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Research Article

Comparison of Movements, Body Weight, and Habitat Selection Between Translocated and Resident Gopher Tortoises

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ABSTRACT Gopher tortoises (*Gopherus polyphemus*) are among the most frequently translocated herpetofauna; yet, determining translocation success is difficult because tortoises are slow-growing, long-lived organisms with low reproductive potential. Comparing behavioral traits of translocated individuals with those of sympatric or nearby resident individuals can provide an ecologically relevant baseline to determine if translocated individuals show behavioral traits consistent with those of long-term residents. We used radio telemetry to concurrently monitor 21 translocated and 15 resident gopher tortoises across 2 sites in southern Georgia and compared movement patterns, body weights, and multi-scale habitat selection between treatments. Translocated tortoises moved farther and had larger home ranges than resident tortoises but showed similar patterns of site fidelity. We observed no differences in body weight change between treatments. Patterns of habitat selection were similar between treatments in that tortoises selected structurally open habitats at all scales. Our study suggests that more extensive post-release movements compared to resident individuals may not necessarily lead to lower site fidelity in translocated individuals. We suspect that the presence of structurally suitable habitat within the release area and retaining translocated individuals within a pre-release enclosure for 10 months contributed to high site fidelity. Although comparing translocated and resident individuals can help inform translocation efforts, we caution that using resident individuals from ecological sinks may lead to misleading results. © 2014 The Wildlife Society.

KEY WORDS Chelonian, conditional logistic regression, enclosure, *Gopherus polyphemus*, home range, resource selection function, soft release.

Wildlife translocations often are used to restore extirpated populations, supplement existing populations, increase genetic diversity in inbred populations, solve human-animal conflicts, and rescue individuals from potential sources of mortality (Fischer and Lindenmayer 2000, Massei et al. 2010). Among herpetofauna, the gopher tortoise (*Gopherus polyphemus*) is one of the most widely translocated species (Dodd and Seigel 1991). Gopher tortoises are considered a keystone species throughout much their range because their extensive burrows (up to 6 m long and 3 m deep; Hansen 1963, Tuberville and Dorcas 2001) are used by a wide range of species, including many frequent or obligate commensals (Jackson and Milstrey 1989, Lipps 1991). However, gopher tortoises have declined throughout their range because of habitat loss and fragmentation, habitat degradation due to fire suppression and commercial forestry practices, and overcollection (Auffenberg and Franz 1982, Diemer 1986, McCoy et al. 2006). Translocations often are used as a management tool to remove tortoises from development sites, augment existing populations, or reestablish new populations (Enge et al. 2003, Tuberville et al. 2005, Florida Fish and Wildlife Conservation Commission 2007). However, gopher tortoises are slow-growing, long-lived animals, making it difficult to determine if translocations will lead to a viable population within the intended release area. As a result, short-term studies frequently are the only option available for post-release monitoring; yet, relatively few studies have monitored translocated tortoises following release (Tuberville et al. 2005, 2008, Ashton and Burke 2007, Riedl et al. 2008).

Given the difficulties in determining long-term translocation success, many translocation studies use metrics that relate to population viability but can be measured on a shorter time-frame including body condition, stress hormone levels, movement patterns, survival, and reproduction (Fischer and Lindenmayer 2000, Pinter-Wollman et al. 2009, Drake et al. 2012, Whisson et al. 2012). Movement patterns (home range size, distance moved following release) are commonly

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used metrics in post-release monitoring because many studies have reported extensive post-release movements across multiple taxa (Reinert and Rupert 1999, Moehrenschlager and Macdonald 2003, Sullivan et al. 2004, Armstrong and Seddon 2008, Nussear et al. 2012) and such movements may lead to emigration from the release area, reduced survival, and translocation failure (Hester et al. 2008, Germano and Bishop 2009, Roe et al. 2010). Although fidelity to the release area does not guarantee future survival and reproduction, it is a necessary first step to population integration or establishment. Concurrent monitoring of sympatric or nearby resident populations under similar environmental conditions may provide a suitable baseline for determining if the movement patterns or degree of site fidelity of translocated individuals are consistent with those of long-term residents. Several studies have concurrently measured and compared body condition, movement patterns, and survival between translocated and resident individuals and have used the degree of similarity in measured traits as indicators of translocation success (Moehrenschlager and Macdonald 2003, Riedl et al. 2008, Pinter-Wollman et al. 2009, Nussear et al. 2012, Scillitani et al. 2013). However, using traits of resident populations as a baseline for inferring population viability in the absence of direct, long-term data on population performance can potentially be misleading if resident populations represent ecological sinks.

The goal of this study was to compare the behavior of translocated and resident adult gopher tortoises at 2 translocation sites in central and southern Georgia. Recipient sites were conservation lands with ongoing habitat restoration that supported low resident tortoise densities at the time of our study. Historical land use practices at both recipient sites had degraded tortoise habitat and likely was the primary cause of low resident densities. We compared movement patterns, body weight, and habitat selection between resident and translocated tortoises for 1 summer following release. We predicted that translocated tortoises would move farther and have larger home range sizes than resident tortoises. Previous studies suggest that using pre-release enclosures for ≥ 9 months prior to release may increase release-site fidelity in translocated gopher tortoises (Tuberville et al. 2005). Because our study used pre-release enclosures for 10 months prior to release (see Methods for details), we predicted that our translocated tortoises would show similar rates of site fidelity and home range sizes as those reported by Tuberville et al. (2005) for translocated tortoises enclosed for ≥ 9 months prior to release. Conversely, we also predicted that translocated tortoises in our study would show greater site fidelity and smaller home ranges than Tuberville et al. (2005) reported for unenclosed tortoises. Finally, we predicted that translocated and resident tortoises in our study would show similar patterns of weight gain and habitat selection.

STUDY AREA

We obtained translocated tortoises from a disturbed xeric sandhill on private property near Turnpike Creek in Telfair County, Georgia (31.95°N, 82.84°W) in August 2011. We translocated tortoises to the Orianne Indigo Snake Preserve (OISP; 1,025 ha) in Telfair County, Georgia, (31.88°N, 82.84°W) and the Yuchi Wildlife Management Area (YWMA; 3,127 ha) in Burke County, Georgia (33.11°N, 81.74°W; Fig. 1). The OISP consists of xeric sandhills, flatwoods, and creek and riverine floodplain forests. The release area at the OISP was on the middle tract of the OISP (467 ha) in a patch of open-canopy xeric sandhill formerly used for center pivot agriculture that degraded much of the historical land cover. At the time of this study, the ground cover in the release area was dominated by prickly pear cactus (*Opuntia humifusa*) and dog fennel (*Eupatorium* spp.). The understory was primarily oak (*Quercus* spp.) and the release area was surrounded by more closed-canopy forests of either mixed hardwoods or planted slash (*Pinus elliottii*) and longleaf pine (*P. palustris*).

