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PRIMARY RESEARCH PAPER

Conservation implications of somatic growth and length-at-age in *Pseudemys gorzugi*, Rio Grande Cooter

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Abstract Conservation decisions are often based on population models that rely on underlying assumptions made about species' demographic parameters. The Rio Grande Cooter (*Pseudemys gorzugi*) is a conservation-dependent riverine turtle, but our understanding of its population dynamics has been limited due to the absence of long-term surveys. We used mark-recapture data collected between 2016 and 2022 from the Black River, New Mexico, USA, to evaluate *P. gorzugi* somatic growth parameters. Females reached larger maximum size than males but exhibited a slower growth rate. We observed only a slight difference in maximum length and Brody growth coefficient of turtles from different locations, but the growth coefficients were overall significantly lower than any other *Pseudemys* species. Turtles on the Black River represent the northernmost robust population of *P. gorzugi*. In light of the intense human use of the river and riparian areas coupled with the impacts of climate change, it is imperative to maintain commitment to conservation efforts to resist population declines given the slow somatic growth rate of the population.

Keywords Bayesian · Von Bertalanffy growth model · Mark-recapture · *Pseudemys* · Rio Grande Cooter

Introduction

Understanding population dynamics is fundamental to wildlife management and conservation (e.g., Bjorndal et al., 2013; Tuberville et al., 2014). To apply ecological models and make inferences about population growth, it is imperative to know basic life history traits such as age at maturity (Sibly & Hone, 2002; Mazaris et al., 2005; Stawitz & Essington, 2019; Turner Tomaszewicz et al., 2022). For many reptiles, including freshwater turtles, age at maturity is more related to individual size than age (Cagle, 1948). Therefore, somatic growth rates are directly associated with other demographic processes such as fecundity (Armstrong & Brooks, 2014; Stawitz &

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Essington, 2019). Individual growth rates can vary based on habitat quality and environmental conditions that affect resource availability (Sibly & Hone, 2002; Marchand et al., 2018; Stawitz & Essington, 2019), which can serve as an important tool in monitoring population responses to changing environment over time (Tuberville et al., 2014). Growth rates can be affected by environmental conditions and the length of active season, and therefore vary across latitudinal gradients (Litzgus & Brooks, 1998; Marchand et al., 2018). However, obtaining somatic growth rate data in long-lived organisms like turtles is challenging and parameters in population models are often rough estimations (e.g., Mazaris et al., 2005).

Many freshwater turtle species, including turtles of the genus *Pseudemys,* exhibit a similar growth trajectory by which females reach a larger asymptotic size than males, and juveniles exhibit a rapid growth rate until they reach adulthood (e.g., Jackson, 1970; Aresco & Dobie, 2000; Huestis & Meylan, 2004; Lindeman, 2007; Marchand et al., 2018; Edmonds et al., 2021). Growth and age-specific maturity were often estimated based on growth rings (Galbraith & Brooks, 1987; Germano & Bury, 1998). However, growth rings could become ambiguous and may not provide an accurate estimation of age in some species, especially when turtles become older (Galbraith & Brooks, 1987; Germano & Bury, 1998; Wilson et al., 2003). Another approach to studying growth rate and age-specific maturity is to construct a growth model using mark-recapture techniques. Although this method has been increasingly used to study somatic growth pattern and to derive an estimated size and age at maturity in turtles, data on growth parameters of *Pseudemys* turtles remain sparse (see Dreslik, 1997; Lindeman, 2007; Siders et al., 2023).

The Rio Grande Cooter (*Pseudemys gorzugi*) is a medium-sized riverine turtle that occurs in the lower Pecos, Black, and Delaware rivers of New Mexico (Degenhardt et al., 1996), Rio Grande, Pecos, and Devils rivers of Texas (Ernst & Lovich, 2009; Bailey et al., 2014), and the Río Bravo del Norte drainage including the Salado, Sabrina, and San Juan Rivers of Mexico (Legler & Vogt, 2013; Pierce et al., 2016). This westernmost species of its genus is facing numerous threats including primarily habitat degradation and modification, but also commercial pet trade (historically), illegal shooting, and fishhook ingestion (Dixon, 2013; Bailey et al., 2014; Mali et al., 2014; Pierce et al. 2016). The overall density of the Rio Grande Cooter across its range is low, although they can be locally abundant in some areas (Bailey et al., 2014; Mali et al., 2018). Due to the limited distribution and knowledge of the species coupled with profound anthropogenic habitat alteration across much of its range, the Rio Grande Cooter is listed as threatened in New Mexico and Mexico (New Mexico Department of Game and Fish, 2018; Secretaríade Medio Ambiente y Recursos Naturales, 2010), species of greatest conservation concern in Texas (Texas Parks and Wildlife Department, 2012), and near threatened by the International Union for Conservation of Nature (IUCN; Van Dijk, 2011). The species was evaluated for protection under the USA Endangered Species Act, with the final decision made in 2022 to not list the species (Pierce et al., 2016; Endangered and Threatened Wildlife and Plants, 2022).

Based on the peer-reviewed literature, the Rio Grande Cooter was ranked the second least-studied freshwater turtle in the USA and Canada (Lovich & Ennen, 2013). However, since the petition for federal listing in 2012 (Adkins Giese et al., 2012) and subsequent initiation of the Species Status Assessment by the US Fish and Wildlife Service in 2015, many efforts have been made toward understanding various aspects of species ecology: diet and resource partition (Letter et al., 2019; Mahan et al. 2020; Bassett et al., 2022; Suriyamongkol et al., 2022), reproductive biology (Lovich et al., 2016; Letter et al., 2017; Suriyamongkol & Mali, 2019; Bohannon et al., 2022), basking behavior (Suriyamongkol et al., 2021), abundance (Mali et al., 2018), movement and dispersal (Curtis et al., 2017; MacLaren et al., 2017a, b), potential threats (Waldon et al., 2017; Suriyamongkol et al., 2019; Mahan et al., 2022a, 2022b), and survey techniques (MacLaren et al., 2017a; Mali et al., 2018; Mirabal et al., 2018; Bogolin, 2020). Despite these efforts, information on somatic growth rates and age at sexual maturity is still lacking. This is primarily due to relatively low densities across species range and lack of long-term data where the species is locally abundant.

