



## Research Article

# Survival and Movements of Head-Started Mojave Desert Tortoises

JACOB A. DALY,<sup>1,2</sup> *University of Georgia's Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, SC 29802, USA*

KURT A. BUHLMANN, *University of Georgia's Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, SC 29802, USA*

BRIAN D. TODD, *Department of Wildlife, Fish and Conservation Biology, University of California, Davis, One Shields Ave, Davis, CA 95616, USA*

CLINTON T. MOORE, *U.S. Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA 30602, USA*

J. MARK PEADEN, *Department of Wildlife, Fish and Conservation Biology, University of California, Davis, One Shields Ave, Davis, CA 95616, USA*

TRACEY D. TUBERVILLE, *University of Georgia's Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, SC 29802, USA*

**ABSTRACT** Head-starting is a conservation strategy in which young animals are protected in captivity temporarily before their release into the wild at a larger size, when their survival is presumably increased. The Mojave desert tortoise (*Gopherus agassizii*) is in decline, and head-starting has been identified as one of several conservation measures to assist in recovery. To evaluate the efficacy of indoor head-starting, we released and radio-tracked 68 juvenile tortoises from a 2015 cohort in the Mojave National Preserve, California, USA. We released 20 tortoises at hatching (control) in September 2015, and reared 28 indoors and 20 outdoors in predator-proof enclosures for 7 months before releasing them in April 2016. We monitored tortoises at least weekly after release until 27 October 2016, and documented survivorship, movement, and surface activity. We estimated survivorship by treatment and evaluated effects of treatment, proximity to a raven (*Corvus corax*) nest (predator) coincidentally established after release, distance moved between monitoring events, surface activity, and release size on individual fate in a generalized linear model. Although indoor head-start tortoises reached the size of 5–6-year-old wild tortoises by release at 7 months of age, survival did not differ significantly among the 3 treatment groups. Combined annual survival was 0.44 (95% CI = 0.34–0.58). Tortoises that were closer to an active raven nest were significantly more likely to die, as were those seen more often outside their burrows and active aboveground. Predicted estimates for short-term probability of survival approached 1.0 as distance from a raven nest exceeded approximately 1.6 km. Rearing treatment, movement distance, and body size were not significant predictors of fate over the 1-year monitoring period. Head-started tortoises released  $\geq 1.6$  km from areas of raven activity will likely have higher short-term survival. Population recovery through head-starting alone is unlikely to be successful if systemic ecosystem-level issues, such as habitat degradation and conditions that promote human-subsidized predators, are not ameliorated. © 2019 The Wildlife Society.

**KEY WORDS** chelonian, conservation, desert tortoise, endangered species, head-start, Mojave Desert, population augmentation, species recovery, threatened species, turtle.

Population interventions are often controversial as species recovery tools because outcomes of such measures are difficult to predict (Seddon et al. 2014) and are infrequently measured and reported. With ever-increasing anthropogenic effects on wildlife populations, however, interventions may be necessary to prevent extinctions. In recent years, there has been interest in reintroducing extirpated species (e.g., black-footed ferrets [*Mustela nigripes*]; Miller et al. 1994), facilitating dispersal in response to climate change (McLachlan et al. 2007, Hewitt et al. 2011, Seddon et al. 2014), and augmenting small

populations (e.g., Kemp's ridley sea turtles [*Lepidochelys kempii*]; Caillouet et al. 2015).

Head-starting is one approach to population augmentation that involves protecting and rearing animals through early life stages when they are typically most vulnerable before releasing them into the natural environment at a more advanced state of development when survival is presumably greater (Burke 2015). Head-starting has been a useful conservation tool for several species, including California condors (*Gymnogyps californianus*; Cohn 1999), rock iguanas (*Cyclura* spp.; Pérez-Buitrago et al. 2008), Galapagos tortoises (*Chelonoidis hoodensis*; Gibbs et al. 2014), and Blanding's turtles (*Emydoidea blandingii*; Buhlmann et al. 2015). Chelonians, the most threatened group of vertebrates globally (Stanford et al. 2018), may be uniquely suited to head-starting because survivorship in the wild is typically low in early life and high during adulthood under most

Received: 21 February 2019; Accepted: 11 August 2019

<sup>1</sup>E-mail: jacobadaly@gmail.com

<sup>2</sup>Current Address: Camp Parks Reserve Forces Training Area, Directorate of Public Works, Environmental Division, Dublin, CA 94568, USA

natural conditions, and juveniles require no parental care after hatching (Burke 2015). However, efficacy of head-starting is often difficult to evaluate, if examined at all, and some have questioned its effectiveness at increasing populations (Heppell et al. 1996), or expressed concern that it may divert attention and funds from other conservation measures (e.g., habitat preservation; Frazer 1992). Under most circumstances, head-starting is likely practical for turtles only when ongoing causes of adult mortality are addressed (Congdon et al. 1994, Tuberville et al. 2015). There is growing recognition, however, that a combination of conservation measures that target multiple life stages may provide the strongest chances of population recovery in chelonians (Crawford et al. 2014, Spencer et al. 2017).

The Mojave desert tortoise (*Gopherus agassizii*) has been declining because of habitat loss and degradation (U.S. Fish and Wildlife Service [USFWS] 2011), proliferation of human-subsidized predators (i.e., ravens [*Corvus corax*] and coyotes [*Canis latrans*]; Esque et al. 2010), road mortality (Nafus et al. 2013, Peaden et al. 2015), and other anthropogenic effects (Darst et al. 2013, Tuma et al. 2016). Mojave desert tortoises are classified as threatened under the Endangered Species Act (USFWS 1990), and despite considerable conservation effort, populations have continued to decline recently (Allison and McLuckie 2018). Population augmentation, such as head-starting, has been listed as 1 of several concurrent strategies for desert tortoise recovery (USFWS 2011). A few studies have evaluated post-release success of juvenile desert tortoises reared in semi-natural, outdoor, predator-proof pens (Hazard et al. 2015, Nagy et al. 2015*b*, Tuberville et al. 2019). Researchers suggested that released head-started juvenile tortoises should be  $\geq 84$  mm (Hazard et al. 2015) to 110 mm (Nagy et al. 2015*b*) in midline carapace length (MCL) to gain any appreciable increase in post-release survival; however, it can take up to 7 years to rear a juvenile tortoise from size at hatching (~46 mm MCL) to 110 mm MCL outdoors under semi-natural conditions (without supplemental food; Nagy et al. 2015*a*).

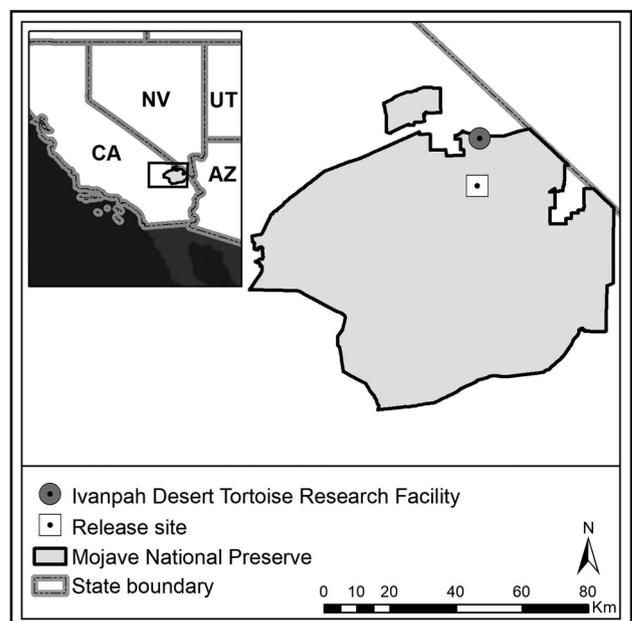
Our objective was to determine if short-term indoor-rearing could yield a tortoise closer to the recommended head-start release size and whether a larger size at release enhances its short-term ability to survive in its release environment. We reared tortoises indoors where they were kept active through the winter instead of undergoing winter dormancy, and we provided supplemental food to enhance their growth and shorten the head-start period. We sought to determine how indoor head-starting would affect survival, post-release dispersal, and surface activity relative to direct-release and outdoor head-starting (testing null hypotheses of no difference among groups).

