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Population Status of the Suwannee Alligator Snapping Turtle (*Macrochelys suwanniensis*) in the Suwannee River, Florida

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ABSTRACT. – Freshwater megafauna populations, which are declining worldwide, are well known but often overlooked and understudied compared with marine and terrestrial megafauna. One species of freshwater megafauna is the Suwannee alligator snapping turtle (*Macrochelys suwanniensis*), which is endemic to the Suwannee River drainage in Georgia and Florida. Several trapping studies have examined *M. suwanniensis* distribution, body size, and population structure, but little information exists regarding its population status. The objectives of our study were to 1) estimate population size, 2) estimate apparent survival, and 3) model population growth rates (λ) by conducting a capture–mark–recapture study of *M. suwanniensis* in the Suwannee River in Florida. From 2011 to 2013, we repeatedly sampled 12 randomly selected 5-km sites along the Suwannee River for *M. suwanniensis* using baited hoop-net traps. We captured 126 individuals and had 29 recaptures. Both adult males and adult females had very high apparent survival (0.99), whereas juveniles had lower apparent survival (0.32). We estimated a population density of 6.6 turtles/river km, indicating a population of 1709 (95% CI, 1205–2694) *M. suwanniensis* from the town of White Springs to the upper limit of the estuary in the main stem of the Suwannee River (approximately 259 river km). We constructed 2 postbreeding census matrix population models for *M. suwanniensis* and incorporated parameters from this study and from the literature. Both matrix population models suggested a slightly decreasing population ($\lambda = 0.99$), but because of the uncertainty around our estimates, we consider the population trend to be unclear. Elasticity analysis revealed that λ was most sensitive to changes in adult survival compared with other model components. This is a conservation concern because adult *M. suwanniensis* may be incidentally killed by fishing gear. Our study was short-term, and our analyses had limitations; therefore, we recommend future areas of research, including long-term population monitoring.

KEY WORDS. – abundance; chelonian; Chelydridae; conservation; demography; ecology; survival

Globally, freshwater megafauna (i.e., aquatic freshwater species ≥ 30 kg) is threatened at increasing rates because of a variety of anthropogenic threats, such as overexploitation, habitat degradation, dam construction, invasive species, and pollution (He et al. 2018). Conservation and research have mostly focused on terrestrial megafauna, leaving freshwater species understudied (Cooke et al. 2013; He et al. 2017). To complicate matters, freshwater megafauna often possess life history traits that make them especially vulnerable to threats; thus, many of them are in urgent need of conservation attention (Winemiller et al. 2015). Consequently, approximately 71% of the 93 species of freshwater megafauna with known population trends are in decline, with 43% of all

freshwater megafauna having insufficient or outdated data (He et al. 2018). These large-bodied freshwater species are important to their ecosystems because they play integral roles in trophic dynamics, nutrient transport, and habitat creation (He et al. 2017). Although research has been conducted on some species and taxonomic groups (e.g., sturgeon), demographic information is lacking for many groups. To establish effective conservation strategies for freshwater megafauna, information on population status is needed (He et al. 2018).

The genus *Macrochelys* (alligator snapping turtles) contains the largest freshwater turtles in North America (Ewert et al. 2006). These large-bodied turtles are known to grow to sizes > 100 kg and inhabit river systems from

Florida to Texas that empty into the Gulf of Mexico (Ewert et al. 2006). The genus *Macrochelys* has experienced significant population declines throughout its geographic range because of extensive commercial harvest, fishing bycatch, hook ingestion, and poaching (Dobie 1971; Pritchard 1989; Ewert et al. 2006). The alligator snapping turtle (*Macrochelys temminckii*) was considered a single, wide-ranging species until Thomas et al. (2014) described 2 new species, *Macrochelys apalachicola* and *Macrochelys suwanniensis*. Although debate exists regarding the validity of *M. apalachicola* as a distinct species, there appears to be agreement that *M. suwanniensis* represents a distinct taxonomic unit (Folt and Guyer 2015; US Fish and Wildlife Service [USFWS] 2021).

Several studies have assessed *M. temminckii* distribution and population structure (Wagner et al. 1996; Trauth et al. 1998; Boundy and Kennedy 2006; Riedle et al. 2008; Folt and Godwin 2013), and robust population studies have been conducted on the species in Arkansas (Howey and Dinkelacker 2013), Oklahoma (East et al. 2013), and Georgia (Folt et al. 2016). However, we know relatively little about the status and population trends of *M. suwanniensis*, which is restricted to a single river drainage (Thomas et al. 2014) and therefore potentially impacted by threats to this watershed (i.e., low population redundancy). Pritchard (1989), citing mainly park naturalists in Florida and Georgia, reported *M. suwanniensis* scarce in the Suwannee River and its headwaters, the Okefenokee Swamp. Only a handful of studies have been conducted on *M. suwanniensis*, and intensive trapping in Georgia failed to detect the species in the upper Suwannee River (Jensen and Birkhead 2003). A study of *M. suwanniensis* in the Santa Fe River, a tributary of the Suwannee River in Florida, examined population structure and body size (Johnston et al. 2015). Recently, a study used survey data to determine the distribution and relative abundance (catch per unit effort) of *M. suwanniensis* throughout its range (Enge et al. 2021).

