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RESEARCH ARTICLE

Survival and behavior of Mojave desert tortoises head-started with and without outdoor rearing

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Abstract

Mojave desert tortoise (*Gopherus agassizii*) populations in some regions have declined by >50% since 2004, prompting the need for more research on ways to recover populations. One possible recovery tool is head-starting (i.e., the act of protecting and raising juvenile tortoises to sizes that increase survival upon release); however, head-starting can have high start-up and maintenance costs that can limit its feasibility. Strategies that reduce cost and rearing duration may foster broader and more effective use. We released and radio-tracked 60 juvenile tortoises in the Mojave National Preserve in California, USA, that had been reared under 2 treatments: those reared 1 year indoors after hatching, then 1 year outdoors (combo) and those reared just 1 year indoors (indoor-only). We tested whether indoor-only rearing alone could be a more efficient means of producing robust head-started tortoises. We examined the behavior, movement, and survival of tortoises after release into the wild from 2020 to 2021 to determine whether these outcomes differed between husbandry treatments. Combo tortoises tended to perform settling behaviors (mean ± 1 SE days to building first burrow = 6.7 ± 0.8, entering dormancy = 23.3 ± 2.1, and emerging from dormancy = 189.6 ± 4.4) earlier than indoor-only tortoises (7.4 ± 0.9, 31.5 ± 2.6, and 193.9 ± 5.9,

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respectively), but this difference was not significant, suggesting the rearing method did not greatly alter settling behavior. Indoor-only tortoises dispersed at least twice as far from their release site (156.2 ± 26.3 m compared with 77.3 ± 20.6 m for combo tortoises), had larger mean use areas (3.7 ± 0.1 ha compared with 2.8 ± 0.3 ha for combo tortoises for 95% Brownian bridge movement model estimates), and greater variability in their movements than combo tortoises (daily average step length post-emergence: 4.3 ± 0.2 m compared with 2.8 ± 0.1 m for combo tortoises). Despite differences in their movements, indoor-only and combo tortoises had similar survival rates over the study, 51% versus 42%, respectively, during a period of extreme drought in 2021. The similarity in survival between groups gives head-starting practitioners freedom in their rearing methods. The indoor-only group had lower site fidelity, which should be considered when this is an undesirable trait for released tortoises.

KEYWORDS

behavior, climate change, *Gopherus agassizii*, head-starting, movement, population augmentation, population recovery, survivorship

Wildlife species worldwide have been declining because of a variety of factors, including habitat loss, climate change, pollution, and human-subsidized predators (Capdevila et al. 2022). When conservation measures are taken to address the underlying causes of decline, many species may still require direct intervention for populations to rebound. Species like California condors (*Gymnogyps californianus*; Kelly et al. 2015) and black-footed ferrets (*Mustela nigripes*; Santymire et al. 2014), for example, required extensive reintroduction efforts to recover. Species with slow life histories are especially vulnerable to decline and are slow to recover (Congdon et al. 1993, Tuberville et al. 2014), often making population augmentation essential for their survival.

Turtles are a particularly threatened taxon, with over half of species threatened with extinction (Lovich et al. 2018). Some traits, like their long lifespans, delayed sexual maturity, and low juvenile recruitment rates, make turtles vulnerable to decline because they cannot adapt quickly to sudden changes in their environment (Stanford et al. 2020, Berry et al. 2021). The Mojave desert tortoise (*Gopherus agassizii*; i.e., desert tortoise, tortoise) is one such turtle species that has experienced chronic declines and has been listed as threatened under the United States Endangered Species Act since 1990 (U.S. Fish and Wildlife Service [USFWS] 1983). Desert tortoises are considered important keystone species because they construct burrows that are used as refugia by other species (Woodbury and Hardy 1948, Agha et al. 2017), they serve as indicators of ecosystem health (Berry and Medica 1995), and they are an iconic species of the Mojave Desert (Kohn 2018). While tortoises have many traits suited to arid environments, including prolonged fasting, periods of inactivity, and seeking shelter in burrows, they can be sensitive to changes in their environment (Nagy and Medica 1986, Bulova 2002). The added stressor of climate variation, especially the extended drought that the southwestern United States has been experiencing since 2000 (Williams et al. 2020, 2022), reduces desert tortoise survival even in otherwise protected areas (Lovich et al. 2014*b*). Increased drought conditions and other threats like wildfires (Brooks 1999), habitat destruction (Morris et al. 1997, Parker et al. 2018), and human-subsidized predators (Kristan and Boarman 2003, Esque et al. 2010) have contributed to population declines of desert tortoises. From 2004–2014, abundance of adult desert tortoises declined in 4 out of 5 USFWS-designated recovery units, and juveniles have declined in all recovery units since 2007 (Allison and McLuckie 2018).

To counter tortoise population declines, recovery tools are being studied and refined in a few locations before wider implementation in areas where population recovery may be needed (USFWS 2011). One recovery tool (i.e., head-starting) is the practice of rearing juveniles to a size at which they are less vulnerable to mortality and then releasing them into the wild (USFWS 2011, Burke 2015). When combined with other recovery tools, head-starting may help jumpstart conservation efforts to restore populations (Spencer et al. 2017). For Mojave desert tortoises, the recommended size at release is approximately 100 mm midline carapace length (MCL), which reduces mortality from exposure (e.g., dehydration) and predation (Nagy et al. 2015*b*). But it may take ≥7 years for juveniles to reach this size when reared outdoors, even with access to supplemental water (Nagy et al. 2015*a*, Daly et al. 2019, Tuberville et al. 2019), which limits the feasibility of head-starting given the cost and time required for husbandry. To accelerate that process, Daly et al. (2019) tested the efficiency of indoor rearing, which involved keeping tortoises indoors where they remained active and growing year-round, including when they would otherwise be dormant over winter. They released 3 groups of tortoises: hatchlings, 7-month old indoor-reared tortoises, and 7-month old outdoor-reared tortoises, and reported that indoor rearing produced tortoises much larger than those reared outdoors, but post-release survival for the first 6 months did not differ significantly among the groups (Daly et al. 2019). To explore whether a longer rearing period would further increase tortoise survival, a husbandry approach called combo rearing was developed that combines an indoor-rearing component for 1 year, during which hatchling tortoises grow rapidly by being fed and kept active year-round, followed by outdoor rearing for 1 year, during which tortoises are kept in predator-proof pens, are exposed to natural environmental cues, and perform behaviors critical to surviving in the wild like building burrows and undergoing winter dormancy (McGovern et al. 2020*a*, 2021). The latter husbandry approach has proven successful in producing healthy tortoises that attained the recommended release size within 2 years and exhibited high survival after release in the wild (McGovern et al. 2020*a*, *b*; Candal 2021). It is unclear, though, whether the high survival of combo-reared tortoises is attributable to exposure to natural environmental cues during their year outdoors or to the larger size attained during their first year indoors. It is also important to understand whether or how different husbandry processes affect tortoise behavior and movement after release. For instance, if tortoises are reared only indoors before release, will they respond appropriately to changes in their environment like settling into burrows for winter dormancy with the onset of colder weather? Likewise, without prior exposure to the outdoors, will tortoises be more likely to disperse away from release locations? Will a particular treatment cause greater individual variability than the other (Shaw 2020)? These factors may lower survival or site fidelity (Nussear et al. 2012), either of which could limit the appeal of indoor-only rearing as a head-starting method.

We tested whether the second year of combo rearing, in which tortoises are reared outdoors, improves the release outcome relative to 1 year of indoor rearing alone to determine whether providing an added year outdoors before release should continue to be a priority for head-start programs. We compared the post-release settling behavior, movement, and first-year survival of combo-reared (1 year indoors after hatching, 1 additional year outdoors; combo) and indoor-reared (just 1 year indoors after hatching; indoor-only) tortoises. We predicted that combo tortoises, which were already exposed to natural environmental cues during outdoor rearing, would settle into their wild habitat more quickly and with less individual variability after release than indoor-only tortoises that experienced only indoor rearing; combo tortoises would have reduced movements and variability in movements before and after settlement; and after accounting for size, husbandry treatment would not affect tortoise survival after release because both husbandry treatments produce robust tortoises that exceed the minimum release size threshold known to increase survival in earlier studies.

