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Special Section on Gopher Tortoise Mark-Recapture

Waif Gopher Tortoise Survival and Site Fidelity Following Translocation

REBECCA K. McKEE,[1] *Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green Street, Athens, GA 30602, USA*
KURT A. BUHLMANN, *University of Georgia's Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, SC 29802, USA*
CLINTON T. MOORE, *U.S. Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit, Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green Street, Athens, GA 30602, USA*
JEFFREY HEPINSTALL-CYMERMAN, *Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green Street, Athens, GA 30602, USA*
TRACEY D. TUBERVILLE,[2] *University of Georgia's Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, SC 29802, USA*

ABSTRACT Gopher tortoises (*Gopherus polyphemus*) are among the most commonly translocated reptiles. Waif tortoises are animals frequently of unknown origin that have been displaced from the wild and often held in human possession for various reasons and durations. Although there are risks associated with any translocation, waif tortoises are generally excluded from translocation projects because of heightened concerns of introducing pathogens and uncertainty about the post-release survival of these individuals. If these risks could be managed, waif tortoises could have conservation value because they can provide the needed numbers to stabilize populations. In the early 1990s, the discovery of an isolated population of gopher tortoises (≤15 individuals) near Aiken, South Carolina, USA, prioritized establishment of the Aiken Gopher Tortoise Heritage Preserve (AGTHP). Because of the population's need for augmentation and the site's isolation from other tortoise populations, the AGTHP provided the opportunity to evaluate the post-release survival of translocated waif tortoises without compromising a viable population. Since 2006, >260 waif tortoises have been introduced to the preserve. Using a Cormack-Jolly-Seber modeling framework to analyze release records and capture histories from trapping efforts in 2017 and 2018, we estimated the long-term apparent survival and site fidelity of this population composed largely of waif tortoises. We estimated annual apparent survival probabilities to be high (≥0.90) for subadult, adult male, and adult female tortoises, and these rates were similar to those reported for wild-to-wild translocated gopher tortoises and those from unmanipulated populations. Of the tortoises recaptured within the boundaries of the preserve, 75% were located within 400 m of their release location. These results suggest that waif tortoises could be an important resource in reducing the extirpation risk of isolated populations. © 2021 The Wildlife Society.

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Translocation, the intentional movement of animals from one location to another, is a common wildlife management technique (Fischer and Lindenmayer 2000, Seddon et al. 2005, Germano and Bishop 2009). With hundreds of translocation projects carried out annually, the practice has been applied to species across multiple taxonomic groups (Griffith et al. 1989). Historically, game management motivated most translocation efforts (Snyder et al. 1999, Hughes and Lee 2015), but the technique has emerged as a conservation measure for imperiled non-game species (Bouzat et al. 2009, Schwartz and Martin 2013, Seddon et al. 2014).

The gopher tortoise (*Gopherus polyphemus*) is a fossorial reptile endemic to the southeastern United States and is among the most commonly translocated reptile species (Tuberville et al. 2008). Because their burrows provide refuge for diverse taxa, the gopher tortoise is considered a keystone species and an ecosystem engineer (Lips 1991, Pike and Mitchell 2013, Catano and Stout 2015). Unfortunately, the species is declining throughout its range, predominantly because of habitat degradation or permanent habitat loss to development (Smith et al. 2006)—with the latter having caused the displacement of thousands of individuals (Mushinsky et al. 2006). The gopher tortoise is federally listed as threatened under the Endangered Species Act in southwestern Alabama, Mississippi, and Louisiana, and is a candidate species for federal listing in the remainder of its range (U.S. Fish and Wildlife Service 1987, 2011). Although protecting and managing existing habitat is fundamental to the species' conservation (U.S. Fish and

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[1] *Current affiliation: Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL 32611, USA*
[2] *E-mail: tubervil@uga.edu*

Wildlife Service 1987, 2011), practitioners have considered strategies of using displaced tortoises to bolster depleted populations to thresholds necessary to achieve viability.

Because of the widespread use of translocation as a management tool for gopher tortoises, numerous studies have attempted to measure the outcomes of wild-to-wild translocations (Heise and Epperson 2005, Ashton and Burke 2007, Riedl et al. 2008, Tuberville et al. 2008, Bauder et al. 2014) and to evaluate strategies to improve the success of future projects (Tuberville et al. 2005). Many studies are limited to short-term evaluations of success, but long-term studies are particularly valuable for understanding how translocation affects survival rates of long-lived species (Dodd and Seigel 1991, Tuberville et al. 2008, Germano and Bishop 2009, Sutherland et al. 2010), including gopher tortoises, which can likely live ≥60 years (Landers et al. 1980). Post-release site fidelity and survival in the first years following release are frequently used to assess project outcomes (Burke 1989, Heise and Epperson 2005, Tuberville et al. 2005, Riedl et al. 2008); however, short-term apparent survival metrics may not be indicative of the long-term viability of translocated populations (Ashton and Burke 2007). For example, 2 long-term studies demonstrated that apparent survival is reduced in the initial 1–2 years following translocation, but populations maintain a high level of adult annual apparent survivorship (≥98%) in subsequent years (Ashton and Burke 2007, Tuberville et al. 2008). Reduced rates of apparent survival in the initial 1–2 years have been predominantly attributed to dispersal rather than direct mortality (Tuberville et al. 2008), and this behavior is reduced as tortoises acclimate to their new environment and establish home ranges (Heise and Epperson 2005, Tuberville et al. 2005). Similar patterns of acclimation have been reported for other translocated tortoise species, including the Mojave desert tortoise (*Gopherus agassizii*; Nussear et al. 2012, Farnsworth et al. 2015) and Hermann's tortoise (*Testudo hermanni*; Pille et al. 2018).

Although translocation is a common management technique for gopher tortoises, waif gopher tortoises have typically been excluded from consideration. Waif gopher tortoises are displaced animals, often of unknown origin, that have been in human possession for various reasons and durations. They include, for example, tortoises that are rehabilitated following injury, surrendered after extended captivity as pets, or confiscated subsequent to their illegal collection from the wild. Waif tortoises are typically perceived as a management dilemma. Because of uncertainties about their origin or conditions in captivity, waif tortoises are generally excluded from translocation efforts because of the possible risk of pathogen introduction into the recipient population (International Union for Conservation of Nature 2000). For example, captive Mojave desert tortoises have exhibited high seroprevalence for known tortoise pathogens and released pets may be a possible source of infection for wild populations (Johnson et al. 2006). Moreover, formerly captive tortoises or previously injured and rehabilitated tortoises may be less able to survive when returned to the wild. Conversely, if these risks could be managed, waif tortoises could provide the needed numbers to stabilize populations that have experienced severe declines and for which alternative options are limited.

In 1993, a small isolated population of gopher tortoises (≤15 individuals) was discovered in Aiken County, South Carolina, USA (Fig. 1; Clark et al. 2001), on private property that was later purchased in 1995 by South Carolina Department of Natural Resources (SCDNR) and designated as the Aiken Gopher Tortoise Heritage Preserve (AGTHP). Because of the site's isolation (>50 km to nearest gopher tortoise population) and the practical certainty of population extirpation without augmentation measures, the AGTHP provided the opportunity to serve as a recipient site and evaluate the outcome of releasing waif tortoises without compromising a viable population. Between 2006–2017, 268 waif gopher tortoises from a variety of origins throughout the species' range were marked and released at the AGTHP. During 2017–2018, we conducted a mark-recapture study to assess the outcome of the recovery project to date.

