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Note

Post-Release Movement and Survivorship of Head-Started Gopher Tortoises

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ABSTRACT Gopher tortoise (*Gopherus polyphemus*) populations are declining throughout their range and recovery requires management intervention to alleviate losses. Population augmentation strategies may prove useful in recovery of depleted populations once threats are mitigated. We head-started and soft-released hatchlings produced from robust donor populations and evaluated their post-release survivorship and movement for the first year following their release. During 2014 and 2015, we head-started and released 145 tortoises, of which we radio-tracked a subset of 41 individuals, from 2 cohorts at 2 release areas within Yuchi Wildlife Management Area in Burke County, Georgia, USA. Movement and mortality of gopher tortoises was highest in the first month after release but declined soon after. Estimated annual survivorship of our first cohort was 60.6%. Annual survivorship of our second cohort was low (7.1%) at the southeast release area but much higher (75.0%) at the northwest release area because of spatial variation in predation. Although survivorship was variable, site fidelity remained high throughout the study and no tortoise moved >122.0 m from its release location. Initial results suggest that head-starting could prove effective as a population recovery tool, but that release strategy and predator mitigation, especially within the first month, are critical to success. © 2018 The Wildlife Society.

KEY WORDS augmentation, Georgia, gopher tortoise, head-start, juvenile, movement, population recovery, survivorship.

Turtles are declining globally and approximately half of all extant species are currently listed as threatened on the International Union for Conservation of Nature (IUCN) red list (Rhodin et al. 2011). Mitigating threats that led to initial declines (e.g., habitat degradation, poaching, disease) is the first step land managers must make to recover depleted populations (Frazer 1992, Seigel and Dodd 2000). Turtle life-history traits include a long adult lifespan, delayed sexual maturity, low offspring survival, and low reproductive output (Gibbons 1987, Congdon and Gibbons 1990, Iverson 1991), which constrain recovery potential when the adult population has been diminished (Congdon et al. 1993). Furthermore, depleted populations may be below the minimum viable population size (MVP) and unable to recover (Shaffer 1981), remaining vulnerable to extirpation even once threats have been mitigated (Hall et al. 1999). Depleted populations can be augmented by introducing individuals to attain or surpass MVP thresholds, thereby decreasing the likelihood of extirpation. Individuals used in augmentation efforts are typically wild-caught or reared in captivity and subsequently translocated (i.e., intentionally released at a within-range location different from their capture location to establish, reestablish, or augment a population; Griffith et al. 1989).

The gopher tortoise (*Gopherus polyphemus*) is native to the southeastern United States, residing primarily in upland habitats on sandy soils of the Coastal Plain physiographic region. Populations have been declining throughout their range (Auffenberg and Franz 1982, McCoy et al. 2006) because of habitat degradation and loss of the longleaf pine (*Pinus palustris*) savanna ecosystem, causing many populations to fall below the estimated 250 adults required to form an MVP (Gopher Tortoise Council 2013, 2014). These population declines are responsible for their current federal listing in the western portion of their range and their status as a candidate for federal listing in the eastern portion (U.S. Fish and Wildlife Service 2011). The displacement of wild gopher tortoises from development sites has contributed to their becoming one of the most widely translocated herpetofauna species (Dodd and Seigel 1991, Seigel and Dodd 2000, Tuberville et al. 2005) making them ideal candidates for evaluating the role that augmentation strategies could play in population recovery.

Although prior studies have evaluated the success of translocating wild gopher tortoises (Ashton and Burke 2007;

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Riedl et al. 2008; Bauder et al. 2014; Tuberville et al. 2005, 2008), the sporadic availability of wild tortoises, many of which are displaced from development sites (Doonan 1986, Burke 1989, Heise and Epperson 2005), make them an unpredictable source for planned population recovery efforts. In contrast, eggs can be readily collected from robust populations and the resulting hatchlings reared under controlled conditions (Quinn et al. 2016). Hatchlings have low annual survivorship in the wild (12.8%; Perez-Heydrich et al. 2012). Pike and Seigel (2006) also reported that in 3 radio-tracking studies all 85 hatchlings died within 2 years of release. This naturally low survival rate, along with an average age at maturity of 14.4 years (range = 10–20 yr; Diemer 1986, Germano 1994, Ashton and Ashton 2008), would make population recovery slow if relying solely on released hatchlings. However, after adult survivorship, population persistence is most sensitive to changes in juvenile survivorship (Tuberville et al. 2009) and increasing juvenile survivorship should be the next priority for augmenting populations. Head-starting, "...the practice of protecting especially vulnerable life stages of a species to increase the likelihood of survivorship for conservation purposes..." (Burke 2015: 299), may offer a suitable or additional alternative to augmenting populations with wild adults. Tortoises head-started in captivity are protected from predation during the most vulnerable hatchling life stage (Frazer 1992). In addition, head-starts are also typically kept active and growing during the dormant season, which allows them to be released at larger sizes and with potentially harder shells relative to same-aged wild conspecifics (Nagy et al. 2011, Buhlmann et al. 2015, Green 2015, Holbrook et al. 2015), presumably further reducing their risk of predation (Heppell et al. 1996, O'Brien et al. 2005). Furthermore, because sexual maturity is dictated largely by body size in tortoises (Iverson 1980, Landers 1982), head-starting to larger size classes may enable head-starts to reach sexual maturity sooner than their wild counterparts, although this has yet to be demonstrated.