The YWMA includes a mixture of xeric sandhills, flatwoods, wetlands, and creek and riverine floodplain forests. The release area at YWMA was located in an open-canopy xeric sandhill surrounded by more closed-canopy stands of planted pine. This sandhill, and much of the YWMA, was formerly densely planted loblolly pine (*P. taeda*) prior to being clearcut and planted with longleaf pine. Ongoing habitat restoration (planting longleaf pine, prescribed fire) began in 2011 at OISP and 2008 at YWMA.

We selected both OISP and YWMA as recipient sites because they historically supported suitable gopher tortoise habitat, but past land-use practices degraded much of the habitat resulting in relatively low tortoise densities at the time of this study. Although habitat conditions varied across the recipient sites, conditions were comparable in the portions of the sites used by the translocated and resident tortoises included in this study. Resident tortoise densities on the middle tract of the OISP were 1.07 tortoises per ha (95% CI = 0.75–1.56; J. Bauder, The Orianne Society, unpublished data), and we confirmed the presence of all age classes and successful reproduction. Resident tortoise densities

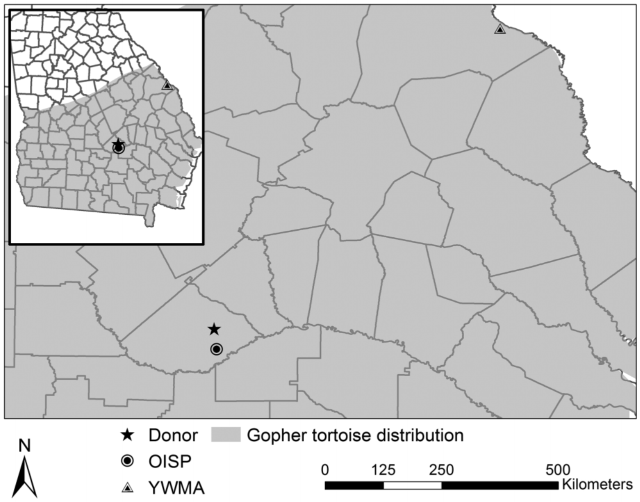

Figure 1. Donor and recipient sites (Orianne Indigo Snake Preserve [OISP] and Yuchi Wildlife Management Area [YWMA]) in a gopher tortoise translocation study from 2011–2013 in central and southern Georgia, USA.

across YWMA were 0.11 tortoises per ha (95% CI = 0.08–0.17; M. Elliott, Georgia Department of Natural Resources, personal communication), and successful reproduction was unconfirmed at the time of this study. Tortoise densities on the middle tract of the OISP were similar to or higher than densities reported from xeric sandhill habitat on conservation lands in southern Georgia, but densities at YWMA were some of the lowest on conservation lands in southern Georgia (Eubanks et al. 2003, Smith et al. 2009).

METHODS

Tortoise Translocation

We collected tortoises from the donor site from 22 August–12 September 2011. We examined active and inactive tortoise burrows at the donor site using a burrow camera system. If the burrow was occupied by a tortoise, we placed a Havaheart® live trap (Woodstream Corp., Lititz, PA) at the entrance of the burrow and shaded the trap with burlap. We checked traps twice per day until we captured the tortoise. We weighed and measured all tortoises following the protocols of McRae et al. (1981*a*). We individually marked each tortoise with a subcutaneous passive integrated transponder (PIT) tag (Biomark, Boise, ID) injected in the foreleg and by notching the marginal scutes using a Dremel® tool (Dremel, Racine, WI) or a triangular file. All translocated tortoises received a full health assessment and tested negative for upper respiratory tract disease prior to translocation. We placed all translocated tortoises in a common circular 1-ha enclosure made of silt fencing at each location. We dug 1 starter burrow approximately 1 m in length haphazardly within each pen for each translocated tortoise using an auger or shovel.

Tortoise Radio Telemetry

In June 2012, we trapped each translocated tortoise within the enclosures using methods described above. We also placed traps opportunistically at the burrows of resident tortoises throughout the release areas at both sites. We weighed and measured each captured tortoise, and individually marked unmarked resident tortoises. We placed radio transmitters on the first 10 (5 M and 5 F) and 11 (6 M, 4 F, and 1 unknown sex) translocated tortoises and 8 (4 M and 4 F) and 7 (4 M and 3 F) resident adult tortoises captured at the OISP and YWMA, respectively. We used 14.5-g RI-2B transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) and 15.3-g R1860 transmitters (ATS, Isanti, MN). We attached transmitters to the posterior of the carapace using epoxy putty (Loctite Interior/Exterior Epoxy Repair Putty, Henkel Corp., Rocky Hill, CT, and J-B Weld Interior/Exterior Epoxy Putty Stick, J-B Weld Company, Sulphur Springs, TX). We secured the antenna to the carapace using epoxy putty at 3 or 4 locations, and covered the intervening lengths of the antenna with silicone sealant (DAP® Auto/Marine Sealant, DAP Products Inc., Baltimore, MD). We released tortoises at their capture location or at the nearest unoccupied burrow if its original burrow had been occupied by another tortoise. After attaching all our radio transmitters we removed the enclosures around the translocated tortoises. We removed the enclosure on 11 June 2012 at the OISP and on 18 June 2012 at YWMA. Translocated tortoises were held within the enclosure for a mean total of 290 days (±3 SD) at OISP and a mean total of 281 days (±19 SD) at YWMA.

We located each telemetered tortoise weekly through the end of October 2012 with the exception of the first 8 days following release at the OISP when we located each tortoise daily. We located tortoises monthly in November, December, February, March, April, and May at the OISP and December, April, and May at YWMA. We tracked tortoises using a 3-element Yagi antenna (Wildlife Materials, Inc., Murphysboro, IL) and an R1000 receiver (Communications Specialists, Inc., Orange, CA), and recorded their locations using a GPSMap76CSx global positioning system (Garmin International, Inc., Olathe, KS). We removed the transmitters from all tortoises that were still present in the study in June 2013. Our study was conducted under permit # 29-WBH-12–14 from the Georgia Department of Natural Resources and we adhered to the Guidelines for use of Live Amphibians and Reptiles in Field Research (American Society of Ichthyologists and Herpetologists 2004) during all field procedures.

