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Aggregated Space Use by Soft-Released Translocated Gopher Tortoises (*Gopherus polyphemus*)

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Abstract: Translocated herpetofauna can exhibit irregular space use and movement patterns when compared with resident conspecifics. In Florida, USA, Gopher Tortoises (*Gopherus polyphemus*) are translocated throughout the state to mitigate habitat loss due to development. The postrelease space use of translocated Gopher Tortoises within soft-release pens can affect population dynamics and population monitoring efficacy, and understanding spatial patterns can aid wildlife managers with population management. We used a combination of time-lapse cameras, animal tracking devices, and burrow distribution surveys to investigate translocated tortoise space use at Eglin Air Force Base, Florida, where tortoises have been translocated since 2015. We investigated 10 soft-release pens that varied in size (4–41 ha) and shape (due to landscape configuration and existing infrastructure). Time-lapse cameras and burrow distribution surveys showed that tortoises used habitat within 20 m of soft-release pens (silt fences) significantly more than the interior of pens. In most pens, the selection of pen-edge habitat resulted in a clustering effect that lessened upon subsequent surveys, after fences were removed. Additionally, our tracking data showed mixed evidence for clustering, where three of the seven tortoises used edge area significantly more than the interior of pens. Such clustering can affect the efficacy of population survey methods while potentially having negative impacts on the health of translocatees by increasing local density.

Key words: Conservation; Florida; Mitigation-driven translocation; Movement; Population monitoring

Conservation translocation is used to recover populations, reduce extinction risk, and reduce human–wildlife conflict, among other purposes (Novak et al. 2021). The process involves intentionally moving organisms to a new area for measurable conservation goals (IUCN 2013) and can take the form of several management strategies, including reintroduction, reinforcement, assisted colonization, and mitigation-driven translocation (Seddon 2010; Germano et al. 2015). Accounting for project-specific complexities (e.g., species' ecology, funding, local perception; Berger-Tal et al. 2019) can increase the probability of translocation success.

The definition of translocation success is nuanced and dependent on specific project objectives (Ewen et al. 2014; Wren et al. 2023). However, success is often contingent on sufficiently high posttranslocation survival, reproduction, population growth, and site fidelity to result in a viable population (Miller et al. 2014; Resende et al. 2021). Monitoring of translocated individuals is crucial in understanding the long-term successes of translocation programs (Ewen et al. 2014). Upon review of the Global Re-introduction Perspectives Series (e.g., Soorae 2018), one of the most highly reported difficulties in translocation success had to do with animal behavior (Berger-Tal et al. 2019) and more specifically, dispersal and movement. Immediate long-term dispersal by translocated individuals, resulting in low site fidelity, is a critical challenge for establishing or augmenting populations. For example, the success of Mojave Desert Tortoise (*Gopherus agassizii*) translocation was negatively affected by homing behavior (returning to a location of origin; Hinderle et al. 2015; Berger-Tal et al. 2019). Behavioral responses of translocatees to novel environments may be initially detrimental to translocation goals but may change over time as individuals behaviorally adapt to the novel environment—a process called "post release behavioral modification" (Berger-Tal and Saltz 2014). With the increased prevalence of spatial ecology technology accessible to wildlife managers, movement behavior can be more readily assessed to evaluate translocation success or at least as a prelude to success (Berger-Tal and Saltz 2014).

Translocated turtle and tortoise species can exhibit irregular movement and spatial use patterns upon release (Bauder et al. 2014). For example, translocated Three-Toed Box Turtles (*Terrapene carolina triunguis*) traveled greater overall distances and used larger home range areas than resident turtles (Rittenhouse et al. 2007). Similarly, translocated Gopher Tortoises (*Gopherus polyphemus*) moved greater distances and exhibited larger home ranges than resident conspecifics (Bauder et al. 2014). Additionally, chelonian species have been known to disperse immediately after translocation (Nussear et al. 2012; Attum and Cutshall 2015; Pille et al. 2017). These examples indicate that translocated individuals may exhibit greater movement distances as they familiarize themselves with a novel environment to locate resources (e.g., food and shelter) or return to a place of origin.

To minimize increased movement of translocated individuals, managers often implement "soft-release" (Griffith et al. 1989) procedures such as temporary penning of animals and providing immediate access to food or shelter (Tetzlaff et al. 2019). Soft-release strategies provide animals more time to acclimate to their new environment, and in the case of penning, reduce

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the probability that individuals will disperse offsite after pens are removed (Tuberville et al. 2005; Knox et al. 2017). The reduction of dispersal through penning implies that individuals have interactions with penning structures that limit their outward movement. Although soft-release penning has immediate benefits of increasing site fidelity, it is unclear how this strategy influences space use both during the period of penning and afterward, with possible consequences for both long-term habitat use and population monitoring (Jones et al. 2023).

In the United States, Gopher Tortoises are frequently translocated as a mitigation technique because their upland habitats, where they serve as keystone species because of their ecologically important burrows, are prime locations for development, and *Gopherus* spp. tortoises can survive the initial stresses of translocation (Tuberville et al. 2005; Field et al. 2007; Drake et al. 2012; Bauder et al. 2014). However, without soft release, translocated tortoises will attempt to disperse back to their site of origin (Hinderle et al. 2015). Penning (soft release) translocated Gopher Tortoises can significantly increase site fidelity even after soft-release pens are removed; however, the length of time tortoises are penned is a factor (Tuberville et al. 2005). In one study, 77% of hard-released Gopher Tortoises dispersed more than 1 km from the core release area, whereas only 8.3% of soft releases did so after 12 mo of temporary enclosure (Tuberville et al. 2005).

Despite knowing that penning tortoises can improve site fidelity, the movement behavior of translocated Gopher Tortoises within pens is relatively unstudied. This is a concern given the large scale of pens now used in Florida recipient sites (e.g., 7–134 ha in Loope et al. 2024) compared with those used in previous movement studies (Tuberville et al. 2005; Bauder et al. 2014). Studies with Mojave Desert Tortoises have revealed greater movement velocity and carapace temperatures when tortoises are near linear structures such as fences and roads (Peaden et al. 2017), and persistent movement and pacing behaviors along barriers and fences (Peaden et al. 2017; Ruby et al. 2023a, b). Understanding the space use and movement behaviors of tortoises in pens is important because the spatial arrangement of translocated Gopher Tortoises can affect the strategies being used to accurately estimate population density to measure success of translocations (Jones et al. 2023). If tortoises maintain high spatial clustering even after pens are removed, local densities experienced by individuals could be higher than they would be otherwise, which could have broad implications for population health, such as disease transfer, and individual survival (Aiello et al. 2014; Cozad et al. 2020). Thus, understanding the spatial ecology of translocated populations of Gopher Tortoises including during the penning phase is important for improving the chances that translocations result in self-sustaining populations.

We investigated a translocation site in northwest Florida, USA that received Gopher Tortoises into soft-release enclosures between 2015 and 2021. We predicted that tortoises would use areas close to pen edges disproportionately compared with the available area, and these spatial patterns would persist short term even after pens had been removed. We used several methods to investigate the space use of translocated Gopher Tortoises, including camera trap arrays, burrow distribution surveys, and global positioning system (GPS) telemetry.

Materials and Methods

Study Site

The study site, Eglin Air Force Base (EAFB), is in the Gulf Coastal Plain of the Florida Panhandle and is the largest US military installation in the Air Force, spanning an area of 186,350 ha (Hudak et al. 2016; Baldwin et al. 2023). The climate is subtropical, exhibiting a mean annual temperature and precipitation of 19.8°C and 158 cm, respectively (Hudak et al. 2016). Much of EAFB is upland sandhill habitat, dominated by pine savanna that is managed by thinning and prescribed burning. Native populations of Gopher Tortoises in this region are historically depleted because of harvesting by humans for food (Auffenberg and Franz 1982) and are predicted to experience continued declines and possible local extinction owed to excessively low densities (Chandler et al. 2020; Folt et al. 2021). Under the Florida Fish and Wildlife Conservation Commission (FFWCC) permits, over 10,000 tortoises have been translocated onto EAFB into areas of existing habitat of Gopher Tortoises since 2015. Although there are resident Gopher Tortoises in Eglin, to our knowledge, none of the sites in our study had any native individuals.