Although trapping studies that collect information on population structure, body size, and species distribution are valuable in conservation, they do not provide estimates of critical demographic parameters that help explain population dynamics. To properly manage a species, it is important to understand aspects of its population dynamics (Lebreton et al. 1992). The objectives of this study were to 1) estimate population size, 2) quantify demographic parameters, and 3) model population growth rates to elucidate the status of *M. suwanniensis* in the Suwannee River in Florida. To that end, we conducted a capture–mark–recapture (CMR) study in 2011–2013 in the Suwannee River in Florida. We used our CMR data to estimate apparent survival and population size. In addition, we used our estimated survival parameters as well as other parameters gleaned from the literature to create 2 discrete matrix population models and investigated population growth rates for *M. suwanniensis* in the Suwannee River. Also, we explored the overall importance of model

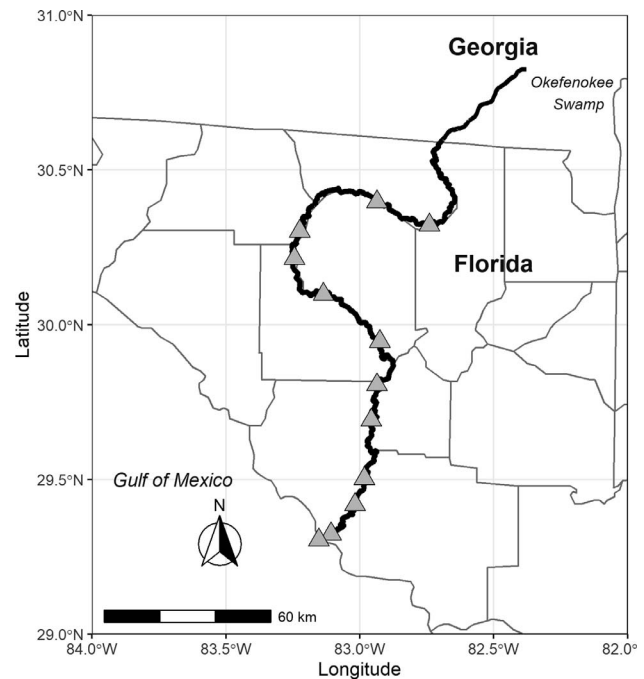


Figure 1. Map showing the twelve 5-km study sites (triangles) in the main stem of the Suwannee River in Florida.

parameters (lower-level demographic parameters) to the long-term population growth rate by using elasticity analyses. Findings from this study could inform management strategies to help conserve this species.

METHODS

Study Site. — The Suwannee River (Fig. 1) is the second largest river drainage in Florida and serves as a key geological and ecological break between the peninsula and panhandle regions. Its major tributaries are the Alapaha, Withlacoochee, and Santa Fe rivers, which were not part of this study. The Suwannee River flows approximately 378 river kilometers (rkm) from the Okefenokee Swamp in southeastern Georgia to the Gulf of Mexico in Florida (Fig. 1). During its course through North Florida, the Suwannee River experiences changes in water chemistry (Ceryak et al. 1983) that led the Suwannee River Water Management District to divide the river into 6 distinct ecological reaches that are characterized by their unique chemical and ecological features (Hornsby et al. 2000).

Data Collection. — To represent this dynamic river, we stratified its main stem into 5-km sections from the town of White Springs downstream approximately 279 rkm to the Gulf of Mexico. Each ecological reach is a relatively homogeneous stretch of river; therefore, we randomly selected two 5-km sites in each ecological reach using ArcGIS (Esri, Redlands, CA), giving us a total of 12 sites (Fig. 1). We believed that sampling these 12 sites adequately represented this system and was at the upper end of what was logistically feasible. We trapped each site for *M. suwanniensis* from summer 2011 to fall 2013. We aimed to sample sites twice per year in 2011–2012 and

once during 2013, but extreme fluctuations in water levels occasionally precluded trapping. Still, we managed to sample each site on at least 5 occasions. During each visit, we typically set 12 large hoop-net traps (122-cm diameter with 6.4-cm mesh) baited with fresh-cut or fresh-ground fish of various species. We set traps parallel to the bank in depths of 1–2.5 m with the funnel opening facing downstream and the current moving directly through the throat of the trap. In the estuary, traps were modified by attaching 2 traps together at the back with cable ties so that funnel openings faced both upstream and downstream. This allowed traps to function in shifting tides, and we considered each modified trap as a single trap (i.e., 24 traps paired for 12 trap sets). All traps were set in the late afternoon and checked and removed the next morning. Captured turtles were released at their capture location after processing.

We recorded straight midline carapace length (CL), precloacal tail length (PTL), and mass of captured turtles. Straight-line measurements were recorded to the nearest 1 mm using either a 40-cm or 95-cm aluminum tree caliper (Haglöf, Langsele, Sweden) or a nylon measuring tape (PTL). Turtles < 20 kg were weighed to the nearest 10 g using 10- and 20-kg spring scales (Pesola, Baar, Switzerland). Turtles > 20 kg were weighed to the nearest 500 g with a 100-kg spring scale (Rubbermaid, Huntersville, NC). We determined sex by size and PTL, where individuals with a CL > 330 mm and a PTL < 115 mm were considered adult females, individuals with a CL > 370 mm and a PTL > 115 mm were considered adult males, and all other individuals were considered juveniles (Dobie 1971). These size classifications are for a different species (*M. temminckii*) but represent the best available metric to determine sex in *M. suwanniensis*. Each turtle was individually marked by drilling holes in posterior marginal scutes (Cagle 1939), and individuals > 150 mm CL were implanted with a passive integrated transponder (PIT tag, Biomark, Boise, ID) in the ventrolateral tail muscle (Trauth et al. 1998).

