



Special Section on Gopher Tortoise Mark-Recapture

Survival of Immature Gopher Tortoises Recruited into a Translocated Population

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ABSTRACT Population manipulations such as translocation and head-starting are increasingly used as recovery tools for chelonians. But evaluating success of individual projects can require decades of monitoring to detect population trends in these long-lived species. Furthermore, there are often few benchmarks from stable, unmanipulated populations against which to compare demographic rates, particularly for the immature stages. We used 8 years of mark-recapture data to estimate apparent survival of immature gopher tortoises (*Gopherus polyphemus*) recruited into an introduced population of gopher tortoises first established on St. Catherines Island, Georgia, USA, in 1987. During 2006–2013, we conducted targeted trapping of immature gopher tortoises and compared survival of the hatchling, juvenile and subadult stages among treatments: individuals released shortly after hatching from eggs obtained from gravid female founders (direct releases), individuals reared in captivity for 6–9 months following hatching (head-starts), and individuals first encountered as free-ranging, wild-recruited offspring (wild recruits). Among the candidate models we examined, the best fit model included additive effects of tortoise stage and treatment; however, overlapping 95% credible intervals among treatments (CrI) suggested that survival did not vary significantly among treatments. Annual apparent survival increased over the immature period, highlighting the importance of calculating separate estimates for the different immature stages. Across all treatments, the additive model estimated annual apparent survival probability to be 0.37 (CrI = 0.25–0.48) for hatchlings, 0.71 (CrI = 0.61–0.81) for juveniles, and 0.83 (CrI = 0.74–0.94) for subadults. Our study, in combination with previous monitoring efforts at St. Catherines Island, provides strong evidence that the translocation and subsequent population augmentation efforts have been successful in establishing a robust population of gopher tortoises. Additionally, our results provide estimates of demographic rates for life stages that are poorly understood but critical to understanding population dynamics of this imperiled species. © 2020 The Wildlife Society.

KEY WORDS apparent survival, augmentation, demographic rates, gopher tortoise, *Gopherus polyphemus*, immature, life stage, population viability, recovery, translocation.

Many turtle species are characterized by long life spans, delayed sexual maturity, and relatively low rates of annual fecundity (Gibbons 1987, Congdon et al. 1993, Heppell 1998). These combined traits make populations vulnerable to chronic demographic perturbations (Congdon et al. 1993) and slow to recover after perturbations have subsided (Bailey and Guyer 1998, Hall et al. 1999, Tucker et al. 2001). Increased anthropogenic threats have made turtles among the most threatened vertebrate groups (Lovich et al. 2018). Increasingly, population manipulations such as translocation (the intentional movement of animals from one location to another) and head-starting (rearing of offspring in captivity until they reach a size less vulnerable to predation) have become important tools for managing turtle

populations (Frazer 1992, Turtle Conservation Fund 2002, Germano and Bishop 2009, Burke 2015). But quantifying population responses to management interventions is challenging and often requires long-term monitoring. In addition, for many turtle species, there are few estimates of demographic rates from stable populations to serve as benchmarks for comparison. As a result, it can be difficult to identify which demographic process is causing the decline or impeding recovery efforts.

Immature stages in particular are often poorly understood, contributing to a major gap in life-history data for most turtle species (Carr 1952, Germano 1994, Pike et al. 2008). Immature turtles are often more cryptic and secretive than adults, and ontogenetic changes in behavior, diet, or habitat associations can make immature turtles more difficult to detect even when adults can be readily found (Carr 1952, Pike et al. 2008). In addition, trapping techniques used for adults may be less effective for capturing smaller size classes,

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contributing to the underrepresentation of immature individuals in turtle population surveys or mark-recapture studies (Hellgren et al. 2000). As a result, immature turtles are often presumed to be in low abundance and to experience high levels of mortality, although these assumptions have been challenged by Pike et al. (2008).