We predicted that indoor-reared tortoises would be larger than outdoor-reared tortoises or direct-release tortoises of the same age, and would thus have greater post-release survival, because larger body size is generally associated with increased survival among turtles (Haskell et al. 1996). We investigated whether treatment group affected dispersal

because post-release movements can be risky for animals (Pedrono and Sarovy 2000, Hazard and Morafka 2002, Farnsworth et al. 2015). Burrows, pallets (short burrows), and vegetative cover provide important thermal and anti-predator refuges for desert tortoises (Woodbury and Hardy 1948, Nafus et al. 2015*a*), and 1 concern is that rearing animals indoors in the absence of these natural resources could affect their use of refuges in the wild. Thus, we sought to determine whether surface activity and cover use differed among treatment groups. Furthermore, juvenile desert tortoises associate with soil substrate that is composed of particles (i.e., rocks) of similar size to their bodies, as opposed to fine sand, in an apparent effort to become more cryptic (Nafus et al. 2015*a*). We predicted that the degree of association with rocks would vary among treatment groups because of body size differences among groups and corresponding availability of rocks of similar body size. Thus, the degree of camouflage afforded by their environment could vary among treatments.

## STUDY AREA

The Mojave National Preserve (MNP) is a 650,000-ha preserve managed by the National Park Service and located in the eastern Mojave Desert, San Bernardino County, California (Fig. 1). Our study took place in Ivanpah Valley, at the northern edge of the MNP (Fig. 1). Typical temperatures ranged from overnight lows of 1°C in winter to daytime highs of 40°C in summer (Hereford et al. 2006). Annual precipitation ranged 8–18 cm, falling primarily in winter (Dec–Feb). Variable monsoonal rains (Jul–Sep) can comprise up to 34% of precipitation (Hereford et al. 2006). Elevation across the study area ranged 800–1,050 m, and elevation within the release site was approximately 1,000 m. Our study area was a gently sloping valley floor dominated



**Figure 1.** Location of study area for a desert tortoise head-start experiment in the Ivanpah Valley of the Mojave National Preserve, California, USA, 2015–2016.

by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*). Mojave yucca (*Yucca schidigera*), Joshua tree (*Y. brevifolia*), and various cacti (Cactaceae) were present at lower density (Turner et al. 1984, Todd et al. 2016). Land use and disturbance at the study area included dirt roads, powerline rights-of-way, and abandoned cattle grazing infrastructure (fencing and corrals). Vertebrate fauna included numerous burrow-digging rodents such as round-tailed ground squirrels (*Xerospermophilus tereticaudus*) and Merriam's kangaroo rats (*Dipodomys merriami*), which provided refugia for juvenile desert tortoises. Predators of juvenile desert tortoises at the study area included common raven, coyote, American badger (*Taxidea taxus*), kit fox (*Vulpes macrotis*), and others. Although desert tortoises are commonly seen in Ivanpah Valley and habitat characteristics appear suitable (Nussear et al. 2009, Todd et al. 2016), tortoise densities declined 7% annually from 2004–2014 (Allison and McLuckie 2018).

## METHODS

### Hatchling Collection and Husbandry

In May 2015, we captured radio-transmittered, free-ranging adult female desert tortoises and radiographed them (Diagnostic Imaging Systems, Poskam, CO, USA) to determine the presence of calcified eggs (Gibbons and Greene 1979). We transferred gravid females to individual, outdoor, predator-proof nesting pens at the Ivanpah Desert Tortoise Research Facility (IDTRF) and provided each with an artificial burrow and natural shrub cover (Daly et al. 2018). We radiographed females every 7–10 days until they laid eggs, then we returned females to their May capture locations. We left eggs to incubate in nests where they were laid. Beginning August–September, we searched pens daily for emerging hatchlings. We weighed each hatchling to the nearest 0.1 g, measured (MCL, width, and height) them to the nearest 0.1 mm, and temporarily housed hatchlings by clutch inside the IDTRF until all potential hatchlings were accounted for. We excluded 4 hatchlings from the study because of especially low body mass (<15.5 g) at hatching or developmental issues (1 had an eye deformity and 2 had very folded shells).

In late September 2015 (within 21–46 days of hatching), we assigned 70 healthy hatchlings to 1 of 3 treatment groups: indoor-reared ( $n = 30$ ), outdoor-reared ( $n = 20$ ), and direct-release ( $n = 20$ ; control group). We selected an unbalanced design, including more indoor-reared animals, because previous cohorts in our head-start program included only releases of outdoor-reared and direct-release neonates. We raised indoor-reared head-start (indoor HS) tortoises in the climate-controlled IDTRF and housed them in 189-L polymer stock tanks with desert sand as substrate, humid hide boxes, and heat lamps (white during day and infra-red at night). We fed indoor HS tortoises a mixture of leafy greens and water-softened tortoise pellets 5 times/week (Daly et al. 2018). We raised outdoor-reared head-start (outdoor HS) tortoises in semi-natural predator-resistant enclosures and offered supplemental food and artificial rain

via garden sprinklers once per week. We allowed outdoor HS animals to undergo winter dormancy, whereas we kept indoor HS animals active throughout the winter. We released direct-release (DR) hatchlings into the natural environment in September 2015, whereas we kept indoor and outdoor HS tortoises in captivity from September 2015 until April 2016 (7 months). See Daly et al. (2018) for more details on husbandry and growth of outdoor HS and indoor HS treatments.

### Experimental Releases

Using ArcGIS (version 10.2, Environmental Systems Research Institute, Redlands, CA, USA), we delineated a 0.7-km<sup>2</sup> rectangular release site (700 m × 1,000 m) of natural, unfenced desert, with the longer side parallel to a powerline service access road (Fig. S1, available online in Supporting Information). We chose this orientation to minimize variability in the distance from the powerline road to the release site (as we occasionally saw ravens perching on these powerlines). We placed the center of the release site 850 m from the powerline road such that locations within the site were 500–1,200 m from the powerline (Fig. S1). We then used the genregularpntsinpolys (Generate Regular Points In Polygons) tool in Geospatial Modeling Environment (GME; version 0.7.3, www.spatial ecology.com, accessed 11 Dec 2018) to generate 70 regularly spaced points 100 m apart to serve as locations of 20-m radius release centers (Fig S1).

We randomly assigned each hatchling to 1 release center. Based on field inspection, we chose a specific release point ≤20 m of the release center that provided large creosote bushes and several kangaroo rat (*Dipodomys* spp.) burrows for hatchling refugia (Todd et al. 2016). Thus, under this protocol for release point selection, the minimum possible distance between any 2 release points was 60 m. We chose this spacing to achieve spatial independence among tortoises as much as possible (Hurlbert 1984) while retaining a small enough study area to make regular radio-tracking logistically feasible.

On 28 September 2015, we released 20 hatchlings from the DR treatment group at 20 of the release points described above. We released all hatchlings in the morning, between 0700–0930 hours, and placed them inside kangaroo rat burrows under creosote bushes to avoid heat exposure. Seven months later (25 Apr 2016), we released 28 indoor HS and 20 outdoor HS tortoises in the same manner. After the 2016 release was already underway, we noted a mated pair of ravens rearing young in a nest on 1 of the powerline towers adjacent to the release plot approximately 500 m from the nearest released tortoise.

