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## COMPARING HUSBANDRY TECHNIQUES FOR OPTIMAL HEAD-STARTING OF THE MOJAVE DESERT TORTOISE (*GOPHERUS AGASSIZII*)

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**Abstract.**—Desert tortoise populations continue to decline throughout their range. Head-starting (the captive rearing of offspring to a size where they are presumably more likely to survive post-release) is being explored as a recovery tool for the species. Previous head-starting programs for the Mojave Desert Tortoise (*Gopherus agassizii*) have reared neonates exclusively outdoors. Here, we explore using a combination of indoor and outdoor rearing to maximize post-release success and rearing efficiency. We assigned 68 neonates (2016 cohort) to one of two treatments: Outdoor head-starting (HS; n = 38), where neonates were reared exclusively in outdoor predator-proof enclosures, and Combination (Combo) HS (n = 30), where neonates were reared indoors for 1 y followed by outdoor rearing for 1 y. After 2 y of captive rearing, we released 24 Outdoor HS and 24 Combo HS juveniles in the Mojave National Preserve, California, USA, on 25 September 2018. We compared pre-release size, body condition, and shell hardness as well as first year post-release movement and survival between the treatment groups. Body condition was not significantly different between groups. Outdoor HS tortoises, however, were significantly smaller and had significantly softer shells than Combo HS tortoises. Released head-starts experienced 78.2% survival through their first year after release. Combo HS tortoises dispersed significantly shorter distances than Outdoor HS animals. Our findings that Combo HS animals were larger and had harder shells at release, and exhibited high survival but low dispersal following release, support the use of combination head-starting as a recovery tool for the Mojave Desert Tortoise.

**Key Words.**—animal movement; Chelonian; conservation; head-starting; reintroduction; reptile; survival; threatened

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### INTRODUCTION

Many wildlife populations are in severe decline globally because of anthropogenic threats (Gibbons et al. 2000; Loh et al. 2008; Vié et al. 2009). In response, conservationists and management agencies have implemented diverse strategies to recover populations (Myers et al. 2000; Lindenmayer et al. 2006; Haag and Williams 2014). While actions to acquire and protect natural habitat remain paramount in conserving wildlife, species with depleted populations often require additional interventions (Ellis et al. 2000; Jachowski and Lockhart 2009; Milinkovitch et al. 2013). Head-starting is an approach in which offspring are protected through their early life stages before release at a larger

size presumed to be less prone to mortality (U.S. Fish and Wildlife Service [USFWS] 2011; Burke 2015). When used alongside management techniques that mitigate the original causes of decline, head-starting has the potential to expedite population recovery (Tomillo et al. 2008; Crawford et al. 2014; Spencer et al. 2017). Head-starting has been used in the recovery of a variety of taxa, such as Mona Island Iguanas, *Cyclura cornuta stejnegeri* (Pérez-Buitrago et al. 2008), Philippine Crocodiles, *Crocodylus mindorensis* (van de Ven et al. 2009), Hellbenders, *Cryptobranchus alleganiensis* (Crane and Mathis 2011), and Mangrove Finches, *Camarhynchus heliobates* (Cunningham et al. 2015). To increase success and efficiency, however, it is important to continue evaluating, improving, and

customizing this management technique for each at-risk species.

The Mojave Desert Tortoise (*Gopherus agassizii*) is a keystone species of the Mojave and Colorado deserts of the southwestern USA that has experienced severe population declines (Luckenbach 1982; Murphy et al. 2011; USFWS 2011; Allison and McLuckie 2018) and has been classified as threatened under the U.S. Endangered Species Act. Populations of this desert endemic species are affected by habitat loss, road mortality, subsidized predators, and the direct and indirect effects of changing climate (Berry 1986; Barrows 2011; USFWS 2011; Peaden et al. 2015; Nafus et al. 2017b). A wide range of management strategies has been suggested to address these threats and recover depleted populations (USFWS 2011), including population augmentation techniques such as head-starting.

The Mojave Desert Tortoise has been the subject of head-starting efforts for nearly 30 y (Morafka et al. 1997). Initial projects involved the rearing of hatchlings in outdoor predator-proof enclosures situated in natural habitat to evaluate the effects of captive rearing enclosures on nest success and hatchling survival and to gather insight into unknown aspects of juvenile tortoise ecology (Morafka et al. 1997). Juvenile survival in predator-proof enclosures was high (>90%; Spangenberg 1996; Morafka et al. 1997), leading to additional head-starting projects (Nagy et al. 2015a; Tuberville et al. 2019). These subsequent projects incorporated the use of supplemental rain in outdoor enclosures to increase growth and improve survival during periods of natural drought. Recent studies continue to build on these earlier findings to identify possible avenues for further improvement of these metrics.

Slow growth rates have burdened conventional outdoor captive-rearing efforts for the Mojave Desert Tortoise (Hazard et al. 2015; Nagy et al. 2015a). Desert tortoises spend roughly 95% of their lives below ground during the thermal extremes of winter and summer (Woodbury and Hardy 1948; Ernst and Lovich 2009). These prolonged bouts of inactivity during inhospitable ambient conditions result in restricted opportunities for foraging and growth (Medica et al. 2012). Previous studies have found that 5–9 y of outdoor captive-rearing is required to raise juveniles to a size that confers a survival advantage upon release into the wild (84–110 mm midline carapace length [MCL]; Nagy et al. 2011; Hazard et al. 2015; Nagy et al. 2015a). To reduce this extended captivity, indoor captive-rearing has recently been used to enhance growth by allowing head-started animals to remain active and foraging year-round (Daly et al. 2018). The expedited growth exhibited by tortoises reared under this technique was significant, producing 7-mo-old, captive-reared tortoises equivalent in size to 5–6-y-old wild animals (Daly et al. 2018).

Tortoises reared indoors for 7 mo, however, had softer shells and slightly lower body condition compared to older animals (3–4 y-old) of similar size reared solely outdoors (Daly et al. 2018). Rearing hatchlings solely indoors also holds the potential of raising tortoises that are naive to their surroundings upon release into the wild (Grueber et al. 2017). Incorporating an outdoor rearing component may serve as pre-release enrichment by providing head-starts with native forage, opportunities for burrowing, and exposure to natural environmental cues. Environmental enrichment has been shown to improve the survival of captive-reared animals released to the wild (Tetzlaff et al. 2019).

We used shell hardness and body condition as metrics for monitoring the possible effects of accelerated growth during the captive period in Mojave Desert Tortoises. Shell hardness has been found to increase with both body size and age in juvenile Mojave Desert Tortoises (Nagy et al. 2011; Daly et al. 2018). Although we did not find studies showing a direct correlation between shell hardness and increased survival, an increase in shell hardness presumably reduces the vulnerability of tortoises to certain predators like Common Ravens (hereafter Ravens, *Corvus corax*; Kristan and Boarman 2003; Nagy et al. 2015b). Body condition, an estimate of relative mass, has been used as a physiological metric of health in previous tortoise studies (Nagy et al. 2002; Loehr et al. 2007; McCoy et al. 2011). Nagy et al. (2015a) found that increased body condition from supplemental watering was associated with higher survival in outdoor predator-proof enclosures during a natural drought. Body condition values may also increase concurrently with the shell ossification process (as harder shells weigh more), highlighting the value of monitoring both metrics.