Thorough research on head-starting as a population recovery tool for a target species (Mitrus 2005, Haegen et al. 2009, Buhlmann et al. 2015, Nagy et al. 2015) is needed before being implemented on a large scale (Snyder et al. 1996, Seigel and Dodd 2000). For head-starting to be effective, head-starts ultimately need to be recruited into the breeding population. However, monitoring released head-starts until maturity is a long-term endeavor and shorter-term metrics are needed to evaluate initial success. We radio-tracked head-started gopher tortoises released into a depleted population at the Yuchi Wildlife Management Area (YWMA) in Burke County, Georgia, USA. Despite half of the release site providing suitable habitat for gopher tortoises, Smith et al. (2009) reported few native tortoises while conducting line transect surveys. Only 27 resident tortoises (89% adult, 4% subadult, and 7% juvenile) were encountered on line transects, resulting in an estimate of 44 resident tortoises (GADNR, unpublished data). The low population density was likely due to historically incompatible silvicultural practices and from tortoise harvest by the public prior to purchase by the state (J. B. Jensen, GADNR, personal observation), threats that largely no longer exist. As part of a separate study conducted by The Orianne Society in collaboration with GADNR, 18 adult tortoises were translocated to YWMA in 2012 (Bauder et al. 2014) with an additional 19 released in 2013 (GADNR, unpublished data). These releases resulted in an estimated 81 adult and sub-adult tortoises with no observations of hatchlings or young juveniles. Yuchi Wildlife Management Area was subsequently chosen by GADNR as a suitable recipient site to help assess the effectiveness of using head-started juveniles to augment tortoise populations. Our goal was to conduct a descriptive study to document annual movement and survivorship of 2 cohorts of head-started gopher tortoises after their release to assess head-starting as a potential population recovery tool.

STUDY AREA

Yuchi Wildlife Management Area is a 3,127-ha protected area near Waynesboro (Burke County), Georgia (33.11°N, 81.74°W) that lies immediately south of the Georgia Fall Line on the Upper Coastal Plain, which is located near the northeastern edge of the gopher tortoise's range. Waynesboro is approximately 50 m above sea level, receives an average annual rainfall of 121.4 cm, and has average annual high and low temperatures of 24.3°C and 11.1°C, respectively. Prior to 1988, YWMA was private land largely managed for timber harvest. The Georgia Department of Natural Resources (GADNR) purchased the land in 1988 and has since restored native longleaf pine. At the time of our study, YWMA was predominantly composed of upland pine (*Pinus* spp.) and pine-scrub oak (*Quercus* spp.) mixtures, with several creek bottoms and wetlands adjacent to the Savannah River. Upland soils were well-drained and sandy (including Lakeland, Troup, Bonifay, Orangeburg, and Lucy), grading into poorly drained flood plain soils (i.e., Osier, Chastain, and Shell Bluff).

We selected 2 release areas for head-start gopher tortoise release and tracking between May 2014 and July 2016. Release areas were centrally located within YWMA to minimize potential for released head-starts to disperse outside YWMA boundaries. The release areas were located on opposite sides of a sandy, infrequently used road (Fig. 1) and were separated by only 275 m. The 2 release areas were in separate but adjacent management compartments that were similar in vegetation structure, with a sparse open canopy of predominantly longleaf pine, absent mid-story, and a diverse understory, making the areas well-suited for gopher tortoises (Landers and Speake 1980, Aresco and Guyer 1999, Nussear and Tuberville 2014). The northwest (NW) release area had been clearcut and replanted with longleaf pine prior to 2010. The southeast (SE) release area had been partially cleared and burned in the winter and spring 2013, but some older trees remained.

METHODS

We collected gopher tortoise eggs from 3 populations in Georgia: St. Catherines Island in Liberty County, Reed Bingham State Park in Cook County, and YWMA. Quinn