Vegetation Measurements

We recorded several habitat variables at each novel telemetry location where the tortoise was in a burrow; we did not use above ground locations. We only recorded habitat data at OISP due to logistical constraints. We recorded canopy cover using a spherical densitometer directly over the burrow entrance and at 5 m in each cardinal direction. We calculated the mean canopy cover for each burrow using the 5 canopy cover values for that burrow. We used the point-quarter method to recorded the distance from the burrow entrance, diameter at breast height (dbh), and species (pine, oak, or other hardwood) of the nearest tree (defined as ≥ 2.5 cm dbh) within 4 quadrants formed by the cardinal directions (i.e., NE, NW, SW, and SE), and then used these data to estimate total tree density (trees/ha) and total basal area (cm^2). We visually estimated shrub cover within a 10-m radius around the burrow into 1 of 5 categories: 0%, 1–25%, 26–50%, 51%–75%, and 76–100%. For each burrow we also calculated relative density, relative basal area, and relative frequency of each species group present within the 4 quadrants around that burrow and summed these 3 variables to generate an importance value for each species group (pine, oak, other hardwoods) which ranged from 0 to 3. The importance value was 3 if all quadrants had the same species group. For all vegetation analysis, we used data from telemetry observations made after all transmitters were deployed (19 June 2012).

Data Analysis

We measured total distance moved, maximum displacement (i.e., maximum distance moved from site of initial capture in June 2012), and the number of unique burrows used by each individual from June through October 2012. We used 2 measures of site fidelity to estimate translocation success. The first was whether a telemetered tortoise moved off and remained off the xeric sandhill containing the enclosure for the 12 months following release. The second followed

Tuberville et al. (2005) and was whether a telemetered tortoise moved >1 km from the burrow it was captured at in June 2012 within the enclosure. We calculated minimum convex polygon (MCP) home ranges from weekly telemetry locations (Jun–Oct 2012) using Geospatial Modeling Environment (Beyer 2012). We also report home range sizes from June to October 2012 estimated using 95% fixed kernel utilization distributions because they provide a more robust estimate of home range size compared to MCP (Kernohan et al. 2001).

Because kernel home ranges are sensitive to bandwidth (h; Worton 1995, Seaman and Powell 1996, Hemson et al. 2005, Kie et al. 2010), we tried multiple approaches for estimating bandwidth. The reference bandwidth (h_{ref}) tended to over-smooth our data resulting in large areas of unused habitat similar to the MCP. The least-squares cross-validation approach either failed to solve or severely under-smoothed our data resulting in many disconnected polygons. We therefore used the method of Berger and Gese (2007) where we incrementally decreased the reference bandwidth by 0.1 until we found the smallest contiguous polygon that included all telemetry observations. This approach resulted in a more appropriate home range estimator for our data given our analysis goals. We had a large number of duplicate telemetry locations at successively used burrows, so we randomly shifted the Universal Transverse Mercator coordinates of every duplicate telemetry observation by 0.25–3 m for both estimators to avoid computational difficulties in estimating the kernel bandwidth. We calculated kernel home ranges using Home Range Tools v2.0 (Rodgers et al. 2013) in ArcGIS 10.1 using scaled variances (i.e., separate variances for the x and y coordinates) and 1–5-m grid cell sizes.

We tested for an effect of treatment (translocated or resident), sex, and a treatment by sex interaction on total distance moved, maximum displacement, number of unique burrows, and MCP and fixed kernel home range sizes using linear mixed-effect models with site (OISP and YWMA) as a random effect. The interaction term was not significant for any analyses so we drew inference from the model with an additive effect of treatment and sex. We tested for differences in body weights in adult translocated tortoises among years (2011, 2012, and 2013) using linear mixed-effects models with individual, sex, and site as nested random effects. We also tested for differences in change in body weight between 2012 and 2013 between adult translocated and resident tortoises using a linear mixed-effects model with sex and site as nested random effects. To meet model assumptions, we log transformed all response variables except total distance moved, which we square root transformed. Although including site as a random effect controlled for site-specific variation in our movement metrics, we conducted a post-hoc test using general linear models to test for an effect of site on each movement metric. We used Fisher's exact tests to compare the proportion of translocated and resident tortoises moving >1 km from their release site. We also used 3 separate Fisher's exact tests to compare the proportion of translocated tortoises moving >1 km from their release site in our study to those of the 3 treatments (no enclosure, 9-months, and 12-months) reported by Tuberville et al. (2005). All means are reported ±1 standard error and we conducted all analyses in R.2.15.2 (R Development Core Team 2012) unless otherwise noted.

We evaluated habitat selection at burrows used by telemetered translocated and resident tortoises at the OISP using resource selection functions (RSF) in a used-available design (Manly et al. 2002, McLoughlin et al. 2010). Because of issues with model convergence, we estimated separate RSF for translocated and resident tortoises at 2 spatial scales, the study area (second-order habitat selection; Johnson 1980) and individual burrow (third-order; Johnson 1980). We initially defined our study area as the portion of the sandhill, delineated by a xeric soils shape file polygon, within 1-km of the enclosure. We selected a 1-km buffer based on the distances moved by the majority of translocated tortoises in an earlier study where tortoises were enclosed prior to release (Tuberville et al. 2005). Only 1 telemetry observation at the OISP was made outside of this buffer so we feel it is an appropriate representation of the available habitat for our study population. This approach assumes that all translocated and resident tortoises had equal access to the entire area, an assumption we felt justified given movement abilities of this species and the lack of potential movement barriers or non-habitat (e.g., wetlands or riparian) within this area. However, both translocated and resident tortoises could potentially move off the sandhill where the vegetation structure was quite different, so we delineated a second study area by adding a 100-m buffer to the portion of the sandhill within 1-km of the enclosure. We expected that including off-sandhill areas within our study area would result in increased selection for open vegetation structure because much of the habitat surrounding the sandhill consisted of planted pine, which we expected tortoises to avoid. We used Hawth's Analysis Tools for ArcGIS (Beyer 2004) and ArcGIS 9.3 (Environmental Systems Research Institute, Inc., Redlands, CA) to randomly select points within each study area. We selected 242 random points from the sandhill and 330 random points from the sandhill and 100-m buffer (i.e., off-sandhill) corresponding to approximately 1.24 points per ha in each study area. We then recorded habitat variables at each random point as described in Vegetation Measurements. We fit 2 sets of RSF (1 for each treatment) using the random points from each study area for a total of 4 sets of study-area scale RSFs. For each of these 4 sets, we randomly subsampled 100 points from the sandhill and off-sandhill random points so the number of random points equaled the number of used points in our analyses. We then fit the study area RSF using mixed-effects generalized linear models (i.e., logistic regression) using the glmer function in the R package lme4 (v. 0.999999-2; Bates et al. 2013). We included tortoise as a random effect to control for variation among individuals and weighted each burrow by the number of telemetry locations observed at that burrow for each telemetered tortoise using the weights argument in the glmer function.

