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Source: Journal of Herpetology, 52(2) : 193-200

Published By: Society for the Study of Amphibians and Reptiles

URL: https://doi.org/10.1670/17-063

Journal of Herpetology, Vol. 52, No. 2, 193–200, 2018

An 18-Year Mark–Recapture Study of Wood Turtles (*Glyptemys insculpta*) in Michigan

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ABSTRACT.—**Wood Turtles (*Glyptemys insculpta*) occupy forested streams at midlatitudes in eastern North America and are listed as endangered by the International Union for Conservation of Nature, but few populations have been rigorously studied. We studied a population of Wood Turtles in Michigan for 18 yr, individually marking 260 different turtles (146 females, 88 males, and 26 unsexed juveniles), including 118 turtles that we followed for one or more years using radiotelemetry. We analyzed our encounter data using a Cormack–Jolly–Seber model in Program MARK; and we estimated total population size using a Bayesian integrated population model that combined Horvitz–Thompson estimates of annual population size, mark–recapture estimates of annual survival, and derived estimates of annual recruitment. Annual adult survival was 0.970 ± 0.016 SD and annual recruitment to age 15 (mean age of first capture) was 0.058 ± 0.019 SD. Over the 18-yr study, estimated population size grew from 770 (95% CI 631–928) to 1,196 (95% CI 977–1,444) individuals.**

Turtles are extremely vulnerable to extinction (Buhlmann et al., 2009), with 52% of the 335 modern species of turtles and tortoises listed as threatened, endangered, or already extinct (van Dijk et al., 2014). In North America, freshwater species such as the Spotted Turtle (*Clemmys gutata*), Blanding's Turtle (*Emydoidea blandingii*), and Western Pond Turtle (*Actinemys marmorata*) all have experienced population declines (Reese and Welsh, 1971; Congdon et al., 1994; Lewis et al., 2004). Although populations of Wood Turtles (*Glyptemys insculpta*) are frequently reported as declining (Harding and Bloomer, 1979; Harding, 1991; Ernst, 2001; Daigle and Jutras, 2005), only two studies have provided direct, long-term monitoring for more than a decade (Garber and Burger, 1995; Parren, 2013), with only the former documenting a decline. The need for such monitoring was identified by Tinkle (1979) and Dodd and Franz (1993) and by recent U.S. federal consideration to list the Wood Turtle under the Endangered Species Act.

Long-term studies face many logistical obstacles, and these obstacles are even more prevalent when studying long-lived species (Tinkle, 1979; Gibbons, 1987; Congdon et al., 1993). For these reasons, there are inadequate data on life-history traits and ecological impacts of many long-lived species (Congdon et al., 1994), which limits the effectiveness of conservation and management plans. Previous studies of long-lived organisms demonstrate that their life-history traits, which coevolve with long life, result in populations having a limited capacity to respond to rapid change (Congdon et al., 1993, 1994). This is concerning because anthropogenic impacts already are accelerating natural rates of climatic change (Axford et al., 2009; Kaufman et al., 2009; Kemp et al., 2015), and Wood Turtles may not have the ability to adapt.

Wood Turtles are found throughout northeastern North America, ranging from northern Virginia to Nova Scotia and west to Minnesota (Ernst and Lovich, 2009). The IUCN Red List classifies Wood Turtles as endangered (van Dijk and Harding, 2016), and although protection efforts are taking place in some states attributable to perceived declines, they are not federally listed under the U.S. Endangered Species Act. One of the most robust examples of Wood Turtle decline is the extirpation of two physically disjunct populations of Wood Turtles in Connecticut over a 10-yr period, coinciding with the opening of natural areas for human recreation (Garber and Burger, 1995). Some major threats implicated in Wood Turtle decline are climate disturbance, habitat destruction and fragmentation, increased predation, illegal collection for the pet trade, and human recreational activities (Harding and Bloomer, 1979; Garber and Burger, 1995; Ernst, 2001).

Wood Turtles are semiaquatic and typically overwinter in rivers and streams and occupy riparian habitats in the spring and fall, with most terrestrial activity occurring in the summer (Holman, 2012). Wood Turtles display slow growth, delayed sexual maturity, low fecundity or reproductive output, and extreme longevity (Ernst and Lovich, 2009), all of which make it difficult for populations to adapt to rapid change. The aforementioned life-history traits also limit the ability of Wood Turtle populations to endure prolonged increases in mortality of any age class (Congdon et al., 1993). In addition, Wood Turtles represent a species with specialized habitat requirements and large home ranges which may make them more susceptible to local extirpation due to habitat fragmentation (Remsburg et al., 2006; Willoughby et al., 2013).

The goal of our study was to provide a detailed demographic assessment of a single population of Wood Turtles through direct, long-term monitoring of marked individuals. By combining annual estimates of population size and annual adult survival into an integrated population model (IPM), we were also able to estimate annual recruitment. This information is valuable for research and management alike as the current body of literature lacks robust population parameter estimates for Wood Turtles, especially for western populations.

MATERIALS AND METHODS

Study Site.—Fieldwork took place along a 37.5-km stretch of river in Michigan (Fig. 1). We divided the stretch of river into three reaches, each ~12.5 km in length, for consistency in data collection among field workers and for our statistical analyses. The forest consists of 44% hardwood, 44% pine (*Pinus* spp.), 5% lowland conifer, 1% mixed swamp hardwood, and 6% open

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DOI: 10.1670/17-063

FIG. 1. Map of our field site in Michigan, the 37.5 km stretch of river, including boundaries for the three river reaches surveyed (red is upper, blue is middle, purple is lower), each ~12.5 km in length.

areas. The river is a sand and gravel-bottomed waterway, and the surrounding terrestrial landscape is predominantly made up of sand and gravel. The river has a mean width of 30 m and mean depth of 1 m, with average summer temperatures of ~20°C (USGS, 2016). This stretch of river receives heavy recreational use, primarily during the summer months of June, July, and August. We chose to withhold all further information on the location of our study site to protect the Wood Turtle population from illegal collection.