Recent efforts to study species natural history on the Black River, New Mexico, accumulated a long-term dataset to begin examining and understanding species' growth rate patterns. Using mark-recapture data, we aimed to estimate somatic growth parameters of male and female *P. gorzugi*. We further evaluate growth patterns which may contribute to sexual size dimorphism and shell biometrics. In addition, we used the estimated sex-specific growth to estimate age and size at sexual maturity. Finally, we analyze the growth parameters from this study in relation to other *Pseudemys* species to draw conservation insights.

Materials and methods

Study site

Our study sites were located on the Black River, a ~ 87 km long tributary of the Pecos River in Eddy County, New Mexico (Fig. 1). Black River represents the northernmost portion of *P. gorzugi* range where the species is abundant and dominant (Mali et al., 2018). The Black River is used for recreation (e.g., fishing), cattle ranching, and irrigation, and is surrounded by oil and gas extraction operations (Martin, 2011; Scanlon et al., 2022). The river has been known to support a relatively large population of Rio Grande Cooters and to our knowledge, it is the only river system in the USA where juveniles and adults are readily observed and captured in hoop-net traps (Degenhardt et al., 1996; Mali et al., 2018). Our surveys focused on several stretches of the river that were readily accessible.

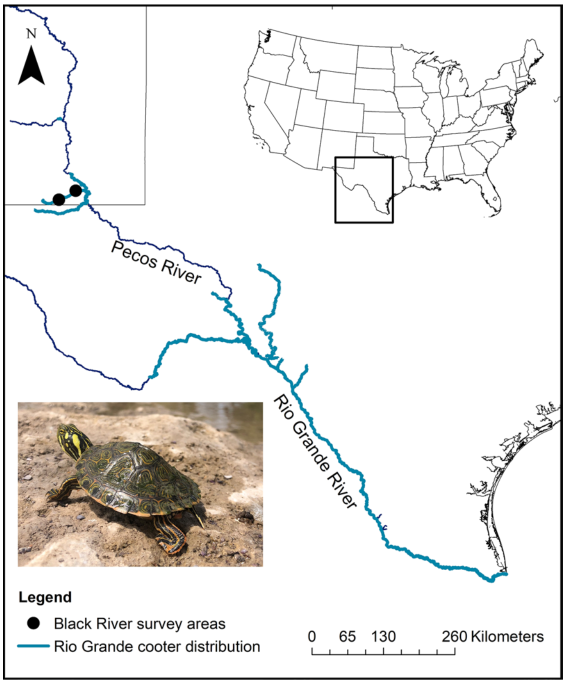

Fig. 1 A map representing *Pseudemys gorzugi* study locations on the Black River (black dots), New Mexico in relation to the rest of the species range (thick blue lines) in the USA. The study was conducted between 2016 and 2022 at two general locations on the Black River: the upstream portion and the downstream portion

The first stretch (hereafter, “upstream”) is ~ 1500 m long, located upstream near the Black River headwaters. This section is managed by the Bureau Land Management (BLM) for public recreational activities. The second stretch (hereafter, “downstream”) is ~ 3000 m long and located about 30 km downstream from the first stretch. Most of the downstream stretch of the river is located within natural gas and oil industry sites as well as private properties. At both stretches, riparian and aquatic vegetation were predominantly monocots such as sawgrass (*Cladium* spp.) and filamentous algae (Letter, 2018), respectively. However, filamentous algae, netleaf hackberry (*Celtis reticulata*), and cottonwood trees (*Populus* spp.) occurred more frequently upstream (Letter, 2018). We occasionally surveyed a ~ 200 m creek that feeds into the mainstem of the river (hereafter, “creek”) and just upstream of the creek confluence (hereafter, “creek confluence”), located approximately 3 km upstream from the downstream site. The exact locations of our study sites cannot be disclosed as some of our survey locations were located on private properties.

Data collection

We conducted annual freshwater turtle surveys from 2016 to 2022 primarily using hoop net traps. Survey months varied among years; however, all surveys were conducted between May and September (Fig. 2). The traps were 54.8 cm in diameter, fiberglass, single-opening, single-throated, wide-mouth, with 2.54 cm mesh size and four hoops per net (Memphis Net and Twine Company, Memphis, Tennessee). Due to the elusive nature of the Rio Grande Cooter, high trapping effort with at least 400 trap days per river kilometer (Mali et al., 2018) was deployed at each trapping occasion for all study sites. However, trapping effort was not consistent among sites for all years. For example, some portions of the downstream

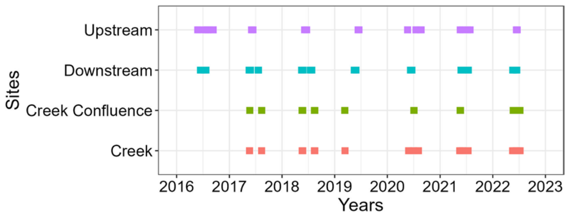

Fig. 2 Survey periods for *Pseudemys gorzugi* between 2016 and 2022 at each survey location on the Black River, New Mexico, USA. Survey period varied among locations, and the survey locations include upstream (purple), downstream (blue), creek confluence (green), and creek (red)

stretch were not surveyed every year due to accessibility and logistical constraints. Unlike the mainstem of the Black River, the creek was surveyed using only a few traps, but it still yielded a high number of captures. Traps were set approximately five meters apart and baited with canned sardines in oil. Sardines were put in a plastic cup with holes on the lid to allow scent to disperse while the bait remained in the trap. In some years, we also placed a single leaf of romaine lettuce in each trap.

