significantly from 0.5 in *C. picta*, *G. geographica*, or *T. s. elegans*, while both *C. serpentina* and *S. odoratus* had significantly male-biased sex ratios. Our failure to observe any changes in the sex ratios over the course of our study does not preclude an impact of the anthropogenic factors on these species of turtles, but suggests that they are not influencing sex ratios in a systematic way in Dewart Lake.**

Keywords. *Chelydra serpentina*, *Chrysemys picta*, *Graptemys geographica*, populations, Reptilia, *Sternotherus odoratus*, temporal trends, *Trachemys scripta elegans*

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Introduction

Animal populations are generally expected to have a 1:1 sex ratio (Fisher 1958). However, anthropogenic factors can potentially cause the sex ratios in a variety of animals, including freshwater turtles, to vary from the expected 1:1 ratio (e.g., Smith and Iverson 2006; Lambertucci et al. 2012; Mondol et al. 2014; Sharma et al. 2014). One major factor that may alter the sex ratios in freshwater turtles with temperature-dependent sex determination is an increase in global temperatures due to anthropogenically-driven climate change (Butler 2019; Janzen 1994; Schwanz et al. 2010). In addition, predicted increases in the variations of temperatures, including increases in the frequency and intensity of heat waves, will potentially have effects on freshwater turtle sex ratios (Carter et al. 2018; Neuwald and Valenzuela 2011; Valenzuela et al. 2019). Changes in precipitation during the nesting period may also influence the sex ratios of freshwater turtles (LeBlanc and Wibbels 2009; Sifuentes-Romero et al. 2018).

Beyond the effects of climate change, other anthropogenic changes in the environment can affect the sex ratios of freshwater turtles. Increased road mortality of freshwater turtles, especially nesting females, can shift sex ratios making them more male-biased, sometimes extremely so (e.g., Aresco 2005; DeCatanzaro and Chow-Fraser 2010; Dupuis-Déormeaux et al. 2017, 2019; Mali et al. 2013; Marchand and Litvaitis 2004; Nicholson et al. 2020; Piczak et al. 2019; Steen and Gibbs 2004; Winchell and Gibbs 2016). However, Dorland et al. (2014) and Vanek and Glowacki (2019) found no relationships between male-biased sex ratios in *C. picta* populations and either road density or other similar factors. Agriculture adjacent to ponds and lakes can alter freshwater turtle sex ratios by changing the thermal conditions of the nest (e.g., Freedberg et al. 2011; Thompson et al. 2018). In addition, any alteration of vegetation cover and canopies at nesting sites can also impact the sex ratios of freshwater turtles (Freedberg and Bowne 2006; Marchand and Litvaitis 2004; Weisrock and Janzen 1999), as can changes in nesting substrate (e.g., sand, soil, gravel; Mitchell and Janzen 2019). Such changes in nest-site characteristics can occur when residential development occurs near freshwater turtle nesting areas (Kolbe and Janzen 2002), and urbanization has been shown to alter the thermal environments of nests leading to sex ratio biases (Bowne et al. 2018;

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but see Vanek and Glowacki 2019). Thus, increasing anthropogenic influences on the environment can have significant impacts on the sex ratios of freshwater turtles. Such variations from a 1:1 sex ratio can have conservation implications for the long-term persistence of freshwater turtle populations (Gibbons et al. 2000).