Data Collection.—We collected data on 260 individual Wood Turtles from May 1998 to August 2015 using similar methods throughout the course of the study. We actively searched the study site from canoes and kayaks for basking Wood Turtles throughout the summer months of May through August, tracked movements of radio-marked turtles using telemetry, and collected data from all Wood Turtles otherwise encountered while moving about the study site. While tracking radio-marked turtles, incidental captures also occurred ($n = 116$). Of these incidental captures, 91 were new turtles and 25 were recaptures. We encountered 20 turtles while driving through the study area, including 18 new captures and two recaptures. All turtles were captured by hand and marked with a triangular file on the marginal scutes of the carapace using a Forest Service numbering scheme, similar to Cagle (1939). We released all turtles at the point of capture within ~1 h. These markings provided each turtle with a distinguishing ID number. Beginning in 2010, all new and recaptured turtles ($n = 64$) were given a unique 15-digit passive integrated transponder (PIT) tag (Biomark, Inc., Boise, ID) using the methods of Buhlmann and Tuberville (1998). We recorded age, sex, body size, mass, and any injuries or distinguishing characteristics for each turtle. We estimated minimum age by counting the annular rings on either the carapacial scutes or the plastral scutes, depending on which were more defined; however, annuli are known to become less reliable after 15–20 yr of growth (Garber, 1989; Kaufmann, 1992; Wilson et al., 2003). By counting annuli multiple times from different scutes, we were able to estimate minimum age more precisely. We determined the sex of all adult turtles (age > 15 yr) based on both plastron concavity and the location of the cloaca relative to the edge of the plastron. We checked female turtles for gravidity by probing anterior to the rear limbs throughout the 18-yr study.

We attached radio transmitters (Advanced Telemetry Systems [ATS], Isanti, MN) weighing <10 g (<2% of the average Wood Turtle mass) to 10–20 turtles per field season. Transmitters were attached to the carapace on a rear costal or marginal scute using 5-min epoxy, with antennas extending horizontally behind the turtles (Boarman et al., 1998). We observed Wood Turtle mounting behavior, which suggested that this positioning would not restrict mating of the radio-marked turtles. Using a 3-element Yagi antenna and a 4-MHZ scanning receiver (ATS), we located and recorded GPS locations accurate to <3 m for individual radio-marked turtles up to 44 times per year between late May and the end of August. This period lies between spring mating and winter hibernation, both of which are aquatic activities, and is associated with the most terrestrial activity (Harding and Bloomer, 1979; Ernst, 1986; Harding, 1990).

We conducted three types of searches for Wood Turtles: 1) river; 2) hiking; and 3) telemetry, including combination searches involving two or more methods. River searches ($n = 115$) involved floating the entire length of one or more reaches and searching for turtles basking on logs in the river or on the riverbank. Hiking searches ($n = 14$) involved searching sites accessible by U.S. Forest Service roads and looking for turtles under vegetation and along any sandy substrate. Telemetry searches ($n = 528$) involved using hand-held antennas to locate radio-marked turtles (average 4.04 encounters per survey), but nonradioed turtles were occasionally encountered during such surveys (0.25 turtles per telemetry-only survey).

Statistical Analysis.—For each captured turtle, we assigned individual covariates for sex, injury, and age at first capture (that we incremented by 1 yr for each year postcapture). Approximately 10% of captured turtles could not be sexed reliably when first captured and were not recaptured when older; we assigned these turtles a covariate value of 0.5 for sex (i.e., intermediate between male = 0 and female = 1). Injuries included missing limbs or tails; cracks, chips, and indentations on the carapace or plastron; lacerations and abnormalities on the body; missing eyes; and cloacal prolapses. We speculated that turtles with severe injuries might have lower survival than uninjured turtles. Estimated age at first capture averaged 14.7 ± 5.2 SD yr (range 1–28 yr).

We assigned each marked turtle two year-specific covariates: telemetry and search effort. Telemetry included a series of 17 dummy variables indicating whether a turtle had a functioning radio at the start of each field season (e.g., $T_{2004} = 1$ for a turtle wearing a functioning radio in 2004) and could, therefore, be found using telemetry. Although radioed turtles were not located during every telemetry visit, on average they were located 10.6 times each year (range 1–44), and no radioed turtle went undetected for an entire season. For nonradioed turtles (including turtles wearing nonfunctional transmitters), search effort varied greatly among years and among reaches within years. To quantify annual search effort for each turtle, we tallied the number and type of searches that occurred each year within that turtle's home river reach. We tallied river and hiking searches as full searches (value = 1), because our data indicated nearly equivalent captures per search for each method (1.36 nonradioed turtles per river search, 1.80 per hiking search). In contrast, telemetry searches had a lower probability of finding nonradioed turtles (0.25 turtles per search); thus, we approximated telemetry searches as providing 0.2 search equivalents for nonradioed turtles. Based on this metric, annual search effort averaged 1.12 (2009) to 17.75 (1998) search equivalents per turtle and ranged from 0 to 35.4 depending on where each turtle lived. If a marked turtle was subject to zero search effort, we coded its capture history for that year using missing value notation rather than a zero (e.g., 1.1 vs. 101) to indicate absence of search effort in year 2 rather than detection failure.