STUDY AREA

The study was conducted in the Ivanpah Valley within the Mojave National Preserve in San Bernardino County, California, USA, from 2018-2021, with the post-release monitoring occurring during 2020-2021. The approximately 150-ha study area is within the Eastern Mojave recovery unit for the Mojave desert tortoise, where the species has experienced the greatest decline in juvenile recruitment (USFWS 2011, Allison and McLuckie 2018), making it an ideal place to study the effect of head-starting augmentation on populations. Land use was primarily as a natural preserve, with occasional recreational use of primitive roads by visitors. We conducted all head-starting at the Ivanpah Desert Tortoise Research Facility. The release site was approximately 15 km south of the research facility and was dominated by yucca woodland vegetation communities, with dominant plants being creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), yuccas (*Yucca brevifolia*, *Y. shidigera*), branched pencil cholla (*Cylindropuntia ramosissima*), and littleleaf ratany (*Krameria erecta*; Todd et al. 2016). The site also contained many small washes and small-mammal burrows used as shelter sites by multiple wildlife species (Todd et al. 2016). Elevation ranged from 940–1,075 m above sea level and the topography was relatively flat. The region has a dry, desert climate with 4 plant phenological seasons including spring (Feb–Apr), summer (May–Aug), fall (Sep–Nov), and winter (Dec–Feb), and a rainy season from approximately November to April. From 2000–2022, the temperatures at the study site ranged from a long-term average high of 40.6°C to an average low of −6°C, and the annual precipitation ranged from 4.7–50.6 cm/year. During our study period, the average annual precipitation was just 5.4 cm/year (Applied Climate Information System 2022).

In October 2020, the Palmer drought severity index (a measure of relative severity of drought conditions over time with 0 representing the average) was −1.9, indicating a period of drought. The Palmer drought severity index remained negative for the rest of the present study through December 2021 and reached a low of −3.9, which is the lowest Palmer drought severity index value reported for the study site in the last 10 years (Abatzoglou 2013; https://app.climateengine.com/climateEngine, accessed 08 May 2022).

METHODS

Obtaining hatchlings

To obtain hatchlings, we captured adult female desert tortoises at the study area during late April—early May in 2018 (*n* = 18) and 2019 (*n* = 28), brought them to the research facility, and radiographed them to check for calcified eggs (Diagnostic Imaging Systems, Poskam, Colorado, USA; 60 kvp, 0.8 mAS, 74 cm focal length; Gibbons and Greene 1979). We immediately returned all non-gravid females to their capture location. We placed gravid females in individual 9-m × 9-m predator-proof nesting pens with pre-made burrows and natural vegetation (McGovern et al. 2020*a*, *b*). We allowed gravid females to nest naturally and gave them supplemental water from an aquifer-fed sprinkler system (Tuberville et al. 2019) and supplemental food. We radiographed females every 10 days to monitor for egg deposition, and when it was confirmed that they had nested, we returned them to the wild at their original capture location. We returned any females that had not laid their eggs within 30 days to their last known burrow location, in accordance with permits. Fifteen females nested in the pens in 2018 and 19 females nested in 2019, with 9 females nesting both years. Once eggs were laid, they incubated naturally in the predator-proof pens. We began searching pens for emerging hatchlings 80 days after the estimated nest date and we marked hatchlings with unique identification numbers assigned by USFWS using the notching technique in Cagle (1939). Each nest from 2018 and 2019 produced hatchlings.

Experimental treatments

We compared 2 experimental rearing treatments: combo rearing and indoor rearing. Combo rearing involved rearing hatchling tortoises inside for 1 year, keeping tortoises active and eating year-round to achieve rapid growth, followed by 1 year of outdoor rearing to provide exposure to natural environmental cues while still protecting the tortoises from predators. Indoor rearing involved rearing tortoises indoors for just 1 year after hatching before releasing them into the wild.

In September 2018, we selected 48 hatchlings for the combo treatment. We assigned tortoises to 1 of 6 large indoor-rearing tubs (8 hatchlings/tub). To account for possible maternal effects, we separated tortoises from the same clutch so no siblings were placed together in a single tub (Nafus et al. 2015). Each tub consisted of a 190-L stock tank (132 × 79 × 30.5 cm) equipped with natural substrate, humid hide boxes to promote normal shell growth and avoid pyramiding (Wiesner and Iben 2003), artificial plastic shelters, and a paper feeding plate. Lighting was provided using a 50-W ZooMed Repti Basking Spot Lamp bulb (Zoo Med Laboratories, San Luis Obispo, CA, USA) for daytime basking (37°C), a ZooMed 50-W Infrared Basking Spot bulb for night-time heat (32°C), and a 26-W Exo-Terra Reptile UVB150 bulb (Rolf C. Hagen Corp., Mansfield, MA, USA) for optimal calcium metabolism and vitamin D_3 conversion (McWilliams 2005), all suspended 30 cm above the tub and set with automatic timers to mimic a natural photoperiod. While tortoises were indoors, we provided food (a mixture of greens and moistened Mazuri® Tortoise Diet; Mazuri Exotic Animal Nutrition, St. Louis, MO, USA; Daly et al. 2018) 3 times a week, supplemental calcium powder twice a week, and soaked tortoises once a week to maintain hydration. Once a month during indoor rearing, we recorded tortoise mass to the nearest 0.1 g, and MCL, shell width, and shell height to the nearest 1 mm.

In fall of 2019, after 1 year of indoor rearing, we measured and weighed tortoises assigned to the combo treatment and placed them in 9-m × 30-m outdoor juvenile pens. The outdoor juvenile pens (different pens than the female nesting pens but of similar materials) were predator-proof, with pre-made burrows, natural terrain, and native vegetation. Once a week during the active season (~Apr–Nov), we provided them with the same type of supplemental food that they had received while indoors and water from a sprinkler system. McGovern et al. (2020*a*) provides further husbandry details. We then selected 48 tortoises that hatched in 2019 for the indoor-only treatment and assigned them to the indoor tubs in the same way the 2018 combo tortoises had been.

By the time of release, tortoises assigned to the combo treatment had spent 1 year indoors, then 1 year outdoors and were 2 years old (2018–2020). Tortoises assigned to the indoor-only treatment had spent 1 year indoors and were 1 year old (2019–2020). Prior to release, we measured and weighed all tortoises to confirm they were fit to be released (i.e., healthy; Berry and Christopher 2001) and around the recommended release size of 100 mm MCL.

Release and monitoring

Using ArcGIS (version 10.5; Esri, Redlands, CA, USA), we identified a release site that met the following criteria: 0.6 km^2 (300 m × 2,000 m) rectangular area (McGovern 2019), parallel to and ≥200 m from a dirt access road to reduce tortoise interaction with the road, and ≥1.6 km from any powerline to reduce common raven (*Corvus corax*) predation (Daly et al. 2019). We divided the area into 3 blocks with a 400-m buffer between blocks to reduce the chance of tortoises settling in a different block than they were assigned. The use of blocks allowed for easier access to track tortoises post-release and reduced the amount of disturbance within the release area. Within each block, we created a grid of 20 release points 50 m apart throughout. We randomly selected 30 of the 48 tortoises from each treatment group to be released (60 tortoises released). Within each of the 3 blocks, we released 10 combo tortoises and 10 indoor-only tortoises, assigning individuals to separate release points, making sure to alternate treatment types assigned to each block. Within 10 m of each release point, we selected a suitable release refugium in the form of a kangaroo rat (*Dipodomys* spp.) burrow beneath a large perennial shrub, and we enlarged the burrow using a hand trowel the day before tortoises were released to provide shelter for each released tortoise. We measured the selected tortoises and fit them with an Advanced Telemetry Systems (Isanti, MN, USA) radio-transmitter (model R1670, 3.1 g or model R1680, 3.6 g) on the fifth vertebral scute with gel epoxy (Devcon 5-minute epoxy gel, ITW Engineered Polymers, County Clare, Ireland). We released all tortoises on 1 October 2020.

