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Abstract.—For many turtle species, life history traits such as body size, age at maturity, and somatic growth rate can vary among individuals and habitats and between the sexes. Therefore, it is important to consider factors that may influence growth when modeling (somatic) growth for turtles. Long-term capture–mark–recapture studies lend themselves to studying somatic growth in turtles due to the repeated measurements of individuals over time. We used a long-term dataset to examine growth patterns of philopatric Diamondback Terrapins (*Malaclemys terrapin*) on Kiawah Island, South Carolina, USA. We used a hierarchical three-parameter von Bertalanffy model to estimate individual growth of 44 female and 36 male Diamondback Terrapins that were each captured 3–17 times between 1983 and 2019. Sex and site (i.e., tidal creeks) were included as second-level model effects. Mean maximum asymptotic size (plastron length; $L_\infty = 173.4$ mm for females and $L_\infty = 104.4$ mm for males) and mean growth coefficients ($K = 0.28$ for females and $K = 0.61$ for males) varied between sexes. Growth variability among individuals was high, ranging from 23 to 56% within species for different parameters, suggesting that models not accounting for individual variability would be pooling dissimilar information. Site was a significant covariate for male growth, but not female growth. Understanding how Diamondback Terrapin somatic growth varies within a population may inform habitat quality as well as population health and vulnerability to anthropogenic stressors. Our model can serve as a comparison for other Diamondback Terrapin populations and provide more detailed information for demographic models that can be used in conservation decisions.

Growth patterns and the resulting size of an organism can be influential to a species' life history, so much so that size is often directly used in population demographic models for species management. Somatic growth is influenced by numerous factors, including genetics (Olsson et al., 1996; Webb et al., 2001), sex (Stamps and Krishnan, 1997; Lindeman, 1999), density-independent factors (e.g., temperature [Ashton et al., 2015], water availability [Purcell et al., 2017], salinity [Holliday et al., 2009], stochastic disturbances [Dodd and Dreslik, 2008], and climatic oscillations [Bjorndal et al., 2017]), and density-dependent factors (e.g., habitat availability [Dodd and Dreslik, 2008], nutrient and food availability and quality [Bjorndal et al., 2000], and fishing mortality [Wolak et al., 2010]). Across numerous animal taxa, growth rates are related to life history traits such as adult survival rates, size and age at maturation, and fecundity (Shine and Iverson, 1995; Armstrong et al., 2018; Congdon et al., 2018). Shine and Iverson (1995) found that reptile species with greater adult mortality rates had higher growth constants and earlier sexual maturation. Conversely, populations with higher adult survival rates tended to exhibit delayed sexual maturation, particularly in females. The dynamic interaction between growth rates and other evolved life history characteristics can provide insight into individual- and population-level health as well as habitat quality (e.g., Armstrong and Brooks, 2014; Moldowan et al., 2015).

Turtles represent an interesting taxonomic group in which to study growth not only because of their unique shelled anatomy and ectothermy (i.e., body temperature is dependent on the surrounding environment) but also because of their life history traits of slow growth, delayed age at reproductive maturity, sexual dimorphism, and extreme longevity (e.g., Shine and Iverson, 1995; Snover et al., 2015). Chelonians are also one of the most threatened vertebrate groups worldwide, and their life history characteristics have left them particularly vulnerable to anthropogenic activities such as climate change, habitat loss, road mortality, emergent diseases, pollution, and over-exploitation (Lovich et al., 2018a; Rhodin et al., 2018). Therefore, in addition to the biological and evolutionary implications of slower somatic growth, there are also conservation implications, because proper conservation strategies for imperiled species require demographic knowledge that can be used to model and assess populations trends and inform management decisions (Ramirez et al., 2021).

Numerous studies have applied a wide variety of growth models to various turtle species. On one extreme are studies that investigate and compare size-at-age (*Actinemys marmorata* [Ashton et al., 2015]) and that do not include a traditional growth model (i.e., a model that estimates change in size over age). The Sergeev (1937) method, as was applied to Wood Turtles (*Glyptemys insculpta* [Marchand et al., 2018]), is another simple approach to investigating somatic growth rates. Studies of size-at-age may be informative for comparing large differences across populations or between sexes; however, in most cases, simple studies do not provide as much information as a conventional growth model. Many conventional growth models applied to turtles have been developed for, and applied to, other taxa (e.g., fish). The popular von Bertalanffy growth model (as commonly parameterized by Beverton and Holt, 1957) has been used with *Graptemys* spp. (Lindeman, 1999), *Chrysemys picta* (Dolph, 2017), *Trachemys scripta* (Lewis et al., 2018), and five species of cheloniid Sea Turtles (reviewed in Ramirez et al., 2021), among others. Other growth models, such as the Gompertz, logistic, and Richards, have been applied to somatic growth in turtles (Dodd and Dreslik, 2008; Wolak et al., 2010; Germano, 2016). Bernstein et al. (2018) ultimately evaluated seven different growth models to find the best model for Ornate Box Turtles (*Terrapene ornata ornata*). In addition to quantifying somatic growth, robust long-term capture–mark–recapture studies, such as Richard et al. (2014), Bjorndal et al. (2017), and Keevil et al. (2021), have investigated the relationship of

climatic and ecological drivers to variation in turtle growth rates. The diversity of growth models and their application to turtles, in addition to many studies being published within the last decade, demonstrate that understanding turtle growth is an active area of study.

Diamondback Terrapins (*Malaclemys terrapin*) are a unique estuarine obligate turtle species with a wide geographic distribution in the United States ranging from Cape Cod, Massachusetts, to Corpus Christi, Texas (Ernst and Lovich, 2009). As sexually dimorphic salt marsh specialists, Diamondback Terrapins experience highly variable, tidally driven environmental conditions such as changes in water level, temperature, salinity, and prey availability. Such extreme variability in dynamic estuarine habitats means that Diamondback Terrapins hold potential for somatic growth variability at the individual and population levels; however, few studies have attempted to investigate their somatic growth. Seigel (1984) used Sergeev's method to compare two neighboring Diamondback Terrapin populations in the southeastern United States and found that individuals from Florida have a slightly faster growth rate than those in North Carolina or in Louisiana. More recently, Tokash (2018) compared growth rates of wild and captive-reared Diamondback Terrapins on Poplar Island, Maryland, by using von Bertalanffy, Gompertz, and logistic models, showing that the rearing treatment, sex, and site may have effects on growth. However, due in part to the challenges of initiating and maintaining long-term capture–mark–recapture studies on Diamondback Terrapins (Levasseur et al., 2019), their growth is largely unreported in scientific literature (Hart and McIvor, 2008; Tokash, 2018).