Mark–Recapture Analysis.—We analyzed encounter data using a Cormack–Jolly–Seber model as implemented in Program MARK (White and Burnham, 1999). Although one nonradio-marked turtle and three radio-marked turtles were found dead during the study, dead recoveries were too sparse to use joint live–dead or telemetry–recapture models (Burnham, 1993; Powell et al., 2000). Except for radio-marked turtles, within season reencounters were too infrequent to use robust-design models (Kendall et al., 1997); thus, we used Horvitz–Thompson (1952) methods for estimating population size.

Cormack–Jolly–Seber models make several important assumptions: 1) after accounting for modeled covariates, all individuals have the same probability of capture and survival; 2) all samples are instantaneous; 3) no animals are killed in the capture process, and their marks are not lost, overlooked, or incorrectly reported; 4) all emigration is permanent (and, therefore, confounded with mortality); and 5) all individuals behave independently (Bonner and Schwarz, 2006). The first assumption is critically important for generalizing from marked individuals to the unmarked population at large, and for estimating total population size by generalizing capture probabilities of recaptured turtles to all turtles in the population, and we therefore used covariates to minimize unmodeled heterogeneity. To test how well this approach worked, we also considered random effects models with latent individual heterogeneity (White and Cooch, 2017). Specifically, we measured latent heterogeneity in detection probability (p) before and after fitting individual covariates on p, and we conducted likelihood ratio tests of both estimates (White and Cooch, 2017). Although samples were not instantaneous and observations were made throughout the summer, simulation studies suggest that violation of this assumption has minimal impact on parameter estimates in mark–recapture studies of long-lived species (O'Brien et al., 2005). Cagle (1939) asserted that notches on marginal scutes will last for a turtle's lifetime, and we observed no potential cases of marker loss (i.e., turtles with damaged shells that could no longer be identified) or capture-induced mortality during our study. Several radios became nonfunctional soon after deployment, but these turtles remained physically marked. Our study population was bounded by a reservoir both upstream and downstream, with no major tributaries between the reservoirs; thus, we believe our population was effectively closed to immigration or emigration for the duration of our study, and φ, therefore, estimates true survival rather than apparent survival. Our extensive telemetry data and limited evidence of movement between reaches by marked turtles supports this assumption. Finally, although we occasionally encountered a pair of turtles during the same capture event, this never happened during multiple years for the same pair of turtles.

For initial analyses of encounter data, we used maximum likelihood estimation (MLE) procedures to assess models where annual survival potentially varied by year, sex, age, and injury status, and annual detection probability potentially varied by year, sex, age, telemetry status, and annual search effort. We also assessed individual variation in survival and detection probability using numerical integration with Gaussian–Hermite quadrature (McClintock et al., 2009; Gimenez and Choquet, 2010). We ranked models based on AICc (Akaike information Criterion with a correction for finite sample size; Burnham and Anderson, 2002) and used these rankings to identify variables to include in our final analysis, which we conducted using Markov chain Monte Carlo (MCMC) procedures in Program MARK. With MCMC estimation procedures (White et al., 2009), we were able to treat year effects as random rather than fixed effects, allowing us to incorporate annual variation using only two parameters (i.e., annual mean $\hat{\mu}$, annual variance $\hat{\sigma}^2$) rather than 16 parameters (i.e., a unique parameter estimate for each study year). For MCMC analysis, we specified vague priors for each estimated parameter and used two chains comprising 15,000 total iterations apiece (4,000 tuning, 1,000 burn-in, and 10,000 retained for modeling posterior distributions). We assessed parameter convergence between duplicate chains using $\hat{R}$ statistics (Gelman, 1996).

For estimating annual population size of catchable turtles (typically age 8+, although 7% of initial captures were aged 1–7), we used a Horvitz–Thompson estimator to calculate total population size of available turtles based on a summation of how many turtles each captured turtle represented:

$$\hat{N}_{jt} = \sum_{i=1}^{m_{jt}} \frac{1}{\hat{p}_{ijt}}$$

where $\hat{N}_{jt}$ represents estimated population size in river reach j during year t, i represents each individual turtle that was captured, m_{jt} is the total number of turtles captured in reach j during year t (including both new captures and recaptures), and $\hat{p}_{ijt}$ represents the predicted capture probability for each captured turtle. Unless $p = 0.5$, uncertainty in $\hat{p}$ results in asymmetrical uncertainty in estimation of N. Rather than use delta method approximations for variance in N, which assumes normal (symmetrical) variances, we implemented bootstrap simulations in Program R to incorporate prediction uncertainty, using 10,000 sets of parameter estimates from the posterior distribution of our MCMC mark–recapture analysis from Program MARK.