Multiple soft-release pens were constructed at EAFB beginning in 2015, all of which varied in shape and size. Pens were often constructed to fit a specific number of tortoises expected to be translocated at a given time, whereas the shape of construction often followed easy-access areas such as roads and was also influenced by available habitat (e.g., excluding wetlands and heavily forested areas), resulting in irregularly sized and shaped pens, which is common practice in Florida recipient sites (see Supplemental Figs. S1–S5, available online). We investigated 10 of these pens (Table 1), which we have named Pen-X, where X represents a unique pen number (e.g., Pen-1, Pen-2, . . . , Pen-10). Each pen had received translocated Gopher Tortoises, which included translocations from sites within EAFB (Eglin relocations) or from multiple sites throughout Florida (off-site translocations; Table 1). Pens were constructed using 3-mm-thick silt fence that stood at approximately 1 m tall, with 20–25 cm buried to prevent tortoises digging underneath the fence and secured to oak fence stakes. The silt fences were regularly maintained to prevent tortoises from escaping, though if any escapes occurred, no tortoises were subsequently found outside of the pens and later returned. Pens were prepared for tortoise translocations by digging starter burrows to improve settlement rates. Starter burrows were dug at least 1 m from silt fences, with entrances angled toward the interior of the pen following permitting guidelines (approximately 2-ft depth at 30–45° angle to the ground; FFWCC 2023). Starter burrows lack the characteristic “apron” found outside of natural burrows of Gopher Tortoises and are considerably shorter; they need to be modified by the translocated Gopher Tortoises to be utilized. Initially, we attempted to dig as many burrows as the number of translocated tortoises in each pen and most of these were near pen edges where newly translocated tortoises tended to cluster. Over time, we began digging more burrows within the interior of pens to encourage interior use, and additionally placed pine

TABLE 1.—Information for each soft-release pen investigated at Eglin Air Force Base, including pen identification (ID), pen size, placement dates, and density for translocated Gopher Tortoises (GT; *Gopherus polyphemus*) within each pen, pen removal date, and original burrow distribution survey dates. Density estimates are for the pen enclosure; available surrounding habitat reduces site density below these values after fence removal. Pen stocking levels were higher than densities of natural sandhill populations (Auffenberg and Franz 1982; Guyer et al. 2012), with the expectation that tortoises would disperse to a more natural density after pen removal.

Pen ID	Size of pen (ha)	Initial GT placed	Last GT placed	Pen removed	Minimum penning duration (mo)	Burrow distribution survey	GT densities (Adults/ha)
Pen-1†	20	April 2018	July 2019	January 2020	7	January 2020	13.9
Pen-2‡	4	April 2015	October 2016	January 2019	15	March 2019	8.3
Pen-3‡	5	April 2019	March 2020	April 2021	13	April 2021	11.1
Pen-4‡	7	April 2017	April 2019	December 2019	7	January 2020	19.4
Pen-5‡	9	July 2020	October 2022	December 2022	2	January 2023	7.1
Pen-6†	31	October 2017	February 2019	February 2020	12	February 2020	17.3
Pen-7†	41	October 2016	September 2017	February 2019	17	March 2019	7.2
Pen-8†‡	24	June 2019	April 2020	Jan 2021	9	March 2021	12.5
Pen-9^†	33	June 2020	April 2021	Feb 2022	10	January 2022	7.0
Pen-10^†	24	February 2021	May 2021	Feb 2022	9	January 2022	10.7

^ Pen fence removed manually; surveys not completed postburn, and therefore pens were still present.

† Off-site tortoise translocations. Tortoises were translocated from sites in Florida outside of Eglin Air Force Base.

‡ Eglin tortoise relocations. Tortoises were translocated from other locations within Eglin Air Force Base.

needle bales perpendicular to silt fences to direct movement away from pen edges (Ruby et al. 2023b); however, we found that tortoises started burrowing underneath bales, and the bales degraded quickly, ultimately reducing their effectiveness at influencing tortoise movement and their use was discontinued.

Burrow Distribution Surveys

We performed burrow distribution surveys across most of the soft-release pens between late January and early March, after silt fences had been removed via winter prescribed burns. We conducted pen surveys before a burn in two of the pens (Pen-9 and Pen-10) because fences were manually removed. Vegetation obstruction can substantially affect an observer's ability to detect burrows of Gopher Tortoises (Howze and Smith 2019); thus, performing surveys after burns is likely to increase overall detection probability. We surveyed pens systematically, ensuring full coverage of pen area, and applied the same approach to a 100-m buffer around each pen. We recorded the location of each burrow using a handheld GPS, and since Gopher Tortoises are known to use multiple burrows over time (FFWCC 2012), we assigned an activity status of either active (evidence of recent tortoise activity, such as footprints or feces), inactive (intact but lacking evidence of recent activity), or abandoned (no longer comprised of a functioning tunnel with tortoise-shaped entrance) to each detected burrow following FFWCC permitting guidelines (FFWCC 2012). For six of the soft-release pens (Pen-1, Pen-2, Pen-4, Pen-6, Pen-7, and Pen-8) we performed a follow-up survey using the same methodology after a prescribed burn 882, 930, 754, 752, 861, and 724 d after pen removal, respectively. These follow-up surveys were part of routine monitoring of translocated tortoises at our site, providing data on distribution, density, and survival.

We wanted to determine whether active burrows were significantly closer to pen edges than random. For each of the 10 survey data sets, we generated several randomly distributed points within the surveyed pen and surrounding 100-m buffer that were equal to the number of active burrows. We calculated the distance of each point to the perimeter of the pen for both observed (detected active burrows) and random burrows (randomly distributed points within the pen and buffer) and then conducted a Wilcoxon rank sum test for both original and follow-up surveys, where distance could indicate burrows within the pen boundary or the surrounding 100-m buffer. We further performed a chi-squared test to compare the proportion of burrows that were within 20 m of the pen edge and those >20 m away for each sample (for both original and follow-up surveys). We decided to perform these two tests since there may only be a pen edge effect within the immediate vicinity (i.e., 20 m) of the pen edge. We chose 20 m to assess the edge effect because this is a short enough distance that burrow site selection of Gopher Tortoises could have been influenced by the fence during the period when the fence was present (it should be noted that fences had already been removed either by hand or during prescribed burns shortly before surveys; Table 1). Additionally, the process of installing fences can disturb relatively large areas (~5 m), and using this distance can also account for GPS error. Therefore, a 20-m edge provides a generous area adjacent to fences that accounts for tortoise movement behavior, but also any error within our data collection.

Tortoise Activity and Movement

Since Gopher Tortoises spend most of their time in and around their burrows (Alexy et al. 2003; Eubanks et al. 2003), mapping and enumerating burrows (as above) is an important tool for understanding their space use and postrelease behavior. However, where individual tortoises dig burrows may not be indicative of where they forage, interact, and mate, among other behaviors. Thus, we used two additional methods to collect evidence of increased tortoise activity and movement near pen edges: time-lapse cameras and GPS loggers.

Time-lapse cameras.—We deployed 14 and 11 time-lapse cameras along the fence lines of Pen-6 and Pen-7 respectively on 23 February 2018, with a minimum distance between cameras of 170 m. We also placed four cameras within the interior area of Pen-6 and Pen-7, attempting to position each interior camera as far away from the fence edge as possible given the pen shape. We therefore spaced interior cameras approximately 200 m from one another at

Pen-7, and between 100 and 200 m for Pen-6. Fences in both pens remained intact throughout the duration of time-lapse camera deployment.

We secured cameras to U-posts approximately 1 m above the ground, and we set each post along the fence at an angle 10° from perpendicular with the ground to maximize coverage of pen edges. We positioned the interior cameras similarly in open areas to maximize potential detection of Gopher Tortoises. We programmed each camera to take a picture every minute from 0500 h to 2100 h. We removed all cameras by 16 February 2019 (358 d of deployment) and 1 December 2018 (281 d of deployment) for Pen-6 and Pen-7 respectively (we removed cameras earlier in Pen-7 in expectation of a winter prescribed burn).

For each of the two pens, we calculated the number of images with Gopher Tortoises taken by each camera and then conducted a Wilcoxon rank sum test on the camera photo counts of tortoises to determine if the distributions of tortoise photos per camera were different between cameras on the edge and the interior.