Even for well-studied turtle species such as the gopher tortoise (*Gopherus polyphemus*), the ecology of immature animals remains elusive. Burrows are commonly surveyed to estimate population size and density of this fossorial species through standardized techniques such as line-transect distance sampling (Smith et al. 2009). But most surveys detect few small burrows, and it is often unclear whether the cause is low abundance of immature tortoises or poor detection of their burrows (Smith et al. 2009, Gaya 2019). Although vegetation structure can impede detection of burrows in all size classes, burrows of immature animals are especially likely to go undetected in vegetation that is overgrown or has not been recently burned (Howze and Smith 2019). In addition to their burrows being difficult to detect, immature gopher tortoises are infrequently encountered on the surface, spending as much as 80% of their time in their underground burrows (Auffenberg and Iverson 1979). Thus, few radio-telemetry studies have focused on immature gopher tortoises.

Of the few survival estimates from mark-recapture studies on gopher tortoises, almost all report only a single estimate for immature animals (Tuberville et al. 2008, 2014; Howell et al. 2020); however, as has been recently reported in the congeneric Mojave desert tortoise (*G. agassizii*; McGovern 2019), survival likely increases with size over the immature period. Except in a few studies (Tuberville et al. 2015, Wright 2016, McKee 2019), separate estimates for hatchling, juvenile, and subadult gopher tortoises are generally lacking and remain an important research need (Germano 1994, Smith et al. 2006, Tuberville et al. 2009). Moreover, because gopher tortoises are declining throughout their range (U.S. Fish and Wildlife Service [USFWS] 2013), it is imperative to quantify these unknown life-history characteristics to better assess the stability of remaining populations.

The population of gopher tortoises on St. Catherines Island has been the subject of long-term monitoring and management. The population was established through multiple translocations starting in 1987, but the primary translocation occurred in 1994. Based on mark-recapture efforts from 1994–2006, Tuberville et al. (2008) estimated high rates of post-release apparent survival in translocated immature and adult gopher tortoises. But because recapture efforts targeted the larger size classes that comprised the majority of the founding population, survival rates of offspring recruited following translocation remain unknown. Moreover, because the authors combined all immature animals into a single stage class, additional analysis is required to fully quantify the dynamics of these smaller size classes. Finally, following initial translocation efforts, additional population augmentation measures have been implemented, including the collection of eggs from gravid female founders and the release of resulting

hatchlings (direct releases) and short-term head-starting of offspring (head-starts; Tuberville et al. 2015). The ultimate success of population manipulations is whether the population can be self-sustaining, and long-term monitoring of the St. Catherines Island gopher tortoise population provided a rare opportunity to assess this metric.

During 2006–2013, we conducted targeted trapping of immature gopher tortoises. Our first objective was to refine estimates of immature survival by calculating separate apparent survival estimates for the hatchling, juvenile, and subadult stages. We predicted that survival would increase over the immature period, with survival lowest in hatchlings and highest in subadults. Our second objective was to determine whether apparent survival varied among direct releases, head-starts, and wild-recruited offspring produced following translocation. We expected that, after accounting for size, survival of immature tortoises would be similar among treatments.

STUDY AREA

St. Catherines Island is a 5,670-ha (16 km long, 3.2–4.8 km wide) privately owned barrier island with limited human access in Liberty County in southeast Georgia, USA, located approximately 6.5 km off the mainland. Elevation at the study site ranged from 0 to 30 m above sea level. Average annual rainfall is 110 cm, with nearly half falling during June–September, but annual rainfall was ≥ 20 cm below average during 4 years of the study period (Smith et al. 2016). Summer (Jun–Aug) high temperatures averaged 32.2°C, with overnight winter (Nov–Feb) lows averaging 7.2°C. Our study took place in a 162-ha pasture at the northern end of the island. The pasture was created in 1950 for cattle grazing, which was discontinued in 1982. The pasture was planted with Bahia grass (*Paspalum notatum*), Bermuda grass (*Cynodon* spp.), spangle grass (*Chamanthium latifolium*), and broomsedge (*Andropogon* spp.) but also retained some native plants, such as narrowleaf silk grass (*Pityopsis graminifolia*), cockspur prickly pear (*Opuntia pusilla*), queen's delight (*Stillingia sylvatica*), hairy lespedeza (*Lespedeza hirta*), and butterfly pea (*Centrosema* spp.; Harris 2014). The former pasture had a sparse overstory of mature pines, including longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pines but no mid-story shrub layer (Fig. 1). The absence of a mid-story shrub layer and the short height of groundcover facilitated detection (and thus targeted trapping) of burrows of immature gopher tortoises (Gaya 2019, Howze and Smith 2019). The open savanna-like conditions were maintained by mowing on an approximate 3-year rotation, with some portion of the pasture mowed each year during winter months (Nov–Feb). The pasture provided habitat for gopher tortoises on the island but has become reduced to approximately 108 ha over time because of natural succession (J. L. Gaskin, Georgia Southern University, personal communication). The potential predators on nests and immature gopher tortoises during the study (2006–2013) included raccoons (*Procyon lotor*), feral hogs (*Sus scrofa*), and red imported fire ants (*Solenopsis invicta*), although coyotes (*Canis latrans*) and