We used a Bayesian state-space model (Kéry and Schaub, 2012) as implemented in program R2jags (Su and Yajima, 2015) to estimate population size in each river reach during 1998–2015. Input data included log population size and precision of log population size based on Horvitz–Thompson estimates from all years with $\geq$3 captures of nonradioed turtles. Annual population growth rate (λ_t) was modeled as the sum of annual survival and recruitment ($\lambda_t = S_t + R_t$) and was log transformed to reflect instantaneous growth rate (r_t). We used the mean survival estimate from our mark–recapture analysis as a prior for S_t (logit[mean.S] $\sim$ Normal[3.74, 1.67], SD[S_t] $\sim$ uniform[0.001,0.02]) and treated annual recruitment as an un-

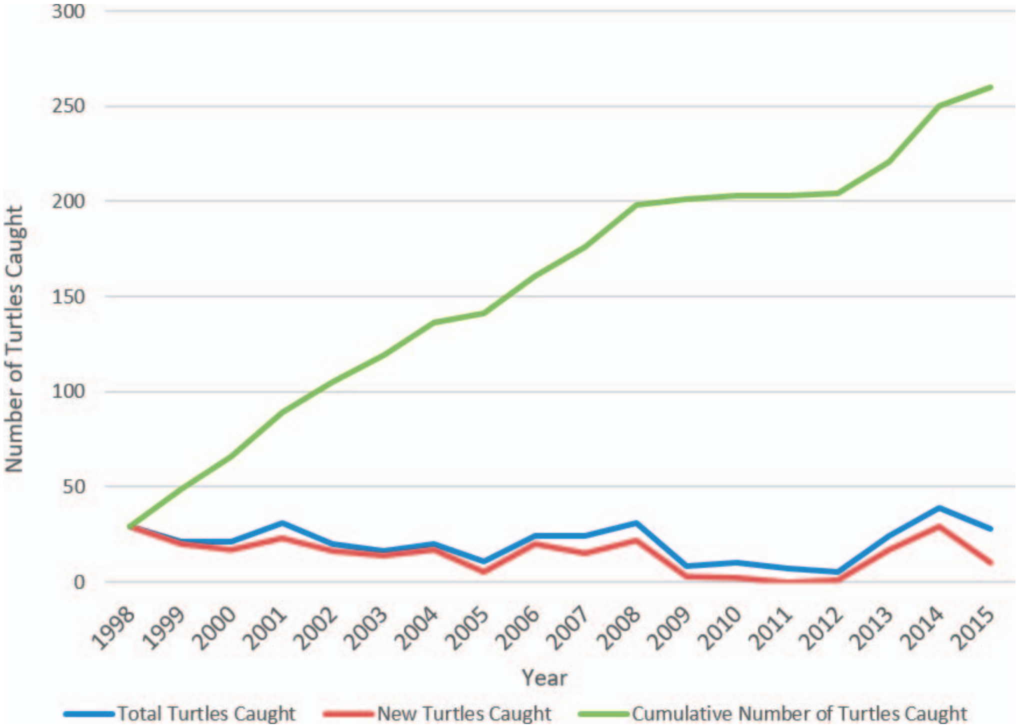

FIG. 2. Summary of total number of turtles captured from 1998–2015 in Michigan, including the total number of turtles caught each year, the number of new turtles caught each year, as well as the cumulative number of turtles caught over time. Low numbers of new turtles from 2009–2012 were attributable to reduced search effort rather than saturation of all turtles marked.

known parameter (mean.R $\sim$ uniform[0,0.1], SD[R_t] $\sim$ uniform[0.001, 0.05]). Given sparse data and shared survival estimates, we modeled a common annual growth rate (r_t) for each river reach. We analyzed 3 MCMC chains totaling 250,000 iterations each, with the first 50,000 iterations discarded as burn-in and every 10th iteration retained for analysis (i.e., 60,000 posterior samples). Total population size was treated as a derived parameter, based on summation of back-transformed population estimates for each river reach, with 95% credible intervals drawn from the 2.5 and 97.5% percentiles of the posterior distribution.

RESULTS

From 1998–2015, we captured and marked 260 individual Wood Turtles, 118 that were radio-marked for 1–5 field seasons and 139 of which were marked only with shell notches. Turtles with functioning radios were reencountered a total of 1,905 times, whereas turtles without radios were reencountered only 49 times at an average of 3 yr since last capture (range 0–14 yr). Only five turtles were observed moving from one reach to another, including two that moved downstream one reach, two that moved upstream one reach, and one that moved upstream two reaches. We detected no radio-marked turtle leaving the study area. On average, we captured 20 turtles per year, including 14 that had not been previously marked. We did not observe a reduction in new turtles caught in the later years of the study, and the cumulative number of marked turtles increased steadily over time (Fig. 2). Female Wood Turtles have been known to mature on average between 14–18 yr (Harding and Bloomer, 1979; Ernst and Lovich, 2009), but we found no gravid females <16 yr of age.

Based on maximum likelihood estimates, annual survival was unaffected by sex, age, or injury status. Including annual variation reduced model deviance by only 3.7 units, despite 16 additional parameters, suggesting that annual variation in survival was slight. Detection probability was strongly affected by functioning radio transmitters and search effort, but not by sex or age, although the parameter estimate for sex indicated lower capture probability for males ($\beta = -0.44 \pm 0.38$ SE). Including annual effects on detection probability resulted in a 24.7 unit reduction in model deviance, which was not enough to overcome the 32 unit AIC penalty for 16 additional parameters but suggested that residual annual variation in p might be important. A model with individual random effects on p but no covariates estimated σ_p at 1.82 ± 0.43 SE on the logit normal scale ($\chi^2 = 24.82$, df = 0,1, $P < 0.0001$), but after accounting for variation attributable to telemetry and search effort, individual random effects became trivial ($\sigma_p = 0.61 \pm 0.47$ SE; $\chi^2 = 0.44$, df = 0,1, $P > 0.5$).