Statistical Analyses and Modeling. — We were unable to investigate CMR data by ecological reach because some reaches lacked captures; therefore, we pooled capture data across sites and compiled a detection history for each turtle during the study. We investigated CMR data structure with a goodness-of-fit test using the R package R2ucare (version 1.0.0; Gimenez et al. 2017). We estimated apparent survival (ϕ) using Program MARK (White and Burnham 1999) with Cormack-Jolly-Seber (CJS) models using the R package RMark (version 2.2.6; Laake 2013). We used a multimodel approach to examine if ϕ and capture probability (p) varied by age-sex state (adult males, adult females, unknown juveniles), over time, or were constant over these potential sources of variation. We used Akaike information criterion (AIC) model selection (Akaike 1973, 1974) and quasi-likelihood AIC_C (QAIC_C) to evaluate models where lower values were considered more parsimonious (Burnham and

Anderson 2002). We used QAIC_C to select the most parsimonious model because our measure of overdispersion (\hat{c}) for our general CJS model was slightly > 3 (3.03), which can be problematic for analyses (Lebreton et al. 1992). In addition, we used Program MARK to generate estimates of the superpopulation size (N) and probability of entrance ($pent$) for each sex with the POPAN formulation of the Jolly-Seber (J-S) model (Schwarz and Arnason 1996) using the R package RMark. The superpopulation is defined as the total number of animals ever present for capture within the study site, whereas $pent$ is the rate at which animals enter the population via births and immigration between the first and the last sampling occasions (see Schwarz and Arnason 1996). We set model parameters such ϕ , $pent$, and N to vary by age-sex stage (group), and we considered capture probability (p) to be constant (i.e., $\phi[\text{group}] p[.] pent[\text{group}] N[\text{group}]$).

Finally, we investigated the asymptotic population growth rate (λ) with 2 different female stage-structured postbreeding census matrix population models (MPMs). We used 3 demographic stages (hatchling, juvenile, and adult) in both models. Model parameters included stage-specific survival probabilities (σ_h , σ_j , σ_a), growth rate of juveniles to the adult stage (γ), the probability of juvenile reproduction (b), and an estimate of annual fecundity (m). We conducted a literature review to obtain life-history parameters for *M. suwanniensis*, but information on this species was limited. Estimates of hatchling survival presently do not exist for *Macrochelys*. Folt et al. (2016) used 0.15 to represent hatchling survival (age 0–1 yr) of *M. temminckii* based on hatchling survival of *Chelydra serpentina*. We also felt this estimate was appropriate and likely a conservative estimate of hatchling survival for *M. suwanniensis*. We used estimates of apparent survival from our CMR data to represent annual juvenile and adult survival. The growth probability (γ) is the probability that juveniles grow to transition to the adult stage. However, this species is long-lived and exhibits slow growth; thus, we were unable to directly estimate this parameter from our short-term CMR data. Therefore, we estimated γ with the asymptotic-age-within-stage method using the R package mpmttools (version 0.2.0; Kendall 2019). Sexual maturity ranges from 13 to 21 yrs in female *M. temminckii* (Tucker and Sloan 1997); therefore, we used the median (17 yrs) to represent sexual maturity for female *M. suwanniensis* (stage duration for juveniles was 16 yrs). We estimated annual fecundity (m) by taking the product of one-half the clutch size (cs), nest survival (ns), and nest hatching success (hs) (e.g., $m = (cs \times ns \times hs)/2$). A study conducted in the lower Apalachicola River in Florida found that the *M. temminckii* mean clutch size was approximately 35 eggs (Ewert et al. 2006), so we used this estimate to represent the clutch size of *M. suwanniensis*. Ewert et al. (2006) also reported nest survival and nest hatching success to be 0.13 and 0.72, respectively, for *M. temminckii* nests in Florida, so we used these parameters for *M. suwanniensis*. We assumed that *M. suwanniensis*

Table 1. Estimates of demographic parameters used in population matrices with associated symbols for Model 1 and Model 2. We used a higher rate of juvenile survival (within our 95% CI) and a higher juvenile to adult transition probability in Model 2. The probability of juvenile reproduction is directly related to the proportion of juveniles that transition to adulthood.

Parameter	Symbol	Model 1 estimate	Model 2 estimate
Hatchling survival	σ_h	0.15	0.15
Juvenile survival	σ_j	0.32	0.75
Growth probability	γ	0.000001	0.003
Adult survival	σ_a	0.99	0.99
Juvenile reproduction probability	b	0.000001	0.003
Fecundity	m	1.64	1.64

lays a single clutch based on limited data for this species (Allen and Neill 1950) and for *M. temminckii* (Dobie 1971; Ewert and Jackson 1994). We assumed the hatchling sex ratio is 1:1; incubation temperature influences sex determination in *Macrochelys* (Ewert et al. 1994). Although juveniles do not reproduce, we accounted for the individuals that survive and make the transition from the juvenile stage to the adult stage and reproduce (b) after the just-passed breeding season (Mills 2013; Kendall et al. 2019). See Table 1 for the demographic rates, which were used to form population matrices that followed the form:

$$A = \begin{bmatrix} 0 & mb & m\sigma_a \\ \sigma_h & \sigma_j(1 - \gamma) & 0 \\ 0 & \sigma_j\gamma & \sigma_a \end{bmatrix}$$