We restricted our model set for all habitat selection analyses to 6 single-variable models, which included tree density, basal area, mean canopy cover, shrub cover (condensed to 2 levels: 0–25% and > 25%), importance values for pine, and importance values for oak. We used second-order Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002) to calculate ΔAIC_c and model weights (w_i) for each model. To evaluate how well our models predicted use by translocated and resident tortoises, we used a 10-fold cross-validation approach (Johnson et al. 2006, Lele et al. 2013) and quantified predictive performance using Lin's (1989) concordance correlation coefficient (CCC; Zeller et al. 2014). The CCC statistic measures the correlation between expected and predicted values as their deviance from a line with intercept = 0 and slope = 1. Because 100 random points may not adequately describe the range of available habitat features throughout the study area, we used bootstrapping by repeating our random subsampling procedure 1,000 times (500 for CCC model evaluation) with replacement. We took the median of the resulting distributions of each model's fixed-effects regression coefficients, ΔAIC_c, w_i, and CCC with 95% confidence intervals.

At the burrow scale, we considered habitat availability within an area potentially accessible to tortoises based on their movement in the interval between successive telemetry locations (approximately 1 week). To measure habitat availability at this scale, we fit a Weibull distribution to the empirical distributions of weekly movement steps for translocated and resident tortoises separately and weighted all random points on and off the sandhill (defined as above) by the Weibull probability density of the movement steps (Fig. 2). This allowed us to assess availability within a burrow neighborhood based on an empirically estimated probability of taking a step of any given length (Addicott et al. 1987). We fit separate RSFs for each treatment and set of random points for a total of 4 sets of burrow-scale RSFs. Because the unit of analysis at this scale is the individual burrow, rather than the individual tortoise, we used conditional or case-controlled logistic regression to pair each used burrow with the Weibull-weighted average from all random points to represent the available habitat unique to each burrow (Compton et al. 2002, Boyce et al. 2003, Johnson et al. 2004). This allows habitat availability to vary in space and time, which is appropriate for fine-scale tests of resource selection. We further used mixed-effects conditional logistic regression to account for any lack of independence among burrows from the same individual using random effects (Duchesne et al. 2010) and included individual as a random slope effect. We fit the RSF by first differencing the habitat values at each burrow by the appropriate Weibull-weighted mean value across all random points and used the lmer function in the lme4 package to fit a model with no intercept to these differences. We also weighted each burrow by the number of telemetry locations observed at that burrow for each telemetered tortoise using the weights argument in the lmer function. If a model failed to converge, we used the slope estimated from its fixed-effect conditional logistic regression counterpart as a starting value after which convergence of the mixed-effects model occurred. We evaluated differences in selection between translocated and resident tortoises by comparing model rankings and parameter estimates with 95% confidence intervals within their respective spatial scales. We evaluated model predictive performance as described for the study area scale analysis, except we estimated CCC for the best-supported model.

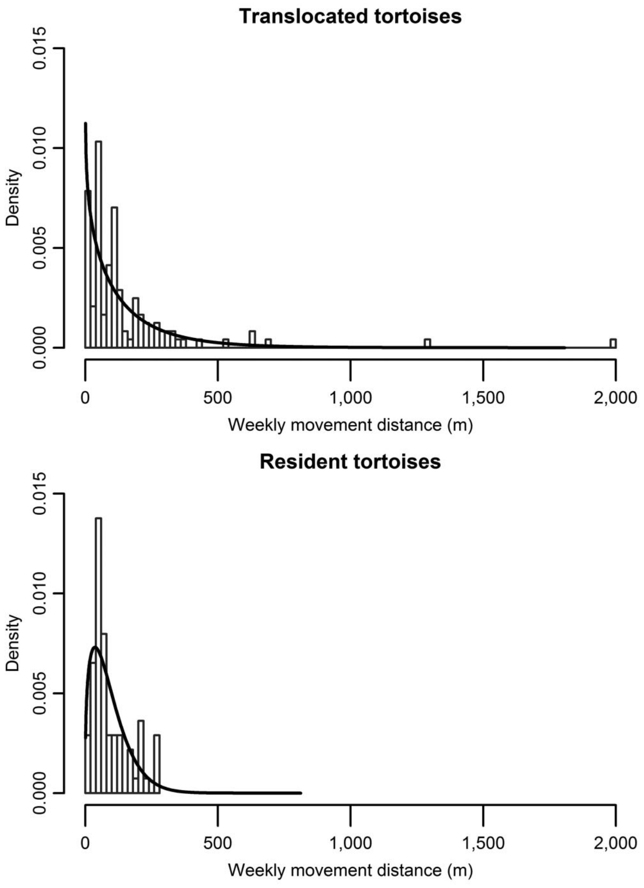

Figure 2. Weibull probability distributions fit to weekly movement distances (meters per week) of translocated and resident gopher tortoises at the Orianne Indigo Snake Preserve in southern Georgia from June through October 2012.

RESULTS

We captured 32 adult gopher tortoises at the donor site for translocation. We translocated 16 tortoises to the OISP, and the remaining 16 to the YWMA. We translocated an additional adult male and subadult of unknown sex to the YWMA in October 2011 from a third donor site. At the OISP, we detected all 16 translocated tortoises within the enclosure in June 2012 and recaptured 13 (7 F and 6 M). At YWMA, we detected 13 of 16 translocated tortoises within the enclosure in June 2012 and recaptured 11 (6 M, 4 F, and 1 subadult). The median number of days to capture a tortoise during June 2012 was 3.0 (inter-quartile range = 3.0–5.0) and did not differ between translocated and resident tortoises ($P = 0.97$). Although we examined each burrow within the enclosure with the burrow camera and placed traps at burrows where burrow occupancy was questionable, we did not detect all the tortoises released inside the enclosure at YWMA. We recaptured 1 translocated tortoise (a male released in Oct 2011) outside of the enclosure at YWMA

Table 1. Movement summaries for adult translocated and resident gopher tortoises in central and southern Georgia monitored with radio telemetry from June through October 2012. Values reported are medians with 25th and 75th percentiles in parentheses.