An MCMC model that recognized constant annual survival and individually varying recapture probabilities that were a function of year, radio-marking, and annual search effort within each turtle's home reach converged well ($\hat{R} \leq 1.03$) and provided realistic estimates for all parameters. Annual survival (φ) averaged 0.964 on the real scale, with 90% minimum credible intervals (90% MCI) ranging from 0.933 to 0.997. Annual recapture probability for nonradioed turtles averaged −4.17 (90% MCI: −4.69–−3.69) on the logit scale, with annual process variation (σ_t) averaging 0.32 (90% MCI: 0.03–0.68). Logit(p) increased by 0.049 (90% MCI: 0.004–0.096) for each survey equivalent and by 7.52 (90% MCI: 6.50–8.60) if the turtle was already radio-marked. On the real scale, estimated detection probabilities averaged 0.024 ± 0.009 SD per year for

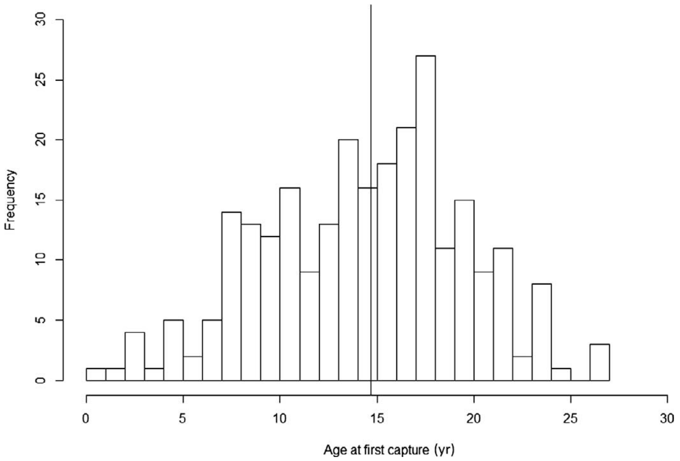

FIG. 3. Minimum age at first capture for Wood Turtles in our study in Michigan, based on counting annular rings of the scutes. Note that growth rings may become unreliable after turtles reach 15–20 yr of age (Garber, 1989; Kaufmann, 1992; Wilson et al., 2003); therefore, the reduction in older age classes is likely attributable to underestimating the age of older turtles, and, hence, our estimated mean age at first capture of 14.7 yr (represented by the vertical line) is likely an underestimate. The paucity of younger age turtles (e.g., <8 yr of age) is presumably attributable to lower capture probabilities of juvenile turtles.

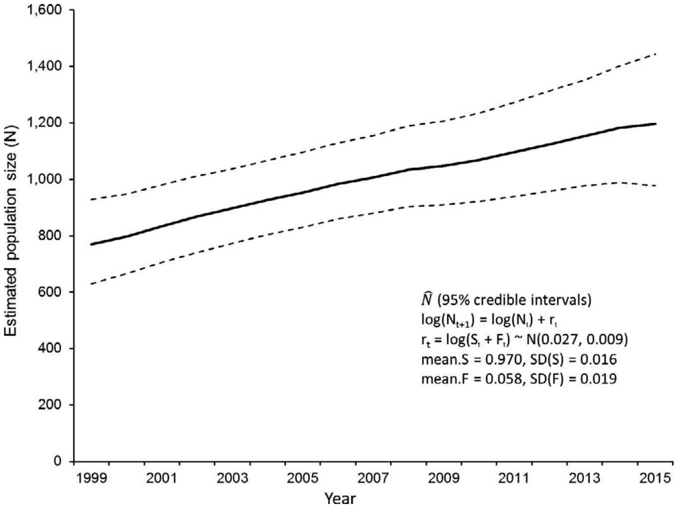

FIG. 4. Estimated population size of Wood Turtles in Michigan, based on a Bayesian integrated population model that combined Horvitz–Thompson estimates of annual population size on three river reaches, mark–recapture estimates of annual survival, and derived estimates of annual recruitment.

nonradioed turtles at average annual search effort and 0.978 ± 0.010 SD per year for radioed turtles.

For estimation of annual population size, each radioed turtle represented approximately one turtle ($\bar{x} = 1.03$), but each nonradioed turtle represented an average of 42.9 turtles (range 16.5–69.7). Annual survival was estimated at 0.970 ± 0.016 SD and annual recruitment to mean age at first capture (14.7 yr; Fig. 3) was 0.058 ± 0.019 SD. Annual population growth (r_t) from the IPM averaged 0.027 ($\sigma_t = 0.009$), but 95% credible intervals included zero for all years. Over the 18-yr study, the population grew from an estimated 770 (95% CI 631–928) to 1196 (95% CI 977–1444) individuals (Fig. 4).

DISCUSSION

We used 18 yr of capture–mark–recapture data from a Michigan Wood Turtle population to develop an integrated population model (IPM) that estimated annual abundance, survival, and recruitment to mean age of first capture. Our IPM indicated that this population had high survival, with recruitment that was sufficient to allow the population to grow by an average rate of 2–3% per year.

Given concerns about population declines of Wood Turtles throughout their range (Harding and Bloomer, 1979; Harding, 1991; Ernst, 2001; Daigle and Jutras, 2005), and the reported historical decline of this population found by Willoughby et al. (2013), our most surprising finding was a positive growth rate for this population, which increased from ~800 to 1,200 turtles from 1998–2015. Our population estimates (20–32 turtles km^{-1}), however, are well within the range of other studies that have reported population estimates per river km (Walde et al., 2003; Daigle and Jutras, 2005; Brown et al., 2017; Table 1). Willoughby et al. (2013) reported evidence of a historical decline in this population of Wood Turtles using genetic data and a coalescent theory model (MSVar). The comparison between this study and our own is of interest because the genetic study provides information over an evolutionary time frame whereas our study is a recent snapshot of the demography of this population. We found evidence of a recent increase in population size over the past 18 yr that, considering the historical decline found using genetic data, provides evidence that this population may be rebounding after a previous decline.