Long-distance dispersal away from the release site is the primary reason for failure in herpetofaunal release programs (Germano and Bishop 2009). In Mojave Desert Tortoises, translocated adults have larger home ranges and move greater distances compared to residents, particularly during the first year following release (Farnsworth et al. 2015; Hinderle et al. 2015). Thus, as a possible indicator of short-term success, we assessed post-release movement. For head-starting to ultimately succeed, released animals must survive to maturity and reproduce successfully (Pritchard 1981). However, monitoring a released juvenile tortoise to first reproduction may take over 10 years. As a more immediate metric of this ultimate goal, we monitored survival during the first-year post-release.

In this study, we introduce the use of combination head-starting, defined as initial captive-rearing indoors followed by conventional outdoor captive-rearing prior to release. This novel approach maximizes tortoise growth during indoor rearing and exposes tortoises

to environmental cues during outdoor rearing. The outdoor rearing period should also promote shell ossification through exposure to natural ultraviolet (UV) light (Acierno et al. 2006).

We compared two head-starting treatments for the Mojave Desert Tortoise using animals from the same year cohort: solely outdoor captive-rearing for 2 y, and combination head-starting, consisting of 1 y of indoor captive-rearing followed by 1 y of outdoor captive-rearing. We compared size, body condition, and shell hardness at release and movement and survival from release to dormancy and during the first year post-release. Ultimately, by reducing the duration of the captive rearing period and decreasing the cost of implementing this technique, combination head-starting may increase the efficiency and success of population augmentation efforts.

#### MATERIALS AND METHODS

**Study site.**—We conducted the study in the Ivanpah Valley in the Mojave National Preserve (MNP), San Bernardino County, California, USA, which is within the Eastern Mojave recovery unit of the Mojave Desert Tortoise (Nussear et al. 2009; USFWS 2011). We conducted the husbandry portions of this study at the Ivanpah Desert Tortoise Research Facility (IDTRF), which lies at 820 m elevation. The release site, located approximately 15 km away, occurred at 1,000–1,100 m elevation. The release site was dominated by Yucca Woodland habitat composed primarily of Creosote (*Larrea tridentata*) and White Bursage (*Ambrosia dumosa*), with yuccas (*Y. brevifolia*, *Y. shidigera*), Pencil Cholla (*Cylindropuntia ramosissima*), and Littleleaf Ratany (*Krameria erecta*) heavily intermixed (Todd et al. 2016). Limited anthropogenic disturbances at the release site included abandoned cattle corrals, a powerline, and seldom-used dirt roads. The Eastern Mojave recovery unit has experienced the highest documented decrease in the proportion of juvenile Mojave Desert Tortoises among all five recovery units for the Mojave Desert Tortoise (Allison and McLuckie 2018), suggesting a paucity of wild juveniles across the region, and thus a low probability of interspecific competition between released head-starts and wild resident juveniles.

**Obtaining hatchlings.**—In April 2011, we initiated the IDTRF head-starting program by capturing, attaching transmitters (RI-2B, Holohil Systems Ltd., Ontario, Canada), and radio-tracking 30 adult female Mojave Desert Tortoises in the Ivanpah Valley of the MNP. We tracked females at least monthly using a 3-element Yagi antenna (AF Antronics, Inc., Urbana, Illinois, USA) and an R1000 receiver (Communications Specialists, Inc., Orange, California, USA). In April 2016, we

brought all radio-tracked females to the IDTRF and radiographed them to check for the presence of calcified eggs (Diagnostic Imaging Systems, Poskam, Colorado, USA; 60 kvp, 0.8 mAS, 74 cm focal length; Gibbons and Greene 1979). We immediately released all non-gravid females at their point of capture. We placed gravid females in individual nesting enclosures and allowed them to nest naturally. These predator-proof nesting enclosures measured 5 × 9 m and included pre-made burrows, natural cover and forage, as well as sprinkler systems for supplemental watering (Tuberville et al. 2019). After their initial placement in the enclosures, we radiographed females weekly to monitor for egg deposition. If nesting was confirmed, we immediately released females at their point of capture. In accordance with our permits, we released all females that did not nest within 30 d at their last known burrow location.

We allowed eggs to incubate naturally in the predator-proof enclosures. Approximately 80 d after the estimated nesting date, we began searching pens daily for emerged hatchlings. We removed hatchlings as they emerged from nests and marked them by notching unique combinations of marginal scutes (modified from Cagle 1939) using numerical codes assigned by the USFWS. We also searched nests for any unhatched eggs or unemerged hatchlings. After all hatchlings from the 2016 cohort had emerged and been uniquely marked, we used a matched pairs design to assign all healthy neonates (evenly separating siblings between treatments; Daly et al. 2018; Tuberville et al. 2019) from our 2016 cohort to one of two treatment groups: solely outdoor head-started (Outdoor HS) or combination (indoor + outdoor) head-started (Combo HS). We reared both treatment groups in captivity for 2 y prior to release.

**Outdoor Head-starting.**—On 7 September 2016, we moved the 38 hatchlings assigned to the Outdoor HS treatment to outdoor predator-proof enclosures at the IDTRF. Captive rearing enclosures measured 9 × 9 m and included pre-made starter burrows (53-cm long, 10-cm diameter perforated plastic pipes buried at 20° angles), natural cover and forage, as well as rotating sprinkler systems (Nafus et al. 2015b; Daly et al. 2018; Tuberville et al. 2019). We placed 8–10 animals into each of four pens (0.10–0.13 tortoises/m<sup>2</sup>) and separated siblings from the same clutch into different pens. We have not altered the maximum juvenile density since the onset of our project (2011) due to evidence that tortoises in our pens continue to have species-appropriate body condition, high annual survival, and above-average growth (Daly et al. 2018; Tuberville et al. 2019). By using rotating garden sprinklers (always between 0700–1100 and with temperatures < 35° C), we provided artificial rain once every 1–2 weeks for 30 min

during the active season (March–October). Watering sustained native plant growth (Beatley 1974), allowed hatchlings to drink, and encouraged tortoises to feed on supplemental food.