Using a 3-element Yagi antenna (AF Antronics, Inc., Urbana, IL, USA) and a R1000 receiver (Communications Specialists, Orange, CA, USA), we radio-tracked tortoises 24 hours after release, twice a week for the first 3 weeks, then once a week until winter dormancy (fall 2020). After all tortoises ceased moving and entered winter dormancy in mid-November 2020, we reduced tracking to once every 10–14 days. In March 2021, when tortoises started emerging from winter dormancy, we resumed weekly tracking. We radio-tracked until December 2021 (15 months of monitoring). At each tracking event, we collected data on the tortoise's location to the nearest 3 m using a handheld global positioning system unit (Garmin GPSMAP 76CSx, Olathe, KS, USA), cover usage (burrow or pallet, surface hidden, surface open), approximate distance from last tracking location, and time of day. We visually confirmed the location of the tortoise unless it was deep enough inside a burrow that it could not be seen. When we found a dead tortoise, we photographed the tortoise remains and attempted to determine cause (i.e., mammalian predator, avian predator, exposure).

Data analysis

Settling behaviors

We characterized settling behavior using 3 metrics: timing of first burrow establishment, winter dormancy initiation, and spring emergence. Although we provided each tortoise with a burrow at release, we considered the milestone of a tortoise constructing its own first burrow as an early indication of the tortoise settling into its new environment. Burrows provided shelter from predators and temperature extremes, and thus were likely to influence tortoise survival (Bulova 2002, McGovern et al. 2021, Tuberville et al. 2021). We defined the initiation of winter dormancy as the date tortoises remained in the same burrow for 2 weeks in fall. Initiation of winter dormancy was another indication of settling behavior as tortoises generally cease movement on the surface for several months, although they may occasionally emerge from their burrows to bask on warm winter days (Nagy and Medica 1986). Finally, we defined the spring emergence for each individual as the date on which the tortoise was documented to have moved ≥1 m from its winter dormancy burrow, even if only to bask and return to the same burrow. Spring emergence was an important behavior for gauging tortoises' sensitivity to the seasonal change in environmental conditions.

We predicted that tortoises in the combo group would build their first burrows, initiate winter dormancy, and emerge from dormancy in spring earlier than those in the indoor-only group. We also predicted that the naïve indoor-only tortoises might exhibit greater variability in these behaviors compared to the more experienced combo tortoises. While in captivity, only combo tortoises had the opportunity to create their own burrows and be exposed to natural environmental cues during their second year when they were in outdoor enclosures. Thus, timing of post-release settling behaviors and variability among individuals might differ between combo and indoor-only tortoises. For each settling metric (i.e., response variable), we used Levene's tests (Carroll and Schneider 1985) to compare homogeneity of variances in days to the behavior between husbandry treatments. We used generalized linear models (GLM) to compare means in settling behaviors between husbandry treatments. Each response variable was measured as days since release. Because each metric was constrained to be positive, real values, we used negative binomial models, with husbandry treatment as a categorical predictor variable and the number of days until each behavior was initiated as the response variable.

Movement and use areas

We predicted that the combo group would have smaller use areas, shorter dispersal distances, shorter step lengths, and less variability in these movement metrics than the indoor-only group. Individual variability in animal movement can be caused by multiple factors and affect the local population and community as a whole, either positively, such as dispersing widely throughout the foraging area, or negatively, when larger movements take a greater energy toll and potentially reduce survival (Shaw 2020). To evaluate use area sizes, we calculated 95% and 50% Brownian bridge movement models (BBMM; Horne et al. 2007) for each tortoise using their locations during the first full active season following release (~Apr–Nov 2021). The BBMM is traditionally used for calculating home ranges, but because we only had 1 active season within the study, we use the term use areas to define the area used by tortoises during their first active season. We chose the BBMM approach because 4 individuals shifted the location of their use areas mid-season, and BBMMs prevent use areas from being overestimated by accounting for temporal autocorrelation resulting from large movement. Unlike the standard kernel density estimator, BBMMs create a use area based on the path an animal took while excluding the areas it likely did not use along the way (Horne et al. 2007). The BBMM has also been recommended for use in reptile studies using very high frequency tracking because it works well with tracking data and provides estimates with less error than standard kernel density estimator or minimum convex polygon (MCP) approaches (Silva et al. 2020). For the purposes of comparison with other similar studies, we also calculated the 95% MCP use area. For the calculations of the BBMM and MCP, we excluded data prior to their final settling metric (i.e., spring emergence) to focus on the active season and to avoid inflated use area estimates associated with exploratory behavior immediately after release (Richter et al. 2024). We included in the use area estimates 1 location associated with their first winter dormancy burrow from which they emerged in spring 2021, 1 location associated with their second winter dormancy burrow at the end of the 2021 active season (if applicable), and all locations between these time points. We included the winter dormancy locations in the use area analysis because of the importance of dormancy burrows for tortoise survival and the extensive amount of time (~4.5 months) tortoises spend in them (Nagy and Medica 1986, Daly et al. 2019). We calculated use areas for individuals with ≥10 locations in the 2021 active season (*n* = 28 combo, 30 indoor-only), although most (*n* = 36) spanned March-November 2021; the average number of tracking locations for each tortoise was 22.

After calculating the 50% and 95% BBMMs, we used Levene's tests to compare homogeneity of variances in use area sizes between husbandry treatments. For each use area estimator (50%, 95% BBMMs, 95% MCP), we then compared use area size using a gamma GLM with husbandry treatment as the predictor variable and use area size (in ha) as the response variable. We performed calculations and analyses using the packages adehabitatHR and adehabitatLR (Calenge 2018) in Program R (R Core Team 2020).

We assessed site fidelity of released head-starts using ArcGIS and the tracking data to calculate Euclidian dispersal distances (straight-line distance between 2 points) for the following 4 dispersal periods: pre-dormancy (release location to first dormancy location), post-dormancy (first dormancy location to end of the study location), total dispersal for tortoises that died or went missing (release location to last known alive location), and total dispersal for the tortoises that survived (release location to end of study location). When we found tortoises depredated, we used their last known alive location to calculate their total dispersal instead of where they were found dead to avoid the potential bias of predators carrying a tortoise away. For each dispersal period, we used Levene's tests to compare homogeneity of variances in dispersal distances between husbandry treatments. For each dispersal metric, we compared means using gamma GLMs (McGovern et al. 2020*a*) with husbandry treatment as the predictor variable and distance (m) as the response variable. Gamma GLMs are widely used in analyses that involve continuous, non-negative and positive-skewed data, which in this case were appropriate for distances.

We calculated daily movement using the average daily step length for each tortoise for 2 time periods: 4 weeks post-release and 8 weeks post-emergence in spring. Calculating daily step lengths provided a way to standardize our weekly tracking. We chose these time periods because within approximately 4 weeks after release, ≥40% of tortoises had initiated winter dormancy, and within 8 weeks following spring emergence, most tortoises (71.7%) had slowed their movements as part of summer estivation. For each time period, we calculated daily average step length as distance (m) from the last observation divided by the number of days since last observation for every tracking event. Thus, each tortoise had a step length estimated for each date within both time periods. We tracked all tortoises at the same frequency, allowing for detection of between-treatment differences. We also created a binomial response for each step length that assigned a value of 1 if the tortoise had moved on that date and 0 if not.

We then assigned the step-length estimates to the week after release or after emergence to assess the effect of time. We used Levene's tests to compare homogeneity of variances in step lengths between husbandry treatments. Within each time period, we compared the step lengths of each treatment group using a zero-inflated gamma hurdle model. A zero-inflated gamma hurdle model uses a binomial model to quantify the probability of a tortoise moving (1 if tortoise moved, 0 if not) and a gamma model to compare the step lengths of tortoises that did move. For both sub-models, we included husbandry treatment and week after event as predictor variables. We performed all calculations and analyses for the model sets using the statistical package lme4 (Bates et al. 2017) in Program R. All averages are reported as the mean (±1 SE).

Survival

We predicted that survival of head-started desert tortoises would not differ between treatments. We used Kaplan-Meier survivorship curves to determine the 15-month survival of all head-started tortoises released and to compare survival between treatments (Kaplan-Meier 1958). We censored tortoises that went missing during the study from the models to account for their unknown fates. We also used a Cox proportional hazard model (Cox 1972) to examine the effect of husbandry treatment and release MCL on survival of head-starts. The minimum number of observations for any individual was 9 observations, or 243 days after release. We performed all calculations and analyses for survival models using the statistical package survminer (Kassambara et al. 2021) in Program R.