We think that the recent increase in population size may be attributable to road closures within the riparian zone that occurred within the study area during the late 1980s and early 1990s. In 1988, a new management plan was created by the U.S. Forest Service to protect our study site. The management plan identified numerous unregulated roads within the river corridor, and once the plan was implemented several of these were closed to vehicles and horses to minimize negative impact in the riparian zone (USFS, 1988), which likely benefited Wood Turtles (Garber and Burger, 1995).

One important limitation of our study was that capture and recapture rates of nonradioed turtles were extremely low. Consequently, we continued to capture old unmarked turtles throughout the study, except during 2009–2012 when we had low sampling effort (Fig. 2). Therefore, although our study has been ongoing for 18 yr, we estimate that >70% of this population has never been captured, and the low probabilities of recapture contribute to large uncertainty in most parameter estimates. Other studies of Wood Turtles have reported similar low encounter rates. Spradling et al. (2010) conducted intensive marking efforts of an Iowa Wood Turtle population over 4 yr, logging more than 1,500 search hours per year but only managed to mark about half of their study population based on captures of marked and unmarked turtles. Lovich et al. (1990) studied a Wood Turtle population in Pennsylvania over 24 yr but averaged <3 captures per turtle. Given the low estimated recapture rates in our study ($p = 0.024$ for nonradioed turtles), each captured turtle represented 42 estimated turtles in the study population (i.e., $0.024^{-1} = 42$). We note that two potential sources of bias in our estimates of detection probability would have led us to underestimate true population size and rate of population growth: 1) unmodeled heterogeneity in capture probability leads to overestimates of p and

TABLE 1. Wood Turtle population densities (turtles/river km) from published studies for comparing our work in Michigan (20–32 turtles per river km is within the range of other studies, and seems reasonable for a healthy population).

Location	km River	$\hat{N}$	Turtles/km	Source
Quebec	7.5	238	31.7	Walde et al., 2003
Michigan	37.5	770	20.5	Our study
Michigan	37.5	1196	31.9	Our study
Iowa		77		Spradling et al., 2010
W Virginia		331		Spradling et al., 2010
Quebec	5.7	52.4	9.2	Daigle and Jutras, 2005
Quebec	5.7	25.6	4.5	Daigle and Jutras, 2005
MN–BO	0.5	4.57	9.1	Brown et al., 2017
MN–CUT	0.5	7.65	15.3	Brown et al., 2017
MN–GLN	0.5	6.61	13.2	Brown et al., 2017
MN–IL	0.5	76.72	153.4	Brown et al., 2017
MN–LG	0.5	36.36	72.7	Brown et al., 2017
MN–NLG	0.5	9.95	19.9	Brown et al., 2017
MN–SP	0.5	43.36	86.7	Brown et al., 2017
MN–TR	0.5	62.15	124.3	Brown et al., 2017

underestimates of *N* (White and Cooch, 2017); and 2) recapture probability tended to decrease throughout our study, although the effect was not significant (the 95% CI overlapped zero); but, had we included this downward trend in detection in our MCMC model, it would have caused population estimates to increase even more.

Based on known captures, we observed a female-biased sex ratio of 1.66:1 (146 F, 88 M), which is similar to other Wood Turtle studies that have captured a preponderance of females (Lovich et al., 1990, table 4). Point estimates from a model that included a sex effect on recapture, however, suggested that females in our study had 1.5-fold higher capture probabilities than males, although the 95% confidence interval for this parameter included 0. Therefore, the female-biased sex ratio we observed in our data may have been an artifact of greater capture probability for females; or the true population sex ratio may be female biased.

Although we found no evidence that capture probability was affected by age, we note that we had only 19 marked turtles <8 yr old with which to test for an effect of age on capture probability of very young turtles. Daigle and Jutras (2005), however, reported much lower capture probabilities for juvenile Wood Turtles in Quebec, and the low numbers of young turtles that we captured suggests they are less detectable during active searches. Because our model assessed recruitment to capture age, which averaged nearly 15 yr-old in our study but was highly variable (Fig. 3), our annual recruitment estimate of 0.058 ± 0.019 SD is not necessarily biologically meaningful as it cannot be directly compared to recruitment estimates for other turtle populations. Our estimate should be interpreted as the product of fecundity and juvenile and adult survival up until first capture. Nevertheless, it represents the only missing vital rate in our balance equation, and provided survival and population estimates are unbiased, our estimate of recruitment properly captures the unmeasured vital rates of the population (Robinson et al., 2014).

Our survival estimate of 0.964 ± 0.016 SD is near the upper end of published annual adult female survival rates for multiple North American freshwater turtles, which ranged from 0.76 (*Chrysemys picta*) to 0.97 (*Chelydra serpentina*; Shine and Iverson, 1995). These results are also consistent with delayed sexual maturity of Wood Turtles occurring between 14 and 18 yr of age (Harding and Bloomer, 1979; Ernst and Lovich, 2009) and follow the general trend that species with deferred maturity have greater survival (Shine and Iverson, 1995). Our telemetry data also confirm that adult Wood Turtles have high annual survival rates; only 3 radioed turtles were found dead during 178 collective telemetry years, which equates to 0.983 apparent survival.