Supplemental feeding coincided with watering. We fed tortoises a mixture of leafy greens and water-soaked Mazuri® Tortoise Diet 5M21 (Mazuri Exotic Animal Nutrition, St. Louis, Missouri, USA) on a centrally located concrete slab (40 × 40 cm) level with the soil surface. The greens included Dandelion (*Taraxacum officinale*), Mustard (*Brassica juncea*) greens, Turnip (*Brassica rapa*) greens, Collards (a cultivar of *Brassica oleracea*), Endive (*Cichorium endivia*), and Escarole (*C. endivia latifolia*). The weekly combination of greens varied by availability, though always consisted of at least three different types to approximate the nutritional properties of the natural diet of desert tortoises (Jarchow et al. 2002). We provided food *ad libitum*, but we monitored the amount provided to each pen and removed uneaten food to avoid attracting ants and rodents.

**Combination Head-starting.**—We reared 30 Combo HS tortoises in mesocosms in the indoor climate-controlled IDTRF for the first year (September 2016 to September 2017) before moving them to an outdoor predator-proof enclosure for the second year (September 2017 to September 2018). We set ambient temperature inside the IDTRF to a constant 24.4° C. We constructed indoor mesocosms from 189 L (50-gallon) Rubbermaid (Atlanta, Georgia, USA) stock tanks (132 × 79 × 30.5 cm), and we lined them with natural substrate (Daly et al. 2018). We prepared six identical tanks, each of which held five tortoises (n = 30; 4.81 tortoises/m<sup>2</sup>). Each tank contained three hides made from longitudinally halved plastic pipe (11.5 cm in diameter and 12 cm in length), a paper feeding plate, and a humid hide box. Humid hide boxes have been shown to promote smooth shell growth in tortoises (Wiesner and Iben 2003). We made hide boxes from Rubbermaid Roughneck tote boxes (40 × 26 × 18 cm), and we filled them with approximately 4 cm of peat moss, which we moistened every 3–4 d and replaced every two weeks. Tortoises were able to enter the hide box through a burrow-shaped entrance hole cut into each tote. We suspended Mini Combo Deep Dome Dual Lamp Fixtures (ZooMed Laboratories Inc., San Luis Obispo, California, USA) 30 cm over each tank with a 50-W ZooMed Repti Basking Spot Lamp bulb for daytime basking (37° C) and a ZooMed 50-W Infrared Basking Spot bulb for nighttime heat (32° C). We provided each tub with a 26 W Exo-Terra Reptile UVB150 bulb (Rolf C. Hagen Corp., Mansfield, Massachusetts, USA) 45 cm above substrate for optimal calcium metabolism and vitamin D3 conversion. We connected all lights to automatic timers, regulated monthly to reflect the natural photoperiod. We held

indoor conditions constant to allow juveniles to remain active and forage year-round (Diez et al. 2009).

We fed the Combo HS group *ad libitum* 4–5 times per week during the indoor rearing period (Diez et al. 2009), using the same food mixture as described above for the Outdoor HS treatment, placing the food on a single paper plate in each tank. Twice per week, we supplemented their food with a light dusting of Rep-Cal Calcium with Vitamin D3 (Rep-Cal Research Labs, Los Gatos, California, USA). We soaked Combo HS tortoises weekly for 15–30 min in 1–2 cm of water. In September 2017, we moved all Combo HS tortoises outdoors to a single 10 × 30 m predator-proof enclosure at the IDTRF for their second year of rearing. This larger enclosure contained all of the previously described enclosure components (refugia, natural vegetation, sprinklers) while maintaining a similar tortoise density (0.11 tortoises/m<sup>2</sup>) to the Outdoor HS treatment. We provided supplemental rain to this pen weekly during the active season (March–October).

**Morphometrics.**—We weighed and measured (hereafter measured) all hatchlings immediately after emergence from the nest. We then measured Outdoor HS tortoises once each spring and fall during the captive rearing period. We measured Combo HS tortoises monthly while indoors (September 2016 to September 2017) and then on the same cycle as the Outdoor HS treatment thereafter. We recorded mass to the nearest 0.1 g (Model HH320, OHAUS Corporation, Parsippany, New Jersey, USA); when tortoise mass exceeded 300 g, we recorded mass to the nearest 1 g (My Weigh 6001, HBI Technologies, Phoenix, Arizona, USA). We recorded midline carapace length (MCL), maximum shell height, and maximum shell width on the bridge to the nearest 0.1 mm using dial calipers (Series 505, Mitutoyo, Aurora, Illinois, USA).

**Body condition.**—We calculated body condition (BC) for all animals from both treatment groups using measurements taken at hatching (initial), 1 y post-hatching (Year 1; when we moved the Combo HS group outdoors), and immediately prior to release (release; 2 y post-hatching) based on the formula described by Nagy et al. (2002):

$$\text{Body condition } \left(\frac{\text{g}}{\text{cm}^3}\right) = \frac{\text{weight (g)}}{\text{shell volume (cm}^3\text{)}}$$

$$\text{Shell volume (cm}^3\text{)} = \frac{\pi \times \text{MCL} \times \text{width} \times \text{height}}{6000}$$

**Shell hardness.**—We measured shell hardness of all juveniles (n = 48) after 1 y of captive rearing (September 2017) and again just prior to release (September 2018).

To calculate shell hardness index (SHI) we first used a 4-inch (10.2-cm) tension-calibrated micrometer (model 3732XFL-4, L.S. Starrett Company, Athol, Massachusetts, USA) to measure the uncompressed shell height (UCSH) at the center of the third vertebral scute (Nagy et al. 2011) of each tortoise. We then measured compressed shell height (CSH) by turning the micrometer spindle and compressing the shell between the two measuring faces until the spindle ratchet slipped continually for approximately 270° (Daly et al. 2018). We used these measurements to calculate a shell hardness index as described by Nagy et al. (2011), in which a SHI value of 100 corresponds to maximum hardness (i.e., an incompressible shell):

$$\text{Shell Hardness Index (SHI)} = \frac{\text{CSH}}{\text{UCSH}} \times 100$$

**Experimental releases.**—We released Outdoor HS (n = 24) and Combo HS animals (n = 24) concurrently and in the same release area. We chose our release location based on the 1.6-km minimum recommended distance from raised structures such as powerlines that could serve as perching sites for Ravens (Daly et al. 2019), accessibility for frequent tracking, and habitat quality (Baxter 1988; Nafus et al. 2015a; Todd et al. 2016). At our study site, juvenile Mojave Desert Tortoises select for microhabitats with sandy soils, high-density perennial shrubs, abundant rodent burrows, and washes (Todd et al. 2016). Washes influence movement (Nafus et al. 2017a; Peaden et al. 2017) and provide increased forage (Jennings and Berry 2015). Using ArcGIS (version 10.5; Esri, Redlands, California, USA), we first created a 0.6-km<sup>2</sup> rectangular release plot (300 × 2,000 m) parallel to an access road. We then used the Fishnet function to generate release points every 50 m throughout the plot. From there, we set an interior buffer (buffer in from plot edge) of 50 m and removed all points within the buffered area. We then selectively removed interior points to create three equally spaced blocks (block edges 300 m apart), each containing 26 release points for a total of 78 release points. We buffered 10 m around each release point to maximize our ability to select a release refugium consisting of a large perennial shrub and an intact kangaroo rat (*Dipodomys* spp.) burrow (Nafus et al. 2015a; Todd et al. 2016; Daly et al. 2019). Prior to release, we enlarged the burrow to provide a refuge large enough to fully conceal the released animal. Under this release protocol, the minimum possible distance between release burrows was 30 m. Release points were far enough apart for the behavior and fate of individual tortoises to presumably be independent of each other while close enough to facilitate radio-tracking a large number of animals. Final release points ranged between 150 and 350 m from the access road and between 1.9 and 2.5 km to the closest powerline.