Figure 1. Gopher tortoise habitat at St. Catherines Island in southeast Georgia, USA, 2006–2013. Periodic mowing is used to maintain the open landscape, which is a former cattle pasture with sparse mature pines, no shrub midstory, and a grassy understory that retains some native herbaceous species. Note white stakes in the right foreground marking the patch of sand associated with the burrow of an immature gopher tortoise naturally recruited into the translocated population. Photo by K. Buhlmann.

nine-banded armadillos (*Dasypos novemcinctus*) have since become established on the island (T. M. Norton, St. Catherines Island Foundation, personal observation).

METHODS

Study Population and Sampling

Gopher tortoises occur on the adjacent mainland but were not native to St. Catherines Island. The St. Catherines Island population was established through multiple translocations and subsequent natural recruitment. St. Catherines Island Foundation (SCIF) staff released an estimated 25–30 tortoises between 1987 and 1994, although they did not record details. In 1994, SCIF staff translocated a population of 74 tortoises from a development site in Bulloch County, Georgia to the island (Jones 1996, Tuberville et al. 2008). Starting with the primary translocation in 1994, biologists permanently marked all tortoises by notching unique combinations of marginal scutes (as described in Jones 1996) prior to release. During 2006–2013, we released 21 individual waif (i.e., primarily injured and subsequently rehabilitated) tortoises. We also permanently marked any unmarked tortoises we encountered. We presumed unmarked adults were translocated prior to 1994 and unmarked juveniles resulted from post-translocation reproduction (i.e., wild recruits). Based on growth rates of immature tortoises on St. Catherines Island, it takes hatchlings ≥ 10 years to reach maturity (Harris 2014); thus, we felt confident assigning unmarked animals to 1 of the 2 categories.

Additionally, we obtained eggs from gravid females or wild-collected nests during 2005–2009 to study the population's mating system and to evaluate head-starting as a management tool (Tuberville et al. 2011, 2015). We obtained hatchlings from 7–16 clutches/year (Tuberville

et al. 2015). We uniquely marked all resulting hatchlings prior to release. We directly released some (39–58 mm midline carapace length [MCL] at release) shortly after hatching in fall, whereas we retained others (53–80 mm MCL at release) for indoor head-starting and fed and kept them active until the following spring. Tuberville et al. (2015) describe husbandry and release details. An estimated 45 potential adult females were present in the population (Tuberville et al. 2011). Assuming that, on average, 73% of mature female gopher tortoises reproduce each year (Diemer and Moore 1994), head-starts and direct releases represented only a portion of immature tortoises available for capture in the population because we did not detect all nests in any given year.

During 2006–2013, we targeted burrows of immature tortoises for trapping by placing live wire traps (models 201, 202, 205; Tomahawk Live Trap LLC, Tomahawk, WI, USA) at entrances of active burrows. In addition to conducting informal transect surveys throughout the mowed pasture, we marked and mapped burrows of immature tortoises encountered while tracking radio-telemetered tortoises and while searching for nests as part of head-starting and mating-system studies (Tuberville et al. 2011, 2015; Harris 2014). We shaded traps with burlap cloth or cut vegetation and checked traps at least twice daily. Trapping effort varied among years and we did not record details of effort. We identified marked tortoises by their unique notch code, measured their MCL to the nearest 1 mm, weighed them to the nearest 1 g, and released them at their point of capture ≤ 24 hours later. We assigned a notch code to unmarked animals at their first capture but otherwise handled them similarly. We used MCL to assign tortoises to demographic stage classes as follows: hatchlings (< 68 mm), juveniles (68 mm to < 130 mm), and subadults (130 mm to < 230 mm, without male secondary sex characteristics such as plastron concavity or gular protrusion). We performed all procedures in accordance with Georgia scientific collecting permits (29-WCH-07-137, 29-WCH-07-74, 29-WBH-08-188, 29-WBH-09-68, 29-WBH-10-99, 029-WBH-12-166, 29-WJH-13-83) and University of Georgia Animal Use Permits (A2005-10247, A2008-10198, A2011 05-20-Y1).

