WILDLIFE BIOLOGY

Research article

Population dynamics of a desert riverine turtle, *Pseudemys gorzugi*, at the northern edge of its range

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Wildlife Biology
2025: e01355
doi: 10.1002/wlb3.01355
Subject Editor: Kaya Klop Toker
Editor-in-Chief: Ilse Storch
Accepted 07 September 2024

Estimating the key demographic parameters of animal populations can enhance our understanding of system dynamics and assist in developing and improving conservation decision–support models. The Rio Grande cooter *Pseudemys gorzugi* is a conservation reliant freshwater turtle native to lower Rio Grande River Basin (USA and Mexico), with limited knowledge regarding its natural history and population dynamics. In this study, we used seven years of capture–mark–recapture data from the northern edge of the species' range to estimate survival probabilities, changes in abundance, and the probability of transitioning between different size classes while explicitly accounting for the sampling process. We found relatively high survival probabilities across different strata, with large juveniles exhibiting the highest survival (0.98) and small juveniles the lowest (0.71). However, transition probabilities between strata were low, indicating slow somatic growth rates. Our pattern-oriented modelling revealed a low overall mean estimate of egg survival (0.024), warranting further empirical confirmation. Our study provides the first comprehensive demographic analysis of *P. gorzugi* encompassing an array of size and sex classes. Overall, we consider the population of *P. gorzugi* in the Black River robust, highlighting the importance of this river system to the species' persistence in the northern extent of its range, where the population is isolated from its broader distribution. The demographic estimates and ecological insights provided by our study offer critical data for parameterizing decision-support models to ensure that *P. gorzugi* conservation strategies are grounded in the best available science.

Keywords: Demography, desert rivers, *Pseudemys*, riverine turtle, survival probability

Introduction

Conservation strategies often use decision-support models to predict the response of animal populations to changing environmental conditions in order to evaluate tradeoffs in the face of uncertainty (Peterson and Kwak 1999, Kjelland et al. 2015, Duarte et al. 2016, Peterson and Duarte 2020). These models are often highly sensitive to the underlying assumptions pertaining to system dynamics, particularly key

demographic parameters (Duarte et al. 2017, Arnold et al. 2018, Kendall et al. 2019, Riecke et al. 2019). Unfortunately, species of conservation concern often have a dearth of information related to their ecology, population dynamics, and their role in ecosystem functions. In such cases, this often leads to the reliance on parameter estimates from surrogate species or different populations of the same species to parameterize models (Hernández-Camacho et al. 2015, Raimondo et al. 2020, Hostetler et al. 2021). Although this is a useful and often necessary approach, ontogenetic niche partitioning (Diaz et al. 2024), size- and age-specific demographic rates (Duarte et al. 2014, Mullin et al. 2020, Kastle et al. 2021, Knoerr et al. 2021), and general spatial and/or intraspecific differences in these processes can wield significant influence over population dynamics (Snover et al. 2015, Gilligan-Lunda et al. 2024). Therefore, whenever feasible, it can be useful to collect site-, population- and species-specific data to enhance the quality of the best available scientific knowledge used in models aimed at informing conservation decision making.

Turtles, a group of vertebrates that have persisted for over 200 million years, are now facing a dire situation as one of the most endangered vertebrate groups globally (Lovich et al. 2018). Remarkably, human activities have placed over half of all turtle species at risk of extinction (Lovich et al. 2018, Rhodin et al. 2018, Stanford et al. 2020). These threats encompass a wide spectrum, including overharvest for the meat market and pet trade (Mali et al. 2014a, Sung et al. 2021), agricultural expansion (Mui et al. 2016), urbanization (Hamer et al. 2018), and the proliferation of subsidized predators (Moldowan 2023). In general, turtle populations rely on high adult survivorship to counterbalance the naturally higher mortality rates of eggs and hatchlings (Lovich et al. 2018). Consequently, populations experiencing increased adult mortality are likely to decline within a relatively short timeframe (Congdon et al. 1994). While it is well understood that improving adult survival plays a key role in bolstering populations (Páez et al. 2015), recent research suggests that targeting earlier life stages can also be imperative for the recovery of imperiled populations (Knoerr et al. 2021, Bougie et al. 2022).

