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Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*)

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Abstract

Efforts to evaluate the efficacy of translocation as a conservation tool have mostly been inadequate, particularly for reptiles and amphibians, leading many biologists to discount translocation as a viable management option. Nevertheless, with two-thirds of the world's tortoise and freshwater turtle species at risk, translocation may be one of the few remaining options for re-establishing extirpated populations and reconnecting fragmented ones. We translocated 106 gopher tortoises (*Gopherus polyphemus*) to a protected area within the historical range but with no resident tortoises and tested the effects of penning on site fidelity and activity area size. We assigned 38 adults and subadults to one of three penning treatments (9 months, 12 months and no penning) and radio-tracked them for 2 years. Penning significantly increased site fidelity and resulted in smaller activity areas. Our data suggest that translocation coupled with penning will improve the likelihood of establishing self-sustaining tortoise populations.

INTRODUCTION

Translocation – the intentional release of individuals of a species at a within-range location different from their capture location in order to 'establish, reestablish, or augment a population' (Griffith *et al.*, 1989) – is commonly used in the management of native mammals and birds. However, success rates have differed between game (86%) and non-game species (46%) and varied depending on factors such as number of animals released, habitat quality at the release site and location of the release site within the species' range (Griffith *et al.*, 1989; Wolf *et al.*, 1996). Many valid biological and political concerns are associated with the intentional movement of wildlife (Berry, 1986; Dodd & Seigel, 1991; Seigel & Dodd, 2000; Zug, Vitt & Caldwell, 2001), although some can be avoided or minimised by releasing animals at sites without resident populations (Berry, 1986). Careful planning prior to translocation is critical for achieving effective conservation and minimising the risk of unintended consequences (Conant, 1988; Kleiman, 1989; IUCN, 1998).

Compared to birds and mammals, very little research has been conducted on translocation of reptiles and amphibians and the success rate for known projects (19%) is much lower (Dodd & Seigel, 1991). However, reptiles and amphibians around the world are experiencing declines (Alford & Richards, 1999; Gibbons *et al.*,

2000; Stokstad, 2004; Stuart *et al.*, 2004). Two-thirds of the world's turtle species are considered threatened by the IUCN, and many of the remaining third have not been evaluated (Turtle Conservation Fund, 2002). Human exploitation of turtles has resulted in population declines, local extirpations and even extinction of some species (Thorbjarnarson *et al.*, 2000). As exploitation and habitat alteration continue, translocations and repatriations will play an increasingly important role in turtle conservation. A recent global action plan for tortoises and freshwater turtles lists translocation and repatriation as critical conservation components for the most threatened species (Turtle Conservation Fund, 2002).

Out of all the amphibian and reptile species of the southeastern United States, the gopher tortoise (*Gopherus polyphemus*) has been the target of the most numerous and extensive relocations (i.e. displacement of animals from their habitat to avoid immediate threats such as development: Dodd & Seigel, 1991). Because the primary goal of most relocations is the welfare of individual animals rather than conservation of populations or species, very little subsequent monitoring has been conducted to evaluate the overall success of projects. Despite the controversy associated with the deliberate movement of wildlife and the paucity of data available to evaluate its effectiveness as a management tool for reptiles and amphibians, translocation may sometimes be the only option for re-establishing extirpated populations and reconnecting fragmented ones.

The goals of this project were to: (1) re-establish a protected, viable population of gopher tortoises within

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the species' natural range and (2) test whether use of temporary outdoor enclosures (hereafter referred to as 'penning') and penning duration affected site fidelity and activity area size during the first 2 years following release. One of the primary concerns associated with translocation projects is post-release site fidelity. Techniques that encourage the acclimation of translocated animals to the release area have been recommended as ways to increase translocation success in mammals (e.g. bobcats *Felis rufus*, Diefenbach *et al.*, 1993; swift foxes *Vulpes velox*, Moehrensclager & MacDonald, 2003) and may enhance translocation success in tortoises. Although the effectiveness of short-term penning (i.e. <25 days) in promoting site fidelity by gopher tortoises has been disputed (Doonan, 1986; Burke, 1989), we predicted that long-term penning would facilitate the acclimation of tortoises to the release site and result in increased site fidelity and smaller activity areas. If long-term penning can be demonstrated to be effective, it is relatively inexpensive and easy to implement, making it a prime candidate technique for future conservation efforts.

METHODS

Study animal

The gopher tortoise is a large (maximum carapace length (CL) = 381 mm), herbivorous, long-lived terrestrial turtle, attaining reproductive maturity at 230–255 mm CL and 10–21 years (Iverson, 1980; Landers, Garner & McRae, 1980; Ernst, Lovich & Barbour, 1994). They construct large underground burrows (up to 6 m long and 3 m deep: Hansen, 1963; Tuberville & Dorcas, 2001) and individual tortoises will use multiple burrows throughout their lifetime, often even within a single year (Diemer, 1992; Smith, Breininger & Larson, 1997; Eubanks, Michener & Guyer, 2003). Gopher tortoises are social animals – they occur in local 'colonies' and frequently visit each other at their respective burrows (Waddle, 2000; Boglioli, Guyer & Michener, 2003). Although they tend to occupy burrows singly (McRae, Landers & Garner, 1981; Diemer, 1992; Smith *et al.*, 1997), several tortoises may sequentially occupy a given burrow throughout the active season. In addition, because the burrows themselves are also long-lived (Guyer & Hermann, 1997), they may be used by many different individuals over multiple years.