We examined the long-term trends in sex ratios of five species of freshwater turtles in Dewart Lake in northern Indiana in 30 different years within a 35-year study period (1979–2014). The species investigated were: Common Snapping Turtles (*Chelydra serpentina*), Painted Turtles (*Chrysemys picta*), Common Map Turtles (*Graptemys geographica*), Red-eared Sliders (*Trachemys scripta elegans*), and Common Musk Turtles (*Sternotherus odoratus*). Turtle populations have been studied in Dewart Lake for over 50 years (see Wade and Gifford 1965), and the populations of the different species of turtles have been under relatively regular study from 1979–2014 (*C. serpentina*: Smith and Iverson 2004; Smith et al. 2006, 2018; *C. picta*: Smith et al. 2017, 2018, 2020; *G. geographica*: Iverson et al. 2019; Smith et al. 2018, 2020; *S. odoratus*: Smith and Iverson 2004; Smith et al. 2006, 2017; and *T. s. elegans*: Lewis et al. 2018; Smith et al. 2018, 2020). All of the species we examined have temperature-dependent sex determination (*C. serpentina*, Ewert et al. 2005; Janzen 1992; Rhen and Lang 1998; St. Juliana et al. 2004; *C. picta*, Ewert et al. 2004; Rhen and Lang 1998; Schwarzkopf and Brooks 1985, 1987; *G. geographica*, Bull 1985; Vogt and Bull 1984; *S. odoratus*, Ewert et al. 2004; and *T. s. elegans*, Carter et al. 2017; Dodd et al. 2006), and thus their sex ratios might be influenced by any changes in environmental temperatures. There is evidence that the temperatures in Indiana have increased during the last quarter of the 20th century and the start of the 21st century, as has precipitation (Frederick 2018). In addition, the local environment around Dewart Lake has changed over the study period, including increased residential development, shoreline modification (i.e., concrete seawalls, increased coverage by manicured lawns), and improved recreational facilities (e.g., paved boat launches), as well as increased road and boat traffic (J.B. Iverson, G.R. Smith, and J.E. Rettig, pers. obs.). These are all changes that could potentially alter the sex ratios of the freshwater turtles in Dewart Lake.

Materials and Methods

This study examined the freshwater turtle community in Station Bay (area = 4.5 ha) in the SE corner of Dewart Lake near Syracuse, Kosciosko County, Indiana, USA. Turtles were surveyed in late July to early August nearly annually from 1979 to 2014, for a total of 30 years of sampling effort. Prior to 1992, all trapping was carried out with aquatic wire funnel traps (n = 5 to 15; see Iverson 1979 for design). Starting in 1993, all trapping used 2.5 cm mesh fyke nets (n = 2 to 12) with 15 m (50') leads between a pair of 90 cm (3') hoop-diameter funnel traps (although a single fyke net and multiple wire traps were used in the transitional year of 1992). Traps were checked every 2–3 hours from sunrise until 1–2 hours post-sunset. No turtles entered the traps during the night (Smith and Iverson 2004). All captured turtles were sexed, retained, and subsequently released at the end of each sampling period (2–5 days). Males were sexed based on the presence of the following secondary sex characteristics for each species (also see Ernst and Lovich 2009): *C. serpentina* plastron shape, relative location of cloaca on tail (Mosimann and Bider 1960); *C. picta* relative tail size, elongated foreclaws (Smith et al. 2017); *G. geographica* tail length, placement of cloacal opening (Iverson et al. 2019); *S. odoratus* plastral size, tail size, scale patches on rear legs of males (Risley 1930); and *T. s. elegans* elongated foreclaws, tail length (Readel et al. 2008). Individuals without these characteristics, which were at or larger than the size at which male secondary sex characteristics would be apparent for each species, were considered females. By using these criteria, we were consistent across years in how the sex ratios were assessed relative to sexual maturity (see Lovich et al. 2014). In addition, for the four species which were permanently marked (*C. serpentina*, *C. picta*, *G. geographica*, and *T. s. elegans*), we were able to repeatedly sex individuals across years and confidently assign sex to individuals (and retrospectively adjust sex ratios as needed).

The proportions of males were tallied for *C. serpentina, C. picta*, *G. geographica*, *S. odoratus*, and *T. s. elegans* relative to the total number of individuals that were sexed each year. Trapping techniques can potentially show biases in terms of observed sex ratios (Browne and Hecnar 2005; Ream and Ream 1966; Thomas et al. 1999; see also Gibbons 1970, 1990; Lindeman 2013). However, since there is no reason to expect that any trapping bias would change over time, even if the observed sex ratios were potentially biased, they should allow for an assessment of the temporal changes in sex ratios. A trap type independent variable is included in the analyses to account for any possible effect of trap type on sex ratios. The observed sex ratios of trapped turtles can also vary seasonally due to sexual differences in activity (e.g., Moldowan et al. 2018; Vanek and Glowacki 2019). However, because trapping was always conducted during the same period each year (late July–early August), if such biases were present, they would have been constant throughout the study, and so any changes in observed sex ratios should reflect a change in the underlying sex ratio of the population.