Understanding demographic changes in freshwater turtle populations presents a unique challenge due to their remarkable longevity, difficulty to age in the field, and delayed maturity. Collectively, this often requires turtle population studies to span multiple years, and ideally, even decades to collect the data needed to accurately estimate demographic parameters (Enneson and Litzgus 2008, Spencer 2018, Howell et al. 2019, Escoriza et al. 2020). Unfortunately, monitoring and conservation plans are rarely developed on such extended timescales (Gibbons et al. 2000). Furthermore, collecting comprehensive data on all life stages of turtles is a daunting task (Enneson and Litzgus 2008, Blamires and Spencer 2013). In particular, juvenile turtles pose a significant challenge for survey and monitoring efforts because surveyors do not readily capture or observe juveniles in natural populations (Iverson 1991, Blamires and Spencer 2013, Howell et al. 2019). It is often suspected that juvenile turtles have low encounter rates due to the sampling process. For example, juvenile turtles may inhabit different habitats and exhibit distinct behaviors compared to adults with some evidence suggesting that many turtle sampling methods are tailored to the adult segment of the population (Flaherty et al. 2008, Howley and Dinkelacker 2013, Ferreira et al. 2018, Selman 2018). However, it is also possible that juvenile turtles within a population are simply scarce. Given that turtle populations can persist as 'ghost populations' for extended periods, where the continued survival of long-lived adults masks a complete absence of recruitment (Howell et al. 2019), assessing the proportion of juveniles within a population is paramount for gaining a comprehensive understanding of overall population trends.

The Rio Grande cooter *Pseudemys gorzugi* is a medium-sized freshwater turtle that inhabits the Lower Rio Grande Basin of the southwestern United States of America (USA) and northern Mexico, making it the westernmost species within its genus (Ernst and Lovich 2009). This turtle inhabits rivers that wind through rugged desert and semiarid landscapes (Pierce et al. 2016). Ward (1984) first designated Rio Grande cooter as a subspecies of the river cooter (i.e. *P. concinna gorzugi*). Despite separating *P. gorzugi* from *P. concinna* and recognizing it as a unique species by early 1990s (Seider 1994), only a handful of published studies have focused on its ecology and biology (reviewed by Pierce et al. 2016). For decades, this species has grappled with numerous threats, chiefly stemming from alterations in river flow caused by dam construction, channelization, water extraction for fracking, and the effects of climate change (Mahan et al. 2022, Vandewege et al. 2024). Furthermore, incidental fishing catch and unlawful recreational shooting present sources of mortality that can threaten population persistence (Pierce et al. 2016). Although the US Fish and Wildlife Service (USFWS) recently considered the species for federal protection under the US Endangered Species Act (ESA), the proposal was ultimately rejected based on the Species Status Assessment (USFWS 2021). The scarcity of historical demographic data has made assessing its conservation status challenging, which also complicates the evaluation of tradeoffs in potential management actions.

Recent systematic survey efforts in the Black River, the northernmost region known to harbor a relatively robust *P. gorzugi* population (Mali et al. 2018), have yielded a valuable dataset, offering a unique opportunity to assess the species' demographic parameters. The system is unique not only due to the species' relative abundance but also because a significant proportion of the population is comprised of juvenile turtles (Mali et al. 2018), a typically uncommon observation. Using seven years of capture–mark–recapture data, we sought to estimate survival probabilities, changes in abundance, and the probability of transitioning between different size classes while explicitly accounting for the sampling process. These baseline demographic estimates can inform conservation strategies for *P. gorzugi* in the northernmost edge of its range. Additionally, these data provide baseline estimates for

comparison with future studies in other parts of the species' range and can potentially be applied to the conservation of other co-occurring freshwater turtle species.

Material and methods

Study sites

The Black River is ~ 87 km tributary of the Pecos River in Eddy County, New Mexico, USA (Fig. 1). Riparian vegetation consists primarily of netleaf hackberry *Celtis reticulata*, Fremont cottonwood *Populus fremontii*, baccharis willow *Baccharis salicina*, and broadleaf cattail *Typha latifolia* (Letter et al. 2019). We surveyed turtles at two 1500 m stretches located ~ 30 km apart. While riverine turtles have the capacity to traverse long distances, the presence of 7 km of subterranean flow between the two sites presents a significant barrier to gene flow (Vandewege et al. 2024) and we have not observed movement of turtles between these sites. The Bureau of Land Management (BLM) manages the upstream stretch, which is used primarily for recreational activities (i.e. kayaking, fishing, swimming), while the downstream stretch is located within private properties. Apart from the growing oil and gas industry, particularly notable in the lower section, no drastic environmental changes have been observed throughout our study period. However, a flood event in late June 2021, after annual surveys were completed for that year, impacted both sections of the river. For example, between 28 June and 30 June, the mean flow of the river increased to ~ 1 $m^3 s^{-1}$, reaching a maximum of 3.3 $m^3 s^{-1}$ on 29 June (USGS station 08405450). Before the flood, the mean flow in June 2021 was approximately 0.3 $m^3 s^{-1}$. Several known nesting locations were submerged for numerous days.

Surveys

We surveyed turtles using traditional hoop net traps (Memphis Net and Twine Co., Memphis, Tennessee, USA). The traps are 50.8 cm in diameter, single throated, wide mouth, with 2.5 cm mesh size and 4 hoops per net. Although hoop net traps are typically not deemed effective for capturing predominantly herbivorous *Pseudemys* turtles, both historical and recent surveys conducted on the Black River have shown the efficacy of this survey method when employing high trap effort (Degenhardt et al. 1996, Bailey et al. 2008, Mali et al. 2018). The relatively small mesh size of the trap prevents juvenile turtles from escaping while the relatively large diameter of the trap mouth allows for adult *P. gorzugi* to be captured. We stretched the traps using two hand-made wooden poles and placed a flotation device in every trap to prevent turtles from drowning. We set the traps with mouth facing downstream and tied them with a rope to available live riparian vegetation. We baited the traps with canned sardines placed in perforated containers that allowed scent dispersal but prevented bait consumption.

