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Effects of head-starting on multi-year space use and survival of an at-risk tortoise

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A R T I C L E I N F O

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A B S T R A C T

A major challenge in the recovery of long-lived at-risk taxa like turtles is low juvenile recruitment. Head-starting—the raising of juveniles to larger sizes to improve survival—is one tool that can be used in circumstances where juvenile recruitment is limited. Due to declining populations and difficulty detecting juveniles, however, lack of knowledge of the ecology of juveniles can hinder efforts to develop and evaluate head-starting programs for many turtle species. We sought to inform recovery efforts of Mojave desert tortoises by quantifying multi-year space use and survival of head-started juveniles after release. We radio-tracked tortoises head-started under three different husbandry treatments that varied in rearing duration (from two to over six years) and whether head-starting included an indoor rearing component the first year. We compared post-release space use and survival as a function of treatment, release size, and time since release. We found that space use, including home range size and site fidelity, varied by husbandry treatment, with smaller and younger tortoises having smaller home ranges and higher site fidelity. Additionally, home range size decreased and site fidelity increased with time since release across treatments. Tortoises with an indoor-rearing component experiencing increased risk of mortality as movement increased compared to tortoises reared solely outdoors. Nevertheless, survival did not differ among treatments or with tortoise age or size. Regardless of husbandry treatment, head-started tortoises exhibited similar space-use and survival overall. Our study provides insight into juvenile tortoise behavior and head-starting as a tool for tortoise conservation.

1. Introduction

Biodiversity loss is accelerating globally due to human activities, including habitat destruction and over-exploitation (Todd et al., 2010). Reptiles especially have undergone precipitous declines, resulting in increased conservation attention in recent decades (Buhlmann et al., 2009; Cox et al., 2022; Todd et al., 2010). Due to their delayed maturity and high juvenile mortality, animals with slow life histories are vulnerable to population threats and it may take decades to realize outcomes of conservation and recovery actions (Congdon et al., 1993; Germano and Bishop, 2009; Tuberville et al., 2014). Delayed responses to recovery actions, combined

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with few long-term monitoring efforts to date, have limited our understanding of the success of recovery efforts for long-lived species in general (Burke, 2015; Congdon et al., 1993; Germano and Bishop, 2009).

Conservation actions, such as population augmentation via head-starting—raising an animal to a life stage less vulnerable to mortality—are increasingly being explored as potential recovery tools for at-risk species, including turtles (Burke, 2015; Seddon, 1999; Tear et al., 1993). The effectiveness of head-starting and other translocation efforts has historically been viewed with skepticism (see Dodd and Seigel, 1991, Frazer, 1992, Heppell et al., 1996), due in part to a lack of long-term post-release monitoring or because translocated animals dispersed from release areas (Germano and Bishop, 2009; Hoy et al., 2020). Additionally, head-starting is labor-intensive, often necessitates specialized facilities, and can be costly (Burke, 2015; Cohn, 1999). Despite these challenges, head-starting has shown promise for many species (Buhlmann et al., 2015; Cohn, 1999; Gibbs et al., 2014; McGovern et al., 2020a), especially when used in concert with other management actions (Spencer et al., 2017).

The Mojave desert tortoise (*Gopherus agassizii*), hereafter "desert tortoise," is a species native to the desert southwest of North America and was listed as "Threatened" under the Endangered Species Act in 1990 (US Fish and Wildlife Service, 1990). Recovery efforts in recent years have included relocation of displaced wild tortoises, installation of fencing and underpasses to mitigate road mortality, predator management, and head-starting (US Fish and Wildlife Service, 2011). Initial head-starting efforts were largely limited to the protection of tortoises in outdoor enclosures (Nagy et al., 2015). Due to long periods of dormancy during which tortoise activity and growth cease, tortoises took 5–9 years to reach the recommended release size of 100 mm midline carapace length (MCL), the size at which juvenile survival approaches that of mature tortoises (Hazard and Morafka, 2002; Nagy et al., 2015). Consequently, more recent efforts have incorporated an initial year of indoor-rearing, allowing hatchling tortoises to reach the 100 mm threshold size in just one year through year-round activity and growth (McGovern et al., 2020b). Monitoring during the first year after release has shown that increased tortoise size was associated with higher survival, but also greater movement, as there is often an "exploratory phase" following release (Candal, 2021; McGovern et al., 2020a). However, tortoises have an extended juvenile period lasting up to 15–20 years in the wild (Nagy et al., 2015; Woodbury and Hardy, 1948), and survival can vary greatly year to year based on stochastic events (Nagy et al., 2015). Additionally, post-release movement, which can influence survival, is often greatest in the first year after release (Farnsworth et al., 2015; Field et al., 2007; Nussear et al., 2012), though relatively few studies have followed released head-started tortoises more than one year after release (Candal, 2021; McGovern et al., 2020a; but see Nagy et al., 2015). Consequently, the duration of post-release monitoring to date limits our understanding of the long-term outcome of head-starting efforts, including the extent to which different head-starting techniques contribute to conservation success and efficiency.

To increase the potential for head-starting to contribute to recovery efforts, conservation efforts must assess the benefits of head-starting and identify protocols that maximize success (Burke, 2015). However, due to the slow population-level responses in most turtle species (Congdon et al., 1993), these assessments have been challenging. Here, we evaluated the outcome of three head-starting approaches that varied in rearing duration and whether or not head-starting included an indoor rearing component. We quantified multi-year movement and space use, including post-release settling time, home range size, site fidelity, and survival in desert tortoises and examined the role of head-starting treatment, tortoise release size, and time since release. By evaluating the outcomes of head-starting efforts over multiple years, we aim to improve the efficiency and efficacy of head-starting and recovery efforts for this long-lived species.

2. Methods

2.1. Study site

We conducted our study in the northeastern portion of the Mojave National Preserve, San Bernardino County, California, USA, at the southern end of the Ivanpah Valley. The release areas for head-started tortoises were open flats of 940–1112 m elevation dominated by creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), little-leaf ratany (*Krameria erecta*), big galleta (*Pleuraphis rigida*), Mojave yucca (*Yucca shigidera*) and cholla cacti (*Cylindropuntia sp.*), with an abundance of rodent burrows for shelter sites and small rocks for camouflage (Todd et al., 2016). Our study site was within the Eastern Mojave Recovery Unit, which has the lowest density of juvenile tortoises of the five Mojave Desert Tortoise Recovery Units (Allison and McLuckie, 2018; US Fish and Wildlife Service, 2011).

2.2. Obtaining hatchlings

We reared all tortoises at the Ivanpah Desert Tortoise Research Facility (IDTRF), located 15 km north of our release sites. Each May, starting in 2011, we collected wild adult female tortoises and used radiographs to detect calcified eggs (Gibbons and Greene, 1979). We placed gravid females in 5 × 9 m predator-proof nesting pens until they laid their eggs or for 30 d, whichever came first, after which we returned females to their capture location. The eggs developed in situ until they hatched, approximately 90 d after oviposition. We individually marked each hatchling by notching their marginal scutes (Cagle, 1939). We distributed hatchlings from each clutch among treatment groups due to potential maternal effects on hatchling size and survival (Nafus et al., 2015).