Statistical Analyses

We used the information collected at first handling (release for head-starts and direct releases, initial capture for unmarked wild-recruited individuals) and subsequent captures to construct a capture history for each tortoise. For every year (t) of the study (2006–2013), we represented each individual's capture status as a value of 1–5 based on its stage class (c): 1 = pre-hatch, 2 = hatchling, 3 = juvenile, 4 = subadult, 5 = unknown or dead. We used a size-based categorization for our stage classes because body size likely influences many factors that affect survival, such as susceptibility to predation. Moreover, because tortoises exhibit different growth rates depending on habitat quality and length of growing season (Mushinsky et al. 1994, Aresco and Guyer 1999) and because chelonians are difficult to reliably age (Wilson et al. 2003), size rather than age may

better enable comparisons among populations. Finally, sexual maturity (and thus transition from subadult to adult class) is based on size rather than age (Mushinsky et al. 1994). Because the trap size deployed in our study excluded most adult tortoises, we omitted the adult stage class from our analysis. For individuals recovered dead ($n=2$), we fixed the capture state to 5 for all subsequent years.

We used an open-population multistate Cormack-Jolly-Seber model (Brownie et al. 1993, Schwarz et al. 1993) to estimate stage class-specific annual probabilities of capture (p_c), apparent survival (ϕ_c), and transition to the next stage class given survival (Ψ ; Fig. 2). We allowed capture probability to also vary by year. Because direct releases and head-starts were hatched in captivity, we fixed the capture probability of these groups to 1 for the pre-hatch class. We also fixed the pre-hatch capture probability of wild recruits to zero. Because tortoises could potentially disperse from the study area during the study period, we chose to estimate apparent rather than true survival. To account for the unequal sample sizes of the hatchling size class in each treatment group, we allowed capture rate of the hatchling size class to vary by treatment. We defined the treatments as wild recruit (first encountered as a free-ranging unmarked animal), direct release (hatched in captivity but released within 4–6 weeks of hatch date), and head-start (reared in captivity for 6–9 months prior to release). Using the described parameterization (Fig. 2), we fit the data to 3 candidate models. The first model considered survival to vary only by the tortoise stage class (stage-only model), the second included an additive effect between tortoise stage and treatment (additive model), and the third included an interactive effect between tortoise stage and treatment (interactive model). We compared the candidate models using Deviance Information Criterion (DIC) and model weights (w_i ; Spiegelhalter et al. 2002).

We analyzed our models in a Bayesian framework following the approach of Kéry and Schaub (2012). We used Markov chain Monte Carlo (MCMC) sampling in JAGS (Plummer 2003) via R (version 3.5.1; www.r-project.org, accessed 6 Oct 2019) using the package runjags (Denwood 2016) to approximate the posterior distribution of all model parameters. We used uniform priors for all transition and survival probabilities. We tested for chain convergence using the Gelman-Rubin statistic (Gelman et al. 2003) and extended simulations to meet the minimum iteration suggestion of the Raftery-Lewis diagnostic (Bernardo et al. 1992). We considered convergence likely when the Gelman-Rubin statistic dropped below 1.1 for all monitored parameters. We ran all models for $\geq 30,000$ iterations.

RESULTS

We captured an average of 59 immature tortoises/year (range = 13–133). Overall, we recorded 473 captures of 284 individual immature tortoises, with individuals captured on average 1.7 times (range = 1–8 times). Of these, 170 individuals were direct releases (238 captures), 41 were head-starts (78 captures), and 73 were wild recruits (157 captures). We recovered 2 dead tortoises (both direct releases).

Based on DIC, the best model was the additive model (stage + treatment; DIC = 911.5, $w_i = 0.78$). The stage-only model ($\Delta DIC = 3.0$, $w_i = 0.18$) and the interactive model ($\Delta DIC = 6.1$, $w_i = 0.04$) received less support. We used the additive model to estimate annual apparent survival for each tortoise stage class and treatment (Fig. 3). However, the 95% credible intervals (CrI) for apparent survival rates within each stage overlapped considerably, suggesting there was no significant difference in apparent survival rate among treatments.