### Post-Release Monitoring

Prior to release, we marked each tortoise by notching marginal scutes in unique patterns (modified from Cagle 1939) and attached a radio-transmitter (BD-2, Holohil Systems, Ontario, Canada) to the fourth vertebral scute using gel epoxy (Devcon 5-min epoxy gel, ITW Engineered Polymers, County Clare, Ireland). All methods followed procedures approved by the University of Georgia Animal Care and Use Committee (number A2013 02-017-Y1-A0)

and permits issued by USFWS (number TE-17838A-2), United States National Park Service (number MOJA-2011-SCI-0056 [under study MOJA-00258]), and California Department of Fish and Wildlife (number SC-0011221). We used a 3-element Yagi antenna (AF Antronics, Urbana, IL, USA) and a R1000 receiver (Communications Specialists, Orange, CA, USA) to locate tortoises. We located each animal daily for the first 4 days following release in September 2015 (DR) and April 2016 (indoor and outdoor HS) to ensure radio-transmitters were working properly and observe that tortoises were not exhibiting unexpected behavior relative to foraging activity and use of cover. After the first 4 days, we tracked tortoises twice per week (every 3–4 days), a temporal resolution sufficient to detect mortality when tortoises were most active but not so frequent as to attract predators. We reduced tracking to once per week (every 5–9 days) temporarily during winter dormancy (Nov–Feb) and then permanently (starting mid-May 2016) when tortoises began sustaining high levels of predation.

### **Movement, Surface Activity, and Microhabitat Use**

At each tracking event, we recorded tortoise location to the nearest 3 m using a handheld global positioning system (Garmin model GPSMAP 76, Olathe, KS, USA) and recorded attributes about the tortoise's activity and microhabitat use. When we observed the detected tortoise on the surface, we recorded its location and behavior when first seen. Otherwise, we recorded its burrow location. We categorized cover type as shrub (identified to species), rock, burrow, or pallet (shorter than burrow, with length < width). We estimated amount of the animal covered when looking down from directly above the tortoise and categorized percent tortoise covered in the ranges <1%, 1–10%, 11–25%, 26–50%, 51–75%, 76–95%, and 96–100%. We categorized activity as walking, digging, foraging, resting, or sheltering. We also counted the number of tortoise-sized rocks around animals at each tracking. To enumerate, we placed a 1 m × 1 m quadrat around the tortoise (with sides parallel to the tortoise's longitudinal axis, or squarely in front of the burrow or pallet if inactive) and counted the number of rocks within half to 1.5 times of the mean MCL (at most recent measurement) of the treatment group to which the tortoise belonged; by this standard, we considered tortoise-sized rocks to be 24.4–73.2 mm, 26.0–77.9 mm, and 43.6–130.8 mm for DR, outdoor HS, and indoor HS animals, respectively.

We subsequently converted percent of tortoise covered to a binary variable for analyses, such that a tortoise was considered covered if >50% of its body was covered from above. We also categorized activity to a binary variable: surface active (not in a burrow or pallet) or not surface active (at least part of its body inside a burrow or pallet). We used generalized linear models to evaluate differences in cover state (binomial response, logit link), surface activity state (binomial response, logit link), and number of tortoise-sized rocks (Poisson response, log link), and we used a gamma

hurdle model (Mullahy 1986) to evaluate distance moved between tracking events (log link for nonzero component, logit link for binary component) among the 3 treatment groups from 25 April to 27 October 2016 (when all 3 treatment groups were in the field). We fit all models under a Bayesian estimation framework with the brms package in R (R version 3.5, [www.r-project.org](http://www.r-project.org), accessed 11 Dec 2018). The brms package uses RStan (version 2.18.1, Stan Development Team, <http://mc-stan.org/rstan/>, accessed 11 Dec 2018) to implement the No-U-Turn sampler, a variation of Hamiltonian Monte Carlo. We considered differences among treatment groups to be significant if 95% Bayesian credible intervals (BCIs) of model predictions were non-overlapping. In each model, we included the random effect of individual to specify that repeated measures on individuals were not independent. We sampled treatment group effects from noninformative improper flat priors (uniform distribution on the real line). For each model, we ran 4 chains, each with 10,000 iterations and a thinning rate of 1, and we discarded the first 1,000 iterations as burn-in. We observed no evidence of lack of convergence ( $\hat{R} < 1.04$  for all monitored parameters).

We used the `point.distances` function in GME to calculate each tortoise's distance from its release point at the end of the movement study (by 27 Oct 2016). Because post-release survival varied among individuals and thus affected number of days radio-tracked, we plotted distance from release point over time for individuals that survived the entire study to determine which individuals to include in our analysis of final distance from release point. For these plots, we grouped individuals by release event: DR and HS release (combining indoor and outdoor HS). Plots for both groups had a clear asymptote, a point in time at which individuals stopped moving farther from their release points. If animals lived past that threshold date (29 Oct 2015 [31 days post-release] for DR and 18 Aug 2016 [115 days post-release] for HS), we included them in the analysis of final distance from release point. We natural log transformed final distance from release point to improve normality. We back-transformed means and confidence intervals for reporting. We compared distance from release point among treatment groups with 1-way analysis of variance (ANOVA) followed by Tukey's tests.

### **Survivorship and Mortality Risk Factors**

For each tortoise found dead, we carefully examined the area for signs of predators such as digging, tracks, or scat, and we noted the location and condition of the carcass. We photographed each carcass *in situ* and then collected it for further analysis. We classified carcasses or chewed transmitters that were found adjacent to excavated burrows, or that had clear tooth marks, as predated by mammal. We classified carcasses or transmitters that were found up in, or directly beneath, Mojave yucca and Joshua trees as predated by bird because we often saw ravens perching on these plants. We classified dead tortoises with damage to their bodies, but without visible tooth-marks or that were not directly in or under yucca plants as predated by unidentified

predator. We classified tortoises found intact and upside down (flipped on their carapace) or dead inside winter burrows as killed by exposure. We classified individuals lost because of radio failure (battery failure or the unit fell off) as unknown fate. We estimated survival for each treatment group using a Kaplan-Meier estimator (Pollock et al. 1989) within the survival package in Program R. We right-censored data, meaning that we made no assumptions about the fate of animals lost from the study and for which fate could not be determined.

Using only data from animals for which fate was known, we evaluated the effect of treatment group and individual-level metrics (i.e., potential risk factors) on individual fate. We included treatment group, average step length (distance moved between consecutive monitoring events; Quinn et al. 2018), average surface activity, size at release, and average distance from the documented raven nest as potential predictors in a generalized linear model (quasibinomial response with logit link; alive = 1 and dead = 0). We characterized average surface activity as the proportion of all observations for which the tortoise was surface active. Because of seasonal differences during which the HS (indoor and outdoor) and DR groups were tracked, we corrected each individual score of surface activity and step length by subtracting the treatment group mean score from the individual score. Similarly, we corrected size at release (MCL in mm) by treatment group mean size. Therefore, the resulting individual metrics for average step length, average surface activity, and size at release indicated how far the individual deviated from its treatment group mean. For each individual, we calculated average distance from the raven nest during all post-release monitoring observations of the living animal using the `point.distances` function in GME. From the model, we generated predictions and 95% confidence intervals of survival based on distance from the raven nest and average surface activity for each treatment group. We obtained predictions over a range of each effect by holding other model effects fixed at mean values.

## RESULTS

All (20/20) outdoor HS tortoises survived in their head-start pens until their release on 25 April 2016. Twenty-nine of 30 (96.7%) indoor HS tortoises survived the rearing period. We found 1 indoor HS tortoise dead of unknown causes in its mesocosm (6.6 months into the indoor rearing period). One other indoor HS tortoise had a temporary skin condition from which it later recovered, but we excluded it from the HS release and did not consider it further. Therefore, we released 68 tortoises into the natural environment: 20 DR, 20 outdoor HS, and 28 indoor HS. Growth during the HS period varied greatly by treatment group. At time of HS release (25 Apr 2016), mean MCL was  $87.2 \pm 1.0$  (SE) mm for the indoor HS group and  $51.9 \pm 1.6$  mm for the outdoor HS group. At mid-March 2015 (when we recaptured DR tortoises for transmitter replacement), average MCL was  $48.8 \pm 1.4$  mm for the DR group (Daly et al. 2018).