2.3. Experimental treatments

Head-started tortoises included individuals from three experimental treatments. The Combo treatment consisted of two-yr old tortoises raised in naturalistic indoor mesocosms for their first year, followed by one year outdoors in natural habitat inside predator-proof enclosures. The Outdoor Two treatment, obtained from the same cohort of hatchlings as the Combo treatment, included tortoises raised solely in outdoor pens from hatching to two years of age. The Outdoor Six+ treatment consisted of tortoises reared solely in outdoor pens from hatching to 6–7 years of age. When reared outdoors, tortoises dug their own burrows and were inactive during winter months. Because Combo tortoises spent their first winter indoors, during which they remained active and feeding, they did not experience a winter dormancy period and thus reached sizes comparable to the Outdoor Six+ tortoises in a single year. The Outdoor Two treatment group tortoises were smaller. For detailed information on pre-release husbandry information, see Daly et al. (2018) and McGovern et al. (2020b).

2.4. Releases

We conducted two releases using similar release protocols. Release 1 occurred on 25 September 2018 (total n = 78, Combo = 24, Outdoor Two = 24, Outdoor Six+ = 30) and Release 2 on 19 September 2019 (total n = 72, Combo = 24, Outdoor Two = 24, Outdoor Six+ = 24). We released tortoises in an area > 4.0 km from heavily trafficked roads to reduce road mortality and ≥ 1.6 km from power lines, a distance shown to reduce the risk of depredation by ravens (*Corvus corax*) that commonly use powerline towers as perching and nesting structures (Daly et al., 2019). We randomly assigned tortoises to release locations that were separated into three blocks. For Release 1, blocks were 150 m x 450 m and spaced 350 m apart from one another. Within each block, release locations were spaced 50 m from one another. Release 2 was similar to Release 1 except blocks were 180 m x 300 m due to a slight difference in the number of tortoises released. We selected release site refugia that consisted of an intact rodent burrow beneath a perennial shrub within 10 m of each pre-determined release point (see further release information in Candal, 2021 and McGovern et al., 2020a).

2.5. Post-release monitoring

The first year after release, we tracked tortoises twice per week (beginning within 24 h of release) until 31 October, then weekly until winter dormancy. We defined tortoises as "dormant" when they remained in the same burrow for more than two weeks and we classified "active" locations as all locations leading up to the first day of winter dormancy. Once tortoises were dormant, we tracked them every two weeks through winter, then increased tracking frequency to weekly following spring emergence in March. Once tortoises emerged from winter dormancy, we considered them "active." After the first year of post-release monitoring, we tracked tortoises weekly during their active season (Mar–Oct) and every two weeks during winter dormancy (Nov–Feb). At each location, we collected UTM coordinates using handheld GPS units with an accuracy of ± 3 m (Garmin model GPSMAP 76, Olathe, KS). If a tortoise was found dead, we recorded the location and any signs of potential predators. We replaced radio-transmitters each September, with all surviving individuals receiving a 3.6-g R1680 (Advanced Telemetry Systems, Insanti, MN, USA) transmitter until September 2020, when we reduced the number of tortoises being monitored via radio-telemetry to 15 tortoises per treatment (n = 45) per release year. We radio-tracked all remaining tortoises until 1 October 2021, resulting in three years of monitoring for Release 1 and two years for Release 2 animals.

2.6. Data analysis: settling date

Prior to establishing a home range, tortoises typically exhibit greater movements in the first few weeks following release, although the duration of this settling phase can vary among species and individuals (Tuberville et al., 2005; Quinn et al., 2018; Daly et al., 2019; Tuberville et al., 2021). Greater exploratory movements during the settling phase can lead to greater surface activity, which can contribute to greater mortality risk from predation or exposure (Quinn et al., 2018; Daly et al., 2019; Tuberville et al., 2021). For each tortoise in this study, we used two different settling metrics that captured different biologically relevant movement parameters to estimate the time—in days since release—that it took tortoises to settle. Settling date$_{DSL}$ was determined based on daily step length (DSL; meters traveled per day by an individual tortoise, calculated by dividing the distance between successive locations by the number of days between tracking events.) and settling date$_{DND}$ was based on daily net displacement from release site (DND; defined as the straight-line distance from the current location of the tortoise to the initial release location standardized by the number of days since release; for similar analyses, see Franks et al., 2011). Settling date$_{DSL}$ captured the daily movement of each individual tortoise, indirectly measuring time spent on the surface. Settling date$_{DND}$ identified the extent to which tortoises continued to move away from their initial release location. Settling date$_{DSL}$ was standardized for duration between tracking events, whereas settling date$_{DND}$ was standardized for days since release to account for animals that survived longer having had greater opportunity to move farther from the release site.

We used linear piecewise splines (Wold, 1974) to model an inflection point threshold corresponding to the time—measured as number of days after release—at which DSL or DND changed for each individual tortoise to obtain the settling date$_{DSL}$ and settling date$_{DND}$ (Suppl. Fig. 1). Piecewise splines are used to quantify distinct changes in animal behaviors and survival (e.g., MacNulty et al., 2014, Kohl et al., 2019). We created separate sets of candidate models for each response variable (settling date$_{DSL}$, settling date$_{DND}$), with each set including three models: a one-knot, a two-knot, and a linear model. A knot corresponds to an inflection point or time point (days since release) at which an individual tortoise's movement changed. Individuals for which a one-knot model is the top model would exhibit a single shift in movement behavior, with the single knot representing the settling date. This would occur when an animal's post-release movement slows until a point when movement stabilizes. Two-knot models accommodate multiple distinct shifts in movement behavior by individuals, with the second knot corresponding to the estimated settling date. If the linear model was identified as the top model, this would indicate that an individual's movement behavior did not change during the monitoring period and a settling date could not be estimated. For each settling metric, we ranked the three models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson, 2002) to identify the model that best explained settling behaviors for each tortoise ($\Delta AIC_c < 2.0$). Because most of the top models were two-knot models, we selected all individuals with a two-knot model for comparison and excluded individuals with a one-knot or linear model as the top model.

To determine how estimated settling date differed based on the movement metric used, we used an unpaired t-test to compare the mean values of settling $date_{DSL}$ and settling $date_{DND}$. We used an unpaired t-test because we could not obtain settling dates from two-knot models for every individual. Though the settling dates were significantly different from one another, in subsequent analyses we still constructed candidate model sets for both, as they measure two different patterns of behavior and have different implications regarding release outcome.

We used linear models to determine how settling date varied with treatment group, release year (1 vs. 2), and release MCL. We considered both treatment group and release MCL as covariates in the linear models as head-starting treatment might be expected to influence tortoises beyond affecting their size, such as through duration of captivity and whether they experienced indoor rearing. We log-transformed the response variable of 'days since release' to ensure data were normally distributed. We used AIC_c to evaluate model fit ($\Delta AIC_c < 7.0$). If multiple models were within 7 AIC_c, we used all of those models to generate predictions, then averaged those predictions using the "modavgPred" tool in the "AICmodAvg" package in R (v. 4.1.0) to account for uncertainty in model selection (Mazerolle, 2020), then evaluated trends in predicted days since release based on our covariates.