We took standard measurements (method D; Iverson & Lewis, 2018) for each capture which included straight-line carapace length (CL), carapace width (CW), plastron length (PL), plastron width (PW), and body depth (BD). Sex was identified based on secondary sex characteristics by which males possess long, straight front claws, long tail with the cloacal opening extending past the carapace, and concave plastron, while females have shorter tail and are often larger in size (Ernst, 1990). When sex could not be identified, turtles were regarded as juveniles. In addition, reproductive status of females (i.e., the presence of shelled eggs or oviductal follicles) was evaluated in 2018 (Suriyamongkol & Mali, 2019), 2021, and 2022 (unpublished data) using an ultrasound (Mindray Digi Prince DP-6600 ultrasound; Mindray Medical International Ltd., Shenzhen, China) or X-ray (MinXray 308; MinXray Inc., Northbrook, Illinois). Each turtle was marked using one of three different marking techniques depending on the size of turtles. For larger turtles (CL > 110 mm), we used a Dremel rotary tool 8220 (Dremel, Racine, Wisconsin) to mark turtles using marginal scute notching technique (Cagle, 1939). For individuals with a CL of less than 110 mm, excluding small juveniles, we inserted Passive Integrated Transponder (PIT) tags into the inguinal region parallel to the spine (Buhlmann & Tuberville, 1998). For very small juveniles, we used a combination of toe-clipping technique and plastron pattern for identification (Suriyamongkol & Mali, 2018).

Modeling growth

von Bertalanffy growth model

We used the Fabens (1965) mark-recapture version of the von Bertalanffy growth model (von Bertalanffy, 1934) to model the sex-specific growth of *Pseudemys gorzugi* across the carapace length, plastron length, and body depth measurements (Eq. 1).

$$\widehat{L}_{t,m,i} = L_{\infty,m,j} - \left(L_{\infty,m,j} - L_{t-1,m,i}\right) e^{-k_{m,j}\Delta t_i} \tag{1}$$

where m denotes measurement, j denotes sex, i denotes individual, $\widehat{L}_t$ is the expected length at capture in time t, L_∞ is the asymptotic length (also the average maximum length), L_{t-1} is the length in the past capture event, k is the Brody growth coefficient (the proportion of $L_\infty - L_t$ obtained per unit time), and Δt is the amount of time between t and $t-1$ in fractions of a year. We assumed the expected length, $\widehat{L}_{t,m,i}$ describes the mean of a normal likelihood with σ denoting the variability in growth around the expected length (Eq. 2).

$$L_{t,m,i} \sim N\left(\widehat{L}_{t,m,i}, \sigma_{m,j}\right) \tag{2}$$

where $L_{t,m,i}$ is the observed length at capture in time t. As we had capture histories of individuals, we incorporated the individual variability in growth using a random effect for individual (Eqs. 3 and 4).

$$\log\left(L_{\infty,m,i}\right) = \log\left(L_{\infty,m,j}\right) + \beta_{i,m,L_\infty} \tag{3}$$

$$\operatorname{logit}\left(k_{m,i}\right) = \operatorname{logit}\left(k_{m,j}\right) + \beta_{i,m,k} \tag{4}$$

where $\beta_{i,m}$ is the random effect for L_∞ and k for a given measurement, m. As each individual had multiple measurements at each capture, we wished to directly estimate the correlation between growth parameters (L_∞ and k) for each measurement. We did so by structuring the individual growth parameter random effects as a set drawn from a multivariate normal distribution (Eq. 5).

$$\left\{\begin{matrix} \beta_{i,\mathrm{CL},L_\infty} \\ \beta_{i,\mathrm{CL},k} \\ \beta_{i,\mathrm{PL},L_\infty} \\ \beta_{i,\mathrm{PL},k} \\ \beta_{i,\mathrm{BD},L_\infty} \\ \beta_{i,\mathrm{BD},k} \end{matrix}\right\} \sim MVN\left(\left\{\begin{matrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{matrix}\right\}, \Sigma\right) \tag{5}$$

where the mean of the individual random effects is zero for each transformed growth parameter and Σ is the covariance matrix of the multivariate normal distribution. For the sake of easing the fitting of this correlation, we decomposed the covariance matrix into the Cholesky factorization (see Siders et al., 2023).

Predicted length at age and derived age at maturity

We also estimated the expected length at age and its uncertainty from the joint distribution of the growth parameters. To do so, we used measurements of size at hatch (birth), L_0, and assumed these measurements came from a half-normal distribution (bounded above zero) (Eq. 6).

$$L_{0,m} \sim N\left(\mu_{L_0,m}, \sigma_{L_0,m}\right) \tag{6}$$

and this L_0 was used in the length-at-birth formulation of the von Bertalanffy growth model (1934) to predict the length at age (Eq. 7).

$$\widehat{L}_{t,m,j} = L_{\infty,m,j} - \left(L_{\infty,m,j} - L_{0,m}\right)e^{-k_{m,j}t} \tag{7}$$

where Eq. 9 is analogous to Eq. 1 but using t instead of $\Delta t$where t is equal to a vector of ages to predict length at age at, ranging from age zero to 50 and an interval of a tenth of a year.

Bayesian implementation

We fit the multidimensional mark-capture von Bertalanffy growth model (Fabens, 1965) using STAN and the *cmdstanr* package (STAN Development Team, 2020; Gabry & Češnovar, 2022). We specified priors following Siders et al. 2023. We fit the model in STAN using four chains with 5,000 warmup and 1,000 sampling iterations per chain using the NUTS sampler. We assessed chain convergence using the Gelman-Rubin statistic (Gelman & Rubin, 1992). From the fitted model, we wished to understand if there was structure to the individual random effects we estimated by capture location. We pulled the median L_∞ and k individual random effects and visualized the clustering according to capture location: upstream, near creek, or downstream. We also tested whether said clusters were significantly different with a multivariate ANOVA.