A better understanding of Diamondback Terrapin growth could yield insights into the life history of such a widely distributed estuarine species, and more information about sex-specific size-at-age could help with improved demographic models to evaluate their population status and help inform management decisions, particularly regarding the Blue Crab (*Callinectes sapidus*) fishery. Diamondback Terrapin populations across their range have exhibited declines, in large part because of high bycatch mortality rates in Blue Crab traps (Lovich et al., 2018b). Thus, Diamondback Terrapin has been listed for protection in multiple states (Butler et al., 2006; Hart and Lee, 2006). One Diamondback Terrapin metapopulation in decline is the subject of an on-going, long-term ecological research project in the tidal creek tributaries of the Kiawah River, South Carolina, USA (Gibbons et al., 2001; Dorcas et al., 2007; Witczak et al., 2014). Although narrow in spatial scale, the capture and multiple recapture nature of this long-term study provides an excellent opportunity to study growth variability at the individual level. In fact, some recent studies have investigated individual growth variability (*Chelydra serpentina* [Armstrong and Brooks, 2014]) and built upon that work by applying state–space models to examine relationships between indeterminate growth, reproduction, and survival (Armstrong et al., 2018). We used a hierarchical three-parameter von Bertalanffy growth model to estimate individual somatic growth of 80 Diamondback Terrapins from the Kiawah River over a 36-yr period. Specially, we examined how somatic growth of this species varied by 1) individual, 2) sex, and 3) tidal creek site.

MATERIALS AND METHODS

Study Site and Data Collection.—Kiawah Island Diamondback Terrapin populations have been surveyed regularly since 1983 as part of a long-term, ongoing capture–mark–recapture research program (Gibbons et al., 2001; Dorcas et al., 2007; Witczak et al., 2014). Diamondback Terrapins for our study were collected within five *Spartina alterniflora*–dominated salt marsh tidal creek tributaries of the Kiawah River, Charleston County (80°08′W, 32°36′N), at the southwestern end of Kiawah Island: Terrapin Creek (1983–2019), Oyster Creek (1986–2019), Fiddler Creek (1987–2019), Stingray Slough (1990–2019), and Sandy Creek (1992–2019). No Diamondback Terrapin sampling occurred in 2000, 2001, 2002, and 2018. For a map of the tidal creeks, see Dorcas et al. (2007), and for a more detailed description of the study site, see Gibbons and Harrison (1981), Tucker et al. (1995), and Gibbons et al. (2001).

Diamondback Terrapins were captured primarily at low tide by using seines and trammel nets, yielding more than 1,500 individuals captured from more than 3,000 total captures (including recaptures) since 1983 (Lovich and Gibbons, 1990; Tucker et al., 1995). Although our sampling techniques can be sex biased, Lovich and Gibbons (1990) found that recapture probability was the same for both sexes. For each Diamondback Terrapin captured, plastron length (PL) was measured to the nearest 1 mm and individually marked by notching the marginal scutes (Cagle, 1939). Sex was determined using overall body shape and size, tail length, and the position of the cloaca relative to the carapace margin. Age at initial capture was estimated based on growth rings on the carapace and plastron scutes (Cagle, 1946; Roosenburg et al., 1997), which was typically only performed for turtles ≤10 yr old (Gibbons et al., 2001; Dorcas et al., 2007), when there was greater accuracy for reading growth rings. For consistency, recaptured individuals were always measured by only a few scientists who used the same ruler. PL was used as the most reliable measure of size. Age was not re-estimated upon each recapture, but rather was calculated using the age at initial capture plus known years at-large since initial capture. We are aware of the criticisms regarding the accuracy of using scute annuli to estimate turtle age (e.g., Wilson et al., 2003). However, despite criticisms of aging turtle by scute annuli numbers, counts of scute rings have been shown to be accurate in many cases for aging juvenile turtles that are growing rapidly (Germano and Bury, 1998; Wilson et al., 2003; Germano and Riedel, 2015), and this technique has been shown to be reliable in this population with the use of interannual recapture data (for details, see Gibbons et al., 2001).

Growth Modeling.—Based on the nature of general turtle growth, we first considered different nonlinear growth functions that have been used to model growth in other turtle species: the von Bertalanffy model (Beverton and Holt, 1957; Eguchi et al., 2012; Dolph, 2017), Gompertz model (Gompertz, 1825; Wolak et al., 2010), logistic model (Bernstein et al., 2018), and Richards model (Richards, 1959; Bury et al., 2010; Bernstein et al., 2018). For most of these models, forms exist that include different parameterizations and different numbers of parameters. We selected the three-parameter von Bertalanffy model to use with our Diamondback Terrapin data. We recognize that other models also may perform well; however, other three-parameter models are less common and have less support in the literature, and models that have four parameters tend to be beneficial for datasets where there is particularly good coverage at small sizes and young ages (e.g., Tokash, 2018), which is not the case for our dataset. In addition, the use of the three-parameter von Bertalanffy model permits our model estimates to be the most translatable to other turtle growth studies.

Given the resolution of our data and repeated measurements of known individuals over time, we sought to use a model that would quantify individual variation in growth while also providing population-level growth estimates. In other words, we did not want to run separate growth functions on individuals (nor would nonlinear functions fit to individuals with low numbers of recaptures and/or a lack of contrast in size and age), but we also did not want to run one growth model with all individuals pooled. Our solution to modeling both individuals and the population was to use a hierarchical form of the von Bertalanffy model (Midway et al., 2015), in which varying parameters could be attributed to individuals, while still estimating population-level parameters. Furthermore, we adopted a Bayesian framework in which to fit our models, which provides several benefits including direct comparison of parameter estimates that would allow a probabilistic interpretation of the magnitude of growth differences among individuals. The hierarchical three-parameter von Bertalanffy model took the following form:

$$y_{ij} = L_{\infty j}\left(1 - e\left(-K_j(t_{ij} - t_{0j})\right)\right) + \varepsilon_{ij} \qquad (1)$$

$$\varepsilon_{ij} \sim N(0, \sigma^2) \qquad (2)$$

$$\log\begin{pmatrix} L_{\infty j} \\ K_j \\ t_{0j+10} \end{pmatrix} \sim MVN(\boldsymbol{\mu}, \boldsymbol{\Sigma}) \qquad (3)$$