Gopher tortoises are diurnal, but even during the day spend a large proportion of the time underground in their burrows. They also have discrete seasonal activity patterns, with a winter dormancy period during which they may bask at the burrow entrance on warm days but will rarely travel away from or between burrows (McRae *et al.*, 1981; Diemer, 1992). Although the duration of the dormancy period varies throughout the species' range (with longer periods of inactivity in the northern populations), gopher tortoises in all regions are active from at least April–October (Douglass & Layne, 1978; Eubanks *et al.*, 2003).

The gopher tortoise is the only tortoise species inhabiting the southeastern USA, where it is occurs in

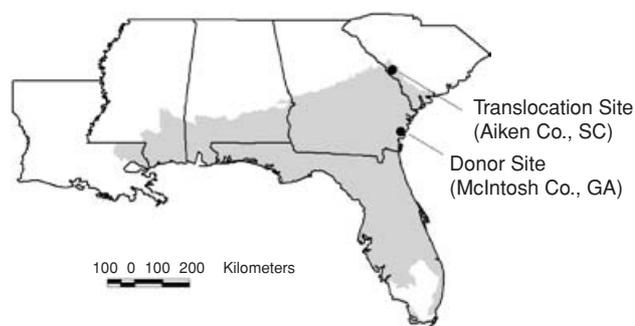


Fig. 1. Distribution of gopher tortoises (shaded) with locations of donor site and translocation site indicated. Range map is adapted from Iverson (1992).

the Coastal Plain and Sandhills physiographical provinces (Fig. 1). It is associated with deep sandy soils and a wide variety of xeric habitats. Its historical habitat was the longleaf pine (*Pinus palustris*) forest, of which only about 2% remains (Noss, LaRoe & Scott, 1995). Due primarily to habitat loss, the gopher tortoise is federally-threatened in the western portion of its range (i.e. western Alabama, Mississippi, Louisiana: USFWS, 1987) and is considered to be declining throughout its range (Auffenberg & Franz, 1982; Smith, Tuberville & Seigel, 2006).

Founder population

The donor site was a 40-ha industrial development site in southeast Georgia, USA (Fig. 1). Primary habitats at this disturbed site included recent clearcuts and densely-planted young pine forests on sandy soils (Lakeland, Kleg and Ona series: USDA, 1961). During August–October 2001 (Autumn), we located and trapped as many intact tortoise burrows as we could find (144 out of 173 burrows were intact) at the donor site. We captured 74 tortoises (including adults, subadults and juveniles) by hand, with pitfall traps at burrow entrances, or by manual excavation of burrows. In addition, 32 were hatched in the lab from seven nests encountered in the field, for a total founder population size of 106 tortoises.

Study site

The recipient site was the Savannah River Site (SRS, Aiken County, South Carolina, USA), an 800 sq km government reserve approximately 217 km north of the donor site (Fig. 1). The SRS is owned by the U.S. Department of Energy and managed by the U.S. Forest Service (White & Gaines, 2000). Although Holbrook (1842) noted that tortoises were historically 'numerous in Edgefield and Barnwell districts,' which border the recipient site, no resident population of gopher tortoises was present on the SRS at the time this study was initiated, probably as a result of historical intensive agriculture in the region (White & Gaines, 2000). A small, isolated population of gopher tortoises was discovered in 1992 approximately 17 km to the northeast of the SRS (Clark, Tsaliagos & Pittman, 2001).