We conducted annual surveys from 2016 to 2022 during warm spring/summer months (May–August) when the activity of turtles is generally high (Suriyamongkol et al. 2021). We conducted surveys at each site for 6 to 12 consecutive days, maintaining consistent survey effort among years in terms of total trap effort, calculated as the number of traps deployed multiplied by the number of days the traps were in the water. However, short-term project goals for each year and the availability of traps determined trap distribution and length of the survey period. From 2016 to 2018 and in 2021, we divided each site into two equal length segments. We trapped one segment using 50 traps for 6 consecutive days, after which all traps were moved to the second segment and trapped for

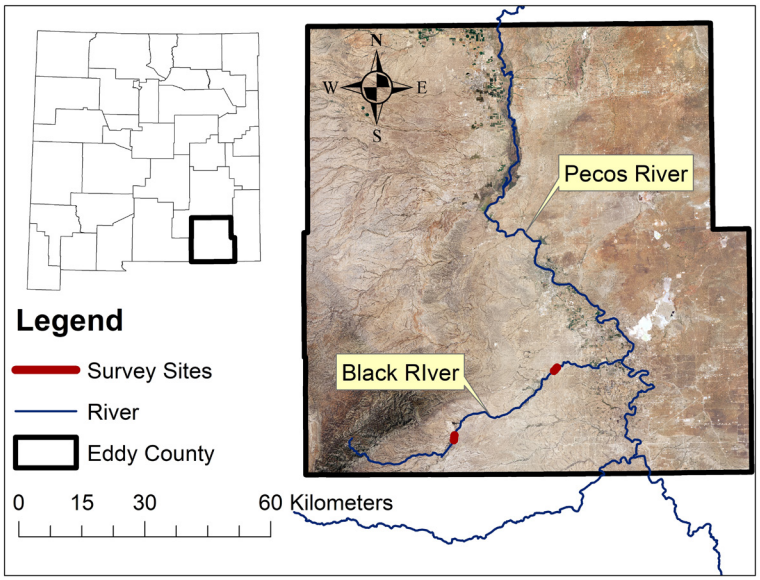

Figure 1. A map of New Mexico (top left) with bolded Eddy County, and zoomed in Eddy County, outlining approximate locations of the two study sites in the Black River where Rio Grande cooters *Pseudemys gorzugi* were surveyed from 2016 to 2022 (right).

another 6 consecutive days. This effort equaled 300 trap days per segment per site for a total of 600 trap days per site over 12 day period. In 2019 and 2022, we distributed 80 traps across the entirety of each site and surveyed the turtles for 8 consecutive days (i.e. 640 trap days per site). In 2020, we distributed 100 traps across the entirety of each site and surveyed the turtles for 6 consecutive days (i.e. 600 trap days per site). We marked turtles by notching marginal scutes for adults (Cagle 1939), inserting a PIT tag in the anterior inguinal region for juveniles (Buhlmann and Tuberville 1998), or by identifying natural plastral patterns for juveniles too small to PIT tag (Suriyamongkol and Mali 2018).

Capture–recapture analyses

We fit multistate robust design models (Kendall and Nichols 1995, Kendall et al. 1995) with a conditional likelihood abundance estimator (Huggins 1989) to our capture–recapture data to estimate apparent survival probability (ϕ), capture probability (p), and the probability of transitioning among life history stages or strata (ψ). Apparent survival is the probability an individual survives and does not permanently emigrate from a site from one primary occasion (i.e. year) to the next. Our analysis assumed population closure at a site within a primary occasion and that turtles did not exhibit temporary emigration. We related each of the estimated probabilities to covariates using logistic regression. We evaluated if apparent survival differed based on site, stratum, and flood event. We also evaluated if site and stratum influenced capture probability along with other potential covariates such as trap arrangement (above for more detail), day of year, the interaction between day of year and stratum (to account for potential differences in seasonal behavior between different strata), and a potential capture effect (i.e. probability of recapture was different than the initial probability of capture for an individual within a primary occasion). Finally, we evaluated if transition probabilities differed based on stratum and site. Turtles were divided into five strata: 1) small juveniles ≤ 80 mm straight line carapace length (CL), 2) large juveniles 80–120 mm CL, 3) small females 120–190 mm CL, 4) large females ≥ 190 mm CL, and 5) males ≥ 120 mm CL. At ~ 120 mm CL we were confident in identifying males from females based on secondary sex characteristics of males (i.e. long tails and foreclaws, and cloaca extending beyond carapace rim). We assumed that all males ≥ 120 mm are sexually mature. We further divided females in two strata based on reproduction data, assuming that all females ≥ 190 mm CL are mature and most females 120–190 mm CL are subadults (Suriyamongkol and Mali 2019, Suriyamongkol et al. 2024).