$$\boldsymbol{\mu} = \log(L_\infty, K, t_0) \qquad (4)$$

In equation 1, y_{ij} is the PL (mm) for measurement i from turtle j, and t_{ij} is the estimated age measurement i from turtle j. $L_{\infty j}$, K_j, and t_{0j} are the three von Bertalanffy model parameters that estimate the asymptotic length, Brody's growth coefficient, and the predicted organism size at time 0, respectively. We assumed that the natural log of the model parameters came from a multivariate normal distribution with a population mean $\boldsymbol{\mu}$ and variance–covariance $\boldsymbol{\Sigma}$. $\boldsymbol{\mu}$ contains the population-average estimates for the three von Bertalanffy parameters, which describe the growth model across all individuals. ε_{ij} is the residual error and is assumed to be independent and identically distributed as $N(0, \sigma^2)$. Model fitting was improved by adopting the Kimura (2008) approach of using the logarithmic scale to estimate parameters. (Note that 10 is added to t_0 because negative t_0 are not possible, even though it may be negative, when estimated on the log scale.) Finally, within species for $L_{\infty j}$ and K_j, as a post hoc test, we ran comparisons of all pairwise 95% credible intervals for overlap. We were not specifically interested in comparisons of individual Diamondback Terrapins; however, the overall percentage of intervals that did not overlap (i.e., that differed) can provide an estimate of the quantity of individual differences in growth.

In addition to evaluating individual Diamondback Terrapin growth, we modeled the estimated K_j and $L_{\infty j}$ parameters based on site of capture (i.e., tidal creek), to quantitatively address the question of whether different creeks are associated with different patterns of growth. The site factor for each individual was determined as the place where the most captures and recaptures took place. Strong site philopatry (Gibbons et al., 2001; Tucker et al., 2001) was observed because the vast majority of Diamondback Terrapins were captured and recaptured exclusively at the same site (89% of females and 86% of males were only ever sampled at one site). Diamondback Terrapins

that were found at more than one site typically showed dominance to one site (and captured only once at a different site), which was assigned as their home site. For Diamondback Terrapins having been caught in different creeks, the creek with the most recaptures became the assigned site. To compare creeks, we added a second level to the model as follows:

$$\log\begin{pmatrix} L_{\infty j} \\ K_j \\ t_{0j+10} \end{pmatrix} = \begin{pmatrix} \gamma_0 \times \text{creek}_j \\ \gamma_1 \times \text{creek}_j \\ t_{0j+10} \end{pmatrix} \qquad (5)$$

where γ_0 and γ_1 are fixed effects represented the estimated parameters (on the log scale) for each of j creeks (where $j = 4$ creeks for males and $j = 5$ creeks for females). The two regressions effectively function like an analysis of variance on the estimated growth parameters, with significance determined by nonoverlapping 95% credible intervals among different creeks.

For all models, prior probability distributions for σ, $\boldsymbol{\mu}$, and $\boldsymbol{\Sigma}$ were diffuse, with a uniform distribution given to σ, a normal distribution given to $\boldsymbol{\mu}$, and a scaled inverse-Wishert distribution given to $\boldsymbol{\Sigma}$ (Gelman and Hill, 2006). However, we made one modification to the t_0 prior probability distribution in one of the model runs (discussed below). We ran three concurrent Markov chains beginning each chain with a different value. From a total of 600,000 iterations, the first 100,000 iterations of each chain were discarded as burn-in. We then thinned the remaining chains by retaining every third value, resulting in a total of 100,000 values for analysis. Posterior distributions were assessed for convergence visually and with the Brooks–Gelman–Rubin statistic, $\hat{R}$, where any values <1.1 indicated convergence. JAGS v4.3.0 (Plummer, 2003) was used to fit the models, all of which we ran within R (R Core Team, 2020).

Data Use.—Once the model form was selected, we made some minor modifications to the data used in the models. First, we modeled males and females separately (i.e., in separate models) due to the strong sexual dimorphism of Diamondback Terrapins. We did not need an overall (pooled sex) growth estimate, nor did we need the possibility of shrinkage estimators for one sex being influenced by another sex. Second, we excluded individual Diamondback Terrapins for which there was only a low-to-moderate confidence score in the number of growth rings counted that would be used to estimate age. Third, if an individual Diamondback Terrapin was caught more than once in a given year, we only included age and size from the first capture of a given year. Fourth, we excluded individual Diamondback Terrapins for which there had been fewer than three total captures. Although the partial pooling feature of Bayesian estimation would permit us to model individuals with fewer captures (even one capture), the uncertainty for a nonlinear growth estimate became very high for many individuals with low captures. As such, it was determined that the additional information provided by these low-capture individuals was not outweighed by the noise and uncertainty that they also added. Fifth, even if an individual Diamondback Terrapin has been captured three or more times with a reliable age estimate, we excluded it from the dataset if the PL did not change due to sequential recaptures being close in time (e.g., a capture late in one year and early in the next) and therefore no variability in the observations.