RESULTS

At the time of release (1 Oct 2020), the mean MCL of combo tortoises (2018 cohort; $n = 30$) was 110.8 ± 8.7 mm (range = 94.0–126.9 mm) and that of indoor-only tortoises (2019 cohort; $n = 30$) was 102.6 ± 8.9 mm (range = 90.4–128.8 mm). We found strong evidence that combo tortoises were larger than indoor-only tortoises at release ($Z = -3.1$, $P = 0.002$).

Settling behaviors

Overall, tortoises took an average of 7.0 ± 0.6 days (range = 1–19) after release to build their first burrow, 27.4 ± 1.7 days (range = 5–53) to initiate dormancy, and 191.8 ± 3.6 days (range = 80–249) since release to emerge in spring (Table 1). These averages corresponded to the dates of 8 October 2020 for building a burrow, 28 October 2020 for initiating dormancy, and 10 April 2021 for spring emergence. The average dormancy duration was 164.4 ± 4.3 days (range = 49–238). There was no evidence of differences in the variances of settling behaviors between treatments (days to burrow: $F = 0.08$, $P = 0.77$; days to dormancy: $F = 1.69$, $P = 0.19$; days to emergence: $F = 1.50$, $P = 0.22$). Combo tortoises tended to build their first burrow <1 day sooner than indoor-only tortoises, but there was little evidence that this difference was significant (Table 2). Combo tortoises initiated dormancy >8 days sooner and emerged from winter dormancy >4 days sooner than indoor-only tortoises on average, but we only found evidence for a difference between treatments for dormancy initiation (Tables 1 and 2).

Movement and use areas

We estimated the 50% and 95% BBMM and 95% MCP use areas of 58 tortoises (30 indoor-only, 28 combo), excluding 2 combo tortoises that were depredated within 15–49 days of their spring emergence and therefore did

TABLE 1 Means and ranges for timing of settling behaviors and movement of head-started juvenile Mojave desert tortoises released on Mojave National Preserve, California, USA, 2020–2021, by husbandry treatment type: combo rearing and indoor-only rearing. Settling behaviors represent the number of days since release (1 Oct 2020) when each settling behavior (building first burrow, initiating dormancy, and spring emergence) was performed by tortoises. Use area size is the calculated Brownian bridge movement model (BBMM) or minimum convex polygon (MCP) use area in hectares. Dispersal distances represent the Euclidian distance tortoises dispersed (m) pre-dormancy (release point to first dormancy point), post-dormancy (first dormancy point to last point), total dispersal (release point to last point) for tortoises that went missing or died, and total dispersal for tortoises that survived the study. Step lengths represent the daily average distance moved (m) for 4 weeks post-release and 8 weeks post-emergence when tortoises moved. For all metrics, *n* = 30 unless otherwise noted.

Metric	Treatment	$\bar{x}$	SE	Range
Settling behaviors (days since release)				
Building burrow	Indoor-only	7.4	0.9	1.0-19.0
	Combo	6.7	0.8	1.0-15.0
	All (*n* = 60)	7.0	0.6	1.0-19.0
Dormancy initiation	Indoor-only	31.5	2.6	8.0-53.0
	Combo	23.3	2.1	5.0-53.0
	All (*n* = 60)	27.4	1.7	5.0-53.0
Spring emergence	Indoor-only	193.9	5.9	80.0-249
	Combo	189.6	4.4	151-249
	All (*n* = 60)	191.8	3.7	80.0-249
Use area size (ha)				
50% BBMM area	Indoor-only	0.4	0.0	0.1-0.9
	Combo (*n* = 28)	0.2	0.0	0.0-0.5
95% BBMM area	Indoor-only	3.7	0.1	2.3-8.0
	Combo (*n* = 28)	2.8	0.3	2.2-4.0
95% MCP area	Indoor-only	0.3	0.09	0.0-2.0
	Combo (*n* = 28)	0.1	0.02	0.01-0.6
Dispersal distances (m)				
Pre-dormancy dispersal	Indoor-only	85.0	13.9	4.3-360
	Combo	59.5	7.30	10.1-158
Post-dormancy dispersal	Indoor-only	106.1	23.2	4.50-546
	Combo	46.8	8.80	1.41-197
Total dispersal for missing and dead	Indoor-only (*n* = 15)	154.1	41.7	8.9-598
	Combo (*n* = 21)	73.3	10.5	5.9-153
Total dispersal for surviving	Indoor-only (*n* = 15)	156.2	26.3	42.1-388
	Combo (*n* = 9)	77.3	20.6	15.5-203

(Continues)

TABLE 1 (Continued)

Metric	Treatment	$\bar{x}$	SE	Range
Daily step lengths (m)				
Daily step length post-release	Indoor-only	14.5	0.6	0.6-74.0
	Combo	12.6	0.5	0.5-95.0
Daily step length post-emergence	Indoor-only	4.3	0.2	0.1-26.3
	Combo	2.8	0.1	0.1-15.3

TABLE 2 Results of statistical comparisons of settling behaviors and movements of head-started juvenile Mojave desert tortoises released in the Mojave National Preserve, California, USA, 2020–2021. The values shown include back-transformed treatment effect size, 95% confidence interval (CI), *Z* or *t* value, and *P*-value of each comparison between indoor-only or combo head-started tortoises. We compared settling behaviors using negative binomial generalized linear models (GLM; *Z* value), use area sizes using gamma GLMs (*t* value) for Brownian bridge movement models (BBMMs) or the minimum convex polygon (MCP), dispersal distances using gamma GLMs (*t* value) for pre-dormancy (release point to first dormancy location), post-dormancy (first dormancy location to last point), total dispersal (release point to last known alive point) for tortoises that went missing or died, and total dispersal for tortoises that survived the study.

Metric	Treatment effect size	95% CI	*Z* or *t*	*P*
Settling behaviors (days since release)				
Building burrow	1.11	0.80, 1.55	0.61	0.54
Dormancy initiation	1.36	1.07, 1.72	2.53	0.01
Spring emergence	1.02	0.950, 1.10	0.571	0.57
Use area size (ha)				
50% BBMM area	1.73	1.28, 2.35	3.55	0.001
95% BBMM area	1.34	1.13, 1.57	3.46	0.001
95% MCP area	0.003	0.00, 0.17	−2.49	0.016
Dispersal distances (m)				
Pre-dormancy dispersal	1.43	0.96, 2.14	1.75	0.09
Post-dormancy dispersal	2.27	1.28, 4.0	2.84	0.01
Total dispersal for missing and dead	2.10	1.21, 3.71	2.61	0.01
Total dispersal for surviving	2.02	1.10, 3.59	2.35	0.03

not have ≥10 observation points. On average, we found moderate evidence that the indoor-only tortoises had larger use areas than the combo tortoises for both BBMM and MCP calculations (all *P*-values < 0.016; Table 2). We also found moderate evidence that the variance was greater for indoor-only tortoises compared with combo tortoises for both 50% ($F = 4.30$, $P = 0.04$) and 95% ($F = 8.08$, $P = 0.01$) BBMM use areas. The 4 individuals that shifted their use areas mid-active season were all indoor-only tortoises.