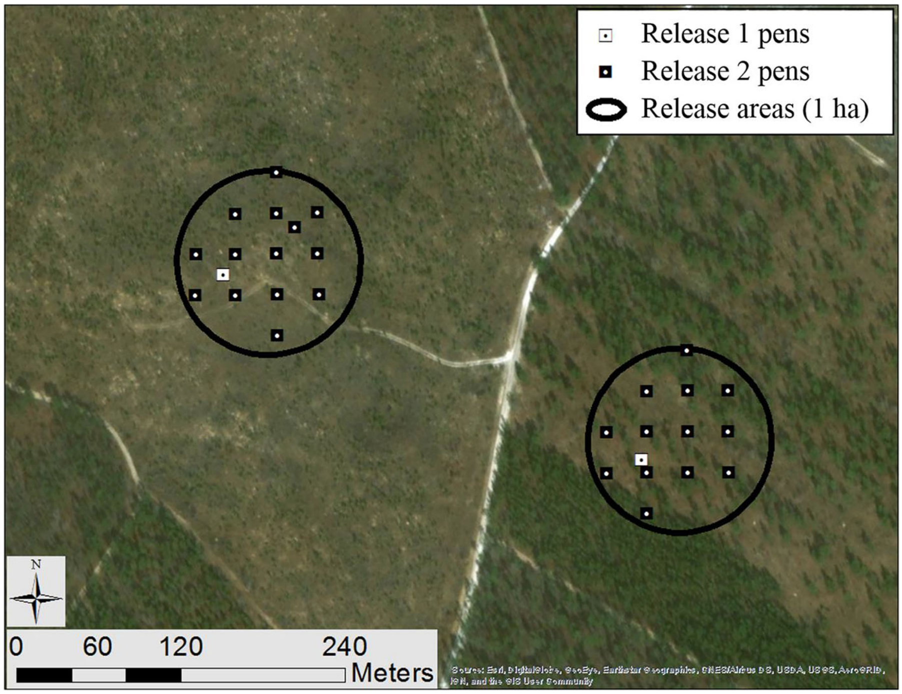

Figure 1. Soft-release pen locations used within 2 1-ha release areas (NW and SE) for release 1 (summer 2014) and release 2 (summer 2015) head-started gopher tortoises at Yuchi Wildlife Management Area, Georgia, USA. During release 2, 14 pens were distributed within a 1-ha circular area at both release areas using a grid pattern such that no pen was within 25 m of another pen. However, 1 pen in the NW release area was moved just prior to release because of presence of fire ants.

et al. (2016) provide a description of egg collection methods, incubation, and hatching success. We head-started tortoises indoors for 8–9 months on St. Catherines Island and at the University of Georgia's Savannah River Ecology Laboratory (SREL; Aiken County, South Carolina, USA) before releasing them the spring following hatching. Quinn (2016) provides a description of head-starting procedures. We weighed tortoises to the nearest 0.1 g using a DeltaRange® Mettler PE 3,600-g scale (Mettler Toledo, Columbus, OH, USA) and measured straight mid-line carapace length (SCL) to the nearest 0.1 m using dial calipers (Mitutoyo, Aurora, IL, USA) after hatching and just prior to release. Sizes and weights are reported as means (±1 SE). We permanently marked tortoises just before release by notching a unique combination of marginal scutes (Ernst et al. 1974).

Releases

During 2014 and 2015, we released 145 head-start tortoises, of which we radio-tracked 41 to evaluate post-release movement and survivorship (Table 1). We first soft-released head-starts by placing tortoises in temporary pens to increase site fidelity by allowing them time to acclimate to the release site and establish a burrow. We initially planned to pen head-starts for 30–50 days, staggering releases over several days. The intended penning duration was based on our observations of head-started desert tortoises (*Gopherus agassizii*), which exhibit greatest movement within the first 1–2 months following release (K. A. Buhlmann, University of Georgia, unpublished data). However, because of issues encountered during the penning period (see release 2 results), actual penning duration varied from 4 to 47 days. Prior to placing head-starts in pens, we attached radio-transmitters (Advanced Telemetry Systems Model R1680, 3.6 g, Isanti, MN, USA) to the fourth vertebral scute using WaterWeld epoxy (J-B Weld®, Sulphur Springs, TX, USA). We had 2 release groups: release 1 (2013 cohort, $n = 12$) and release 2 (2014 cohort, $n = 133$).

For release 1, we installed 2 pre-fabricated chain link pens (Fig. 2A) 280 m apart (1 in each release area). To accommodate the larger sample size for release 2, we created 28 smaller soft-release pens made of galvanized hardware cloth (Fig. 2B). Approximately 3 weeks prior to soft-release, we treated release sites for fire ants (*Solenopsis invicta*) by broadcasting AMDRO® (AMBRANDS, Atlanta, GA, USA) within an approximately 3-m perimeter around the outside edge of each pen (application rate not quantified). Within each pen, we constructed 5–10 starter burrows approximately 30–40 cm deep by pounding a 7.5-cm-diameter pipe at an approximately 35° angle using a post driver. Starter burrows were provided as initial refugia, which gopher tortoises could expand or use until they constructed their own. During soft-release we randomized tortoises, 5–6 in each pen, but no pen contained siblings from the same clutch. After the soft-release period, we removed pens and initiated post-release monitoring of transmittered gopher tortoises.

Post-Release Monitoring

For both releases, we monitored survivorship and movement of transmittered tortoises for 1 year following release (i.e., pen removal). We tracked tortoises 2–3 times a week during

Table 1. Releases of head-started gopher tortoise at Yuchi Wildlife Management Area, Georgia, USA, and their known fates 1 year post-release, summarized by release groups (release 1 or release 2) and release area (NW or SE). Soft-release date is the date tortoises were placed in pens; release date is the date when soft-release pens were removed. Survival estimates are based on Kaplan-Meier (KM) survivorship analyses of tracked tortoises.

	Releases			
Parameters	Release 1 NW area	Release 1 SE area	Release 2 NW area	Release 2 SE area
Cohort	2013	2013	2014	2014
Release year	2014	2014	2015	2015
Soft-release date	30 May 2014	30 May 2014	5 Jun 2015	5 Jun 2015
Release date	16 Jul 2014	16 Jul 2014	Staggered[a]	9 Jun 2015
Number released	5	6	62	71
Number tracked	5	6	16	14
Number survived	4	1	12	1
Number deceased	1	3	4	13
Number censored	0	2	0	0
% KM annual survivorship estimate	80.0%	33.3%	75.0%	7.1%

[a] Staggered releases from 6 July 2015 through 22 July 2015; mean number of days in pens = 39 days.