2.7. Home range size

We estimated home range for each tortoise for each monitoring year to examine variation among treatments and over time (i.e., years since release). To avoid inflated home range estimates due to exploratory behavior immediately following release, we only included post-dormancy locations for Year 1 calculations. Additionally, we only used locations collected during the "active" season (between spring emergence and winter dormancy) to calculate subsequent annual home ranges for each individual for each active season. Because the limited number of locations per individual per season precluded the use of other home range estimators, we constructed 95% minimum convex polygon (MCP; Mohr, 1947) annual home ranges for each tortoise using the "adehabitatHR" package in R (Calenge, 2006) for any individual tortoise having at least 10 tracking locations in the corresponding active season (range: 10–36 locations). Depending on the number of years an individual tortoise survived, we constructed up to three annual home ranges for Release 1 tortoises (2019; $n = 68$, 2020; $n = 59$, 2021; $n = 40$) and two for Release 2 tortoises (2020; $n = 68$, 2021; $n = 41$).

We used linear mixed effects models to examine how home range size differed by treatment group, release year, year since release, and release MCL, with home range size (ha) as the response variable and tortoise ID as a random effect to account for repeated measures of the same individual (R package "lme4″; Bates et al., 2015). We log-transformed home range size prior to analysis to meet assumptions of normality. We used AIC_c to evaluate model fit ($\Delta AIC_c < 7.0$). If multiple models were within 7 AIC_c, we used prediction averaging as described above and then evaluated trends in predicted home range size based on our covariates.

2.8. Site fidelity

Using the annual home ranges described above, we compared between-year site fidelity among tortoises reared under different head-starting treatments to examine how space use changed from year to year. We evaluated site fidelity for each tortoise using four metrics: 1) distance between release location and initial settling location, 2) distance between initial settling location and Year 1 home range center, 3) distance between annual home range centers, and 4) home range overlap (proportion of home $range_t$ included in home $range_{t+1}$). Home range centers for each annual home range were determined by calculating the average easting and northing of the points used to generate MCPs for each tortoise.

We built separate model sets for each site fidelity metric. For both distance from release location to settling location and settling location to the Year 1 home range center, we used a linear model to examine how distance differed by treatment, release year, and release MCL. For the distance between home range centers and annual home range overlap analyses, we used linear mixed effects models to examine how each site fidelity metric differed based on treatment, release year, years since release, and release MCL, with tortoise ID as a random effect to account for repeated sampling of individuals. We log-transformed all response variables to ensure data were normally distributed and then used AIC_c to evaluate model fit ($\Delta AIC_c < 7.0$). If multiple models in a set were within 7 AIC_c, we used prediction averaging as described above and evaluated trends in predicted home range size based on our covariates. Results for all movement and space use metrics are presented as the mean $\pm$ 1 SE of the non-transformed variable.

2.9. Survival

We quantified annual survival of head-started desert tortoises by treatment group for the first three years after release. We evaluated the effects of head-starting treatment, DSL (m) during the active season (calculated as the distance between weekly locations over the number of days between tracking events), release MCL, and release year (1 vs. 2) on annual survival using individuals of known fate at the end of the study. We ran a Cox proportional hazard model (Cox, 1972) with a weekly binary response (1 =alive, 0 =dead), which included weeks that tortoises were dormant, with release year (1 vs. 2) as a strata variable in the "survival" package in R (Therneau, 2022). We used AIC_c to evaluate model fit ($\Delta AIC_c < 7.0$), using the "AICcmodavg" packages in R (v. 4.1.0) to account for uncertainty in model selection.

3. Results

We collected 12,821 locations on 150 tortoises between 25 September 2018 and 01 October 2021. Of the 150 tortoises released ($n = 78$ in Release 1, September 2018; $n = 72$ in Release 2, September 2019), 55 tortoises were killed by predators, 27 tortoises were removed from the study in September 2020 to reduce tracking effort, and 17 tortoises were lost from the study due to radio failure and their fate was unknown. Fifty-one tortoises were continually radio-tracked and known to have survived until September 2021.

3.1. Settling date

Using the two-knot models, we were able to calculate settling date$_{DSL}$ (daily step length in m traveled per day) for 127 tortoises and settling date$_{DND}$ (daily net distance in m per day) for 122 tortoises. We found that mean settling date$_{DSL}$ and mean settling date$_{DND}$ differed significantly from one another ($t = -4.15$, $df = 247$, $p < 0.05$), with settling date$_{DSL}$ occurring earlier (mean $= 6.6 \pm 0.5$ days, range 2–33 days post-release) than settling date$_{DND}$ (mean $= 9.5 \pm 0.5$ days, range 2–40 days; Table 1). Mean settling date$_{DSL}$ did not differ among treatment groups, between releases, or as a function of release MCL. Mean settling date$_{DND}$ also did not differ significantly among treatment groups, nor between releases, or as a function of release MCL. None of the seven candidate models for the settling date$_{DSL}$ or settling date$_{DND}$ garnered > 0.36 or > 0.24 of the AIC$_c$ model weight, respectively, indicating high uncertainty in the model selection (Suppl. Table 1, Suppl. Table 2).

3.2. Home range size

Mean annual home range size across all tortoises and all years was 0.7 ± 0.3 ha ($n = 276$) and ranged from < 0.1–54.8 ha (Table 1). The most parsimonious model for home range area included just treatment and years since release, garnering 95% of the AICw (Suppl. Table 3). All other models had a ΔAIC of ≥ 6.56 (Suppl. Table 3). When predictions of all models within 7 AIC$_c$ were averaged, home range size differed by treatment and years since release (Table 1). Tortoises in the Six + treatment had larger home ranges (1.6 ± 0.8 ha) than the Combo (0.2 ± 0.0 ha) and Outdoor Two treatment groups (0.2 ± 0.1 ha, $p < 0.05$). Home range size decreased with each year since release, but did not differ between releases (Fig. 1).

3.3. Site fidelity

Across all treatment groups and both releases, the mean distance between the release location and the settling location was 203.5 $\pm$ 32.4 m and ranged from 2.2–2867.1 m (Table 1). When predictions of all models within 7 AIC$_c$ were averaged, distance from release to settling location differed among treatment groups (Suppl. Table 4). Outdoor Six+ tortoises and Outdoor Two tortoises settled farther

Table 1
Means, standard errors, and ranges of settling dates, home range size, and site fidelity metrics for head-started desert tortoises (*Gopherus agassizii*) in the Mojave National Preserve, California, USA from 2018 – 2021. DSL refers to daily step length (m) and DND refers to daily net displacement from the initial release area (m). Home ranges were calculated using 95% minimum convex polygons (MCP). *Year 3 home ranges and site fidelity metrics could only be calculated for tortoises in Release 1.