On average, indoor-only tortoises moved about twice the distance of combo tortoises based on all 4 dispersal metrics (Table 1; Figure 1). The farthest an indoor-only tortoise dispersed was 598.1 m from its release

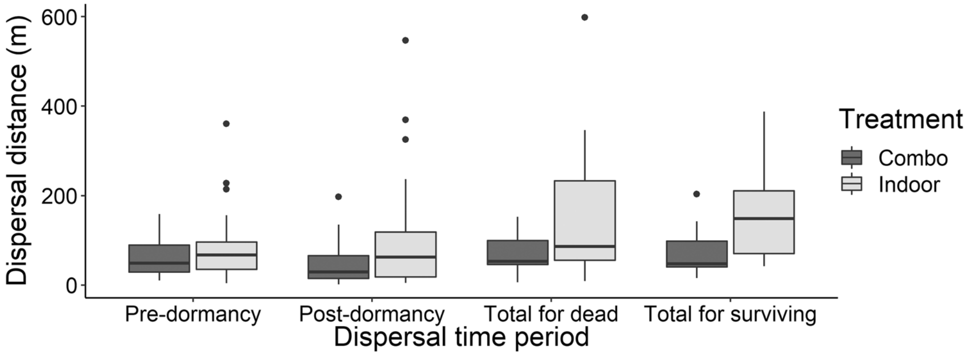

FIGURE 1 Euclidian dispersal distances (m) of head-started juvenile Mojave desert tortoises released on Mojave National Preserve, California, USA, October 2020, by husbandry treatment type: combo rearing and indoor-only rearing. We calculated pre-dormancy dispersal from the release point to first dormancy location ($n = 60$), post-dormancy from the first dormancy location to the end of the study ($n = 60$), total dispersal for the deceased and missing tortoises ($n = 35$; total for dead) from the release point to their last known alive point, and total dispersal for the surviving tortoises ($n = 25$; total for surviving) from the release point to the end of the study.

site, whereas the farthest a combo tortoise dispersed was 203.2 m from its release site. We found moderate evidence that the variance in movements for the post-dormancy dispersal and total dispersal for dead and missing tortoises was greater for indoor-only tortoises than combo tortoises ($F = 5.9$, $P = 0.01$ and $F = 5.12$, $P = 0.03$, respectively). On average, indoor-only tortoises moved farther than combo tortoises, and we found strong evidence for differences between the 2 treatment groups for all dispersal periods except for pre-dormancy (Tables 1 and 2).

We calculated the daily average step length for all 60 tortoises for 4 weeks post-release and 8 weeks post-emergence to assess their daily movement. The average daily step length of indoor-only tortoises 4 weeks after release was 14.5 ± 0.6 m (range = 0.6-74), whereas that of combo tortoises was 12.6 ± 0.5 m (range = 0.5-95; Table 1). Eight weeks post-emergence, the average daily step length of indoor-only tortoises was 4.3 ± 0.2 m (range = 0.1–26.3), whereas that of combo tortoises was 2.8 ± 0.1 m (range = 0.1–15.3; Table 1). We found very strong evidence that the variance among indoor-only tortoises' step lengths was greater than that for combo tortoises for both time periods (post-release: $F = 6.2$, $P = 0.01$ and post-emergence: $F = 39.1$, $P < 0.01$). After release, we found very strong evidence that the probability of movement for all tortoises decreased over time ($P < 0.001$). While we found very strong evidence that indoor-only tortoises initially had a lower probability of movement than combo tortoises ($P < 0.001$), by the end of the 4 weeks after release, indoor-only tortoises had a greater probability of moving than combo tortoises ($P < 0.001$, Figure 2A). The daily step lengths of tortoises after release decreased over time ($P < 0.001$), although we found no evidence that daily step lengths differed between indoor-only tortoises and combo tortoises for the entire 4-week period ($P = 0.517$; Figure 2B).

After spring emergence, there was very strong evidence that the overall probability of movement decreased over time ($P = 0.001$), but for an indoor-only tortoise, the probability of movement actually increased over time ($P = 0.005$; Figure 2C). By the end of the 8-week period, there was no evidence that probability of movement differed between treatment groups ($P = 0.345$; Figure 2C). We found moderate evidence that indoor-only tortoises initially had greater daily step lengths after emergence than combo tortoises ($P = 0.011$), but by the end of the 8-week time period, there was very strong evidence that combo tortoises had greater daily step lengths than indoor-only tortoises ($P < 0.001$; Figure 2D).

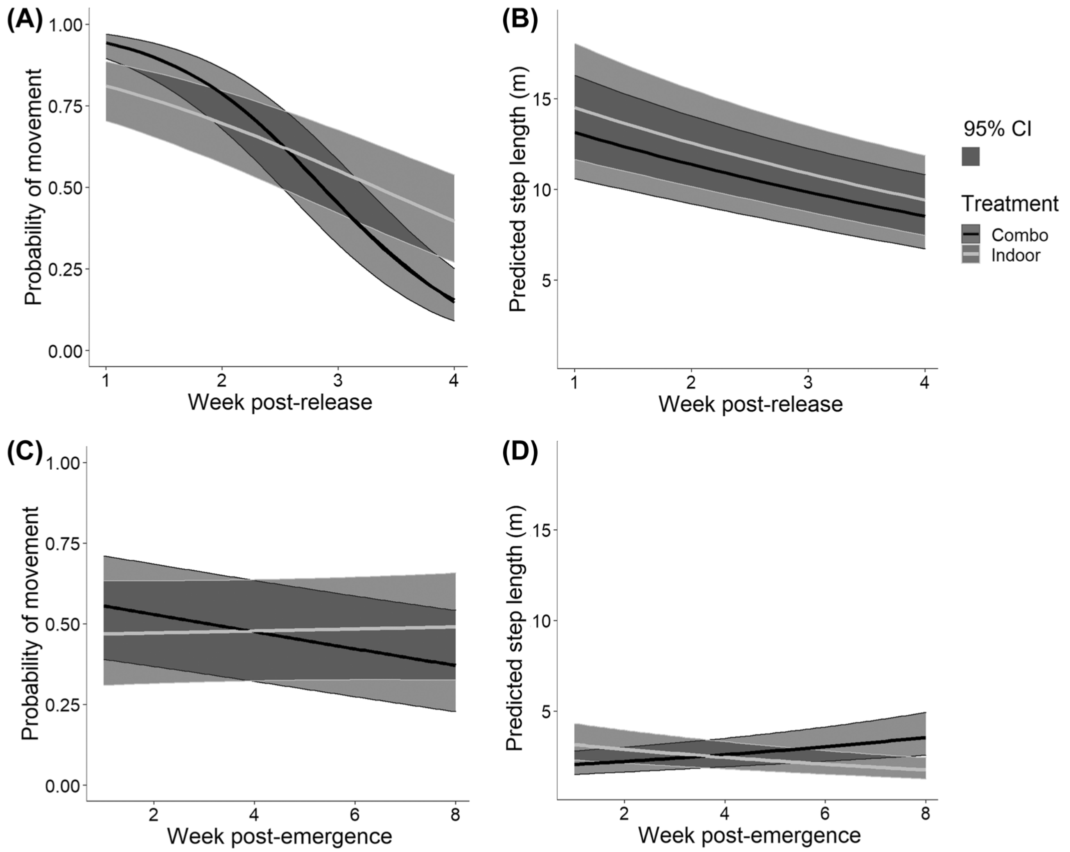

FIGURE 2 Step-length predictions of head-started juvenile Mojave desert tortoises released on Mojave National Preserve, California, USA, in October 2020 by husbandry treatment type: combo rearing and indoor-only rearing. Graphs show A) the probability of movement post-release, B) predicted step length (m) post-release, C) probability of movement post-emergence, and D) predicted step length (m) post-emergence. Shaded regions show 95% confidence intervals (CI).

Survival

Of the 60 head-started tortoises, all survived through their first dormancy (November 2020–April 2021), and 25 (41.7%) were known to have survived to their second dormancy at the end of the study 15 months after release (December 2021). Thirty (50%) tortoises died (29 from predation, 1 from exposure), and 5 (8.3%) tortoises went missing during the 2021 active season and were censored from analyses. We determined mammalian predators were the causes of loss to predation in all cases based on the presence of bite marks and the nature of the broken shell fragments. The exact species could not be pinpointed; however, mammal mesopredators such as coyotes (*Canis latrans*), kit foxes (*Vulpes macrotis*), or American badgers (*Taxidea taxus*) were suspected because of the jaw strength needed to break tortoise shells into pieces. Survival across both treatments for the 15 months after release was estimated at 0.47 (95% CI = 0.4–0.6) after accounting for censored tortoises (those missing with unknown fates). Overall, 0.42 (95% CI = 0.3–0.7) of combo tortoises and 0.51 (95% CI = 0.4–0.7) of indoor-only tortoises survived (Figure 3). We found no evidence that survival of tortoises differed between treatments ($Z = 0.1$, $P = 0.92$), but there was weak evidence that tortoises with a larger release MCL were more likely to survive ($Z = 1.7$, $P = 0.07$).