increased activity periods post-release (Jun–Aug) and then ≥1 time/week through the remainder of the study. We recorded each telemetry location to the nearest ± 3 m using a Garmin GPSMAP® 64 (Garmin International, Olathe, KS, USA). We marked all burrows used by transmittered tortoises by placing a uniquely numbered aluminum tag (Forestry Suppliers, Jackson, MS, USA) adjacent to the burrow apron using a landscaping staple. When we tracked tortoises to burrows, we documented the burrow identification, location, and if the tortoise had moved since its previous tracking event. We could not verify state (alive or dead) for each tracking event without disturbing tortoises or their burrows, thereby potentially influencing their movement patterns. However, if we suspected that tortoises were dead inside their burrows because of presence of numerous fire ants, or lack of movement or signs of recent tortoise activity within the previous 2 weeks (i.e., no freshly excavated sand on the apron, collapsing burrow entrance, prolonged absence of tracks, foliage on apron), we inspected the burrow with a burrow scope (Environmental Management Systems, Canton, GA, USA) to determine the tortoise's status (alive or dead). If a tortoise was found deceased above or below ground, we attempted to determine the most likely cause of death by inspecting for damage to the shell and transmitter package. If a dead tortoise or its transmitter showed evidence of teeth marks, we assumed it was depredated by a mammal. When we found a dead tortoise intact, but covered with fire ants, we assumed fire ants to be the direct cause of death. In release 2 we also used wildlife cameras at soft-release penning sites to aid in predator verification.

For evaluating movement and survivorship to winter dormancy, we defined 15 November as the end of the activity season based on other Georgia studies (McRae et al. 1981, Harris et al. 2015). We visually confirmed each tortoise's status by inspecting its burrow with a burrow scope at the beginning of dormancy, and again when tortoise burrows began to show signs of activity in spring. During dormancy we continued tracking but did not scope burrows to prevent disturbing tortoises. We scoped burrows a final time a year post-release to document tortoise status. All methods followed protocols approved by the University of Georgia Institutional Animal Care and Use Committee (number A2014 08-006-Y1-A0) and by permits provided by GADNR Wildlife Resources Division (numbers 29-WJH-14-93, 29-WJH-13-83), and Georgia State Parks and Historic Sites Division (number 172014).

Analysis

For each release, we created survivorship curves with monthly intervals for the first year after release from their pens based on whether head-starts were dead, alive, or censored. Even though we could not determine state for each tracking event, we verified state of animals that had not exhibited movement or other signs of activity for >2 weeks. Thus, our monthly survival estimates should accurately reflect true survival. Using the asbio package in Program R (Aho 2015), we estimated annual survivorship using the Kaplan–Meier estimator for staggered entry, which models a proportion of censored animals as being alive (Pollock et al. 1989). Survivorship data are presented as means ± 95% confidence intervals. We compared annual survivorship between release 1 and release 2 and between the NW and SE areas (release 2 only) using log-rank tests, with $\alpha = 0.05$ (Pollock et al. 1989).

All movement analyses are based on burrow locations used by radio-tracked tortoises. We used the Spherical Law of Cosines (Movable Type Ltd. 2015) to calculate step distances (i.e., linear distances between successive burrow locations) and linear displacement from release sites (i.e., linear distance from each burrow used by a tortoise to the tortoise's release pen location) to calculate the number of steps, mean step length, maximum step length, minimum step length, and cumulative step length (i.e., sum of all step lengths) for each tortoise. We also used burrow locations to calculate mean displacement, minimum displacement, maximum displacement, and final displacement from release sites (i.e., displacement 1 yr post-release) for each tortoise. We averaged all movement values for a given metric across individuals within a release group. However, because tortoise mortality resulted in different monitoring durations among individuals, we also averaged movement metrics across only those individuals that survived to 1 year post-release in each release group.

Figure 2. Soft-release pens for head-started gopher tortoises at Yuchi Wildlife Management Area, Georgia, USA. A) Portable chain link pens used for release 1 soft-release (3-m L × 3-m W × 1.8-m H; 5.1-cm mesh; MidWest Black E-Coat Exercise Pens, Midwest Pet Products, Irvine, CA, USA). We modified each chain link pen to prevent escape of tortoises and trespass of predators by attaching aluminum flashing to the inside perimeter of pens, sinking the pens into the ground approximately 15 cm, and placing 1.9-cm (0.75-in) mesh cloth netting over the tops to exclude avian predators. B) Hardware cloth pens used for release 2 soft-release (1.2-m L × 1.2-m W × 0.6-m H; 6.4-mm mesh; Jackson Wire International, Houston, TX, USA). We excavated a narrow, 15-cm deep trench in dirt to place the pen walls, which we reinforced with wooden stakes at all 4 corners to help add stability to the hardware cloth. Once we placed tortoises in the pens, we secured the top to the sides of the pen with zip ties to exclude mammalian and avian predators.

RESULTS

Release 1 (2013 Cohort)

We head-started all 12 hatchlings at St. Catherines Island for an average of 250 ± 2 days; all survived the head-starting period. While in captivity, tortoises gained an average of 48.5 ± 4.0 g (initial = 38.1 ± 0.9 g; final = 86.5 ± 4.4 g) and reached an average SCL of 71.2 ± 1.2 mm (range = 65.6–81.8 mm) by 30 May 2014, the time we placed them in soft-release pens (Fig. 2A). We released 11 of 12 head-starts from pens on 16 July 2014 by removing the pens. One head-start was depredated by fire ants during penning and was excluded from further analyses. Of the 11 head-starts released, 8 survived (72.7%) to their first winter dormancy (i.e., 15 Nov 2014), with none censored. All 8 tortoises alive at the beginning of winter dormancy survived through the entire dormancy period (i.e., 100% dormancy survivorship) until mid-April, when they began moving again. After dormancy, one head-start died and 2 were censored. By 1 year post-release, 4 had died, 2 were censored, and 5 were alive, resulting in an estimated annual survivorship of 60.6% (95% CI = 30.1–91.0%; Fig. 3A) for both NW and SE areas combined. Although survivorship estimates varied between release areas (i.e., 80.0% at the NW area and 33.3% at the SE area), the difference was not statistically significant ($\chi^2_1 = 1.30$, $P = 0.25$).