Specifically, the objectives of this descriptive study were to estimate the long-term apparent survival of a population predominantly composed of waif tortoises and evaluate tortoises' fidelity to their release point. Because the recipient site occurred at the northern periphery of the species' range and waif tortoises originated across a range of latitudes, we also assessed whether distance and bearing from origin influenced survival. Lastly, we assessed whether a tortoise's fidelity to its release point was related to time since its release.

STUDY AREA

In 1995, SCDNR purchased 148 ha to create the AGTHP. Located 30 km east of Aiken, South Carolina, the AGTHP protected the northernmost extant population of gopher tortoises and was separated from the nearest known gopher tortoise population by >50 km (Clark et al. 2001). Average annual rainfall was 130 cm, with approximately 30% falling during summer (Jun–Aug) and 25% falling in winter months (Dec–Feb). Average annual high and low temperatures were 33.3°C and 0.6°C, respectively. Average elevation at the site was 86.2 m. The land cover was remnant sandhills with xeric soils (Lakeland, Troup, and Fuquay), an herbaceous understory dominated by wiregrass (*Aristida beyrichiana*) and bluestem (*Andropogon* spp.), a midstory dominated by turkey oak (*Quercus laevis*), and a sparse canopy of longleaf pine (*Pinus palustris*). There was a small stream that formed 3 small ponds on the property. Potential predators of gopher tortoises that were present included coyotes (*Canis latrans*) and feral dogs. Other fauna commonly associated with longleaf landscapes, including red-cockaded woodpecker (*Picoides borealis*), eastern fox squirrels (*Sciurus niger*), and upland snakes such as coachwhips (*Masticophis flagellum*), occurred on the property. Beyond activities associated with restoring the sandhills ecosystem, the primary use of the preserve during the time of our study was for low-impact recreation (hiking, horseback riding) and hunting by the public. South

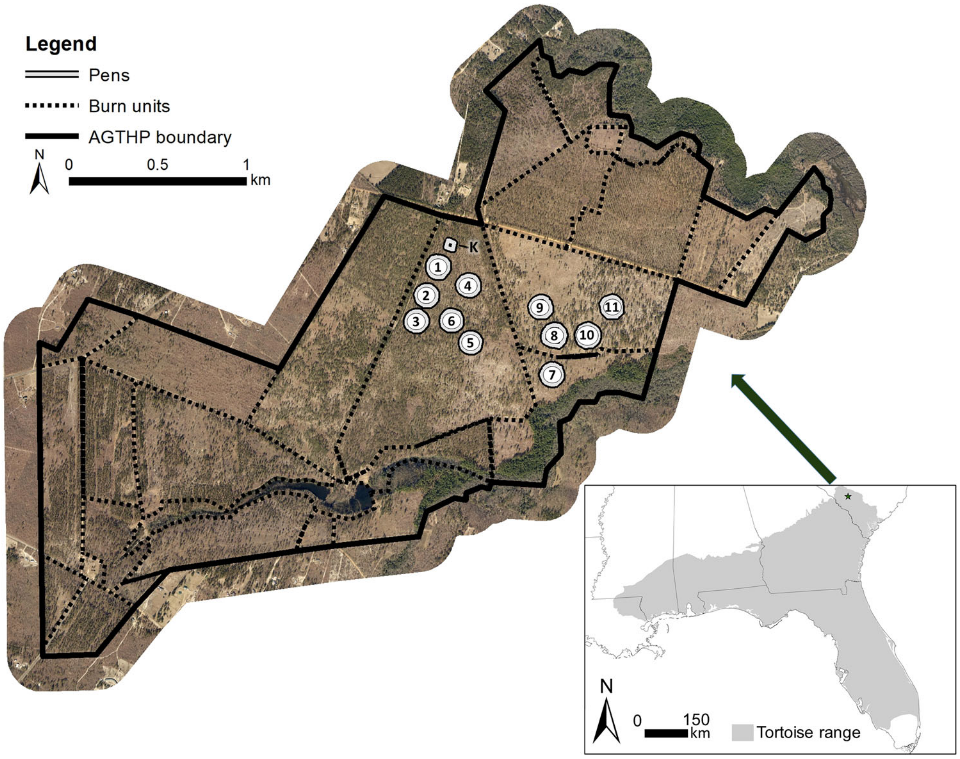

Figure 1. Burn units (management compartments) and tortoise release pens at the Aiken Gopher Tortoise Heritage Preserve in Aiken County (AGTHP), South Carolina, USA. We released the waif tortoises and captured residents into pens (1–11, K) from 2006–2017 and recaptured tortoises in 2017–2018. Tortoises acclimated in pens ≥10 months before pen walls were lowered. The inset shows the location of the preserve (star) in the context of the gopher tortoise range (shaded area). The preserve is the northernmost known gopher tortoise population in the species' range. Map image is the intellectual property of Esri and is used herein under license. Copyright © 2020 Esri and its licensors. All rights reserved.

Carolina Department of Natural Resources managed the AGTHP with prescribed fire, manual thinning, and periodic applications of broadleaf herbicide (Moule 2013) to promote longleaf savanna and the herbaceous forbs that provide important forage for gopher tortoises. Since the preserve's establishment, SCDNR purchased additional surrounding properties to enlarge the preserve to its current size of 656 ha. Waif tortoise releases at AGTHP began in 2006 and were ongoing (as of 2020), but our study included release records for individuals released between 2006 and 2017. Our recapture efforts occurred in the summers of 2017 and 2018.

METHODS

Prior Population Survey and Augmentation Efforts

Burrow surveys and mark-recapture efforts conducted in 1995 and 2001 (prior to augmentations), indicated that AGTHP supported ≤15 resident tortoises (K. A. Buhlmann, Savannah River Ecology Laboratory, unpublished data). As part of those efforts, all resident tortoises encountered on the property were weighed, measured for their midline carapace length (MCL; the distance between the nuchal scute and supercaudal scute), checked for plastral concavity (a secondary sex characteristic in adult males), permanently marked by scute notching (modified from Cagle [1939]), and photographed. Without augmentation, the AGTHP population faced near-certain extirpation, but no populations in South Carolina were suitable as donor sites because of their small population sizes (Auffenberg and Franz 1982, Tuberville and Dorcas 2001, Smith et al. 2006). Acquiring wild tortoises from other states was also unfeasible because many populations in other states were declining (Hermann et al. 2002, McCoy et al. 2006, Ennen et al. 2010) and managers retained those tortoises for their in-state augmentation efforts. Given the AGTHP's isolation and its need for augmentation, translocation of waif tortoises began in 2006 as part of an ongoing effort to recover the population.

With the assistance of SCDNR, we obtained waif tortoises from wildlife rehabilitation facilities, state wildlife agencies, zoos, and other partners throughout the eastern United States, including states outside the species' native range. We typically acquired waifs as single animals or in small groups, but in one case, as a group of 58 adult tortoises. Prior to release, we weighed, measured, photographed, and permanently marked each individual. We determined the sex of adult tortoises by noting plastral concavity. We visually inspected all tortoises and did not release any tortoises displaying clinical signs of upper respiratory tract disease, such as ocular or nasal discharge (Brown et al. 1999) but did not screen tortoises for pathogens prior to release because of lack of funding. We provided starter burrows to waif tortoises and 14 previously captured adult and immature resident tortoises (native to AGTHP) and penned them in groups in 1-ha circular pens (0.7-m tall aluminum flashing) at the AGTHP for ≥10 months (Table 1; Fig. 1; following methodology of Tuberville et al. [2005]) to promote site fidelity and, in the case of resident tortoises, consolidate individuals from across the preserve. To the extent possible, we penned animals from the same source or acquisition cohort together, but we often placed animals from multiple sources in the same pen. We stocked pens with an average of 13 adult tortoises (range = 3–22) and an average of 18 total tortoises (including juvenile and subadult animals). With SCDNR, we constructed additional pens over time as needed to house newly acquired waif tortoises. Following penning (12–70 months after placement of first tortoise in pen and ≥10 months after placement of last tortoise in pen), we removed pen walls to allow tortoises to move beyond the pen footprint (Table 1). Except for a thorough burrow trapping effort conducted in pen 1 in 2009, we did not conduct comprehensive surveys to confirm that all tortoises placed in pens were alive in pens at the time pen walls were removed.