## Activity and Microhabitat Use

Tortoises in the 3 treatment groups were similar in their use of cover and levels of surface activity post-release but differed in the number of tortoise-sized rocks around them. Sample sizes for these analyses were 15 for the DR group (reflecting 5 losses from this treatment group over winter), 28 for the indoor HS group, and 20 for the outdoor HS group. Mean probability of being >50% under cover during tracking observations was 0.86 (95% BCI = 0.79–0.91) for DR, 0.86 (95% BCI = 0.82–0.90) for indoor HS, and 0.89 (95% BCI = 0.79–0.95) for outdoor HS, and these values did not differ (based on overlapping credible intervals). Mean probability of being surface active during tracking observations was 0.19 (95% BCI = 0.13–0.26) for DR, 0.27 (95% BCI = 0.18–0.38) for indoor HS, and 0.17 (95% BCI = 0.11–0.23) for outdoor HS, and treatment groups did not differ. On average, indoor HS tortoises had significantly fewer tortoise-sized rocks around them than either DR tortoises or outdoor HS tortoises. Direct-release tortoises had nearly 6 times more tortoise-sized rocks around them than indoor HS tortoises (11.9 [95% BCI = 7.6–18.5] vs. 2.0 [95% BCI = 1.3–2.9]). Similarly, outdoor HS tortoises were surrounded by nearly 4 times as many tortoise-sized rocks (7.9 [95% BCI = 6.3–10.0]) as indoor HS tortoises.

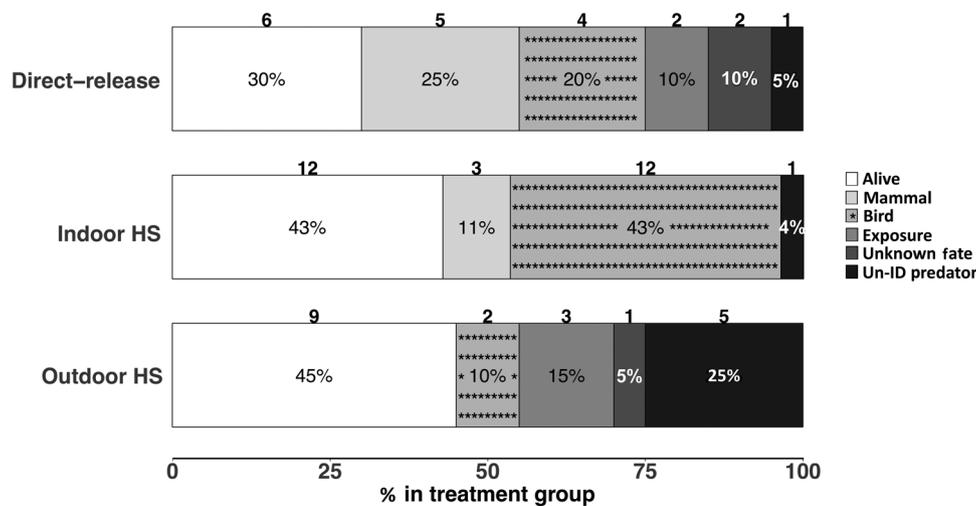
## Movement

The hurdle model indicated that treatment groups did not differ in probability of moving between tracking events. Probability of moving was 0.39 (95% BCI = 0.28–0.51) for the DR group, 0.35 (95% BCI = 0.26–0.43) for the indoor HS group, and 0.42 (95% BCI = 0.32–0.51) for the outdoor HS group. When tortoises moved, indoor HS tortoises moved significantly farther between tracking events on average (25.3 m [95% BCI = 20.9–30.6 m]) than either outdoor HS tortoises (8.2 m [95% BCI = 6.0–11.0 m]) or DR tortoises (14.3 m [95% BCI = 9.8–20.5 m]).

Final distance from release site (27 Oct 2016; 13 months after DR release and 6 months after HS release) differed among treatment groups ( $F_{2,37} = 6.83$ ,  $P = 0.003$ ). Mean final distance from release site was 163.9 m (95% CI = 93.6–286.9 m) for the DR group ( $n = 16$ ), 75.1 m (95% CI = 41.2–136.6 m) for the indoor HS group ( $n = 14$ ), and 31.9 m (95% CI = 15.7–64.7 m) for the outdoor HS group ( $n = 10$ ). Direct-release tortoises moved >5 times farther, on average, than did outdoor HS tortoises ( $t_{37} = 3.67$ ,  $P = 0.002$ ). Indoor HS and DR groups did not differ ( $t_{37} = -1.93$ ,  $P = 0.144$ ), nor did indoor HS and outdoor HS groups ( $t_{37} = 1.87$ ,  $P = 0.161$ ), in final distance from release site.

## Survivorship and Mortality Risk Factors

Of the 68 released tortoises, we confirmed 27 (39.7%) alive at the end of this study (6 Nov 2016). We confirmed that 38 of the 68 tortoises died (55.9%), and predation by birds was responsible for the greatest proportion of mortality. Eighteen (26.5% of released tortoises) were predated by birds, 8 (11.8%) were predated by mammals, 7 (10.3%) were killed by unidentified predators, and 5 (7.3%) died from exposure. We were unable to determine fate for 3 (4.4%) tortoises lost to radio



**Figure 2.** Fates of 68 juvenile desert tortoises released into the eastern Mojave Desert, California, USA. Direct-release neonates (control group,  $n = 20$ ) were released in September 2015, whereas indoor head-started (HS;  $n = 28$ ) and outdoor HS ( $n = 20$ ) juveniles were released in April 2016 after 7 months of head-starting. Bold numbers above bar segments are the number of individuals with each fate. Values within bar segments are percentage of animals with each fate by treatment group rounded to the nearest percent. Tortoises categorized as alive survived the 58-week study period. The categories bird and mammal correspond with predator taxa, whereas others were predated without clear evidence of predator taxa (un-ID predator). Others died from exposure and some went missing with unknown fate because of radio failure.

failure (Fig. 2). Annual survival (all treatment groups combined, Sep 2015–Sep 2016, including the rearing period) for the 70 tortoises was 0.44 (95% CI = 0.34–0.58). Overall survival for the entire study period (28 Sep 2015–6 Nov 2016, 58 weeks, including the rearing period) was 0.43 (95% CI = 0.32–0.56). Estimated survival was 0.37 (95% CI = 0.20–0.66) for the DR group (both annual and 58-week; Fig. 3A). Estimated annual survival was 0.45 (95% CI = 0.30–0.67) and 58-week survival was 0.41 (95% CI = 0.27–0.64) for the indoor HS group (Fig. 3B). Estimated survival was 0.50 (95% CI = 0.32–0.77) for the outdoor HS group (both annual and 58-week; Fig. 3C). Overlapping 95% confidence intervals for survival estimates throughout the study indicate no difference in survival among treatment groups at any point in time (Fig. 3).

Proportion of surface-active observations (relative to treatment group mean;  $\hat{\beta} = -6.808$ ,  $t_{61} = -3.04$ ,  $P = 0.004$ ) and distance from the raven nest ( $\hat{\beta} = 0.004$ ,  $t_{59} = 2.57$ ,  $P = 0.013$ ) were the only significant predictors of fate. Treatment group, size at release, and step length were not significant predictors of fate ( $P \geq 0.39$  in each case). All surviving tortoises were surface-active on <30% of observations (Fig. 4). Tortoises that were the least surface-active had the highest predicted survival probability (Fig. 4). Tortoises that were farther from the raven nest were also more likely to survive (Fig. 5). Odds of survival increased by 51.5% for every 100 m distant from the raven nest (Fig. 5). None of the tortoises that were on-average  $\geq 1,250$  m from the raven nest died. Our modeled predictions of survival probability approached 1.0 at approximately 1,600 m from the raven nest (Fig. 5).