Across all treatments, the additive model estimated annual apparent survival probability (ϕ_c) to be 0.37 (CrI = 0.25–0.48) for hatchlings, 0.71 (CrI = 0.61–0.81) for juveniles, and

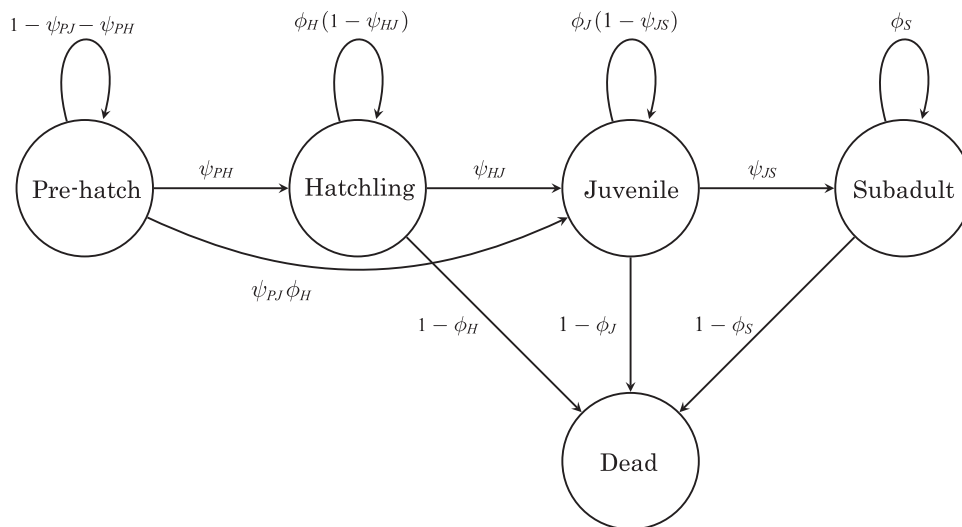


Figure 2. Diagram illustrating the Bayesian multistate mark-recapture model used to analyze survival and transition probabilities between size classes of immature gopher tortoises recruited into a translocated population at St. Catherines Island in Georgia, USA, based on mark-recapture conducted from 2006–2013. Multistate parameters include transition probabilities between size classes (ψ) and apparent survival probabilities (ϕ) for each size class: pre-hatch (P), hatchling (H), juvenile (J), and subadult (S).

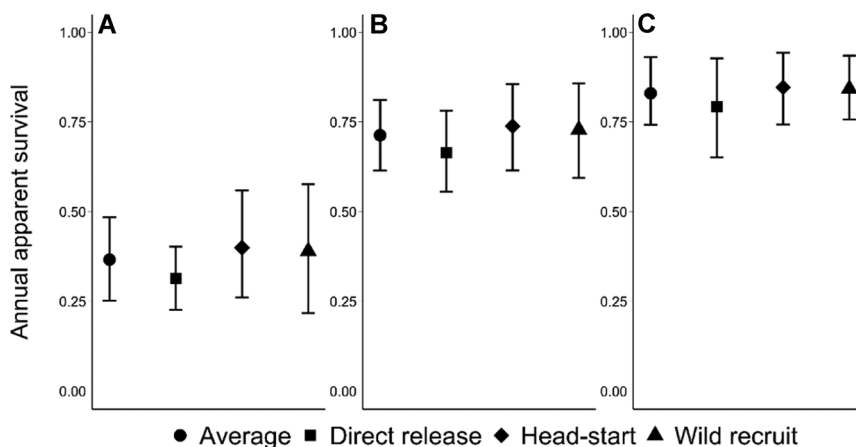


Figure 3. Apparent survival for immature gopher tortoises recruited into a translocated population at St. Catherines Island in Georgia, USA, 2006–2013, based on our additive model. We assigned tortoises to a stage class (hatchling [A], juvenile [B], or subadult [C]) based on their midline carapace length. There were 3 treatment groups defined as wild recruit (first encountered as a free-ranging unmarked animal), direct release (hatched in captivity but released within 4–6 weeks of hatch date), and head-start (reared in captivity for 6–9 months prior to release). We also estimated an average for each stage class across all treatments.

