

## Establishing Reference Demography for Conservation: A Case Study of *Macrochelys temminckii* in Spring Creek, Georgia

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**ABSTRACT:** The conservation of large, long-lived turtle species can be a challenging issue because their life-history strategies make populations sensitive to changes in adult survivorship and populations may be difficult to sample. The Alligator Snapping Turtle (*Macrochelys temminckii*) is a large freshwater turtle species occurring in North America for which commercial harvest has severely reduced populations throughout the species range. Given recent population declines and a general deficit of demographic knowledge for *Macrochelys*, we conducted a mark-recapture study of *M. temminckii* from 1997–2013 in Spring Creek, Georgia, USA. We made 166 captures of 75 individuals using baited hoop-net traps and skin-diving searches. The observed and estimated population structure described the adult sex ratio as even and adults as more abundant than juveniles. Apparent survival was higher for adult males (0.98) and females (0.95) than for juveniles (0.86), and we estimated a population density of 13–14 turtles/stream kilometer. The survival estimates for adult *M. temminckii* are among the highest of all freshwater turtle species reported in the literature. We used the empirical demographic parameters described here and a literature review to build an updated population model for *M. temminckii*; the model estimated a finite rate of population increase consistent with a growing population ( $\lambda = 1.036$ ) at Spring Creek, and population viability analysis found the population growing over the next 50 yr in 100% of simulations. Application of our model to published survival estimates from two impacted western populations indicated a declining population ( $\lambda = 0.563$ ) with a high risk of extirpation in Oklahoma and a population with a slow rate of decline ( $\lambda = 0.978$ ) but approaching stability in Arkansas. Simulations identified combinations of survival values which generate viable populations and also characterized population structure resulting from viable scenarios. This is the first study to document a stable and viable population of *Macrochelys*. We suggest that the population parameters described at Spring Creek are the best approximation of reference demographic conditions for *Macrochelys* to date, and this study provides a general framework applicable for large, long-lived, endangered turtle species for which demographic data are unavailable.

**Key words:** Alligator Snapping Turtles; Conservation; Demography; *Macrochelys temminckii*; Mark-recapture; Population model; Population structure; Survival

LIKE MANY long-lived species, turtles are susceptible to declines resulting from chronic disturbances, such as human harvest, because their life history strategies are characterized by low recruitment, slow growth, high adult survival, and long generation time (Iverson 1991; Congdon et al. 1993, 1994; Cunnington and Brooks 1996; Gibbons et al. 2000; Webb et al. 2002; but see Fordham et al. 2007). In recent history, large freshwater, marine, and terrestrial turtles have been harvested by humans as a food source (Klemens and Thorbjarnarson 1995; Thorbjarnarson et al. 2000), and harvest is thought to have caused extreme population declines of some of the world's largest turtles, including the critically endangered Mangrove Terrapins (*Batagur baska*; Das 1997; Platt et al. 2000), the Arrau Turtles (*Podocnemis expansa*; Pritchard and Trebau 1984; Peñaloza et al. 2013), the critically endangered Yangtze Giant Softshell Turtles (*Rafetus swinhoei*; Jian et al. 2013), Tortoises (Pritchard 1967; Swingland and Klemens 1989), and Alligator Snapping Turtles (Pritchard 1989). For many large, imperiled species, population declines occurred during the 20th Century, and demographic studies of natural, undisturbed populations have not been performed. In the absence of such studies, basic population vital rates are unavailable, information which is needed to build population models and inform conservation theory and practice. The ability to address these deficits is further hindered because large turtles appear to possess lifespans that can be greater than those of researchers (sensu Tinkle 1979). For these reasons,

studies of natural population dynamics have not been performed for many large, declining turtle species, resulting in a lack of knowledge which hinders conservation efforts.

Alligator Snapping Turtles (*Macrochelys* spp.) are the largest freshwater aquatic turtles in North America, with large males able to reach body sizes of up to 80 cm standard carapace length and 110 kg in mass (Lovich 1993). Members of the genus occur in Gulf Coastal drainages from the San Antonio River, Texas, USA east to the Suwannee River, Florida, USA (Ernst and Lovich 2009). *Macrochelys* are dietary generalists that consume a wide variety of prey (reviewed in Ernst and Lovich 2009) and, given the broad diet, the species may be an important member of the riparian food web of Gulf coastal drainages of the southern United States. *Macrochelys* appear to be extremely long-lived: the longevity record is a male who, after being collected from the wild as an adult, lived over 70 yr in the Bronx Zoo before dying (Gibbons 1987).

Because of their large size and the relative ease of collection using hoop-net traps and set lines, *Macrochelys* were heavily targeted by commercial collectors in the 1960s and 70s to support a demand for turtle meat used predominately in soups. This commercial collection is thought to have caused population declines throughout the southeastern United States (Pritchard 1989); in particular, populations in Florida, Georgia, Alabama, and Mississippi were significantly reduced. In light of declines, members of the genus *Macrochelys* are now considered to be species of conservation concern and are protected in each state where

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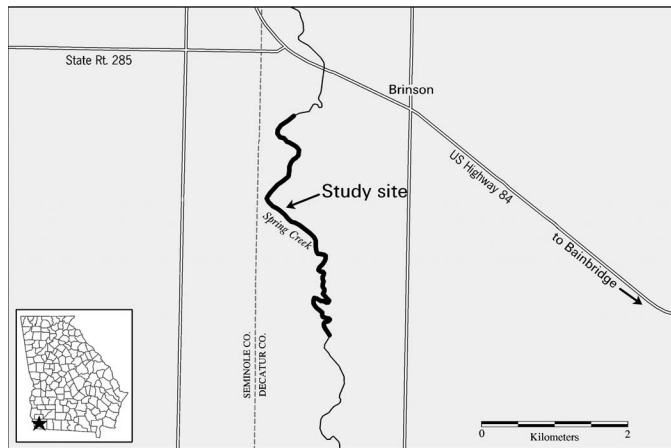


FIG. 1.—Map of the study area, a 4.5 stream-kilometer distance of Spring Creek, Decatur County, Georgia. The bold line indicates the contour of the creek where sampling efforts occurred. Inset bottom left: a county-level map of Georgia with the study area labeled with a star.

they occur (Boundy and Kennedy 2006; Adkins Giese et al. 2012).

To better understand the current distribution, abundance, and conservation status of *Macrochelys*, a number of recent studies have sampled representative populations throughout the genus range. Unfortunately, a general issue with understanding the current ecology and conservation status of *Macrochelys* is that we lack historical data characterizing reference population conditions prior to apparent population declines (Boundy and Kennedy 2006). Studies to date, however, have revealed a number of worrisome patterns. In Missouri, USA, *M. temminckii* were significantly smaller from areas with historical take than were individuals from less-impacted areas (Shipman and Riedle 2008). Further, a historically harvested population in Arkansas supported a highly female-biased sex ratio (6:1; Howey and Dinkelacker 2013); although sex ratios can be driven by uneven hatchling sex ratios and intersexual differences in migration, age at sexual maturity, adult mortality, and trap biases (Gibbons 1990), the female-biased Arkansas population was suspected to have been caused by selective collection of the larger males (Howey and Dinkelacker 2013). Together, these studies suggest that harvest pressure can cause dramatic shifts in population structure, similar to other studies of emydid turtles (Close and Seigel 1997; Gamble and Simons 2004). In the Flint River, Georgia, a river exploited by commercial collectors at an estimated rate of 3–4 tons of live turtles per day in the early 1970s (Pritchard 1989), capture rates of *M. temminckii* were among the lowest anywhere in the state, suggesting that historic commercial collection heavily depleted the population (Jensen and Birkhead 2003). In general, populations appear to be declining in many areas, and the distribution of *M. temminckii* appears to be shrinking in the northern and western extent of its range, such as in Missouri (Lescher et al. 2013), Oklahoma (Riedle et al. 2005; East et al. 2013), Kentucky (Baxley et al. 2014), and Illinois (Bluett et al. 2011). Consequently, this pattern of decline provided the major impetus for a recent petition by the Center for Biological Diversity to the US Fish and Wildlife Service for the listing of *Macrochelys* populations

under the Endangered Species Act (Adkins Giese et al. 2012).