During 2006–2017, we released 282 tortoises into pens at the AGTHP, including 14 resident and 268 waif tortoises. For purposes of analysis, we assigned tortoises to a stage class at the time of their release based on MCL and the presence of plastral concavity. The released tortoises included 66 tortoises released as hatchlings (<68 mm MCL), 31 as juveniles (≥68 mm but <130 mm MCL), 34 as subadults (flat plastron and ≥130 mm but <230 mm MCL), 67 adult males (concave plastron and ≥180 mm MCL), and 84 adult females (flat plastron and ≥230 mm MCL). At the time of trapping (see below), SCDNR had removed the walls of pens 1–7 and pen 9 but pens 8, 10, 11 and K were still intact (Table 1; Fig. 1; McKee [2019] provides further details). We included tortoises residing in intact pens in our study because, although constrained in their ability to disperse, they were still subject to mortality factors such as disease and predation. Because waif tortoise introductions are ongoing at the AGTHP, an additional pen was constructed in the summer of 2018; however, no tortoises released after 2017 were included in our analysis.

Trapping Effort in This Study

Because of the fossorial nature of gopher tortoises, many monitoring methods for the species depend on the detection of their burrows (Burke and Cox 1988, Breininger et al. 1991, Smith et al. 2005). To locate tortoise burrows, we walked parallel transects spaced 15 m apart in all suitable habitat throughout the preserve during May–June 2017 and February–May 2018. We considered low-lying riparian areas to be unsuitable for tortoises and excluded them from surveys (roughly 18% of the site). We recorded the location of all observed burrows using a global positioning system (±5 m; 76CSx GPS, Garmin Limited, Olathe, KS, USA) and classified them as active, inactive, or collapsed based on criteria described in Cox et al. (1987). We measured all intact (active and inactive) burrows by recording burrow height and width (cm) at a depth of 0.5 m inside the mouth

Table 1. Summary of gopher tortoises placed into soft release pens at the Aiken Gopher Tortoise Heritage Preserve in Aiken, South Carolina, USA. Tortoises were released between 2006–2017 and recaptured in 2017–2018. Temporary confinement in 1-ha circular pens allowed tortoises time to acclimate to the release site. We assigned individuals to stage classes (juvenile, subadult, adult male, and adult female) based on their midline carapace length and the presence of secondary sex characteristics. We did not include hatchlings ($n = 66$) in analyses or in the pen totals. Tortoises originated from a variety of locations within the species' range. The unknown column refers to the number of individuals with origins that were completely unknown. The state only column refers to number of tortoises in each pen where origin could only be identified to the state-level. Average distance and average bearing refer to the mean Euclidean distance (km) and bearing (°) calculated for tortoises in each pen with known origin locations (exact or county locations).

			Stage class of tortoises released in pens					Origin of tortoises released in pens				
Pen	Last tortoise added	Pen walls removed	Juvenile (*n*)	Subadult (*n*)	Adult male (*n*)	Adult female (*n*)	Total (*n*)	Unknown (*n*)	State only (*n*)	Known origin (*n*)	Average distance (km)	Average bearing (°)
1	Jul 2008	Jul 2009	2	1	8	11	22	3	14	5	224	199
2	Oct 2010	Apr 2013	5	3	3	3	14	0	1	13	0	180
3	Nov 2008	Apr 2013	10	1	3	2	16	0	2	14	117	167
4	Aug 2012	Aug 2013	2	2	8	14	26	1	0	25	591	191
5	Aug 2012	Aug 2013	1	3	7	11	22	5	1	16	667	183
6	Oct 2012	Aug 2013	0	4	11	9	24	2	0	22	737	184
7	Oct 2013	Apr 2016	2	2	4	6	14	6	2	6	312	199
8	Apr 2015	Jul 2018	0	2	0	3	5	1	3	1	352	184
9	Mar 2014	Aug 2016	4	4	5	5	18	3	2	13	352	184
10	Jul 2017	Still standing[a]	2	7	6	6	21	3	3	15	748	174
11	Sep 2016	Jul 2018	3	5	9	12	29	2	1	26	699	176
K	Jul 2015	Still standing[a]	0	0	3	2	5	1	2	2	737	184

[a] Pens K and 10 were still standing at the end of study (Aug 2018).

of the burrow. We used a burrow camera to determine occupancy of each active burrow (Smith et al. 2005) and marked intact burrows with uniquely numbered aluminum tags on metal stakes that were able to withstand the frequent prescribed fires.

We trapped tortoises during 22 May–19 July 2017 and 8 May–17 July 2018. This effort represented the first systematic attempt to capture all gopher tortoises residing on AGTHP after waif introductions began. If the burrow camera revealed a tortoise in the burrow, we immediately placed a wire box trap covered in shade cloth at the mouth of the burrow (Aresco and Guyer 1999). We checked traps multiple times daily to prevent captured tortoises from overheating. We also opportunistically captured any tortoise encountered outside of a burrow during the trapping period. We recorded the point of capture for all live tortoises and for tortoise remains (i.e., shells). Because of a concurrent radio-telemetry project designed to assess movement and survival of hatchlings and head-started yearlings, we did not attempt to trap tortoises from these age classes. We measured, photographed, and identified tortoises by their notch codes. We referenced all identifications against the historical capture database and photographs of released animals. We used MCL and plastral concavity to assign tortoises to a stage class at each capture. We handled unmarked individuals similarly and marked them as described previously. We returned tortoises to their point of capture within 24 hours.

In addition to formal trapping conducted in 2017 and 2018, we recorded incidental observations of live tortoises and recovery of shells from dead individuals during 2006–2016. We also incorporated records from the 2009 trapping effort conducted within pen 1 prior to removal of that pen's walls. We conducted all work in accordance with appropriate permits (SCDNR Scientific Collection Permit Number SC-04-2017, SC-06-2018) and approved University of Georgia Institutional Animal Care and Use Committee protocols (AUP A2017 05-022-Y1-A0).

Survival Analysis

We used the information collected at first handling (release for waifs, initial capture for resident tortoises and unmarked individuals), subsequent captures, and dead recoveries to construct a capture history for each tortoise. A capture history was an array of 13 digits with each digit representing an individual's capture status for each year t of the study (2006–2018). For live captures or release of a tortoise, the corresponding year's digit was assigned a value of 1–4 based on its stage class (c) as follows: 1 = juvenile, 2 = subadult, 3 = adult male, and 4 = adult female. We assigned a value of 5 if the tortoise was recovered dead. We also assigned this value to any living tortoise opportunistically encountered off-site during our study ($n = 1$) or in years prior ($n = 2$), reasoning that the finding represented permanent dispersal from the preserve. Although we returned such tortoises to the preserve, we treated the event as a functional removal from the population (and we excluded future captures of the tortoise from analysis) to be consistent with our objectives of estimating apparent annual survival (the probability of an animal surviving 1 year and remaining in the study site) associated with our reintroduction approach. Similarly, prior to 2017, 1 tortoise had been injured by a dog, treated by a wildlife veterinarian, and later returned to the population. Because the individual might not have survived without our intervention, we also classified this tortoise as code 5. We assigned the value 6 if the tortoise was not observed (neither captured alive nor recovered dead).