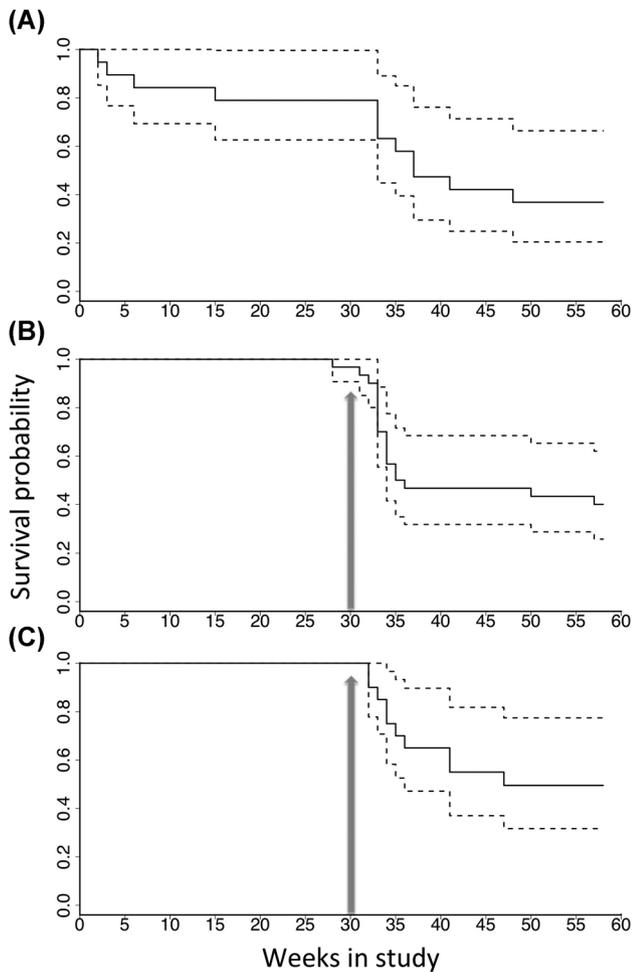
## DISCUSSION

Although there has been considerable research on head-starting as a management technique, head-starting has only

recently been attempted in desert tortoises (Hazard and Morafka 2002; Hazard et al. 2015; Nagy et al. 2015a, b). Our survival estimates of released juvenile desert tortoises build on previous work that has elucidated how ravens affect juvenile tortoises (Kristan and Boarman 2003, Hazard et al. 2015).

Counter to our expectation, we found no difference in survival among treatment groups despite the indoor-reared tortoises' substantially larger body sizes at release (the size of 5–6-yr-old wild tortoises; Turner et al. 1987, Curtin et al. 2009). Previous desert tortoise head-start studies (Hazard et al. 2015, Nagy et al. 2015b) reported that larger juvenile tortoises were more likely to survive. Nagy et al. (2015b) reported that released outdoor-reared HS juveniles >100 mm MCL were more robust to predation than smaller tortoises, and they did not find any raven-predated tortoises >80 mm MCL. An analysis of data from released HS tortoises at the same site by Hazard et al. (2015) indicated that outdoor-reared juveniles were more likely to survive if they were >84 mm in MCL at release. By these measures, we expected our indoor HS tortoises (87 mm mean MCL) to exhibit higher survival than the much smaller tortoises from the outdoor HS or DR treatments. Outdoor-reared tortoises from previous studies (Hazard et al. 2015, Nagy et al. 2015b), however, were older ( $\geq 8$  yrs) when they approached the size of our indoor HS tortoises, and likely had harder, more puncture-resistant shells (Daly et al. 2018).

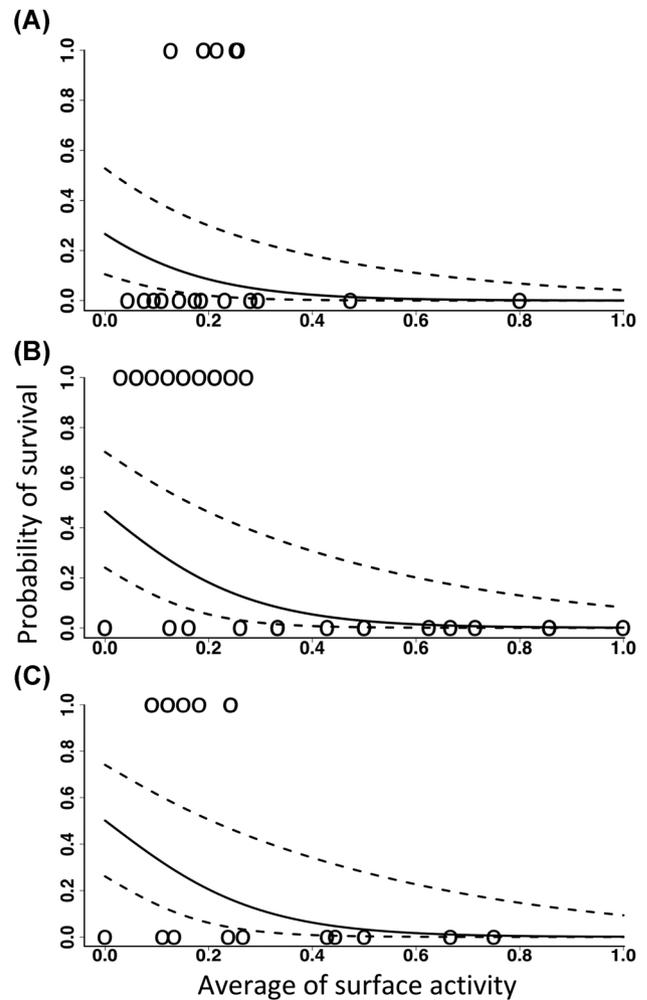
Our study yields rare and valuable estimates of first-year survival for juvenile desert tortoises. Few survival estimates are reported for juvenile desert tortoises because animals of this size are difficult to find in the wild and because radio-transmitters small enough for them to carry have short-lived batteries (Morafka 1994, Bjurlin and Bissonette 2004, Tuberville et al. 2019). Our estimate



**Figure 3.** Kaplan-Meier survival curves for 70 desert tortoises in Mojave National Preserve, California, USA, in 3 treatment groups: direct-release (A), indoor head-started (B), and outdoor head-started (C). Estimates are shown from 28 September 2015 until 6 November 2016 (58 weeks). Direct-release tortoises ( $n = 20$ ) were released into the natural environment at week zero (28 Sep 2015), whereas indoor ( $n = 30$ ) and outdoor ( $n = 20$ ) head-started tortoises were released at week 30 (25 Apr 2016; indicated by grey arrow). We right-censored data to avoid assumptions about the fate of lost or missing animals. Dashed lines show 95% confidence intervals.