We fit models using program MARK (ver. 9.0; White and Burnham 1999) called from program R (www.r-project.org) using the package 'RMark' (ver. 2.2.7; Laake 2013). We standardized continuous covariates to have a mean of zero and a standard deviation of one prior to fitting models. We constrained the transition probabilities so that an individual turtle never changed sex and never transitioned to a smaller size class. Thus, transition probabilities we estimated were small juvenile to big juvenile, small female, big female, or male; big juvenile to small female, big female, or male; and small female to big female. All other potential transitions were assumed biologically unrealistic and were fixed to zero.

We implemented an exploratory model selection approach and used Akaike's information criterion corrected for small sample size (AIC_C) for model comparisons (Akaike 1976), where we fit all combinations of covariates and selected the model with the lowest AIC_C and highest AIC_C weight. We then estimated abundance (N) as a derived parameter from our selected model. We described model parameters by their mean, standard error, and 95% confidence interval (CI). We also interpreted our logistic regression results using predicted probabilities on the real scale and odds ratios (ORs) that were calculated from model coefficients (Hosmer and Lemeshow 2000).

Pattern orientated modeling

Our capture–recapture analyses allowed us to estimate survival of juveniles from the size at which we were able to capture them in our traps until adult life stages; however, no direct information was available to estimate egg-to-small juvenile survival. Given the potential importance of this demographic parameter to population dynamics, we aimed to estimate it using a pattern orientated approach (Swannack et al. 2009). We developed a simulation model that linked the estimated large female and small juvenile abundances in year t to the estimated small juvenile abundance in year t+1 at each site. For this simulation, we assumed the number of eggs per clutch could be approximated using a triangle distribution with a range of 5 to 14 eggs and a mode of 9.33 (Suriyamongkol and Mali 2019). We further assumed that 50% of the large females would have two clutches per year. Multiple clutching has been reported for this population, but the frequency of such events is unknown (Suriyamongkol and Mali 2019). However, multiple clutching has been readily observed in other *Pseudemys* turtles, including geographically closest *Pseudemys texana* (Mali et al. 2014b, Rose and Mali 2023). Abundances were sampled using log-normal distributions with estimates that matched the site and year specific derived abundances for each stratum from our capture–recapture analyses. The number of new small juveniles in year two through year seven was estimated as the number of small juveniles the previous year that survived and did not transition to another stratum (again, based on site-specific estimates from our capture–recapture analyses). We used a beta distribution to sample both probabilities and a binomial distribution to simulate both processes. We estimated the number of new small juveniles at a site as the difference between the number of small juveniles that year and the estimated number of small juveniles the previous year that survived and did not transition to another stratum. Egg survival was then estimated as the ratio between the estimated number of new small juveniles at the site and the number of eggs estimated the previous year. In some rare cases the stochastic nature of our simulations resulted in the number

Table 1. Comparison of the top 10 multistate robust design capture–mark–recapture models for the Rio Grande cooter *Pseudemys gorzugi* in the Black River, New Mexico, USA, sorted by Akaike's information criterion corrected for small sample size (AIC_C). We used the top model to estimate apparent survival probability (ϕ), capture probability (p), and transition probabilities among life history stages or strata (ψ).

Model	k	AICc	ΔAICc	w_i
ϕ (stratum), ψ (stratum + site), p (site + trap density + stratum + recapture + day of year + stratum × day of year)	23	14861.26	0	0.248
ϕ (stratum), ψ (stratum + site), p (site + trap density + stratum + recapture + day of year)	19	14861.54	0.28	0.216
ϕ (site + stratum), ψ (stratum + site), p (site + trap density + stratum + recapture + day of year + stratum × day of year)	24	14863.26	2.00	0.091
ϕ (stratum + flood), ψ (stratum + site), p (site + trap density + stratum + recapture + day of year + stratum × day of year)	24	14863.30	2.04	0.089
ϕ (site + stratum), ψ (stratum + site), p (site + trap density + stratum + recapture + day of year)	20	14863.55	2.29	0.079
ϕ (stratum + flood), ψ (stratum + site), p (site + trap density + stratum + recapture + day of year)	20	14863.57	2.31	0.078
ϕ (stratum), ψ (stratum × site), p (site + trap density + stratum + recapture + day of year + stratum × day of year)	26	14864.83	3.57	0.042
ϕ (site + stratum + flood), ψ (stratum + site), p (site + trap density + stratum + recapture + day of year + stratum × day of year)	25	14865.31	4.05	0.033
ϕ (stratum), ψ (stratum × site), p (site + trap density + stratum + recapture + day of year)	22	14865.37	4.11	0.032
ϕ (site + stratum + flood), ψ (stratum + site), p (site + trap density + stratum + recapture + day of year)	21	14865.59	4.33	0.029

of estimated new small juveniles being greater than the total number of small juveniles. When this occurred, we truncated the estimated number of new small juveniles to zero. We simulated this process for each site 1000 times using program R (www.r-project.org) with the 'triangulr' (ver. 1.2.1; Nursalim 2021) and 'popbio' (ver. 2.8; Stubben et al. 2024) packages. We then summarized egg survival using the mean, standard deviation, and the 0.025th and 0.0975th quantiles (hereafter referred to as the 95% CI) for each year and across all years.