		Combo	Outdoor Two	Outdoor Six+	Release 1	Release 2	All
Settling Date							
DSL	Mean (days) ± SE	6.9 ± 0.7	5.5 ± 0.6	7.1 ± 1.0	6.2 ± 0.4	6.9 ± 0.9	6.5 ± 0.5
	Range (days)	2 – 20	2 – 17	2 – 33	2 – 18	2 – 33	2 – 33
DND	Mean (days) ± SE	10.5 ± 0.8	8.3 ± 0.8	9.6 ± 1.0	8.8 ± 0.6	10.3 ± 1.0	9.5 ± 0.6
	Range (days)	3 – 22	2 – 24	3 – 40	3 – 24	2 – 40	2 – 40
Home Range Size							
Year 1 Home Range	Mean (ha) ± SE	0.3 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.2 ± 0.1	0.4 ± 0.1
	Range (ha)	0 – 3.4	0 – 4.4	0 – 5.7	0 – 5.7	0 – 3.4	0 – 5.7
Year 2 Home Range	Mean (ha) ± SE	0.1 ± 0.0	0.1 ± 0.0	3.8 ± 2.1	2.3 ± 1.2	0.2 ± 0.1	1.4 ± 0.7
	Range (ha)	0 – 0.7	0 – 0.5	0 – 54.8	0 – 54.8	0 – 3.4	0 – 54.8
Year 3 Home Range*	Mean (ha) ± SE	0.1 ± 0.0	0.1 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	–	–
	Range (ha)	0 – 0.3	0 – 0.5	0 – 0.8	0 – 0.8	–	–
Site Fidelity							
Release to Settling	Mean (m) ± SE	92.5 ± 26.0	152.7 ± 26.4	349.0 ± 80.1	231.2 ± 55.3	175.8 ± 34.0	203.5 ± 32.4
	Range (m)	4.1 – 1184.7	2.2 – 957.1	4.5 – 2867.1	4.1 – 2867.1	2.2 – 1494.2	2.2 – 2867.1
Settling to Year 1 Center	Mean (m) ± SE	100.4 ± 16.8	132.8 ± 39.8	84.1 ± 12.0	102.7 ± 17.9	106.3 ± 22.1	104.5 ± 14.2
	Range (m)	4.9 – 533.0	3.9 – 1380.8	5.7 – 402.5	4.9 – 795.3	3.9 – 1380.8	3.9 – 1380.8
Year 1-Year 2 Center	Mean (m) ± SE	22.4 ± 2.8	18.6 ± 3.1	105.7 ± 42.3	73.4 ± 25.6	17.3 ± 1.8	50.4 ± 15.3
	Range (m)	4.6 – 76.7	2.0 – 76.5	3.1 – 1269.9	3.9 – 1269.9	2.0 – 45.5	2.0 – 1269.9
Year 2-Year 3 Center*	Mean (m) ± SE	15.2 ± 3.3	15.6 ± 5.0	22.0 ± 3.6	17.6 ± 2.3	–	–
	Range (m)	1.7 – 39.0	1.1 – 71.8	6.9 – 45.8	1.1 – 71.8	–	–
Overlap Year 1-Overlap Year 2	Mean (%) + SE	27.3 ± 4.3	28.0 ± 4.3	35.4 ± 4.7	38.6 ± 3.6	18.5 ± 2.8	30.4 ± 2.6
	Range (%)	0.1 – 99.9	1.0 – 97.2	0.0 – 100.0	0.0 – 100.0	0.0 – 62.6	0.0 – 100.0
Overlap Year 2-Overlap Year 3*	Mean (%) + SE	27.0 ± 5.8	23.5 ± 4.3	38.1 ± 6.7	29.5 ± 3.4	–	–
	Range (%)	0.0 – 72.1	4.8 – 54.9	10.4 – 70.5	0.0 – 72.1	–	–

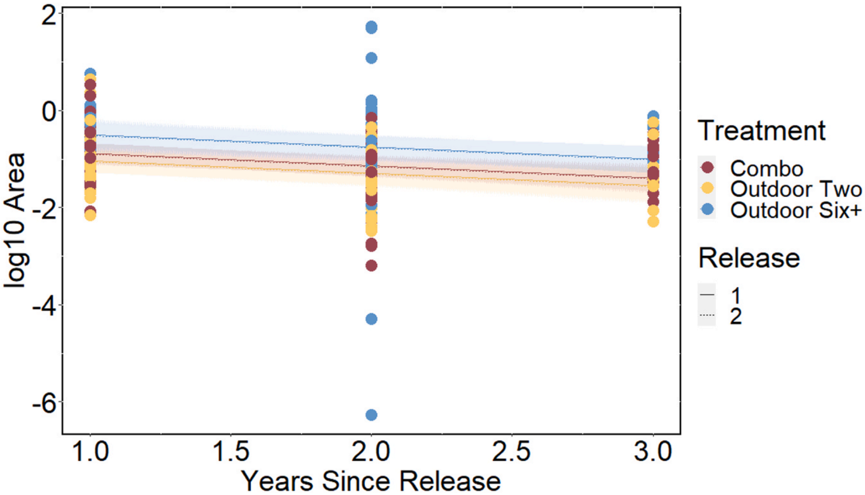

Fig. 1. Prediction averaged change in log10 annual home range area (95% minimum convex polygons in ha) over time (years since release) for each treatment group for head-started Mojave desert tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA. Tortoises in the Outdoor Six+ treatment group had larger home ranges than Combo and Outdoor Two treatment tortoises, with home range size decreasing over time in each head-starting treatment group.

from their release points (349.0 ± 80.1 m and 152.7 ± 26.4 m, respectively) than did Combo tortoises (92.5 ± 26.0 m, Table 1). Distance between release and settling location did not differ between releases or vary with MCL at release.

Across all treatment groups and both releases, the mean distance between the settling location and Year 1 home range center was 104.5 ± 14.2 m (n = 136) and ranged from 3.9–1380.8 m (Table 1). When predictions of all models within 7 AIC_c were averaged (Suppl. Table 5), mean distance between settling and Year 1 home range center did not differ significantly among treatments. Distance between the settling location and Year 1 home range center was best explained by the interaction between MCL and release year; the distance differed between Release 1 and Release 2 and increased as tortoise size increased for tortoises in Release 2.

Across treatments and years, the distance between annual home range centers ranged from 1.1–1269.9 m, with a mean of 41.2 ± 11.1 m (n = 139, Table 1). Predictions of all models for distance between annual home range centers within 7 AIC_c were averaged (Suppl. Table 6). Distance between home range centers was greater for the Outdoor Six+ tortoises (83.1 ± 31.2 m) than for the Combo (20.4 ± 2.3 m) and Outdoor Two treatments (17.7 ± 2.6 m, Table 1). Finally, distance between home range centers decreased with time since release. Distance between home range centers did not vary with MCL at release, and decreased slightly between Release 1 and 2.