Comparing maturity estimates

Lastly, we wished to compare the length and age at maturity between those derived from the growth models using life-history invariants and those predicted from observations of male secondary sexual characters and female maturation measurements. To calculate the life-history invariants (Beverton & Holt, 1959; Jensen, 1996; Prince et al., 2015), we used the Gibbons et al. (1981) proportions of L_∞ where sex-specific maturity might occur in *Pseudemys* (Eq. 8).

$$L_{mat} = \left(\frac{\overline{L_{mat}}}{L_\infty}\right) * L_\infty \tag{8}$$

where $\left(\frac{\overline{L_{mat}}}{L_\infty}\right)$ is the average proportion of L_∞ at which L_{mat} occurs. It is worth noting this is a derived estimate but was successful at estimating length at maturity for other *Pseudemys* species (Siders et al., 2023). For male length at maturity, we assumed length at maturity was 120 mm CL from the observed field measurements of secondary sexual characteristics. For female length at maturity, we fit a logistic length at maturity model to the measurements of the presence of follicles or eggs in females (Eqs. 9 and 10).

$$p_{mat} = \left(\frac{1}{1 + \exp\left(\frac{L - \widehat{L}_{mat}}{\widehat{L}_{mat} * \eta}\right)}\right) \tag{9}$$

$$P_{mat} \sim Bernoulli\left(p_{mat}\right) \tag{10}$$

where p_{mat} is the probability of maturity described by a logistic function with the parameters of length at 50% maturity ($\widehat{L}_{mat}$) and maturation rate (η) and P_{mat} is the observed maturity described by a Bernoulli distribution. Using the three estimates of length at maturity, life-history invariant derived, female measurement estimated, or male secondary sexual characteristic, we derived the expected age at the respective length (Eq. 11).

$$t_{mat} = \left(\frac{1}{k}\right)\log\left(\frac{L_\infty - L_0}{L_\infty - L_{mat}}\right) \quad (11)$$

where t_{mat} is the age at maturity and L_{mat} is the corresponding length. By predicting length at age and estimating a derived L_{mat} and t_{mat} within the model, we ensure that all error in the model estimates of the growth parameters propagates to these predictions/derivations (Lovich & Gibbons, 1992).

Results

Sampling

From 2016 to 2022, a total of 3090 captures were made in the Black River of 688 individual *P. gorzugi* over 220 different sampling days. The number of sampling days ranged from 24 to 40 days per year (median of 32 days). Most of the captures were from the upstream location (1072), followed by the downstream location (1061), then in the creek (150), and the fewest captures in the creek confluence location (110). Although the turtles can freely move between the creek and the river, such encounters were relatively infrequent. Of these captures, 127 individuals were only captured as juveniles and thus, were not included in the sex-specific von Bertalanffy mark-recapture models. These juveniles most frequently occurred in the creek (30% of captures) or downstream (26% of captures). Removing juvenile-only records left 561 individuals, 301 females, and 260 males, and resulted in 2025 valid straight carapace lengths ranging from 43 to 278 mm, 2026 valid plastron lengths ranging from 39 to 251 mm, and 2018 valid body depths ranging from 21 to 116 mm. Individuals had a median of three recaptures with a range of 1 to 21. Six hatchlings were used to make measurements of L_0, three from the Albuquerque Zoo and three from the Black River with a mean straight carapace length of 36 mm, mean plastron length of 32.8 mm, and mean body depth of 16.8 mm. Ultrasound surveys of 110 females were performed, with a median of 2 per turtle (range: 1–5), resulting in 216 surveys. Of these, 82 were not gravid, 94 were gravid with follicles, and 40 were gravid with shelled eggs.

Somatic growth

The median estimated size at birth (L_0) from the hatchling measurements and the mark-recapture growth data was 36, 33, and 17 mm for CL, PL, and BD, respectively (Table 1; Fig. 3). Female asymptotic lengths (L_∞) were higher than male asymptotic length for carapace length, plastron length, and body depth with a ratio of 1.35, 1.4, and 1.45 females to males, respectively. Female Brody growth coefficients were lower than males for all measurements (Table 1).

Table 1 Measurement- and sex-specific growth parameters for the Black River *Pseudemys gorzugi* population. Measurements were carapace length (CL), plastron length (PL), and body depth (BD) for females (F) and males (M)

θ	Meas	Sex	Value
L_0	CL	–	36.02 (34.83–37.26)
	PL	–	32.81 (31.82–33.84)
	BD	–	16.81 (15.86–17.87)
L_∞	CL	F	242.06 (236.26–248.66)
	CL	M	182.01 (177.41–186.71)
	PL	F	221.56 (216.73 – 227.58)
	PL	M	161.59 (157.55–165.81)
	BD	F	88.09 (84.77–91.87)
	BD	M	61.91 (59.72–64.7)
k	CL	F	0.05 (0.05–0.06)
	CL	M	0.08 (0.07–0.09)
	PL	F	0.05 (0.05–0.06)
	PL	M	0.08 (0.07–0.09)
	BD	F	0.05 (0.04–0.06)
	BD	M	0.07 (0.06–0.08)
σ	CL	F	2.51 (2.43–2.61)
	CL	M	2.15 (2.06–2.23)
	PL	F	2.11 (2.03–2.2)
	PL	M	2.08 (2.01–2.17)
	BD	F	2 (1.92–2.07)
	BD	M	1.8 (1.73–1.87)
$L_{t=1}$	CL	F	46.37 (42.16–50.68)
	CL	M	46.84 (42.75–50.78)
	PL	F	42.51 (38.96–46.49)
	PL	M	42.2 (38.42–45.93)
	BD	F	20.38 (16.99–23.81)
	BD	M	19.75 (16.65–22.96)

Reported is the median value and, in parentheses, the 90% credible interval. Asymptotic length (L_∞), growth variability (σ), size at hatch (L_0), and size at one-year-old $(L_{t=1})$ are reported in millimeters while the Brody growth coefficient (k) in proportion per year