Finally, because initial model runs showed some uncertainty in the estimate of t_0, we added a randomly drawn hatchling size observation to each individual Diamondback Terrapin instead of putting an informative prior distribution on t_0. Despite t_0
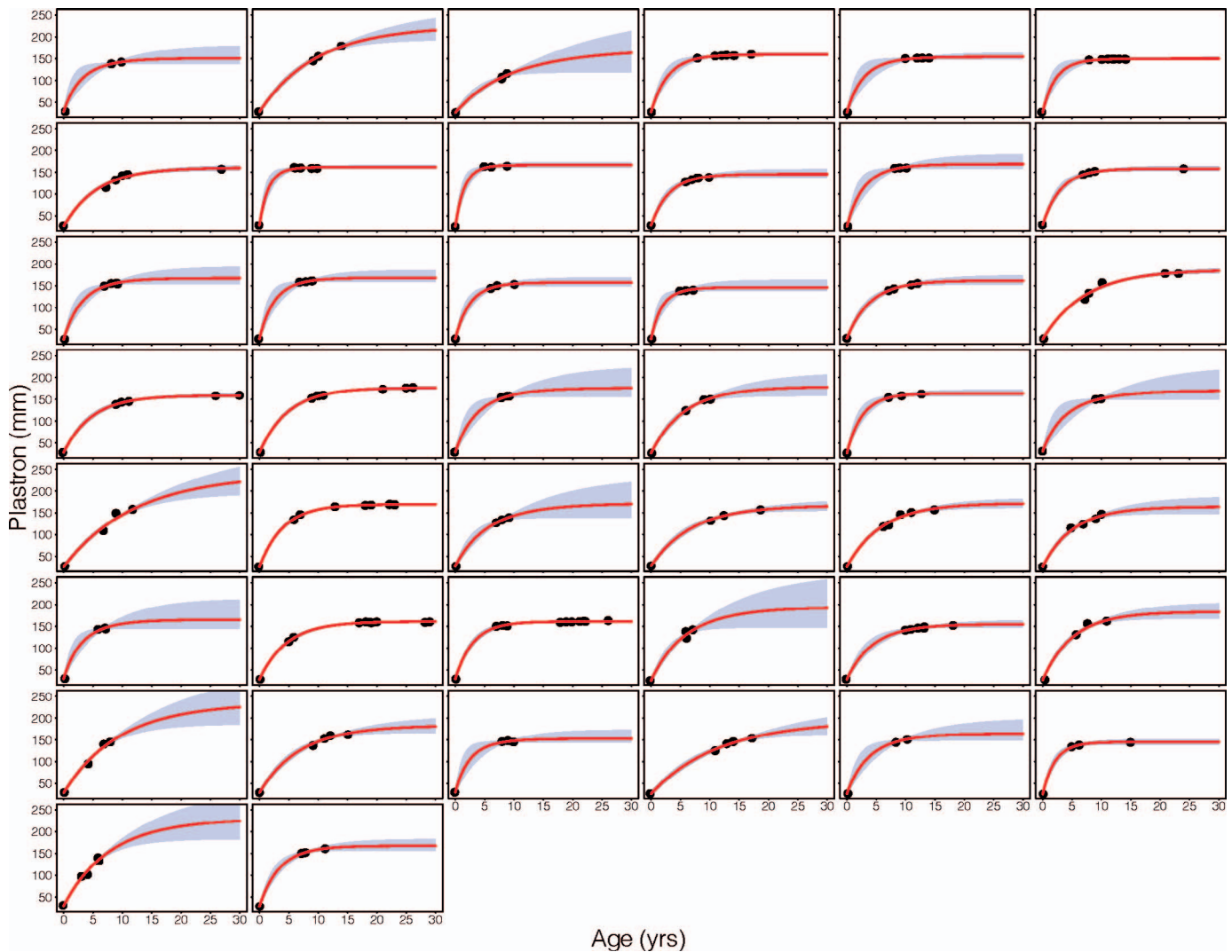
FIG. 1. Individual growth model fits for 44 female Diamondback Terrapins. Red lines represent the individual von Bertalanffy model fits for the corresponding plastron-at-age observations, which are represented with black dots. The 95% credible regions are shown in the blue-shaded region.

being considered an artificial model parameter (i.e., not biologically meaningful), it can be informed by small-sized individuals, such as hatchlings. Although size was not an actual observation in our study, Diamondback Terrapins have a narrow range of hatchling sizes. The model realism that is gained by anchoring the individual growth curves to a realistic hatchling size was considered to vastly outweigh any concerns with adding an unobserved hatchling size. Wild-hatched hatchling sizes were informed by two previous studies that both report mean and uncertainty surrounding hatchling PL: Seigel (1980) reported hatchling PL (from $n = 29$ *Malaclemys terrapin tequesta* in Florida) as 27.9 mm ($s = 1.4$ mm), and Roosenburg et al. (2003) reported hatchling PL (from $n = 565$ *Malaclemys terrapin* in Maryland) as 27.7 mm ($s = 1.57$ mm). Although hatchling size estimates are from different parts of the geographic range, which can affect egg and hatchling size (Siegel, 1980; Allman et al., 2012), they are very similar in value. The mean PLs also represent some of the few morphometric data from wild-hatched hatchlings (vs. captive reared). Thus, we combined the two estimates to create a normal distribution with parameters $\mu = 27.8$ and $\sigma = 1.48$. Using these parameters, we then drew $n = 1,000$ random values to create a hatchling PL distribution. Each individual Diamondback Terrapin in our dataset was then randomly assigned a value from this hatchling PL distribution with the associated age = 0.