Results

Although we had competing models ($\Delta AIC_C \leq 2$) in our final model set (Table 1), the parameter estimates varied little across these two competing models. Therefore, we based our inferences on the top model. Apparent survival varied by stratum (Table 2, Fig. 2). The odds of survival were 1.3, 8.0, and 3.9 times lower for large females, small juveniles, and males, respectively, when compared to small females. In contrast, the odds of survival were 2.3 times greater for big juveniles relative to small females. There was no evidence to support an effect of site or the 2021 flood event on apparent survival probability.

Transition probabilities varied by stratum and site, where turtles grew faster at the upper site (Fig. 3). As expected, turtles tended not to skip strata. For example, small juveniles likely stayed the same size or transitioned to large juvenile and rarely jumped to a small female, a large female, or a male. Similarly, a large juvenile likely stayed the same size or transitioned to a small female or male. They were not likely to skip to a large female stratum.

Capture probability was lower at the lower site (OR = 0.63), increased with greater number of traps in the water at once (OR = 2.02), and increased following initial capture (OR = 1.82). Although the odds of capture were 1.16 times higher for large juveniles when compared to small females, the odds of capture were 1.74, 1.53, and 1.07 times lower for large females, small juveniles, and males respectively. Capture probability decreased with day of year for small females, large females, big juveniles, and males, but it increased with day of year for small juveniles.

Abundance estimates varied across years and strata, with mean abundances generally greater in the upper site (Fig. 4). For example, for the larger female class size, the mean annual abundance estimates ranged from 10 to 72 and 41 to 187 at the lower and upper sites, respectively. However, small juveniles had similar overall means for both sites. The annual estimates of small juveniles also varied the most, from 5 to 98 at the lower site and 3 to 59 at the upper site. Based on our pattern orientated modeling, egg survival ranged from 0.004 to 0.13 at our lower site, with an overall mean estimate of 0.045 (SD = 0.064, 95% CI: < 0.001–0.210) across our study period. Egg survival was lower at our upper site, ranging from 0.002 to 0.071 with an overall mean estimate of 0.024 (SD = 0.032, 95% CI: < 0.001–0.111) across our study period.

Discussion

Through intensive capture–mark–recapture surveys conducted over seven consecutive years, our study provides the first comprehensive demographic analysis of *P. gorzugi* encompassing an array of size and sex classes. Previously, the only survival estimate for *P. gorzugi* was a combined male and female adult annual survival rate of 81% from the Devils River, Texas (Sirsi 2021). In the recent Species Status Assessment (SSA), the USFWS used the slider turtle *Trachemys scripta* and painted turtle *Chrysemys picta* as a surrogate species to describe demographic estimates of nest survival and cumulative juvenile survival from 1–4 years of

Table 2. Parameter estimates with mean, standard error (SE) and 95% confidence intervals (CI) for apparent survival probability (ϕ), capture probability (p), and the probability of transitioning among life history stages or strata (ψ) for the Rio Grande cooter *Pseudemys gorzugi* on the Black River, based on the selected model.

Parameter	Mean	SE	Lower CI	Upper CI
Φ				
Intercept	2.97	0.50	2.00	3.94
Stratum: big female	−0.27	0.64	−1.52	0.99
Stratum: juvenile	−2.08	0.54	−3.14	−1.02
Stratum: big juvenile	0.82	0.97	−1.08	2.72
Stratum: male	−1.36	0.51	−2.37	−0.36
Ψ				
Intercept	−3.01	0.26	−3.53	−2.50
Stratum: big female	−2.16	0.45	−3.04	−1.28
Stratum: big juvenile	3.36	0.34	2.69	4.03
Stratum: male	0.21	0.23	−0.25	0.67
Site: upper	1.61	0.27	1.08	2.15
p				
Intercept	−2.80	0.10	−2.98	−2.61
Site: upper	−0.46	0.07	−0.59	−0.33
Trap density: high	0.70	0.06	0.59	0.82
Stratum: big female	−0.55	0.11	−0.77	−0.33
Stratum: small juvenile	−0.42	0.16	−0.74	−0.11
Stratum: big juvenile	0.15	0.10	−0.04	0.34
Stratum: male	−0.06	0.09	−0.24	0.11
Recapture	0.60	0.06	0.48	0.72
Day of year	−0.24	0.08	−0.39	−0.10
Stratum: big female × day of year	−0.02	0.11	−0.23	0.19
Stratum: small juvenile × day of year	0.32	0.14	0.06	0.59
Stratum: big juvenile × day of year	0.07	0.10	−0.12	0.26
Stratum: male × day of year	0.13	0.09	−0.03	0.30