The mean home range overlap across treatments and years was 30.1 ± 2.1% (n = 136) and ranged from 0–100% (Table 1). When

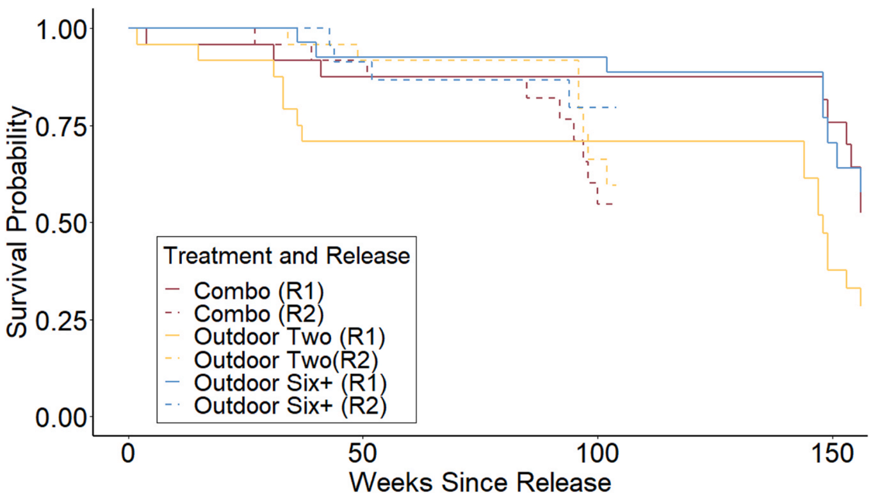

Fig. 2. Cox survival curve for head-started Mojave desert tortoises (*Gopherus agassizii*) from three treatment groups and two different releases in Mojave National Preserve, California, USA from 2018 – 2021. Release 1 included 78 tortoises released in 2018 and radio-tracked for up to three years; Release 2 included 72 tortoises released in 2019 and followed up to two years. There was no significant difference in annual survival among treatments ($p > 0.05$), but there was a significant interaction between daily step length (m) and treatment ($p < 0.05$).

predictions of all models within 7 AIC_c were averaged (Suppl. Table 7), home range overlap did not differ significantly among treatment groups but differed between release years, with tortoises in Release 2 having less overlap than tortoises in Release 1.

3.4. Survival

As of 1 October 2021, a total of 55 tortoises were confirmed to have died during the study, with all mortalities attributed to predation—five to avian predators (9.1% of known mortalities), 48 to mammalian predators (87.3%), and two to unidentified predators (3.6%). Post-release survival over three years to the end of the study for Release 1 was 0.45 (95% CI, 0.34–0.60, Fig. 2, Table 2), with annual survival ranging from 0.55–0.98 across all treatments. Post-release survival over two years to the end of the study for Release 2 was 0.63 (95% CI, 0.51–0.77, Fig. 2, Table 2), with annual survival ranging from 0.72–0.87 across all treatments. Most mortalities (32 of 55) occurred in 2021 (Year 3 for Release 1, Year 2 for Release 2).

The best fitting Cox proportional hazards model included an interaction between the effect of daily step length (m) and treatment on survival. The top model garnered 95% of the AIC_c weight and included daily step length, treatment group, and their interaction (Suppl. Table 8), revealing that as daily step length increased, survival decreased differently among the three treatment groups. There was no significant difference in survival due to treatment alone, nor by daily step length alone. There was, however, a significant effect of movement per day on risk of mortality to the Combo treatment ($\beta = 0.33$, 95% CI = 0.17, 0.48, Table 3). The hazard ratio for this effect was 1.38 (95% CI: 1.19–1.62), indicating an increase in risk of mortality of 38% for every additional meter moved per day for tortoises from the Combo rearing treatment. There was nevertheless no significant difference in overall risk of mortality for the Outdoor Two and Outdoor Six+ treatment groups compared with the Combo treatment group ($\beta = -0.10$, 95% CI = −0.12, 1.76, $\beta = -0.24$, CI = −0.64, 1.32, respectively, Table 3). While the interaction did not differ significantly among treatment groups, we observed a lower relative risk of death for both Outdoor Two and Outdoor Six+ tortoises as movement per day increased compared with Combo tortoises. Release year, years since release, and size (MCL) were not significant predictors of tortoise survival.

4. Discussion

It is important to evaluate conservation practices to ensure success and maximize effectiveness. Head-starting is a conservation practice increasingly used for many species (Cohn, 1999; Gibbs et al., 2014; Buhlmann et al., 2015; Nagy et al., 2015; McGovern et al., 2020a). Certain life history traits like prolonged time to sexual maturity make it difficult to evaluate head-starting effectiveness in long-lived taxa like turtles, especially when multi-year monitoring is rarely implemented. Different husbandry practices may affect post-release space-use and survival—factors that directly contribute to population recovery (Germano and Bishop, 2009; Nagy et al., 2015). Here, we monitored desert tortoises from three different head-starting treatment groups for up to three years after release. We found that Outdoor Two tortoises settled slightly earlier than Outdoor Six+ and Combo tortoises, whereas Outdoor Six+ tortoises had larger home ranges than both Combo and Outdoor Two tortoises. Additionally, home range size of tortoises from all treatments decreased with time since release, while site fidelity increased over time based on decreased distance between home range centers and percentage of home range overlap. While home range overlap did not differ among treatment groups, distance between home range centers was larger in the Outdoor Six+ tortoises than the Combo and Outdoor Two treatment groups, indicating that the older Outdoor Six+ tortoises shifted the location of their home ranges year-to-year more than other treatment groups. Finally, annual survival did not differ significantly among treatment groups, but tended to be greater in the treatment groups with larger tortoises (i.e., the Combo and Outdoor Six+ groups).

Settling $date_{DSL}$ (settling date calculated by daily step length) is an indirect measure of time spent on the surface, when tortoises may be exposed to predators or harsh conditions during the initial settling period. In contrast, settling $date_{DND}$ (calculated as daily net displacement) accounts for the distance a tortoise has moved away from its release location—influencing the area in which a tortoise finally settles. Tortoises tended to reduce their daily movement within one week of release, but took slightly longer to stop moving farther away from their release locations, resulting in an earlier settling $date_{DSL}$ compared to settling $date_{DND}$. Thus, settling $date_{DND}$ was a more conservative metric than settling $date_{DSL}$ in our study in that while tortoises may have been shortening movements, thereby decreasing daily step length, they continued to move away from their release sites, requiring continued surface activity. By identifying differences among treatment groups, settling $date_{DND}$ may serve as a better metric for quantifying settling behavior in future studies.

Table 2
Summary of post-release survival rates for head-started Mojave desert tortoises (*Gopherus agassizii*) in the Mojave National Preserve, California, USA from 2018–2021.

		Annual Survival			Proportion Alive at End of Study
		2018 – 2019	2019 – 2020	2020 – 2021	
Release 1	Combo	0.88	1.00	0.60	0.53
n = 78	Outdoor Two	0.71	1.00	0.40	0.28
	Outdoor Six+	0.9	0.96	0.65	0.56
	All	0.83	0.98	0.55	0.45
Release 2	Combo	-	0.88	0.63	0.55
n = 72	Outdoor Two	-	0.92	0.65	0.60
	Outdoor Six+	-	0.83	0.92	0.76
	All	-	0.87	0.72	0.63

Table 3
Beta estimate values used for survival of head-started Mojave desert tortoises (*Gopherus agassizii*) in the Mojave National Preserve, California, USA from 2018 – 2021. Combo is the reference group for this model set; thus, no coefficient estimate is provided in a categorical analysis. Movement is the daily mean step length. **Bold** indicates significant differences between the covariate and the model intercept.

Cox Model Variables	Post-Release Survival β Estimates
Treatment Outdoor Two	0.823
Treatment Outdoor Six+	0.303
Movement:Treatment Combo	**0.327**[a]
Movement:Treatment Outdoor Two	-0.102
Movement:Treatment Outdoor Six+	-0.241

[a] Denotes the model's intercept value.