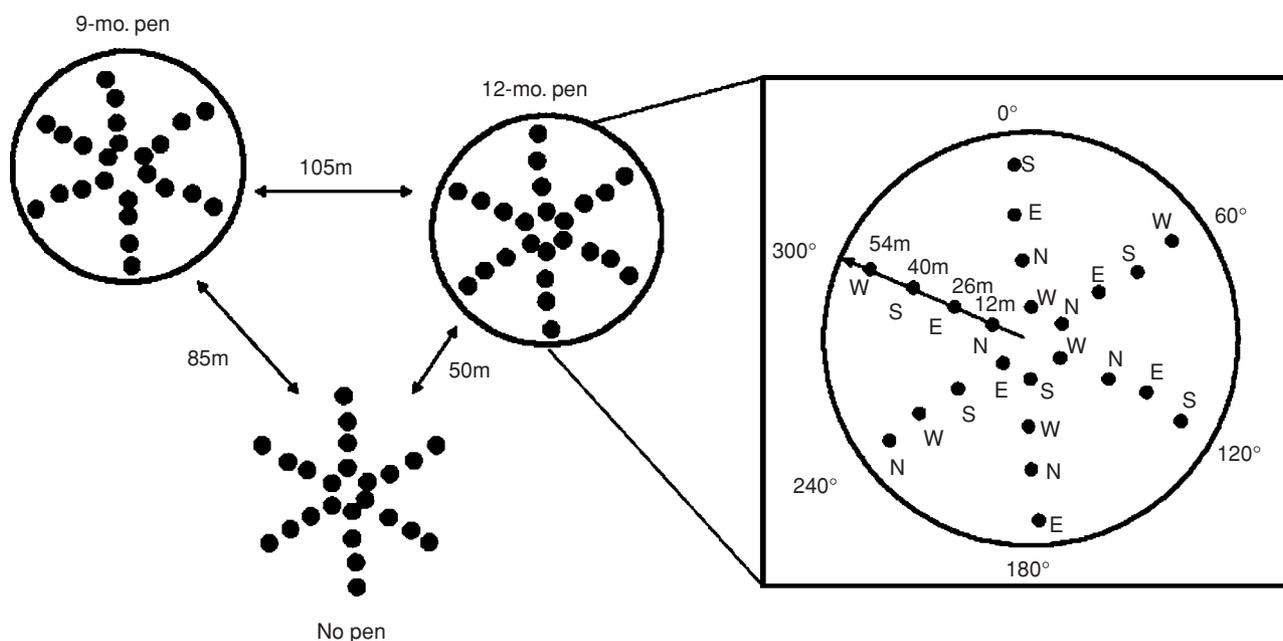


Fig. 2. Relative locations of 9 month penning (9-mo. pen), 12 month penning (12-mo. pen) and no-penning arrays used for experimental releases. Inset illustrates one of the burrow arrays. Dots represent starter burrows with the position and orientation of burrow entrances indicated.

The release site was located in the northeast corner of the SRS, in an 882 ha timber management compartment with sandy soils (Lakeland and Troup series). The forest type is primarily open-canopy longleaf pine (52% of compartment area), flanked by floodplain sweetgum (*Liquidambar styraciflua*) forests (13%) and interspersed with small patches of other upland forest types. The estimated age of the timber stand is approximately 50–60 yrs (P. Johnston, pers. comm.). The understory comprises mixed-oak (*Quercus* spp.) shrub and a diverse herbaceous layer. Management is directed towards improving site conditions for the federally-endangered red-cockaded woodpecker (*Picoides borealis*: USFWS, 1970) and re-establishing wiregrass (*Aristida stricta*), a dominant understory species of the longleaf pine ecosystem eliminated prior to the establishment of the SRS due to intensive agriculture (White & Gaines, 2000). The release site is treated with prescribed fire approximately every 3 years and was burned during spring/summer 2001.

Experimental release pens

Three separate arrays of starter burrows were constructed in the core release area (Fig. 2) at the centre of the timber compartment. Arrays were 50–105 m apart and positioned so that approximately 50% of each array contained wiregrass, an important food item for gopher tortoises (Garner & Landers, 1981; MacDonald & Mushinsky, 1988). Two out of the three arrays were enclosed by 92-cm tall aluminum flashing buried approximately 30 cm in the ground and reinforced with wooden stakes; the third was not enclosed. The arrays were 1 ha in size.

Each array consisted of 24 starter burrows (Fig. 2). Burrows were created using a gas-powered auger with a 46 cm bit placed at a 30 degree angle to excavate

burrows to approximately 1 m in length. Burrow entrances were manually shaped to more closely resemble tortoise-constructed burrows and the excavated sand was used to form a mound to imitate the ‘apron’ typically found outside burrow entrances. Each burrow was permanently marked and its location recorded using GPS technology.

Experimental subjects and penning treatments

All tortoises were measured (only mid-line CL to nearest mm reported here) and permanently marked by drilling or filing notches in unique combinations of marginal scutes (Gibbons, 1990). Tortoises measuring > 235 mm CL were considered to be adults and identified as male or female based on the degree of plastral concavity (Iverson, 1980; Landers *et al.*, 1980). Tortoises measuring 181–235 mm CL were classified as subadults. Although the founder population included many juveniles (≤ 180 mm CL), only adults and subadults were intensively monitored in this study (Fig. 3). Data on juveniles will be presented elsewhere. All adults and subadults were assigned to one of three penning treatments, each treatment consisting of 12–13 animals, with similar sex ratios and size distributions between treatments. Tortoises from all three treatments were temporarily held offsite until transported to the release site (approx. 25 km away). Each tortoise was fitted with two radio-transmitters (No. LF-2-2/3A-CTM-RS-T, LL Electronics, Mahomet, IL; wt 40 g with epoxy) mounted on the anterior-most costals – one on each side of the carapace.