Because we intentionally did not trap hatchling tortoises, our analyses were conditioned on releases of tortoises only in the juvenile and larger stages. We used a multistate version of a Cormack-Jolly-Seber model (Brownie et al. 1993, Schwarz et al. 1993) for joint live-capture and dead-recovery data (Burnham 1993, Barker et al. 2005) to estimate stage-class-specific probabilities of apparent survival (φ_c), transition to the next stage class given survival (Ψ_c for $c = 1$ or 2 only), capture of live animals ($p_{c,t}$), and recovery of dead animals (r_c). We also estimated 1 parameter not specific to stage class: probability of transitioning into the adult stage class as male rather than female (γ; Table S1, available online in Supporting Information).

Because tortoises were penned in groups prior to their release and because some pens were still intact during our searches, we considered pen number (Table 1; Fig. 1) to be a random effect for survival probability within each model. We listed unmarked tortoises found on site during the 2017–2018 surveys as having no pen (N). To separate potential effects of penning group from other effects in subsequent models, we expressed survival probability as a linear-logit function of stage class and the random pen effect.

Because of sparseness of data, the only parameter for which we considered temporal variation was capture probability (p; Table S2, available online in Supporting Information). We assumed that recovery and capture rates varied by size of tortoise. In contrast, we assumed no variation in recovery and capture rates by sex because we reasoned that the sexes were equally vulnerable to trapping, which yielded the majority (77%) of captures, and incidental captures were relatively evenly divided between males (54%) and females (46%). Therefore, we estimated a common recovery rate of dead adult tortoises ($r_A = r_3 = r_4$) and capture probability for live adult tortoises ($p_{A,t} = p_{3,t} = p_{4,t}$), regardless of sex. We modeled annual capture probability as a fixed effect of annual search effort. We defined search effort as whether we conducted trapping for tortoises in a given year or not (i.e., whether we discovered tortoises only incidentally to other field activities). We estimated capture probability separately for each year that trapping occurred (2009, 2017, 2018), but we estimated a common capture probability for years without a trapping effort.

Given that our study site was at the northern extent of the species' range, tortoise survival could be influenced by the geographic origin of the tortoise. For tortoises with known origin (which we considered as either an exact location, or the centroid of the county of origin), we calculated the Euclidean distance (km) and bearing (degrees from true north) between the origin and the coordinates for the preserve using the package geosphere (Hijmans et al. 2019) in program R (R Core Team 2020). For tortoises with unknown origin, we developed prior probability distributions to characterize our uncertainty. When we knew origin only to the state level, we assumed that the tortoise could have originated with equal probability from any of the state's counties within the species' range. When origin was completely unknown, we assumed that the tortoise could have originated with equal probability from any county within the entire range. For individuals that had been in captivity outside the species' range, we used the tortoise's original location within the range to calculate distance and bearing, but if original location was unknown, we assigned its location to one of the prior distributions described above. We assumed that unmarked tortoises found on the preserve were resident individuals undetected in earlier surveys, and we assigned as origin coordinates the center coordinates for the preserve.

We considered 5 candidate models for annual apparent survival probability with our simplest model (1) including tortoise stage class as the sole fixed effect. We formed other models by adding covariates related to origin to the stage-class effect in alternative combinations: distance only (2), bearing only (3), both distance and bearing (4), and the interaction between distance and bearing (5; and including the constituent main effects). Because each model could be represented by removing specific parameters from model 5, we applied an indicator variable selection procedure within the interaction model and assessed the posterior frequency of each indicator (Kuo and Mallick 1998). We derived the posterior relative probability of each model by computing the posterior frequency of relevant combinations of indicators.

Because of sparsity of the data, our prior assumptions for unknown origins, and desire to incorporate random pen effects, we chose to analyze models in a Bayesian framework following the approach of Kéry and Schaub (2012). The approach uses a state-space representation in which tortoises progress among states through the annual processes of survival, stage-class transition, and recovery (i.e., of shells). These processes are modeled as latent mechanisms that are probabilistically observable. Other than our use of the logit link to model annual apparent survival as a function of covariates (i.e., stage class, distance and bearing covariates, pen random effects), we modeled all parameters directly as probabilities. We used Markov chain Monte Carlo sampling in JAGS (Plummer 2003) via R using package R2jags (Su and Yajima 2020) to approximate the posterior distribution of all model parameters. We used non-informative priors, and we provided random initial values to each of 3 chains. We performed 10,000 simulations of each chain, discarding the first 2,000 as burn-in and retaining every sixth sample, yielding 4,000 simulated values across the chains to construct posterior distributions. We checked for chain convergence using the Brooks-Gelman-Rubin statistic (Brooks and Gelman 1998) cutoff of $\hat{R} < 1.1$ and by visually inspecting the trace plots for evidence of mixing. From the posterior distributions, we reported mean ± standard deviation ($\bar{x} \pm 1$ SD) and 95% Bayesian credible intervals.

Site Fidelity Analysis

For each individual captured during 2017–2018, we calculated the displacement distance of the capture location from the release location (the center point of the pen). Because we exclusively surveyed areas within the AGTHP footprint, we captured only tortoises that exhibited site fidelity to the preserve. The minimum distance between the pens and the nearest preserve boundary averaged 437.3 m (range = 201.1–641.9). Tortoises that dispersed from the preserve would not have been detected in our surveys, and thus inferences on displacement distance do not reflect such dispersal events. Because the preserve is >656 ha in area, tortoises could exhibit widely different degrees of fidelity to their soft-release pen without dispersing beyond the boundary of the site (Fig. 1).

For live tortoises recaptured on-site during the 2017–2018 trapping period, we calculated the Euclidean distance between the center point of the tortoise's release pen and its first recapture location (distance to first observation). For individuals captured on >1 occasion, we also calculated the Euclidean distance between the center point of the tortoise's release pen and its last capture occasion (distance to last observation). Additionally, for individuals captured alive in both 2017 and 2018, we calculated the distance from the location of its first observation in 2017 to the location of its first observation in 2018 (distance between years). Because 4 pens (pens 8, 10, 11, K; Fig. 1) had walls still standing during the trapping period, we excluded individuals confined to these pens from site fidelity analyses. We assessed the effect of time-since-release on movement using a generalized linear model with a log link. We used distance to first observation (m) as the response variable and years since the pen walls were removed as the predictor variable. We considered the time-since-release effect significant if the observed *P*-value was <0.05. We used program R to calculate all distances (geosphere package) and to conduct all statistical analyses.