RESULTS

Growth of Females.—We modeled a total of $n = 44$ female Diamondback Terrapins that were caught between 1984 and 2019 from five different sites. Of the 44 females, only 2 females were first captured between the ages of 1 and 4 yr. Each Diamondback Terrapin was captured (including recaptures) between 3 and 10 times. The smallest female captured measured 95 mm PL, the largest captured measured 179 mm PL, and the mean female PL was 147.9 mm. All individual growth models converged (Fig. 1). The mean estimate for the K for all female turtles was estimated as 0.28, and the mean estimate for the maximum asymptotic size (L_∞) for all female Diamondback Terrapins was estimated as $L_\infty = 173.4$ mm. Based on all combinations (946) of pairwise 95% credible intervals, 24% of females differed in their estimates of L_∞ and 29% of females differed in their estimates of K (Fig. 2). For female Diamondback Terrapins, tidal creek (site) was not a significant predictor in describing the variability in growth parameters K and L_∞ (Fig. 3).
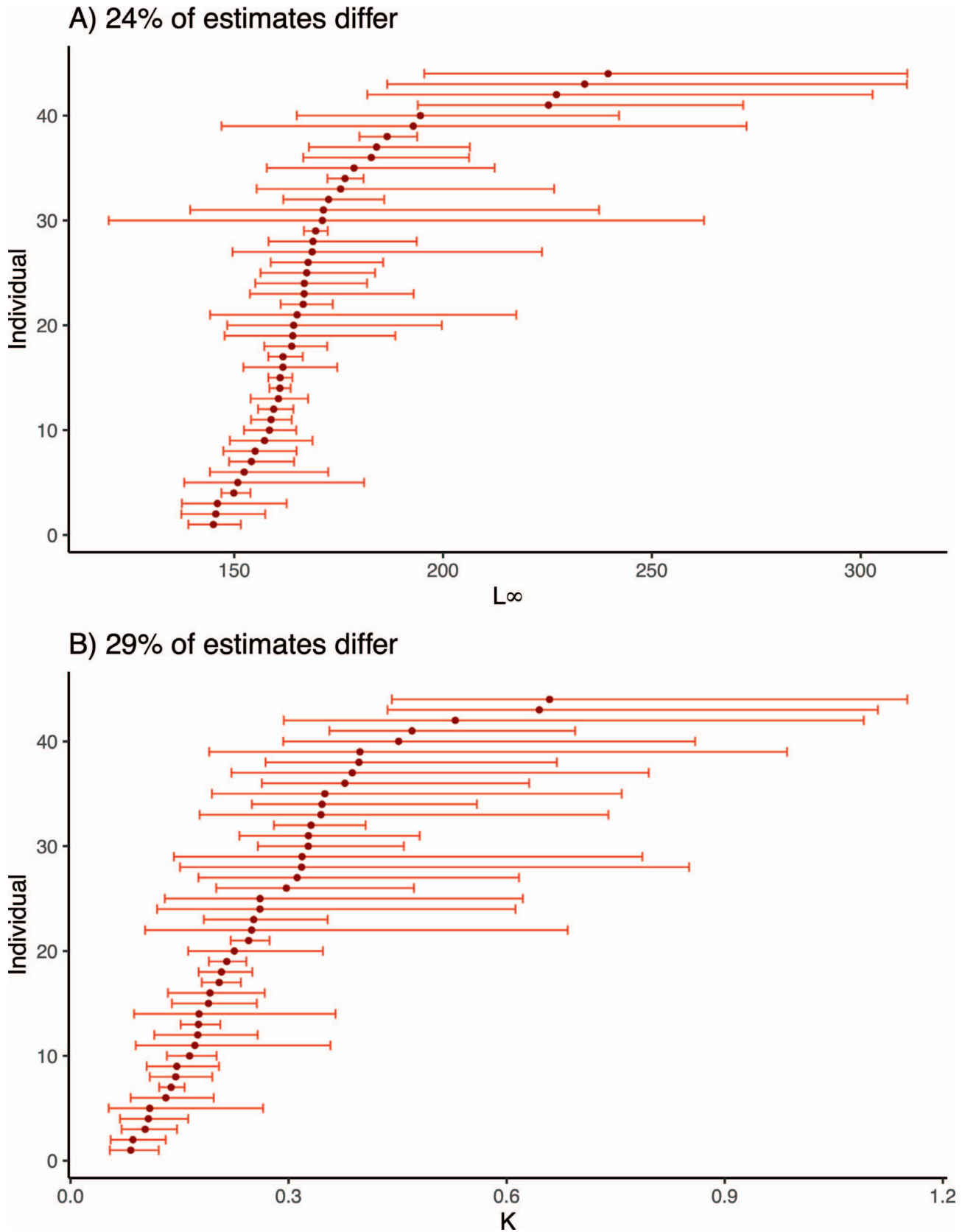
FIG. 2. L_∞ (A) and K (B) parameter estimates (black dots) and 95% credible intervals (red lines) for individual female Diamondback Terrapins. In both panels, individuals are ordered from smallest to largest mean estimates; 24% of L_∞ estimates differ (i.e., 95% credible intervals do not overlap), whereas 29% of K estimates differ.
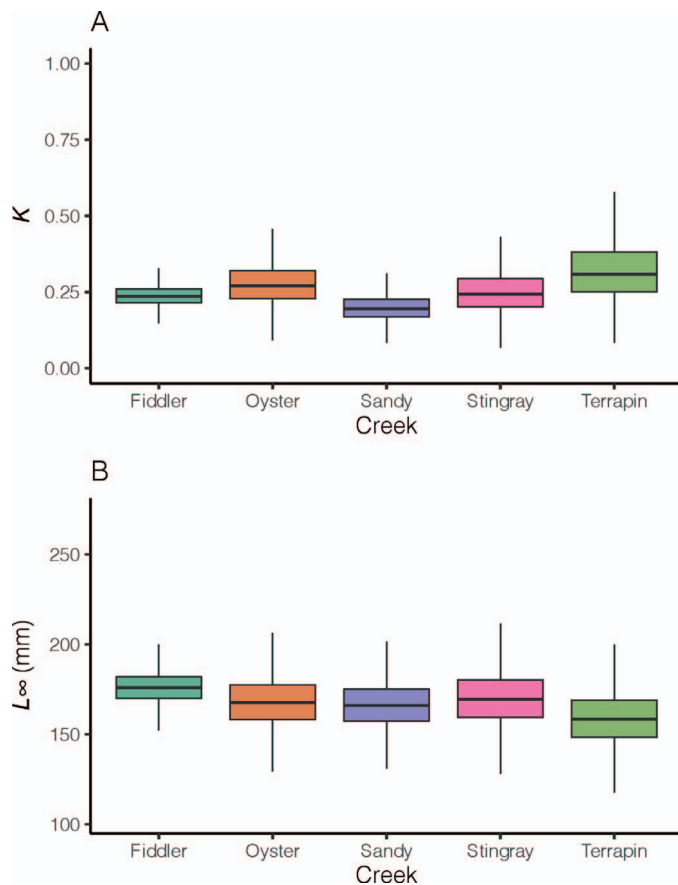
Fig. 3. Boxplots of parameter estimates of K (A) and L_∞ (B) from level 2 of the growth model. For female Diamondback Terrapins, creek was not significantly associated with any of the variability in the growth parameters. Boxes represent the interquartile range (IQR), the horizontal line in the middle of the box represents the mean, and the vertical whiskers extend to $1.5 \times$ IQR.

Growth of Males.—We modeled a total of $n = 36$ male Diamondback Terrapins that were caught between 1983 and 2019 from four different sites. Of 36 males, only 4 males were first captured between the ages of 1 and 4 yr. Each Diamondback Terrapin was captured (including recaptures) between 3 and 17 times. The smallest male captured measured 91 mm PL, the largest captured measured 114 mm PL, and the mean male PL was 102.7 mm. All individual growth models converged (Fig. 4). The mean estimate for the K value for all male Diamondback Terrapins was estimated as 0.61, and the mean estimate for L_∞ for all male Diamondback Terrapins was estimated as 104.4 mm. Based on all combinations (630) of pairwise 95% credible intervals, 56% of males differed in their estimates of L_∞ and 23% of males differed in their estimates of K (Fig. 5). For male Diamondback Terrapins, creek (site) was a significant predictor. Male K values were significantly larger in Terrapin Creek than in Fiddler Creek (Fig. 6). Tidal creek (site) was not a significant predictor in describing the variability in L_∞, indicating that although male Diamondback Terrapins may approach their maximum size at different rates in different creeks, they all achieve a similar L_∞ (Fig. 6).