Settling date$_{DND}$ differed among treatment groups, with Outdoor Two tortoises settling slightly earlier than Combo and Outdoor Six+ tortoises. In contrast, settling date$_{DSL}$ did not differ among treatment groups; rather, all tortoises may have been reducing their daily step length around the same time post-release, likely because they were all experiencing the same cooling temperatures ahead of winter. Overall, tortoises from all treatment groups settled within 10 d of release. Hazard and Morafka (2002) reported similar settling times (~7 d post-release) for neonate and head-started desert tortoises, though older juveniles moved more often. Post-release settling behavior was likely influenced by both pre-release intrinsic factors—like age and size of the individuals at release and time and experiences while in captivity—and extrinsic factors—like the quality of the habitat where they were released (Nafus et al., 2017; Stamps and Swaisgood, 2007). Our releases were conducted in the Fall, which may have facilitated settling behavior as the onset of winter forced tortoises to become less active on the surface as temperatures dropped (Pille et al., 2018; Daly et al., 2019).

Outdoor Six+ tortoises consistently had the largest home ranges compared to the Combo and Outdoor Two tortoises. While the Outdoor Six+ tortoises were similar in size to the Combo tortoises, they were at least four years older than both the Combo and Outdoor Two tortoises, suggesting that post-release home range size may be driven by age more so than size. Annual home ranges averaged 0.7 ha for all head-started tortoises, with many of the home ranges $<$ 0.5 ha, consistent with the few home range estimates available for juvenile congeners (*G. polyphemus*: 0.01 ha; Diemer, 1992). Home ranges of immature tortoises tend to be smaller than for adult tortoises, as with Sonoran Desert tortoises (*G. morafkai*; Averill-Murray et al., 2020). The larger home ranges of older Outdoor Six+ juveniles may indicate that these tortoises were reaching the subadult stage at which they are likely to disperse (McRae et al., 1981; Tuberville et al., 2014; Tuma et al., 2016).

As predicted, annual home ranges in each treatment group decreased with time since release, even when excluding the settling period in the first year. A similar trend has been reported for wild-to-wild translocations, with home range size decreasing the first year after release in desert tortoises (Farnsworth et al., 2015; Nussear et al., 2012), gopher tortoises (Tuberville et al., 2005), ornate box turtles, *Terrapene ornata*, (Doroff and Keith, 1990) and timber rattlesnakes, *Crotalus horridus*, (Reinert and Rupert, 1999). Our results corroborate previous studies in which space use decreases over time when tortoises are released in suitable habitat.

We assessed site fidelity using four different metrics, and while the factors driving site fidelity differed depending on the metric used, all groups exhibited high site fidelity that increased over time since release. The distance between settling location and Year 1 home range center varied widely among individuals (1.1–1269.9 m), though tortoises on average established their initial home range centroid within ~ 105 m of the settling location. Similarly, both Nafus et al. (2017) and Nagy et al. (2015) reported that head-started desert tortoises generally settled within 100–200 m of their initial release location. The distance between home range centers decreased between years in all three treatments, showing increased site fidelity over time. Home range overlap between years averaged ~30%, was similar among treatments, and did not differ among years. While estimates of site fidelity over multiple years post-release are limited for tortoises, our results mirror previous studies that have found tortoises show increased site fidelity over time since release (Nussear et al., 2012; Tuberville et al., 2005). The high site fidelity exhibited by head-started desert tortoises in our study may in part be due to the high-quality habitat at the release site, which supported preferred plant communities and was relatively homogenous (Todd et al., 2016).

Annual survival rates prior to 2021 (0.83–0.98 across treatment groups and releases) were higher than those previously reported for head-started juvenile desert tortoises (0.44–0.79; Nagy et al., 2015, Nafus et al., 2017, Daly et al., 2019); the larger size of tortoises released in the current study (mean=107.1 mm MCL, compared to mean = 69.55 mm MCL in Daly et al., 2019) likely played a role. McGovern et al. (2020a), released tortoises with a broad size range (68.00–145.00 mm MCL) and found that size was an important predictor of survival of head-started desert tortoises during the first year after release, but size may not always be the best predictor. Size can interact with physiological stress to influence survival (Candal, 2021), and its relative importance can vary for different predators (e.g., ravens versus coyotes (*Canis latrans*); Richter, 2022). Although treatment alone did not influence annual survival here, the interaction between movement and treatment was the most significant predictor of survival in our study; as daily movements increased, the risk of mortality also increased across all treatments, though Combo differed significantly in its increase of risk with increasing movement compared to Outdoor Two and Outdoor Six+. Increased movement likely resulted in increased surface activity, which has been associated with mortality risk in head-started desert tortoises and gopher tortoises (Quinn et al., 2018; Daly et al., 2019; McGovern et al., 2020a). While the interaction between movement and survival did not differ significantly among treatment groups, Combo tortoises—which experienced only a single year of outdoor rearing—had a greater increase in relative mortality risk as movement per day increased than did Outdoor Two and Outdoor Six+ tortoises—which experienced extended outdoor rearing of two to six or more years. Outdoor rearing in natural enclosures may provide a form of pre-release conditioning, which has been shown to decrease post-release movement in some turtles (Tetzlaff et al., 2019), and which may lead to increased survival. However, more than a single year of outdoor rearing may be needed to mitigate the increased risk of mortality observed in those Combo tortoises that exhibited greater daily movement.

Most tortoise mortalities in our study were attributed to mammalian predators, as has been reported in some other studies (Nagy et al., 2015), including earlier releases at our study site (McGovern et al., 2020a; Candal, 2021). In contrast, Daly et al. (2019) reported common ravens as the primary predator during earlier releases at our study site, and showed that mortality risk due to ravens extended 1.6 km from powerlines that served as perching and nesting structures. The preponderance of mammalian predation in the current study likely stems from two factors. First, following the recommendations of Daly et al. (2019), we released all tortoises ≥ 1.6 km away from the nearest powerline, thereby likely mitigating much raven predation. Second, the greatest mortality was observed in the final year of monitoring—2021—which coincided with a marked decrease in precipitation and onset of extreme drought conditions. An average of 7.6–12.7 cm of rainfall typically occurs each year in the Mojave National Preserve, with most occurring in the spring (Mar–Apr; US Department of the Interior, 2022). However, in spring of 2021, our study area received no rainfall, and tortoises delayed emergence from their winter dormancy burrows by several months. With the onset of the summer monsoon, however, tortoises emerged en masse, making them particularly vulnerable to predators. Additionally, coyotes are known to prey more heavily on desert tortoises during drought years when jackrabbits (*Lepus californicus*)—their usual primary prey—become scarce (Esque et al., 2010). Annual survival of Release 1 tortoises (across all treatments) dropped from 0.98 in 2020 to 0.55 in 2021 and survival of Release 2 tortoises dropped from 0.87 in 2020 to 0.72 in 2021. Survival of 0.98 in 2020 for our tortoises in Release 1 may provide an indication of what survival may look like for head-started tortoises in their second-year post-release under "normal" conditions. The decrease in survival in 2021 due to mammal predators also occurred irrespective of tortoise size, likely masking any significant differences in survival among treatments. Our results followed a similar pattern to Nagy et al. (2015), where survival rates increased with size and with time since release until extreme drought conditions led to increased predation of all released tortoises, regardless of size. It is also worth noting that while size did not appear to confer any survival benefit during the drought year of 2021, its influence on survival in non-drought years means that more tortoises were alive on the landscape due to head-starting prior to the drought bottleneck, and thus more tortoises remained afterward despite the heavy toll the drought in 2021 imposed on study animals.