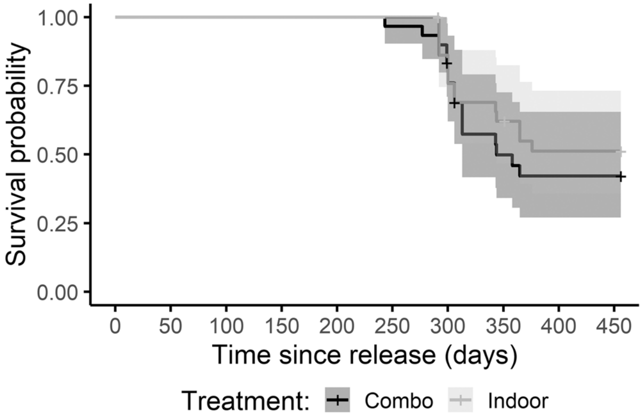

FIGURE 3 Survival probability curves of head-started juvenile Mojave desert tortoises released on Mojave National Preserve, California, USA, in October 2020 over the 15-month study by husbandry treatment type: combo rearing and indoor-only rearing. Shaded regions show 95% confidence intervals. By the end of the 15-month post-release monitoring period, combo head-starts had a survival rate of 0.42 (95% CI = 0.3–0.7) and indoor-only tortoises had a survival rate of 0.51 (95% CI = 0.4, 0.7).

DISCUSSION

We found that although head-starting treatment did not influence settling behavior, indoor-only tortoises dispersed farther from their release location, had larger use areas, and exhibited greater variation in movement following release compared to combo tortoises. Despite these differences, survival did not differ significantly between our treatments. Overall survival for tortoises in our study was lower than the first-year survival of other recent releases at our study site (McGovern et al. 2020*a*, Candal 2021), likely from elevated predation by coyotes and other mesopredators associated with the worsening drought severity in California and our study site throughout 2021 (Esque et al. 2010, Williams et al. 2022).

The timing of settling behaviors was not strongly influenced by husbandry treatment, except for dormancy initiation. Because all tortoises still initiated dormancy within a normal timeframe (~Oct–Nov), any biological difference between the treatment groups was not detectible. Therefore, our prediction that combo tortoises would exhibit settling behaviors earlier than indoor-only tortoises was not supported. During spring emergence, we also observed several tortoises, including those from previous releases being radio-tracked concurrently as part of a separate study, that emerged much later than normal, with the latest being in early June. We speculate that the extreme drought conditions with a lack of rainfall in late winter and early spring in 2021 kept some tortoises from emerging and becoming fully active within the normal time, similar to how drought conditions can reduce movements and activity of adult tortoises (Duda et al. 1999).

Animals released as part of a head-starting or translocation program often have a period of exploratory movement before settling into their release environments (Rittenhouse et al. 2007, Russell et al. 2010, Hazard et al. 2015, Rueda et al. 2021, Smetzer et al. 2021). For turtles, this exploratory period is usually associated with increased surface activity, which in turn can leave individuals vulnerable to predation (Hazard and Morafka 2002, Rittenhouse et al. 2007, Daly et al. 2019). Large post-release movements can also lead individuals away from habitat or alter their ability to thermoregulate (Hazard and Morafka 2002, Rittenhouse et al. 2007, Stamps and Swaisgood 2007, Roe et al. 2010). Because of this vulnerability and because dispersal from the release site is a leading cause of failure in reptile translocations (Germano and Bishop 2009), a common goal for turtle translocations is having individuals demonstrate high site fidelity to their release site. Our prediction that combo tortoises would have higher site fidelity than indoor-only tortoises was supported, with combo tortoises tending to stay closer to their release sites than indoor-only tortoises. Indoor-only tortoises also showed greater variability in most of the movement metrics than combo tortoises, and indoor-only tortoises had larger use areas than combo tortoises. Greater variability could stem from indoor-only tortoises not having been able to explore a larger area before release, unlike combo tortoises. Despite the larger use areas and movements of indoor-only tortoises after release, both treatment groups still showed high site fidelity overall compared to other juvenile tortoises (McGovern et al. 2020*a*), with most tortoises settling within 200 m of their release location.

Although indoor-only tortoises tended to move more often and farther than combo tortoises, survival did not differ between the treatment groups. Similarly, McGovern et al. (2020*a*) reported no significant difference in the survival of combo and exclusively outdoor-reared tortoises, suggesting that all 3 head-starting methods produce tortoises that survive similarly in the wild after release. Body size did not have a statistically significant effect on survival in our study, but a biologically meaningful trend that survival increased with size has been reported by others. Juvenile tortoises across a broader range of sizes had higher survival with increasing size before a plateau around release sizes of approximately 100 mm MCL (Nagy et al. 2015*b*, McGovern et al. 2020*b*). We likely did not find a significant effect of body size in the present study because all tortoises had an MCL of ≥90 mm and were close to, or exceeded, 100 mm MCL, and because droughts and associated heightened predation levels may more broadly affect tortoises of all sizes.

Survival of both treatment groups, 42% for combo tortoises, 51% for indoor-only tortoises, was lower than those from previous releases at the study site (96% for McGovern et al. 2020*a*, 79.3% for Candal 2021). We suspect that lower survival in the present study stems from worsening drought conditions compared with earlier studies, eventually reaching an extreme drought designation with a near absence of rainfall in the winter and spring following the present releases. Drought conditions like these tend to reduce the amount of available forage and free-standing drinking water, both of which tortoises rely on for survival (Peterson 1996). Drought has also been associated with reduced tortoise survival and movements in wild adult tortoises (Peterson 1994, Duda et al. 1999, Longshore et al. 2003, Lovich et al. 2014*a*).

We observed an increase in tortoise predation from mesopredators during the current study relative to previous releases at the site. When small-mammal populations in the desert are low, as happens during prolonged droughts (Beatley 1969), coyotes and kit foxes eat desert tortoises more often, thus reducing local tortoise populations (Nagy et al. 2015*b*, Kelly et al. 2021). Also, when mammal populations are low, rodent burrows may become less abundant, negatively affecting juvenile tortoises that rely on small-mammal burrows for refugia (Todd et al. 2016). All these factors likely contributed to the lower survival observed in the present study compared with earlier releases at the same study site (McGovern et al. 2020*b*, Candal 2021). Further investigation into the effects of climate on head-started tortoises could provide valuable insights into how tortoises are affected by changing climate and the best strategies for when to release tortoises for maximal survival and recruitment to aid population recovery.

Another possibly confounding effect that we were unable to explore is the effect of differing ages between the treatment groups. Because of the nature of the treatments, we could not parse out the effect of treatment type versus tortoise age. The differences in behavior and movement that we observed may have occurred because the combo tortoises had experienced a naturalistic environment during their time in the outdoor pen, or because they were 1 year older than the indoor-only group. Whether behavior and movement patterns are largely instinctual or affected by interactions with their environments over time has yet to be studied in desert tortoises.

One major challenge of captive rearing for reintroduction is ensuring animals are physically and behaviorally equipped for the wild. Animals reared in captivity may be unable to perform natural, learned behaviors needed to survive in the wild if not given the opportunity to experience suitable environmental conditions before being released (Einum and Fleming 2001, Mathews et al. 2005). One method used by captive-rearing practitioners to equip animals with wild behaviors is to provide them with enrichment, like natural habitat features in enclosures, anti-predator training, or foraging training (Reading et al. 2013, Tetzlaff et al. 2019). In a literature review of captive rearing and translocations, Tetzlaff et al. (2019) reported that animals released from captivity were more likely to survive if they had been given some type of enrichment before being released. In our study, the outdoor rearing component of combo rearing could be considered enrichment because tortoises were provided with opportunities to build burrows, respond to weather, forage on native plants, and experience winter dormancy before being released into the wild. Our results suggest that an outdoor-rearing component was not strictly necessary for tortoise survival during their first year following release but may provide valuable experience to head-started desert tortoises that reduces variability in their movements and encourages the highest site fidelity. It is not clear, however, whether these results would have differed under better climate conditions that might reveal an advantage of combo-reared tortoises having experienced a year of exposure to the outdoors that indoor-only tortoises did not experience. Future investigation into the influence of drought on tortoises after release using multiple years of data would allow us to determine whether the drought conditions in 2020–2021 masked an effect of treatment on tortoise survival.