GPS loggers.—We epoxied GPS loggers (Advanced Telemetry Systems W519-AA GPS logger) with very-high-frequency transmitters (Advanced Telemetry Systems R2220) to one female and six male adult tortoises that were translocated from outside of EAFB. We ensured that the total attached equipment weighed <5% of the body mass of each tortoise. We tracked tortoises in Pen-9 ($n = 1$ tortoise), Pen-10 ($n = 2$), Pen-11 ($n = 2$), and Pen-12 ($n = 2$). We attached transmitters and then immediately placed individuals within soft-release pens once the epoxy had hardened. Each GPS logger recorded a location, or fix, twice per day at 1000 h and 1400 h Central Time, which we downloaded every 2 mo. We tracked tortoises between May 2021 and July 2022 for an average of 264.4 d (range 192–373 d) and we only included data for tortoises tracked while fences were still up. We truncated the final downloaded GPS data by removing any fixes where the horizontal dilution of precision (HDOP) value was >1.5 (19.01% percent of points) to remove highly inaccurate fixes (Lewis et al. 2007; Recio et al. 2011). Our selection of a 1.5 HDOP threshold was based on the distribution of final HDOP values and provided a relatively conservative removal of possible inaccurate locations.

We created random movement paths for comparison with the observed movements of telemetered individuals to test if there was a difference in the proportion of locations within 20 m of the pen edge. We calculated the step length and turning angles on the basis of the GPS fixes from each telemetered animal using the bayesmove v0.2.1 package (Cullen and Valle 2021). We randomized each set of step length and turning angle 1,000 times, maintaining the pairing of each as calculated from the original fixes (i.e., as observed during actual tortoise movement). Thus, we created 1,000 random movement data sets matching the number of fixes, step lengths, and turning angles exhibited by the actual individual (Fig. 1). We limited the random movements within the boundary of the soft-release enclosure, redrawing step lengths and turning angles if a movement would have placed the animal outside of the pen (Fig. 1).

We calculated the proportion of time steps that were within 20 m of the pen edge for the observed movements and for each random-movement data set. We further determined if the proportions from our observed sample were significantly greater than the distribution of simulated proportions by calculating the one-sided *P*-value as the fraction of the simulated values greater than the observed value.

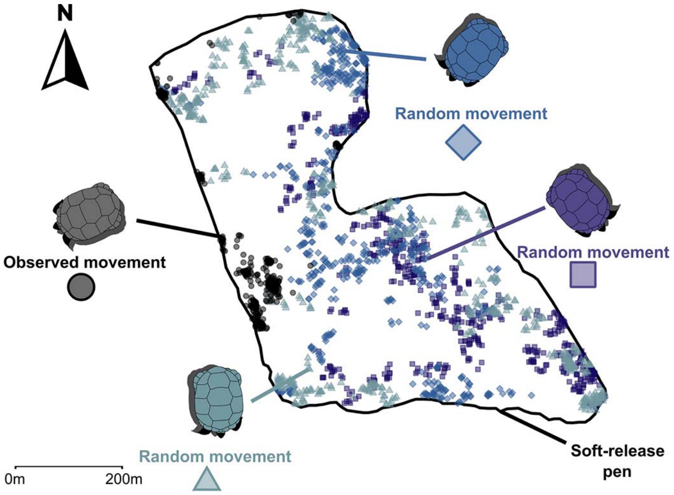

FIG. 1.—An example of the simulated movement derived from the step length and turning angles observed from global positioning system-tracked Gopher Tortoises (*Gopherus polyphemus*) at Eglin Air Force Base, Florida, USA. Circles show the observed movements from a tracked individual; the other shaped points (squares, diamonds, and triangles) delineate the simulated movement from three random permutations. The soft-release pen boundary is depicted by the solid black line. Increased opacity of points represents where more points overlap one another. A color version of this figure is available online.

RESULTS

Burrow Distribution Surveys

We found that an average of 31.8% (range 22.1–46.1%) of all active tortoise burrows were within 20 m of a pen edge (Table 2; Fig. 2). Because of the varying size and shape of each soft-release pen, the percentage of pen area that was within 20 m of the boundary was between 12.6 and 39.1% (Table 2). In the five pens where we performed a follow-up survey (Pens-1, 2, 4, 6–8), we observed an average of 20.9% (range 12.7–27.3%) of all active burrows within 20 m of a pen edge (Table 2; Fig. 3).

We generally recorded more burrows closer to the pen edge for our observed burrows than our randomly distributed points in the initial surveys of 10 pens (Fig. 2). On the basis of our Wilcoxon rank sum test, burrows were significantly closer to pen edges than expected by chance for 7 of the 10 pens (Pens-1, 4, 6–10; Table 2). In addition, on the basis of our chi-squared test, burrows were more often within 20 m of a pen edge compared with >20 m away in 4 of the 10 pens (Pens-1, 6, 8, 9). There appears to be an association between the source of relocated animals and edge clustering: all five of our off-site relocation pens had significant clustering, whereas only two of our five on-site relocation pens had significant clustering. However, the three pens without evidence of clustering (Pens-2, 3, 5) also tended to have smaller areas and lower stocking densities (Table 1). Although these patterns are suggestive, determining which (if any) of these features influence clustering may benefit from more data.

TABLE 2.—Summary of burrow distribution surveys of Gopher Tortoises (*Gopherus polyphemus*) from the original and follow-up survey at Eglin Air Force Base, Florida, USA between March 2019 and January 2022. Values represent the number of active burrows detected within 20 m of a pen boundary (fence) during a survey. The fourth column shows the percentage of the overall pen area within 20 m of the pen edge. NA indicates pens scheduled for a follow-up burrow distribution survey. Bold text highlights significant results.

Pen ID	Percentage of active edge burrows (original survey)	Percentage of active edge burrows (follow-up survey)	Percentage of pen area	Wilcoxon rank sum test (*P*)	Chi-squared test (*P*)
Pen-1	39.3	18.3	17.7	**<0.0001**	**<0.0001**
Pen-2	30.8	27.3	39.1	0.47	0.63
Pen-3	33.9	NA	32.4	0.87	1
Pen-4	46.1	26.7	34.9	**0.01**	0.13
Pen-5	31.3	NA	25.9	0.35	0.32
Pen-6	31.8	19	18.8	**<0.001**	**0.04**
Pen-7	22.1	21.3	12.6	**0.001**	0.13
Pen-8	28.5	12.7	16.7	**<0.0001**	**<0.001**
Pen-9	29.9	NA	19.5	**<0.001**	**<0.001**
Pen-10	24	NA	19.6	**0.004**	0.07

We conducted follow-up surveys on six pens (Fig. 3). In five of the pens, we detected no evidence that detected burrows were closer to pen edges than our randomly distributed samples on the basis of Wilcoxon rank sum tests and the proportion of burrows <20 m from an edge in our chi-squared tests (Pen-1, $P_{\mathrm{cs}} = 0.44$, $P_{\mathrm{wt}} = 0.77$; Pen-2, $P_{\mathrm{cs}} = 0.7$, $P_{\mathrm{wt}} = 0.32$; Pen-4, $P_{\mathrm{cs}} = 0.32$, $P_{\mathrm{wt}} = 0.64$; Pen-6, $P_{\mathrm{cs}} = 1$, $P_{\mathrm{wt}} = 0.64$; Pen-8, $P_{\mathrm{cs}} = 0.41$, $P_{\mathrm{wt}} = 0.21$ [CS = chi squared; WT = Wilcoxon rank sum test]). However, in one pen the Wilcoxon rank sum test indicated that burrows were closer to pen edges, although the proportion of burrows <20 m and >20 m from an edge in our chi-squared tests were not different (Pen-7, $P_{\mathrm{cs}} = 0.32$, $P_{\mathrm{wt}} = 0.04$).