A challenge with previous studies is that marked *Macrochelys* are rarely recaptured during subsequent sampling efforts. Mark-recapture data from repeated observations of individuals through time can inform models that account for imperfect detection (Lebreton et al. 1992; Mazerolle et al. 2007) and estimate vital rates of populations (e.g., survival, abundance, population structure) and individuals (e.g., growth). However, with low return rates of marked individuals in studies of *Macrochelys*, researchers have struggled to apply mark-recapture analyses to model population parameters, and thus our understanding of population biology for *Macrochelys* is severely lacking. This knowledge gap is particularly troubling because it inhibits our ability to build accurate population models to describe population dynamics, forecast population viability, and inform potential management actions.

Given deficits in demographic knowledge and population declines of *M. temminckii* and other large freshwater turtles worldwide, we undertook a long-term mark-recapture study of *M. temminckii* in Spring Creek, Georgia. We sampled the population over a 16-yr period to maximize the proportion of recaptured individuals relative to other studies conducted over shorter periods. Because the Spring Creek population was previously reported as the most abundant of postharvest populations in Georgia (Pritchard 1989), and because recent survey efforts were consistent with this pattern (Jensen and Birkhead 2003), we sought to characterize demography at Spring Creek to potentially serve as a comparative reference for other populations which may have experienced historical harvest both in Georgia and throughout the species range. Herein we used our mark-recapture data to describe important deficits in our knowledge of the population demography of *Macrochelys*. We then combined the empirical survival estimates described here with other demographic parameters from the literature to build an updated population transition matrix, and we applied this model in a population-viability framework to project population growth and forecast viability at Spring Creek and two western populations of *M. temminckii* in Arkansas and Oklahoma.

## MATERIALS AND METHODS

### Study Area

Our study site was Spring Creek, Decatur County, Georgia, USA (Fig. 1). The Spring Creek drainage basin occurs within the karst topography of the Dougherty Plain ecological region of southwestern Georgia (Ward et al. 2005) and is a component of the Apalachicola River drainage. The creek is considered a “nonalluvial clear water river” (Wharton 1978) and is in part spring fed, receiving input from artesian ground waters of the Upper Floridian Aquifer via blue spring “boils” emerging at various sites along the creek bottom and other adjacent short, clear-water runs. Although the creek receives significant clear water input, Spring Creek drains a highly erodible agricultural landscape, with minimally forested buffers (Sterrett et al. 2010), which can contribute heavy sediment loads downstream following heavy or persistent rainfall. Thus, depending on the amount and timing of rainfall in the basin, visibility conditions of

Spring Creek can range from extremely clear to highly turbid with little to no visibility.

While historic commercial harvest of *M. temminckii* severely depleted the population in the nearby Flint River, it is unclear whether or to what extent trapping efforts occurred in Spring Creek. However, the population had previously been reported to be the most abundant among postharvest populations in the state (Pritchard 1989), and recent survey efforts were consistent with this pattern (Jensen and Birkhead 2003); thus, we selected Spring Creek as our study site because we hoped the demographics here would be the closest representation of reference population conditions available. We focused our sampling efforts on a stretch beginning ca. 0.8 km downstream from the US Highway 84 bridge (30.96994°N, 84.74922°W; datum NAD83) and extending 4.5 stream-km south (30.94304°N, 84.74520°W; Fig. 1). The study area extended downstream to the creek's confluence with Lake Seminole, a large impoundment that captures Spring Creek and both the Flint and Chattahoochee rivers. Flow throughout the study area was unaltered by damming activities in Lake Seminole and was above the point where most recreational boaters travel up the creek from the lake.

Within the study area, the width of Spring Creek ranges from ca. 6–12 m during typical flow conditions and is bordered by fairly abrupt banks in most places. The dominant overstory vegetation along the banks consists of Baldcypress (*Taxodium distichum*), Water Elm (*Planera aquatica*), and oaks (*Quercus* spp.), and the understory is characterized by a dense and diverse shrub layer including Sebastian Bush (*Sebastiania fruticosa*), Possum Haw (*Viburnum nudum*), and Deciduous Holly (*Ilex decidua*). Stream substrate is sand in most places, but limestone is present in scattered areas, especially near spring emergences. Rock shelters among limestone areas, log jams, hollow logs, tree buttresses, and undercut banks provide the microhabitats typically used as refugia by *M. temminckii*.

#### Study Species

All populations of *Macrochelys* had been traditionally regarded as a single, wide-ranging species, *Macrochelys temminckii* (Troost in Harlan 1835), until Thomas et al. (2014) used morphological and mitochondrial genetic variation to describe two new species, *Macrochelys apalachicola* (Choctawhatchee–Ochlockonee drainages) and *Macrochelys suwanniensis* (Suwannee drainage), and restricted *M. temminckii* to western populations (Alabama–San Antonio drainages). The study population in Spring Creek occurs within the Apalachicola River drainage and would be assigned as *M. apalachicola* by the geographic distribution; however, we follow Folt and Guyer (2015), who retained *M. apalachicola* within *M. temminckii* until a proper morphological or molecular diagnosis documents the two as representing separate individuals. Therefore, we refer to our study population as *M. temminckii*.

#### Sampling Methods

During 13 nonconsecutive years from 1997 to 2013, we sampled *M. temminckii* in the study area using two methods: baited hoop-net traps and skin-diving surveys. During trapping efforts, we used single-entrance hoop-net traps (Champlin Net Company, Jonesville, Louisiana) comprising

four, 1.2-m diameter hoops and a 2.5 m net (Vogt 2012). Mesh diameter of the nets was ca. 10 cm. Because *M. temminckii* are known to select microhabitats associated with structure (Sloan and Taylor 1987; Harrel et al. 1996; Riedle et al. 2006; Shipman and Riedle 2008; Howey and Dinkelacker 2009), we baited and deployed traps non-randomly by tying traps 10–20 m upstream from a significant structure, such as log jams and undercut banks, especially those associated with sharp stream bends. In this fashion, downstream scent transmission from bait was intended to lure turtles out of microhabitat refuges, attract them upstream, and cause them to enter traps. Traps were typically tied to tree limbs, trunks, or stumps along the shoreline or in shallow waters; in all cases the interior first or second hoop emerged partially from the surface of the water to allow captured turtles access to air. Trap entrances were weighted down in the water column in slightly deeper areas to facilitate the capture of animals walking along the stream bottom. In 1997, we used cut fish or chicken entrails to bait traps, but chicken entrails were discontinued as bait in all subsequent seasons after fish was determined to be more effective for *M. temminckii* (Jensen 1998). We set traps in late afternoon and checked the following morning; this timeframe was intended to maximize capture success of the nocturnally active focal species (Ewert et al. 2006) while reducing bait-stealing by diurnal turtles (e.g., *Trachemys scripta*). During trapping sessions spanning multiple nights, we replenished bait as necessary. A typical night of trapping had 9–13 traps deployed (mode = 10).

Sampling effort occurred opportunistically from 1997–2013. We sampled most frequently in the warmer spring and summer months; however, in an effort to study the reproductive cycles of the species (Teare 2010), some trapping was performed in cooler months. No sampling took place in the months of January and February or in the years 1999, 2000, 2011, and 2012. Seventy-six percent of the sampling effort was during 2008–2010.

From 2000–2009, we augmented our trapping efforts by performing diurnal visual encounter searches with snorkels or scuba gear through the study site (hereafter referred to as “skin-diving searches”). Nine skin-diving searches were performed: one per year in 2000, 2001, 2004, 2005, 2006, 2008, and 2009 and two in 2007; none was performed in 2002 and 2003. Searches were typically performed (1) during August, although the 2005 search was in October and the first 2007 search was in June, and (2) on days when the visibility of the creek was expected to be high and a large number of volunteers were available to help. During these searches, 5 to 20 participants paddled down the creek searching for microhabitats favored by *M. temminckii*; upon locating apparently suitable microhabitats, participants searched underwater for turtles with the assistance of snorkels or scuba gear.