0.83 (CrI = 0.74–0.94) for subadults. Hatchlings had a lower apparent survival than the other immature classes (Fig. 3). Although the point estimate was higher for the subadult stage class relative to the juvenile stage class, their 95% credible intervals overlapped considerably (Fig. 3). Across all stages, directly released individuals had the lowest estimated apparent survival (0.54; CrI = 0.21–0.80) of the 3 treatments, followed by wild recruits (0.62; CrI = 0.32–0.88) and head-starts (0.63; CrI = 0.33–0.88).

Estimated annual conditional probability for hatchlings transitioning to the juvenile stage (given survival) was 0.89 (CrI = 0.78–0.98). The probability of transitioning from a juvenile to a subadult was 0.35 (CrI = 0.24–0.45). Our additive model estimated the mean hatchling capture probability to be 0.49 (CrI = 0.38–0.61) for direct releases, 0.41 (CrI = 0.28–0.55) for head-starts, and 0.37 (CrI = 0.22–0.51) for wild recruits. For juveniles, the mean capture probability was 0.43 (CrI = 0.30–0.57) for direct releases, 0.52 (CrI = 0.33–0.70) for head-starts, and 0.45 (CrI = 0.28–0.65) for wild recruits. The 95% credible intervals for these capture probability estimates overlapped for all treatments. The mean capture probability for subadults for all treatments was 0.43 (CrI = 0.33–0.53).

DISCUSSION

Survival of gopher tortoise offspring recruited on St. Catherines Island increased over the immature period, with the lowest annual apparent survival in the hatchling size class and greatest survival in the subadult size class. Our findings conform to the general trend of type III survivorship first documented in turtles by Iverson (1991), in which mortality is inversely related to age (or size) class. Several recent studies have reported that survival of immature gopher tortoises is significantly lower than that of adults, with immature annual apparent survival ranging from 70–84% among sites compared to 87–98% in adults (Tuberville et al. 2008, 2014; Howell et al. 2020). The wide range in

immature apparent survival estimates among sites is likely due in part to site-specific factors such as habitat quality or predator abundance (Smith et al. 2013, Tuberville et al. 2014) but may also be influenced by the size distribution of animals comprising the immature class. Predicted annual survival increases with increasing size in immature desert tortoises (from 54% at 60 mm MCL to 95% at 150 mm MCL; McGovern 2019) and age in other turtle species (Fernández-Chacón et al. 2011, Arsovski et al. 2018); however, few studies have investigated whether survival also increases over the immature period in gopher tortoises. Wright (2016) and McKee (2019) reported that annual apparent survival of subadult gopher tortoises is significantly higher than that of juveniles, although neither provided separate estimates for the hatchling stage.

Estimates of first-year survival of hatchling gopher tortoises have varied among studies, in part because attempts to precisely estimate survival have been plagued by high mortality rates and low sample sizes. Based on a meta-analysis of 4 previous studies (Smith 1992, Butler and Sowell 1996, Epperson and Heise 2003, Pike and Seigel 2006) with sample sizes of 20–48 individuals in which annual survival ranged from 0–40%, Perez-Heydrich et al. (2012) estimated hatchling annual survival at 12.8%. The authors also conducted one of the few multi-year field studies and reported that hatchling survival varied from 6.5–52.9% among 3 cohorts, for an average annual survival of 22.9%. A previous study at St. Catherines Island reported that $\geq 20.0\%$ and $\geq 28.6\%$ of hatchlings from the 2008 ($n = 30$) and 2009 cohorts ($n = 56$), respectively, survived their first year following release, based on the proportion recaptured through 2010 (Tuberville et al. 2015). The current study estimated hatchling annual apparent survival at 37% based on 8 years of mark-recapture data from 201 individuals first released or first captured as hatchlings, providing a more robust estimate of long-term average annual apparent survival of hatchlings in our study population.