Time-Lapse Cameras

In Pen-6, all 14 of the pen-edge cameras captured images of Gopher Tortoises, resulting in 91,561 images (Fig. 4) and a mean of 6,540 images per camera (range 290–27,956 images). In the same pen, only two of the four interior cameras captured

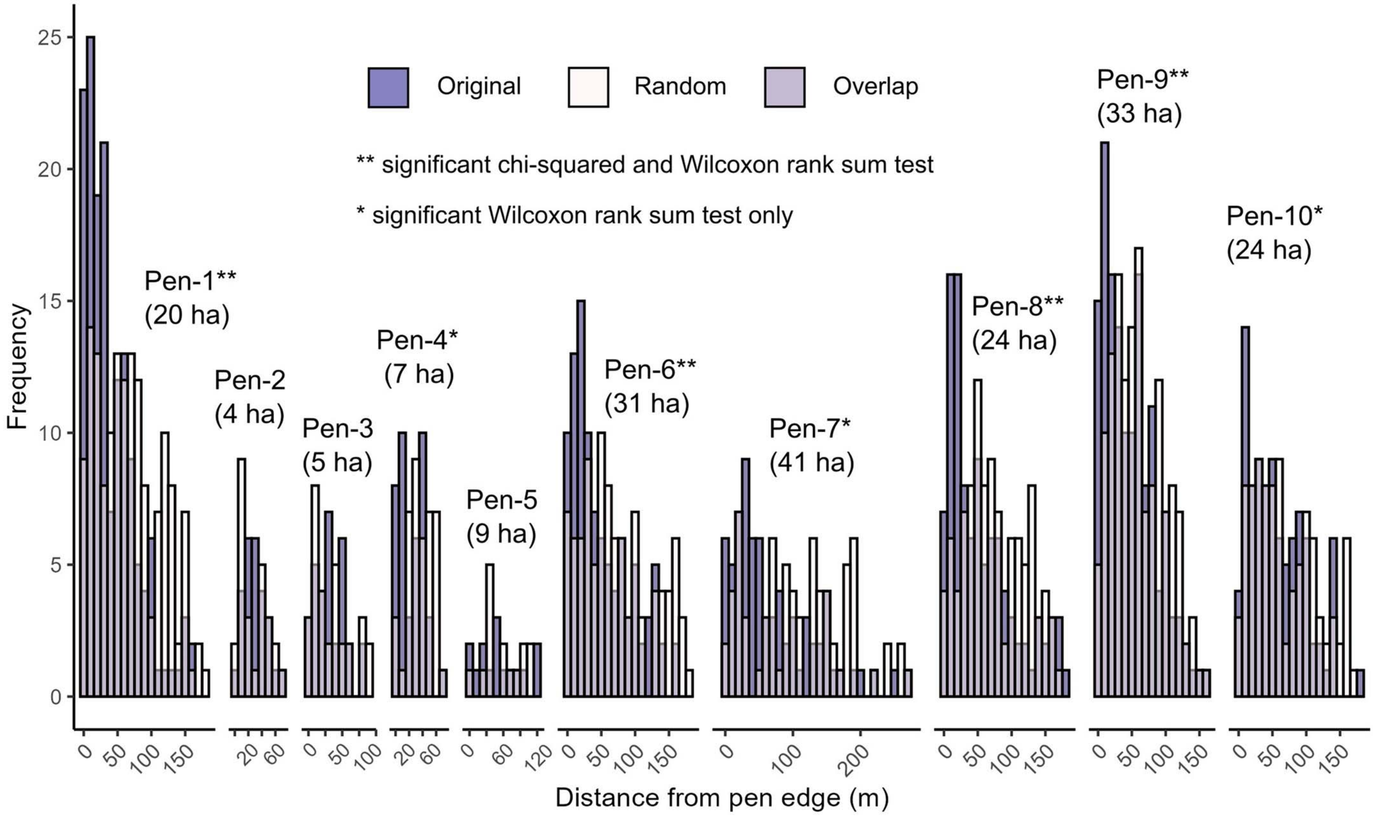

FIG. 2.—Frequency of active burrows of Gopher Tortoises (*Gopherus polyphemus*) located within an increasing distance from pen edge for active burrows found in the original survey: Original (dark purple) and a randomly distributed sample of points: Random (white), at Eglin Air Force Base, Florida, USA, between March 2019 and January 2022. Distance from pen edge can either be toward the interior or exterior of pens. Text above each histogram highlights the pen identification and size. Single and double asterisks depict that a significant relationship was detected in a chi-squared test or a chi-squared and Wilcoxon rank sum test respectively. Light purple bars represent overlapping results for observed active burrows in the original surveys and randomly distributed points. A color version of this figure is available online.

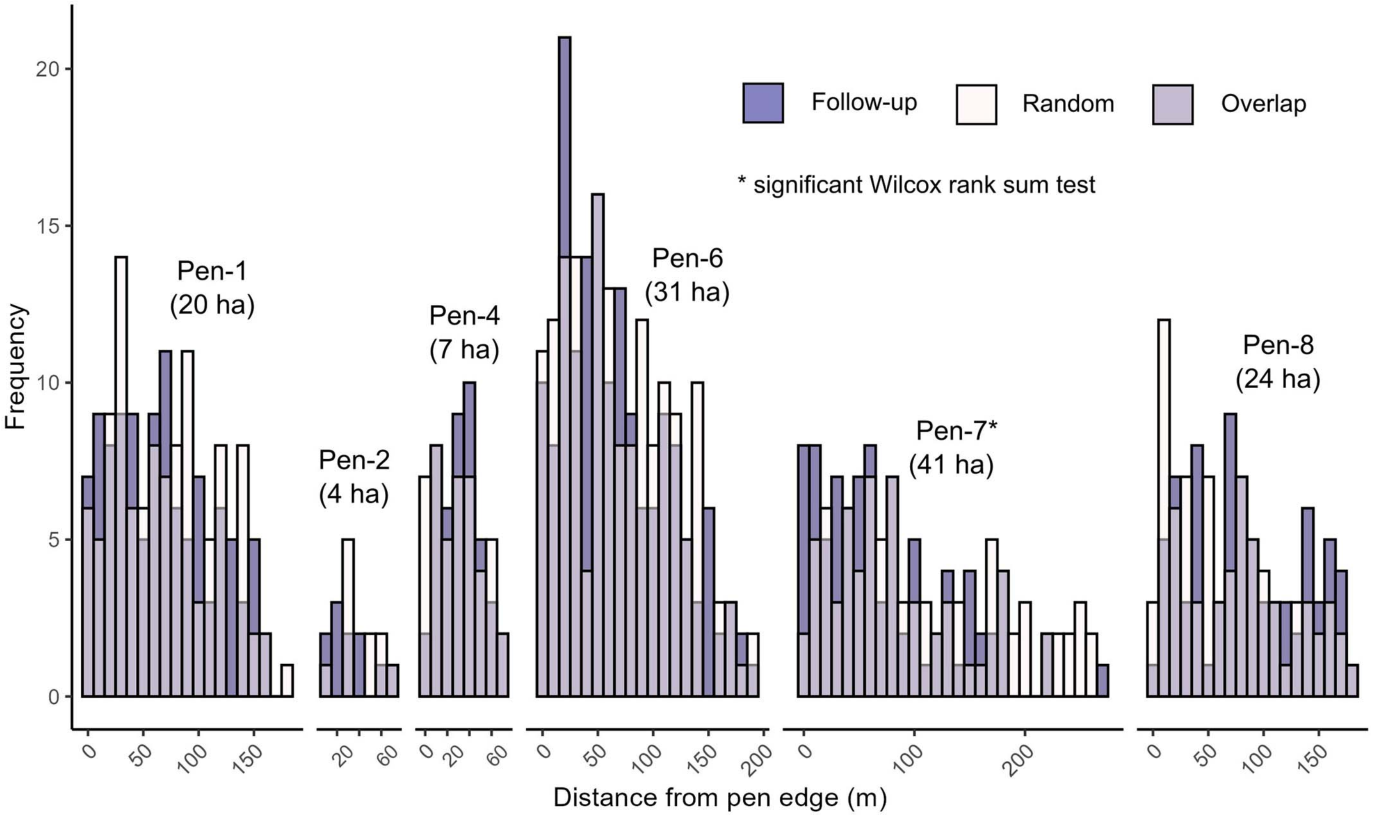

FIG. 3.—Number of active burrows of Gopher Tortoises (*Gopherus polyphemus*) located within an increasing distance from pen edge for active burrows found in the follow-up burrow distribution survey: Follow-up (dark blue) and a randomly distributed sample of points: Random (white), at Eglin Air Force Base, Florida, USA, between March 2019 and January 2022. Text above each histogram highlights the pen number and size. Light purple bars represent overlapping results for observed active burrows in the follow-up surveys and randomly distributed points. A color version of this figure is available online.

images of Gopher Tortoises, with an average of 1 image per camera (range 0–3 images) and a total of 4 images. For Pen-6, the number of images detected on edge cameras was significantly different from interior cameras ($W = 44$, $P = 0.005$). For Pen-7, all 11 pen-edge cameras captured images of Gopher Tortoises, with a mean of 623 images per camera (range 24–3,553 images) and a total of 6,855 images (Fig. 4), and three of the four interior cameras captured images of Gopher Tortoises, averaging 2 images per camera (range 0–3 images), with a total of 8 images. In Pen-7, the number of images detected on pen-edge cameras was significantly different from interior cameras ($W = 56$, $P = 0.003$). Combining data from Pen-6 and Pen-7, a total of 98,445 tortoise images were captured, 99.97% (98,416) of which occurred at pen-edge cameras and only 0.03% (29) at interior cameras.