Individuals were measured for standard (midline) carapace length (CL; cm) with 100-cm Haglof calipers and measured for mass (kg) with a 91-kg Viking scale. We classified individuals as adult males, adult females, or juveniles using the following criteria. We first classified individuals as adult males by assessing the location of the vent relative to the edge of the carapace (Dobie 1971; Teare 2010), by probing the vent for the presence of a penis, or both. For individuals not identifiable as males, we used an



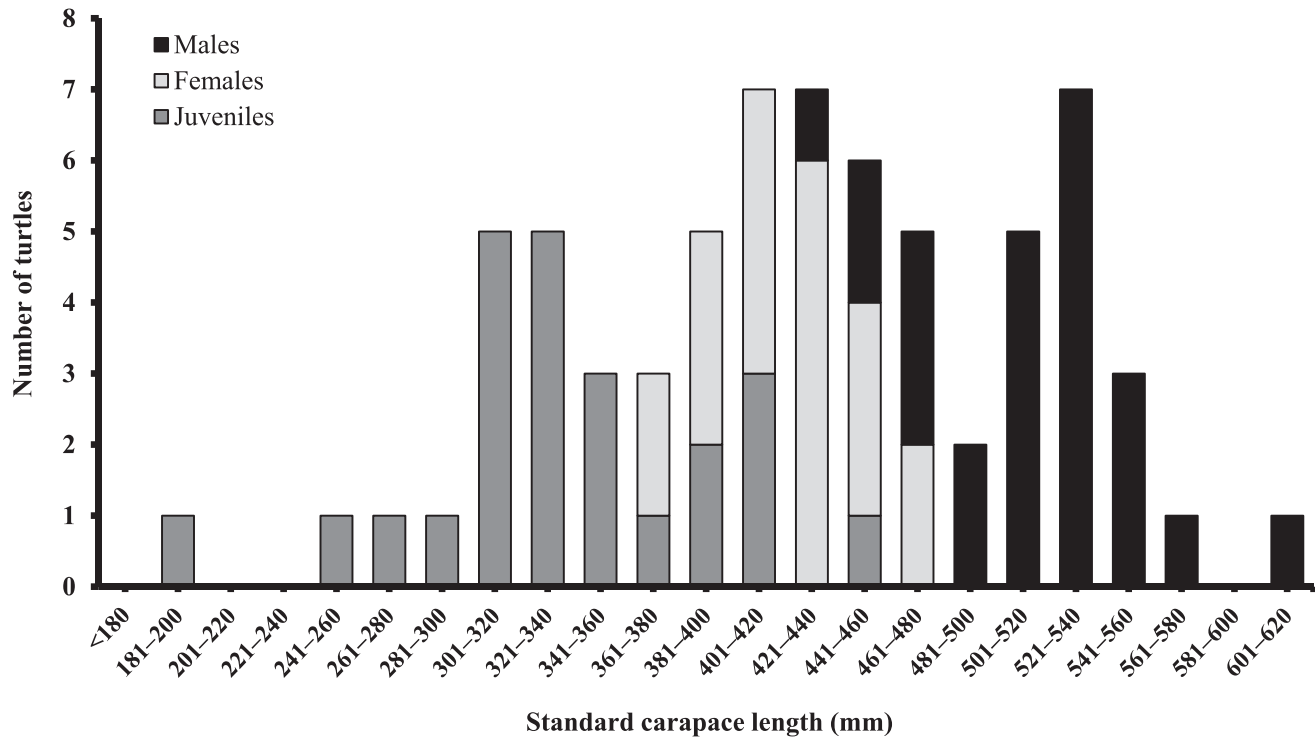


FIG. 2.—Size distribution of juvenile, female, and male *Macrochelys temminckii* collected in Spring Creek, Georgia. For individuals captured multiple times during the study period, carapace length was averaged over all observations. The largest juveniles (361–460 mm) may represent subadult males that we were unable to identify to sex.

arbitrary size threshold to classify adult females ( $\geq 36$  cm CL) and juveniles ( $< 36$  cm CL). We acknowledge that this may have misclassified large juvenile males as adult females. However, during the most intense period of trapping from 2008–2010, we confirmed external identification of sex for 54% of individuals with ultrasound examination using a SonoSite 180 Vet Plus with a variable C11/7–4 MHz transducer (SonoSite Inc.). Turtles were placed in dorsal recumbency during examination, coupling gel was applied to the skin in the inguinal area, and the ultrasound transducer was positioned therein, cranial to the hind-limb, creating an acoustic window that the ultrasound waves could penetrate (Rostal 2005). Both left and right sides were scanned. If ovarian follicles or shelled eggs were present, the individual was classified as female. This method identified sexually mature females ranging from 38.1–46.2 cm CL, which was generally consistent with the CL threshold used to classify juveniles and adult females. Individuals that could not be identified to sex using ultrasound were considered juveniles. This resulted in the classification of seven relatively large individuals as juveniles, which we interpret to likely represent subadult juvenile males. We also acknowledge that, during years with ultrasound, we may have misclassified individuals for whom we could not identify female reproductive structures as subadult juvenile males. However, in general, age–sex classification with and without the use of ultrasound were generally consistent, and we think few, if any, errors of classification occurred.

In general, these criteria resulted in our classification of individuals into four age–sex classes that are delineated by CL: sex-unknown juveniles ( $< 36$  cm), adult females (36–48 cm), subadult juvenile males (36–48 cm), and adult males

( $> 44$  cm; Fig. 2). To facilitate identification upon recapture, individuals were marked with a unique combination of holes through the marginal scutes (Cagle 1939) using an electric drill and by injecting a Passive Integrated Transponder (PIT) tag (Biomark, Boise, Idaho) subdermally and dorsally in the base of the tail. Lastly, all turtles were released at their capture site.

#### Population Model and Statistical Analyses

To understand population demographics of *M. temminckii* at the study site, we first characterized the body-size distribution of juveniles, females, and males. Each individual was placed into a size-class category based on CL; for individuals captured multiple times during the study, we averaged CL across observations to derive a mean body size estimate and then used this estimate to categorize the size class of that individual during the study period (Fig. 2). Because adults typically comprise 70% of freshwater turtle population structure (Bury 1979), and because other studies of *Macrochelys* have found juvenile-dominated structure, biased sex ratios, or both, we tested whether the observed ratios of adults:juveniles and males:females deviated from 1:1 with Pearson's chi-square ( $\chi^2$ ) tests. Because a population of *M. temminckii* experienced a shift in population structure that was consistent with a population decline over a comparable time period as our study (East et al. 2013), we tested for changes in size of adult males and adult females in Spring Creek across the study period using linear regression. For these analyses, we evaluated statistical significance with alpha set at 0.05.

We used the trap data to compile detection histories for each individual marked during the study period; detection

histories were binned by sample year. We then built Cormack-Jolly-Seber open population models (CJS) to estimate apparent annual survival and detection probability of individuals. We first assessed structural goodness-of-fit (GOF) and overdispersion of the general CJS model (time- and group-dependent survival and recapture probability) using a goodness-of-fit procedure in Program RELEASE as run through Program MARK (White and Burnham 1999) implemented by the package RMarked (Laake 2013) in the statistical program R (R Core Team 2015). Because different age and sex groups of *M. temminckii* are thought to differ in life history strategies that may influence survival and detection probability, and our trapping effort varied through the study, we then used a multi-model approach to evaluate whether apparent survival and detection probability varied by all combinations of groups (females, males, juveniles) and by time-varying or constant apparent survival ( $\phi$ ) and recapture probability ( $P$ ). Few of the juveniles in the dataset were recaptured after having transitioned to the adult stage, so individuals were grouped based on the assignment at the first capture; this structure allowed us to evaluate whether juveniles, females, and males differed in apparent survival or recapture probabilities in the population (Tuberville et al. 2014). We ranked and evaluated relative support for each competing model with AIC and  $\Delta$ AIC (Akaike 1974); we were unable to calculate AIC<sub>c</sub> because the number of parameters ( $n = 72$ ) approached the sample size of the dataset ( $n = 73$ ) for some models, which prohibits the calculation of AIC<sub>c</sub>. We considered models with  $\Delta$ AIC < 2.0 to represent good candidates for inference (Burnham and Anderson 2002). The detection histories were organized into yearly intervals and the interval spacing was adjusted between sampling periods to account for 4 yr in which no trapping occurred. We selected the most well-supported models from the CJS analysis (those with  $\Delta$ AIC < 2.0) and then applied those parameters to build Jolly-Seber models with the POPAN extension to estimate abundance and probability of entrance for each group during the study period. We also tested whether the estimated ratios of adults:juveniles and males:females deviated from 1:1 with Pearson's  $\chi^2$  tests. The CJS and POPAN models were performed with maximum likelihood estimation with the function *crm()* from the package RMarked in R (Laake et al. 2013).