age (0–83% and 18.4%, respectively; USFWS 2021). The demographic insights gained through our study will improve future assessments and inform the development of more targeted conservation strategies. Blamires et al. (2005) pointed out that the difference in somatic growth rate and maximum body size among similar species of freshwater turtles can lead to different estimates of population growth rates, and therefore congeners are not always good surrogates for determining demographic influences on population growth. Our estimates, in combination with the recent study of somatic growth for this population (Suriyamongkol et al. 2024), likely provide more accurate information when developing life tables for *P. gorzugi* and estimating population growth.

Remarkably, the Black River population we studied not only boasts a higher overall abundance than that observed in mainstem rivers like the Pecos and Rio Grande but also features a notable presence of juveniles. To the best of our knowledge, Black River is the sole river system in New Mexico, and possibly across the entire species' distribution, where small juveniles are observed and captured using hoop-net traps. We were able to estimate juvenile demographic parameters, a parameter typically challenging to obtain for

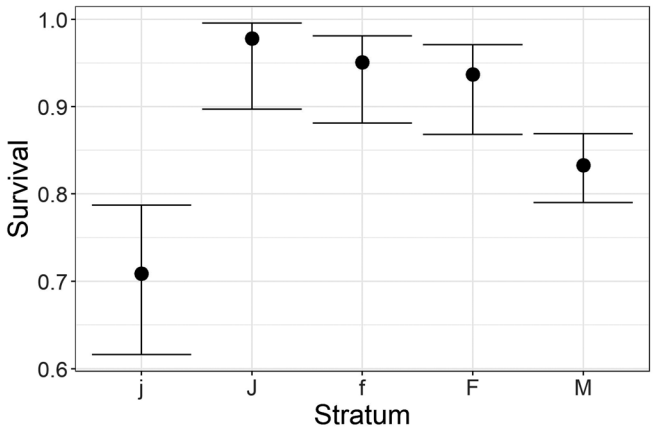

Figure 2. Mean annual survival probabilities (including 95% confidence intervals) of the Rio Grande cooter *P. gorzugi* in the Black River, New Mexico, based on the capture–mark–recapture surveys (top model in Table 1), conducted at two distinct sections of the river and divided into five life history stages (strata): j – small juveniles, J – large juveniles, f – small females, F – large females, and M – males (see capture–recapture analyses for more details).

freshwater turtle populations due to the generally low capture success of smaller individuals (Pike et al. 2008, Garcés-Restrepo et al. 2019). Our observed population composition sharply contrasts with locally abundant populations in Texas. For example, surveys of *P. gorzugi* in the pristine Devils River have revealed a notable lack of juvenile turtles and an abundance of adults, skewed toward males, and generally larger than the adults captured in the Black River (Bailey et al. 2014, Pierce et al. 2016, Sirsi 2021). Whether the apparent lack of juvenile turtles is an artifact of low detection, or a true representation of the Devils River population can only be speculated at this time. Regardless, this difference raises questions about population dynamics and conservation strategies across the species range. This uncertainty, along with the growing evidence that the Black River population is isolated from its broader distribution (Vandewege et al. 2024), suggests the Black River provides important habitat at the northern extent of *P. gorzugi* range that may be essential for the species' persistence.

As anticipated, the smallest size class exhibited the lowest survival (Fig. 2), likely due to higher susceptibility of smaller turtles to predation (Janzen et al. 2000, Micheli-Campbell et al. 2013, Mullin et al. 2020). On average, the survival probability of small juveniles in the Black River (71%) aligns with indirect estimates of juvenile survival for turtles (65%; Pike et al. 2008). We consider the survival estimates of small juveniles in the Black River robust based on freshwater turtle natural history. The sustainability of chelonians relies disproportionately more on high adult survival to offset naturally high mortality of eggs, with even the slightest increase in adult mortality (e.g. ≥ 2%) often posing a threat to population persistence (Congdon et al. 1994, Spencer et al. 2017). Both small and large females exhibited relatively high survival, which is within the range observed in other freshwater turtle populations (79–97%; Shine and Iverson 1995,