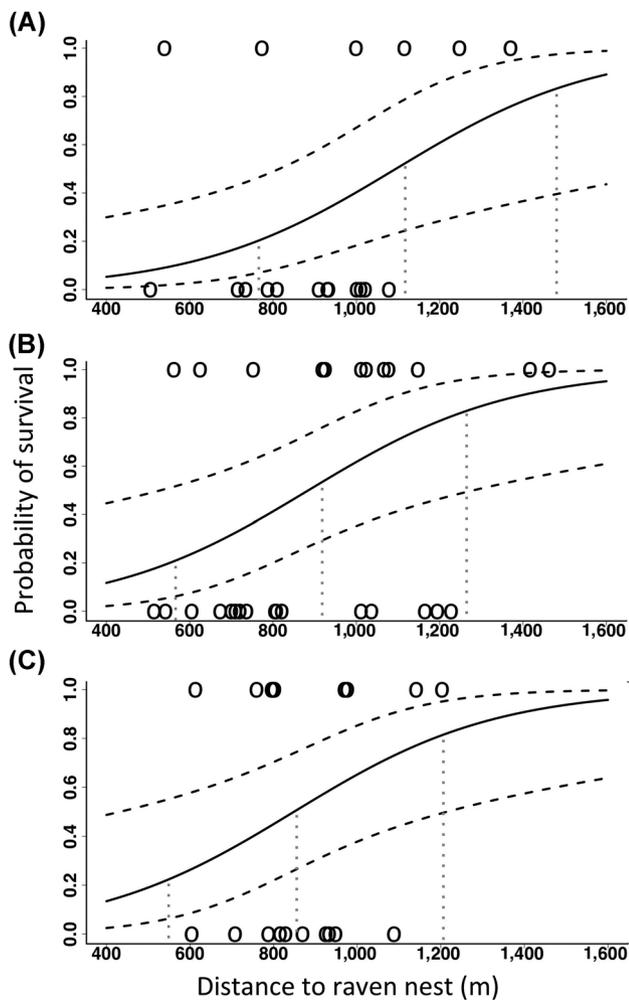
of combined annual survival (including the rearing period and combining the 3 treatment groups) was 0.44, and the largely unmanipulated DR group had an annual survival estimate of 0.37. These numbers are slightly lower but comparable to the annual survival estimate of 0.48 for free-ranging juvenile tortoises (released at 0–18 months old) from an earlier study at the same site (Tuberville et al. 2019), before the increased raven activity seen in the present study. Our survival estimates are lower than the 0.68 first-year, post-release annual survival estimate reported by Nafus et al. (2017) of juvenile tortoises (age 0.5–4 yrs) at several other locations in the Mojave Desert.

The sources of mortality varied by treatment. For example, no indoor HS tortoises died from exposure during the study, whereas 2 DR and 3 outdoor HS tortoises were presumed to have succumbed to exposure. Of the 5 exposure-related mortalities, 4 were found toppled on their carapace and 1



**Figure 4.** Observed survival fates (open circles) and predicted survival probabilities based on average surface activity (proportion of observations where surface active) for juvenile desert tortoises in Mojave National Preserve, California, USA, 2015–2016 in 3 treatment groups: direct-release (A), indoor head-started (B), and outdoor head-started (C). We predicted survival probability for each treatment group by setting average distance moved per tracking event, size at release, and average distance to an active raven nest (known predator) to the respective treatment group means. We then varied average surface activity from 0 to 1 and generated predictions of survival probability along that curve. Solid lines are predicted model estimates and dashed lines are upper and lower limits of 95% confidence intervals.

(a DR) died inside its winter burrow. The indoor HS tortoises' larger size may have reduced their risk of toppling on their carapace, or they may have been more successful in righting themselves once toppled. The larger size of indoor HS tortoises may have also prevented exposure-related deaths by reducing their risk of desiccation. For many species, water loss is negatively associated with size (Murphy et al. 2016), such that larger tortoises have greater water reserves (Nafus et al. 2015b), and body size affects heating and cooling rates (Harris et al. 2015). Therefore, larger indoor HS tortoises would likely have more time to right themselves than smaller outdoor HS and DR tortoises before expiring from heat exposure or water loss, and we would expect them to generally be more robust to exposure mortality overall.



**Figure 5.** Observed survival fates (open circles) and predicted survival probabilities based on average distance from a raven nest for juvenile desert tortoises in Mojave National Preserve, California, USA, 2015–2016, in 3 treatment groups: direct-release (A), indoor head-started (B), and outdoor head-started (C). We predicted survival probability for each treatment group by setting average distance moved per tracking event, size at release, and average surface activity to the respective treatment group means. We then varied distance from the raven nest from 400 m to 1,600 m and generated predictions of survival probability along that curve. Solid lines are predicted model estimates and dashed lines are upper and lower limits of 95% confidence intervals. Vertical grey dotted lines indicate the places along each curve where predicted survival probabilities are 0.2, 0.5, and 0.8 to facilitate visual comparison of the 3 plots.

Our study documented 33 predation events of juvenile tortoises. Predation by birds (presumably the brood-rearing ravens we regularly saw) was the largest known source of mortality in our study (26.5%), especially among the indoor head-start group (42.9%). The large proportion of mortalities of outdoor HS tortoises attributed to unidentified predators makes it difficult to compare mortality sources among treatments. Because the indoor HS group tortoises were larger than other treatment groups, ravens may have spotted them more easily. Moreover, indoor HS tortoises were associated with fewer body-sized rocks compared to other treatment groups, suggesting that they may have been more conspicuous (Nafus et al. 2015a), resulting in increased predation. Rocks at our site were uniformly

small; thus, the site offered little opportunity for tortoises to select habitat patches varying in cryptic ground cover. Also, indoor HS tortoises may have been less wary of avian predators because of routine feeding in captivity; juvenile desert tortoises can become habituated to overhead stimuli (Germano et al. 2017). Although hardness of a juvenile tortoise's shell is thought to confer protection against ravens (Nagy et al. 2011), only 3 of the 18 tortoises in our study that were confirmed as preyed upon by ravens actually had holes pecked through the carapace (considered an indicator of predation by ravens). In most cases, the ravens removed the tortoise's head, front limbs, and entrails without puncturing the shell. This suggests that even if shell hardness had been greater in tortoises in our study, the tortoises would likely still have been susceptible to ravens.

Although we knew that ravens occasionally perched on the powerlines near our release plot (500 m to the nearest edge), we did not anticipate the raven nest established at our release site, which we discovered after we initiated our head-start release in April 2016. Prior releases of juvenile tortoises in and near our site (age = hatched to 18 months at release) had no confirmed incidences of raven predation during the first year after release (Tuberville et al. 2019). Furthermore, previous research reported that breeding ravens in the Mojave Desert spend most of their foraging time  $\leq 600$  m (and 75% of foraging time  $\leq 400$  m) from their nests (Sherman 1993), suggesting that most of the tortoises at our release site should have experienced relatively low predation risk from the breeding ravens (only 5 of 68 were  $\leq 600$  m from the raven nest). In contrast, we found that tortoises were most likely to survive if they were on average  $\geq 1.6$  km from an active nest, suggesting that raven predation risk persists much farther from nesting sites than the 600 m previously suspected.

These findings have implications for protocols of lethal raven control (i.e., shooting) under depredation permits for conservation. Current federal government protocols for lethal control of ravens target only offending ravens, and ravens are only considered offending if juvenile tortoise carcasses are found within the presumed territories of the ravens (USFWS 2008). Searching a brood-rearing raven's entire 8-km<sup>2</sup> territory for tortoise carcasses is unrealistic (Boarman 2003). Furthermore, surveys for carcasses below established raven nests may not be a reliable indicator of raven predation; none of the 18 bird-killed tortoises in our study were found within 400 m of the nest. Thus, identifying offending ravens may prove difficult (Boarman 2003). Because ravens are opportunistic predators (Sherman 1993, Liebezeit and George 2002, Boarman 2003), any raven likely poses some threat to juvenile desert tortoises when found in desert tortoise habitat.

Although the siting of head-start projects is constrained by where monitoring access is logistically feasible, managers also desire sites that minimize predation pressure on newly released juveniles. Thus, knowledge of how predation risk varies with distance from man-made structures that host avian predators (e.g., powerlines or communication towers)

is important to consider when releasing tortoises. Although many ravens are predictably found at areas of high human activity like construction sites, nesting sites are more widely distributed, making their location and attendant predation risk difficult to predict (Boarman 2003, Kristan and Boarman 2003). Furthermore, raven populations have increased because of human-produced food subsidies like agriculture and garbage, and ravens are increasingly moving into natural areas such as the MNP (Liebezeit and George 2002, Boarman 2003).