RESULTS

After excluding hatchlings, we marked and released 13 resident (4 juvenile, 3 subadult, 3 adult male, 3 adult female) and 203 waif (27 juvenile, 31 subadult, 64 adult male, 81 adult female) tortoises prior to 2017. Of the released waifs, 22 were acquired from locations outside the species' range. We assigned exact or county-level origins for 165 tortoises released at AGTHP, including 7 unmarked resident tortoises located on the preserve during the 2017–2018 surveys (Fig. 2). The average distance between origin and the preserve was 497.4 km (range = 0–879 km; Fig. 2) and the average bearing was 181.7° (range = 124.9–285.7°). We could identify a state (but not county) of origin for

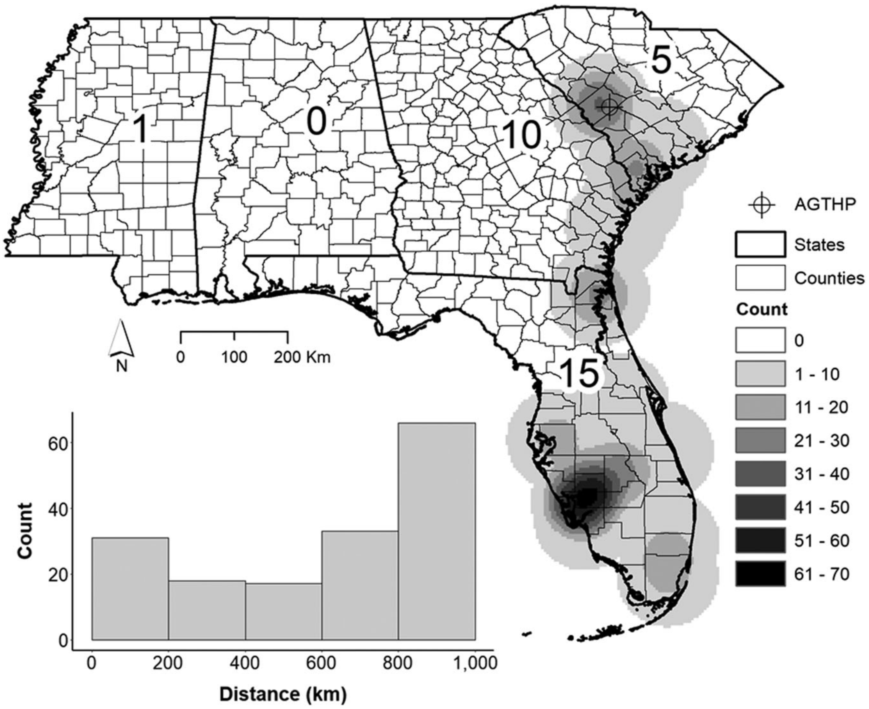

Figure 2. Known origins of gopher tortoises prior to release at the Aiken Gopher Tortoise Heritage Preserve (AGTHP) from 2006–2017 in Aiken County, South Carolina, USA. Shading corresponds to the number (count) of tortoises that originated from a given location. Large numbers on each state indicate the number of tortoises originating from the state but that lacked a specific county of origin. In total, we could assign only state-level origin to 31 tortoises. Additionally, origin for 27 tortoises was entirely unknown and not assignable to a specific state. The inset shows a histogram of Euclidean distances from the tortoises' origins (if known) to the AGTHP. Map image is the intellectual property of Esri and is used herein under license. Copyright © 2020 Esri and its licensors. All rights reserved.

31 tortoises (Fig. 2), and 27 tortoises were from completely unknown origins.

During 2017, we captured 60 live tortoises (including 1 individual we found offsite and returned to the preserve) and recovered 7 shells. During 2018, we captured 111 live tortoises and recovered 2 shells. In total, we captured 124 unique, live juvenile, subadult, and adult tortoises, of which 45 were captured in both years. All recovered shells were marked tortoises and their identities known. Of the 124 live individuals observed, 117 had been marked and released into a pen prior to 2017 (5 released as juveniles, 23 as subadults, and 89 as adults). Of the 117 previously marked tortoises, 10 were resident tortoises and 107 were waifs, including 11 waifs obtained from outside the species' range. The 7 unmarked animals had never been released into a pen and were assumed to be resident tortoises overlooked in earlier surveys but could have been released by private citizens without our knowledge or, in the case of the unmarked juvenile, recruited into the population.

Survival

We found no evidence that distance to origin (model 2; $\beta = -0.08 \pm 0.10$), bearing to origin (model 3; $\beta = -0.11 \pm 0.09$), or the distance × bearing interaction (model 5; $\beta = -0.02 \pm 0.03$) were correlated with apparent survival. Posterior predictions of relative model probability placed nearly all weight (0.84) on model 1, which included stage only (i.e., with no origin covariate effects; Table 2).

Under model 1, estimated annual apparent survival probability (φ_c) was 0.93 ± 0.05 for adult females, 0.90 ± 0.07 for adult males, 0.91 ± 0.07 for subadults, and 0.25 ± 0.15 for juveniles (Fig. 3). Overlapping 95% credible intervals indicated no significant difference among the annual apparent survival rates for the adult male, adult female, and subadult stages (Fig. 3). Annual apparent survival for juvenile tortoises was significantly lower than the 3 other stages (Fig. 3). Among pens, tortoises in pens 2 and 11 exhibited greater odds of annual apparent survival relative to tortoises

Table 2. Candidate models used to estimate annual apparent survival of gopher tortoises released at the Aiken Gopher Tortoise Heritage Preserve in Aiken County, South Carolina, USA, from 2006–2017 and recaptured in 2017–2018. Tortoise stage class (juvenile, subadult, adult male, and adult female; hatchlings excluded) was the sole predictor of survival in the simplest model (model 1). Because tortoises originated from throughout the species' range, we calculated the Euclidean distance and bearing between a tortoise's origin and the preserve and considered these covariates as additive and interactive effects in subsequent models (models 2–5). Relative probabilities indicate the level of support for each model. Models are displayed in order of support.

Model number	Fixed effects included in model	Relative probability
1	Stage only	0.84
3	Stage + bearing	0.09
2	Stage + distance	0.06
4	Stage + distance + bearing	0.01
5	Stage + distance × bearing	0.00

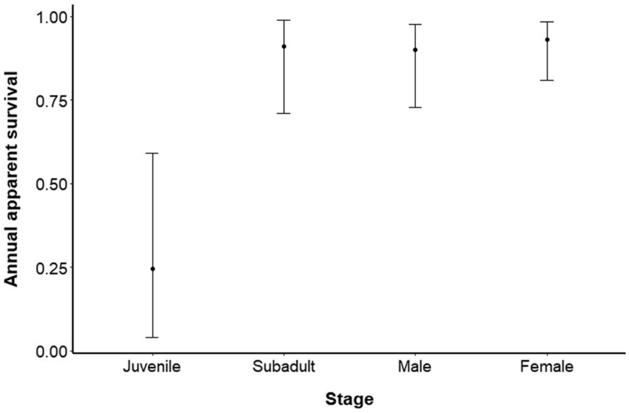

Figure 3. Mean annual apparent survival probabilities and 95% Bayesian credible intervals for juvenile (excluding hatchlings), subadult, adult male, and adult female stage classes of waif gopher tortoises, based on estimates from a joint live-dead multistate Cormack-Jolly-Seber model. Data for the model included tortoise release and incidental recapture records from 2006–2017 and recapture data collected in 2017–2018 at the Aiken Gopher Tortoise Heritage Preserve, Aiken County, South Carolina, USA.

in other pens, while tortoises in pens 7, 10, and K exhibited lower relative odds of survival (Fig. 4).

Estimated annual conditional probability (Ψ_1) for juveniles transitioning to subadult stage was 0.28 ± 0.15. For subadults the estimated annual probability of transitioning (given survival) to an adult male ($\Psi_2 \times \gamma$) was 0.03 ± 0.02 and the annual probability of transitioning (given survival) to an adult female ($\Psi_2 \times [1{-}\gamma]$) was 0.13 ± 0.04. Collectively, the estimated conditional transition probability from subadult to an adult regardless of sex (Ψ_2) was 0.16 ± 0.04.