	Translocated		Resident	
	Males	**Females**	**Males**	**Females**
Total distance (m)[a,b]	1,637 (549–6,640)	894 (250–3,064)	1,410 (461–2,236)	237 (30–2,305)
Maximum displacement (m)[a]	553 (87–1,825)	566 (108–1,766)	189 (78–407)	79 (25–696)
Number of unique burrows[b]	6 (2.8–11.8)	4 (2.0–9.6)	6 (2.4–9.8)	2 (2.0–4.7)
Minimum convex polygon (ha)[a,b]	2.2 (0.5–146.6)	2.3 (0.2–16.5)	2.5 (0.3–12.6)	0.1 (0.0–3.3)
95% fixed kernel (ha)[a]	5.6 (1.1–256.2)	20.2 (1.4–49.3)	6.1 (0.7–63.5)	1.4 (0.1–10.1)

[a] $P < 0.05$ for treatment (translocated vs. resident).

[b] $P < 0.05$ for sex.

while trapping for resident tortoises. After 1 year post-release (Jun 2013), 8 of 10 and 10 of 11 telemetered translocated tortoises were present at OISP and YWMA, respectively. We lost 3 telemetered translocated tortoises because of unknown causes. All resident tortoises were present at their respective sites 1 year post-capture.

Tortoise Movement and Body Weight

Treatment (resident vs. translocated) had a strong effect ($P \leq 0.03$) on all movement metrics, with the exception of the number of unique burrows ($P = 0.05$; Table 1). Positive parameter estimates for treatment across all metrics indicate that telemetered tortoises moved more extensively than resident tortoises. No telemetered translocated or resident tortoises permanently emigrated off the sandhills containing the enclosures during 2012 (Fig. 3). One translocated tortoise at OISP moved 1.99 km east of the enclosure but then returned to the eastern edge of the sandhill. Another translocated tortoise at YWMA crossed a mesic creek channel northwest of the enclosure but then returned to the sandhill containing the enclosure. Only 5 of 21 telemetered translocated tortoises (24%) moved >1 km from their enclosure during their first summer following release, whereas no resident tortoises moved >1 km from their capture point and these proportions were marginally different ($P = 0.06$). However, by the end of October 2012, all but 1 of the telemetered translocated tortoises and all resident tortoises were <1 km from the enclosure ($P = 1.00$). The proportion of translocated tortoises that moved >1 km from their release site was lower than the no-enclosure treatment ($P < 0.001$) but similar to the 9-month and 12-month treatments from Tuberville et al. (2005) ($P \geq 0.38$; Table 2).

Males moved greater total distances ($P = 0.01$), used a greater number of unique burrows ($P < 0.001$), and had larger MCP home ranges ($P = 0.02$) than females (Table 1). However, we did not find a difference in maximum displacement ($P = 0.58$) or fixed kernel home range size ($P = 0.21$) between males and females (Table 1). A post-hoc analysis found no support for differences in our movement metrics between OISP and YWMA ($P \geq 0.13$) with the exception of number of unique burrows ($P < 0.001$). Tortoises at OISP used a median of 6 unique burrows (inter-quartile range = 4.0–8.8), whereas tortoises at YWMA used a median of 5 unique burrows (inter-quartile range = 2.0–5.0).

Body weight of translocated tortoises did not differ by year ($P \geq 0.10$) but trended upwards over the course of our study (annual means: 2011 = 4.70 ± 0.18 kg; 2012 = 4.81 ± 0.19 kg; 2013 = 4.85 ± 0.15 kg). Change in body weight between 2012 and 2013 did not differ between translocated and resident tortoises ($P = 0.679$).

Habitat Selection and Use

We recorded a mean of 18 telemetry observations per tortoise after 19 June and each tortoise was located at a mean of 4.8 unique burrows (SE = 0.20, range = 2–10). Habitat selection varied by treatment, scale, and whether or not we used off-sandhill areas to define habitat availability. At the scale of the study area, the model containing oak importance values

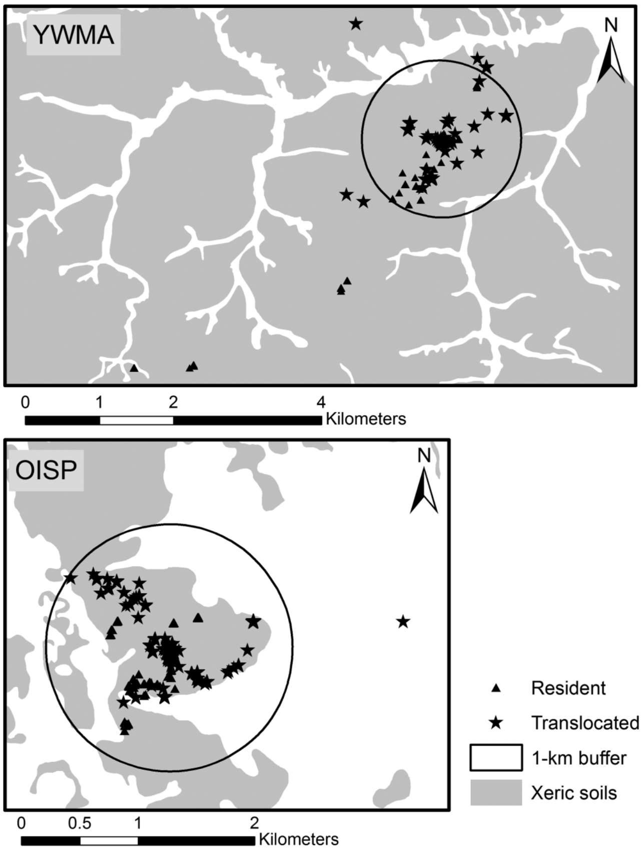

Figure 3. Radio telemetry locations of translocated and resident gopher tortoises at the Orianne Indigo Snake Preserve (OISP) and Yuchi Wildlife Management Area (YWMA) in Georgia from June through October 2012. A 1-km buffer around the pre-release enclosure is denoted by the circle in each image. Shaded areas represent xeric soils.

Table 2. Home range size (minimum convex polygon [MCP]) and site fidelity from multiple radio telemetry studies on translocated and resident gopher tortoises. Means, ranges, and sample sizes are reported unless otherwise noted. Proportion emigrating follows Tuberville et al. (2005) unless otherwise noted.