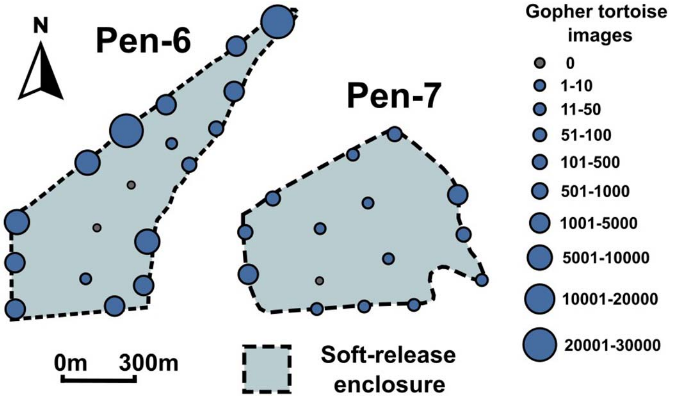

FIG. 4.—Total number of time-lapse camera images of Gopher Tortoises (*Gopherus polyphemus*) for Pens-6 and 7, captured at Eglin Air Force Base, Florida, USA. The number of images for Pen-6 represents camera deployment between 23 February 2018 and 16 February 2019. The number of images for Pen-7 represents camera deployment between 23 February and 1 December 2018. Circles represent the locations of time-lapse cameras and the size of the circle depicts the number of images of Gopher Tortoises captured. Scale bar represents the size of pens and not the distance between them. A color version of this figure is available online.

Our fence cameras caught multiple instances of Gopher Tortoises walking along pen edges (Fig. 5A) and mating behavior at edge burrows (Fig. 5B). A separate camera used to specifically observe a tortoise burrow on the pen edge (not used for photo count analysis above) detected multiple tortoises using this single burrow (Fig. 5C).

Telemetry

The proportion of fixes that were within 20 m of a pen edge for the observed GPS data was significantly greater than the proportion calculated from random movements in three tracked individuals (Fig. 6; Tortoise #3, $P \leq 0.01$; Tortoise #5, $P = 0.04$; Tortoise #6, $P \leq 0.01$). The proportions from the remaining four individuals were not significantly greater than randomly generated movements (Fig 6; Tortoise #1, $P = 1$; Tortoise #2, $P = 0.99$; Tortoise #4, $P = 0.05$; Tortoise #7, $P = 0.69$).

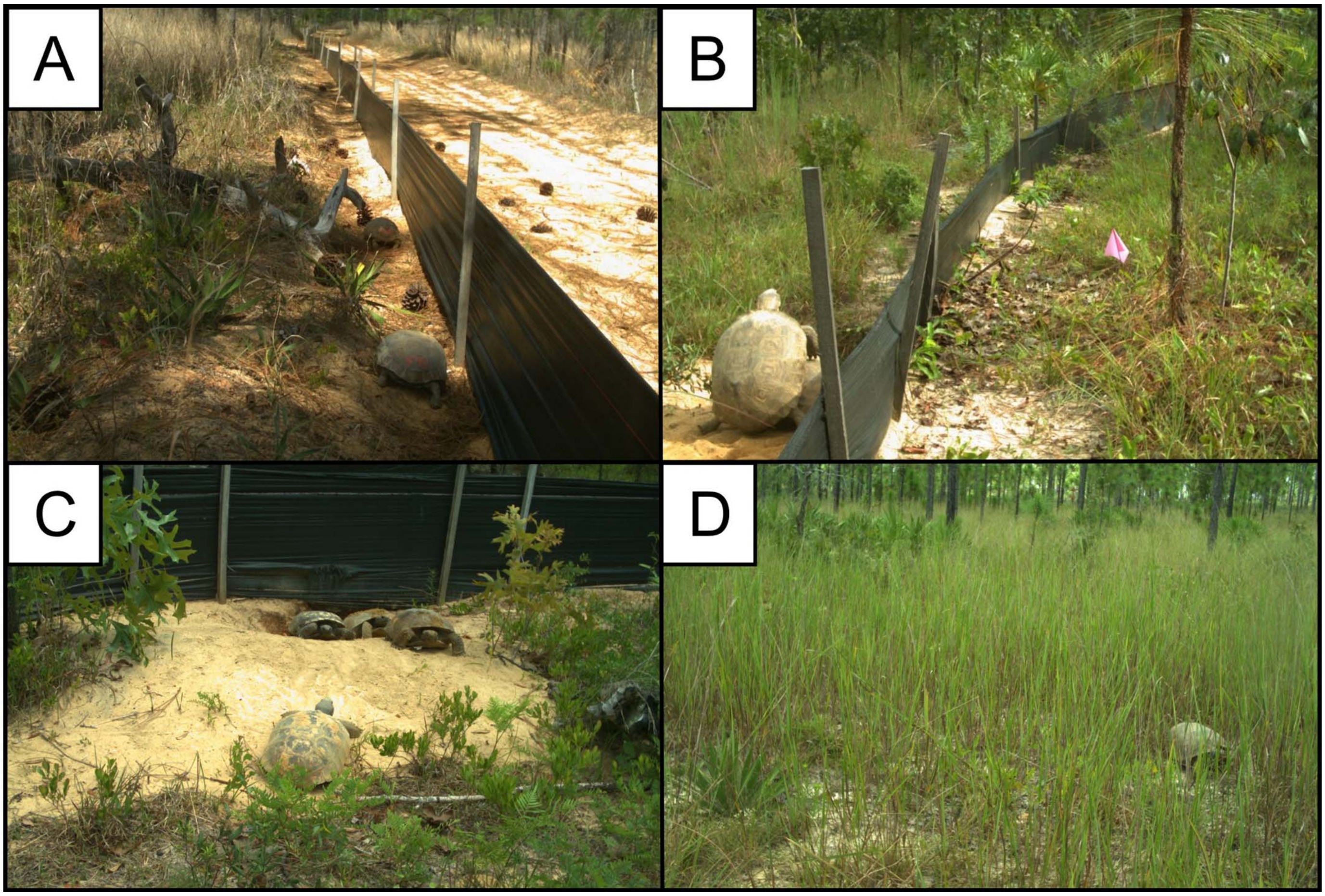

FIG. 5.—Time-lapse camera images of Gopher Tortoises (*Gopherus polyphemus*) captured at Eglin Air Force Base, Florida, USA between 23 February 2018 and 16 February 2019. (A) Two Gopher Tortoises active, walking along the pen perimeter. (B) Mating behavior exhibited by a pair of Gopher Tortoises outside a burrow dug on fence line. (C) Multiple Gopher Tortoises using a single burrow (using a camera positioned to specifically monitor the burrow) dug directly on the fence line. (D) A tortoise detected on an interior camera. A color version of this figure is available online.