From this formulation, we created 2 different MPMs under 2 different scenarios. Model 1 incorporated our apparent survival estimates for juveniles (0.32) and adult females (0.99), while Model 2 used a higher estimate for juvenile survival (0.75) and thus a higher juvenile to adult transition probability. We derived this estimate by simulating ($n = 10,000$) values from our original distribution and discarding values < 0.65 . This allowed us to use a higher juvenile survival by focusing on the upper tail of the juvenile survival distribution from Model 1. The higher juvenile survival estimate is also more aligned with the reference parameter for *M. temminckii* (see Folt et al. 2016). We then calculated the asymptotic λ for both models and determined elasticity to ascertain how λ responded to proportional changes to different model components (Caswell 2001) using the R package popbio (version 2.4.4; Stubben and Milligan 2007). We generated the 95% confidence interval (CI) for λ with the delta method (see Caswell 2001). We considered estimates of λ , where $\lambda > 1$ indicates a growing population, $\lambda = 1$ suggests a stable population, and $\lambda < 1$ indicates a declining population. We used the R package tidyverse (Wickham et al. 2019) for data exploration and visualization. All analyses were conducted in R (version 3.5.2; R Core Team 2018) implemented in RStudio (version 1.1.463; RStudio Team 2016).

Table 2. Model selection table showing CJS models for *Macrochelys suwanniensis* in the Suwannee River, Florida. Models allowed apparent survival (ϕ), probability of capture (p) to vary by age-sex group (g), time (t), or remain constant (\cdot).

Model	Parameters	$\Delta QAIC_C$	Model weight
$\phi(g) p(\cdot)$	4	0.00	42.31
$\phi(\cdot) p(\cdot)$	2	0.57	31.79
$\phi(\cdot) p(g)$	4	1.84	0.16
$\phi(g) p(g)$	6	3.87	0.06
$\phi(g) p(t)$	7	6.58	0.01
$\phi(t) p(\cdot)$	5	6.87	0.00
$\phi(t) p(t)$	8	13.41	0.00
$\phi(g^*t) p(\cdot)$	13	16.52	0.00
$\phi(g) p(g^*t)$	15	16.93	0.00
$\phi(g^*t) p(g^*t)$	24	42.35	0.00

RESULTS

We recorded 155 *M. suwanniensis* captures (29 were recaptures) at our 12 sites. The sample consisted of 27 (21%) juveniles, 21 (17%) adult females, and 78 (62%) adult males, and the entire sample exhibited a right skew toward individuals with larger CLs. The overall goodness-of-fit test for the CMR modeling did not show any significant transient effects or trap happiness (or shyness) within the sample. Our most parsimonious CJS model possessed age-sex-determined ϕ and a constant p (Table 2), and we used this model to provide ϕ estimates for each group. Estimates for ϕ were extremely high and near the boundary with 1.0 for adult males (0.99; SE < 0.001 ; 95% CI, 0.99–1.00) and adult females (0.99; SE < 0.001 ; 95% CI, 0.99–1.00) but were much lower for juveniles (0.32; SE = 0.22; 95% CI, 0.06–0.77). Our J-S model with the POPAN formulation estimated the superpopulation to have 330 (95% CI, 233–520) *M. suwanniensis* in our trapping sites in the river main stem (excluding the 2 estuarine sites), but population size estimates varied by age-sex group (Table 3). Density was calculated at 6.6 (95% CI, 4.7–10.4) turtles/rkm, indicating an estimated 1709 (95% CI, 1205–2694) *M. suwanniensis* occur in the Suwannee River main stem from the town of White Springs to the upper estuary (approximately 259 rkm). We did not include the estuary in the calculation of density because only 1 turtle was captured there during the study,

Table 3. Estimates of the superpopulation (N) and density (turtles/rkm) with associated standard error (SE) by sex/age class (male, female, juvenile) for *Macrochelys suwanniensis* in 10 sites (excluding the 2 estuary sites) in the Suwannee River, Florida. The superpopulation is defined as the total number of animals ever present for capture within the study site (see Schwarz and Arnason 1996).

	N	SE	95% CI	Density	95% CI
Female	51	12.2	35–86	1.1	0.7–1.7
Male	177	28.3	135–249	3.5	2.7–5.0
Juvenile	102	29.5	63–185	2.0	1.3–3.7
Total	330	—	232–520	6.6	4.7–10.4

Table 4. The elasticity (proportional sensitivity) of the population growth rate (λ) to changes in lower-level demographic parameters for Model 1 and Model 2.

Parameter	Model 1 elasticity	Model 2 elasticity
σ_h (hatchling survival)	< 0.001	0.002
σ_j (juvenile survival)	< 0.001	0.009
σ_a (adult female survival)	0.999	0.988
γ (growth rate)	< 0.001	0.002
b (juvenile reproduction probability)	< 0.001	< 0.001
m (fecundity)	< 0.001	0.002

suggesting the estuary may not provide suitable conditions for long-term occupancy by *M. suwanniensis*. In addition, we did not project our density estimates to the portion of the Suwannee River upstream of White Springs, because no turtles have been trapped there. Estimates of *pent* were higher for adult females (0.18; 95% CI, 0.11–0.28) and juveniles (0.16; 95% CI, 0.10–0.25) than for adult males (0.14; 95% CI, 0.08–0.21).

Our first female-based MPM (Model 1) suggested that the population is decreasing ($\lambda = 0.99$; 95% CI, 0.98–0.99), whereas our second female MPM (Model 2), which used a higher juvenile survival rate, also suggested a decreasing population ($\lambda = 0.99$; 95% CI, 0.99–1.00). Notably, due to our estimates being around 1.0 and because of the uncertainty around our estimates, this species' population trend is uncertain. Additionally, elasticity analysis of both models revealed that λ was much more sensitive to proportional changes in adult survival compared with other parameters (Table 4). Furthermore, Model 2 used a much higher juvenile survival rate and higher juvenile-to-adult transition probability, but adult female survival was still by far the most sensitive model component (Table 4).