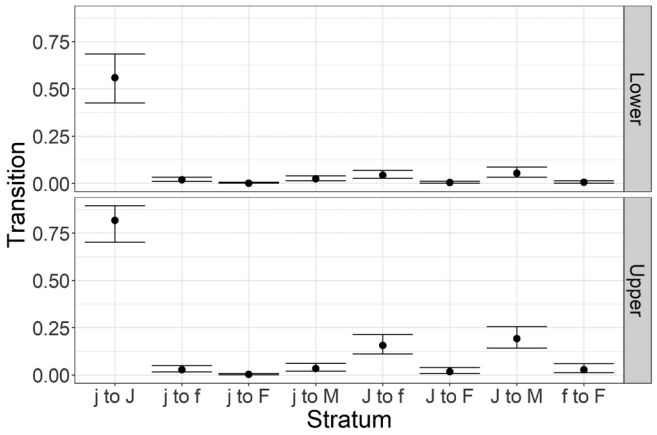

Figure 3. Mean transition probabilities (including 95% confidence intervals) between different life history stages (strata) of the Rio Grande cooter *P. gorzugi* in the Black River, New Mexico, based on the capture–mark–recapture surveys conducted at two distinct sections of the river (lower and upper); j – small juveniles, J – large juveniles, f – small females, F – large females, and M – males (see capture–recapture analyses for more details).

Flaherty et al. 2008, Rees et al. 2009, Feng et al. 2019). Despite the positive outcome for juveniles, the odds of survival for large juveniles are two times greater when compared to small and large females, which raises questions about the sources of mortality in female turtles, their impact on population persistence, and the potential for addressing these issues through conservation measures.

Although abundance estimates were generally higher in the upper site, our analysis revealed a gradual decline of large females and males from 2017 to 2020 (Fig. 4). Reports of fishhook ingestion, a notable contributor to additive mortality for freshwater turtles (Steen et al. 2014, Steen and Robinson 2017), raise concerns for the *P. gorzugi* population. Additionally, documented cases of recreational shooting for target practice in the Black River (Pierce et al. 2016, Suriyamongkol et al. 2019) further exacerbate these concerns, even in the upper reaches of the river which are predominantly utilized for recreational activities. An increase in the predation of nesting females may also contribute to the observed abundance patterns. Northern racoon *Procyon lotor* is common in the area and is a major predator of *P. gorzugi* nests (unpubl.). Since adult females spend a disproportionately greater amount of time on land (e.g. for nesting) compared to males and juveniles, there is a possibility that *P. lotor* may also prey on female turtles (Feinberg and Burke 2003, Karson et al. 2018). At the upper site, we incidentally found five turtle shells on land, including some from turtles we had previously marked. While the exact causes of mortality for these turtles remain unclear, at least one shell exhibited a bullet wound and another showed signs of carnivore predation, underscoring the variety of threats these turtles face.

Reptiles have a significant positive relationship between somatic growth and adult mortality rates (Shine and Iverson 1995). A somatic growth rate assessment for *P. grozugi* in the Black River revealed exceptionally low Brody growth coefficients (i.e. 0.05 and 0.08 for females and males, respectively), lower than any other *Pseudemys* species (Suriyamongkol et al. 2024). Suriyamongkol et al. (2024) also found slightly greater somatic growth rates in the upper segment of the river, which is in concordance with higher transition probabilities we estimated in the upper segment. The river segments near springs and closer to the headwaters may offer more favorable conditions regarding water quality and food availability (Suriyamongkol et al. 2022), potentially accounting for