Maximum displacement of the 11 head-starts from their release pens ranged from 22.3–122.0 m (Table 2). The 5 head-starts that survived the first year post-release had a maximum displacement of 27.9–88.8 m. Final displacement distances of head-starts at 1 year post-release were similar to maximum displacement distances (Table 2). All head-starts combined (i.e., those that did and did not survive 1 year post-release) constructed an average of 3.1 additional burrows (range = 1–8) and moved an average of 23.5 m (range = 10.7–41.5 m) between burrow locations. The maximum single movement (i.e., step) of individual head-starts ranged from 15.8–109.5 m.

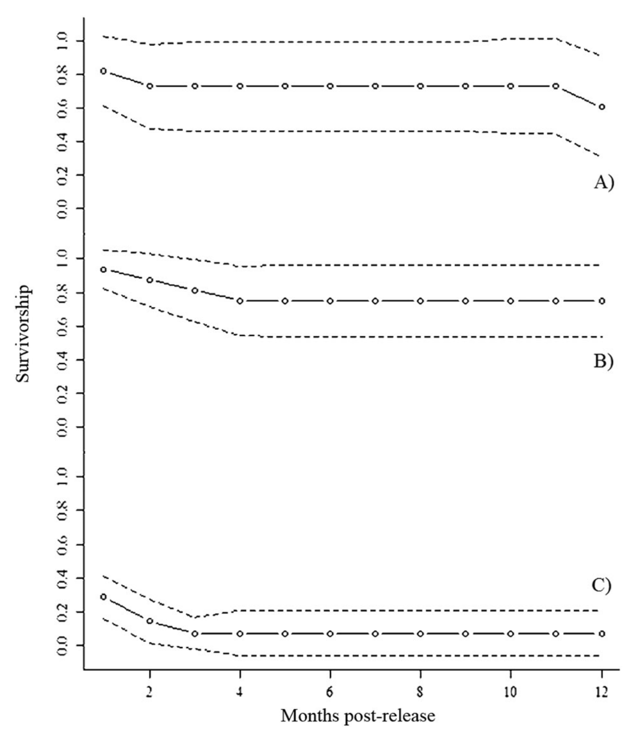

Figure 3. Post-release Kaplan-Meier survivorship curves by month (large dashes with open circles) with 95% confidence intervals (small dashes) for transmittered head-started gopher tortoises at Yuchi Wildlife Management Area, Georgia, USA for A) release 1 ($n = 11$; 2013 cohort released in 2014); B) release 2 in the northwest release area ($n = 16$; 2014 cohort released in 2015); and C) release 2 in the southeast release area ($n = 14$; 2014 cohort released in 2015).

Table 2. Movement metrics of radio-tracked head-started gopher tortoises during their first year following release at Yuchi Wildlife Management Area, Georgia, USA. Values are averaged across individuals from the same release group and are calculated for all individuals released (i.e., including deceased using subscript all) and for only tortoises surviving through the first year post-release (subscript surv). Steps represent movements between successive burrows and cumulative step is the sum of all step lengths between burrows. Displacement is the linear distance between burrows and release site, with final displacement indicating the distance between release site and most recent burrow used at the end of the 1-year monitoring period. Data are presented as means with ranges presented in parentheses.

	Release group			
Metric	Release 1_{all}	Release 1_{surv}	Release 2_{all}	Release 2_{surv}
n	11	5	30	13
Days in study	254.5 (2–365)	365	171.7 (3–365)	365
Number of steps	4.5 (1–14)	5 (2–9)	2.5 (0–9)	5 (0–9)
Mean step (m)	23.5 (10.7–41.5)	21.2 (10.7–32.8)	11.8 (0.0–119.1)	12.6 (0.0–24.7)
Min. step (m)	14.5 (0.1–41.5)	8.4 (4.8–15.9)	8.3 (0.0–119.1)	5.7 (0.0–21.9)
Max. step (m)	49 (15.8–109.5)	50.9 (15.8–84.4)	17.1 (0.0–119.1)	22.5 (0.0–54.5)
Cumulative step (m)	84.9 (22.3–220.0)	92.3 (41.9–146.9)	38.2 (0.0–216.8)	66.9 (0.0–216.8)
Mean displacement (m)	48.8 (15.3–114.5)	48.9 (19.0–82.9)	14 (0.0–119.1)	15.5 (0.0–41.3)
Min. displacement (m)	41.8 (8.2–109.5)	38 (8.2–76.5)	11.7 (0.0–119.1)	10.7 (0.0–41.3)
Max. displacement (m)	55.2 (22.3–122.0)	55.9 (27.9–88.8)	17.9 (0.0–119.1)	23.9 (0.0–62.5)
Final displacement (m)	49.5 (22.3–122)	47.2 (22.5–88.8)	13.7 (0.0–119.1)	15 (0.0–37.8)

Head-starts that survived 1 year constructed on average 3.4 burrows during their first year post-release (range = 2–5 burrows), moving an average of 21.2 m (range = 10.7–32.8 m) between burrows. The maximum individual movement made by gopher tortoises surviving their first year post-release ranged from 15.8–84.4 m (Table 2).