We saw no differences among treatment groups in frequency of cover use or surface activity. An initial concern of ours was whether indoor HS tortoises would be able to dig suitable refugia because they did not have the opportunity to dig burrows while in captivity and were too large at release to fit in many of the unmodified small-mammal burrows in the wild. From the first day post-release, however, we observed indoor HS tortoises enlarging small-mammal burrows or constructing their own burrows. Smaller tortoises from the other treatment groups mostly used small-mammal burrows, although some were also seen digging their own. In short, tortoises from each treatment group used cover and burrow refugia similarly.

Ultimately, beyond determining survival of tortoises in each of the treatment groups, we were most interested in identifying useful predictors of their post-release fate. Step length was not a significant predictor of fate, but tortoises that were surface active more often had lower predicted survival probability. This pattern is likely influenced by tortoises that died shortly after release during the time they were dispersing and therefore more surface active (autumn for DR, and spring for indoor and outdoor HS). These animals did not survive into the less-active seasons (winter and summer), and thus had greater proportion of surface activity observations. In other words, surface activity was correlated with lower survival, but it may not have caused it.

The tortoises in our study showed high site fidelity. In most cases, tortoises from each treatment group had ceased dispersing  $\leq 30$  days after their release, and average final distance from their release point at the end of the study ranged from 31.9–163.9 m among treatment groups. Outdoor HS tortoises exhibited the highest level of site fidelity. Unlike tortoises in the DR and indoor HS groups, outdoor HS tortoises had experience living in burrows, which may have allowed them to settle into suitable refugia and cease dispersing more readily. Compared to data reported by previous work on outdoor head-started desert tortoises (Hazard and Morafka 2002, Hazard et al. 2015, Nagy et al. 2015b), both of our HS treatment groups (indoor and outdoor) exhibited high site fidelity. Furthermore, a study of 5 released head-started Ploughshare tortoises (*Astrochelys yniphora*) claimed success because the juveniles stayed  $\leq 750$  m from their release points, in addition to surviving the 325-day study (Pedrono and Sarovy 2000). By this measure, all but 1 tortoise in our study (a DR tortoise that was 928 m from its release site) showed high site fidelity. Direct-release tortoises moved

significantly farther from their release sites than outdoor HS tortoises. However, they too did not move far (mean final distance from release = 164 m), and their dispersal distances were similar to those reported for other juvenile head-started desert tortoises (Hazard and Morafka 2002, Hazard et al. 2015, Nagy et al. 2015b) and juvenile head-started gopher tortoises (*Gopherus polyphemus*; Quinn et al. 2018).

## MANAGEMENT IMPLICATIONS

The 7-month indoor HS method is not sufficient to produce raven-resistant tortoises without additional measures to reduce predation risk. For example, tortoises reared indoors for longer periods may obtain the size and shell ossification to withstand raven predation. All things being equal, post-release survival of head-started desert tortoises is most likely to be greatest when they are released  $\geq 1.6$  km from raven nests or raised man-made structures that could attract ravens. Our work suggests that all ravens found in desert tortoise habitat pose a threat to young tortoises; targeting only offending individuals for lethal control may not fully address raven predation risk. The timing of releases may also be important in mitigating predation risk to released head-start tortoises. Releasing head-start tortoises in fall, rather than spring, would ensure that HS tortoise dispersal does not coincide with raven brood-rearing (raven nestlings fledge by mid-summer), and it would also allow managers to identify areas of raven activity and nesting to avoid in the spring and summer, prior to HS tortoise release in the fall. Future studies that incorporate modifications to husbandry or release protocols to reduce predation risk by ravens could provide valuable insight into the potential role of indoor head-starting in desert tortoise recovery.

## ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. K. A. Nagy, M. W. Tuma, and M. G. Nafus offered helpful advice in the early stages of the project. L. P. Chiquoine and M. A. Steele assisted with fieldwork and husbandry. J. H. Waddle reviewed an early version of this manuscript. Funding was provided by the National Park Service (PSAC-CESU Cooperative Agreement number P08AC00193) and California Energy Commission (Agreement number 500-10-20). Additional support was provided by United States Department of Agriculture National Institute of Food and Agriculture Hatch project CA-D-WFB-2097-H to BDT, the Department of Energy under Award Number DE-FC09-07SR22506 to the University of Georgia Research Foundation, and the Desert Tortoise Council through the David J. Morafka Memorial Research award to JAD.