The mean proportion of males across all years was compared to the expected 0.5 using a one-sample t-test for each species to determine whether there was a consistent bias in the sex ratios. For each species, a generalized linear model with a binomial distribution and logit link was used to examine the effects of year, trap type (e.g., fyke net year versus non-fyke net year), and total number of individuals examined per year on the proportion of males. It is worth noting that trap type was not included for *C. serpentina* because this species was never caught in the wire funnel traps. An α value of 0.05 was used to indicate significance, and data are reported as mean ± 1 S.E. The program JMP Pro 15.1 (SAS Institute Inc., Cary, North Carolina, USA) was used for all statistical analyses.

Results

Sample sizes. The overall mean (± 1 S.E.) annual sample sizes (including only years when at least one individual was captured) were:

- *C. serpentina,* 11.2 ± 1.5 (*n* = 18 years; range: 1–23);
- *C. picta,* 93.5 ± 11.4 (*n* = 30 years; range: 13–259);
- *G. geographica,* 12.5 ± 1.7 (*n* = 28 years; range: 1–42);
- *S. odoratus*, 79.0 ± 9.2 (*n* = 30 years; range: 4–189);
- *T. s. elegans,* 9.9 ± 1.3 (*n* = 22 years; range: 1–18).

Chelydra serpentina. The overall mean proportion of males by year was 0.66 ± 0.04 (*n* = 18), which is significantly different from 0.5 (t_{17} = 3.56, p = 0.0024). Using only years with > 10 individuals, the mean proportion of males was 0.69 ± 0.03 (*n* = 10), which is also significantly different from 0.5 (t_9 = 5.86, p = 0.0002). The proportion of males was not affected by year, trap type, or the total number of individuals (Table 1).

Chrysemys picta. The overall mean proportion of males by year was 0.47 ± 0.02 (*n* = 30), which is not different from 0.5 (t_{29} = -1.52, p = 0.14). Year, trap type, and the total number of individuals had no effect on the proportion of males found in a given year (Table 1).

Graptemys geographica. The overall mean proportion of males by year was 0.53 ± 0.04 (*n* = 28), which is not significantly different from 0.5 (t_{27} = 0.69, p = 0.50). The mean proportion of males in years with > 10 individuals was 0.46 ± 0.04 (*n* = 14), which is also not significantly different from 0.5 (t_{13} = -0.94, p = 0.36). The proportion of males in a year was not affected by year, trap type, or the total number of individuals (Table 1).

Sternotherus odoratus. The mean proportion of males by year was 0.66 ± 0.01 (*n* = 30), which is significantly different from 0.5 (t_{29} = 12.66, p < 0.0001). The mean proportion of males in years with > 10 individuals was 0.65 ± 0.012 (*n* = 28), which is significantly different from 0.5 (t_{27} = 12.33, p < 0.0001). The proportion of male *S. odoratus* observed in a year was not affected by year, trap type, or the total number of individuals caught (Table 1).

Trachemys scripta elegans. The mean proportion of males by year was 0.44 ± 0.04 (*n* = 22), which is not significantly different from 0.5 (t_{21} = -1.38, p = 0.18). If only years with > 10 individuals are considered, the mean proportion of males was 0.47 ± 0.06 (*n* = 10), which was not significantly different from 0.5 (t_9 = -0.57, p = 0.58). Year, trap type, and total number of individuals had no significant effects on the proportion of male *T. s. elegans* in a given year (Table 1).

Discussion

Over the course of our study (1979–2014), none of the five species (*C. serpentina*, *C. picta*, *G. geographica*, *S. odoratus,* and *T. s. elegans*) showed a significant temporal trend in sex ratio, and indeed they each showed remarkably consistent sex ratios (i.e., proportion of males) across the study period (Fig. 1). A previous analysis of the temporal variation in the sex ratio in *S. odoratus* in Dewart Lake also found a consistent male-bias from 1979–2000 (Smith and Iverson 2002). Previous studies of sex ratio trends in freshwater turtles have often reported shifts in the sex ratios, but they have ascribed these shifts to a variety of reasons. For example, there has been a significant trend for increased male bias in the sex ratio of freshwater turtles in the United States from 1928 to 2003, which has been ascribed to increases in road density (Gibbs and Steen 2005; see also citations in the **Introduction** related to road mortality). In addition, Tucker et al. (2008) found that the sex ratio of *T. s. elegans* became more male biased over their 13-year study, probably due to the warming trends during the course of their study leading to an expansion of the nesting period to include additional clutches laid during the part of the season that produces males. Jones (2017) found shifts from a male-biased sex ratio before 2000 to unbiased sex ratios after 2000 in *Graptemys oculifera*,

Table 1. Results of generalized linear models examining the effects of year, trap type (fyke net versus non-fyke net years), and number of individual turtles examined on the proportion of males observed in a given year for each of the five species of freshwater turtles from Dewart Lake. *n* is the number of years with data for each species.