Release 2 (2014 Cohort)

In 2014, we head-started 143 tortoises from 22 clutches collected from 3 source populations (Quinn et al. 2016). Tortoises were in captivity for an average of 273 ± 1 day and all survived the head-starting period. While in captivity, tortoises gained an average of 70.1 g (initial = 32.6 ± 0.4 g; final = 102.8 ± 2.5 g) and reached an average SCL of 76.0 ± 0.7 mm (range = 58.3–96.7 mm) by 5 June 2015, when we placed them in soft-release pens (Fig. 2B). Of the 143 tortoises, we used 133 for soft-release (i.e., release 2) with the remaining 10 used for a later study. We staggered pen removal in the NW release area between 6 July and 22 July 2015, as initially planned. However, 3 radio-tracked head-starts were depredated by fire ants during penning at the SE release area and were replaced by placing transmitters on tortoises initially intended for release without transmitters at the same release area. Because of a fire ant invasion of pens at the SE release area, we removed all pens from that area on 9 June 2015 after only 4 days.

Of the 30 transmittered head-starts released from pens, 13 (43.3%) survived until dormancy. All 13 tortoises alive at the beginning of their first dormancy survived through the dormancy period (100% dormancy survivorship) and through to the end of their first year post-release. Thus, overall, 13 survived, 17 died, and none were censored after 1 year (Table 1). Estimated annual survivorship was 12.5% (95% CI = 6.1–18.8%). However, tortoises suffered far fewer casualties at the NW release area ($n = 4$; 25% mortality) compared to the SE release area ($n = 13$; 92.9% mortality), resulting in significantly higher estimated annual survivorship at the NW release area (75.0%; 95% CI = 53.8–96.2%; Fig. 3B) compared to the SE area (7.1%; 95% CI = 0.0–20.6%; $\chi^2_1 = 19.1$, $P < 0.001$; Fig. 3C).

Maximum displacement of all 30 head-starts from their release pens ranged from 0–119.1 m ($\bar{x} = 17.1$ m). Maximum displacement of head-starts surviving 1 year ranged from 0–62.5 m ($\bar{x} = 23.9$ m). Final displacements showed a similar trend (Table 2). All head-starts combined (i.e., those that did and did not survive 1 year post-release) constructed an average of 0.9 additional burrows (range = 0–3), and moved an average of 11.8 m between burrow locations (range = 0–119.1 m). The single largest step made by individual head-starts also ranged from 0–119.1 m ($\bar{x} = 17.1$ m). Surviving tortoises constructed an average of 1.7 additional burrows (range = 0–3) during their first year post-release and moved an average of 12.6 m (range = 0–24.7 m) between burrow locations. The single largest movement made by surviving head-starts ranged from 0–54.5 m ($\bar{x} = 22.5$ m; Table 2).

Release 1 and Release 2 Combined

Both mortality and step distance were highest immediately following release, with 71.4% of mortality and 73% of all steps >40 m occurring within the first 30 days post-release (Fig. 4). The majority of movements between successive burrows during the first year post-release were <20 m (79.2%; Fig. 5). The maximum displacement of any tortoise from its release pen was 122.0 m.

During release 2, tortoise survivorship was significantly lower in the SE release area compared to the NW. Thus, we compared head-start survivorship of release 1(all) to release 2 (NW and SE release areas, separately). Release 1 (all) survivorship was similar to release 2 survivorship in the NW area ($\chi^2_1 = 0.5$, $P = 0.48$) but significantly higher than release 2 in the SE area ($\chi^2_1 = 10.4$, $P = 0.001$), allowing us to pool data for all but release 2 SE area. Pooled annual survivorship of head-started tortoises excluding release 2 SE area was 70.0% (95% CI = 52.2–87.7%).

Causes of Mortality

All tortoises in both releases appeared to be clinically healthy prior to release (Quinn 2016) and none of the mortalities during this study appeared to be due to factors other than predation. All mortalities while animals were in pens ($n = 4$)

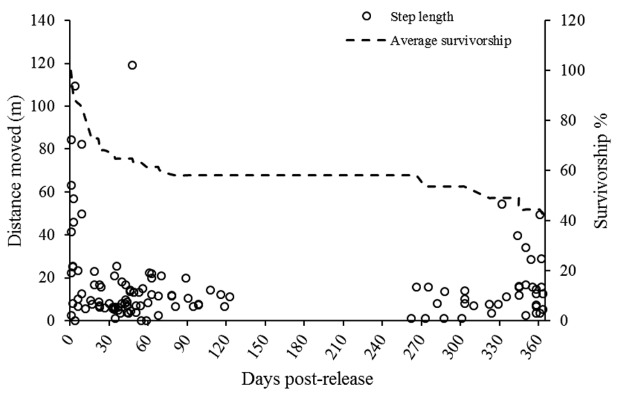

Figure 4. Step lengths and average survival post-release for all (i.e., release 1 and release 2) radio-tracked head-start gopher tortoises ($n = 41$) at Yuchi Wildlife Management Area, Georgia, USA. Dots represent all step lengths between burrows. Day 126 corresponds to the average post-release day when the dormancy period began (i.e., 15 Nov of each release year) and thus no movement occurred until the following spring.