Individuals in the ‘no-penning’ treatment remained at the offsite holding area until 29 March–3 April 2002 (Spring 2002; approx. 190 days offsite), when they were transported to the core release area and placed into starter burrows in the ‘no pen’ burrow array. Individuals in

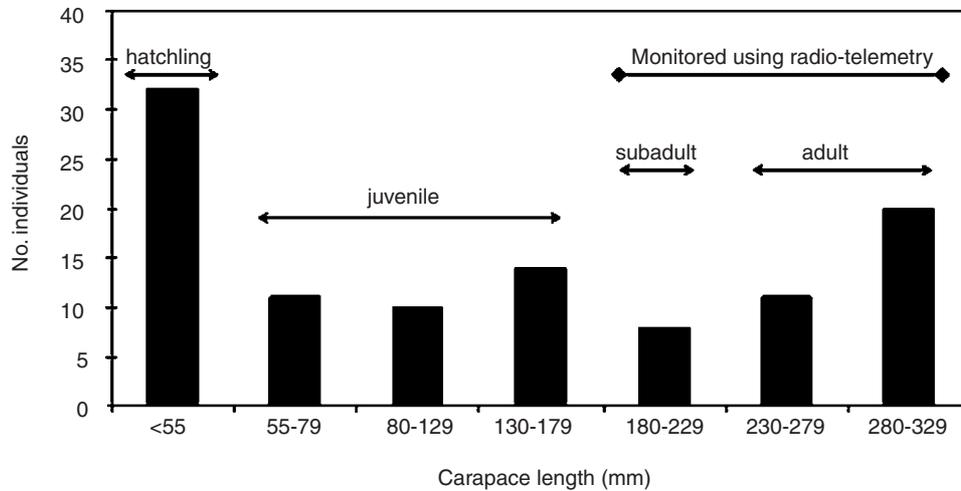


Fig. 3. Size (carapace length (CL) in mm) frequency distribution of founder population ($n = 106$) indicating the size classes for different life stages (as defined in this study). Only subadults and adults were monitored using radio-telemetry.

the 9 month (9-mo) penning and 12 month (12-mo) penning treatments were transported from the offsite holding area in October 2001 (Autumn; approx. 60 days offsite) and placed into starter burrows in their respective burrow arrays, where they spent the first winter. The 9-mo penning group was 'released' on 8 July 2002 by removing the aluminum flashing encircling their burrow array. The 12-mo penning group was similarly 'released' on 23 September 2002.

Post-release monitoring

Following release, animals were located daily through October 2002, then approximately once per week through 30 November 2002 (Year 1 post-release). From March–October 2003 (Year 2), tortoises were located approximately 2–3 times per week. Burrows constructed by tortoises were assigned a unique number and permanently marked. All tortoise and new burrow locations were recorded using GPS technology (Trimble Pro-XR, Sunnyvale, CA, with sub-metre accuracy).

Tortoises that travelled more than 1 km from the core release area (i.e. the burrow arrays) without establishing a burrow were considered to have dispersed from the release site. Dispersers were retrieved and re-released in the core release area. Although we continued to monitor these animals, they were considered to be translocation 'failures.'

Data processing and statistical analyses

Site fidelity was evaluated by comparing the proportions of dispersers and non-dispersers between the release groups using tests for goodness of fit. Separate analyses were conducted for Year 1 and Year 2 (both including and excluding animals that attempted to disperse in Year 1 but were returned to the core release area). Because each animal had two radio-transmitters, individuals lost from the study were presumed to have dispersed great distances.

Activity areas were minimum convex polygons (MCP) calculated for each individual for Year 1 and Year 2

using ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) and the MOVEMENT extension (Hooge & Eichenlaub, 1997). Activity areas include all points where animals were located, including all dispersal attempts by an individual. Because the release date – and, therefore, the number of days individuals were tracked – in Year 1 varied with penning treatment, Year 1 activity areas were calculated using only the first 50 tracking locations. Previous analyses of home range data for gopher tortoises by Eubanks *et al.* (2003) suggest that samples of at least 50 consecutive locations are sufficient to eliminate the potential effects of serial autocorrelation on activity area (i.e. home range) estimates. All 2003 tracking dates were used for calculating Year 2 activity areas. Four individuals were lost during the first 15 days following initial release and were eliminated from the analyses of activity areas. Activity areas for both Year 1 and Year 2 could be calculated for the remaining individuals.

Activity area values were \log_{10} -transformed to reduce variance between groups. Activity areas were compared among penning treatments and between sexes (adult males (M), adult females (F) and subadults (S)) using separate two-way ANOVAs (Statistical Analysis System V8e, Cary, NC, USA) for each year. Post-hoc comparisons of means were conducted for main effects and interactions found to be statistically significant. Because we suspected that activity area sizes for individuals would change between years, we performed separate paired *t*-tests (Year 1 versus Year 2) for each release group. All means are reported ± 1 Standard Error (SE) and alpha was set at 0.05 for all statistical procedures. Additional Year 1 data and analyses are presented in Clark (2003).

RESULTS

Site fidelity

Site fidelity varied significantly between penning treatments during Year 1 ($\chi^2 = 12.15$, $df = 2$, $P = 0.0023$).