DISCUSSION

Using a 36-yr capture–recapture dataset on a South Carolina Diamondback Terrapin population, we found that growth varied among individuals, between sexes (females grew larger but slower), and across sites (in males, but not females). Specifically, L_∞ for female Diamondback Terrapins (173.4 mm) was larger than that of males (104.4 mm), but the estimated K for males (0.61) was larger than that for females (0.28), indicating females grow more slowly, but reach a larger body size than males. Although this is the first growth study of Kiawah Island Diamondback Terrapins, the mean asymptotic sizes we estimated do not conflict with previously published estimated sizes at maturity for both sexes (males: 90 mm PL, 3–4 yr old; females: 138 mm PL, 6–7 yr old [Lovich and Gibbons, 1990]). Our study did, however, quantify both individual growth and differences in individual growth. For example, we found that between 23 and 56% of turtles do not share at least one growth model parameter estimate. Our observed differences are strong evidence that pooling individuals (even within sex) for a population growth curve should be done with caution because any pooled growth curve includes individual growth curves that are not the same.

Our findings are congruent with the life history traits of many other long-lived, sexually dimorphic species in which one sex displays faster growth (higher K), earlier maturity, and a smaller asymptotic size (L_∞; i.e., sexual bimaturism [Stamps and Krishnan, 1997]). With emydid turtles specifically, males are smaller and exhibit faster somatic growth, earlier sexual maturity, or both, than larger females (Congdon et al., 1994; Lindeman, 1999; Rowe, 1997; Ernst and Lovich, 2009; Lewis et al., 2018; Marchand et al., 2018). Although there are measurable costs associated with delayed sexual maturity (e.g., increased juvenile mortality risk, longer generation times [Congdon et al., 1994]), there are also clear benefits for females, such as increased quality (e.g., egg size) and/or quantity of offspring (e.g., clutch size), increased energy storage capacity, and decreased adult mortality risk (Brooks et al., 1992; Congdon et al., 1994; Shine and Iverson, 1995).

Across all sites, female Diamondback Terrapins displayed a wide range of estimates for L_∞ and K, a finding that is likely due to sex-specific differences in adult body size that are related to resource acquisition and allocation. More specifically, males primarily allocate their energy toward somatic growth, whereas females allocate their energy to somatic growth and reproductive output that is variable by age. When female turtles allocate resources to egg production, less energy is available for somatic growth, and because larger female turtles are documented to have greater reproductive output (e.g., clutch size), this energy allocation trade-off can affect an individual's fecundity (Edmonds et al., 2020). It is also well documented that differential growth rates in turtles can, in turn, affect adult body size (Shine and Iverson, 1995) and maturation rate of individuals, with higher growth rates resulting in not only earlier maturation age (Lindeman, 1996; Dodd and Dreslik, 2008; Bury et al., 2010; Germano, 2010) but also greater mortality rates (Shine and Iverson, 1995).

Individual differences can have population-level implications for reproductive success and survival (Congdon and van Loben Sels, 1991; Iverson et al., 1997; Rowe, 1997; Congdon et al., 2013; Kern et al., 2016; Armstrong et al., 2018), which can ultimately affect long-term population recovery and viability (Dodd and Dreslik, 2008; Ashton et al., 2015). A possible source of growth variability comes from the fact that younger age classes are largely absent from our 36-yr database. These missing age classes are likely due to aquatic sampling bias against smaller, secretive, and more terrestrial Diamondback Terrapins (Lovich
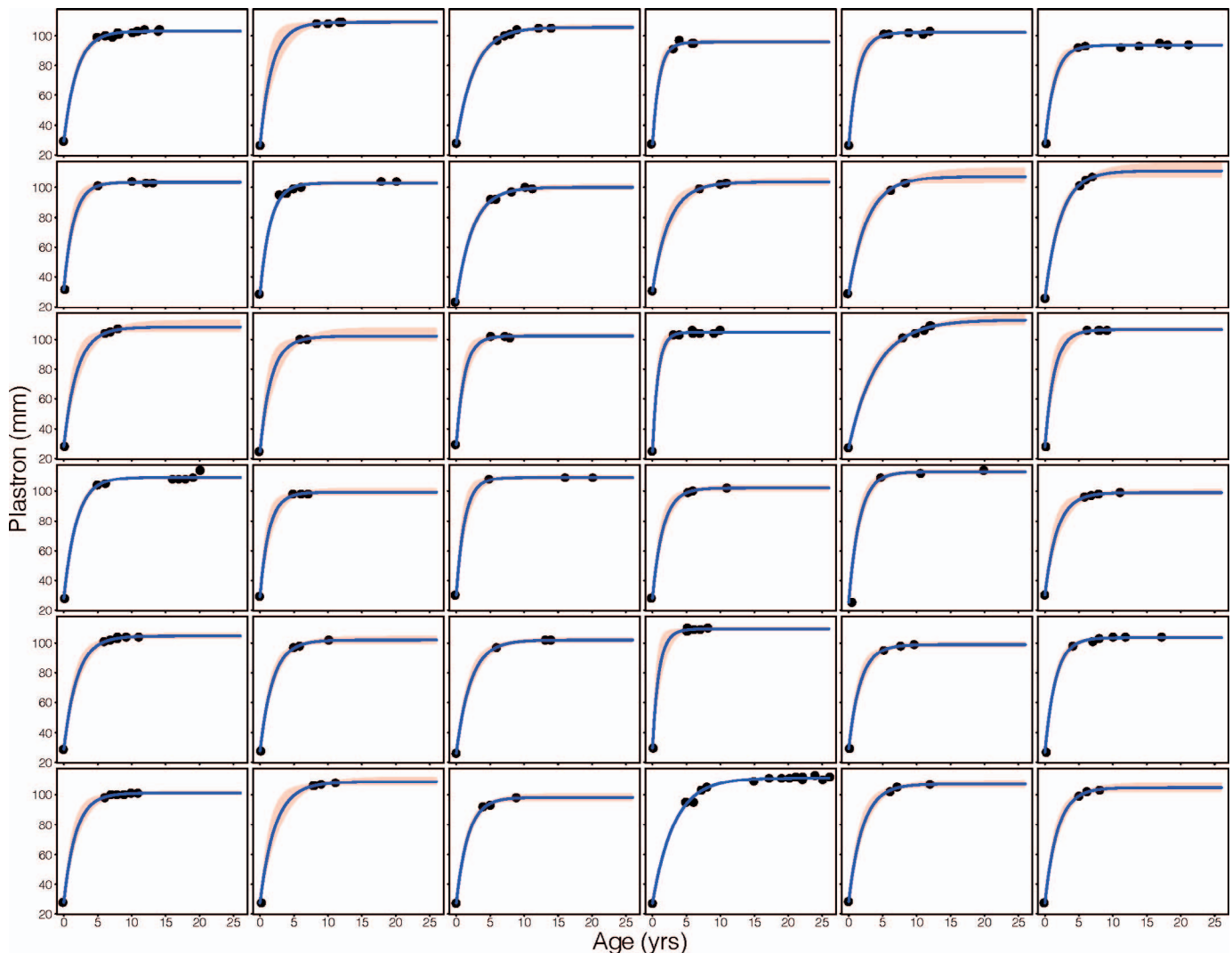
F<small>IG</small>. 4. Individual growth model fits for 36 male Diamondback Terrapins. Blue lines represent the individual von Bertalanffy model fits for the corresponding plastron-at-age observations, which are represented with black dots. The 95% credible regions are show in the pink-shaded region.