We chose to release animals in different release blocks to allow us to track blocks individually, facilitating the tracking of this many animals, and to minimize our activity in each block.

**Post-release monitoring.**—We attached Advanced Telemetry Systems (ATS; Advanced Telemetry Systems, Isanti, Minnesota, USA) radio-transmitters to the fifth vertebral scute with gel epoxy (Devcon 5-minute epoxy gel, ITW Engineered Polymers, County Clare, Ireland). We fitted Outdoor HS with R1670 transmitters (3.1 g) and Combo HS with the slightly larger R1680 model (3.6 g). Before the epoxy hardened, we applied a thin coat of sand to camouflage the transmitter package (Kazmaier et al. 2002). We checked each animal within 24 h of release to make sure the transmitter was working. After the initial 24-h post-release check, we tracked animals within each release block twice per week for the first three weeks (25 September to 15 October 2018) before reducing tracking frequency to once per week until dormancy. During the dormancy period (November 2018 to February 2019), we tracked juveniles every 10–14 d before returning to a weekly tracking schedule in March for the remainder of the study (March to September 2019). We continued tracking during the winter dormancy period, though at a reduced rate, because juvenile Mojave Desert Tortoises may be surface active when weather is favorable in winter months and because we were interested in monitoring winter mortalities (Morafka 1994; Wilson et al. 1999). At each tracking occasion, we recorded the location of each tortoise to the nearest 3 m using a handheld GPS unit (Garmin model GPSmap 76CSx, Olathe, Kansas, USA).

**Statistical methods.**—We performed all statistical tests in Program R (R Core Team 2018), with all inferences supported at a threshold Type I error rate (alpha) of 0.05. We present all data as group means ± 1 standard error (SE). We used graphical visualization of model residuals and Shapiro-Wilk tests to test model assumptions of normally distributed residuals. When necessary, we transformed the data to meet model assumptions, which met parametric assumptions after transformation.

We used Linear Mixed Effects models (LME; nlme package, lme function) to test for differences between treatment groups in MCL, mass, BC, and SHI. We compared these response variables at hatching (initial; except SHI), after 1 y of captive rearing (Year 1), and at the end of the 2-y captive-rearing period (release). We set the metric of interest as the response variable and included mother identity as a random effect in all models to account for maternal effects (Steyermark and Spotila 2001; Nafus et al. 2015b). We included MCL

as a continuous covariate in models testing the effect of treatment on SHI, allowing us to evaluate whether animals differed in shell hardness between treatments at similar sizes. We also tested for interaction between MCL and treatment group in both (Year 1 and release) SHI models. In any model in which the interaction was not significant, we retained MCL as a covariate but removed the interaction term from the final model.

We used an online calculator (<https://www.movable-type.co.uk/scripts/latlong.html>) to calculate distances between successive tracking locations. For each individual, we calculated mean distance moved per tracking event (excluding dormancy tracking events from 1 November 2018 to 5 March 2019), displacement at dormancy (31 October 2018) from the original release burrow, distance between the dormancy burrow and location at the end of the study (27 September 2019; for all animals surviving through dormancy), and final displacement from release burrow until the animal died, went missing, or until the end of the study (27 September 2019; for all animals surviving > 25 d post-release). We chose to include all animals surviving more than 25 d post-release in the latter analyses because animals in both treatment groups reached a clear asymptote for displacement from the release site within 25 d. We did not include the dormancy period (1 November 2018 to 5 March 2019) in our movement analyses because no movement was recorded during this time (also seen in Rautenstrauch et al. 1998), though we did document scat on burrow aprons throughout the winter, which we presumed to be evidence of basking activity during sunny winter days.

We used a Gamma Hurdle model (Mullahy 1986) to compare distance moved per tracking event (log link for nonzero distance component, logit link for binary outcome of moved/not moved) between treatment groups (for all animals that emerged post-dormancy; Daly et al. 2019). We fit this model under a Bayesian estimation framework using the *brms* package in R (R Core Team 2018) which implements Markov chain Monte Carlo (MCMC) sampling of the posterior distributions of model parameters. To account for the non-independence of repeated measures on the same individuals, we included individual identification number as a random factor in our model. We used noninformative improper flat priors (uniform distribution on the real line) to sample treatment group effects. We ran four chains of the MCMC sampler, each with 10,000 iterations and a thinning rate of one, while discarding the first 1,000 iterations as burn-in (Daly et al. 2019). We considered treatment group differences to be significant if 95% Bayesian credible intervals (BCIs) of model predictions did not overlap.

To compare pre-dormancy movement distance, post-dormancy movement distance, and final displacement

between treatment groups, we used a Generalized Linear Model (gamma family, log link) with the movement metric as the response variable and treatment group as a categorical predictor variable. For both pre-dormancy movement distance and final displacement, we included only those animals surviving > 25 d post-release (21 October 2018;  $n = 46$ ). We included all animals that survived the dormancy period and emerged in spring 2019 ( $n = 45$ ) in the post-dormancy movement comparison. We added 0.1 m to all pre-dormancy and post-dormancy movement data to eliminate zeros contained in the data. We report data as raw means  $\pm$  1 SE in text, tables, and figures for ease of interpretation, unless otherwise noted.

**Survivorship.**—Upon finding a dead tortoise, we thoroughly examined the surrounding area for clues of cause of death. We photographed each carcass, including any signs of predation, and removed carcass remnants for further analysis. We attributed deaths to one of five sources of mortality: (1) mammal depredated, (2) bird depredated, (3) unidentified predator, (4) exposure, or (5) unknown fate. Signs of predation included digging, tracks, scat, and condition of the carcass or transmitter. We classified carcasses that were found near clear digging activity or that had obvious tooth marks as mammal depredated. We classified remains in perch sites or with clear signs of being punctured by a beak as bird depredated. We considered remains found without tooth marks or lacking evidence of avian predation depredated by an unidentified predator. We presumed animals found intact on the surface or dead in their burrow to have died due to exposure. We gave an unknown-fate classification to animals lost due to radio failure (faulty batteries or the antenna became damaged), and we right censored (no assumption of fate) these animals in our survival analysis. We estimated survival rates in the field from release until dormancy (25 September to 31 October 2018) and from release until the end of the tracking period (September 2018 to September 2019) using the Kaplan-Meier estimator in the R package *survival* for each treatment group.