DISCUSSION

Using multiple lines of evidence, we demonstrated that penning as a soft-release strategy for Gopher Tortoises sometimes resulted in clustering near pen edges, and the percentage of active burrows near pen edges sometimes remained relatively high (though often nonsignificant) after pen removal. Camera trapping efforts in two soft-release enclosures, soon after tortoises were placed in the pens, revealed high activity of tortoises around pen perimeters. Nearly all images captured occurred at cameras along fences (99.97%), as compared with only a few images captured at interior cameras (0.03%; Fig. 4). The images themselves reveal high rates of perimeter walking (or "pen-pacing" [Cozad et al. 2020]; also observed in Desert Tortoises [Brand et al. 2016]) by multiple individuals, but also that the silt fences and associated buildup of sandy areas with limited canopy cover may provide ideal locations for burrows and natural behaviors (Figs. 4, 5; Jones and Dorr 2004). There is higher visibility at the pen edges because of the installation of silt fences (less vegetation obstruction), which may bias detection in image processing; however, it is unlikely that such a substantial number of interior tortoises were missed because of observer error, and so this potential bias does not discount our inference of greater pen-edge use by tortoises. Additionally, our telemetry data showed that three of seven individuals exhibited a significantly greater proportion of time steps within 20 m of a pen edge than randomly generated data sets. This suggests that some tortoises exhibit a propensity for the pen edge, but this was not the case for all translocated individuals.

Initial burrow distribution surveys demonstrated a high proportion of active burrows within 20 m of a pen edge (mean 31.8%, range 24–46.1%, $n = 10$; Table 2). On follow-up surveys, the bias toward the pen edge was reduced in general, either due to greater interior area use or dispersal from the pen area (mean 20.9%, range 12.7–27.3%, $n = 6$; Table 2; Fig. 3). Our initial surveys showed that detected active burrows were significantly closer to pen edges than randomly generated locations for 7 of 10 pens. In addition, for 5 of 10 pens, there was a significantly greater proportion of observed active edge burrows (20 m from edge) than random. We dug starter burrows, which is a common practice in translocation of Gopher Tortoises (e.g., Tuberville et al. 2005; Bauder et al. 2014), that were at least 1 m from pen edges, and although we do not know the proportional use of these starter burrows by translocated tortoises (proportional to digging unique burrows away from starter burrows), their presence could be positively affecting the detection of edge burrows because of their use by translocated individuals.

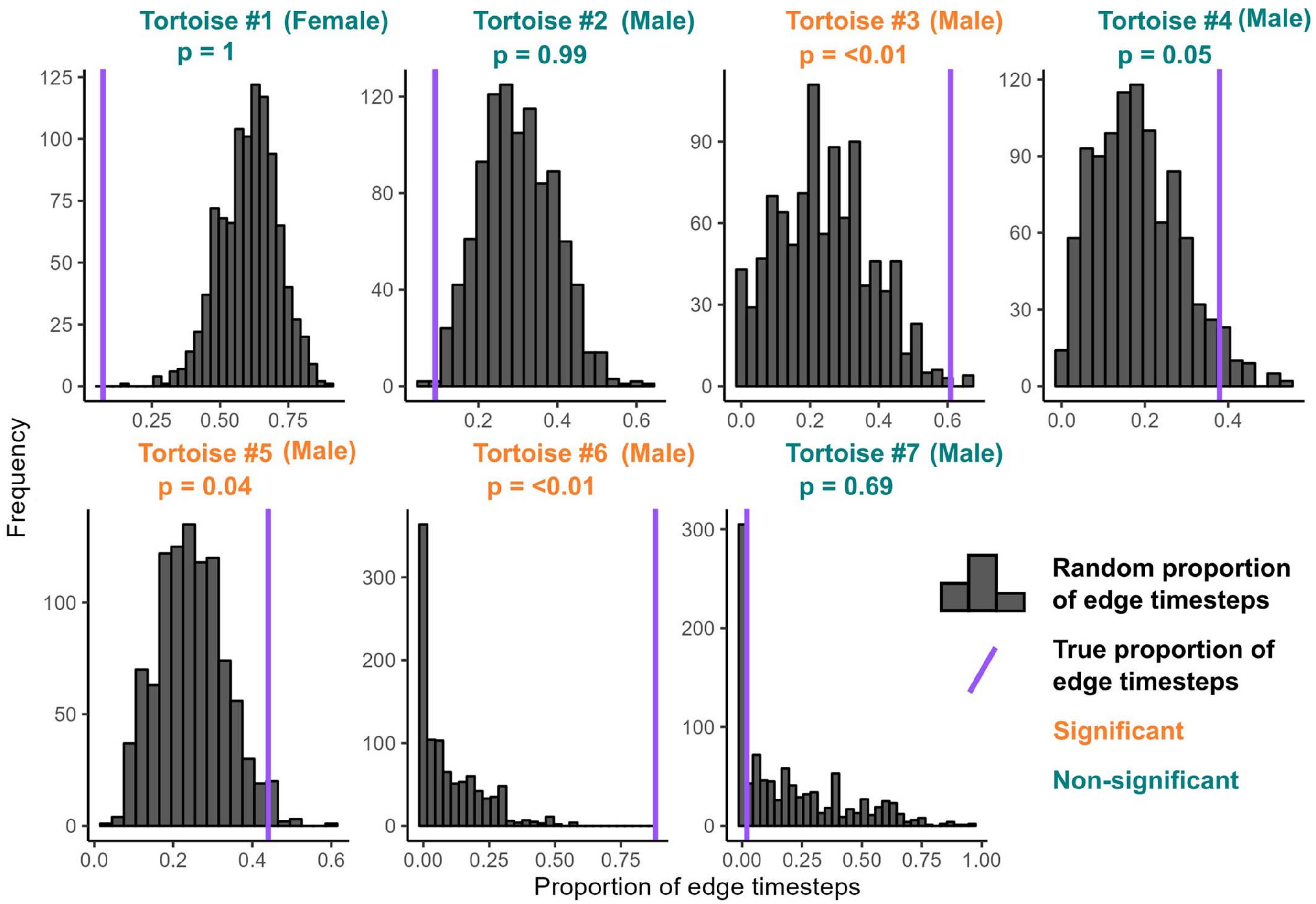

FIG. 6.—Gray histograms show the distributions of the proportion of simulated time steps that were within 20 m of a pen edge from each of our randomly simulated samples ($n = 1{,}000$) for each of seven global positioning system (GPS)-tracked Gopher Tortoises (*Gopherus polyphemus*) at Eglin Air Force Base, USA, between 14 May 2021 and 28 July 2022. The purple vertical line represents the observed proportion of GPS fixes that were within 20 m of a pen edge from our telemetered tortoise. Each histogram is displayed on uniquely scaled axes and should be interpreted individually. A color version of this figure is available online.

Quinn et al. (2018) tracked 41 head-started juvenile Gopher Tortoises across two release sites and reported that only one individual that survived after the annual study period remained within a starter burrow modified by the tracked tortoise, suggesting a propensity for individuals to dig their own burrows. However, we attempted to control for the presence of starter burrows by only using active burrows in our analyses, reducing the inclusion of previously modified and subsequently abandoned starter burrows dug near pen edges. Because unused starter burrows look vastly different from burrows modified by Gopher Tortoises (lack of an apron, shape difference of burrow entrance, only 2 ft in length), any unused starter burrows were not recorded during burrow surveys. Additionally, we conducted initial burrow distribution surveys at least 1 yr after (typically several years after; Table 1) digging starter burrows, which would have given translocated tortoises ample opportunity to construct new burrows at preferred locations. The aggregation of results from time-lapse cameras, GPS telemetry, and burrow distribution surveys suggests that translocated Gopher Tortoises exhibited aggregated space use near pen edges, resulting in a clustering effect that appeared to be transient for all but one of the pens with follow-up surveys.

The clustering of burrows can violate the spatial assumptions of line transect distance sampling (Buckland et al. 2001), which is a practical and accurate survey tool for populations of Gopher Tortoises (Smith et al. 2009; Stober and Smith 2010; Castellón et al. 2015). The issues of clustering arise because of the variable encounter rates of individuals along linear landscape features (in this case, pen fences), causing a density gradient across the sampling frame (Thomas et al. 2010; Marques et al. 2012). Specifically, if these clusters are not accounted for when delineating transect lines, gross over- or underestimation of density estimates may occur (Jones et al. 2023). We therefore suggest that postrelease monitoring of individuals take considerable care when evaluating the movement behavior and spatial arrangement of burrows at recipient sites. An evaluation of pen edge clustering by managers of recipient sites of Gopher Tortoises may help with designing future monitoring surveys (Jones et al. 2023). In addition to the implications that clustering can have on monitoring approaches for translocated Gopher Tortoises, it can also affect the biology and fitness of populations. Specifically, high local density may facilitate disease transmission (Aiello et al. 2014) and has been linked to higher rates of mortality in translocated populations that likely experience disease (Cozad et al. 2020; Loope et al. 2024), but it may also cause social stress (Texeira et al. 2007) and increase intraspecific competition (Rodríguez-Caro et al. 2016).