Our model estimated the capture probability ($p_{c,t}$) in trapping years 2009, 2017, and 2018, respectively, to be 0.51 ± 0.09, 0.44 ± 0.05, and 0.81 ± 0.06 for adults, 0.22 ± 0.19, 0.24 ± 0.11, and 0.81 ± 0.13 for subadults, and 0.43 ± 0.28, 0.22 ± 0.18, and 0.69 ± 0.21 for juveniles. In years without a trapping effort, estimated capture probability was 0.02 ± 0.01 for adults, 0.05 ± 0.03 for subadults, and 0.16 ± 0.19 for juveniles. The recovery rate of dead tortoises (r_c; i.e., probabilities of detecting dead animals) was 0.37 ± 0.08 for adults, 0.31 ± 0.17 for subadults, and 0.22 ± 0.08 for juveniles.

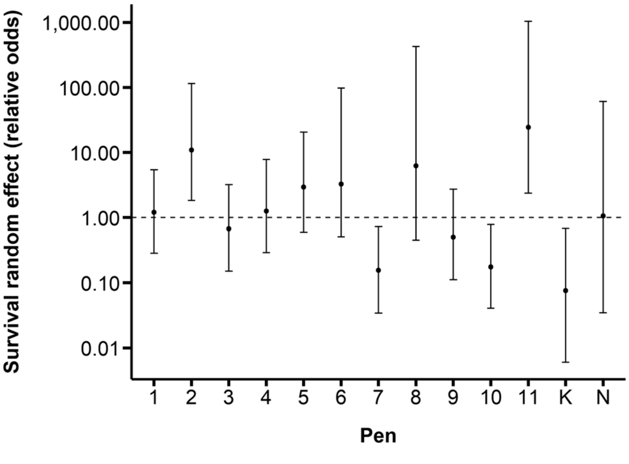

Figure 4. Estimated mean individual pen effects (and 95% Bayesian credible intervals) on annual apparent survival (relative odds with log scaling used for clarity) of gopher tortoises marked between 2006–2017 and recaptured 2017–2018 on the Aiken Gopher Tortoise Heritage Preserve, Aiken County, South Carolina, USA. Tortoises remained in pens for ≥10 months prior to release. We analyzed mark-recapture data in joint live-dead multistate Cormack-Jolly-Seber models and included pen as a random effect in all candidate models. Pen N (no pen) includes unmarked tortoises found on site during the 2017–2018 surveys; all other numbers and letters listed refer to physical pens. Pens 10, 11, and K were still standing during 2017–2018 capture efforts.

Site Fidelity

After excluding tortoises still in pens, we recaptured 73 live tortoises on ≥1 occasion. Of these, we found 41 tortoises on ≥2 occasions with 36 tortoises found in both 2017 and 2018. The median distance to first observation was 191 m ($\bar{x} = 307$ m, range = 8–1,453 m) and 75% of live tortoises encountered had moved <400 m (Fig. 5A). Number of years since release was a significant predictor of distance to first observation ($Z = 58.62$, $P < 0.001$); we encountered tortoises released earlier farther from their release location than tortoises released more recently (Fig. 6; Table 1).

Patterns were similar for the distance to last observation, with a median distance of 230 m ($\bar{x} = 340$ m, range = 33–1,517 m; Fig. 5B). Of the 36 tortoises captured in both 2017 and 2018, 10 (28%) were captured at the same burrow in both years and 23 (64%) were recaptured within 100 m of their 2017 capture point. The median distance between years was 68 m ($\bar{x} = 158$ m, range = 0−1,141 m; Fig. 5C). Although most individuals moved relatively short distances for all 3 metrics calculated, distance to first observation was >1 km for 3 individuals, and 2 additional individuals moved >1 km between 2017 and 2018 (Figs. 5A and 6).

DISCUSSION

Our study estimates the survival of waif gopher tortoises following release into the wild. Translocated adult waif gopher tortoises exhibited apparent survival rates similar to those reported for wild *in situ* populations (Ozgul et al. 2009, Tuberville et al. 2014, Howell et al. 2020, Goessling et al. 2021). Our best model (model 1) estimated annual apparent survival to be 0.93 for adult females and 0.90 for adult males, which falls within the range of rates of 0.87 to 0.98 reported for adults from 2 populations in Georgia and Alabama (Tuberville et al. 2014). A mark-recapture study on 10 tortoise populations in central Florida estimated annual apparent survival probability to be 0.95 ± 0.04 for females and 0.89 ± 0.04 for males (Ozgul et al. 2009). The observed difference between male and female survival was not significant in either study (Ozgul et al. 2009, Tuberville et al. 2014), although apparent survival was estimated to be 9% lower for males at the Georgia site (Tuberville et al. 2014). Similarly, although our adult male survival estimate was slightly lower than our adult female survival estimate, the overlap in the 95% credible intervals suggest that this difference is also not statistically different (Fig. 3).

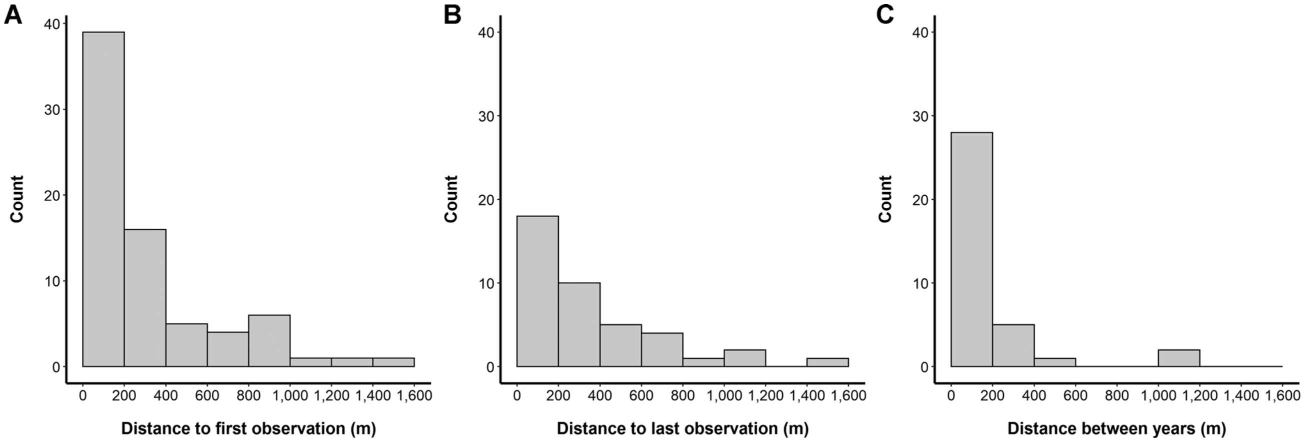

Figure 5. Observed distribution of gopher tortoise dispersal distance (m) following release at the Aiken Gopher Tortoise Heritage Preserve, Aiken County, South Carolina, USA. Distance to first observation is the Euclidean distance from the center point of the tortoise's release pen to the location of its first observation during 2017–2018 (A). The distance to the last observation is the Euclidean distance between the center point of the tortoise's release pen and its last recapture location (B). For tortoises observed in both 2017 and 2018, distance between years refers to the Euclidean distance between its first points of observation in 2017 and 2018 (C).