Juvenile annual apparent survival in the current study was very similar to that reported for a gopher tortoise population established via wild-to-wild translocation, in which annual apparent survival of translocated juveniles averaged 73.7% (range = 57.1–81.3% among years, based on raw percentages of animals recaptured; Tuberville et al. 2015). Juvenile annual apparent survival in both studies was nearly 3 times that reported for a waif population (25.0%; McKee 2019). Whether the disparity in juvenile survival rates is due to different predator communities (Small et al. 2018) or because waif juveniles exhibit lower apparent survival rates than wild-to-wild translocated juveniles or juveniles recruited following translocation is unknown and merits further investigation. However, our values fall within range of those reported for a naturally occurring population, in which juvenile annual apparent survival ranged from 69.0–88.9% among 4 study sites close to each other but that varied in vegetation structure, quality of the surrounding habitat, and the size and demography of the resident population (Wright 2016). We suspect that our estimates of apparent survival closely approximate true survival because limited radio-tracking at our site indicated that immature gopher tortoises use a small number of closely spaced burrows (typically ≤ 20 m apart; B. B. Harris and T. D. Tuberville, University of Georgia, unpublished data) and tortoises are rarely encountered outside the ruderal areas on the island.

Offspring recruited on St. Catherines Island exhibited an annual apparent survival rate of 71.3% as juveniles and 83.0% as subadults. There are few benchmarks against which to compare our estimates for these stage classes: a naturally occurring population in southwest Georgia (Wright 2016) and a population in South Carolina, USA, comprised almost exclusively of released formerly captive (waif) tortoises (McKee 2019). Although individual estimates vary among sites, the 3 studies exhibit similar trends in that, within a population, the point estimate of juvenile apparent survival is consistently lower than the point estimate of subadult apparent survival. The congruence among studies underscores the importance of calculating separate estimates for subadult and juvenile survival, as recommended by Wright (2016). Our subadult apparent survival estimate (83.0%) was lower than those reported by Wright (2016; 91.6%) and McKee (2019; 96.0%), but we were unable to estimate the transition rate of subadults to adults because of the trap size deployed in our study. Because some subadult animals that were not captured again may have simply grown too large for the trap size, our apparent survival estimate is likely a conservative estimate for this stage class.

Our study site is unique in several respects that may affect apparent survival rates. First, predator abundance or species composition may differ between island and mainland populations (Iverson 1991), although raccoons and fire ants—2 species commonly preying gopher tortoise nests and young—are both present on the island (Epperson and Heise 2003, Smith et al. 2013, Dziadzio et al. 2016, Quinn et al. 2018). But even in mainland populations, predation on small gopher tortoises varies among sites and at small spatial

and temporal scales (Butler and Sowell 1996, Pike and Seigel 2006, Quinn et al. 2018). Additionally, because St. Catherines Island is a privately owned island with limited access by humans, the resident tortoise population may be better buffered from other threats (e.g., road mortality, poaching) that affect survival in other populations. Finally, the former cattle pasture where our study took place differed in vegetation structure, species composition, and land use history from many natural areas the gopher tortoise has historically occupied (Nussear and Tuberville 2014). Howell et al. (2020) demonstrated that demographic rates can vary between ruderal and more natural land cover types. Given the growing reliance of gopher tortoises on ruderal plant communities as natural areas become increasingly fragmented or fire-suppressed (Baskaran et al. 2006, Howell et al. 2020), understanding population dynamics of gopher tortoises in these frequently disturbed areas will be important for managing this imperiled species.

We found little support for differences in apparent survival based on treatment. Although treatment was included in the top model, the broadly overlapping credible intervals suggest survival of immature gopher tortoises did not vary among treatments. In other words, after accounting for stage (i.e., size class), survival did not vary among offspring produced by founders, regardless of whether those offspring were directly released, head-started, or wild recruited. To account for the potentially confounding effects of size and treatment on head-started gopher tortoises, we assigned their treatment as head-start but assigned them to their initial size class based on size at release, such that we considered head-starts < 68 mm MCL to be hatchlings and those ≥ 68 mm MCL to be juveniles when they entered the population. The lack of differences among treatments suggests that the any benefits due to head-starting are influenced by size at release, as has been suggested for head-started desert tortoises (McGovern 2019). Furthermore, the fact that head-started gopher tortoises survive as well as wild-recruited offspring suggests that animals reared in captivity did not incur measurable negative effects on survival following their release; however, the estimate for apparent survival of wild-recruited hatchlings we report in this study was based on only 11 tortoises, so direct comparisons among treatments for the hatchling size class should be interpreted cautiously. Our findings closely match those reported by Quinn et al. (2018), who reported 70.0% annual survival (pooled across 2 releases) for head-starts reared to juvenile size, and Radzio et al. (2019:17), who concluded that released head-started gopher tortoises “...exhibit natural attributes required to thrive in the wild.” Additionally, because all treatment groups were comprised of offspring of translocated adults, our survival estimates help to quantify recruitment in manipulated gopher tortoise populations and emphasize the potential for translocated adults to produce viable offspring.