## RESULTS

Sixteen females collectively laid 92 eggs, resulting in 68 successfully emerged hatchlings (73.9% emergence) after an average incubation period of 87 d (range 74–106 d). We randomly selected 48 hatchlings (which represented 15 of the 16 females that successfully nested) for release in this study, retaining the remaining animals for future releases.

**Morphometrics.**—Neither mean MCL ( $45.2 \pm 0.3$  mm) nor mean mass ( $20.8 \pm 0.3$  g) at hatching (initial)

differed between treatment groups (MCL:  $F_{1,32} = 0.442$ ,  $P = 0.511$ ; mass:  $F_{1,32} = 0.235$ ,  $P = 0.631$ ; Table 1). After 1 y of captive rearing (Year 1; September 2017), when the Combo HS treatment was transitioned to outdoor rearing pens, Combo HS tortoises (MCL:  $102.5 \pm 1.5$  mm; mass:  $205.8 \pm 7.2$  g) were significantly larger (MCL) and heavier than Outdoor HS tortoises (MCL:  $66.5 \pm 1.5$  mm,  $F_{1,32} = 291.9$ ,  $P < 0.001$ ; mass:  $62.6 \pm 7.4$  g,  $F_{1,32} = 194.0$ ,  $P < 0.001$ ). Combo HS tortoises (MCL:  $117.2 \pm 1.7$  mm, mass:  $300.6 \pm 10.7$  g) retained their size advantage through release (September 2018; Outdoor HS MCL:  $83.7 \pm 1.7$  mm,  $F_{1,32} = 193.9$ ,  $P < 0.001$ ; Outdoor HS mass:  $115.9 \pm 10.7$  g,  $F_{1,32} = 148.6$ ,  $P$

$< 0.001$ ), with Combo HS tortoises weighing on average nearly three times that of Outdoor HS tortoises and achieving the MCL of an 8-y-old wild tortoise (Medica et al. 2012).

**Body condition.**—The average initial BC was  $0.533 \pm 0.004$  g/cm<sup>3</sup> ( $n = 48$ ) and did not differ between treatment groups ( $F_{1,32} = 2.965$ ,  $P = 0.095$ ; Table 1). Body condition values remained similar between treatment groups at both Year 1 (September 2017; Combo HS:  $0.575 \pm 0.009$ ; Outdoor HS:  $0.570 \pm 0.009$ ;  $F_{1,32} = 0.130$ ,  $P = 0.721$ ) and at release (September 2018; Combo HS:  $0.571 \pm 0.007$ ; Outdoor HS:  $0.572 \pm 0.007$ ;

**TABLE 1.** Summary statistics of growth metrics for juvenile Mojave Desert Tortoises (*Gopherus agassizii*) reared under two husbandry treatments (Outdoor head-started, Outdoor HS, and Combination head-started, Combo HS) at the Ivanpah Desert Tortoise Research Facility, San Bernardino County, California, USA. Measurements were taken shortly after hatching in fall 2016 (initial), after 1 y of captive rearing in fall 2017 (Year 1; when Combination head-starts were transitioned outdoors), and before release in fall 2018 (Release). Intervals are reported at 95% confidence (CI). *P*-values (significant values in bold) correspond to linear mixed effects models (with maternal ID as random effect). Abbreviations are SE = standard error, Min = minimum value, Max = maximum value, MCL = midline carapace length, BC = body condition, and SHI = shell hardness index.

Metric	Treatment	n	Mean	SE	Lower CI	Upper CI	Min	Max	<i>P</i> -value
Initial MCL (mm)	Outdoor HS	24	45.4	0.4	44.6	46.1	41.4	47.6	0.511
	Combo HS	24	45.0	0.4	44.2	45.8	41.0	47.7	
Initial mass (g)	Outdoor HS	24	21.1	0.5	20.1	22.1	16.5	23.6	0.631
	Combo HS	24	20.9	0.5	19.8	21.9	16.8	25.0	
Initial BC (g/cm <sup>3</sup> )	Outdoor HS	24	0.54	0.01	0.53	0.55	0.49	0.60	0.095
	Combo HS	24	0.53	0.01	0.51	0.54	0.45	0.58	
Year 1 MCL (mm)	Outdoor HS	24	66.5	1.5	63.4	69.5	52.2	76.9	<b>&lt; 0.001</b>
	Combo HS	24	102.5	1.5	99.6	105.5	84.9	116.6	
Year 1 mass (g)	Outdoor HS	24	62.6	7.4	47.9	77.5	34.3	85.5	<b>&lt; 0.001</b>
	Combo HS	24	205.8	7.2	191.4	220.3	124.0	302.0	
Year 1 BC (g/cm <sup>3</sup> )	Outdoor HS	24	0.57	0.01	0.56	0.58	0.51	0.63	0.721
	Combo HS	24	0.59	0.01	0.57	0.60	0.50	0.65	
Year 1 SHI	Outdoor HS	24	94.8	1.31	92.1	97.4	90.2	97.2	0.391
	Combo HS	24	95.9	0.6	94.8	97.1	92.9	98.2	
Release MCL (mm)	Outdoor HS	24	83.7	1.7	80.2	87.1	68.6	97.8	<b>&lt; 0.001</b>
	Combo HS	24	117.2	1.7	113.7	120.6	102.3	136.7	
Release mass (g)	Outdoor HS	24	115.9	10.7	94.3	137.4	67.3	175.9	<b>&lt; 0.001</b>
	Combo HS	24	300.6	10.7	279.0	322.2	200.0	421.0	
Release BC (g/cm <sup>3</sup> )	Outdoor HS	24	0.57	0.01	0.56	0.58	0.47	0.61	0.931
	Combo HS	24	0.57	0.01	0.56	0.58	0.52	0.63	
Release SHI	Outdoor HS	24	95.7	0.6	94.5	96.8	92.5	97.2	<b>&lt; 0.001</b>
	Combo HS	24	97.9	0.4	97.0	98.7	94.9	99.1	

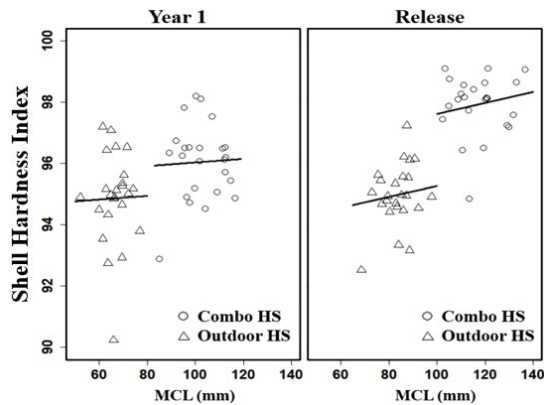


FIGURE 1. Predicted (lines) and measured (symbols) shell hardness index (SHI) versus midline carapace length (MCL) at Year 1 (left; September 2017) and Release (right; September 2018) for 2016 cohort juvenile Mojave Desert Tortoises (*Gopherus agassizii*) reared under two husbandry treatments at Ivanpah Desert Tortoise Research Facility, San Bernardino County, California, USA. Acronyms are Combo HS = Combination head-started and Outdoor HS = Outdoor head-started treatments. The shell hardness index was calculated using Nagy et al. (2011) protocol.