Previous studies on translocated wild gopher tortoises have observed temporary reductions in survival in the first 2 years after release (the establishment phase), followed by high long-term survival rates thereafter (Ashton and Burke 2007, Tuberville et al. 2008). The AGTHP population was not consistently sampled in the years immediately following the multiple ongoing releases. Thus, we are unable to determine if released waif gopher tortoises also exhibited a temporary reduction in apparent survival; however, long-term annual apparent survival rates were high. Although many of the waif gopher tortoises in our study were held in captivity for extended periods, adult waif tortoises exhibited survival rates comparable to those documented in wild-to-wild translocated and *in situ* wild gopher tortoises. This finding

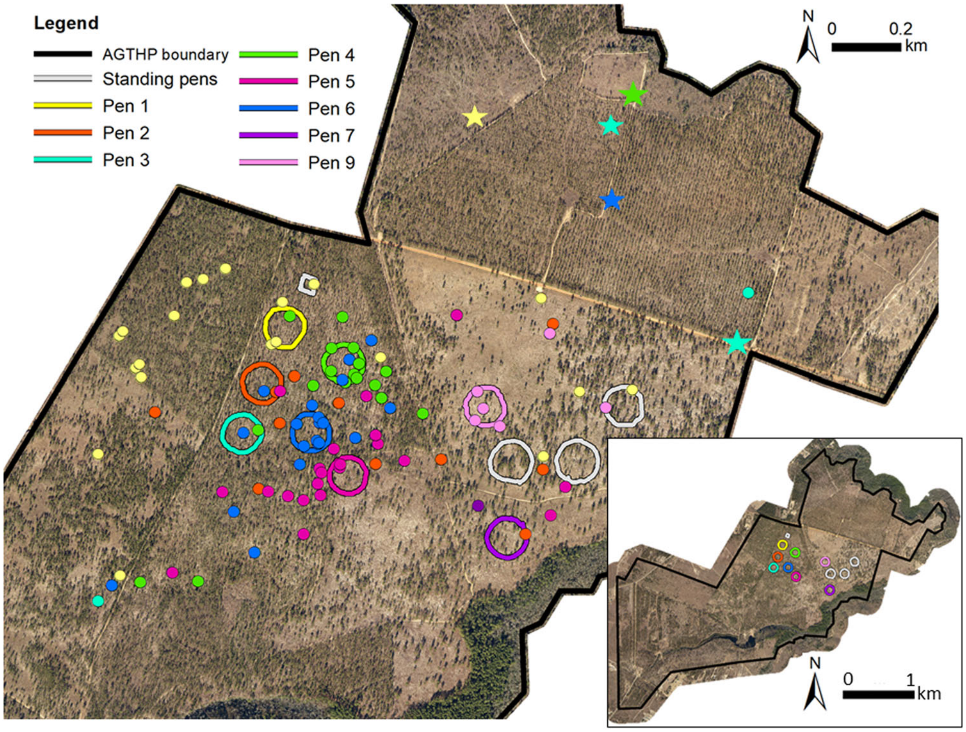

Figure 6. Gopher tortoise capture locations in 2017–2018 at the Aiken Gopher Tortoise Heritage Preserve (AGTHP) in Aiken County, South Carolina, USA. We released tortoises from 2006–2017 into 1-ha pens where they were held for ≥10 months. Capture locations of tortoises are color coded according to their respective release pen. Stars indicate capture locations of 3 tortoises (2 from pen 3 and 1 from pen 1) that moved >1 km between their release point and first observation and locations of 2 tortoises (1 from pen 4 and 1 from pen 6) that moved >1 km between 2017 and 2018. Pens 8, 10, 11, and K (grey) were still standing at the time of the survey and we excluded tortoise capture locations associated with these pens in the site fidelity analysis. The inset shows the entire footprint of the AGTHP. Map image is the intellectual property of Esri and is used herein under license. Copyright © 2020 Esri and its licensors. All rights reserved.

is consistent with studies on other chelonians, such as the Hermann's tortoise (Bertolero et al. 2018), European pond turtle (*Emys orbicularis*; Canessa et al. 2016), and Mojave desert tortoise (Field et al. 2007), which indicated that formerly captive individuals can exhibit long-term survival rates comparable to wild conspecifics. Although, in general, translocations of wild individuals tend to be more successful than those involving formerly captive individuals (Fischer and Lindenmayer 2000, Harrington et al. 2013), reptiles may be more resistant than other taxa to potential adverse effects of captivity, possibly because of their higher physiological and behavioral plasticity (Germano and Bishop 2009, Rummel et al. 2016).

Previous studies of *in situ* gopher tortoise populations have focused on estimating survival of either hatchling (Epperson and Heise 2003, Pike and Seigel 2006, Perez-Heydrich et al. 2012, Smith et al. 2013) or adult stage classes (Ozgul et al. 2009). As a result, very few studies have reported apparent survival rates for immature tortoises, and even fewer have calculated separate survival estimates for the juvenile and subadult stage classes. In 2 *in situ* populations in Alabama and Georgia, immature annual apparent survival was estimated to be between 0.70 and 0.82 (Tuberville et al. 2014). Similarly, for an *in situ* population in Florida, mean survival for immature tortoises was estimated to be 0.74 (Howell et al. 2020). Immature annual apparent survival in a wild-to-wild translocated population on a barrier island in Georgia was estimated to be 0.45 ± 0.26 in the first year following release and 0.84 ± 0.05 thereafter (Tuberville et al. 2008). As with many other chelonians, including the Mojave desert tortoise, gopher tortoises have lacked reliable survival estimates for distinct stage classes (hatchling, juvenile, subadult) and instead relied on aggregate estimates for immature classes (Brand et al. 2016, Harju et al. 2020). To accurately model population dynamics and trajectories, stage-specific survival estimates are essential (Smith et al. 2006, Tuberville et al. 2009). Because we used a multistate modeling framework to distinguish stage-specific transition probability from survival, our study is among the first to separately estimate annual apparent survival for subadult (0.91 ± 0.07) and non-hatchling juvenile gopher tortoises (0.25 ± 0.15). Using a similar analytical approach, a recent study estimated apparent annual survival to be 0.71 for juveniles and 0.83 for subadult gopher tortoises recruited into a population following translocation (Tuberville et al. 2021). Although estimates from additional populations are required to fully address this historical gap in life-history information, our estimates will serve as an important benchmark, particularly for manipulated populations.

We obtained waif tortoises from sources located both within and outside the species' geographic range to augment the AGTHP population but found no evidence that survival of waif gopher tortoises varied as a result of distance or bearing from their origin. Low representation of waifs from western states (LA, AL, MS) and a preponderance of waifs obtained from Florida could have reduced our ability to detect slight differences in survival among tortoises of different origins. Additional mark-recapture effort at AGTHP in future years and better information on origin of future waif acquisitions could further illuminate any potential effects of origin on apparent survival. In addition, future genomic analyses could help assign waifs to their genetic population of origin, as has been done in Mojave desert tortoises (Edwards and Berry 2013). Because the origin of 31 individuals in our study could only be identified to the state-level and the origin of 27 tortoises remains completely unknown, genetic analyses could resolve these uncertainties and confirm the accuracy of the origin assignments for the remaining 165 tortoises. Finally, genomic analysis may reveal the extent to which reproductive and social integration occurs among tortoises from different origins or acquisition groups in this social reptile (Tuberville et al. 2011). These aspects are important considerations in translocation efforts for chelonians (Tuberville et al. 2011, Mulder et al. 2017, Cozad et al. 2020) and other taxa (Muller et al. 2018, Poirier and Bianchet 2018, Bacon et al. 2019, Goldenberg et al. 2019, Franks et al. 2020).