DISCUSSION

Our study is the first to investigate the population status of *M. suwanniensis*, and our MPMs were unable to infer whether this population is stable or declining. This uncertainty in population status is a conservation concern, as many of the world's freshwater megafauna species are in decline (He et al. 2017). In fact, studies on *M. temminckii* estimated declining populations in Arkansas (Howey and Dinkelacker 2013) and Oklahoma (East et al. 2013). Our MPM used our CJS model estimates of apparent survival for the juvenile and adult stages. Apparent survival differs from true survival because the CJS model cannot distinguish mortality from permanent emigration (Lebreton et al. 1992). Therefore, the treatment of gain and loss in our MPMs is somewhat asymmetric. We caution readers against making generalizations about this population's status based on deterministic projection matrices. In addition, our study was short-term and may not reflect the true long-term dynamics that are typical of

wild populations. More research is needed to acquire more precise estimates, which could strengthen future population assessments.

Our estimates of apparent survival were extremely high for both adult males (> 0.99) and adult females (0.99). This is not surprising, because *Macrochelys* is long-lived, and adults have few natural predators (Pritchard 1989). Considering the relatively short duration of our study (~ 2 yrs), one would expect high survival rates for such a long-lived species. The Suwannee River was never heavily commercially harvested and likely received minimal amounts of noncommercial harvest (P.E. Moler, pers. comm., January 2012). Florida prohibited the sale of *Macrochelys* in 1972 and limited personal possession to 1 turtle in 1973, effectively banning commercial harvest. However, incidental take of adult *M. suwanniensis* may occur when turtles ingest fishing tackle or become entangled in fishing line (Enge et al. 2014; Steen and Robinson 2017).

Our estimate of apparent juvenile survival (0.32) for *M. suwanniensis* was low compared with that of *M. temminckii* in a Georgia population (0.88; Folt et al. 2016). The main stem of a large, free-flowing river may negatively impact juvenile survival, or the high proportion of large adult male turtles (70.5% had a CL > 500 mm) in our study sites may have impacted our ability to capture juveniles, which may inhabit floodplain and other shallow-water habitats that we did not trap. This potentially creates a source of permanent juvenile emigration from our sites, which could affect our juvenile apparent survival estimates. Therefore, our lower juvenile survival may reflect increased movement of juveniles out of the river main stem into areas that are more hospitable to smaller individuals.

Elasticity analysis suggested that λ is much more sensitive to changes in adult survival in Model 1. This would be expected under low reproductive rates, lower juvenile survival, and small transition probabilities coupled with extremely high adult survival. Although Model 2 showed that λ had some sensitivity to other parameters, it still suggested that λ is most sensitive to changes in adult female survival. This agrees with other turtle studies that highlighted the importance of adult survival (Congdon et al. 1993, 1994; Heppell 1998; Enneson and Litzgus 2008). These results indicate that protecting adults (especially adult females) from mortality should be a conservation and management priority. In fact, our results suggest that a small increase in adult female mortality could potentially cause significant population declines, as has been found for other long-lived turtle species (Congdon et al. 1994; Bowen et al. 2004).

The US Fish and Wildlife Service (USFWS) proposed that *M. suwanniensis* be listed as threatened under the Endangered Species Act (USFWS 2021). In its species status assessment (SSA) of *M. suwanniensis*, the USFWS (2020) used a female, stage-structured population model that predicted a decline in abundance, with the species

facing extinction in 50 yrs. The listing SSA used an annual adult female survival of 0.95 based on the Folt et al. (2016) study, which was conducted over a longer time period than our study. Future modeling efforts would be greatly improved with further study of *M. suwanniensis* biology, demography, response to and prevalence of threats, and how these vary across the species' range (USFWS 2020). Our study provided demographic data for the Suwannee River main stem in Florida and found that the population status is uncertain. Furthermore, our MPM models have several limitations. For example, hatching survival is poorly understood, and our estimates of nest predation and hatching success came from a single study conducted on a different species (*M. temminckii*) in the Apalachicola River, which is a drastically different system. In addition, other models used multiple stages to represent juvenile turtles (see Crouse et al. 1987), whereas we assumed a constant survival for juvenile *M. suwanniensis*. This assumption is likely unrealistic because juvenile survival is related to size (Kessler 2020), and the size differences in our defined juvenile class were substantial. Also, the standard error associated with our estimate of juvenile apparent survival was large. More research is needed to obtain system-specific model parameters and to estimate juvenile survival more accurately in the Suwannee River. In addition, future models should incorporate environmental and demographic stochasticity, which may provide more robust estimates.

Overall, our model estimated abundance at 6.6 turtles/rkm, indicating approximately 1709 *M. suwanniensis* occur in the river main stem from White Springs to the estuary. However, our mean density estimate is much lower than studies of *M. temminckii* found: 28–34 turtles/km in 2 small Oklahoma streams (Riedle et al. 2008), 18 turtles/km in an Arkansas stream that had been commercially harvested in the past (Howey and Dinkelacker 2013), and 13–14 turtles/km in Spring Creek, Georgia (Folt et al. 2016). Several possible explanations exist for our low densities, including the fact that we studied a different species, although its natural history is apparently similar to that of *M. temminckii*. Other studies were conducted mostly in smaller streams and rivers, whereas our study was conducted in the main stem of a large, free-flowing river with a population of large adults that might decrease the abundance of smaller turtles or restrict them to shallow-water habitats and other areas that could not be effectively trapped. The presence of many large adults suggests that the Suwannee River experienced relatively little past harvest, although extensive trapping in the main stem upstream of White Springs failed to capture *M. suwanniensis* in Georgia and Florida (Jensen and Birkhead 2003; Enge et al. 2021). Historical commercial harvest was identified as one explanation for the paucity of *M. suwanniensis* in Georgia (Jensen and Birkhead 2003). Georgia did not prohibit commercial harvest until 1989, 17 yrs later than Florida, but major commercial trapping likely did not occur in the upper Suwannee River

regardless of this lack of regulation (P.E. Moler, *pers. comm.*, January 2012). Overall, our results indicate that *M. suwanniensis* is widely distributed and more abundant in the Suwannee River in Florida than previously thought.