5. Conclusions

The current study examined space use and survival of head-started desert tortoises for up to three years following release. Overall, head-started tortoises—regardless of treatment—showed high post-release site fidelity, with fidelity increasing with years since release. Annual survival was also high except in the final year of monitoring when tortoises had to contend with extreme drought conditions at the study site. Most differences in space use among treatments were associated with larger home ranges and less between-year site fidelity in the oldest tortoises, which had been head-started outdoors for six to seven years prior to release. Combo-reared tortoises attained release sizes similar to the Outdoor Six+ treatment in just two years of head-starting investment, thereby reducing head-starting costs given the far fewer overall feedings required and several years less time invested during husbandry. Thus, our results corroborate those of McGovern et al. (2020a), (2020b), (2021) and Candal (2021), showing that combination rearing—i.e., one year of indoor rearing followed by one year of outdoor rearing—is a viable head-starting method for producing large juvenile tortoises relatively quickly without altering behavior or compromising survival. By incorporating an indoor rearing component into pre-release husbandry, wildlife managers and conservationists can improve the efficiency of tortoise head-starting projects (Dodd and Seigel, 1991; Cohn, 1999), thereby making head-starting a more feasible recovery tool that can be more broadly implemented.

CRediT authorship contribution statement

Collin J. Richter: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Brian D. Todd**: Conceptualization, Methodology, Resources, Validation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Kurt A. Buhlmann**: Conceptualization, Methodology, Validation, Writing – review & editing, Supervision, Project administration. **Carmen M. Candal**: Methodology, Investigation, Data curation, Writing – review & editing. **Pearson A. McGovern**: Methodology, Investigation, Data curation, Writing – review & editing. **Michel T. Kohl**: Conceptualization, Methodology, Resources, Software, Formal analysis, Resources, Validation, Writing – review & editing, Supervision, Project administration. **Tracey D. Tuberville**: Conceptualization, Methodology, Resources, Validation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02774.

References

Allison, L.J., McLuckie, A., 2018. Range-wide monitoring of the Mojave desert tortoise (*Gopherus agassizii*). Herpetol. Conserv. Biol. 13, 433–452.
Averill-Murray, R.C., Fleming, C.H., Riedle, J., 2020. Reptile home ranges revisited: a case study of space use of Sonoran desert tortoises (*Gopherus morafkai*). Herpetol. Conserv. Biol. 15, 253–271.
Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.
Buhlmann, K.A., Akre, T.S.B., Iverson, J.B., Karapatakis, D., Mittermeier, R.A., Georges, A., Rhodin, A.G.J., van Dijk, P.P., Gibbons, J.W., 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. Chelonian Conserv. Biol. 8, 116–149.
Buhlmann, K.A., Koch, S.L., Butler, B.O., Tuberville, T.D., Palermo, V.J., Bastarache, B.A., Cava, Z.A., 2015. Reintroduction and head-starting: tools for Blanding's turtle (*Emydoidea blandingii*) conservation. Herpetol. Conserv. Biol. 10, 436–454.
Burke, R., 2015. Head-starting turtles: learning from experience. Herpetol. Conserv. Biol. 10, 299–308.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed..,. Springer-Verlag Publishers,, USA.
Cagle, F.R., 1939. A system of marking turtles for future identification. Copeia 1939, 170–173.
Calenge, C., 2006. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. Ecol. Model. 197 (3-4), 516–519.
Candal, C.M. 2021. The role of stress physiology in head-starting success for Mojave desert tortoises. Thesis. University of Georgia. Athens, GA, USA.
Cohn, P., 1999. Saving the California condor years of effort are paying off in renewed hope for the species' survival or wildlife. Bioscience 49, 864–868.
Congdon, J.D., Durham, A., Van Loben Sels, R., 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conserv. Biol. 7, 826–833.
Cox, D., 1972. Regression models and life-tables. J. R. Stat. Soc. 34, 187–220.
Cox, N., Young, B.E., Bowles, P., Fernandez, M., Marin, J., Rapacciuolo, G., Böhm, Monika, Brooks, T.M., Hedges, S.B., Hilton-Taylor, C., Hoffman, M., Jenkins, R.K.B., Tognelli, M.F., Alexander, G.J., Allison, A., Ananjeva, N.B., Auliya, M., Avila, L.J., Chapple, D.G., Cisneros-Here, Y., 2022. A global reptile assessment highlights shared conservation needs of tetrapods. Nature 605, 285–290.
Daly, J.A., Buhlmann, K.A., Todd, B.D., Moore, C.T., Peaden, J.M., Tuberville, T., 2018. Comparing growth and body condition of indoor-reared, outdoor-reared, and direct-released juvenile Mojave desert tortoises. Herpetol. Conserv. Biol. 13, 622–633.
Daly, J.A., Buhlmann, K.A., Todd, B.D., Moore, C.T., Peaden, J.M., Tuberville, T.D., 2019. Survival and movements of head-started Mojave desert tortoises. J. Wildl. Manag. 83, 1700–1710.
Diemer, J.E., 1992. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. J. Herpetol. 26, 158–165.
Dodd, C., Seigel, R., 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47, 336–350.
Doroff, A.M., Keith, L., 1990. Demography and ecology of an ornate box turtle (*Terrapene ornata*) population in south-central Wisconsin. Copeia 1990, 387–399.
Esque, T.C., Nussear, K.E., Drake, K.K., Walde, A.D., Berry, K.H., Averill-Murray, R.C., Woodman, A.P., Boarman, W.I., Medica, P.A., Mack, J., Heaton, J., 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endanger. Species Res. 12, 167–177.
Farnsworth, M.L., Dickson, B.G., Zachmann, L.J., Hegeman, E.E., Cangelosi, A.R., Jackson, T.G., Scheib, A., 2015. Short-term space-use patterns of translocated Mojave desert tortoise in southern California. PLoS One 10, 1–18.