Species	*n*	Intercept	Year	Trap type	Number of individuals	Whole model P
Chelydra serpentina	18	–36.1	0.018	—	0.05	0.78
Chrysemys picta	30	–18.3	0.009	–0.25	0.001	0.99
Graptemys geographica	28	–16.6	0.008	–0.12	–0.03	0.92
Sternotherus odoratus	30	–16.2	0.008	–0.06	–0.002	0.998
Trachemys scripta elegans	22	–90.0	0.045	0.49	–0.02	0.67

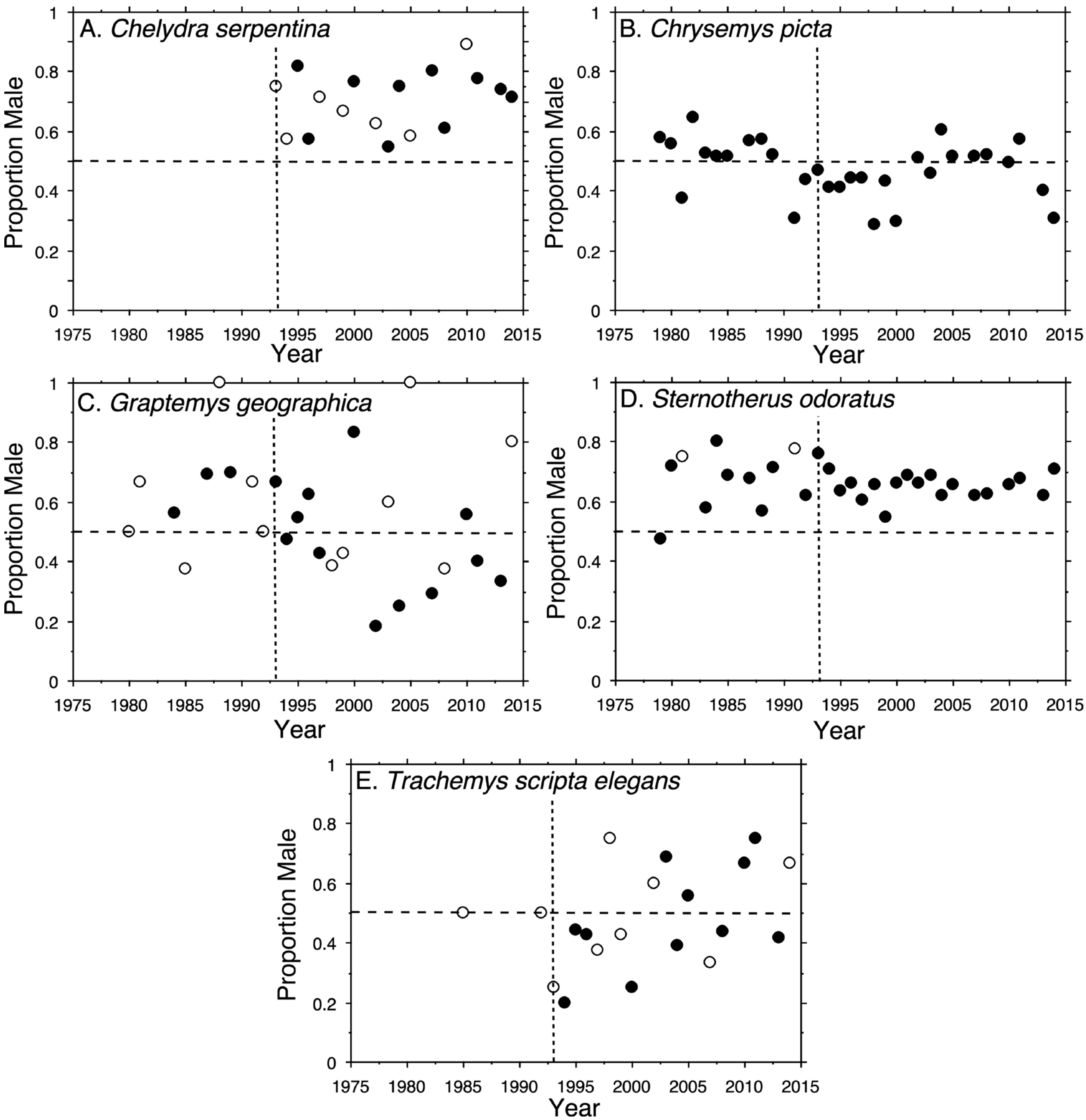

Fig. 1. Proportions of males for **(A)** *Chelydra serpentina*, **(B)** *Chrysemys picta*, **(C)** *Graptemys geographica*, **(D)** *Sternotherus odoratus*, and **(E)** *Trachemys scripta elegans* over the course of the 37-year study in Dewart Lake, Indiana, USA. Open circles indicate years when < 10 individuals were captured, and closed circles indicate years when ≥ 10 individuals were captured. The vertical dashed lines indicate the transition from non-fyke net years to fyke net years, and the horizontal dashed lines represent a 1:1 sex ratio (i.e., 50% males).

possibly due to greater predation on the males, which are smaller than the females. The observed sex ratio in *T. scripta* in South Carolina varied among years (from the late 1960s to the mid-1980s) but with no significant directional temporal trend (Gibbons 1990). A study in Spain found that the sex ratio of *Emys orbicularis* was fairly constant from 1997 to 2018 in one region, but showed a recent increase in male bias in another region (Escoriza et al. 2020). The tendency in observed shifts in turtle sex ratios that have been reported in previously published studies may be a result of publication bias, with studies showing no change in sex ratios simply not being published. The paucity of long-term studies on turtle populations also likely contributes to uncertainty regarding how the sex ratios are changing (or not) in turtle populations.

Overall, the mean proportion of males in this study did not differ significantly from 0.5 (i.e., on average it was not significantly different from a 1:1 sex ratio) in *C. picta*, *G. geographica*, and *T. s. elegans*. In contrast,

Table 2. Populations of the turtle species found in Dewart Lake (Indiana, USA) that have been reported to exhibit biased or unbiased observed sex ratios by US state or Canadian province.