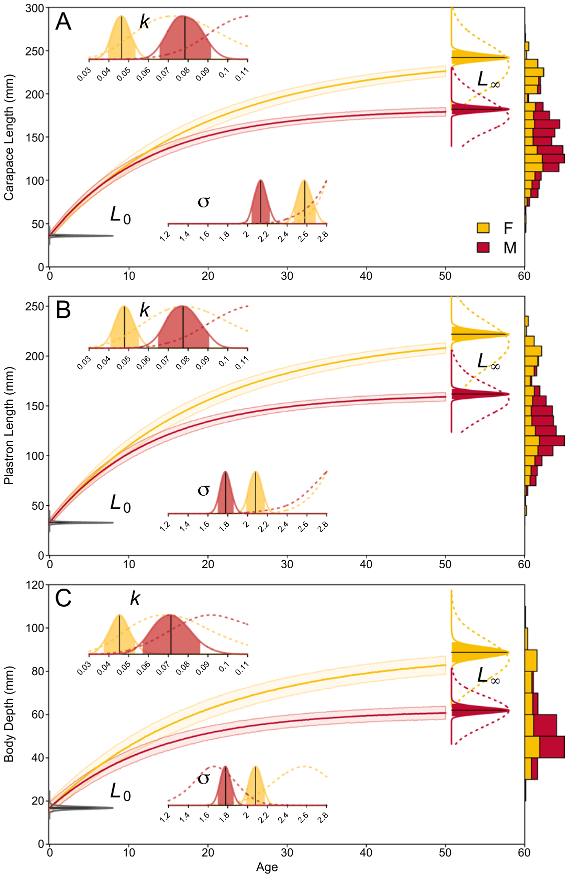

Fig. 3 Predicted measurement length at age for **A** carapace length, **B** plastron length, and **C** body depth for females (yellow) and males (red). For each prediction, the solid line indicates the median predicted length at age while the shaded region indicates the 90% credible interval. Inset parameter distributions (L_∞, k, σ, L_0) indicate the posterior distribution (shaded region), the median posterior value (vertical black line), and, where applicable, the prior distribution (dashed lines). The relative numbers of turtles across size classes are represented along the y-axis on the right of the graphs

Variability in growth, σ, was highest for carapace length and lowest for body depth with females significantly more variable in carapace length than males (Fig. 3). Integrating these values results in markedly similar first-year growth $\left(L_{t=1}\right)$ of females and males but with males slightly larger than females across all three measurements (Table 1). This trend continues for carapace length and plastron length until 10 years of age while body depth diverged earlier between sexes around 5 years of age (Fig. 3). The sexual dimorphism index, following Lovich & Gibbons (Heppell et al., 1999), based on the ratio of L_∞ between males and females was 0.33, 0.37, and 0.45 for carapace length, plastron length, and body depth, respectively. Asymptotic length, L_∞, and Brody growth coefficient, k, were highly correlated for carapace ($\rho = -0.58$) and plastron length ($\rho = -0.55$) but, surprisingly, were uncorrelated for body depth ($\rho = 0.01$) (Table 2). As expected, carapace and plastron length growth parameters were highly correlated but were weakly negatively correlated for body depth L_∞ and moderately positively correlated for body depth k (Table 2).

Individual variation

Individual random effects were weakly separated by capture location, likely reflecting the diverse set of encounter histories in the dataset (Fig. 4). On average, turtles caught at the upstream location were within 0.5 mm of the population-wide L_∞ but had higher growth coefficients indicating they reached asymptotic length faster than other locations (Table 3). Downstream, carapace and plastron length were slightly longer, 1–2 mm, while body depth was slightly lower, 0.2–0.3 mm, on average than the population estimate but k values across measurements

Table 2 Median correlation between the L_∞ and k individual random effects for each measurement of *Pseudemys gorzugi* population in the Black River, New Mexico, USA

$L_{\infty,\mathrm{CL}}$	-0.63	0.98	-0.61	0.51	-0.58
-0.63	k_{CL}	-0.62	1	0.08	0.94
0.98	-0.62	$L_{\infty,\mathrm{PL}}$	-0.61	0.51	-0.58
-0.61	1	-0.61	k_{PL}	0.1	0.94
0.51	0.08	0.51	0.1	$L_{\infty,\mathrm{BD}}$	-0.08
-0.58	0.94	-0.58	0.94	-0.08	k_{BD}

Measurements were carapace length (CL), plastron length (PL), and body depth (BD)

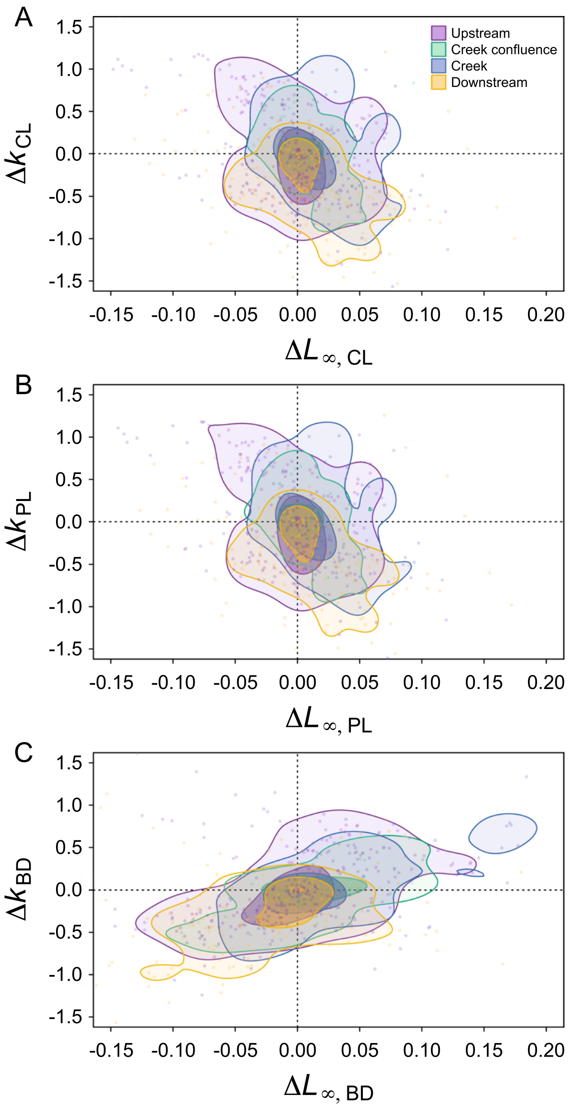

Fig. 4 Individual random effects for **A** carapace length (CL), **B** plastron length (PL), and **C** body depth (BD) of *Pseudemys gorzugi* population in the Black River, New Mexico, USA. Each point corresponds to a pair of for L_∞ and k median random effect values for an individual and are colored by the capture location of said individual. The shaded regions correspond to the 90th (lightly shaded) and 50th percentiles (darkly shaded) of the bivariate kernel density estimate of the capture-location individual random effects. Note that ΔL_∞ affects $L_{\infty,i}$ on the log-scale and Δk affects k_i on the logit-scale (Eqs. 3 and 4)