MANAGEMENT IMPLICATIONS

If the goal of a Mojave desert tortoise head-starting program is to produce tortoises that exhibit high survival in the wild after release, our study suggests that indoor-only and combo rearing are equally successful, as we did not detect a measurable influence of husbandry on survival. Indoor-only rearing, without a subsequent year of outdoor rearing, is the more cost- and time-efficient means of producing tortoises given that less infrastructure and fewer resources are necessary than for combo rearing. When rearing tortoises indoors, the upfront cost of large rearing tubs and lighting fixtures is considerably less than outdoor pens and requires little space and less maintenance, potentially making indoor rearing more appealing to managers.

If managers wish to release tortoises with more predictable use area sizes and higher site fidelity, combo-reared tortoises would exhibit less among-individual variation in their movements and settling behaviors, perhaps making the higher cost of combo rearing justifiable. The absence of large dispersal outliers among the combo group may give more credence to a second year of outdoor rearing if low dispersal is a priority of reintroduction. We also recommend that when severe drought conditions occur or are forecast, managers consider not releasing tortoises to avoid the high rate of predation from mesocarnivores that we observed during the present study. Ultimately, management decisions must be made by balancing the benefits, risks, and costs of each rearing option.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All work was conducted in accordance with permits issued by the USFWS (TE-17838A-3), United States National Park Service (MOJA- 2018-SCI0016 [under study MOJA-00258]), and California Department of Fish and Wildlife (SC0011221). Animal protocols were approved by the University of Georgia's Institutional Animal Care and Use Committee (A2017 01-021-Y3-A3, A2020 01-025-Y2-A2).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Abatzoglou, J. T. 2013. Development of gridded surface meteorological data for ecological applications and modelling. International Journal of Climatology 33:121–131.

Agha, M., A. L. Smith, J. E. Lovich, D. Delaney, J. R. Ennen, J. Briggs, L. J. Fleckenstein, L. A. Tennant, S. R. Puffer, A. Walde, et al. 2017. Mammalian mesocarnivore visitation at tortoise burrows in a wind farm. Journal of Wildlife Management 81:1117–1124.

Allison, L. J., and A. M. McLuckie. 2018. Population trends in Mojave desert tortoise (*Gopherus agassizii*). Herpetological Conservation and Biology 13:433–452.

Applied Climate Information System. 2022. NOWData—NOAA Online Weather Data. <https://www.weather.gov/wrh/Climate?wfo=vef>. Accessed 24 Apr 2022.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, G. Grothendieck, and P. Green. 2017. lme4: linear mixed-effects models using 'Eigen' and S4. Version 1.1-13. http://lme4.r-forge.r-project.org/

Beatley, J. C. 1969. Dependence of desert rodents on winter annuals and precipitation. Ecology 50:721–724.

Berry, K. H., L. J. Allison, A. M. McLuckie, M. Vaughn, and R.W. Murphy. 2021. *Gopherus agassizii*. The IUCN Red List of Threatened Species 2021:e.T97246272A3150871.

Berry, K. H., and M. M. Christopher. 2001. Guidelines for the field evaluation of desert tortoise health and disease. Journal of Wildlife Diseases 37:427–450.

Berry, K. H., and P. A. Medica. 1995. Desert tortoises in the Mojave and Colorado deserts. Pages 135–137 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.

Brooks, M. L. 1999. Does protection of desert tortoise habitat generate other ecological benefits in the Mojave Desert? Pages 68-73 *in* Wilderness Science in a Time of Change Conference. U.S Department of Agriculture, U.S. Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA.

Bulova, S. J. 2002. How temperature, humidity, and burrow selection affect evaporative water loss in desert tortoises. Journal of Thermal Biology 27:175–189.

Burke, R. L. 2015. Head-starting turtles: learning from experience. Herpetological Conservation and Biology 10:299–308.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 3:170–173.

Calenge, C. 2018. adehabitat: analysis of habitat selection by animals. Version 1.8.20. https://cran.r-project.org/package=adehabitatHR

Candal, C. M. 2021. Pressure to perform: the role of stress physiology in head-starting success for Mojave desert tortoises. Thesis, University of Georgia, Athens, USA.

Capdevila, P., N. Noviello, L. McRae, R. Freeman, and C. F. Clements. 2022. Global patterns of resilience decline in vertebrate populations. Ecology Letters 25:240–251.

Carroll, R. J., and H. Schneider. 1985. A note on Levene's tests for equality of variances. Statistics and Probability Letters 3:191–194.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society: Series B (Methodological) 34:187–202.

Daly, J. A., K. A. Buhlmann, B. D. Todd, C. T. Moore, J. M. Peaden, and T. D. Tuberville. 2018. Comparing growth and body condition of indoor-reared, outdoor-reared, and direct-released juvenile Mojave Desert tortoises. Herpetological Conservation and Biology 13:622–633.

Daly, J. A., K. A. Buhlmann, B. D. Todd, C. T. Moore, J. M. Peaden, and T. D. Tuberville. 2019. Survival and movements of head-started Mojave desert tortoises. Journal of Wildlife Management 83:1700–1710.

Duda, J. J., A. J. Krzysik, and J. E. Freilich. 1999. Effects of drought on desert tortoise movement and activity. Journal of Wildlife Management 63:1181–1192.

Einum, S., and I. Fleming. 2001. Implications of stocking: ecological interactions between wild and released salmonids. Nordic Journal of Freshwater Research 75:56–70.

Esque, T. C., K. E. Nussear, K. K. Drake, A. D. Walde, K. H. Berry, R. C. Averill-Murray, A. P. Woodman, W. I. Boarman, P. A. Medica, J. Mack, et al. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endangered Species Research 12:167–177.

Germano, J. M., and P. J. Bishop. 2009. Suitability of amphibians and reptiles for translocation. Conservation Biology 23: 7–15.

Gibbons, J. W., and J. L. Greene. 1979. X-Ray photography: a technique to determine reproductive patterns of freshwater turtles. Herpetologica 35:86–89.

Hazard, L. C., and D. J. Morafka. 2002. Comparative dispersion of neonate and headstarted juvenile desert tortoises (*Gopherus agassizii*): a preliminary assessment of age effects. Chelonian Conservation and Biology 4:406–409.

Hazard, L. C., D. J. Morafka, and S. Hillard. 2015. Post-release dispersal and predation of head-started juvenile desert tortoises (*Gopherus agassizii*): effect of release site distance on homing behavior. Herpetological Conservation and Biology 10:504–515.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Kassambara, A., M. Kosinski, P. Biecek, and S. Fabian. 2021. survminer: drawing survival curves using 'ggplot2'. Version 0.4.9. https://rpkgs.datanovia.com/survminer/index.html

Kelly, E. C., B. L. Cypher, and T. L. Westall. 2021. Predation on desert tortoises (*Gopherus agassizii*) by desert canids. Journal of Arid Environments 189:104476.

Kelly, T. R., B. A. Rideout, J. Grantham, J. Brandt, L. J. Burnett, K. J. Sorenson, D. George, A. Welch, D. Moen, J. Rasico, et al. 2015. Two decades of cumulative impacts to survivorship of endangered California condors in California. Biological Conservation 191:391–399.

Kohn, H. 2018. The desert's canary: a narrative examination of the socio-political role of the threatened desert tortoise. Thesis, Humboldt State University, Arcata, California, USA.

Kristan, III, W. B., and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology 84:2432–2443.

Longshore, K. M., J. R. Jaeger, and J. M. Sappington. 2003. Desert tortoise (*Gopherus agassizii*) survival at two eastern Mojave Desert sites: death by short-term drought? Journal of Herpetology 37:169–177.

Lovich, J. E., M. Agha, C. B. Yackulic, K. Meyer-Wilkins, C. Bjurlin, J. R. Ennen, T. R. Arundel, and M. Austin. 2014*a*. Nest site characteristics, nesting movements, and lack of long-term nest site fidelity in Agassiz's desert tortoises at a wind energy facility in southern California. California Fish and Game 100:404–416.

Lovich, J. E., J. R. Ennen, M. Agha, and J. W. Gibbons. 2018. Where have all the turtles gone, and why does it matter? BioScience 68:771–781.

Lovich, J. E., C. B. Yackulic, J. Freilich, M. Agha, M. Austin, K. P. Meyer, T. R. Arundel, J. Hansen, M. S. Vamstad, and S. A. Root. 2014*b*. Climatic variation and tortoise survival: Has a desert species met its match? Biological Conservation 169:214–224.