Turtles that were captured ≥ 5 yr after their initial capture provided us with more reliable minimum age estimations for these turtles than the minimum ages estimated from counting the annular rings of the scutes. In 2015, one turtle was estimated to be 22 yr old by counting annuli, but based on minimum age at first capture plus subsequent recaptures, this turtle must have been at least 36 yr of age. A different turtle also was aged at 22 yr in 2015 by counting annuli, but based on recaptures must have been at least 29 yr old. These results confirm that annular rings become less reliable after 15–20 yr of age (Garber, 1989; Kaufmann, 1992; Wilson et al., 2003) and should not be used as a standalone method for determining the age of Wood Turtles ≥ 15 yr of age.

Management priorities for this population of Wood Turtles should focus on increased quality of nest sites, as well as improvements to nest protection protocols to hopefully increase the quantity of protected nests each year. This may help to increase annual juvenile recruitment and continue the upward trajectory of population growth. Range-wide management priorities should focus on mitigating human impact on Wood Turtle populations. Therefore, protecting and restoring riparian habitat or implementing regulations to minimize human recreation in areas where Wood Turtles are present is imperative. Future Wood Turtle population monitoring should refer to Brown et al. (2017), who used a systematic survey approach involving multiple surveys with multiple observers along small 0.5 km river stretches, resulting in much higher detection rates than we were able to obtain with our methods. Although we lacked the resources to implement surveys using this level of effort, smaller targeted applications conducted every 5–10 yr might allow us to confirm whether the true population size is 4–5 times larger than the marked population size.

Acknowledgments.—This research would not be possible without the long-term collaboration and logistical support of the Huron–Manistee National Forest (U.S. Forest Service). We thank the University of St. Thomas and Wittenberg University for funding and logistical assistance. We thank 38 students of Team Turtle for fieldwork. This research was monitored under University of St. Thomas IACUC Protocol 51 and 51a.

Literature Cited

Axford, Y., J. P. Briner, C. A. Cooke, D. R. Francis, N. Michelutti, G. H. Miler, J. P. Smol, E. K. Thomas, C. R. Wilson, and A. P. Wolfe. 2009. Recent changes in a remote Arctic lake are unique within the past 200,000 years. Proceedings of the National Academy of Sciences 106: 18443–18446.

Boarman, W. I., T. Goodlett, G. Goodlett, and P. Hamilton. 1998. Review of radio transmitter attachment for turtle research and recommendations for improvement. Herpetological Review 29:26–33.

Bonner, S. J., and C. J. Schwarz. 2006. An extension of the Cormack-Jolly-Seber Model for continuous covariates with application to *Microtus pennsylvanicus*. Biometrics 62:142–149.

Brown, D. J., M. M. Cochrane, and R. A. Moen. 2017. Survey and analysis design for wood turtle population monitoring. Journal of Wildlife Management 2017:1–10.

Buhlmann, K. A., and T. D. Tuberville. 1998. Use of passive integrated transponder (PIT) tags for marking small freshwater turtles. Chelonian Conservation and Biology 3:102–104.

Buhlmann, K. A., T. S. B. Akre, J. B. Iverson, D. Karapatakis, R. A. Mittermeier, A. Georges, A. G. J. Rhodin, P. P. van Dijk, and J. W. Gibbons. 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. Chelonian Conservation and Biology 8:116–149.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pp. 199–213 in J. D. Lebreton and P. M. North (eds.), Marked Individuals in the Study of Bird Populations. Birkhäuser Basel, Switzerland.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference. 2nd ed. Springer-Verlag, USA.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

———. 1994. Demographics of common snapping turtles (*Chelydra serpentine*): implications for conservation and management of long-lived organisms. American Zoologist 34:397–408.

Daigle, C., and J. Jutras. 2005. Quantitative evidence of decline in a Southern Quebec wood turtle (*Glyptemys insculpta*) Population. Journal of Herpetology 39:130–132.

Dodd, C. K., and R. Franz. 1993. The need for status information on common herpetofaunal species. Herpetological Review 24:47–49.

Ernst, C. H. 1986. Environmental temperatures and activities in the wood turtle, *Clemmys insculpta*. Journal of Herpetology 20:222–229.

———. 2001. An overview of the North American turtle *Clemmys* Ritgen, 1828. Chelonian Conservation and Biology 4:211–216.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. 2nd ed. Johns Hopkins University Press, USA.

Garber, S. D. 1989. A comparison of two populations of *Clemmys inscuplta*, the North American wood turtle. Plastron Papers 19:32–35.

Garber, S. D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. Ecological Applications 5:1151–1162.

Gelman, A. 1996. Inference and monitoring convergence. Pp. 131–143 in W. R. Gilks, S. Richardson, and D. J. Spiegelhalter (eds.), Markov Chain Monte Carlo in Practice. Chapman and Hall/CRC, USA.

Gibbons, J. W. 1987. Why do turtles live so long? BioScience 37:262–269.

Gimenez, O., and R. Choquet. 2010. Individual heterogeneity in studies on marked animals using numerical integration: capture–recapture mixed models. Ecology 91:951–957.

Harding, J. H. 1990. A twenty-year wood turtle study in Michigan: implications for conservation. Pp. 31–35 in K. R. Beaman, F. Caporaso, S. McKeown, and M. Graff (eds.), Proceedings of the First International Symposium on Turtles and Tortoises: Conservation and Captive Husbandry. Chapman University, USA.

———. 1991. Comments on herpetological collecting: the need for considering life history data in management and regulatory planning. Bulletin Chicago Herpetological Society 26:157–159.

Harding, J. H., and T. J. Bloomer. 1979. The wood turtle, *Clemmys insculpta* . . . a natural history. Herp–Bulletin of the New York Herpetological Society 15:9–26.

Holman, J. A. 2012. The Amphibians and Reptiles of Michigan: A Quaternary and Recent Faunal Adventure. Wayne State University Press, USA.