were lower indicating turtles downstream grow slower than the rest of the population (Table 3). In the creek location, L_∞ values were on 1–4 mm average higher than population for all three measurements while k values were slightly lower for all three measurements while at creek confluence location, L_∞ (0.2–0.6 mm) and k values were slightly higher on average for the three measurements than the population (Table 3). This indicates the creek-dwelling turtles are growing larger overall and faster, as L_∞ and k are negatively correlated, while the creek confluence turtles are solely growing faster to similar sizes as the population mean. In terms of multivariate growth, upstream turtles were expected to be smaller overall, downstream turtles to be longer but flatter, creek turtles to be far larger overall, and creek confluence turtles to be slightly larger overall primarily in length and not body depth (Table 3).

Maturation

Female length at maturity derived from the von Bertalanffy growth model using life-history invariants closely aligns with the female length at maturity estimated using the logistic maturity model fit to the female follicle or egg presence, approximately 211 mm carapace length (Table 4). The former uses 87.2% of L_∞ as the length at maturity (Siders et al., 2023). Using the male-specific percentage (71.2% of L_∞), male length at maturity occurred at much smaller sizes, ~ 131 mm carapace length, and roughly 109% greater than observed secondary sexual characteristic cutoff of 120 mm carapace length. Age at maturity was 36–37 years across measurements using the life-history invariants for females and corresponded to the estimated age at maturity, 37 years, using the logistic maturity model parameters. Male age at maturity was roughly a third of the female age at maturity with the median across measurements using life-history invariants of 14 years and an age at maturity using the secondary sexual characteristic cutoff of 10 years.

Discussion

Understanding species' basic demographic parameters such as somatic growth, age at maturity, fecundity, and survival can be used to evaluate population growth and assess the need for conservation measures (Heppell et al., 1999). Somatic growth can also provide insights into the adaptive strategy of species across various geographic locations and

Table 3 Median change in the L_∞ and k parameter values by location for carapace length (CL), plastron length (PL), and body depth (BD) from the sex-specific population value of *Pseudemys gorzugi* population in the Black River, New Mexico, USA

Location	Sex	$\Delta L_{\infty,\mathrm{CL}}$	Δk_{CL}	$\Delta L_{\infty,\mathrm{PL}}$	Δk_{PL}	$\Delta L_{\infty,\mathrm{BD}}$	Δk_{BD}
Upstream	F	– 0.2	0.0069	– 0.24	0.0075	– 0.18	0.0044
Upstream	M	– 0.15	0.0099	– 0.17	0.01	– 0.13	0.0058
Creek confluence	F	4.1	0.0041	3.7	0.0045	2.7	0.0025
Creek confluence	M	3.1	0.0059	2.7	0.0063	1.9	0.0032
Creek	F	5.7	– 0.00078	5.2	– 0.0008	3.5	– 0.001
Creek	M	4.3	– 0.0011	3.8	– 0.0011	2.5	– 0.0014
Downstream	F	2	– 0.012	1.8	– 0.013	– 1.5	– 0.01
Downstream	M	1.5	– 0.018	1.3	– 0.019	– 1.1	– 0.014

Medians were calculated from the median individual random effect by location and the median sex-specific parameter value

Table 4 Comparison between length at maturity (L_{mat}) in millimeters and age at maturity (t_{mat}) in years calculated from the life-history invariant methods using the von Bertalanffy growth function (VBGF), from the logistic maturity function fit to female maturation data (Logistic), and from male secondary sexual characteristics

θ	Method	Meas	Sex	Value
L_{mat}	VBGF	CL	F	211.12 (206.06–216.88)
		CL	M	130.67 (127.37–134.04)
		PL	F	193.24 (189.03–198.49)
		PL	M	116.01 (113.11–119.04)
		BD	F	76.83 (73.94–80.13)
		BD	M	44.44 (42.88–46.45)
	Logistic	CL	F	211.54 (199–217.85)
	Secondary Characteristic	CL	M	120
t_{mat}	VBGF	CL	F	36.79 (32.54–41.67)
		CL	M	13.64 (11.6–15.76)
		PL	F	35.91 (31.8–40.8)
		PL	M	13.64 (11.56–15.74)
		BD	F	35.71 (31.13–41.45)
		BD	M	13.75 (11.59–16.7)
	Logistic	CL	F	36.87 (29.9–43.07)
	Secondary Characteristic	CL	M	10.17 (9.16–11.26)

Length at maturity and age at maturity were estimated respective to the measurement (*CL* carapace length, *PL* plastron length, *BD* body depth) and respective to sex (*F* females, *M* males)

environmental conditions (Gibbons et al., 1981). Our study is the first to provide estimates of somatic growth for *P. gorzugi*, a species of conservation concern. Based on the growth models, we also estimated size- and age- at sexual maturity, drawing comparisons with studies on other *Pseudemys* species. By incorporating known somatic growth rate parameters and accounting for variations among localities and individuals, we can inform population models, thereby facilitating more effective management planning for this poorly understood species (Bjorndal et al., 2013; Armstrong et al., 2018; Harden et al., 2021).