were due to fire ants and occurred at the SE release area. Post-release predation was attributed to fire ants and mammals. Of the 41 tortoises radio-tracked post-release, 21 were depredated: 12 (57.1%) by mammals, 8 (38.1%) by fire ants, and 1 (4.8%) could not be determined conclusively. Although most post-release mortality occurred at the SE release area ($n = 16$), predation occurred at the NW release area as well ($n = 6$). Using wildlife cameras following release 2, we documented raccoons (*Procyon lotor*) searching the footprints of the soft-release pens. Although stray dogs were also detected by visual observation, both the camera evidence and inspection of head-start carcasses suggested that raccoons were the primary mammalian predators on head-starts.

DISCUSSION

Head-start survivorship during the first year post-release varied between release areas. However, when we could follow

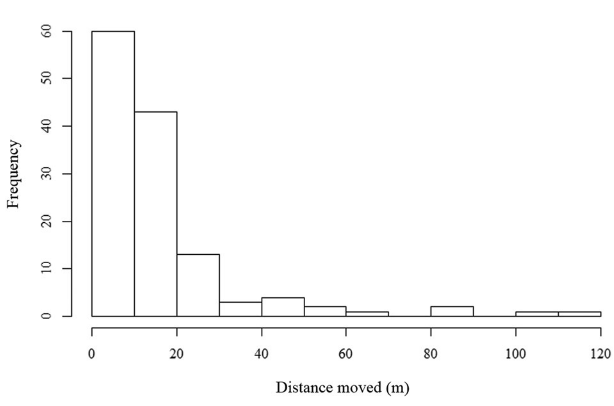

Figure 5. Frequency distribution of individual step lengths (i.e., movements between burrow locations) by transmittered head-started gopher tortoises during their first year post-release at Yuchi Wildlife Management Area, Georgia, USA. Data for release 1 and release 2 ($n = 41$ tortoises) are combined to include all transmittered head-starts released in both years and at all release areas.

the planned release protocol (i.e., excluding release 2 at the SE release area), average annual survivorship of both releases combined was 70.0%, >4 times the 12.8% annual survivorship of wild hatchlings estimated by Perez-Heydrich et al. (2012) from several field studies. Few comparative data are available for wild yearlings. Although >50% of the 14 hatchlings radio-tracked by Butler and Sowell (1996) survived through the first year, none of the remaining 1-year-old tortoises survived the following year. The markedly higher survivorship of our head-starts suggests they may have a survival advantage, presumably because of their increased size relative to wild, same-age counterparts. Tuberville et al. (2015) monitored 1-year-old head-started gopher tortoises following their release using mark-recapture and reported 3.1–100% annual survivorship, necessitating additional research because mortality could not be distinguished from dispersal. The head-starts in our study were comparable in size to 2–3-year-old wild juveniles (Landers 1982, Mushinsky et al. 1994, Aresco and Guyer 1999) and exhibited survivorship rates on par with older, wild juveniles (1–4 yr; 64–130 mm SCL; 65.6% survivorship; Wilson 1991).

Fire ants and mammals were the only known causes of mortality for head-starts in our study. Although fire ants are a threat to young turtles (Allen et al. 2001, Buhlmann and Coffman 2001), including gopher tortoises (Epperson and Heise 2003; Dziadzio et al. 2016*a,b*), mammalian meso-predators such as raccoons, skunks (*Mephitis* spp.), armadillos (*Dasypus novemcinctus*), and stray dogs are typically considered the primary predators of hatchling and juvenile gopher tortoises (Douglass and Winegarner 1977, Butler and Sowell 1996, Epperson and Heise 2003, Smith et al. 2006, Smith et al. 2013). Although mammalian predators were not a major source of mortality in release 1, they contributed significantly to mortality in release 2, particularly at the SE release area after soft-release pens had to be removed prematurely because of fire ant predation. Thus, fire ants are clearly a management issue for future gopher tortoise head-starting efforts, but meso-predators, particularly raccoons, continue to pose risks to released head-starts.

Mortality levels were significantly greater in the SE release areas during release 2, despite being separated from the NW release area by only 280 m. After fire ants gained access to some SE release area pens during release 2, we chose to remove those pens after only 4 days. However, we never detected any large, obvious fire ant mounds at our sites. Instead, fire ants seemed to be distributed diffusely throughout the landscape, hindering our ability prior to release to assess and mitigate potential threats posed by fire ants. Although it is unclear why fire ant predation varied over such a small spatial scale, the SE release area had more herbaceous ground cover, which has been reported to be more conducive to fire ant colonization (Lubertazzi and Tschinkel 2003). Human habitat alterations also attract fire ants (Todd et al. 2008) and clear-cutting and tree planting at the SE release area occurred more recently than in the NE release area. Treatment of enclosures with fire ant bait has previously reduced predation of gopher tortoise nests and hatchlings by fire ants (Dziadzio et al. 2016*a*). However, pre-release broadcast treatment of our release sites with AMDRO® did not prevent predation of head-starts by fire ants, perhaps because the lack of obvious centralized mounds prevented us from detecting areas of core fire ant activity.