Species	Male-biased	Unbiased	Female-biased
Chelydra serpentina	Minnesota (DonnerWright et al. 1999)	Florida (Aresco and Gunzburger 2007; Johnston et al. 2008)	
	Missouri (Glorioso et al. 2010)	Illinois (Cagle 1942)	
	North Carolina (Hanscom et al. 2020)	Michigan (Lagler and Applegate 1943)	
	Ontario (Galbraith et al. 1988)	Ontario (Galbraith et al. 1988)	
		Quebec (Mosimann and Bider 1960)	
		Tennessee (Froese and Burghardt 1975)	
		West Virginia (Major 1975)	
Chrysemys picta	Illinois (Refsnider et al. 2014; Vanek and Glowacki 2019)	Michigan (Gibbons 1968)	Idaho (Lindeman 1996)
		Washington (Lindeman 1996)	Illinois (Cagle 1942)
	Minnesota/Wisconsin (DonnerWright et al. 1999)	Minnesota (Refsnider et al. 2014)	Michigan (Sexton 1959)
	New York (Bayless 1975)	Missouri (Glorioso et al. 2010)	Ontario (Balcombe and Licht 1987)
	Ontario (DeCatanzaro and Chow-Fraser 2010)	New Mexico (Refsnider et al. 2014)	
	Quebec (Dupuis-Désmoreaux et al. 2017)	New York (Zweifel 1989)	
	Wisconsin (Ream and Ream 1966)	Ontario (DeCatanzaro and Chow-Fraser 2010)	
Graptemys geographica	Pennsylvania (Pluto and Bellis 1986)	Illinois (Anderson et al. 2002)	Ohio (Tran et al. 2007)
(also reviewed in Lindeman 2013, Table 4.22)	Quebec (Gordon and MacCulloch 1980; Flaherty 1982)	Indiana (Conner et al. 2005)	Ontario (Browne and Hecnar 2007; Bennett et al. 2009)
		Minnesota/Wisconsin (DonnerWright et al. 1999)	
	Wisconsin (Vogt 1980)	Missouri (Pitt and Nickerson 2012)	
		Ontario (Barrett Beehler 2007; Bulté and Blouin-Demers 2009)	
Sternotherus odoratus	Florida (Aresco 2005)	Florida (Aresco 2005)	Alabama (Dodd 1989)
	Indiana (Smith and Iverson 2002)	Missouri (Glorioso et al. 2010)	Illinois (Cagle 1942)
	Ontario (Edmonds and Brooks 1996)	Various locations pooled (Tinkle 1961)	Michigan (Risley 1933)
	Texas (Swannack and Rose 2003; Munscher et al. 2019)		
	Virginia (Holinka et al. 2003)		
Trachemys scripta elegans	Florida (Aresco 2005)	Florida (Aresco 2005)	Illinois (Cagle 1942)
	Oklahoma (Hays and McBee 2010)	Illinois (Cagle 1950)	North Carolina (Hanscom et al. 2020)
		Missouri (Glorioso et al. 2010)	
		Oklahoma (Hays and McBee 2010)	
		Texas (Munscher et al. 2019)	