Based on long-term monitoring of the introduced St. Catherines Island population, the translocation and subsequent augmentations with directly released hatchlings and head-started juveniles have been successful in establishing a

robust population of gopher tortoises. A previous analysis of 12 years of mark-recapture data revealed that both immature and adult founders experienced high long-term annual apparent survival following release (Tuberville et al. 2008). As adults, translocated tortoises exhibited successful reproduction, although reproductive success varied among males and appeared to be influenced by residency time (Tuberville et al. 2011). The abundance of burrows of smaller size classes (J. L. Gaskin, Georgia Southern University, unpublished data) and the large number of immatures captured (this study) provide evidence of sustained recruitment following translocation. Our targeted trapping of immature tortoises in the current study also revealed that offspring produced following translocation experienced apparent survival rates comparable to those in the only naturally occurring population for which separate estimates are available for juveniles and subadults (Wright 2016). Likewise, point estimates of annual apparent survival rates for gopher tortoises in both stages met or exceeded the 73.0% annual survival rate estimated by Pike et al. (2008) as needed to maintain a stable population in this species.

Although criteria for evaluating success of translocation or reintroduction projects vary, there is general consensus that the ultimate measure of success is that the population eventually becomes self-sustaining (Griffith et al. 1989, Fischer and Lindenmayer 2000, Germano and Bishop 2009). Population manipulations of long-lived species such as turtles are particularly challenging because they may require multiple interventions over many years to ensure long-term persistence of the population (Seddon 1999, Canessa et al. 2016). Likewise, it may take decades of monitoring to know whether a particular project is successful (Dodd and Seigel 1991); thus, the success of many reintroduction projects remains unknown (Fischer and Lindenmayer 2000, Germano and Bishop 2009). In a review of 47 reptile translocation projects, only about a third had been monitored long enough to be considered successful, with the outcome of approximately 40% of projects still uncertain (Germano and Bishop 2009). As a result, most studies report on short-term measures of success, such as site fidelity or evidence of reproduction by released animals (Riedl et al. 2008, Germano and Bishop 2009). To our knowledge, ours is the first study in gopher tortoises to report on the fate of offspring recruited into a population following translocation and to be of sufficient duration (19 years following the primary translocation) to evaluate long-term success. The only similar efforts published in the literature for other reptile species include long-term studies of Hermann's tortoises (*Testudo hermanni*) in Spain (Fernández-Chacón et al. 2011), giant Galapagos tortoises (*Chelonoidis hoodensis*) in Española Island (Gibbs et al. 2014), and eastern collared lizards (*Crotaphytus collaris collaris*) in Missouri (Templeton et al. 2011, Sites 2013). Although continued long-term monitoring will be required to confirm persistence of the St. Catherines Island population and to determine whether additional interventions are necessary (Seddon 1999), the current study, in combination with results of prior monitoring efforts, provides

important demographic rates for incorporating into formal population viability analyses.

MANAGEMENT IMPLICATIONS

Our study demonstrates that immature gopher tortoises recruited on-site following translocation can experience apparent survival rates predicted to support stable populations. Thus, our work provides encouraging evidence that population manipulations such as translocation and head-starting can facilitate species recovery. Additionally, populations in some ruderal plant communities, on which gopher tortoises are increasingly reliant, can support sustained recruitment and survival of immature animals provided the canopy remains open. Because apparent survival can vary among size classes of immature gopher tortoises, we recommend calculating separate estimates for the hatchling, juvenile, and subadult stages. The suite of demographic rates capable of maintaining viable populations varies among populations; however, our estimates of apparent survival rates of immature gopher tortoises help address an important knowledge gap in the population dynamics of this imperiled species.

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