To better understand the population status of *M. temminckii* in Spring Creek, we built a stage-class population model for the females and utilized a population projection matrix to project the female population size and structure through time using simulations. Our model divided the life cycle into three discrete stages: (1) eggs/hatchlings, (2) juveniles, and (3) adults. To create the stage-based project matrix, we compiled estimates which describe the reproductive output ( $F_i$ ), the probability of surviving and remaining within a stage ( $P_i$ ), and the probability of surviving and transitioning into the next age class ( $G_i$ ) for each age class; together, these estimates can describe the population dynamics in the form of a matrix:

$$A = \begin{bmatrix} P_1 & F_2 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{bmatrix},$$

where subscripts 1–3 indicate matrix components for eggs/hatchlings, juveniles, and adults, respectively.

To obtain estimates for each of these parameters, we first referenced Reed et al. (2002), who reviewed the literature and built a stable life table for the species. However, at the time of that study, empirical data for many population parameters were unavailable for *Macrochelys*, and the authors relied on estimates from *Chelydra serpentina*. To address this limitation, we reviewed the recent literature for estimates of fecundity and nest success and then incorporated the survival parameters derived from our analysis that were specific to *M. temminckii* and, when possible, our study area in the Apalachicola River drainage.

The egg/hatchlings stage was defined as including eggs laid in nests (age 0) and all individuals that emerged from nests and were ages 0–1 yr. We modeled this stage by compiling estimates of nest survival (the proportion of nests that were not depredated), nest success (the proportion of individuals that hatched and emerged from undepredated nests), sex ratios, and hatchling survival. Nest survival and nest success were reported from a population in the lower Apalachicola drainage (Ewert et al. 2006); we modeled nest survival as the survival of nests from predators (e.g., Raccoons, *Procyon lotor*) with a beta-distributed variable,  $\mu = 0.13$  ( $\sigma^2 = 0.03$ ), and nest success as the proportion of individuals that hatched and emerged from nests with a beta-distributed variable,  $\mu = 0.723$  ( $\sigma^2 = 0.100$ ). Sex determination of *M. temminckii* is dependent on incubation temperatures within nests: males predominantly are produced at incubation temperatures of 24–27°C and females at temperatures above and below the male threshold (Pattern II temperature-dependent sex determination; Ewert et al. 1994). However, in the absence of published data on hatchling sex ratios from natural nests, we accounted for the production of males by assuming a 1:1 sex ratio across nests and modeled the proportion of hatchling females as a beta-distributed variable,  $\mu = 0.50$  ( $\sigma^2 = 0.04$ ). After emerging from nests, annual survival of hatchlings is unknown in nature; therefore, we assessed values reported for *C. serpentina* (0.47; Congdon et al. 1994) and other turtle species (Heppell 1998) and ultimately made a conservative estimate of hatchling survival as 0.15 ( $\sigma^2 = 0.06$ ). We used the four parameters described here (nest survival, nest success, sex ratio, hatchling survival) to generate a single estimate of female egg/hatchling survival and transition to the juvenile stage ( $G_1$ ) in the transition matrix. No individuals were modeled as remaining within the hatchling stage ( $P_1 = 0$ ).

We defined the juvenile life stage as comprising all individuals >1 yr old that had not yet reached sexual maturity. To estimate the proportion of individuals that survived and remained within the juvenile age class annually ( $P_2$ ), we used the estimates of juvenile survival from our mark-recapture analysis (see Results) and modeled juvenile survival with a beta distribution ( $\mu = 0.86$ ,  $\sigma^2 = 0.10$ ). Because juvenile females are thought to reach sexual maturity at 13–21 yr (Tucker and Sloan 1997), we modeled the proportion of females that survived and transitioned from the juvenile to adult stages annually ( $G_2$ ) as the inverse of the mean age of maturity, as estimated with a log-normal distribution ( $\mu = 17$  yr, SD = 4.5; e.g.,  $G_2 = 0.059$ ). Other population models of long-lived turtle species have divided

the juvenile stage into two or more discrete stages (e.g., *Caretta caretta*; Crouse et al. 1987). However, no study to date has demonstrated differential survival and growth within juvenile *M. temminckii*, and a study of *C. serpentina* found juveniles from ages 1–11 yr to have fairly constant survival (Congdon et al. 1994). Therefore, we modeled juveniles as a single stage with relatively constant survival but with a transition probability that may vary in ways that reflect variance in age of maturity; we believe this is a reasonable approach until more data are available. Because juvenile females do not reproduce, the  $F_2$  parameter was set to zero.

Apparent survival of adult females ( $P_3$ ) was estimated by the parameters derived by our mark–recapture analysis and modeled with a beta distribution ( $\mu = 0.95$ ,  $\sigma^2 = 0.035$ ; see Results). We used two variables to parameterize fecundity ( $F_3$ )—reproductive rate of females and clutch size. Females are generally thought to reproduce one clutch of eggs annually, but Dobie (1971) suggested that not all females may reproduce in a given year. Therefore, we estimated the proportion of nesting females per year with a beta distribution as  $\mu = 0.98$  ( $\sigma^2 = 0.01$ ). Fecundity (clutch size) was reported for a population in the lower Apalachicola drainage (Ewert et al. 2006), and we modeled it as a log-normal distribution with  $\mu = 35$  (SD = 15). The two parameters described were used to generate a single estimate of per capita fecundity in the transition matrix ( $F_3$ ).

We used the above parameter estimates to construct a population transition matrix and replicated simulations ( $n = 100$ ) to calculate the population growth rate ( $\lambda$ ), stable stage distribution, generation time, and age-class reproductive values. Population growth rate ( $\lambda$ ) describes whether the projection matrix will result in an increasing ( $\lambda > 1.00$ ), stable ( $\lambda \sim 1$ ), or decreasing population size ( $\lambda < 1.00$ ). The stable stage distribution described the proportion of hatchlings, juveniles, and adults generated as a result of the population matrix, and we hereafter refer to this metric as stable population structure.