$F_{1,32} = 0.008, P = 0.931$ ). We also found no difference when comparing mean BC at release for animals found dead prior to spring emergence ( $n = 3; 0.582 \pm 0.009$ ) to those known to survive dormancy ( $n = 45; 0.568 \pm 0.007; F_{1,32} = 0.523, P = 0.396$ ).

**Shell hardness.**—Year 1 mean SHI did not differ between Combo HS ( $95.9 \pm 0.6\%$ ) and Outdoor HS tortoises ( $94.8 \pm 1.3\%$ ;  $t = -0.81, df = 30, P = 0.391$ ; Table 1; Fig. 1). Two Outdoor HS animals were unavailable for measurements in Year 1 due to early hibernation. After 2 y of captive rearing, Combo HS tortoises ( $97.9 \pm 0.4\%$ ) had significantly harder shells than Outdoor HS tortoises ( $95.7 \pm 0.6\%$ ;  $t = -3.86, df = 31, P < 0.001$ ) at release. Because treatment so strongly affected size, size (MCL) in the presence of the treatment effect was not a significant predictor of SHI in the models ( $P > 0.370$  for both Year 1 and release; Fig. 1), nor was the interaction between treatment and size ( $P > 0.345$  for both Year 1 and release).

**Movement.**—Combo HS and Outdoor HS tortoises did not differ in probability of moving or in distance moved per movement event during the 1-y post-release study period based on overlapping 95% Bayesian Credible Intervals (95% BCI). Probability of moving between tracking events was 0.42 (95% BCI = 0.38–0.47) for the Combo HS group, and 0.41 (95% BCI = 0.37–0.45; Table 2) for the Outdoor HS group. During movement events, Combo HS tortoises moved an average of 38.5 m (95% BCI = 31.8–46.5 m) per event, compared to 40.4 m (95% BCI = 32.8–49.9 m) by Outdoor HS tortoises.

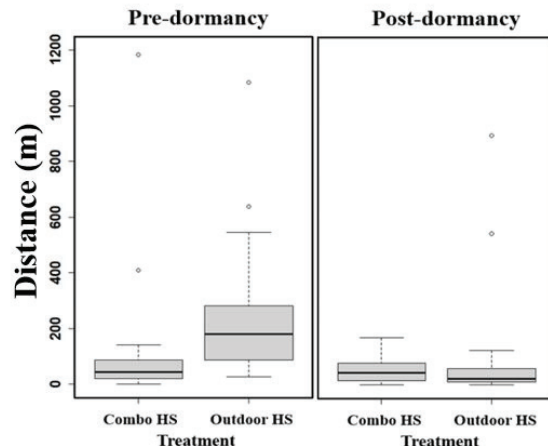


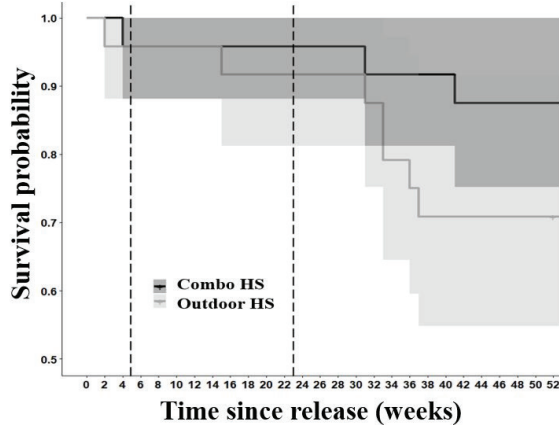
FIGURE 2. Distance moved from release site (Mojave National Preserve, California, USA) during pre-dormancy dispersal (left; 25 September to 31 October 2018) and distance moved from dormancy burrow after one-y post-release (right; 5 March to 27 September 2019) by juvenile Mojave Desert Tortoises (*Gopherus agassizii*) from two treatment groups: Combo HS (Combination head-started) and Outdoor HS (Outdoor head-started treatments). The error bars correspond to  $\pm 1.5$  times the interquartile range (IQR).

Between release and dormancy (pre-dormancy; 25 September to 31 October 2018), Outdoor HS tortoises dispersed nearly twice as far from their release burrows ( $n = 23; \bar{x} = 255 \pm 89$  m) as did Combo HS tortoises ( $n = 23; \bar{x} = 114 \pm 40$  m; Table 3; Fig. 2); however, this difference was not significant compared to within-group variation ( $t = 1.63, df = 45, P = 0.155$ ). Between emerging from dormancy and the end of the study (post-dormancy; 5 March to 27 September 2019), Outdoor HS tortoises reduced their movement away from their release location ( $n = 22; \bar{x} = 95 \pm 34$  m) and exhibited similar displacement distances between their dormancy location and final location when compared to Combo HS tortoises ( $n = 23; \bar{x} = 52 \pm 18$  m;  $t = 1.05, df = 44, P = 0.224$ ). Removing the two longest-distance post-dormancy movers from the Outdoor HS group

TABLE 2. Post-release movements for 48 juvenile Mojave Desert Tortoises (*Gopherus agassizii*) from two treatment groups (Outdoor head-started, OHS, and Combination head-started, CHS) released in September 2018 in the Mojave National Preserve, California, USA. Tortoises were tracked ~weekly from 25 September 2018 to 27 September 2019. Movement probability is defined as the probability of moving between any subsequent tracking events. Abbreviations Treat. = treatment, Est. = estimate, LBCI = lower 95% Bayesian credible interval, UBCI = upper 95% Bayesian credible interval, and NSD = not significantly different. We accepted significance if BCIs did not overlap.

Metric	Treat.	n	Est.	LBCI	UBCI	Result
Movement probability	OHS	22	0.41	0.37	0.45	NSD
	CHS	23	0.42	0.38	0.47	
Distance moved per event (m)	OHS	22	40.4	32.8	49.9	NSD
	CHS	23	38.5	31.8	46.5	





**FIGURE 3.** Kaplan-Meier survival curves for 48 Mojave Desert Tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA, from two treatment groups: Combination head-started (Combo HS; n = 24) and Outdoor head-started (Outdoor HS; n = 24). Estimates are shown from 25 September 2018 until 27 September 2019 (52 weeks). Data were right-censored, meaning no assumptions were made about the fate of lost or missing animals (n = 2). Dashed vertical lines represent the beginning and end of the dormancy period (31 October 2018 to 5 March 2019). Shaded bands are 95% confidence intervals.