Horvitz, D. G., and D. J. Thompson. 1952. A generalization of sampling without replacement from a finite universe. Journal of the American Statistical Association 47:663–685.

Kaufmann, J. H. 1992. Habitat use by wood turtles in central Pennsylvania. Journal of Herpetology 26:315–321.

Kaufman, D. S., D. P. Schneider, N. P. McKay, C. M. Ammann, R. S. Bradley, K. R. Briffa, G. H. Miller, B. L. Otto-Bliesner, J. T. Overpeck, and B. M. Vinther. 2009. Recent warming reverses long-term arctic cooling. Science 325:1236–1239.

Kemp, D. B., K. Eichenseer, and W. Kiessling. 2015. Maximum rates of climate change are systematically underestimated in the geological record. Nature Communications 6:8890.

Kendall W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Kéry, M., and M. Schaub. 2012. Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective. Elsevier Academic Press, USA.

Lewis, T. L., J. M. Ullmer, and J. L Mazza. 2004. Threats to spotted turtle (*Clemmys guttata*) habitat in Ohio. Ohio Journal of Science 104:65–71.

Lovich, J. E., C. H. Ernst, and J. F McBreen. 1990. Growth, maturity, and sexual dimorphism in the wood turtle, *Clemmys insculpta*. Canadian Journal of Zoology 68:672–677.

McClintock, B. T., G. C. White, M. F. Antolin, and D. W. Tripp. 2009. Estimating abundance using mark–resight when sampling is with replacement or the number of marked individuals is unknown. Biometrics 65:237–246.

O'Brien S., B. Robert, and H. Tiandry. 2005. Consequences of violating the recapture duration assumption of mark–recapture models: a test using simulated and empirical data from an endangered tortoise population. Journal of Applied Ecology 42:1096–1104.

Parren, S. G. 2013. A twenty-five year study of the wood turtle (*Glyptemys insculpta*) in Vermont: movements, behavior, injuries, and death. Herpetological Conservation and Biology 8:176–190.

Powell, L. A., M. J. Conroy, J. E. Hines, J. D. Nichols, and D. G. Krementz. 2000. Simultaneous use of mark–recapture and radiotelemetry to estimate survival, movement, and capture rates. Journal of Wildlife Management 64:302–313.

Reese, D. A., and H. H. Welsh. 1971. Use of terrestrial habitat by western pond turtles, *Clemmys marmorata*, implications for management. Pp. 352–357 in Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles. An International Conference. New York Turtle and Tortoise Society, USA.

Remsburg, A. J., T. L. Lewis, P. W. Huber, and K. A. Asmus. 2006. Home ranges of wood turtles (*Glyptemys insculpta*) in northern Michigan. Chelonian Conservation and Biology 5:42–47.

Robinson, R. A., C. A. Morrison, and S. R. Baillie. 2014. Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. Methods in Ecology and Evolution 5:1361–1372.

Shine, R., and J. B. Iverson. 1995. Patterns of survival, growth, and maturation in turtles. Oikos 72:343–348.

Spradling, T. A., J. W. Tamplin, S. S. Dow, and K. J. Meyer. 2010. Conservation genetics of a peripherally isolated population of wood turtle (*Glyptemys insculpta*) in Iowa. Conservation Genetics 11:1667–1677.

Su, Y., and M. Yajima. 2015. R2jags: Using R to Run "JAGS". R package version 0.5-7. Available from: https://CRAN.R-project.org/package=R2jags.

Tinkle, D. W. 1979. Long-term field studies. BioScience 29:717.

USFS (U.S. Forest Service). 1988. Au Sable National Scenic River Management Direction. Eastern Region, Forest Service U.S. Department of Agriculture:1–70.

USGS (U.S. Geological Survey). 2016. National Water Information System. Available from: https://nwis.waterdata.usgs.gov. Accessed 4 January 2017.

van Dijk, P. P., and J. Harding. 2016. Glyptemys insculpta. The IUCN Red List of Threatened Species 2016: e.T4965A97416259. Accessed 17 November 2016.

van Dijk, P. P., J. B. Iverson, A. G. J. Rhodin, H. B. Shaffer, and R. Bour. 2014. Turtles of the World. 7th ed. Annotated Checklist of Taxonomy, Synonymy, Distribution with Maps, and Conservation Status. Conservation Biology of Freshwater Turtles and Tortoises. Chelonian Research Monographs 5:329–479.

Walde, A. D., J. R. Bider, C. Daigle, D. Masse, J. C. Bourgeois, J. Jutras, and R. D. Titman. 2003. Ecological aspects of a wood turtle, *Glyptemys insculpta,* population at the northern limit of its range in Quebec. Canadian Field Naturalist 117:377–388.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Supplement 46:120–138.

White, G. C., and E. G. Cooch. 2017. Population abundance estimation with heterogeneous encounter probabilities using numerical integration. Journal of Wildlife Management 81:322–336.

White, G. C., K. P. Burnham, and R. J. Barker. 2009. Evaluation of a Bayesian MCMC random effects inference methodology for capture–mark–recapture data. Environmental and Ecological Statistics 3:1119–1127.

Willoughby, J. R., M. Sundaram, T. L. Lewis, and B. J. Swanson. 2013. Population decline in a long-lived species: the wood turtle in Michigan. Herpetologica 69:186–198.

Wilson, D. S., C. R. Tracy, and C. R. Tracy. 2003. Estimating age of turtles from growth rings: a critical evaluation of the technique. Herpetologica 59:178–194.

Accepted: 22 December 2017.