Tortoise apparent survival varied by pen, with 3 pens exhibiting lower rates of annual apparent survival (Fig. 4). Although annual apparent survival might have been expected to be highest in intact pens because resident tortoises could not disperse, 2 of the intact pens (10, K) exhibited the lowest survival (Fig. 4). We cannot say conclusively why these pens exhibited lower survival; however, we observed a higher prevalence of the known tortoise pathogen *Mycoplasmopsis agassizii* in pen 10 than in other pens (McKee 2019). Because tortoises in pens may come into frequent contact with each other, an infected individual may negatively affect the survival of other individuals housed in the same pen. Although the density of pen 10 did not differ from the other pens (Table 1), higher release densities in pens housing multiple acquisition groups of translocated tortoises have been linked to elevated mortality (Cozad et al. 2020). By limiting the number of individuals housed in each pen, the number of tortoises affected by an infectious agent may also be minimized, although this must be balanced with the labor and expense associated with constructing additional pens. In cases where disease screening is not possible, visual health assessments and ongoing monitoring during the penning period when animals are effectively quarantined could reduce the risk of introducing pathogens to the entire population.

Penning increases site fidelity of wild-to-wild translocated tortoises (Tuberville et al. 2005), and the use of pens at AGTHP likely contributed substantially to the high rates of apparent survival we observed. Tortoises released more recently were found closer to their release location than tortoises released earlier in the study. Even though the tortoises included in the site fidelity analysis had been released from pens 2–9 years prior to our trapping effort, we located the majority of recaptured tortoises <200 m from their release location and 75% of recaptured tortoises ≤400 m from their release location (Figs. 5A and 6). This distance is larger than the estimated diameter of annual home range sizes reported for resident gopher tortoise populations in Florida ($\bar{x} = 1.7$ ha or ~147.1 m diameter; Smith et al. 1997), Mississippi ($\bar{x} = 1.09$ ha or ~117.8 m diameter; Yager et al. 2007), and Georgia ($\bar{x} = 0.4$ ha or ~71.4 m diameter for females and 1.1 ha or ~118.3 m for males; Eubanks et al. 2003). Because home ranges are generally calculated annually, it is unclear if the AGTHP tortoises moved at an increased rate or if the larger distance we observed is due to the longer time frame of this study; however, given that time-since-release was an important predictor of dispersal distance, difference in time scale likely at least partially explains the larger distance between captures observed in our study. One home range study provided the maximum displacement distance between the 2 most distant telemetry locations used by individual tortoises within a year, which ranged from 116–1,359 m among 31 tortoises in south Florida but averaged 220–394 m depending on sex and land cover type (mesic flatwoods or scrub; Castellón et al. 2018). As part of a long-term mark-recapture study in northern Florida, Berish et al. (2012) noted that of the 17 resident tortoises first captured during 1981–1992 and recaptured in 2009, 88% were captured within 200 m of their original capture location but 1 male had moved >800 m. Although comparable data are limited, the distances we observed do not appear to be uncharacteristic for the species, particularly given the time scale over which recaptures occurred.

Even with penning, a small fraction of individuals may disperse from the release site (Tuberville et al. 2005, Bauder et al. 2014). Based on the average minimum distance between the pens and the preserve perimeter ($\bar{x} = 437.3$), it was possible for tortoises to disperse beyond the boundary of the site. Although we did not survey areas outside the preserve's footprint, 4 individuals were incidentally observed on roadways or nearby private property since the initial tortoise releases began in 2006. Additionally, 3 individuals captured on the preserve had a distance to first observation >1 km from their release pen. Occasional long-distance dispersal events have also been reported in translocated Mojave desert tortoises (Nussear et al. 2012) and resident gopher tortoises (Eubanks et al. 2003). This pattern highlights the importance of considering release site characteristics, such as proximity to roads and total available habitat.

Because tortoise site fidelity and survival rates can also vary depending on the quality of the habitat (Howell et al. 2020), it is important to note that the AGTHP was and continues to be regularly burned, thinned, and managed for tortoises. Provided such intensive habitat management efforts continue, the preserve can provide up to 525 ha of high-quality habitat for gopher tortoises. This represents >5 times the consensus threshold reserve size (100 ha of high-quality habitat) recommended for supporting a viable tortoise population of ≥250 adults (Gopher Tortoise Council 2014). On this basis, there is sufficient habitat at AGTHP for all tortoises released to date and to accommodate additional waifs that become available (Moule 2013). Efforts by SCDNR to expand and manage the AGTHP likely also contributed to the high rates of apparent survival we observed in this study. Because habitat loss and degradation are the main threats to this species (Smith et al. 2006), translocation and population augmentation efforts are likely only effective when implemented in conjunction with habitat protection, restoration, and management of the recipient site.

Our study provides insight into an emerging management issue—whether the growing number of waif gopher tortoises in captivity are suitable candidates for release into the wild. As the first study to evaluate waif gopher tortoise translocation, it also provides important considerations for future gopher tortoise management. Adult survival following release historically has been an important parameter for determining the success or failure of translocation projects (Dodd and Seigel 1991, Ashton and Burke 2007, Tuberville et al. 2008) because of the sensitivity of population viability to adult mortality in many turtle species (Seigel and Dodd 2000). Because waif tortoises are often housed in captivity for extended periods, it was uncertain if waifs at this site would exhibit high levels of survival following release; however, the annual apparent rates of survival observed in this study were comparable to rates observed *in situ* (Ozgul et al. 2009, Tuberville et al. 2014, Howell et al. 2020) and in wild-to-wild translocated tortoise populations (Ashton and Burke 2007, Tuberville et al. 2008). The high survival rates we observed in our study suggest that waif tortoises can be used to augment or re-establish tortoise populations in circumstances where the risk to an existing or neighboring population is low and other recovery options are limited. Because many tortoise species globally are held as pets (Edwards and Berry 2013), these findings are important not only to gopher tortoises but for other tortoise species as well, including the ploughshare tortoise (*Astrochelys yniphora*; Mandimbihasina et al. 2020), Greek tortoise (*Testudo graeca*; Salinas et al. 2011, Pérez et al. 2012), and desert tortoise (*Gopherus* spp.; Edwards et al. 2010). Moreover, because illegal wildlife trade is a major threat to chelonians (Mendiratta et al. 2017, Sung and Fong 2018) and wildlife more broadly (Rosen and Smith 2010), it is increasingly important to find ways of using confiscated and formerly captive individuals for conservation objectives. Because this is the first effort to quantify the survival of waif gopher tortoises following translocation, additional monitoring of outcomes for other populations augmented with waifs is important to assessing the broader application of our results for gopher tortoises and other species facing similar management dilemmas.

MANAGEMENT IMPLICATIONS

As gopher tortoise populations continue to decline, waif tortoises could play an important role in the conservation of isolated populations facing extirpation, while also reducing the number of waifs relegated to permanent captivity. Because waif tortoises have the potential to introduce novel pathogens, caution is still warranted. The use of waif animals to augment populations is most appropriate for situations where the recipient site does not or is unlikely to support a viable population using lower risk management interventions alone, such as habitat improvement or nest protection, and is geographically isolated from the nearest population by either a distance that greatly exceeds the dispersal distance of translocated tortoises or is surrounded by features impermeable to a dispersing tortoise (e.g., large bodies of water). Additionally, health assessments prior to release (and when possible, pathogen screening) can minimize the risk of disease introduction. Although historically perceived as a management dilemma, waif gopher tortoises, especially the adults, are valuable, irreplaceable individuals that can be repurposed for recovery of wild populations.

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