Mark–recapture studies permitting estimation of demographic parameters for *M. temminckii* have been performed at two other sites: a 2-yr study at East Fork Cadron Creek, Arkansas (hereafter, the Arkansas population, Howey et al. 2013) and a 14-yr study at Sequoyah National Wildlife Refuge, Oklahoma (hereafter, the Oklahoma population; East et al. 2013). To understand the comparative viability, population structure, and extinction probability of the population in Spring Creek relative to the two western populations, we input estimates of juvenile and adult female survival ( $\phi$ ) and population structure from the Arkansas and Oklahoma populations into the population transition model from Spring Creek and measured  $\lambda$ , stable population structure, and generation time for the Arkansas and Oklahoma populations. We then applied the population transition matrix to perform replicated population projections ( $n = 100$ ) at each site over a simulated 50-yr interval. We parameterized juvenile and female survival as 0.80 (0.40–0.96 95% confidence interval [CI]) and 0.88 (0.42–0.99), respectively, for the Arkansas population (Howey and Dinkelacker 2013) and as 0.46 (0.11–1.00) and 0.31 (0.05–0.78), respectively, for the Oklahoma population (East et al. 2013). Abundance of juveniles and adult females for each population were input as initial values—for Spring Creek, we input an average of the two population estimates from our

results section, assuming a 1:1 juvenile sex ratio; for Arkansas, we used the total population estimate and observed juvenile:adult and female:male ratios to estimate the starting population size (90 juveniles, 90 females; Howey and Dinkelacker 2013); and for the Oklahoma population, we used the population estimates for 1997–2001 by East et al. (2013; 31 juveniles, 31 females), assuming a 1:1 sex ratio of juveniles and adults. In the absence of data for the hatchling stages, abundance of the hatchling age class was set at zero for the initial population size of each matrix. We assessed extinction risk of each population by calculating the proportion of replicates in which adult female abundance declined by >50%, declined by 0–50%, increased by 0–50%, or increased by >50% by year 100 of the simulations.

To assess how  $\lambda$  is influenced by variation in the transition matrix, we simulated changes to components in the transition matrix using elasticity analysis (e.g., Crouse et al. 1987; Caswell 2001). Elasticity analysis assesses the sensitivity of matrix components in a relative fashion, such that elasticity estimates sum to 1.00. Each metric was estimated 100 times by simulation, and the mean and 95% CI were recorded. To explicitly understand what thresholds of juvenile and adult survival are generated by matrices of stable or growing populations ( $\lambda \geq 1.00$ ), we estimated  $\lambda$  and the stable population structure under different combinations of juvenile and adult survival using simulations. Juvenile and adult survival were manipulated from 0.30–0.975 ( $\sigma^2 = 0.10$ ) and 0.50–0.975 ( $\sigma^2 = 0.05$ ) with increments of 0.025, and simulations ( $n = 100$ ) were used to estimate mean values of  $\lambda$  and stable population structure at each combination of adult and juvenile survival values. We used R (v3.2.2, 2015, R Development Core Team, Vienna, Austria) to perform all population simulations, and the package popbio (Stubben and Milligan 2007) was used to calculate  $\lambda$ , stable-stage distributions, generation times, reproductive values, and elasticities.

## RESULTS

From 1997–2013, we made 152 captures of 72 individual *M. temminckii* during 715 trap nights. During skin-diving searches we made 14 additional captures, 12 of which were also collected during trapping and 2 of which were only collected during skin-diving efforts. In total, our sampling efforts resulted in 166 captures of 74 individuals. Of the turtles collected during trapping efforts, we recaptured 55.5% during at least one subsequent sampling event of either trapping or skin-diving, and recaptured individuals were collected an average of 3.2 times (range = 2–10). The majority of individuals collected during skin-diving occupied rock crevices/ledges, logs, or log jams, but some individuals were found within cypress buttresses, undercut banks, or on the creek bottom.

The majority of individuals captured ranged from 30–56 cm in CL (Fig. 2). Juveniles typically ranged from 18–38 cm in CL, but some individuals from 38–46 cm likely were subadult males. We collected no individuals smaller than 19.7 cm SCL. Average female and male CL was 42.1 cm ( $\pm 2.8$  SD) and 51.3 cm ( $\pm 4.1$  SD), respectively (Fig. 2). We collected a greater number of adult males ( $n = 25$ ) than females ( $n = 20$ ), an observed adult sex ratio (1.25:1.00 male:female) that did not deviate from 1:1 ( $\chi^2 = 0.56$ ,  $df = 1$ ,



TABLE 1.—Model selection table identifying the most parsimonious Cormack-Jolly-Seber mark-recapture models for survival of Alligator Snapping Turtles (*Macrochelys temminckii*) at Spring Creek, Georgia, from 1997–2013. Apparent survival ( $\Phi$ ) and recapture probability ( $p$ ) were modeled as a result of group (juvenile, female, male), as constant probabilities ( $\cdot$ ), and as functions of time ( $t$ ), or as interactions of these covariates.

Model	No. of parameters	AIC	$\Delta$ AIC	Model weight
$\Phi(\cdot) p(t)$	13	362.10	0.00	0.54
$\Phi(g) p(t)$	15	362.51	0.41	0.44
$\Phi(t) p(t)$	24	370.41	8.32	0.01
$\Phi(\cdot) p(g)$	4	372.78	10.68	0.00
$\Phi(g) p(g)$	6	376.67	14.57	0.00
$\Phi(\cdot) p(\cdot)$	2	377.86	15.77	0.00
$\Phi(g) p(\cdot)$	4	378.32	16.23	0.00
$\Phi(\cdot) p(g^{*t})$	37	378.67	16.57	0.00
$\Phi(t) p(g^{*t})$	48	381.78	19.68	0.00
$\Phi(t) p(g)$	15	386.61	24.51	0.00
$\Phi(t) p(\cdot)$	13	390.55	28.45	0.00
$\Phi(g^{*t}) p(t)$	48	411.55	49.45	0.00
$\Phi(g^{*t}) p(g^{*t})$	72	425.38	63.28	0.00
$\Phi(g^{*t}) p(g)$	39	429.20	67.10	0.00
$\Phi(g^{*t}) p(\cdot)$	37	431.63	69.53	0.00

$P = 0.46$ ). We observed a greater number of adults ( $n = 45$ ) than juveniles ( $n = 24$ ) in our sample, a ratio (1.9:1.0) that differed significantly from 1:1 ( $\chi^2 = 6.39$ ,  $df = 1$ ,  $P = 0.01$ ). We observed a 0.28 cm ( $\pm 0.32$  95% CI) decrease in female standard CL per year and a 0.30 cm ( $\pm 0.31$  95% CI) increase in male standard carapace length, but these changes were not significant ( $P = 0.09$ ,  $P = 0.06$ , respectively).

The CJS model-selection process (Table 1) identified two models with strong support. The top model described apparent survival as constant among groups (0.96, 0.87–0.99 95% CI) and recapture probability varying among years (model weight = 0.54). The second-best model (model weight = 0.44) described survival as varying among groups and recapture varying through time. Parameter estimates for the second-best model estimated apparent survival as higher for males (0.98, 0.84–1.00 95% CI) and females (0.95, 0.79–0.99) than for juveniles (0.86, 0.66–0.95). No models in the top model set described survival as varying through time. Because the second model generated biologically meaningful results with juvenile survival as lower than that of adults (e.g., a pattern for most turtles, including chelydrids; Heppell 1998), and the model was strongly supported, we interpret those survival parameters as the best approximation of juvenile, female, and male apparent survival in the study population and used those parameter estimates for the population model.

Both models in the CJS top-model set identified support for time-varying recapture probability. Estimates were

TABLE 2.—Stage-class population model for female Alligator Snapping Turtles (*Macrochelys temminckii*) based on a literature review for the species and empirical demographic data from the population in Spring Creek, Georgia. Stage classes are (1) = eggs/hatchlings, (2) = juveniles, (3) = adults. See Methods section for explanations for the construction of variables. Values shown here are means from 1000 simulations.

Stage class	1	2	3
1	0	0	31.8
2	0.007	0.863	0
3	0	0.061	0.950

TABLE 3.—Survival parameters and the resulting stable stage distribution and reproductive values for population models of Alligator Snapping Turtles (*Macrochelys temminckii*) at Spring Creek, Georgia, East Fork Cadron Creek, Arkansas, and Big Vian Creek, Oklahoma. Stage numbers (1) = eggs/hatchlings; (2) = juveniles; (3) = adult females. Aside from varying apparent survival, all other parameters were modeled the same for each population.