In recent years, there has been a distinct recognition surrounding the ecological importance of fences, particularly regarding the impact and response of wildlife to these structures (Jakes et al. 2018; McInturff et al. 2020; Wilkinson et al. 2021). Despite the widespread prevalence of fences across multiple ecological contexts, there remains a paucity in studies focusing on fences when compared with other ubiquitous infrastructure such as roads and railway networks (Jakes et al. 2018). It is particularly easy for temporary fencing structures to be overlooked within the broader fence ecology literature. In the soft-release process of Gopher Tortoises in Florida, silt fences are typically maintained for at least 6 mo, with shorter periods likely undermining their importance and thus affecting translocated animals or other species using that landscape. For example, there appears to be some impact from temporary fences on populations of Gopher Frogs (*Lithobates capito*), and creative solutions to provide crossing locations via bespoke wooden ramps is currently being investigated (V.H. Porter, personal observation). Furthermore, it has only recently become regular practice to include the locations of pen edges within the submitted material during the Florida permitting process (FFWCC 2023). We suggest that future fence ecology frameworks consider the prevalence of temporary soft-release fencing, and that this adds another layer of complexity to the dynamic nature of fences already discussed in McInturff et al. (2020). We demonstrate that spatial clustering can result from the presence of pen edges, including unique behavioral responses such as pen pacing (anecdotally reported in Brand et al. 2016, Desert Tortoises and Cozad et al. 2020, Gopher Tortoises), and that this could be the case for animals within other fenced environments.

Given our mixed results, further evidence is needed to demonstrate the propensity for Gopher Tortoises to cluster at pen edges, as well as the legacy of such clustering for populations, and future studies could adopt our methodology at a larger scale to assess tortoise space use across multiple pens, or even translocation sites. Our results demonstrate that aggregated space use can occur because of soft-release strategies, but there is variability among individuals, and may be further affected by penning duration and pen characteristics (e.g., stocking density, pen shape, pen size, etc.). Future work could increase the frequency of follow-up surveys to once or twice a year to evaluate a time-since-release effect as demonstrated in other studies (McKee et al. 2021). An evaluation of aggregated tortoises near pen fences by managers of recipient sites of Gopher Tortoises may also help with designing future monitoring surveys. Although clustering and associated density gradients can be controlled for by appropriate design for monitoring efforts (Thomas et al. 2010; Marques et al. 2012; Jones et al. 2023), the potentially negative impact of these clusters on the health of translocatees may drive managers to develop best practices for limiting these clusters (e.g., internal starter burrows, directional fencing, lower stocking density) at translocation sites moving forward.

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SUPPLEMENTAL MATERIAL

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LITERATURE CITED

Aiello, C.M., K.E. Nussear, A.D Walde, T.C. Esque, P.G. Emblidge, P. Sah, S. Bansal, and P.J. Hudson. 2014. Disease dynamics during wildlife translocations: Disruptions to the host population and potential consequences for transmission in desert tortoise contact networks. Animal Conservation 17:27–39.

Alexy, K.J., K.J. Brunjes, J.W. Gassett, and K.V. Miller. 2003. Continuous remote monitoring of gopher tortoise burrow use. Wildlife Society Bulletin 31:1240–1243.

Attum, O., and C.D. Cutshall. 2015. Movement of translocated turtles according to translocation method and habitat structure. Restoration Ecology 23:588–594.

Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). Pp. 95–126 in North American tortoises: Conservation and Ecology, Wildlife Research Report (R.B. Bury, ed.). US Fish and Wildlife Service, USA.

Baldwin, A.J., C.M. Chini, S.J. Schuldt, and J.D. Delorit. 2023. Modeling potential damages of hurricanes at the facility scale: A case study of Eglin Air Force Base. Journal of Infrastructure Systems 29:1–11. DOI: https://doi.org/10.1061/JITSE4.ISENG-2217

Bauder, J.M., C. Castellano, J.B. Jensen, D.J. Stevenson, and C.L. Jenkins. 2014. Comparison of movements, body weight, and habitat selection between translocated and resident gopher tortoises. Journal of Wildlife Management 78:1444–1455.

Berger-Tal, O., and D. Saltz. 2014. Using the movement patterns of reintroduced animals to improve reintroduction success. Current Zoology 60: 515–526.

Berger-Tal, O., D.T. Blumstein, and R.R. Swaisgood. 2019. Conservation translocations: A review of common difficulties and promising directions. Animal Conservation 23:121–131.

Brand, L.A., M.L. Farnsworth, J. Meyers, B.G. Dickson, C. Grouios, A.F. Scheib, and R.D. Scherer. 2016. Mitigation-driven translocation effects on temperature, condition, growth, and mortality of Mojave Desert tortoise (*Gopherus agassizii*) in the face of solar energy development. Biological Conservation 200:104–111.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations, 1st edition. Oxford University Press, UK.

Castellón, T.D., B.B. Rothermel, and S.Z. Nomani. 2015. A comparison of line-transect distance sampling methods for estimating gopher tortoise population densities. Wildlife Society Bulletin 39:804–812.

Chandler, H.C., S.J. Goodman, J.A. Smith, T.A. Gorman, and C.A. Haas. 2020. Understanding occupancy patterns in a low-density gopher tortoise (*Gopherus polyphemus*) population. Herpetological Conservation Biology 15:536–546.

Cozad, R.A., S.M. Hernandez, T.M. Norton, T.D. Tuberville, N.I. Stacy, N.L. Stedman, and M.J. Aresco. 2020. Epidemiological investigation of a mortality event in a translocated gopher tortoise (*Gopherus polyphemus*) populations in northwest Florida. Frontiers in Veterinary Science 7:1–15.

Cullen, J.A., and D.R. Valle. 2021. bayesmove: Non-parametric Bayesian Analysis of Animal Movement, R package Version 0.2.1. Available at https://cran.r-project.org/package=bayesmove. R Foundation for Statistical Computing, Austria. Accessed on 1 January 2024.

Drake, K.K., K.E. Nussear, T.C. Esque, A.M. Barber, K.M. Vittum, P.A. Medica, C.R. Tracy, and K.W. Hunter, Jr. 2012. Does translocation influence physiological stress in the desert tortoise? Animal Conservation 15:560–570.

Eubanks, J.O., W.K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). Herpetologica 59:311–321.

Ewen, J.G., P.S. Soorae, and S. Canessa. 2014. Reintroduction objectives, decisions and outcomes: Global perspectives from the herpetofauna. Animal Conservation 17:74–81.

Field, K.J., C.R. Tracy, P.A. Medica, R.W. Marlow, and P.S. Corn. 2007. Return to the wild: Translocation as a tool in conservation of the desert tortoise (*Gopherus agassizii*). Biological Conservation 13:232–245.

FFWCC (Florida Fish and Wildlife Conservation Commission). 2012. Gopher tortoise management plan. Available at https://myfwc.com/media/1819/gt-management-plan.pdf. Florida Fish and Wildlife Conservation Commission, USA. Accessed on 1 January 2024.

FFWCC (Florida Fish and Wildlife Conservation Commission). 2023. Gopher tortoise permitting guidelines. Available at https://myfwc.com/media/11854/gt-permitting-guidelines.pdf. Florida Fish and Wildlife Conservation Commission, USA. Accessed on 1 January 2024.

Folt, B., J.M. Goessling, A. Tucker, C. Guyer, S. Hermann, E. Shelton-Nix, and C. McGowan. 2021. Contrasting patterns of demography and population viability among gopher tortoise populations in Alabama. Journal of Wildlife Management 85:617–630.

Germano, J.M., K.J. Field, R.A. Griffiths, S. Clulow, J. Foster, G. Harding, and R.R. Swaisgood. 2015. Mitigation-driven translocations: Are we moving wildlife in the right direction? Frontiers in Ecology and the Environment 13:100–105.