(896 m and 543 m), however, reduced mean post-dormancy movement distance to 33 m for the Outdoor HS treatment group. Total displacement from release burrow until the end of the study (25 September 2018 to 27 September 2019) was heavily influenced by pre-dormancy dispersal away from the release burrow, leading to a significant difference in final displacement between treatment groups ( $t = 2.05$ ,  $df = 45$ ,  $P = 0.041$ ). Outdoor HS tortoises (n = 22;  $\bar{x} = 333 \pm 95$  m) dispersed over two times the distance of Combo HS tortoises (n = 23;  $\bar{x} = 142 \pm 41$  m) during the 1-y post-release monitoring period. We observed large variation in final displacement within treatment groups, ranging from 10–1,178 m (Combo HS) and 11–1,041 m (Outdoor HS) based on all animals that survived dormancy.

**TABLE 3.** Post-release movements for 48 juvenile Mojave Desert Tortoises (*Gopherus agassizii*) from two treatment groups (Outdoor head-started, Outdoor HS, and Combination head-started, Combo HS) released in September 2018 in the Mojave National Preserve, California, USA. Displacement pre-dormancy represents dispersal from release burrow until dormancy for all animals surviving to dormancy (n = 46; 25 September 2018 to 31 October 2018). Displacement post-dormancy represents movement from dormancy burrow until the end of the study for all animals that emerged post-dormancy (n = 45; 5 March 2019 to 27 September 2019). Total displacement represents the distance from release burrow until the end of the study for all animals that emerged post-dormancy (n = 45; 25 September 2018 to 27 September 2019). Abbreviations are SE = standard error, Min = minimum value, and Max = maximum value. Significant P-values ( $\leq 0.05$ ) are in bold.

Metric	Treatment	n	Mean (m)	SE (m)	Min (m)	Max (m)	P-value
Displacement pre-dormancy	Outdoor HS	23	255	89	26	1084	0.155
	Combo HS	23	114	40	0	1183	
Displacement post-dormancy	Outdoor HS	22	95	34	0	896	0.224
	Combo HS	23	52	18	0	169	
Total Displacement	Outdoor HS	22	333	95	11	1041	<b>0.041</b>
	Combo HS	23	142	41	10	1178	

**Post-release survivorship.**—Survival from release to dormancy (five weeks post-release; 25 September to 31 October 2018) was equally high for both treatment groups at 96% (n = 23/24 Combo HS and n = 23/24 Outdoor HS; Fig. 3). During dormancy, we found one Outdoor HS tortoise dead after a mammalian predator had removed it from its winter burrow, as evidenced by signs of digging at the burrow. At the end of the first-year post-release (25 September 2018 to 27 September 2019), 36 (75.0%) of the 48 released head-starts were confirmed alive. Of the 12 not confirmed alive, two went missing with an unknown fate and thus were censored in the survival analysis. The remaining 10 animals were all lost due to predation; no animals died due to exposure. Six head-starts were depredated by mammals (12.5% of released tortoises; four from Outdoor HS and two from Combo HS), three were killed by avian predators (6.2% of released tortoises; all from Outdoor HS group), and one was killed by an unidentified predator (2.1% of released tortoises; a Combo HS tortoise). We found the head-started tortoise killed by an unidentified predator buried in its burrow. The burrow entrance showed signs of mammalian digging, while both the burrow and tortoise carcass were covered in harvester ants (*Veromessor* sp.). Overall estimated survival for the 48 head-starts during their first year post-release (September 2018 to September 2019) was 0.79 (95% CI, 0.69–0.92; Fig. 3). Annual survival was 0.88 (95% CI, 0.75–1.0) for the Combo HS treatment and 0.71 (95% CI, 0.55–0.92; Fig. 3) for the Outdoor HS treatment, with overlapping 95% confidence intervals indicating no statistical difference between treatment groups.

**DISCUSSION**

After two years of captive rearing, Combo HS tortoises were both larger and had harder shells than Outdoor HS tortoises from the same cohort. Combo HS tortoises were the size of an 8-y-old wild juvenile with

the shell hardness of an 11 y-old wild tortoise (Nagy et al. 2011; Medica et al. 2012) and weighed nearly three times more than same-aged Outdoor HS tortoises. Outdoor HS tortoises, however, were also large for their age when compared to wild counterparts, attaining the size of 4–5 y-old wild tortoises with just 2 y of captive rearing outdoors (Medica et al. 2012). Outdoor HS animals grew 19.3 mm MCL/y, an enhanced rate that can be attributed to the supplemental food and water they were provided weekly during the active season (March–October). Tuberville et al. (2019) reported growth rates of 12.7 mm MCL/y for juvenile tortoises reared outdoors without supplemental food at the IDTRF. Collectively, these results lend support for providing supplemental food to Mojave Desert Tortoises during outdoor captive rearing, particularly as vegetation in the pens may become depleted over time.

The growth rate of Combo HS tortoises during their year indoors (4.7 mm/mo) was similar to that found by Daly et al. (2018) for tortoises reared indoors under nearly the same protocols (4.3 mm/mo), highlighting the significant growth advantage of indoor captive rearing for head-starting Mojave Desert Tortoises. Combo HS tortoises surpassed the Nagy et al. (2015b) recommended release size of 100 mm MCL after just one year of indoor rearing ( $\bar{x}$  = 102.5 mm MCL), while Outdoor HS tortoises reached a mean size equivalent to the Hazard et al. (2015) recommendation of 84 mm MCL after two years outdoors ( $\bar{x}$  = 83.7 mm MCL). Throughout the 2-y captive rearing period, tortoises in both treatment groups had similar body conditions, agreeing with the findings of Daly et al. (2018). Body condition of head-started tortoises ranged from 0.47–0.65 g/cm<sup>3</sup> across treatments over the captive rearing period. Nagy et al. (2002) determined prime body condition values for wild Mojave Desert Tortoises were between 0.6–0.7 g/cm<sup>3</sup>, which 21–27% of individuals in our study attained. Prime body condition values represent peak nutritional status in spring, however. We measured tortoise body condition in September, corresponding with emergence from summer aestivation when Mojave Desert Tortoises can actually weigh less than they did the previous spring (Nagy and Medica 1986). Nonetheless, after initial measurements, all individuals in our study had body condition values above the Nagy et al. (2002) threshold value for a dehydrated Mojave Desert Tortoise (0.45 g/cm<sup>3</sup>). Likewise, using the body condition formula from Loehr et al. (2004), the tortoises in our study were well within the range of body condition values for adult Speckled Tortoises (*Chersobius signatus*; Loehr et al. 2004), which are similar in size to the juvenile Mojave Desert Tortoises in our study.