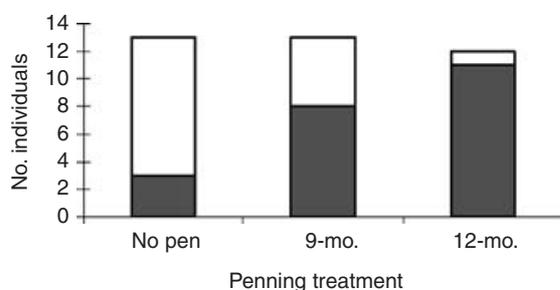


Fig. 4. Site fidelity by penning treatment during Year 1. Dispersers (unshaded) are animals that travelled more than 1 km from the core release area without establishing a burrow.

Only 23.1% (3 out of 13) of no-penning animals stayed in the release site (i.e. timber management compartment) without attempting to disperse, whereas 61.5% (8 out of 13) of the 9-mo penning and 91.7% (11 out of 12) of the 12-mo penning animals remained during the first year after release (Fig. 4). Four tortoises (no pen: 1F, 1S; 9-mo pen: 1F; 12-mo pen: 1F) were lost from the study within 15 days of release during their initial dispersal attempt, presumably because they travelled out of signal range between daily tracking periods. Tortoises that dispersed during Year 1, on average, made the initial attempt 25 days post-release (range: 6–94 days; $n = 16$; Clark, 2003). After excluding those lost from the study, length of penning treatment also resulted in differences in the number of dispersal attempts made by tortoises during Year 1. Half of the no-penning dispersers attempted to disperse 2–4 times before settling in the release site. In contrast, the four 9-mo penning dispersers (2F, 1M, 1S) attempted to disperse only once. The single 12-mo penning disperser was lost from the study.

The proportion of individuals dispersing during Year 2 was not significantly different between penning treatments regardless of whether we considered all animals (i.e. including Year 1 dispersers that were retrieved and returned to the core release area; $\chi^2 = 0.4979$, $df = 2$, $P = 0.7796$) or included only animals not attempting to disperse in Year 1 ($\chi^2 = 1.0476$, $df = 2$, $P = 0.5923$). During Year 2, only 4 out of the 34 remaining animals (some of which attempted to disperse in Year 1) attempted to disperse (11.7% overall; no pen: 1M (dispersed twice), 1F; 9-mo pen: 1F; 12-mo pen: 1M). Except for the male from the 12-mo penning treatment, all Year 2 dispersers had also attempted to disperse during Year 1. Although we cannot say how far animals would have dispersed if we had not retrieved them, male no. 7 (no-penning treatment) travelled 5.1 km N and established a burrow on private property before we located and retrieved him.

Activity areas

Year 1 activity areas varied significantly between penning treatments ($F_{2,25} = 19.19$, $P < 0.0001$) and among sexes ($F_{2,25} = 6.66$, $P = 0.0048$; Figs 5(a) & 6(a)). Year 1 activity areas were significantly smaller for the 12-mo penning treatment (1.96 ± 1.07 ha) than either

no-penning (93.54 ± 33.43 ha) or the 9-mo penning treatments (37.06 ± 14.08 ha); no-penning and 9-mo penning treatments were not significantly different. Activity areas of both males (45.23 ± 23.67 ha) and females (64.12 ± 18.45 ha) were significantly larger than activity areas of subadults (12.16 ± 6.90 ha) but were not significantly different from each other. The group \times sex interaction was nearly significant ($F_{4,25} = 2.54$, $P = 0.0653$), with females exhibiting a weaker response to penning than males or subadults. When animals that attempted to disperse during Year 1 were excluded from analyses, the main effects of penning treatment ($F_{2,14} = 5.24$, $P = 0.02$) and sex ($F_{2,14} = 5.99$, $P = 0.0132$) were still significant.

Year 2 activity areas were not significantly different between penning treatments (Figs 5(b) & 6(b)), regardless of whether animals that attempted to disperse in Year 1 were included in ($F_{2,25} = 0.73$, $P = 0.4910$) or excluded from ($F_{2,21} = 0.69$, $P = 0.5155$) the analyses. Similar to the results of Year 1, activity areas in Year 2 varied between sexes ($F_{2,25} = 12.04$, $P = 0.0002$), with adult male (22.19 ± 12.33 ha) and adult female (12.13 ± 6.69 ha) activity areas being significantly larger than activity areas of subadults (0.52 ± 0.44 ha) but not different from each other.

Overall, activity areas were smaller in Year 2 than in Year 1 (Figs 5 & 6), even though Year 1 activity areas only included the first 50 daily tracking locations, whereas Year 2 activity areas were based on 48–72 tracking locations per individual collected over the entire activity season (230 days). The difference between years was significant for the no-penning treatment ($t = -2.30$; $n = 11$, $P = 0.0440$), nearly significant for 9-mo penning ($t = -1.95$, $n = 12$, $P = 0.0776$), but not for 12-mo penning treatment ($t = 1.14$, $n = 11$, $P = 0.2791$). Year 2 activity areas were more similar to the home ranges reported for naturally occurring populations, particularly when dispersers were excluded from the analyses (Table 1).