et al., 1991) and/or population level reproductive failure resulting in low recruitment (Gibbons et al., 2001). When Diamondback Terrapins are first captured around age 5 yr, the males are more likely to already be mature (Gibbons and Lovich, 1990) and thus have largely approached their asymptotic adult size. Females, in contrast, are more likely to be juveniles at age 5 yr and continue growth for a few years before approaching their asymptotic maximum size.

Tidal creek (site) was a significant factor for male growth, but not for female growth. Specifically, male growth rate was greater at Terrapin Creek than at Fiddler Creek. The site differences in male growth rate may be due to decades of urbanization-based changes in tidal creek habitat quality (e.g., habitat loss, siltation, overfishing, and contamination) along the Kiawah River, specifically near Terrapin Creek (Tucker et al., 2001; Dorcas et al., 2007; Witzcak et al., 2014). Furthermore, site-specific growth may differ between sexes because males and females exhibit differences in dispersal and movements among creeks that are associated with sex-specific habitat requirements such as partitioned foraging and nesting activities (Tucker et al., 1995; Gibbons et al., 2001; Sheridan et al., 2010). Gibbons et al. (2001) found that in the Kiawah Island Diamondback Terrapin population, the frequency of movement from Terrapin Creek

was substantially higher (24.5%) than the average of all other creeks, reducing density-dependent factors that can limit growth rate (Bjorndal et al., 2000). Other Kiawah Island Diamondback Terrapin studies also have noted site-specific differences in limb loss (presumably due to interactions with predators) and in survivorship, with Terrapin Creek having higher rates of limb loss (Cecala et al., 2009) and the lowest survivorship estimates (Witczak et al., 2014).

Data on distribution, demographics, and growth of coastal turtle species such as Diamondback Terrapins are critical for understanding and mitigating the effects of anthropogenic threats such as climate change and fisheries interactions. It is projected that climate change–linked sea level rise ($\sim$1 m by 2100) will have a 30.3% overlap with the geographic range of Diamondback Terrapins, increasing coastal salinity levels (Woodland et al., 2017; Agha et al., 2018). Higher salinity can increase the energetic cost of osmoregulation (reviewed in Harden and Williard, 2018) and decrease individual growth rates (Holliday et al., 2009; Ashley et al., 2021), which could impact other life history characteristics such as age at maturity and survival.