The slow growth and delayed maturity of chelonians stem from their investment in maintenance and growth of a protective shell (Klemens 2000). The level of

protection, and presumably the ability to withstand attacks from predators, can best be measured by quantifying shell hardness, which increases with both size and age in healthy turtles (Hill 1999; Nagy et al. 2011). Though significantly larger, Combo HS tortoises at Year 1 had shell hardness values similar to Outdoor HS tortoises at Year 1. It seems that one year of indoor conditions (i.e., UV lighting, calcium supplementation, and accelerated growth) or one year of outdoor conditions (i.e., supplemental food and water as well as natural sunlight) at our site both result in nearly equal shell hardness values; however, Combo HS tortoises at Year 2 had significantly harder shells at release than 2-y-old Outdoor HS tortoises and had SHI values equivalent to those calculated for an 11-y-old wild Mojave Desert Tortoise (Nagy et al. 2011). Through combining the accelerated growth of indoor captive rearing and the natural shell ossification of outdoor captive rearing, we were able to significantly increase the shell hardness of 2-y-old captive-reared Mojave Desert Tortoises relative to both wild counterparts and tortoises captive-reared solely outdoors.

Extreme post-release dispersal can remove individuals from optimal habitat, result in higher incidence of exposure and predation, and ultimately impede translocation or reintroduction efforts (Stamps and Swaisgood 2007; Germano and Bishop 2009; Roe et al. 2010). In our study, with the exception of two individual outliers (> treatment mean + 2 standard deviations), released head-starts did not move far from their release burrows. Means of both treatment groups were within the range (about 100–400 m) of mean initial (< 2 mo) dispersal distances reported for head-started or translocated juvenile Mojave Desert Tortoises (Germano et al. 2017; Nafus et al. 2017a). Although pre-dormancy dispersal distance of Outdoor HS tortoises was twice that of Combo HS tortoises, the difference was not significant. Likewise, probability of movement and mean distance per movement were similar between the treatments.

Roughly 80% of the total dispersal by both treatment groups occurred in the first three weeks post-release, corroborating previous studies of post-release movement of head-started Mojave Desert Tortoises (Hazard et al. 2015; Nagy et al. 2015b; Daly 2017; Germano et al. 2017) and Gopher Tortoises (Quinn et al. 2018). Germano et al. (2017) also reported a secondary dispersal event after the first dormancy period, during which 13% of released juvenile Mojave Desert Tortoises engaged in movements away from the release site. Similarly, seven tortoises (15%) in our study dispersed > 100 m (range, 107–896 m) away from their dormancy burrows the following spring (spring 2019). Post-dormancy dispersal was slightly greater (about 20 m) for Combo HS tortoises than Outdoor HS tortoises

when two extreme movers were removed from the data, possibly due to the larger size of Combo HS tortoises necessitating a slightly larger home range to acquire all necessary resources (Slavenko et al. 2016; though see Harless et al. 2009). Total displacement during the 1-y study period, however, differed significantly between the two treatments and was predominantly driven by pre-dormancy dispersal from the release burrow. One year after release, Combo HS tortoises had settled nearly 200 m closer to their release burrows than Outdoor HS tortoises. Reducing initial dispersal allows for targeted management within conservation areas and facilitates continued monitoring of population recovery.

When compared to previous releases of juvenile Mojave Desert Tortoises (Morafka et al. 1997; Hazard and Morafka 2002; Nagy et al. 2015b; Germano et al. 2017; Nafus et al. 2017a), including those from our release area (Tuberville et al. 2019; Daly et al. 2019), tortoises in our study exhibited particularly high survival rates. This finding was especially pronounced when considering the survival of our Combo HS group, whose 88% annual survival marks the highest survivorship reported for any size-class of juvenile Mojave Desert Tortoises (79%, Nagy et al. 2015b; 69%, Germano et al. 2017; 68%, Nafus et al. 2017a; 44%, Daly et al. 2019; 48%, Tuberville et al. 2019). Mortality risks for juvenile tortoises released at our sites in Ivanpah Valley have changed over time. Earlier releases at our study site focused on identifying appropriate microhabitats for release as well as establishing baseline survival rates for newly hatched or very young tortoises (Tuberville et al. 2019). The small size of tortoises in that study (40.8–61.5 mm MCL) likely gave rise to the many mortalities due to exposure, resulting in an annual survival estimate of 48%. Smaller juveniles experience increased rates of water loss as well as faster heating and cooling rates and are thus at a greater risk for desiccation and thermal stress during post-release activities (Berry and Turner 1986; Geffen and Mendelssohn 1989; Wilson et al. 2001; Harris et al. 2015). Over 15% of head-starts released by Tuberville et al. (2019) died due to suspected exposure, greatly outnumbering the single loss attributed to a bird predator. Ravens became a significant source of mortality in a later release at our site by Daly et al. (2019), with nearly 27% of all released tortoises lost to these opportunistic predators in the first year post-release (Sherman 1993; Boarman 2003). In turn, Daly et al. (2019) recommended releasing tortoises over 1.6 km away from powerlines, a known nesting structure for Ravens. Incorporating this recommendation as part of our release protocols, not releasing tortoises in spring when Ravens are actively nesting, and the larger size of our Combo HS tortoises may account for the higher survival rates documented in our study. By building on previous efforts, we have increased the success and efficiency of our head-starting program.

**Management implications.**—Both post-release site fidelity and survival were high for both head-starting treatment groups. By releasing tortoises in late September, we were able to minimize the amount of time available for dispersal prior to dormancy, likely increasing the probability that animals settled near their release sites. The fall release also appeared to give tortoises sufficient time to establish burrows and become familiar with areas for resource acquisition before the especially vulnerable spring activity period documented in this and other studies of released juvenile Mojave Desert Tortoises (Nagy et al. 2015a; Daly et al. 2019). The combination of a fall release when Raven activity is lower and the selection of release sites > 1.6 km from potential perching sites (Daly et al. 2019) likely contributed to the high post-release survival exhibited by both treatment groups in our study.

In only two years of captive rearing, combination head-starting produced tortoises that exceeded previously published recommendations for minimum size at release for the Mojave Desert Tortoise (Nagy et al. 2015b; Hazard et al. 2015). Combo HS tortoises, equivalent in size to 8 y-old wild tortoises (Medica et al. 2012), also had nearly prime body condition values and a shell hardness index similar to an 11 y-old wild tortoise (Nagy et al. 2002; Nagy et al. 2011). In addition, Combo HS tortoises dispersed significantly shorter distances in the first year post-release than their solely outdoor-reared siblings while exhibiting high survivorship. In sum, it appears that combination head-starting supports a significant advancement in producing robust, healthy juvenile tortoises compared to more traditional outdoor-only rearing. Moreover, an annual survival difference of 17% (88% vs 71%) between Combo HS and Outdoor HS tortoises may be biologically relevant if our findings persist over the lives of the animal. Only continued monitoring will reveal the longer-term success of head-starting and reintroduction efforts, but our study provides encouraging early support for this innovation in husbandry that increases the efficiency of head-starting and enhances its value as a tool in recovering declining tortoise populations.

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## Herpetological Conservation and Biology



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