Because of the uncertain population status of *M. suwanniensis* in the Suwannee River, resource managers should be vigilant regarding threats to this species, because even a slight decrease in adult survival, especially in females, could result in a significant population decline. Mortality of freshwater turtles from ingested fish hooks has been identified as a threat in southeastern US rivers (Steen et al. 2014), and the probability of a turtle ingesting a hook and dying from it was estimated at 1.2%–11% (Steen and Robinson 2017). Ingested fish hooks can perforate the digestive tract lining and eventually cause mortality in turtles, and associated fishing line attached to the hook can cause injury or death (Borkowski 1997; Casale et al. 2008; Steen et al. 2014). Although Florida prohibited the harvest of all *Macrochelys* in July 2009 and listed *M. suwanniensis* as threatened in 2018, some incidental mortality likely occurs from fishing tackle ingestion or entanglement. We observed and had reports of dead *Macrochelys* and of turtles containing hooks, but the incidence of mortality from hooks is unknown. The large size of adult *Macrochelys* makes them potentially susceptible to drowning from getting snagged and entangled in fishing line associated with abandoned bush hooks (i.e., limb lines), which has been observed with *M. temminckii* in Florida (J.D. Mays, *pers. comm.*, June 2015). Three of 25 *M. suwanniensis* radiographed during this study had fish hooks lodged in their upper gastrointestinal tracts, and one turtle had 3 hooks (Enge et al. 2014). The species action plan developed by the Florida Fish and Wildlife Conservation Commission (2018) identified the need to investigate the effects of trotlines and bush hooks on *Macrochelys* spp. A bush hook typically consists of a piece of heavy monofilament or nylon line with a weighted, baited hook that is tied to an overhanging branch. Rule 68A-23.004, F.A.C. (Florida Department of State 2008) requires that these hooks be permanently and legibly marked with the harvester's name and address, checked every 24 hrs, and promptly removed when done fishing, but we observed that bush hooks are often left unattended for long periods and are sometimes abandoned. Because a small increase in adult mortality from hook ingestion can cause population declines in turtles (Steen and Robinson 2017), the potential threat posed by bush hooks needs to be investigated. If future research finds evidence of significant adult mortality of *M. suwanniensis* from bush hooks, prohibiting their use in the Suwannee drainage could be considered, as Rule 68A-23.002, F.A.C., already does in portions of other rivers and some lakes in Florida. Less restrictive conservation actions include banning the use of stainless-steel hooks, initiating an educational campaign to inform stakeholders of current bush hook regulations and the potential threat of

abandoned bush hooks, and organizing “cleanup” efforts of abandoned fishing gear in the drainage.

In conclusion, our study was the first to report on the status of *M. suwanniensis* in the Suwannee River in Florida, and although this species’ population status was found to be uncertain, it is important to understand that our study represents a short-term “snapshot” of the population. Many studies are considered stand-alone investigations, but single studies rarely provide definitive results (Nichols et al. 2019). Therefore, we recommend additional research in the following areas: 1) investigate age- and size-related variation in juvenile survival, 2) determine the impact of bush hooks in the Suwannee drainage, and 3) institute long-term population monitoring to accumulate information that can be used to effectively manage this important species of freshwater megafauna.