Following early pen removal in the SE release area during release 2, some tortoises were quickly subjected to mammalian predation. Tortoise depredation may have been accelerated by the release of multiple tortoises at the same time in a relatively small area before they had time to construct burrows deep enough to protect them from predators. By releasing head-starts early, we may have prevented further fire ant depredations caused by keeping them in a confined space but increased their risk to mammalian predators.

Head-started tortoises demonstrated remarkably high site fidelity. Indeed, one head-start that survived the annual study period in release 2 never constructed a separate burrow apart from the modifications it made from the starter burrow we provided (i.e., why the burrow construction and distance ranges included 0 in some instances). No head-start made a single movement >119.1 m, traveled farther than 122.0 m from their release pen, or left the boundaries of YWMA. The longest movements occurred soon after release and corresponded with the lowest survivorship period of our study. Of movement steps >40 m, 73% occurred within the first 30 days post-release and corresponded with 71.4% of known mortalities. We suspect that naïve tortoises dispersing from their pen sites are learning their landscape and searching for locations to construct burrows, and are thereby more vulnerable to predators, leading to increased mortality. However, once tortoises establish a burrow, both movement and mortality decline. Prior studies have demonstrated that hatchling gopher tortoises also experience the lowest survivorship in the first 30 days post-release (Epperson and Heise 2003), especially when mammalian meso-predators are present (Smith et al. 2013), suggesting that the first month post-release can be a critical time for young, naïve gopher tortoises.

Movements by head-starts in our study were comparable to those reported in the literature for wild juveniles. Wild hatchling and yearling gopher tortoises move an average of 8.0–17.1 m (Butler et al. 1995, Pike 2006) between successive burrow locations and the maximum distance ranged from 139.4–150.0 m. Wild hatchlings have also been documented moving >70 m from their natal nests (Pike 2006), more than most of our head-starts moved from their release pens. Thus, head-starts exhibited high post-release site fidelity.

Long-term (≥9–12 months) soft-release penning increases site fidelity for adult translocated gopher tortoises (Tuberville et al. 2005). Thus, we suspected that some duration of penning would benefit released hatchlings and head-starts (Smith et al. 2013, Tuberville et al. 2015). However, the benefits of penning juveniles may be context-dependent. Confining head-starts in enclosures made some of our study animals more vulnerable to fire ant predation. Furthermore, our head-starts demonstrated very little movement from their release sites, despite being in pens for far less time than is recommended for adults (Tuberville et al. 2005). This high site fidelity after so little time suggests that head-starts may need little to no penning to achieve high site fidelity. The primary benefit of pens or enclosures may be in the ability to exclude mammalian predators (Smith et al. 2013) rather than in promoting site fidelity, although fire ant predation could reduce the effectiveness of pens in this regard.

When choosing a release site for head-started tortoises, some factors to consider include habitat quality, size of the recipient site, the distance to site boundaries, and density of tortoises released. Gopher tortoises have important social networks (Guyer et al. 2014) and our long-term goals include head-starts surviving to maturity and become socially, and thereby reproductively, integrated with the resident population. Thus, we intentionally released head-starts over a relatively small area that overlapped with the residents. However, higher densities at release could have enabled predators, or even an individual predator, to repeatedly target the release site. Even if only 1 or a small number of predators learn habit depredation (Leopold 1933), predation can greatly hinder recovery efforts for gopher tortoises.

By monitoring post-release movement survival, our study is among the first to evaluate the potential for head-starting to augment depleted gopher tortoise populations in areas where habitat is suitable. Although we head-started tortoises for only 9 months, head-starting for longer time periods, as has been employed in desert tortoises (Nagy et al. 2015) and wood turtles (*Glyptemys insculpta*; Michell and Michell 2015), could potentially further increase post-release survivorship. Although the benefits of extending the head-starting period merit further study, rearing animals for >1 year reduces the number of animals per cohort that can be head-started. Because captive head-starting requires significant infrastructure, time, energy, and financial resources, maximizing the cost-benefit relationship where head-starting provides population-level recovery benefits while minimizing duration of captivity is especially important.

Our study, which was limited to 1 year post-release at 1 site, demonstrated that success of released head-starts can vary over even small temporal or spatial scales and in response to predator activity. To fully evaluate the utility of head-starting to gopher tortoise conservation, released head-started tortoises would ideally be monitored until reproductive maturity at several sites throughout their range. However, given that most movement and mortality of head-starts in our study occurred within the first month, the first year post-release may arguably be the most critical time period to evaluate release success. The high post-release survivorship and site fidelity exhibited by tortoises in our study demonstrate that head-starting shows promise as an effective management option for augmenting populations.

MANAGEMENT IMPLICATIONS

We recommend that species recovery biologists consider the outcome of multiple releases before determining whether head-starting is an appropriate management tool for a site.

Small-scale pilot releases may also reveal whether predator control (e.g., treatment for fire ants; Dziadzio et al. 2016*a*) may be warranted. We recommend that releases of head-starts be staggered over space and time to reduce predation on naïve tortoises. To better quantify the benefit of head-starting gopher tortoises, future research should experimentally compare post-release performance of hatchling and head-start tortoises. Finally, soft-release penning may not be necessary for head-started juveniles and may increase their vulnerability to predation by fire ants. We recommend that future efforts evaluate the effectiveness of hard-releases or releasing head-starts into existing adult burrows in the landscape. A few, easy-to-implement modifications to release protocols may increase the initial efficacy of head-starting for augmenting gopher tortoise populations.

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