## LITERATURE CITED

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

- Bjurlin, C. D., and J. A. Bissonette. 2004. Survival during early life stages of the desert tortoise (*Gopherus agassizii*) in the south-central Mojave Desert. *Journal of Herpetology* 38:527–535.
- Boarman, W. I. 2003. Managing a subsidized predator population: reducing common raven predation on desert tortoises. *Environmental Management* 32:205–217.
- Buhlmann, K. A., S. L. Koch, B. O. Butler, T. D. Tuberville, V. J. Palermo, B. A. Bastarache, and Z. A. Cava. 2015. Reintroduction and head-starting: tools for Blanding's turtle (*Emydoidea blandingii*) conservation. *Herpetological Conservation and Biology* 10:436–454.
- 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* 1939:170–173.
- Caillouet, C. W., Jr., D. J. Shaver, and A. M. Landry, Jr. 2015. Kemp's Ridley sea turtle (*Lepidochelys kempii*) head-start and reintroduction to Padre Island National Seashore, Texas. *Herpetological Conservation and Biology* 10:309–377.
- Cohn, J. P. 1999. Saving the California condor: years of effort are paying off in renewed hope for the species' survival. *Bioscience* 49:864–868.
- Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *American Zoologist* 34:397–408.
- Crawford, B. A., J. C. Maerz, N. P. Nibbelink, K. A. Buhlmann, and T. M. Norton. 2014. Estimating the consequences of multiple threats and management strategies for semi-aquatic turtles. *Journal of Applied Ecology* 51:359–366.
- Curtin, A. J., G. R. Zug, and J. R. Spotila. 2009. Longevity and growth strategies of the desert tortoise (*Gopherus agassizii*) in two American deserts. *Journal of Arid Environments* 73:463–471.
- 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.
- Darst, C. R., P. J. Murphy, N. W. Strout, S. P. Campbell, K. J. Field, L. Allison, and R. C. Averill-Murray. 2013. A strategy for prioritizing threats and recovery actions for at-risk species. *Environmental Management* 51:786–800.
- 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, and J. S. Heaton. 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.
- Farnsworth, M. L., B. G. Dickson, L. J. Zachmann, E. E. Hegeman, A. R. Cangelosi, T. G. Jackson, Jr., and A. F. Scheib. 2015. Short-term space-use patterns of translocated Mojave desert tortoise in southern California. *PLoS ONE* 10(9):e0134250.
- Frazer, N. B. 1992. Sea turtle conservation and halfway technology. *Conservation Biology* 6:179–184.
- Germano, J. M., M. G. Nafus, J. A. Perry, D. B. Hall, and R. R. Swaisgood. 2017. Predicting translocation outcomes with personality for desert tortoises. *Behavioral Ecology* 28:1075–1084.
- Gibbons, J. W., and J. L. Greene. 1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. *Herpetologica* 35:86–89.
- Gibbs, J. P., E. A. Hunter, K. T. Shoemaker, W. H. Tapia, and L. J. Cayot. 2014. Demographic outcomes and ecosystem implications of giant tortoise reintroductions to Espanola Island, Galapagos. *PLoS ONE* 9(11):e110742.
- Harris, B. B., T. M. Norton, N. P. Nibbelink, and T. D. Tuberville. 2015. Overwintering ecology of juvenile gopher tortoises (*Gopherus polyphemus*). *Herpetological Conservation and Biology* 10:645–653.
- Haskell, A., T. E. Graham, C. R. Griffin, and J. B. Hestbeck. 1996. Size related survival of headstarted redbelly turtles (*Pseudemys rubriventris*) in Massachusetts. *Journal of Herpetology* 30:524–527.
- 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.
- Heppell, S. S., L. B. Crowder, and D. T. Crouse. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications* 6:556–565.
- Hereford, R., R. H. Webb, and C. I. Longpré. 2006. Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893–2001. *Journal of Arid Environments* 67:13–34.
- Hewitt, N., N. Klenk, A. L. Smith, D. R. Bazely, N. Yan, S. Wood, J. I. MacLellan, C. Lipsig-Mummé, and I. Henriques. 2011. Taking stock of the assisted migration debate. *Biological Conservation* 144:2560–2572.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Kristan, W. B., III, and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84:2432–2443.
- Liebezeit, J. R., and T. L. George. 2002. A summary of predation by corvids on threatened and endangered species in California and management recommendations to reduce corvid predation. California Department of Fish and Game, Species Conservation and Recovery Program, Sacramento, USA.
- McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* 21:297–302.
- Miller, B., D. Biggins, L. Hanebury, and A. Vargas. 1994. Reintroduction of the black-footed ferret (*Mustela nigripes*). Pages 455–463 in P. J. Olney, G. M. Mace, and A. T. Feistner, editors. *Creative conservation: interactive management of wild and captive animals*. Springer, Dordrecht, Netherlands.
- Morafka, D. J. 1994. Neonates: missing links in the life histories of North American tortoises. Pages 161–173 in R. B. Bury and D. J. Germano, editors. *Biology of North American tortoises*. National Biological Survey, Fish and Wildlife Research 13. U.S. Department of the Interior, National Biological Survey, Washington, D.C., USA.
- Mullahy, J. 1986. Specification and testing of some modified count data models. *Journal of Econometrics* 33:341–365.
- Murphy, C. M., T. D. Tuberville, J. C. Maerz, and K. M. Andrews. 2016. Evaporative water loss rates of four species of aquatic turtles from the Coastal Plain of the southeastern United States. *Journal of Herpetology* 50:457–463.
- Nafus, M. G., T. C. Esque, R. C. Averill-Murray, K. E. Nussear, and R. R. Swaisgood. 2017. Habitat drives dispersal and survival of translocated juvenile desert tortoises. *Journal of Applied Ecology* 54:430–438.
- Nafus, M. G., J. M. Germano, J. A. Perry, B. D. Todd, A. Walsh, and R. R. Swaisgood. 2015a. Hiding in plain sight: a study on camouflage and habitat selection in a slow-moving desert herbivore. *Behavioral Ecology* 26:1389–1394.
- Nafus, M. G., B. D. Todd, K. A. Buhlmann, and T. D. Tuberville. 2015b. Consequences of maternal effects on offspring size, growth and survival in the desert tortoise. *Journal of Zoology* 297:108–114.
- Nafus, M. G., T. D. Tuberville, K. A. Buhlmann, and B. D. Todd. 2013. Relative abundance and demographic structure of Agassiz's desert tortoise (*Gopherus agassizii*) along roads of varying size and traffic volume. *Biological Conservation* 162:100–106.
- Nagy, K. A., S. Hilliard, S. Dickson, and D. J. Morafka. 2015a. 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. 2015b. Head-started desert tortoises (*Gopherus agassizii*): movements, survivorship and mortality causes following their release. *Herpetological Conservation and Biology* 10:203–215.
- Nagy, K. A., M. W. Tuma, and L. S. Hillard. 2011. Shell hardness measurements in juvenile desert tortoises, *Gopherus agassizii*. *Herpetological Review* 42:191–195.
- Nussear, K. E., T. C. Esque, R. D. Inman, L. Gass, K. A. Thomas, C. S. Wallace, J. B. Blainey, D. M. Miller, and R. H. Webb. 2009. Modeling habitat of the desert tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran Deserts of California, Nevada, Utah, and Arizona. U.S. Geological Survey Open-File Report 2009-1102, Washington, D.C., USA.
- Peaden, J. M., T. D. Tuberville, K. A. Buhlmann, M. G. Nafus, and B. D. Todd. 2015. Delimiting road-effect zones for threatened species: implications for mitigation fencing. *Wildlife Research* 42:650–659.

- Pedrono, M., and A. Sarovy. 2000. Trial release of the world's rarest tortoise *Geochelone yniphora* in Madagascar. *Biological Conservation* 95:333–342.
- Pérez-Buitrago, N., M. A. García, A. Sabat, J. Delgado, A. Álvarez, O. McMillan, and S. M. Funk. 2008. Do headstart programs work? Survival and body condition in headstarted Mona Island iguanas *Cyclura cornuta stejnegeri*. *Endangered Species Research* 6:55–65.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- Quinn, D. P., K. A. Buhlmann, J. B. Jensen, T. M. Norton, and T. D. Tuberville. 2018. Post-release movement and survivorship of head-started gopher tortoises. *Journal of Wildlife Management* 82:1545–1554.
- Seddon, P. J., C. J. Griffiths, P. S. Soorae, and D. P. Armstrong. 2014. Reversing defaunation: restoring species in a changing world. *Science* 345:406–412.
- Sherman, M. W. 1993. Activity patterns and foraging ecology of nesting ravens in the Mojave Desert, California. Thesis, Colorado State University, Fort Collins, USA.
- Spencer, R. J., J. U. Van Dyke, and M. B. Thompson. 2017. Critically evaluating best management practices for preventing freshwater turtle extinctions. *Conservation Biology* 31:1340–1349.
- Stanford, C. B., A. G. Rhodin, P. P. van Dijk, B. D. Horne, T. Blanck, E. V. Goode, R. Hudson, R. A. Mittermeier, A. Currylow, C. Eisemberg, et al., editors. 2018. Turtles in trouble: the world's 25+ most endangered tortoises and freshwater turtles—2018. Turtle Conservation Coalition, Ojai, California, USA.
- 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., T. M. Norton, K. A. Buhlmann, and V. Greco. 2015. Head-starting as a management component for gopher tortoises (*Gopherus polyphemus*). *Herpetological Conservation and Biology* 10:455–471.
- Tuma, M. W., C. Millington, N. Schumaker, and P. Burnett. 2016. Modeling Agassiz's desert tortoise population response to anthropogenic stressors. *Journal of Wildlife Management* 80:414–429.
- Turner, F. B., P. A. Medica, and R. B. Bury. 1987. Age-size relationships of desert tortoises (*Gopherus agassizii*) in southern Nevada. *Copeia* 1987:974–979.
- Turner, F. B., P. A. Medica, and C. L. Lyons. 1984. Reproduction and survival of the desert tortoise (*Scaptochelys agassizii*) in Ivanpah Valley, California. *Copeia* 1984:811–820.
- United States Fish and Wildlife Service [USFWS]. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Mojave population of the desert tortoise. *Federal Register* 55: 12178–12191.
- United States Fish and Wildlife Service [USFWS]. 2008. Environmental assessment to implement a desert tortoise recovery plan task: reduce common raven predation on the desert tortoise. U.S. Fish and Wildlife Service, Ventura, California, USA.
- United States Fish and Wildlife Service [USFWS]. 2011. Revised recovery plan for the Mojave population of the desert tortoise (*Gopherus agassizii*). U.S. Fish and Wildlife Service, Pacific Southwest Region, Sacramento, California, USA.
- Woodbury, A. M., and R. Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizii*. *Ecological Monographs* 18:145–200.

Associate Editor: Cynthia Paszkowski.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.