Population	Stage number	Survival* (95% CI)	Stable stage distribution	Reproductive values
Spring Creek, Georgia	1	—	0.927	1.00
	2	0.86 (0.66–0.95)	0.042	196.54
	3	0.95 (0.79–0.99)	0.030	516.95
East Fork Cadron Creek, Arkansas	1	—	0.926	1.00
	2	0.80 (0.40–0.96)	0.045	178.23
Big Vian Creek, Oklahoma	3	0.88 (0.42–0.99)	0.029	466.65
	1	—	0.913	1.00
	2	0.46 (0.11–1.00)	0.071	102.45
	3	0.31 (0.05–0.78)	0.017	165.95

\* Little is known about nest survival, nest success, and hatchling survival. We modeled these components the same for each population based on estimates of nest survival and success by Evert et al. (2006) and hatchling survival of *C. serpentina* and other turtle species (Congdon et al. 1994; Heppell 1998; see Methods).

generally similar for both models, varying from 0 (1998, 2007) to 0.445 (2008), and the average was 0.165 among years. While the likelihood of recapturing turtles may vary among years, this result may be due to differences in the amount of trapping effort among years. Linear regression of recapture probability by the number of trap nights per year suggested that for each 100 traps increase in trapping effort, we observed a 0.085 increase ( $-0.01$  to  $0.18$  95% CI) in recapture probability, although this relationship did not exceed our threshold for statistical significance ( $P = 0.07$ ). No models in the top model set described recapture probability as varying by group.

The first Jolly-Seber model with the POPAN extension ( $\Phi[\cdot] p[t] N[g] pent[g]$ ) estimated the population to contain 22.0 juveniles, 18.4 females, and 22.9 males. The estimated adult sex ratio (1.24:1.0 male:female) did not deviate from 1:1 ( $\chi^2 = 0.49$ ,  $df = 1$ ,  $P = 0.48$ ), but the ratio of adults to juveniles (1.9:1.0) did ( $\chi^2 = 5.88$ ,  $df = 1$ ,  $P = 0.02$ ). When averaged across the 4.5-km length of the study area, the model estimated a population density of ca. 14 individuals per river kilometer. Probability of entry into the population was estimated to be highest for juveniles (0.072), intermediate for females (0.023), and lowest for males (0.009). The second POPAN model ( $\Phi[g] p[t] N[g] pent[g]$ ) estimated 26.6 juveniles, 16.4 females, and 14.9 males (12.9 individuals/river km) and probability of entry as 0.072 for juveniles, 0.021 for females, and 0.005 for males.

The population transition matrix (Table 2) for Spring Creek described a growing female population with  $\lambda = 1.036$  (1.028–1.044 95% CI). The stable stage population structure was characterized by a greater proportion of juveniles (0.042) than adults (0.030; Table 3). The generation time of the population was 31.2 yr (28.6–34.0 95% CI). Reproductive value was lowest for hatchlings (1.00), intermediate for juveniles (183, 163–204 95% CI), and highest for adults (517, 444–590 95% CI). The population projection described the initial female population size (12 juveniles, 17 adults) to increase to 73 juveniles (67–79 95% CI) and 55 females (52–59 95% CI) over a 50-yr period, and 100% of simulations described increasing abundance of adult females (Table 4).

TABLE 4.—Results of population projection simulations describing changes in abundance of Alligator Snapping Turtles (*Macrochelys temminckii*) at one site each in Spring Creek, Georgia, East Fork Cadron Creek, Arkansas, and Big Vian Creek, Oklahoma. We performed 100 simulated projections; each result was evaluated as declining (>50%; 1–50%) or increasing (1–50%; >50%) in abundance. Simulations suggested an increasing and viable population at Spring Creek, but the Arkansas and Oklahoma populations reported by Howey and Dinkelacker (2013) and East et al. (2013) were projected to decline in all simulations.

Population	Large declines (>50%)	Declines (1–50%)	Increase (1–50%)	Large increase (>50%)
Spring Creek, Georgia	0	0	4	96
East Fork Cadron Creek, Arkansas	100	0	0	0
Big Vian Creek, Oklahoma	100	0	0	0

The model for the Arkansas population described a declining population ( $\lambda = 0.978$ , 0.967–0.989 95% CI) characterized by a stable population structure with a greater proportion of juveniles (0.045) than adults (0.029; Table 3). The generation time was 19.6 yr (18.4–20.8 95% CI). The population projection described the initial female population size (90 juveniles, 90 adults) to decline to 19 juveniles (17–21 95% CI) and 14 females (12–16 95% CI) over a 50-yr period. All simulations predicted a situation of <50% population decline (Table 4). The model for the Oklahoma population described a severely declining population ( $\lambda = 0.563$ , 0.548–0.579 95% CI). The stable-stage distribution for the Oklahoma population was heavily dominated by juveniles (0.071) over adults (0.017; Table 3), and the mean generation time was 6.2 yr (6.0–6.4 95% CI). The 50-yr population projection described the initial female population size (31 juveniles, 31 adults) to decline in 100% of simulations (Table 4).

Elasticity analysis of the Spring Creek population model found  $\lambda$  to be most sensitive to changes in adult survival (Fig. 3); this component of the matrix accounted for 0.587 (0.556–0.617 95% CI) of proportional sensitivity. Juvenile survival also accounted for considerable relative sensitivity (0.283,

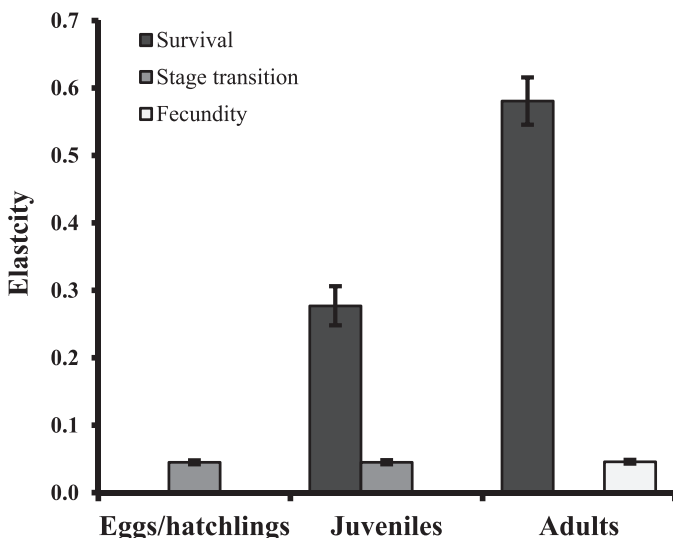


FIG. 3.—The proportional sensitivity (elasticity) of population growth ( $\lambda$ ) to changes in fecundity, survival, and transition states among age classes of Alligator Snapping Turtles (*Macrochelys temminckii*) at Spring Creek, Georgia.

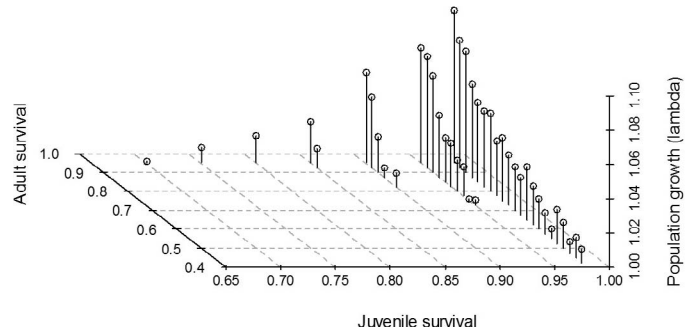


FIG. 4.—Simulated population growth rate ( $\lambda$ ) of female Alligator Snapping Turtles (*Macrochelys temminckii*) under differing degrees of apparent adult and juvenile survival. Only scenarios of viable populations ( $\lambda \geq 1.00$ ) are shown.

0.250–0.315 95% CI), but fecundity and transition components were much lower ( $\sim 0.045$  for each; Fig. 3) and therefore had the proportionally lowest effect on  $\lambda$ . Simulation of  $\lambda$  and stable population structure under different combination of juvenile (0.20–0.975) and adult survival (0.50–0.975) identified combinations of survival values that generate stable or growing populations ( $\lambda \geq 1.00$ ; Fig. 4). Because survival is greater in adults than in juveniles for most turtle species for which demographic data exist (Heppell 1998), and because we interpreted our data from Spring Creek to be consistent with this pattern, we plotted an ellipse in Fig. 5 around simulated values of  $\lambda$  for which adult survival was  $>0.92$  and juvenile survival was  $<0.90$ ; this was meant to represent lambda values produced from population models with realistic survival values. The values within the ellipse and at or above the threshold of  $\lambda \geq 1.00$  represent the range of population structure that could be generated by stable or growing populations of *M. temminckii*.