Traditionally, estimates of somatic growth rates in turtles were based on a single measurement, either carapace length or plastron length (e.g., Dreslik, 1997; Lindeman, 2007). However, recent studies emphasized the importance of accounting for multidimensional growth in turtle shell morphology to better understand sexual dimorphism and sex-specific trade-offs in reproductive requirements (e.g., Hoekstra et al., 2018). Shell curvature and sphericity differ based on sex and age, as an increase in shell curvature may provide more storage capacity for eggs in females (Hoekstra et al., 2018). However, the use of body depth in somatic growth estimation is often neglected. Here, we presented sex-specific growth based on three shell morphometrics, including body depth (i.e., BD) and length (i.e., PL and CL). Similar to other *Pseudemys* species, *P. gorzugi* is sexually dimorphic with females growing to a larger asymptotic size than males for all three measurements and the Brody growth coefficients were lower in females than males. However, the degree of sexual dimorphism can vary among *Pseudemys* species. Siders et al. (2023) reported a strong sexual dimorphism based on CL for *P. c. suwanniensis* and *P. peninsularis* while *P. texana* and *P. nelsoni* showed a weak sexual dimorphism. In our study, females were 133% larger in carapace length, 137% larger in plastron length, and 142% larger in body depth than males at asymptotic size. Variability in growth was dependent on the measurement. Body depth had the highest variability in growth, while carapace length and plastron length had the lowest variability. However, there were minor differences in amount of variability around the mean growth between sexes for PL and BD, while sexual dimorphism was more prominent in CL.

The Brody growth coefficients estimated for *P. gorzugi* (0.05 and 0.08 for females and males, respectively) were exceptionally low in comparison to other *Pseudemys* turtles. *Pseudemys texana*, a species native to Texas and directly to the east of *P. gorzugi*, has estimated *k* values of 0.129 and 0.191 in the South Llano River and 0.23 and 0.20 in Comal Springs-Landa Lake for females and males, respectively (Lindeman, 2007; Siders et al., 2023). The *k* values for *P. gorzugi* are even low relative to temperate systems where growth is likely to be slower. Dreslik (1997) reported the Brody growth coefficient to be 0.087 for female and 0.136 for male *P. concinna* at Round Pond, Illinois, but larger asymptotic sizes than *P. gorzugi* (299 mm PL for females and 219 mm PL for males). The reported asymptotic plastron length of *P. texana* in the South Llano River, Texas, was 231.6 mm for females and 153.1 mm PL for males (Lindeman, 2007), similar to the asymptotic plastron length reported here. In the spring-fed systems, where the temperature allowed for year-round productivity, *P. texana* and *P. concinna suwanniensis* grew to larger asymptotic length and exhibited a faster growth rate than their conspecific in a non-springs habitat (Siders et al., 2023). One possible explanation for the slow growth in *P. gorzugi* may be attributed to a potential scarcity of favored food resources as the Black River exhibits a relatively low abundance of algae, a preferred dietary component of adult *P. gorzugi* (Letter et al., 2019; Bassett et al., 2022). In contrast, spring-fed systems in Texas and Florida boast an abundance of algae and associated food items, while the Round Pond in Illinois is nestled within a Nature Preserve featuring high-quality wetlands and bottomland hardwood forest. While *P. gorzugi* is observed basking year-round (Suriyamongkol et al., 2021), it is plausible that the feeding behavior diminishes during the winter months, likely influenced by the lower temperature characteristic of that season. This reduction of feeding activity could also affect the growth rate.

There was a weak but observable variation in growth across our sampling locations. Variations in asymptotic sizes and shell morphology (i.e., shell arching) were observed among populations of other *Pseudemys* species such as *P. concinna*, which could be attributed to food availability, habitat characteristics, predator pressure, and availability of basking sites for thermoregulation and nutrient assimilation (e.g., Gibbons et al., 1981; Aresco & Dobie, 2000; Munscher et al., 2015). Marchand et al. (2018) found a relationship between growth rate and the number of frost-free days and temperature, by which growth rate declines in cooler temperature. Huestis & Meylan (2004) also showed that growth rates increased during March-September, potentially due to an increase in aerial basking during warmer months. Turtles from the spring-fed system with year-round growth condition exhibited fast growth trajectories (e.g., Jackson, 1970; Munscher et al., 2015; Siders et al., 2023). Siders et al. (2023) showed that these growth rates can be quite extreme with juveniles nearly tripling in size within the first year after hatching. In our study system, survey locations were in relatively close proximity to one another and the mean summer water temperatures were similar for both the upstream and downstream sites, with an average of 26 ºC (Suriyamongkol et al., 2021), although we never measured water temperature in the creek. Similarities in water temperature across our study sites imply that there were other factors which influenced turtle growth, such as habitat quality, food resources, and availability for aerial basking platforms.

Based on vegetation surveys, food availability differs between the upstream and downstream locations, which likely explains why *P. gorzugi* at the two locations have slightly different diets and growth (Suriyamongkol et al., 2022). Although vegetation surveys were not conducted at the creek location, the creek stands out for its clear, heavily vegetated water, a habitat type believed to be particularly favored by *Pseudemys* turtles and most similar to spring fed habitats in other studies (Siders et al. 2023). Since *Pseudemys* turtles are generally herbivorous/algivorous as adults (Letter et al., 2019; Bassett et al., 2022), it is no surprise that the creek-dwelling turtles grow to a larger size and faster than turtles at other locations.

Nonetheless, the variations in growth observed across our study locations were relatively minor. As such, it can be inferred that differences in food availability play only a marginal role in accounting for the slight differences in growth. Furthermore, it is worth noting that *P. gorzugi* in Devils River, Texas, have been documented traveling substantial distances of up to 35.5 km (MacLaren et al., 2017b). Although we have not observed such movements in our study system, one possible explanation for the subtle variations in growth could be the turtles' capacity to move among our study sites, especially in the downstream portion of the river. According to our mark-recapture data, we detected sporadic movement solely occurring between the creek and the creek confluence. Although the turtles could freely move between the two sites, the majority of turtles were recaptured at the locations where they were originally captured. The upstream location is separated from the rest of our survey locations by several kilometers of subterranean flow which appears to act as a significant movement barrier. However, it is perplexing that no observable movement was noted between the downstream site and the creek/creek confluence. Furthermore, we note that all turtles captured in the creek displayed distinct and significant darkening of the carapace (i.e., melanism) in comparison to the rest of the population, suggesting a potential preference for staying within the creek system. Further studies are needed to understand how movement and habitat connectivity affect population dynamics in the Black River.