Mathews, F., M. Orros, G. McLaren, M. Gelling, and R. Foster. 2005. Keeping fit on the ark: assessing the suitability of captive-bred animals for release. Biological Conservation 121:569–577.

McGovern, P. A. 2019. Changing the survival formula for the Mojave desert tortoise (*Gopherus agassizii*) through head-starting. Thesis, University of Georgia, Athens, USA.

McGovern, P. A., K. A. Buhlmann, B. D. Todd, C. T. Moore, J. M. Peaden, J. Hepinstall-Cymerman, J. A. Daly, and T. D. Tuberville. 2020*a*. Comparing husbandry techniques for optimal head-starting of the Mojave desert tortoise (*Gopherus agassizii*). Herpetological Conservation and Biology 15:626–641.

McGovern, P. A., K. A. Buhlmann, B. D. Todd, C. T. Moore, J. M. Peaden, J. Hepinstall-Cymerman, J. A. Daly, and T. D. Tuberville. 2020*b*. The effect of size on postrelease survival of head-started Mojave desert tortoises. Journal of Fish and Wildlife Management 11:494–506.

McGovern, P. A., J. M. Peaden, K. A. Buhlmann, B. D. Todd, and T. D. Tuberville. 2021. Comparing post-release cover and burrow use by differentially head-started Mojave desert tortoises in southern California. Conservation Evidence Journal 18:37–43.

McWilliams, D. A. 2005. Nutrition research on calcium homeostasis in lizards (with recommendations). International Zoo Yearbook 39:69–77.

Morris, R. L., D. A. Devitt, A. M. Crities, G. Borden, and L. N. Allen. 1997. Urbanization and water conservation in Las Vegas Valley, Nevada. Journal of Water Resources Planning and Management 123:189–195.

Nafus, M. G., B. D. Todd, K. A. Buhlmann, and T. D. Tuberville. 2015. Consequences of maternal effects on offspring size, growth and survival in the desert tortoise. Journal of Zoology 297:108–114.

Nagy, K. A., S. Hillard, S. Dickson, and D. J. Morafka. 2015*a*. Effects of artificial rain on survivorship, body condition, and growth of head-started desert tortoises (*Gopherus agassizii*) released to the open desert. Herpetological Conservation and Biology 10:535–549.

Nagy, K. A., L. S. Hillard, M. W. Tuma, and D. J. Morafka. 2015*b*. Head-started desert tortoises (*Gopherus agassizii*): movements, survivorship and mortality causes following their release. Herpetological Conservation and Biology 10: 203–215.

Nagy, K. A., and P. A. Medica. 1986. Physiological ecology of desert tortoises in southern Nevada. Herpetologica 42:73–92.

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.

Parker, S. S., B. S. Cohen, and J. Moore. 2018. Impact of solar and wind development on conservation values in the Mojave Desert. PLOS ONE 13:e0207678.

Peterson, C. C. 1994. Different rates and causes of high mortality in two populations of the threatened desert tortoise *Gopherus agassizii*. Biological Conservation 70:101–108.

Peterson, C. C. 1996. Ecological energetics of the desert tortoise (*Gopherus agassizii*): Effects of rainfall and drought. Ecology 77:1831–1844.

R Core Team. 2020. R: a language and environment for statistical computing. R version 4.0.2. R Foundation for Statistical Computing, Vienna, Austria.

Reading, R. P., B. Miller, and D. Shepherdson. 2013. The value of enrichment to reintroduction success. Zoo Biology 32: 332–341.

Richter, C. J., B. D. Todd, K. A. Buhlmann, C. M. Candal, P. A. McGovern, M. T. Kohl, and T. D. Tuberville. 2024. Effects of head-starting on multi-year space use and survival of an at-risk tortoise. Global Ecology and Conservation 49:e02774.

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

Roe, J. H., M. R. Frank, S. E. Gibson, O. Attum, and B. A. Kingsbury. 2010. No place like home: an experimental comparison of reintroduction strategies using snakes. Journal of Applied Ecology 47:1253–1261.

Rueda, C., J. Jiménez, M. J. Palacios, and A. Margalida. 2021. Exploratory and territorial behavior in a reintroduced population of Iberian lynx. Scientific Reports 11:14148.

Russell, J. C., A. J. C. McMorland, and J. W. B. MacKay. 2010. Exploratory behaviour of colonizing rats in novel environments. Animal Behaviour 79:159–164.

Santymire, R. M., T. M. Livieri, H. Branvold-Faber, and P. E. Marinari. 2014. The black-footed ferret: on the brink of recovery? Pages 119–134 *in* W. V. Holt, J. L. Brown, and P. Comizzoli, editors. Reproductive sciences in animal conservation: progress and prospects. 753. Springer-Verlag, Berlin, Germany.

Shaw, A. K. 2020. Causes and consequences of individual variation in animal movement. Movement Ecology 8:12.

Silva, I., M. Crane, B. M. Marshall, and C. T. Strine. 2020. Reptiles on the wrong track? Moving beyond traditional estimators with dynamic Brownian bridge movement models. Movement Ecology 8:43.

Smetzer, J. R., A. L. Greggor, K. L. Paxton, B. Masuda, and E. H. Paxton. 2021. Automated telemetry reveals post-reintroduction exploratory behavior and movement patterns of an endangered corvid, Alalā (*Corvus hawaiiensis*) in Hawai'i, USA. Global Ecology and Conservation 26:11.

Spencer, R. J., J. U. Dyke, and M. B. Thompson. 2017. Critically evaluating best management practices for preventing freshwater turtle extinctions. Conservation Biology 31:1340–1349.

Stamps, J. A., and R. R. Swaisgood. 2007. Someplace like home: experience, habitat selection and conservation biology. Applied Animal Behaviour Science 102:392–409.

Stanford, C. B., J. B. Iverson, A. G. J. Rhodin, P. P. van Dijk, R. A. Mittermeier, G. Kuchling, K. H. Berry, A. Bertolero, K. A. Bjorndal, T. E. G. Blanck, et al. 2020. Turtles and tortoises are in trouble. Current Biology 30:R721–R735.

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

Todd, B. D., B. J. Halstead, L. P. Chiquoine, J. M. Peaden, K. A. Buhlmann, T. D. Tuberville, and M. G. Nafus. 2016. Habitat selection by juvenile Mojave desert tortoises. Journal of Wildlife Management 80:720–728.

Tuberville, T. D., K. A. Buhlmann, R. Sollmann, M. G. Nafus, J. M. Peaden, J. A. Daly, and B. D. Todd. 2019. Effects of short-term, outdoor head-starting on growth and survival in the Mojave desert tortoise (*Gopherus agassizii*). Herpetological Conservation and Biology 14:171–184.

Tuberville, T. D., D. P. Quinn, and K. A. Buhlmann. 2021. Movement and survival to winter dormancy of fall-released hatchling and headstarted yearling gopher tortoises. Journal of Herpetology 55:88–94.

Tuberville, T. D., B. D. Todd, S. M. Hermann, W. K. Michener, and C. Guyer. 2014. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. Journal of Wildlife Management 78:1151–1160.

U.S. Fish and Wildlife Service [USFWS]. 1983. Endangered Species Act of as amended by Public Law 97-304 (the Endangered Species Act Amendments of 1982). USFWS, Washington, D.C., USA.

U.S. Fish and Wildlife Service [USFWS]. 2011. Revised recovery plan for the Mojave population of the desert tortoise. USFWS, Sacramento, California, USA.

Wiesner, C. S., and C. Iben. 2003. Influence of environmental humidity and dietary protein on pyramidal growth of carapaces in African spurred tortoises (*Geochelone sulcata*). Journal of Animal Physiology and Animal Nutrition 87:66–74.

Williams, A. P., B. I. Cook, and J. E. Smerdon. 2022. Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. Nature Climate Change 12:232–234.

Williams, A. P., E. R. Cook, J. E. Smerdon, B. I. Cook, J. T. Abatzoglou, K. Bolles, S. H. Baek, A. M. Badger, and B. Livneh. 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. Science 368: 314–318.

Woodbury, A. M., and R. Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecological Monographs 18: 145–200.

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