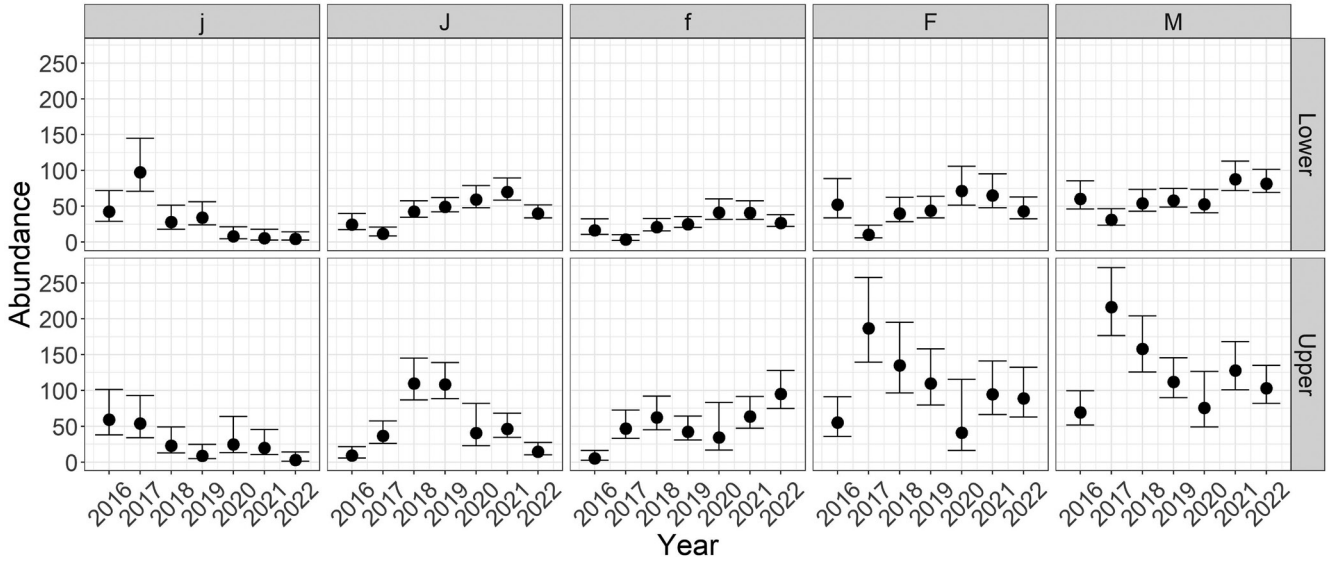

Figure 4. Mean abundance estimates (including 95% confidence intervals) of the Rio Grande cooter *P. gorzugi* in the Black River, New Mexico, based on the capture–mark–recapture surveys conducted at two distinct sections of the river (lower and upper) divided into five life history stages (strata): j – small juveniles, J – large juveniles, f – small females, F – large females, and M – males (see capture–recapture analyses for more details).

the observed differences. We found overall low transition probabilities from large juveniles to small females (0.16 and 0.04 for the upper and lower site, respectively) and especially from small to large females (0.03 and 0.01 for the upper and lower site, respectively), which is also in concordance with slow somatic growth (Suriyamongkol et al. 2024). Given the somatic growth patterns, transition estimates, and the observed smaller body size of adult females in the Black River compared to the Devils River, it is important to maintain monitoring efforts to adaptively respond to any potential changes in survival probabilities, especially in the face of escalating anthropogenic pressures.

Egg survival stands as the sole survival parameter we were unable to estimate from empirical data, primarily due to the challenges posed by the rugged terrain of the Chihuahuan Desert in locating nests. While the egg survival estimates we approximated using a pattern-orientated simulation modeling approach aligns with life history characteristics of turtles, these estimates fall on the lower end of the spectrum compared to findings from studies on other freshwater turtle species (Congdon et al. 1993, Blamires et al. 2005, Bougie et al. 2020, Congdon et al. 2022). Our estimates reflect survival from the egg to the small juvenile, and there is likely a significant gap of several years between these two stages. Although we cannot definitively determine whether most mortality events are linked to eggs or hatchlings, we lean towards the former as a more plausible scenario. Females generally do not show parental care, leaving clutches defenseless against a suite of terrestrial predators, ranging from invertebrates such as red imported fire ants *Solenopsis invicta* to measocarnivores such as *P. lotor*. Additionally, it is important to clarify that our estimates pertain to individual egg survival, and we acknowledge that eggs from the same clutch typically share a common fate, especially in cases of predation or catastrophic environmental events (e.g. floods). Our derived estimate of egg survival represents the first attempt at this key demographic parameter for this unique population. However, these insights underscore the critical need for direct nest survival estimates to deepen our understanding of population dynamics. Until then, the egg survival estimates we present herein should be used with some caution.

Despite significant fluctuations in small juvenile abundance over seven years, the clear evidence of successful reproduction highlights the Black River system's ecological significance and importance for *P. gorzugi* conservation. With the recent decision to withhold federal protection measures, it seems any potential future conservation efforts will likely take on a more localized approach (i.e. lead by state and local environmental services agencies). In the face of uncertainty, decision-support models will likely play a crucial role in guiding these conservation efforts. Such models can help evaluate the potential outcomes of different strategies in achieving multiple (sometimes competing) quantifiable conservation and management objectives, allowing managers to make informed decisions that balance ecological benefits with practical considerations. The demographic estimates and ecological insights provided by our study are likely invaluable in this context, as they offer critical data for parameterizing these models to ensure that *P. gorzugi* conservation strategies are grounded in the best available science.

Acknowledgements – We are grateful to the Bureau of Land Management and private landowners for their support and access to the study sites. We thank numerous undergraduate and graduate students for their help with surveys over the years. A. Duarte would also like to acknowledge support from the U.S.D.A. Forest Service, Pacific Northwest Research Station. The use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.
Funding – This study was supported by the New Mexico Department of Game and Fish and United States Fish and Wildlife Service Endangered Species Conservation Fund Grants: section 6 Program.
Permits – All trapping activities were conducted under New Mexico Department of Game and Fish Scientific Research Permit 3621 and Eastern New Mexico University Institutional Animal Care and Use Committee permits (3-02/2016,04-27/2018, and 2019-0226-010A).

Author contributions

Ivana Mali: Conceptualization (equal); Data curation (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (equal); Writing - original draft (equal); Writing - review and editing (equal). **Adam Duarte**: Conceptualization (equal); Formal analysis (lead); Funding acquisition (supporting); Investigation (supporting); Methodology (equal); Writing - original draft (equal); Writing - review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01355.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.gxd2547vx (Mali and Duarte 2024).

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