both *C. serpentina* and *S. odoratus* had significantly male-biased sex ratios in Dewart Lake. The observed sex ratios for these five species of freshwater turtles in Dewart Lake are within the variations in sex ratios found in previous studies conducted throughout the United States and Canada, in which each of the species had populations with biased and unbiased sex ratios (Table 2). In at least some populations, there is evidence that the observed sex ratio bias is real and not due to trapping bias (e.g., Swannack and Rose 2003). It is not clear why there is variation in the observed sex ratios among the freshwater turtle species in Dewart Lake; however, given the consistency of the ratios across our study period, any explanation for them must account for the relatively long-term difference rather than one that has changed just in recent decades. Similarly, it is not clear why there are differences in sex ratios among populations in cases when there are no obvious anthropogenic factors that could potentially be driving them.

Conclusions

In conclusion, many turtle populations and species are in decline and at risk due to anthropogenic alterations of the environment (Lovich et al. 2018). Our failure to observe changes in sex ratios over the course of this study is also consistent with our failure to observe any temporal trends in the frequency of shell anomalies in this community of turtles over the study period (Smith et al. 2020). The fact that we have found no changes in the sex ratios or frequencies of anomalies in most of the species in Dewart Lake does not preclude any other impacts of the anthropogenic factors on these populations. For example, road mortality may not be as sex-biased towards females as has previously been assumed (Carstairs et al. 2018). In addition, we have observed temporal shifts in the anthropogenic pressures in this community of turtles (e.g., changes in injuries due to boat collisions coinciding with changes in recreational boat use due to economic factors; Smith et al. 2006, 2018). Indeed, there is some evidence for a decline in *C. picta* in Dewart Lake (Smith et al. 2006). Thus, the factors that may contribute to turtle declines are likely not universal, nor do they affect all populations or species similarly, suggesting that we must continue to seek explanations for the observed declines in some turtle populations, but also explanations for why other populations and species do not show such effects. In other words, any homogeneity of response to anthropogenic factors across species of freshwater turtles, or even populations of the same species, should not be assumed.

Tribute to Joseph Mitchell. In June of 1979, Joe Mitchell published a request for information on cannibalism in reptiles in *Herpetological Review* 10(2): 57 (eventually published as an SSAR *Herpetology Circular* in 1986). In response, on 23 July 1979, John Iverson mailed Joe one of his papers demonstrating cannibalism in *Cyclura*. Joe's kind response dated 1 August 1979 informed John of his recent initiation of a long-term field study of the turtles in sites near Richmond, Virginia, and that this work would form the basis of his dissertation through the University of Tennessee. The next week they met for the first time at the annual herpetological meetings in Knoxville, and based on their shared interest in Musk Turtles (*Sternotherus odoratus*), began a life-long friendship. Over the years, they corresponded regularly and co-authored a piece on the importance of herpetological societies and graduate education for supporting education in herpetology in 1998, and a note on kyphosis in Map Turtles in 2019. Joe's influence on and collegiality with John Iverson and so many other herpetologists will remain a huge legacy, along with his over 500 publications. Joe is sorely missed, especially by those of us who call ourselves natural historians.

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