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LITERATURE CITED

- AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N. and Csaki, F. (Eds.). 2nd International Symposium on Information Theory. Budapest: Akademia Kiado, pp. 267–281.
- AKAIKE, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19: 716–723.
- ALLEN, E.R. AND NEILL, W.T. 1950. The alligator snapping turtle, *Macrochelys temminckii*, in Florida. Ross Allen’s Reptile Institute, Special Publication No. 4, 15 pp.
- BORKOWSKI, R. 1997. Lead poisoning and intestinal perforations in a snapping turtle (*Chelydra serpentina*) due to fishing gear ingestion. Journal of Zoo and Wildlife Medicine 28:109–113.
- BOUNDY, J. AND KENNEDY, C. 2006. Trapping survey results for the alligator snapping turtle (*Macrochelys temminckii*) in southeastern Louisiana, with comments on exploitation. Chelonian Conservation and Biology 5:3–9.
- BOWEN, K.D., COLBERT, P.L., AND JANZEN, F.J. 2004. Survival and recruitment in a human-impacted population of ornate box turtles, *Terrapene ornata*, with recommendations for conservation and management. Journal of Herpetology 38:562–568.
- BURNHAM, K.P. AND ANDERSON, D.R. 2002. Model Selection and Multimodel Inference. Second edition. New York: Springer-Verlag, 488 pp.
- CAGLE, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.
- CASALE, P., ABBATE, G., FREGGI, D., CONTE, N., OLIVERIO, M., AND ARGANO, R. 2008. Foraging ecology of loggerhead sea turtles *Caretta* in the central Mediterranean Sea: evidence for a relaxed life history model. Marine Ecology Progress Series 372:265–276.
- CASWELL, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Second edition. Sunderland, MA: Sinauer Associates, 772 pp.
- CERYAK, R., KNAPP, M.S., AND BURNSON, T. 1983. The geology and water resources of the Upper Suwannee River Basin, Florida. Bureau of Geology, Division of Resource Management, Florida Department of Natural Resources and Suwannee River Water Management District, Tallahassee, FL, 165 pp.
- CONGDON, J.D., DUNHAM, A.E., AND SELS, R.V. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist 34:397–408.
- CONGDON, J.D., DUNHAM, A.E., AND VAN LOBEN SELS, R.C. 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.
- COOKE, S.J., LAPOINTE, N.W., MARTINS, E.G., THIEM, J.D., RABY, G.D., TAYLOR, M.K., BEARD, T.D., JR., AND COWX, I.G. 2013. Failure to engage the public in issues related to inland fishes and fisheries: strategies for building public and political will to promote meaningful conservation. Journal of Fish Biology 83: 997–1018.
- CROUSE, D.T., CROWDER, L.B., AND CASWELL, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.
- DOBIE, J.L. 1971. Reproduction and growth in the alligator snapping turtle, *Macrochelys temminckii* (Troost). Copeia 1971:645–658.
- EAST, M.B., RIEDLE, J.D., AND LIGON, D.B. 2013. Temporal changes in an alligator snapping turtle (*Macrochelys temminckii*) population. Wildlife Research 40:77–81.
- ENGE, K.M., STEVENSON, D.J., THOMAS, T.M., JOHNSTON, G.R., JENSEN, J.B., STEGENGA, B.S., CHANDLER, H.C., AND MOLER, P.E. Distribution and relative abundance of the Suwannee alligator snapping turtle (*Macrochelys suwanniensis*). Chelonian Conservation and Biology 20:184–199.
- ENGE, K.M., THOMAS, T.M., AND SUAREZ, E. 2014. Population status, distribution, and movements of the alligator snapping turtle in the Suwannee River, Florida. Final Report, Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Wildlife Research Laboratory, Gainesville, FL, 47 pp.
- ENNESON, J.J. AND LITZGUS, J.D. 2008. Using long-term data and a stage-classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*). Biological Conservation 141:1560–1568.
- EWERT, M.A. AND JACKSON, D.R. 1994. Nesting ecology of the alligator snapping turtle (*Macrochelys temminckii*) along the lower Apalachicola River, Florida. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Final Report, Tallahassee, 45 pp.