DISCUSSION

Our study is the first to provide long-term survival estimates from a nondeclining population of *Macrochelys*. Estimates of apparent survival of adult males and females (0.98 and 0.95, respectively) were higher than those at the

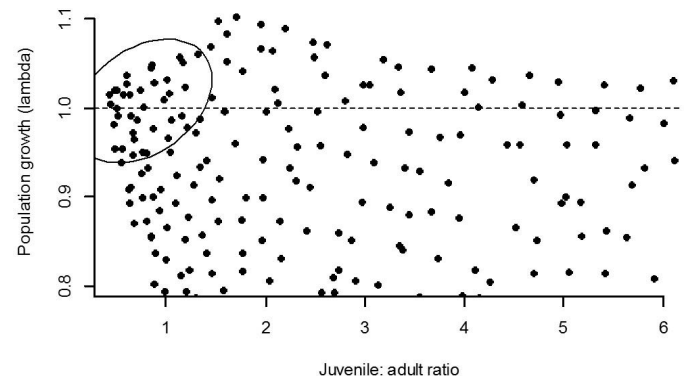


FIG. 5.—Population growth rate ( $\lambda$ ) and juvenile:adult ratios produced by simulated demography with different combinations of apparent adult and juvenile survival. The horizontal dotted line indicates the threshold for population viability ( $\lambda = 1.00$ ). Because survival is generally greater for adults than for juveniles in turtles (Heppell 1998), we emphasized with an ellipse the range of population structure values produced when adult survival  $>0.92$  and juvenile survival  $<0.90$ .



Arkansas (0.96 and 0.88, respectively; Howey and Dinkelacker 2013) and the Oklahoma (0.59 and 0.31, respectively; East et al. 2013) populations. The extremely low Oklahoma estimates resulted from a study period comparable to ours, but were produced from an impacted and declining population (East et al. 2013). In the absence of detailed demographic data for the species, other studies have relied on estimates from the closely related *C. serpentina* to make inferences about observed population parameters of *M. temminckii*. Survival estimates at Spring Creek were comparable to those of adults and juveniles of the closely related *C. serpentina* in unharvested populations (0.97 and 0.77; Galbraith and Brooks 1987; Brooks et al. 1991; 0.93 and 0.77; Congdon et al. 1994). However, our results improve upon this practice by providing fairly robust estimates of adult survival from a nondeclining population, which enabled the construction of a population model with field-validated survival parameters almost entirely specific to *Macrochelys*. The survival estimates for adult *M. temminckii* in Spring Creek are among the highest estimates for freshwater turtles reported in the literature to date (Iverson 1991; Shine and Iverson 1995; Heppell 1998), particularly that of males (0.98). Body size and longevity are positively correlated across diverse taxa (Speakman 2005), including turtles (Shine and Iverson 1995), and high apparent survival of an unimpacted population of *M. temminckii* is consistent with this pattern.

In the absence of studies on verified unharvested populations, natural demographics and population structure are unknown for *Macrochelys* (Boundy and Kennedy 2006; Folt and Godwin 2013), but we suggest that our results from Spring Creek provide the best representation of reference demography for *Macrochelys* available to date. First, the observed and estimated population structure was characterized by an even sex ratio and a greater proportion of adults than juveniles. This structure is consistent with a general prediction for long-lived turtles, where high survival of adults followed by low postmaturity growth rates results in the accumulation of similar-sized adults from different age cohorts (Alford 1980); thus, greater abundance of adults than juveniles is a hypothesized characteristic of stable populations of long-lived turtles (Tuberville et al. 2014). Second, regression analysis did not detect significant changes in observed adult body size during the course of the study, a result which was documented in the declining Oklahoma population (East et al. 2013). Third, and most importantly, the population transition matrix and population projection analysis described the Spring Creek population as growing ( $\lambda = 1.036$ ) and predicted it to increase in 100% of simulations over the next 50 yr, a result which suggests extremely low extinction probability. Together, these analyses all point toward a stable population of *M. temminckii* at Spring Creek, which appears to be at relatively low risk of extinction. This is the first study to suggest population stability and viability for *Macrochelys* to date, an encouraging result for the species from a conservation perspective.

Observed and estimated population structure described more adults than juveniles in Spring Creek, but the population matrix produced a stable population structure that was dominated by juveniles. This discrepancy may have occurred because we were unable to collect any individuals <19 cm CL; the absence of data for this size class prohibited

us from modeling the abundance of these individuals, which likely account for the surplus of juveniles described by the model's stable population structure. Small juvenile age classes are frequently underrepresented in population studies of *Macrochelys* for a few reasons. Trap bias probably exists, where small individuals are more likely to escape from baited hoop-net traps (Pritchard 1989) or smaller individuals may be less likely to enter traps after larger individuals have already entered them, or both. Further, *Macrochelys* have previously been described as occupying both predatory and scavenging trophic roles in the ecosystem (Moll and Moll 2004); we suspect that large juveniles and adults, who have few natural predators, may actively forage for food while juveniles may rely on ambush feeding strategies to decrease risk of predation. If true, then ontogenetic differences in body size and foraging strategies may influence relative capture frequencies and observed size of age classes of *Macrochelys*. Our results did not support trap-bias of juveniles from 20–38 cm CL because the CJS model-selection process did not identify support for recapture probability varying between the age-sex groups; however, this size class may exhibit similar foraging strategies as adults and may be too large to escape traps. Observations of nests and track sign in suspected nesting areas of the population suggest that recruitment is occurring at Spring Creek (JBJ, personal observation), and we observed recruitment into the larger juvenile age class. However, neither of our sampling methods was able to capture the young juvenile age class, and this unsampled age class may account for the abundance of juveniles produced by the model's stable population structure.

Extension of the population transition matrix to two western populations revealed new insights about population viability of western populations. Specifically, Howey and Dinkelacker (2013) inferred the female-biased sex ratio and a high juvenile:adult ratio of the Arkansas population to be a result of historical harvest at the site but suggested that the population may be viable because of high observed estimates of adult survival. Application of the survival estimates from that population to our population transition matrix found that the Arkansas population is likely in decline ( $\lambda = 0.978$ ), and the population projection analysis predicted significant declines in all simulations. However, survival is a dynamic variable and is subject to stochastic variation, and the Arkansas study occurred over a relatively short time period ( $\sim 2$  yr). While the available data predict the population to be in decline, random variation in survival during the study (Howey and Dinkelacker 2013) could have caused the survival values to be lower than true means, and the population may be viable. Regardless, we note that the estimated population growth approached that of viability, and the Arkansas population could be a prime candidate for management practices to increase survival in an attempt to achieve viability.

Similar to East et al. (2013), viability analysis of the Oklahoma population with the model developed here found the Oklahoma population to be in decline. However, our analysis described a much greater decline rate ( $\lambda = 0.56$ ) than previously reported ( $\lambda = 0.94$ ). We suggest this discrepancy likely resulted from the use of different survival estimates for the egg and hatchling stage. Specifically, East et al. (2013) modeled the survival and transition from this

stage as 0.20, roughly following the per capita nest emergence values from Holcomb and Carr (2011), and it appears that nest depredation and mortality of hatchlings after emerging from the nest (age 0–1 yr) were not included in that model. Those two variables resulted in a cumulative effect of 98% of egg and hatchling mortality in our model. Inclusion of those variables likely accounts for the greater decline rate described here for the Oklahoma population.