Maturity in male *Pseudemys* is often determined using the presence of secondary sex characteristics (Cagle, 1944, 1948). When using the cut-off based on those characteristics for *P. gorzugi* in the Black River (120 mm CL), turtles reached maturity at the age of 10 years (Table 4). This finding is slightly higher than the median estimated age at maturity for *P. nelsoni* (8.26 y) and *P. peninsularis* (9.07 y) but is nearly double that of *P. texana* (5.2 y) and more than double that of *P. c. suwanniensis* (4.4 y) in the spring-fed system (Siders et al., 2023). However, this 10 year-old age at maturity is within the range that Dreslik (1997) reported for *P. concinna* (7–15 y) in the temperate system. It is perhaps reasonable, given the very low k values we estimated for *P. gorzugi*, that males mature at 10 years old. However, it is more likely arising from a difference in the definition of age at maturity. The age at maturity estimated using a logistic maturity model or derived from the von Bertalanffy growth model are, by default, assuming that age at maturity occurs at the 50th percentile of length at maturity, L_{50} in common notation. The secondary sexual characteristic cutoff applied here does not correspond to a 50% chance of classifying a turtle as a male but a much higher percentile, such as > 99%. This means the age at maturity is not derived using L_{50} but more likely at $L_{>99}$ entailing that the vast majority of males are mature by 10 years old. Just like with mark-recapture growth, mark-recapture maturation assessment, classifying a turtle as juvenile or male each capture, could be a means of estimating the true L_{50}.

In contrast, females do not develop conspicuous secondary sex characteristics and, therefore, using the cut-off at 120 mm CL is not appropriate for determining maturity in female turtles (Cagle, 1944). Rather, sexual maturity in female turtles is defined by the capability of producing eggs during the next breeding season (Kuchling, 1999). Using the results of ultrasound and X-ray data, we estimated the length of maturity for females at 198 mm CL and the corresponding estimated age at maturity was 37 years, with a similar estimate of 36 years derived with life history invariants (Table 4). This extreme age at maturity estimation does not corroborate with the age at maturity for other *Pseudemys* species (Siders et al., 2023), which ranged from 8.1 to 14.1 years. A couple of processes could be at play. The correspondence between the logistic maturity model and the von Bertalanffy growth model would seem to suggest that the life-history invariant ($L_{mat} = 0.87 * L_{\infty}$) is inappropriate for *P. gorzugi* and that follicle/egg presence in small turtles is undersampled. Here, we list several arguments for our undersampling hypothesis. In our study, females up to 262 mm CL (20 mm CL greater than -L_{∞}) were sampled with ultrasound and X-ray and found to not possess follicles or shelled eggs. The smallest turtle with follicles was 198 mm CL ($t_{mat} = 30.9$ y) while the smallest turtle with shelled eggs was 205 mm CL (t_{mat} 34.3 y). In west Texas, the smallest *P. gorzugi* with shelled eggs was 179 mm PL (Bohannon et al., 2022) in comparison to the 189 mm PL in our study system. Finally, Bohannon et al. (2022) found *P. gorzugi* producing shelled eggs in April, while our surveys did not typically begin until mid-May. However, growth and reproduction are known to vary based on the region, habitat, and resource availability;

therefore, we were hesitant to apply Bohannon et al. (2022) reproduction data on our growth model to adjust estimates of age at maturity. A co-occurring challenge is the same issue as using the secondary sexual characteristic to assign male maturity. In order to have follicles or have shelled eggs, maturation has already occurred and the length at maturity of 211 mm might not correspond to -L_{50}. This means that 36 + years for an age at maturity could be where well above 50% of females are mature. Therefore, we recommend treating our age at maturity estimates for males and females with extreme caution and, instead, hope the lack of corroboration can spur further studies on maturation in *P. gorzugi*.

In conclusion, this is the first study to estimate somatic growth parameters for *P. gorzugi*. The population of *P. gorzugi* on the Black River represents the northernmost population within its range, with locally abundant juvenile and adult turtles. This population represents the last stronghold for *P. gorzugi* in New Mexico, given the lower relative abundances and lack of juveniles in the Pecos and Delaware River (Mahan et al., 2022a; Suriyamongkol et al., 2022). Although our estimates of sexual maturity are extreme and should be taken with caution, more worrisome are the ultra-low estimates of growth coefficients. Whether these estimates are a natural characteristic for this population at the northern extent of its range or a product of changing environment is currently unknown. Although the Black River is considered relatively pristine, an expansion of oil and gas industry in the region puts additional pressures on the river system by potentially altering its flow and increasing the risk of contamination in water (Jiang et al., 2022; Scanlon et al., 2022). In addition, studies found that growth can be suppressed during a period of drought with a shift in age at sexual maturity (e.g., Linderman and Rabe, 1990; Powell et al., 2023). Exposure to prolonged heat is also known to induce stress and reduce growth rate in ectotherms (Kingsolver et al., 2015). Southwestern USA is undergoing one of the worst mega-droughts in modern history (Williams et al., 2022), which could be contributing to the low growth rate observed in our study. Regardless of the underlying causes, the slow growth rates reported here have important conservation implications as slow growth correlates strongly with late maturation, low natural mortality, and low resiliency to additional mortality sources. While *P. gorzugi* has not been granted full protection under the Endangered Species Act, it remains imperative to continue ongoing efforts to safeguard the species from being classified as endangered (e.g., through Conservation Candidate Agreements). This study should be taken into consideration when developing management strategies for *P. gorzugi* in the Black River. Moreover, additional research comparing our estimates to robust populations in more pristine habitats such as the Devils River in Texas is recommended to obtain further insight into *P. gorzugi* growth and to assess how habitat characteristics could influence growth trajectories.

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Data availability The data cannot be shared publicly as it may compromise the locations of species of conservation concern and the private properties where the study was conducted. However, data can be made available upon reasonable requests.

Declarations

Competing interest The authors have no competing interests to declare.

Ethical Statement Research involving Animals- Animal handling and data collection were conducted under Eastern New Mexico Universiy IACUC permit numbers: 03-02/2016, 04-27/2018, and 2019-0226-010A and the New Mexico Department of Game and Fish permit number 3621.

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