- EWERT, M.A., JACKSON, D.R., AND MOLER, P.E. 2006. *Macrochelys temminckii* — alligator snapping turtle. In: Meylan, P.A. (Ed.). *Biology and Conservation of Florida Turtles*. Chelonian Research Monographs 3:58–71.
- EWERT, M.A., JACKSON, D.R., AND NELSON, C.E. 1994. Patterns of temperature-dependent sex determination in turtles. *Journal of Experimental Zoology* 270:3–15.
- FLORIDA DEPARTMENT OF STATE. 2008. Lawful methods for using trotlines and bush hooks or set lines. Rule 68A-23.004. Florida Administrative Code, Florida Department of State, Tallahassee. https://www.flrules.org/Gateway/View_notice.asp?id=5435606.
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION. 2018. A species action plan for Florida's alligator snapping turtles. Tallahassee, FL, 36 pp.
- FOLT, B. AND GODWIN, J.C. 2013. Status of the alligator snapping turtle (*Macrochelys temminckii*) in south Alabama with comments on its distribution. *Chelonian Conservation and Biology* 12:211–217.
- FOLT, B. AND GUYER, C. 2015. Evaluating recent taxonomic changes for alligator snapping turtles (Testudines: Chelydriidae). *Zootaxa* 3947:447–450.
- FOLT, B., JENSEN, J.B., TEARE, A., AND ROSTAL, D. 2016. Establishing reference demography for conservation: a case study of *Macrochelys temminckii* in Spring Creek, Georgia. *Herpetological Monographs* 30:21–33.
- GIMENEZ, O., LEBRETON, J.D., CHOQUET, R., AND PRADEL, R. 2017. R2ucare: goodness-of-fit tests for capture-recapture models. R package version 1.0.0. <https://doi.org/10.1101/192468>.
- HE, F., BREMERICH, V., ZARFL, C., GELDMANN, J., LANGHANS, S.D., DAVID, J.N.W., DARWALL, W., TOCKNER, K., AND JÄHNIG, S.C. 2018. Freshwater megafauna diversity: patterns, status and threats. *Diversity and Distributions* 24:1395–1404.
- HE, F., ZARFL, C., BREMERICH, V., HENSHAW, A., DARWALL, W., TOCKNER, K., AND JÄHNIG, S.C. 2017. Disappearing giants: a review of threats to freshwater megafauna. *WIREs Water* 4: e1208.
- HEPPELL, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998:367–375.
- HORNSBY, D., MATTSON, R.A., AND MIRTI, T. 2000. Surface water quality and biological monitoring. Annual Report 1999. Suwannee River Water Management District Technical Report WR-00-04, 148 pp.
- HOWEY, C.A.F. AND DINKELACKER, S.A. 2013. Characteristics of a historically harvested alligator snapping turtle (*Macrochelys temminckii*) population. *Copeia* 2013:58–63.
- JENSEN, J.B. AND BIRKHEAD, W.S. 2003. Distribution and status of the alligator snapping turtle (*Macrochelys temminckii*) in Georgia. *Southeastern Naturalist* 2:25–34.
- JOHNSTON, G.R., THOMAS, T.M., SUAREZ, E., LAU, A., AND MITCHELL, J.C. 2015. Population structure and body size of the Suwannee alligator snapping turtle (*Macrochelys suwanniensis*) in northern Florida. *Chelonian Conservation and Biology* 14:73–81.
- KENDALL, B.E. 2019. mpmttools: Tools for building and analyzing matrix population models. <https://github.com/BruceKendall/mpmttools>.
- KENDALL, B.E., FUJIWARA, M., DIAZ-LOPEZ, J., SCHNEIDER, S., VOIGHT, J., AND WIESNER, S. 2019. Persistent problems in the construction of matrix population models. *Ecological Modelling* 406:33–43.
- KESSLER, E.J. 2020. Assessment of a freshwater turtle reintroduction. PhD Dissertation, University of Illinois at Urbana-Champaign.
- LAAKE, J.L. 2013. RMark: an R interface for analysis of capture–recapture data with MARK. <https://www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf>.
- LEBRETON, J.-D., BURNHAM, K.P., CLOBERT, J., AND ANDERSON, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- MILLS, L.S. 2013. *Conservation of Wildlife Populations: Demography, Genetics, and Management*. Second edition. Chichester, UK: Wiley-Blackwell, 335 pp.
- NICHOLS, J.D., KENDALL, W.L., AND BOOMER, G.S. 2019. Accumulating evidence in ecology. Once is not enough. *Ecology and Evolution* 9:13991–14004.
- PRITCHARD, P.C.H. 1989. *The Alligator Snapping Turtle: Biology and Conservation*. Milwaukee, WI: Milwaukee Public Museum, 104 pp.
- R CORE TEAM. 2018. R: A Language and Environment for Statistical Computing. Version 3.5.2. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org>.
- RIEDLE, J.D., SHIPMAN, P.A., FOX, S.F., HACKLER, J.C., AND LESLIE, D.M., JR. 2008. Population structure of the alligator snapping turtle, *Macrochelys temminckii*, on the western edge of its distribution. *Chelonian Conservation and Biology* 7:100–104.
- RSTUDIO TEAM. 2016. RStudio: Integrated Development for R. Version 1.1.463. Boston, MA: RStudio, Inc. <https://www.rstudio.com/>.
- SCHWARZ, C.J. AND ARNASON, A.N. 1996. A general methodology for the analysis of open-model capture recapture experiments. *Biometrics* 52:860–873.
- STEEN, D.A., HOPKINS, B.C., VAN DYKE, J.U., AND HOPKINS, W.A. 2014. Prevalence of ingested fish hooks in freshwater turtles from five rivers in the southeastern United States. *PLoS One* 9(3):p.e91368.
- STEEN, D.A. AND ROBINSON, O.J., JR. 2017. Estimating freshwater turtle mortality rates and population declines following hook ingestion. *Conservation Biology* 31:1333–1339.
- STUBBEN, C. AND MILLIGAN, B. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22:1–23.
- THOMAS, T.M., GRANATOSKY, M.C., BOURQUE, J.R., KRYSKO, K.L., MOLER, P.E., GAMBLE, T., SUAREZ, E., LEONE, E., ENGE, K.M., AND ROMAN, J. 2014. Taxonomic assessment of alligator snapping turtles (Chelydriidae: *Macrochelys*), with the description of two new species from the southeastern United States. *Zootaxa* 3768:141–165.
- TRAUTH, S.E., WILHILDE, J.D., AND HOLT, A. 1998. Population structure and movement patterns of alligator snapping turtles (*Macrochelys temminckii*) in northeastern Arkansas. *Chelonian Conservation and Biology* 3:64–70.
- TUCKER, A.D. AND SLOAN, K.N. 1997. Growth and reproductive estimates from alligator snapping turtles, *Macrochelys temminckii*, taken by commercial harvest in Louisiana. *Chelonian Conservation and Biology* 2:587–592.
- US FISH AND WILDLIFE SERVICE (USFWS). 2020. Species status assessment report for the Suwannee alligator snapping turtle (*Macrochelys suwanniensis*). Version 1.1. July 2020. Atlanta, GA, 96 pp.
- US FISH AND WILDLIFE SERVICE (USFWS). 2021. Endangered and threatened wildlife and plants; 12-month petition finding and threatened species status with Section 4(d) rule for Suwannee alligator snapping turtle. *Federal Register* 86:10814–18034.
- WAGNER, B.K., URBSTON, D., AND LEEK, D. 1996. Status and distribution of alligator snapping turtles in Arkansas. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 50:264–270.

- WHITE, G.C. AND BURNHAM, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138.
- WICKHAM, H., AVERICK, M., BRYAN, J., CHANG, W., MCGOWAN, L.D., FRANÇOIS, R., GROLEMUND, G., HAYES, A., HENRY, L., HESTER, J., KUHN, M., PEDERSEN, T.L., MILLER, E., BACHE, S.M., MÜLLER, K., OOMS, J., ROBINSON, D., SEIDEL, D.P., SPINU, V., TAKAHASHI, K., VAUGHAN, D., WILKE, C., WOO, K., AND YUTANI, H. 2019. Welcome to the tidyverse. *Journal of Open Source Software* 4:431686.
- WINEMILLER, K.O., HUMPHRIES, P., AND PUSEY, B.J. 2015. Protecting large apex predators. In: Closs, G.P., Krkosek, K., and Olden, J.D. (Eds.). *Conservation of Freshwater Fishes*. Cambridge, UK.: Cambridge University Press, pp. 361–398.

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