Fisheries-related bycatch mortality of terrapins via recreational and commercial crabbing also has been hypothesized to
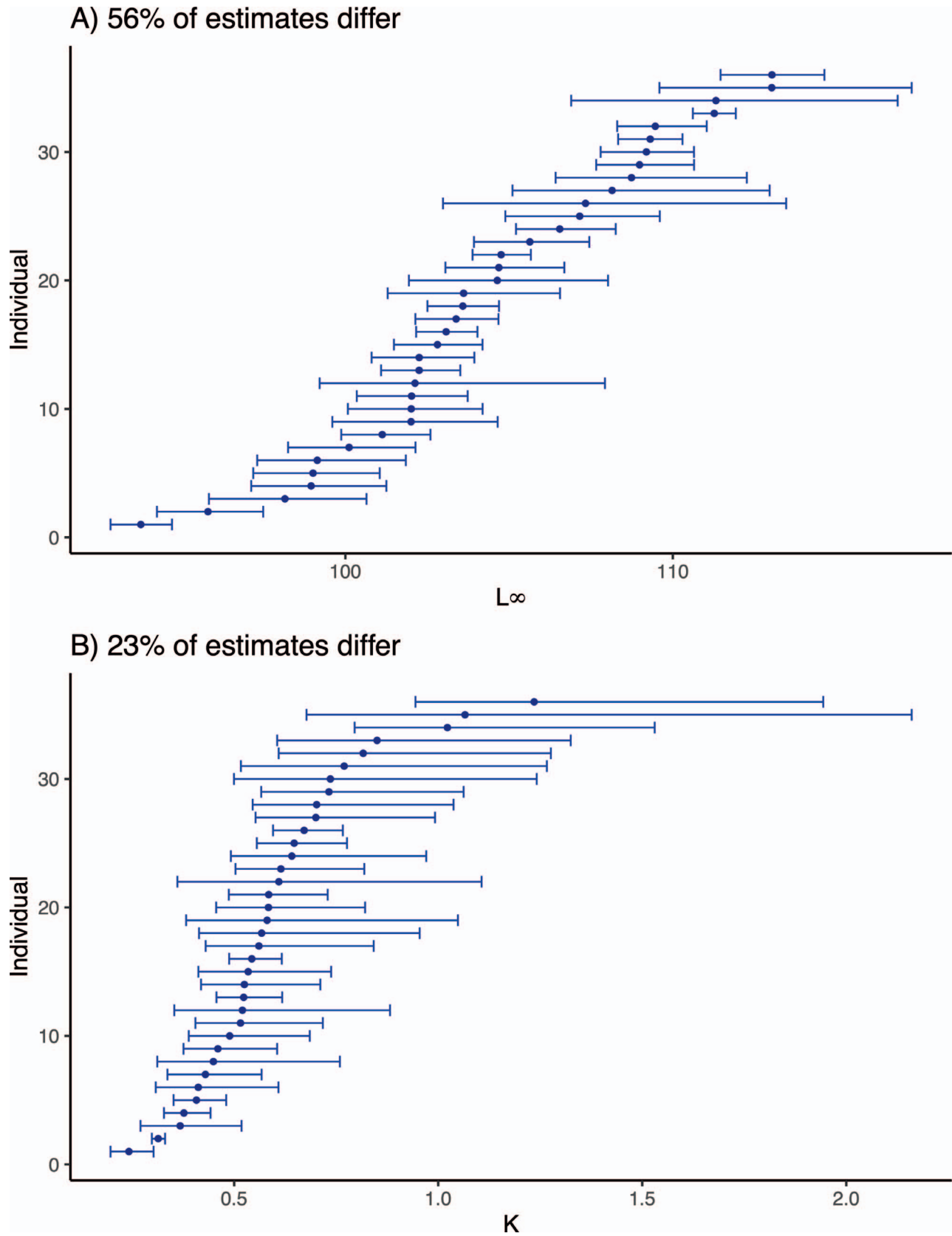
FIG. 5. L_∞ (A) and K (B) parameter estimates (black dots) and 95% credible intervals (blue lines) for individual male Diamondback Terrapins. In both panels, individuals are ordered from smallest to largest mean estimates; 56% of L_∞ estimates differ (i.e., 95% credible intervals do not overlap), whereas 23% of K estimates differ.
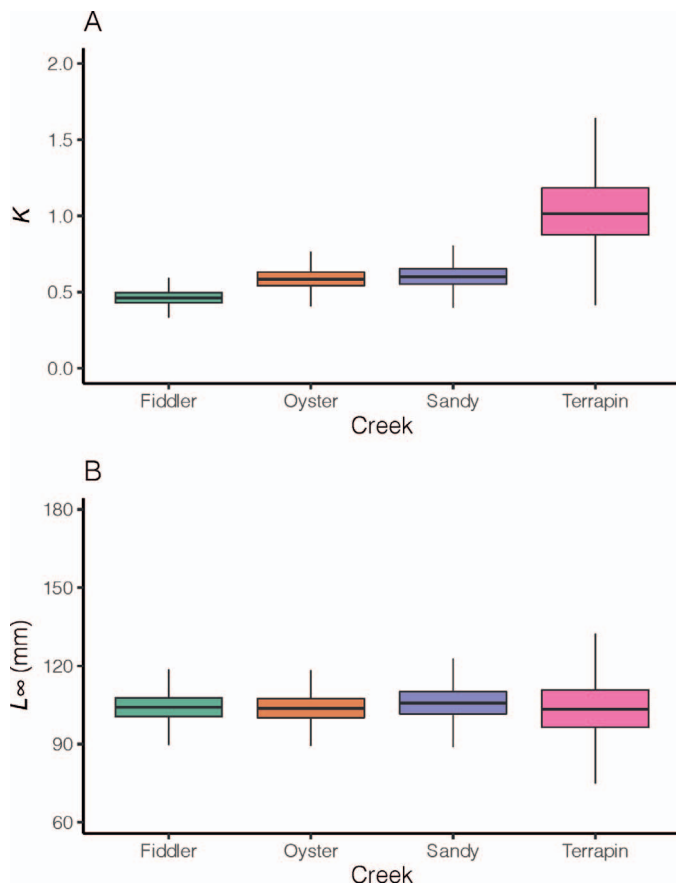
FIG. 6. Boxplots of parameter estimates of K (A) and L_∞ (B) from level-2 of the growth model for males. Creek was not significantly associated with the L_∞; however, males in Terrapin Creek did exhibit significantly greater growth coefficients (K) than males in Fiddler Creek. Boxes represent the interquartile range (IQR), the horizontal line in the middle of the box represents the mean, and the vertical whiskers extend to 1.5 × IQR.

rapid, variable growth to influence individual survival and fitness and ultimately population viability and program success.

Conclusions.—Long-term, capture–mark–recapture studies of long-lived turtles allow researchers to document individual- and population-level variation, providing important life history information that can inform conservation and management of imperiled species (Congdon et al., 1994; Marchand et al., 2018). The results presented here explore individual and sex-specific somatic growth of Diamondback Terrapins, a North American obligate estuarine turtle that is state listed as protected or regulated throughout its range (Roosenburg and Kennedy, 2018). Although our study represents growth estimates from a narrow geographic range in South Carolina, our results may provide detailed information for demographic models and can serve as a comparison for other imperiled terrapin populations in well-studied regions along the Atlantic and Gulf coasts. Because turtle life history traits such as body size at age, age at maturity, and somatic growth rate vary geographically due to environmental factors (e.g., Diamondback Terrapins [Seigel, 1984]; Wood Turtles [Marchand et al., 2018]), it is important to also consider variation in terrapin life history across its geographic range. Thus, we note the need for expanded study and synthesis of Diamondback Terrapin somatic growth rates throughout a geographic range that can contribute important demographic data used to evaluate population trends and help inform conservation management decisions.

impact the body size of a population by selectively removing juveniles, males, and smaller females (Roosenburg, 2004; Dorcas et al., 2007; Wolak et al., 2010; Selman et al., 2019). Roosenburg (1991) and Wolak et al. (2010) suggested that the size-selective mortality from the Blue Crab fishery may exert evolutionary pressure on terrapin populations that favors rapid juvenile somatic growth and terminal size to avoid crab trap mortality. Size-selective mortality of Diamondback Terrapins can be site specific because of their high site fidelity and limited dispersal (Gibbons et al., 2001; Tucker et al., 2001; Szerlag-Egger and McRobert, 2007) and therefore should be considered when collecting regional or range wide demographic data.

Diamondback Terrapin growth and demographic information can also help to inform region-specific management decisions (Hart et al., 2014), particularly as the species' conservation status varies by state. Region and sex-specific growth can help aid development of bycatch reduction device dimensions and configurations to reduce bycatch mortality in Blue Crab traps (Roosenburg et al., 1997; Dorcas et al., 2007; Coleman et al., 2014; Chambers and Maerz, 2018). Finally, results from this study can help to inform head-start programs that have been initiated for research purposes and to augment or establish Diamondback Terrapin populations. Head-start programs must consider the effects of captive-rearing environment on individual hatchling growth rates (Tokash, 2018) and the potential for

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