Citation	Post-release monitoring duration	Release site	Starter burrows dug?	Treatment	MCP home range		Proportion emigrating
					Adult males	Adult females	
This study	5 months	South-central and east-central GA	Yes	10-month enclosure	28.0 (0.4–178.7), $n = 11$	4.9 (0.1–18.3), $n = 9$	0.24
				Resident	3.6 (0.1–14.5), $n = 8$	0.8 (0.0–3.5), $n = 7$	0.00
Tuberville et al. (2005)	2–5 months	West-central SC	Yes	No enclosure	116.5 (0.7–373.7), $n = 6$	84.2 (5.0–145.3), $n = 3$	0.77
				9-month enclosure	12.3 (0.4–50.2), $n = 5$	93.9 (38.9–134.1), $n = 4$	0.38
				12-month enclosure	1.4 (0.1–5.3), $n = 6$	4.4 (0.1–11.6), $n = 3$	0.08
Riedl et al. (2008)[a]	15 months	West-central FL	No	No enclosure	0.08, $n = 3$	0.34, $n = 10$	0.08[b]
				Resident	0.63, $n = 11$	0.78, $n = 8$	0.00
McRae et al. (1981*b*)	8 months	Southwest GA	NA	Resident	0.45 (0.06–1.44), $n = 8$	0.08 (0.04–0.14), $n = 5$	NA
Eubanks et al. (2003)	13 months	Southwest GA	NA	Resident	1.1 (0.0–4.8), $n = 68$	0.4 (0.0–3.4), $n = 51$	0.02[c]
Smith et al. (1997)	20 months	North-central FL	NA	Resident	1.9 (0.3–5.3), $n = 10$	0.6 (0.3–1.1), $n = 4$	NA
Smith (1995)	17 months	Northeast FL	NA	Resident	NA	0.4 (0.0–1.4), $n = 14$	NA

[a] Median MCP values reported.
[b] Proportion of individuals leaving the study area.
[c] Dispersal defined following Berry (1986).

received the highest support for resident tortoises. The bootstrapped AIC$_c$ model weights and parameter estimates were greater (median $w_i = 0.98$ vs. 0.27 and median $\beta = 0.89$ vs. 0.49) when we included off-sandhill areas as available. These changes indicated the strength of selection for oaks increased under this broader definition of available (Table 3). Translocated tortoises selected areas with low tree densities at the study-area scale regardless of whether or not we considered off-sandhill areas available (Table 3). Bootstrapped CCC for the best supported models were high for all 4 sets of RSF at the study-area scale (median CCC ≥ 0.98) indicating a very high correlation between predicted and expected values of burrow use.

At the individual burrow scale, tortoises selected burrows surrounded by low total basal area across all but 1 analysis (Tables 4 and 5). The 1 exception was translocated tortoises when off-sandhill areas were excluded from the analysis; tortoises in this analysis selected burrows surrounded with low tree densities. The best models performed well for all 4 burrow-scale analyses (CCC ≥ 0.74), but model convergence failed during the cross-validation for resident tortoises with sandhill availability (due to complete separation) and for translocated tortoises with off-sandhill availability.

DISCUSSION

Gopher tortoises translocated using soft-releases differed in several behavioral traits from sympatric resident tortoises during the first year post-release. Specifically, translocated tortoises moved more extensively and had larger home range sizes than resident tortoises. However, these increased movements did not result in higher emigration rates by translocated tortoises because rates of site fidelity were similar between treatments, and all telemetered translocated tortoises present at the end of the study were within the intended release area. Greater post-release movements of translocated individuals compared to residents are common in wildlife translocation studies (Hester et al. 2008, Nussear et al. 2012, Scillitani et al. 2012). These movements are likely due to disorientation, attempts to return to the donor site, or searches for suitable habitat or familiar environmental cues (Stamps and Swaisgood 2007, Dickens et al. 2009, Bennett et al. 2013). Post-release movements may result in emigration from the release area, decreased survival, and ultimately translocation failure (Hester et al. 2008, Germano and Bishop 2009, Roe et al. 2010). However, extensive movements after release may suggest that the exploration of novel environments occurs regardless of habitat quality (Pinter-Wollman 2009, Bennett et al. 2013). Greater movements by translocated tortoises than residents in our study did not appear to negatively affect their health or survival compared to resident tortoises because we observed no mortality and translocated and resident tortoises did not differ in their changes in body weight. Additionally, sex-specific differences in movement were similar between treatments in that males of both treatments tended to move farther than females, consistent with other gopher tortoise telemetry studies (McRae et al. 1981*b*, Eubanks et al. 2003).

Table 3. Study-area scale resource selection functions for translocated and resident gopher tortoises at the Orianne Indigo Snake Preserve in southern Georgia, 2012. We report the median and 95% confidence intervals for change in second-order Akaike's Information Criterion (ΔAIC_c), AIC_c model weights (w_i), and model fixed-effects parameter estimates derived from 1,000 bootstraps. Sandhill refers to random points drawn from the xeric sandhill surrounding the release area and off-sandhill includes random points drawn from the sandhill and a 100-m buffer around the sandhill. Importance values are unitless but range from 0–3 and shrub cover is a 2-level categorical variable (1–25% or >25%).

	ΔAIC_c	w_i	Parameter estimates
Resident – Sandhill			
Importance oak	0.70 (0.00–9.17)	0.27 (0.01–0.94)	0.49 (0.08–0.84)
Total basal area (cm^2)	2.05 (0.00–13.55)	0.16 (0.00–0.87)	−0.21 (−0.39–0.15)
Importance pine	2.89 (0.00–11.09)	0.12 (0.00–0.55)	−0.43 (−0.75–0.01)
Total tree density (trees/ha)	4.66 (0.00–15.82)	0.05 (0.00–0.84)	−3.33 (−13.82–28.23)
Shrub cover (%)	5.87 (0.00–18.37)	0.03 (0.00–0.51)	0.39 (−0.34–1.14)
Mean canopy cover (%)	6.38 (0.00–18.39)	0.02 (0.00–0.43)	0.24 (−1.53–4.17)
Resident – off-sandhill			
Importance oak	0.00 (0.00–3.91)	0.98 (0.00.11–1)	0.89 (0.56–1.23)
Total basal area (cm^2)	11.46 (0.00–28.79)	0.00 (0.00–0.71)	−0.31 (−0.48 − −0.1)
Importance pine	12.19 (3.24–28.09)	0.00 (0.00–0.16)	−0.63 (−0.95 − −0.23)
Total tree density (trees/ha)	15.02 (1.27–34.5)	0.00 (0.00–0.31)	−6.58 (−14.85–4.05)
Mean canopy cover (%)	18.89 (6.81–37.71)	0.00 (0.00–0.02)	−1.41 (−2.78–1.01)
Shrub cover (%)	21.34 (7.64–40.62)	0.00 (0.00–0.02)	−0.23 (−0.85–0.54)
Translocated – sandhill			
Total tree density (trees/ha)	0.00 (0.00–6.45)	0.90 (0.04–1.00)	−15.73 (−25.67 − −7.75)
Shrub cover (%)	6.79 (0.00–23.78)	0.03 (0.00–0.92)	−0.89 (−1.46 − −0.21)
Total basal area (cm^2)	9.25 (1.03–24.00)	0.01 (0.00–0.24)	−0.10 (−0.24–0.04)
Mean canopy cover (%)	10.13 (2.52–25.05)	0.01 (0.00–0.12)	−1.44 (−3.14–0.10)
Importance oak	11.19 (1.94–27.84)	0.00 (0.00–0.15)	0.11 (−0.16–0.49)
Importance pine	11.51 (2.44–27.55)	0.00 (0.00–0.12)	−0.08 (−0.45–0.31)
Translocated – off-sandhill			
Total tree density (trees/ha)	0.00 (0.00–17.14)	0.64 (0.00–1.00)	−16.29 (−24.81 − −8.76)
Shrub cover (%)	6.31 (0.00–23.81)	0.04 (0.00–0.99)	−1.46 (−1.95 − −0.98)
Importance oak	7.05 (0.00–25.75)	0.02 (0.00–0.99)	0.69 (0.33–1.06)
Mean canopy cover (%)	14.05 (4.18–28.74)	0.00 (0.00–0.09)	−2.53 (−4.07 − −1.11)
Total basal area (cm^2)	14.14 (4.12–27.89)	0.00 (0.00–0.09)	−0.19 (−0.36 − −0.08)
Importance pine	18.82 (7.37–35.91)	0.00 (0.00–0.02)	−0.36 (−0.73–0.02)