DISCUSSION

Site fidelity

Penning and penning duration dramatically increased site fidelity of translocated gopher tortoises by reducing the proportion of animals attempting to disperse and the number of times an individual attempted to disperse. Most dispersal occurred during the first year following release and most initial attempts occurred within the first 25 days of release. An argument could be made that the low dispersal rate of the 12-mo penning treatment group (September release) was influenced by the onset of the winter inactivity period. However, based on the dispersal behaviour of animals from the previous releases, we believe that the 6 weeks remaining in the activity season allowed adequate time for tortoises from the 12-mo penning treatment to attempt to disperse. Dispersal rates in Year 2 were lower than in Year 1, were not affected by penning treatment and animals remaining in the release

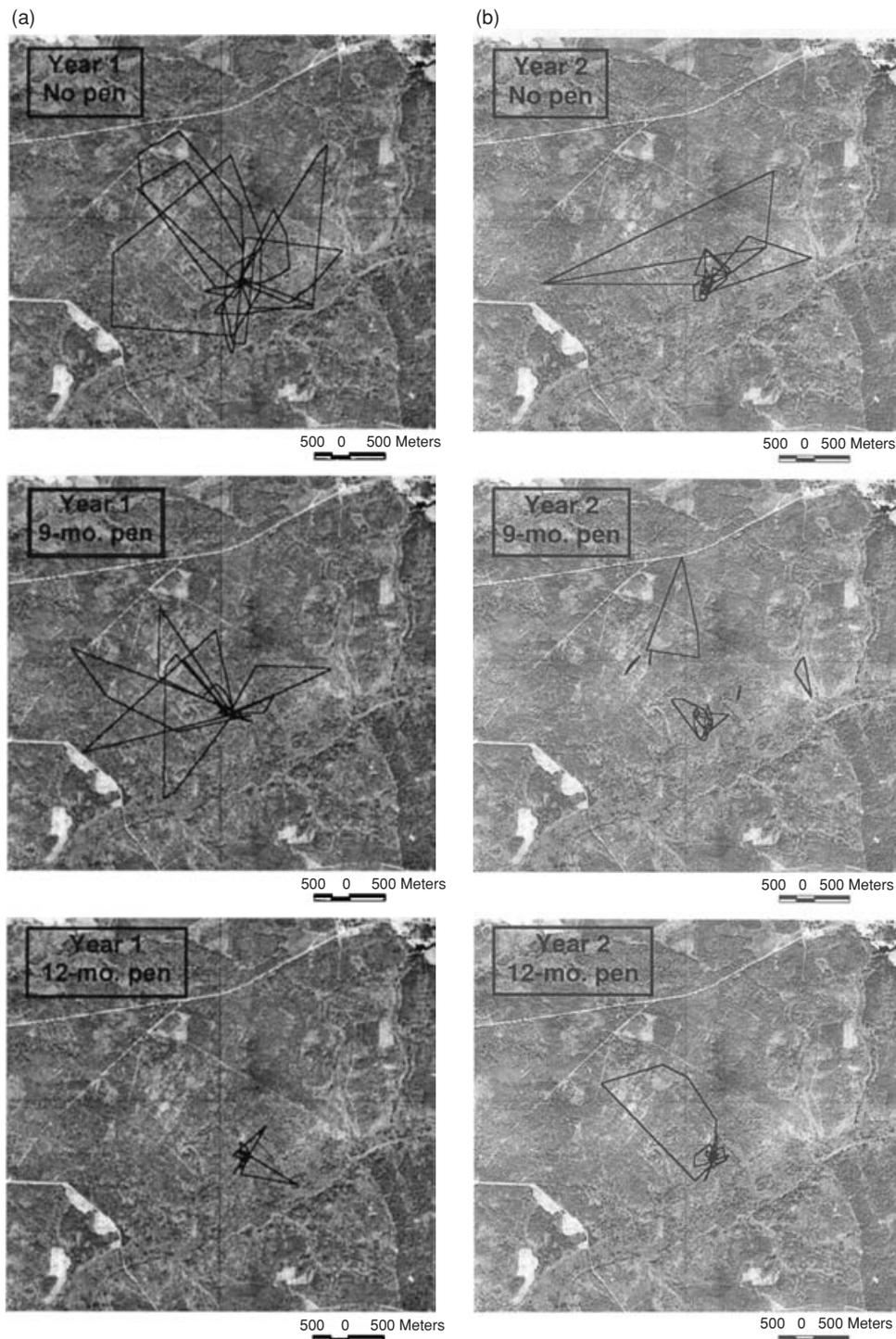


Fig. 5. Minimum convex polygons depicting (a) Year 1 and (b) Year 2 activity areas for tortoises from the no pen, 9 month pen (9-mo.) and 12 month pen (12-mo.) treatments. Year 1 activity areas are based on first 50 daily locations only.

site at the end of Year 1 (whether voluntarily or ‘by force’) tended to eventually settle there.

As predicted, an unnaturally high proportion of translocated animals attempted to disperse shortly after their release. During Year 1, we observed dispersal rates of 76.9% (no-penning), 38.5% (9-mo penning) and 8.3% (12-mo penning), compared to only 2% reported for a naturally-occurring population (Eubanks *et al.*, 2003).