Griffith, B., J.M. Scott, J.W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: Status and strategy. Science 245:477–480.

Guyer, C., V.M. Johnson, and S.M. Hermann. 2012. Effects of population density on patterns of movement and behavior of gopher tortoises (*Gopherus polyphemus*). Herpetological Monographs 26:122–134.

Hinderle, D., R.L. Lewison, A.D. Walde, D. Deutschman, and W.I. Boarman. 2015. The effects of homing and movement behaviors on translocation: Desert tortoises in the western Mojave Desert. Journal of Wildlife Management 79:137–147.

Howze, J.M., and L.L. Smith. 2019. Detection of gopher tortoise burrows before and after a prescribed fire: Implications for surveys. Journal of Fish and Wildlife Management 10:62–68.

Hudak, A.T., B.C. Bright, S.M. Pokswinski, E.L. Loudermilk, J.J. O'Brien, B.S. Hornsby, C. Klauberg, and C.A. Silva. 2016. Mapping forest structure and composition from low density LiDAR for informed forest, fuel, and fire management at Eglin Air Force Base, Florida, USA. Canadian Journal of Remote Sensing 42:411–427.

IUCN (International Union for Conservation of Nature). 2013. Guidelines for Reintroductions and Other Conservation Translocations, Version 1.0. Available at https://portals.iucn.org/library/efiles/documents/2013-009.pdf. International Union for Conservation of Nature, Switzerland. Accessed on 1 January 2024.

Jakes, A.F., P.F. Jones, L.C. Paige, R.G. Seidler, and M.P. Huijser. 2018. A fence runs through it: A call for greater attention to the influence of fences on wildlife and ecosystems. Biological Conservation 227:310–318.

Jones, J.C., and B. Dorr. 2004. Habitat associations of gopher tortoise burrows on industrial timberlands. Wildlife Society Bulletin 32:456–464.

Jones, M.D., L.L. Smith, K.G. Richardson, J.N. DeSha, T. Castellón, D. Hipes, A. Kalfin, N.T. Halstead, and E.A. Hunter. 2023. Simulation modeling to assess line transect distance sampling under a range of translocation scenarios. Journal of Fish and Wildlife Management 14:385–399.

Knox, C.D., S. Jarvie, L.J. Easton, and J.M. Monks. 2017. Soft-release, but not cool winter temperatures, reduces post-translocation dispersal of jeweled geckos. Journal of Herpetology 51:490–496.

Lewis, J., J. Rachlow, E. Garton, and L. Vierling. 2007. Effects of habitat on GPS collar performance: Using data screening to reduce location error. Journal of Applied Ecology 44:663–671.

Loope, K.J., R.A. Cozad, D.B. Breakfield, M.J. Aresco, and E.A. Hunter. 2024 Unexpected effect of geographic origin on post-translocation survival in a long-lived reptile, the gopher tortoise. Animal Conservation 27:685–697. DOI: https://doi.org/10.1111/acv.12946

Marques, T.A., S.T. Buckland, R. Bispo, and B. Howland. 2012. Accounting for animal density gradients using independent information in distance sampling surveys. Statistical Methods and Applications 22:67–80.

McInturff, A., W. Xu, C.E. Wilkinson, N. Dejid, and J.S. Brashares. 2020 Fence ecology: Frameworks for understanding the ecological effects of fences. BioScience 70:971–985.

McKee, R.K., K.A. Buhlmann, C.T. Moore, J. Hepinstal-Cymerman, and T.D. Tuberville. 2021. Waif gopher tortoise survival and site fidelity following translocation. Journal of Wildlife Management 85:640–653.

Miller, K.A., T.P. Bell, and J.M. Germano. 2014. Understanding publication bias in reintroduction biology by assessing translocations of New Zealand's herpetofauna. Conservation Biology 28:1045–1056.

Novak, B.J., R. Phelan, and M. Weber. 2021. U.S. conservation translocations: Over a century of intended consequences. Conservation Science and Practice 3:e394.

Nussear, K.E., C.R. Tracy, P.A. Medica, D.S. Wilson, R.W. Marlow, and P.S. Corn. 2012. Translocation as a conservation tool for Agassiz's desert tortoises: Survivorship, reproduction, and movements. Journal of Wildlife Management 76:1341–1353.

Peaden, J.M., A.J. Nowakowski, T.D. Tuberville, K.A. Buhlmann, and B.D. Todd. 2017. Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. Biological Conservation 214:13–22.

Pille, F., S. Caron, X. Bonnet, S. Seleuze, D. Busson, T. Etien, F. Girard, and J.-M. Ballouard. 2017. Settlement pattern of tortoises translocated into the wild: A key to evaluate population reinforcement success. Biodiversity Conservation 27:437–357.

Quinn, D.P., K.A. Buhlmann, J.B. Jensen, T.M. Norton, and T.D. Tuberville. 2018. Post-release movement and survivorship of head-started gopher tortoises. Journal of Wildlife Management 82:1545–1554.

Recio, M.R., R. Mathieu, P. Denys, P. Sirguey, and P.J. Seddon. 2011. Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. PLOS ONE 6:e28225.

Resende, P.S., A.B. Viana-Junior, R.J. Young, and C.S. Azevedo. 2021. What is better for animal conservation translocation programmes: Soft- or hard-release? A phylogenetics meta-analytical approach. Journal of Applied Ecology 58:1122–1132.

Rittenhouse, C.D., J.J. Millspaugh, M.W. Hubbard, and S.L. Sheriff. 2007. Movements of translocated and three-toed box turtles. Journal of Herpetology 41:115–121.

Rodríguez-Caro, R.C., M. Lima, J.D. Anadón, E. Graciá, and A. Giménez. 2016. Density dependence, climate and fires determine population fluctuations of the spur-thighed tortoise *Testudo graeca*. Journal of Zoology 300:265–273.

Ruby, D.E., W.B. Jennings, G. Goodlett, J.R. Spotila, and H.R. Mushinsky. 2023a. Design of roadway barriers to reduce desert tortoise mortality on paved road infrastructure. Chelonian Conservation Biology 22:103–115.

Ruby, D.E., W.B. Jennings, G. Goodlett, J.R. Spotila, and H.R. Mushinsky. 2023b Experimental designs for tortoise pacing diversion structures and tortoise guards along highway barriers. Chelonian Conservation Biology 22:39–45.

Seddon, P.J. 2010. From reintroduction to assisted colonization: Moving along the conservation translocation spectrum. Restoration Ecology 18:796–802.

Smith, L., M. Elliot, J. Linehan, J. Jensen, and J. Stober. 2009. An evaluation distance sampling for large-scale gopher tortoise surveys in Georgia, USA. Applied Herpetology 6:355–368.

Soorae, P.S. 2018. Global Reintroduction Perspectives: 2018. Case Studies from Around the Globe. IUCN SSC Reintroduction Specialist Group, Switzerland, Environment Agency-Abu Dhabi, AE.

Stober, J.M., and L.L. Smith. 2010. Total counts versus line transects for estimating abundance of small gopher tortoise populations. Journal of Wildlife Management 74:1595–1600.

Tetzlaff, S.J., J.H. Sperry, and B.A. DeGregario. 2019. Effects of antipredator training, environmental enrichment, and soft release on wildlife translocation: A review and meta-analysis. Biological Conservation 236:324–331.

Texeira, C.P., C.S. De Azevedo, M. Mendl, C.F. Cipreste, and R.J. Young. 2007. Revisiting translocation and reintroduction programmes: The importance of considering stress. Animal Behavior 73:1–13.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Stringberg, S.L. Hedley, J.R.B Bishop, T.A. Marques, and K.P. Burnham. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Tuberville, T.D., E.E. Clark, K.A. Buhlmann, and J.W. Gibbons. 2005. Translocation as a conservation tool: Site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). Animal Conservation 8:349–358.

Wilkinson, C.E., A. McInturff, M. Kelly, and J.S. Brashares. 2021. Quantifying wildlife responses to conservation fencing in East Africa. Biological Conservation 256:109071.

Wren, S., P.J. Bishop, A.J. Beauchamp, . . . J.M. Germano. 2023. A review of New Zealand native frog translocation: Lessons learned and future priorities. New Zealand Journal of Ecology 47:3538.

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