Habitat conditions in our release areas may have contributed to our observed movement patterns and site fidelity. High habitat specificity may restrict the post-release movements of translocated individuals if suitable habitat is lacking (Attum et al. 2013). Gopher tortoises are strongly associated with open canopied forests on xeric soils (Boglioli et al. 2000, Hermann et al. 2002, Tuberville et al. 2007). The presence of xeric soils and structurally open habitat within the release areas at OISP and YWMA may have contributed to high rates of site fidelity by translocated tortoises. Patterns of habitat selection in both translocated and resident tortoises on the OISP were consistent with this species' selection for structurally open habitats. Translocated tortoises explicitly selected for low tree density at the study-area scale. Although resident tortoises selected areas with high oak importance from sandhill and off-sandhill areas, most of the oak trees

Table 4. Burrow-scale resource selection functions for translocated and resident gopher tortoises at the Orianne Indigo Snake Preserve in southern Georgia, 2012. We report the change in second-order Akaike's Information Criterion (ΔAIC_c), AIC_c model weight (w_i), and deviance (Dev, defined as $-2 \times \log$ likelihood) for all candidate models. Failed model convergence is denoted by NA. Sandhill refers to random points drawn from the xeric sandhill surrounding the release area and off-sandhill includes random points drawn from the sandhill and a 100-m buffer around the sandhill. Importance values are unitless but range from 0–3 and shrub cover is a 2-level categorical variable (1–25% or >25%).

	Residents			Translocated		
	ΔAIC_c	w_i	Dev	ΔAIC_c	w_i	Dev
Burrow scale – Sandhill						
Total basal area (cm^2)	0.00	1.00	33.32	58.63	0.00	188.46
Importance pine	82.00	0.00	115.32	1,265.6	0.00	1,395.4
Importance oak	90.88	0.00	124.20	NA	NA	NA
Mean canopy cover (%)	126.34	0.00	159.66	103.37	0.0	233.20
Total tree density (trees/ha)	133.84	0.00	167.17	0.00	0.98	129.83
Shrub cover (%)	152.30	0.00	185.63	7.93	0.02	137.76
Burrow scale – Off-sandhill						
Total basal area (cm^2)	0.00	1.00	28.54	0.00	1.00	56.64
Importance oak	76.22	0.00	104.75	64.35	0.00	120.99
Importance pine	107.41	0.00	135.95	170.69	0.00	227.33
Mean canopy cover (%)	119.13	0.00	147.67	163.11	0.00	219.75
Shrub cover (%)	147.03	0.00	175.57	546.01	0.00	602.65
Total tree density (trees/ha)	147.62	0.00	176.16	33.20	0.00	89.85

Table 5. Fixed-effects parameter estimates and 95% confidence intervals in the best-supported resource selection function models at the burrow scale for translocated and resident gopher tortoises at the Orianne Indigo Snake Preserve in Georgia, 2012. Sandhill refers to random points drawn from the xeric sandhill surrounding the release area and off-sandhill includes random points drawn from the sandhill and a 100-m buffer around the sandhill.

	Parameter	Beta	Lower CI	Upper CI
Resident				
Sandhill	Total basal area (cm^2)	−8.28	−13.16	−3.41
Off-sandhill	Total basal area (cm^2)	−5.69	−8.40	−2.98
Translocated				
Sandhill	Total tree density (trees/ha)	−109.65	−217.67	−1.63
Off-sandhill	Total basal area (cm^2)	−2.10	−3.15	−1.06

surrounding the release enclosure were small and shrub-like resulting in a largely open canopy. Additionally, the median bootstrapped model weights for oak importance increased from 0.27 to 0.98 for resident tortoises when off-sandhill habitats were included indicating strong avoidance of the more closed-canopy habitats surrounding the sandhill. Selection for structurally open habitats was also strong at the burrow scale. These results suggest that tortoises strongly avoided habitat features prevalent off the sandhill and that translocated tortoises selected habitat features that were readily available within the release area. Although additional emigration may have been prevented by relatively low availability of open canopied, xeric soils surrounding our release area, we did observe tortoises moving across mesic soils and through dense vegetation. These movements indicate that the presence of suitable habitat alone may not be sufficient to prevent post-release emigration of translocated individuals (Bennett et al. 2013).

Alternatively, increased movements by translocated tortoises may have been related to the availability of fine-scale habitat features we were unable to measure such as groundcover forage (Aresco and Guyer 1999, Tuberville et al. 2007). The release areas at both OISP and YWMA supported low densities of resident tortoises, which may suggest poor-quality habitat within the release area. If the release sites had poor quality habitat translocated tortoises would have been more likely to move away to locate better quality habitat. Although low habitat quality likely explains some of the variation in our data, we do not think it completely explains the greater movement distances observed by translocated tortoises than residents. First, resident tortoise densities are low because of past land-use practices and tortoises likely have not had time to expand into new habitat given the recent habitat restoration actions. Second, resident tortoises were observed within 250 m of the enclosures at both sites, and a third of telemetered translocated tortoises did not move more than 250 m from the enclosure. One translocated tortoise was observed using only a single burrow within the enclosure at YWMA during the entire duration of this study. Finally, prescribed burns within the release area at the OISP in 2011 and 2012 resulted in new ground cover growth, which would have been available to translocated tortoises close to the enclosure immediately following enclosure removal. Translocated tortoises also may have moved farther than resident tortoises because they were held at high densities (16 per ha) within the enclosures. Although we also cannot rule out this possibility, dispersal to avoid high densities of conspecifics does not seem sufficient to explain how far translocated tortoises might move. Translocated tortoises would have had to dispersed only 250 m from the enclosure to achieve a density of 0.81 per ha, which is similar to the mean density reported for several sites across southern Georgia (0.75 per ha; Smith et al. 2009); yet, our median displacement distance was 652 m. Tuberville et al. (2005) used enclosure densities of 12–13 per ha but observed the greatest movement distances with unenclosed tortoises. Using high tortoise densities within pre-release enclosures actually may be beneficial because social interactions among translocated individuals (Tuberville et al. 2005) may enhance population integration (Scillitani et al. 2012, 2013; Bennett et al. 2013).