Most animals that attempted to disperse in Year 2 had also attempted to disperse the previous year, suggesting that certain individuals have a greater propensity to disperse. However, most Year 1 dispersers that were re-released in the core release area did not attempt to disperse in Year 2. Both penning and retrieval of dispersing animals proved to be effective in curbing the initial flight response of tortoises released into their new, unfamiliar environment.

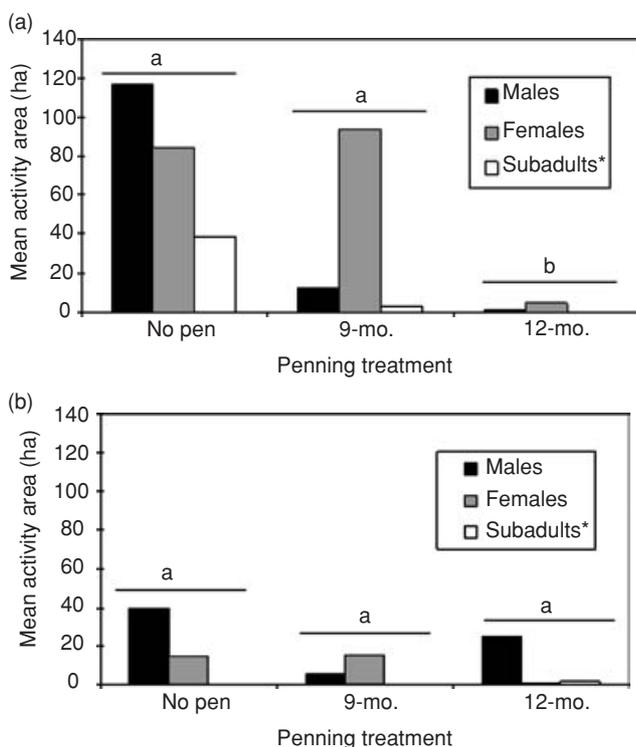


Fig. 6. Comparison of mean activity areas for adult males, adult females and subadults in each penning treatment during (a) Year 1 and (b) Year 2. Significant comparisons between penning treatments are indicated with different letters; significant differences between sexes are indicated with an (*).

Activity areas: comparison among penning treatments

Twelve-month penning was significantly more effective than either 9-mo penning or no penning in reducing the area over which animals roamed during Year 1. Lack of a significant difference in activity area size between 9-mo penning and no-penning was surprising. However, during Year 1, activity areas for adult males and subadults were an order of magnitude smaller for the 9-mo penning compared to the no-penning treatment, whereas activity areas for females from the 9-mo penning treatment were nearly as large as those for females from the no-penning treatment (Fig. 6(a)). These results suggest that the effectiveness of penning varies with sex, with adult females requiring longer term penning.

The variation observed between penning treatments in Year 1 is presumably a result of different penning durations rather than time of year and did not affirm an expectation that ‘translocations may be less successful during late summer-early fall, when tortoises are more likely to disperse’ (Berish, 2001). For example, adult males in naturally occurring populations exhibit peak movement during July–September (Diemer, 1992; Eubanks *et al.*, 2003). Instead, we found that male activity area size decreased for each successive release from spring to autumn (March–September). Likewise, peak activity of adult females from natural populations occurs in September as well as during the May–June nesting season

Table 1. Summary of home-range estimates for gopher tortoises from naturally occurring populations compared to this study of translocated tortoises

Location	Study duration	Mean home ranges (ha)		Land use	Source
		Adult females	Adult males		
Natural populations					
Southwest GA	13 mo	0.4 (0–3.4; n = 53)	1.1 (0–4.8; n = 70)	Ecological preserve	Eubanks <i>et al.</i> (2003)
East-central FL coast	20 mo	0.6 (0.3–1.1; n = 4)	1.9 (0.3–5.3; n = 10)	Military/wildlife refuge	Smith <i>et al.</i> (1997)
North-central FL	24 mo	0.3 (0–1.2; n = 5)	0.9 (0.2–2.9; n = 6)	Wildlife management area	Diemer (1992)
Southwest GA	8 mo	0.1 (0.04–0.14; n = 5)	0.45 (0.1–1.4; n = 8)	Industrial forest	McRae <i>et al.</i> (1981)
Northeast FL	17 mo	0.4 (0–1.4; n = 14)	–	Ecological preserve	Smith (1995)
Translocated population					
West-central SC		Year 1 [†]		Defence facility	This study
No pen		84.2 (5.0–145.3; n = 3)	116.5 (0.7–373.7; n = 6)	”	”
No pen (no dispersers)		5.0 (n = 1)	17.5 (0.7–34.2; n = 2)	”	”
9-mo pen		93.9 (38.9–134.1; n = 4)	12.3 (0.4–50.2; n = 5)	”	”
9-mo pen (no dispersers)		72.2 (38.9–105.5; n = 2)	14.9 (0.4–50.2; n = 4)	”	”
12-mo pen		4.4 (0.1–11.6; n = 3)	1.4 (0.1–5.3; n = 6)	”	”
12-mo pen (no dispersers)		”	”	”	”
		Year 2			
All treatments		12.1 (0.0–55.0; n = 10)	23.5 (0.2–173.3; n = 17)	”	”
All treatments (no dispersers)		2.2 (0–6.1; n = 8)	4.4 (0.2–15.8; n = 15)	”	”

Reported values are mean values (range; number of individuals) to nearest 0.1 ha. Means for this study are reported both including and excluding animals that dispersed from the study site; animals lost from the study are not included because there were too few data to calculate home ranges for those individuals. Means are provided for each penning treatment separately for Year 1 but are combined for Year 2. [†]Year 1 home ranges are based on movement during first 50 daily locations following release.