Field, K.J., Tracy, C.R., Medica, P.A., Marlow, R.W., Corn, P., 2007. Return to the wild: translocation as a tool in conservation of the desert tortoise (*Gopherus agassizii*). Biol. Conserv. 136, 232–245.
Franks, B.R., Avery, H.W., Spotila, J., 2011. Home range and movement of desert tortoises *Gopherus agassizii* in the Mojave Desert of California, USA. Endanger. Species Res. 13, 191–201.
Frazer, N., 1992. Sea turtle conservation and halfway technology. Conserv. Biol. 6, 179–184.
Germano, J., Bishop, P., 2009. Suitability of amphibians and reptiles for translocation. Conserv. Biol. 23, 7–15.
Gibbons, J.W., Greene, J.L., 1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. Herpetologica 35, 86–89.
Gibbs, J.P., Hunter, E.A., Shoemaker, K.T., Tapia, W.H., Cayot, L.J., 2014. Demographic outcomes and ecosystem implications of giant tortoise reintroduction to Española Island, Galapagos. PLoS One 9 (10), 1–15.
Hazard, L.C., Morafka, D.J., 2002. Comparative dispersion of neonate and head-started juvenile desert tortoises (*Gopherus agassizii*): a preliminary assessment of age effects. Chelonian Conserv. Biol. 4 (2), 406–409.
Heppell, S.S., Crowder, L.B., Crouse, D.T., 1996. Models to evaluate head-starting as a management tool for long-lived turtles. Ecol. Appl. 6, 556–565.
Hoy, S., Peterson, R.O., Vucetich, J., 2020. Ecological studies of wolves on Isle Royale, 2019–2020. Ecol. Stud. Wolves Isle R. 2, 1–25.
Kohl, M.T., Messmer, T.A., Crabb, B.A., Guttery, M.R., Dahlgren, D.K., Larsen, R.T., Frey, S.N., Liguori, S., Baxter, R., 2019. The effects of electric power lines on the breeding ecology of greater sage-grouse. PLoS One 14 (1), 25.
MacNulty, D.R., Tallian, A., Stahler, D.R., Smith, D., 2014. Influence of group size on the success of wolves on hunting bison. PLoS One 9, 1–8.
Mazerolle, M.J. 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3–1, ⟨https://cran.r-project.org/package=AICcmodavg⟩.
McGovern, P.A., Buhlmann, K.A., Todd, B.D., Moore, C.T., Peaden, J.M., Hepinstall-Cymerman, J., Daly, J.A., Tuberville, T.D., 2020a. The effect of size on post release survival of head-started Mojave desert tortoises. J. Fish. Wildl. Manag. 11, 494–506.
McGovern, P.A., Buhlmann, K.A., Todd, B.D., Moore, C.T., Peaden, J.M., Hepinstall-Cymerman, J., Daly, J.A., Tuberville, T., 2020b. Comparing husbandry techniques for optimal head-starting of the Mojave desert tortoise (*Gopherus agassizii*). Herpetol. Conserv. Biol. 15, 626–641.
McRae, W.A., Landers, J.L., Garner, J., 1981. Movement patterns and home range of the gopher tortoise. Am. Midl. Nat. 106, 165–179.
Mohr, C., 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37, 223–249.
Nafus, M.G., Todd, B.D., Buhlmann, K.A., Tuberville, T.D., 2015. Consequences of maternal effects on offspring size, growth, and survival in the desert tortoise. J. Zool. 297, 108–114.
Nafus, M.G., Esque, T.C., Averill-Murray, R.C., Nussear, K.E., Swaisgood, R., 2017. Habitat drives dispersal and survival of translocated juvenile desert tortoises. J. Appl. Ecol. 54, 430–438.
Nagy, K.A., Hillard, L.S., Tuma, M.W., Morafka, D., 2015. Head-started desert tortoises (*Gopherus agassizii*): movements, survivorship, and mortality causes following their release. Herpetol. Conserv. Biol. 10, 203–215.
Nussear, K.E., Tracy, C.R., Medica, P.A., Wilson, D.S., Marlow, R.W., Corn, P., 2012. Translocation as a conservation tool for Agassiz's desert tortoises: survivorship, reproduction, and movements. J. Wildl. Manag. 76, 1341–1353.
Pille, F., Caron, S., Bonnet, X., Deleuze, S., Busson, D., Etien, T., Girard, F., Ballouard, J., 2018. Settlement pattern of tortoises translocated into the wild: a key to evaluate population reinforcement success. Biodivers. Conserv. 27, 437–457.
Quinn, D.P., Buhlmann, K.A., Jensen, J.B., Norton, T.M., Tuberville, T.D., 2018. Post-release movement and survivorship of head-started gopher tortoises. J. Wildl. Manag. 82, 1545–1554.
Reinert, H.K., Rupert Jr., R., 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. J. Herpetol. 33, 45–61.
Richter, C. 2022. Multi-year space use and survival of head-started Mojave desert tortoises (*Gopherus agassizii*) and factors influencing risk of predation by subsidized predators. Thesis. University of Georgia. Athens, GA, USA.
Seddon, P., 1999. Persistence without intervention: assessing success in wildlife reintroductions. Trends Ecol. Evol. 14, 503.
Spencer, R.J., Van Dyke, J.U., Thompson, M.B., 2017. Critically evaluating best management practices for preventing freshwater turtle extinctions. Conserv. Biol. 31, 1340–1349.
Stamps, J.A., Swaisgood, R., 2007. Someplace like home: Experience, habitat selection and conservation biology. Appl. Anim. Behav. Sci. 102, 392–409.
Tear, T.H., Scott, J.M., Hayward, P.H., Griffith, B., 1993. Status and prospects for success of the endangered species act: a look at recovery plans. Science 262, 976–977.
Tetzlaff, S.J., Sperry, J.H., DeGregorio, B.A., 2019. Effects of antipredator training, environmental enrichment, and soft release on wildlife translocations: a review and meta-analysis. Biol. Conserv. 236, 324–331.
Therneau, T. 2022. A Package for Survival Analysis in R. R package version 3.3–1. ⟨https://CRAN.R-project.org/package=survival⟩.
Todd, B.D., Willson, J.D., Gibbons, J.W., 2010. The global status of reptiles and causes of their decline. 47–67. In: Sparling, D.W., Bishop, C.A., Krest, S. (Eds.), Ecotoxicology of Amphibians and Reptiles, Second ed. CRC Press, Pensacola, FL, USA.
Todd, B.D., Halstead, B.J., Chiquoine, L.P., Peaden, J.M., Buhlmann, K.A., Tuberville, T.D., Nafus, M.G., 2016. Habitat selection by juvenile Mojave desert tortoises. J. Wildl. Manag. 80, 720–728.
Tuberville, T.D., Clark, E.E., Buhlmann, K.A., Gibbons, J., 2005. Translocation as a conservation tool: Site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). Anim. Conserv. 8, 349–358.
Tuberville, T.D., Todd, B.D., Hermann, S.M., Michener, W.K., Guyer, C., 2014. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. J. Wildl. Manag. 78, 1151–1160.
Tuberville, T.D., Quinn, D.P., Buhlmann, K.A., 2021. Movement and survival to winter dormancy of fall-released hatchling and head-started yearling gopher tortoises. J. Herpetol. 55, 88–94.
Tuma, M.W., Millington, C., Schumaker, N., Burnett, P., 2016. Modeling Agassiz's desert tortoise population response to anthropogenic stressors. J. Wildl. Manag. 80, 414–429.
US Department of the Interior. 2022. *Weather*. National Parks Service. Retrieved July 10, 2022, from ⟨https://www.nps.gov/moja/planyourvisit/weather.htm⟩.
US Fish and Wildlife Service, 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Mojave population of the desert tortoise, 55. Federal Register, pp. 12178–12191.
US Fish and Wildlife Service. 2011. Revised recovery plan for the Mojave population of the desert tortoise (*Gopherus agassizii*). US Fish and Wildlife Service, Pacific Southwest Region, Sacramento, California, USA.
Wold, S., 1974. Spline functions in data analysis. Technometrics 16, 1–11.
Woodbury, A.M., Hardy, R., 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecol. Monogr. 18, 145–200.