We suspect that our use of long-term pre-release enclosures may also have contributed to our high site fidelity although our study was unable to explicitly test this hypothesis. Consistent with our predictions, site fidelity of our translocated tortoises was higher than that reported by Tuberville et al. (2005) for unenclosed translocated tortoises but similar to translocated tortoises enclosed for 9 and 12 months. Tuberville et al. (2005) also found that unenclosed tortoises had larger home range sizes compared to enclosed tortoises and this difference was greatest between unenclosed tortoises and tortoises enclosed for 12 months prior to release. Other Chelonian translocation studies have reported that pre-release enclosures result in reduced movement distances following release (Pedrono and Sarovy 2000). Studies of translocated gopher tortoises using short-term enclosures (i.e., < 1 month) reported high emigration rates (Doonan 1986, Burke 1989). However, Riedl et al. (2008) found no differences in movement patterns or site fidelity between resident and unenclosed translocated tortoises; however, they do not discuss the potential causes behind this lack of difference. Differences in habitat suitability, climate, or the densities and spatial aggregation of resident tortoises may be possible explanations for this lack of difference.

The translocation process did not appear to adversely affect the health of our translocated tortoises relative to resident tortoises as changes in body weight were similar between treatments. Riedl et al. (2008) also reported positive changes in body condition for translocated and resident gopher tortoises in Florida. Additionally, we observed no mortality among translocated tortoises during their first year following translocation. Mortality rates for adult gopher tortoises are generally low (Tuberville et al. 2008). DeGregorio et al. (2012) found high over winter survival of adult translocated tortoises at the northern edge of their range. One translocated individual at YWMA was initially captured outside of the enclosure so it is possible that some of the translocated tortoises at YWMA not captured within the enclosure had escaped during winter. Additionally, YWMA is open to the public and it is possible that some tortoises may have been removed from the enclosure by humans.

We were unable to monitor tortoises in our study beyond 1 year post-release because of logistical constraints. Other studies on translocated Chelonians have reported reduced movement distances following the first year even in the absence of pre-release enclosures (Field et al. 2007, Rittenhouse et al. 2007, Nussear et al. 2012). Tuberville et al. (2005) found that unenclosed gopher tortoises had significantly smaller activity areas in the second year post-release compared to the first year. Additionally, second-year activity areas across all treatments (unenclosed, 9-months, and 12-months enclosed) were similar in size to those from resident gopher tortoise populations across the southeastern United States. Studies on other taxa have also reported reduced movements following some initial period of extensive movement although the length of this period varies. Nussear et al. (2012) found that unenclosed translocated Agassiz's desert tortoises (*Gopherus agassizii*) in Mojave desert scrub and Great Basin conifer woodland exhibited greater first-year movements relative to resident tortoises but showed similar movement patterns during the second and third years post-release. Moehrenschlager and Macdonald (2003) found that translocated adult swift foxes (*Vulpes velox*) had greater daily movement distances than resident foxes within the first 50 days post-release but afterwards their movements were similar. Reinert and Rupert (1999) found that translocated timber rattlesnakes (*Crotalus horridus*) still exhibited more extensive movements than resident rattlesnakes during the second year post-release. Scillitani et al. (2012, 2013) reported that translocated alpine ibexes (*Capra ibex ibex*) needed up to 3 years to conclude exploratory movements and assimilate into resident social groups. These studies illustrate extensive post-release movements are common across many taxa and suggest the importance of strategies, such as pre-release enclosures, designed to minimize extensive first-year movements as a means of improving translocation success.

Some translocations may not be concerned with extensive movements or emigration from the immediate release area if numbers of translocated individuals are large or potential habitat is widespread and available. In this case, survival may be of greater concern than an individual's final location provided individuals come to reside in suitable habitat where they can survive and reproduce. Even with high rates of emigration, individuals that remain in the immediate release area after the first year can contribute to a resident population (Ashton and Burke 2007). However, in many instances, including our study, translocations are conducted with a goal of establishing populations at a specific location (e.g., a specific sandhill). Translocations often involve small numbers of individuals, which itself can lead to lower probability of translocation success (Mateju et al. 2012), and perhaps a greater impact on long-term translocation success. In these instances, short-term studies monitoring site fidelity, as well as survival and reproduction, may be very important in helping mangers ensure long-term translocation success. Although our study did not directly test the effectiveness of pre-release enclosures, our results are consistent with previous studies indicating that pre-release enclosures improve site fidelity. Future studies should examine the interactions between pre-release enclosures and habitat quality in influencing movement patterns and site fidelity of translocated individuals.

MANAGEMENT IMPLICATIONS

Gopher tortoise translocations will likely continue into the future, either as mitigation against land use conversion or to establish or restore populations. Post-release monitoring is essential to ensure that translocated individuals remain and survive within the intended release area and therefore have the potential to become integrated into a viable population. Comparing traits of translocated individuals with nearby or sympatric resident populations allows managers to determine if translocated individuals are behaving like long-term residents. Concurrently monitoring a wide diversity of traits including movement, habitat selection, growth, and survival not only allows for stronger comparisons but may elucidate reasons for observed similarities or differences between translocated and resident individuals. Although behavioral traits of translocated individuals do not necessarily reflect their long-term likelihood of survival and reproduction, such traits (e.g., fidelity to release area, positive growth, high survival) are generally prerequisites for long-term success. We caution that comparisons with resident populations should consider the long-term trajectory of resident populations to avoid using ecological sinks as a baseline for comparison when possible. However, translocations are often intended to augment small, declining resident populations for the very purpose of improving long-term viability. Because site fidelity is a required first step in establishing a population, comparing movement patterns and site fidelity between translocated and resident individuals may still provide useful information informing short-term translocation success.

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