(Diemer, 1992; Eubanks *et al.*, 2003). Hence, the largest Year 1 activity areas for females would have been expected for the 12-mo penning treatment in which activity area, as determined by the first 50 daily locations after release, was based on September–October movement (the nesting period was not represented by Year 1 activity areas for any release group). In Year 1 of our study, greatest activity sizes were observed for females from the 9-mo penning (July–August) and no-penning treatments (late March–early May).

Activity areas: Year 1 vs. Year 2

Compared to Year 1, Year 2 activity areas were smaller, more similar between penning treatments and more similar to the home range sizes reported for residents in naturally occurring populations. The greatest reductions were exhibited by individuals from the no-penning treatment. These results are even more striking considering that the Year 1 activity areas were calculated using only the first 50 tracking locations compared to the full activity season (April–October) for Year 2. Some individuals still roamed over relatively large areas (55–173 ha) during Year 2, but these large activity areas were associated with animals (from all penning treatments) that attempted to disperse during that year.

Site fidelity and activity areas: differences among sexes

Subadults may be more likely than adults to establish home ranges near the release area following translocation. In each penning treatment, adult males and females were more likely than subadults to disperse from the core release area and had larger activity areas. In natural populations of turtles, males tend to travel greater distances and more often than females (Morreale, Gibbons & Congdon, 1984; Gibbons, 1986; Eubanks *et al.*, 2003). However, in this study, female tortoises were more likely than males to disperse immediately following translocation. Three out of four animals lost from the study were females and half of the remaining females were forced to stay in the release site. Based on these findings, in combination with the weaker response of females to penning, we conclude that adult female gopher tortoises may be more sensitive to the disturbance associated with translocation than adult males or subadults. Burke (1989) also reported lower site fidelity by relocated females compared to the overall population average, although sample sizes were small.

Comparison with previous penning experiments in gopher tortoises

Previous studies have implemented different penning protocols for gopher tortoises, with mixed conclusions regarding the technique's effectiveness in promoting site fidelity of translocated animals. However, these studies penned animals individually or in small groups, confined animals for much shorter time periods (< 30 days for adults), included captive animals or animals from multiple localities, inferred site fidelity from burrow surveys

rather than mark–recapture or radio-telemetry methods, or had extremely small sample sizes (Doonan, 1986; Lohoefer & Lohmeier, 1986; Burke, 1989). The effectiveness of our translocation can be attributed to: (1) using longer penning durations more appropriate for long-lived species, (2) translocating an entire, intact population of tortoises that included all size classes and (3) providing opportunity for tortoises within a penning treatment to associate with familiar individuals, thus facilitating social interactions. Our study design did not allow us to make conclusions regarding the importance of penning during the dormancy period (versus activity season only) on post-release site fidelity, but this issue should be explored. Further research is needed to evaluate how other factors such as time of year of release, size of founder population and habitat conditions affect site fidelity, movement patterns and ultimate population demography.

CONCLUSIONS

Although we observed considerable between-individual variation in the dispersal and movement behaviour of translocated tortoises, several patterns emerged: (1) penning and penning duration were important in reducing dispersal rates and activity area size during the first year; (2) during the second year, activity areas were smaller and more similar to those reported for naturally occurring populations; (3) some individuals had a greater propensity to disperse than others, regardless of penning treatment; (4) subadult tortoises had smaller activity areas and may be more likely to settle in the core release area; (5) adult females may require longer penning durations relative to adult male and subadult tortoises. Our data suggest that translocation can be implemented to successfully repatriate gopher tortoises and that relatively inexpensive, easy-to-implement techniques (e.g. penning) may improve the likelihood of establishing self-sustaining, resident populations. Long-term monitoring of the site fidelity, survivorship, and reproduction of this population will be required to determine its viability.

Penning was an effective release technique for the species we investigated and has potential application to other tortoise species with similar space use patterns. However, release techniques and protocols should be tailored to the target species, their habitat and the conservation goals of the project and must be based on a thorough understanding of the species' biology and behaviour. The development of translocation protocols is recognised as a critical component for safeguarding the world's most endangered tortoise and freshwater turtle species. Although it is not a panacea for all species or all situations, translocation should be considered one of the many tools in the conservation toolbox.

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Front cover: Gopher Tortoises (*Gopherus polyphemus*).
Photo credit: Tracey Tuberville and Kurt Buhlmann
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