Previous studies have used estimates of population structure to suggest whether or not populations of *M. temminckii* are stable or to infer effects of historical harvest (e.g., Howey and Dinkelacker 2013). Similarly, Tuberville et al. (2014) recently suggested that greater abundance of adults than juveniles should be expected in stable populations of another long-lived turtle species, Gopher Tortoises (*Gopherus polyphemus*), but our analyses were somewhat inconsistent with this notion for *M. temminckii*. The stable population structure produced from population projection analysis was dominated by juveniles at Spring Creek and the two declining western populations. Further, our simulation of  $\lambda$  and stable population structure under different combinations of juvenile and adult survival did not recover a relationship between population structure and population growth: healthy, growing, and viable populations of *M. temminckii* (characterized by  $\lambda \geq 1.00$ ) can theoretically have wide ranges of population structure, being dominated by adults or juveniles (Fig. 5). Because survival is greater in adults than in juveniles for most turtle species for which demographic data exist (Heppell 1998), and because we interpreted our data from Spring Creek to follow this pattern, restriction of survival values into more realistic thresholds (i.e., the ellipse in Fig. 5) suggests that theoretical population structure estimates for stable or growing populations should range from being adult dominated (0.5:1 juveniles:adult) to juvenile dominated (1.5:1 juveniles:adult). Within this range of potential viable population structure values, the structure of the Spring Creek population is toward the juvenile-dominated end of potential values, due to the relatively high apparent survival of juveniles in the population. Relative to *G. polyphemus*, demography of *M. temminckii* may be more likely to generate a juvenile-dominated population structure because of greater clutch size and recruitment potential.

Elasticity analysis identified that  $\lambda$  is most sensitive to changes in the survival of reproductive adults. This result is consistent with an analysis by East et al. (2013), which found that increases in adult female survival would have greater ability to increase  $\lambda$  of a declining population than increases to hatchling or subadult survival. Reed et al. (2002) previously evaluated whether harvest of *M. temminckii* could be sustainable by generating a stable life table for the species (with  $\lambda = 1.00$ ) and simulated the effects of harvest by decreasing female survival. They observed long-term population declines to result from small decreases in female survival, and used this as evidence to suggest that harvest cannot be sustainable for the species. In some respects, our results actually disagree with their assessment. Our model at Spring Creek described a growing population ( $\lambda > 1.00$ ), and simulations of our model under scenarios of adult survival lower than that observed in the population also recovered growing or stable populations (Fig. 4). This conceivably allows for situations where female survivorship

could be decreased as a result of harvest while still maintaining stable or growing population dynamics ( $\lambda \geq 1.00$ ). However, our opinion is that a sustainable harvest program should be guided by a structured decision-making assessment, which would require a more detailed model with entirely population-specific parameters as well as an analysis evaluating the degree of take that could be allowed while maintaining low extinction probability. Therefore, while the population at Spring Creek appears to be growing and at low risk of extinction, we suggest our results should not be interpreted as evidence to relax protection or to initiate harvest of *M. temminckii* in Georgia or elsewhere. This is especially important given that high-quality reference populations, such as that in Spring Creek, appear to be extremely uncommon throughout the species range.

Our study underscores recent concern about the conservation status and viability of *M. temminckii* in the western portion of the species range. First, our analyses identified that a historically harvested population in Arkansas may be in decline, and our population projection analysis predicted that the population will experience a >50% decrease in abundance over the next 50 yr. The species is currently afforded protection as a species of Special Concern by the state of Arkansas, and take therein is illegal (Howey and Dinkelacker 2013). If the survival estimates observed by Howey and Dinkelacker (2013) at East Fork Cadron Creek are typical for populations throughout the state, this would equate to population declines statewide. However, because estimated population growth of the Arkansas population approached that of viability, greater conservation protection and management could be used to mitigate declines and aid in population persistence in Arkansas. Further, our analyses and those by East et al. (2013) both indicate that the Oklahoma population is at imminent risk of extinction in the immediate future (<15 yr). A previous study already found many historical populations to have declined or been extirpated throughout Oklahoma (Riedle et al. 2005), but the study population within the Sequoyah National Wildlife Refuge was identified as the most robust population in the state (Riedle et al. 2008). Given the protection afforded by being within a national reserve system, the observation of declines at this population are particularly alarming (East et al. 2013). Our results underscore the previous model, but inclusion of more demographic factors here suggest that the previous study may actually have underestimated the decline rate at the Oklahoma population.

Population models and the population viability analysis framework provide helpful tools for conservation biologists seeking to evaluate the sustainability of wildlife populations. Future researchers seeking to understand viability of *Macrochelys* populations can apply parameters derived from a given study population into such a model and can explicitly test the conservation status of local populations. However, our current model is not without its own limitations (Box 1979), and future studies should seek to improve upon lesser-understood components. A general limitation of our model was that we were not able to measure all demographic parameters for the study population. In some cases, we parameterized variables based on estimates from other populations (e.g., fecundity estimates) or based on other turtle species (e.g., hatchling survival). Revisions of the *Macrochelys* population model can be improved in a few

ways. First, future iterations could provide estimates for life-history stages which currently are poorly described or unknown, such as hatchling sex ratios and survival. Indeed, with more available data, future work may reveal that consideration of a juvenile life stage comprising individuals 1–15 yr with constant survival is an oversimplification, as younger juveniles may have different survival than older ones (e.g., *Caretta caretta*; Crouse et al. 1987). Second, future models should seek to use population-specific parameters when possible. While we did not measure fecundity, nest survival, and nest success at Spring Creek, we did use estimates from a nearby population within the same river drainage (Ewert et al. 2006) and assumed minimal differences between the two populations. However, western or northern populations (or both) of *M. temminckii* may experience considerably different thermal regimes for nests, and recruitment may be different in those populations. Therefore, future iterations of the model should seek to describe and employ population-specific parameters. Lastly, models to date have been restricted to females, and no studies have considered aspects which might influence the demography and abundance of males. However, an emerging body of literature supports the notion that reptiles are highly social organisms (Doody et al. 2013), including turtles (Ferrara et al. 2013; Guyer et al. 2014). Our understanding of the local-scale abundance of *M. temminckii* will be improved by description of intraspecific interactions and the species mating system, which collectively will generate a more holistic model for the species.

#### CONCLUSIONS

*Macrochelys temminckii* experienced significant population declines, at least in part due to historic human take, but conservation and management efforts have been hindered without knowledge of basic population parameters for the species. Our study is the first analysis which estimated apparent survival and population structure of a nondeclining population of *M. temminckii*, and the observed survival estimates for adult *M. temminckii* are among the highest estimates of survival reported among all turtles in the world (Iverson 1991; Heppell 1998). We used the empirical survival parameters to build an improved population model for the species, which described the Spring Creek population as growing and at low probability of extinction. For these reasons, we believe that the demographic parameters described here are the best approximation of reference demographic conditions of *Macrochelys* available to date.

Further extension of our model to two western populations of *M. temminckii* with available survival data was consistent with population declines of a population in Sequoyah National Wildlife Refuge, Oklahoma (East et al. 2013) but revealed that a historically harvested population in Arkansas (Howey and Dinkelacker 2013) may also be in decline. These results are consistent with the general consensus among the literature that western populations of *M. temminckii* continue to decline, despite the regulation of human take. However, our results at Spring Creek provide the first empirical support for a stable population of *Macrochelys*, which indicates that viable populations are possible in areas with human presence. Future studies

seeking to evaluate conservation status of *Macrochelys* populations should use the population model here as a starting template to project population size and evaluate viability.

Many other large freshwater turtles have similarly declined from human harvest or influence in the 20th Century (Klemens and Thorbjarnarson 1995; Thorbjarnarson et al. 2000) and, as a result, demographic data from undisturbed populations are absent for many species. Because body size is correlated with longevity and survival across all organisms (Speakman 2005), our results provide a general framework for the survival of large, long-lived turtle species with similar life-history strategies but for whom demographic data are lacking from reference populations. Therefore, population models and conservation agendas for such species could use the adult survival parameters described here as preliminary parameter estimates until more data are available and therefore help inform conservation theory and practice relating to large but endangered freshwater turtles.

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