Articles

The Effect of Size on Postrelease Survival of Head-Started Mojave Desert Tortoises

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Abstract

Captive-rearing conservation programs focus primarily on maximizing postrelease survival. Survival increases with size in a variety of taxa, often leading to the use of enhanced size as a means to minimize postrelease losses. Head-starting is a specific captive-rearing approach used to accelerate growth in captivity prior to release in the wild. We explored the effect of size at release, among other potential factors, on postrelease survival in head-started Mojave desert tortoises *Gopherus agassizii*. Juvenile tortoises were reared for different durations of captivity (2–7 y) and under varying husbandry protocols, resulting in a wide range of juvenile sizes (68–145 mm midline carapace length) at release. We released all animals ($n = 78$) in the Mojave National Preserve, California, United States, on 25 September 2018. Release size and surface activity were the only significant predictors of fate during the first year postrelease. Larger sized head-starts had higher predicted survival rates when compared with smaller individuals. This trend was also observed in animals of the same age but reared under different protocols, suggesting that accelerating the growth of head-started tortoises may increase efficiency of head-starting programs without decreasing postrelease success. Excluding five missing animals, released head-starts had 82.2% survival in their first year postrelease (September 2018–September 2019), with all mortalities resulting from predation. No animals with >90-mm midline carapace length were predated by ravens. Our findings suggest the utility of head-starting may be substantially improved by incorporating indoor rearing to accelerate growth. Target release size for head-started chelonians will vary among head-start programs based on release site conditions and project-specific constraints.

Keywords: desert tortoise; species recovery; head-starting; size; survival

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Introduction

Survival increases with size in a variety of taxa (Wilbur and Collins 1973; Swingland et al. 1979; Murie and Boag 1984; Williams et al. 1993). This relationship is especially evident in long-lived organisms exhibiting type III survivorship, where mortality is inversely related with age, and thus, often size (Iverson 1991). Chelonians, generally characterized by low hatchling survival, slow growth, delayed maturity, and high adult survival, are a prime example of an organism with type III survivorship (Iverson 1991; Congdon et al. 1993; Heppell 1998). Adult chelonians' high survivorship has been attributed to age-related increases in size, thermal and hydric homeostasis, mobility, and shell hardness (Wilson 1991; Haskell et al. 1996; Wilson et al. 2001; Nagy et al. 2011). Though the most obvious difference in survival rates in chelonians is seen when comparing adults and juveniles (Pike et al. 2008), size differences across the range of juvenile life stages presumably also lead to differential survival within this age class (Haegen et al. 2009; Nagy et al. 2015b; Arsovski et al. 2018).

Growth rates are often highly variable in ectotherms and they are affected by a wide range of environmental, climatic, demographic, and genetic factors (Ernst 1975; Rhen and Lang 1995; Steyermark and Spotila 2001; Mack et al. 2018). Ernst (1975) measured the growth rates of a northern population of spotted turtles *Clemmys guttata* and found that growth was limited by the length of the active season and the corresponding water temperatures. Koper and Brooks (2000) measured growth rates of juvenile painted turtles *Chrysemys picta* and corroborated previous findings that warmer, longer active seasons increase growth (Parmenter 1980; Frazer et al. 1993). Studies have also found that snapping turtles *Chelydra serpentina* grow faster in habitats with high productivity (Brown et al. 1994), and that rapid growth in gopher tortoises *Gopherus polyphemus* may be attributed to high-quality habitat achieved through active management (Mushinsky et al. 1994). These studies suggest that factors like habitat quality and food availability could potentially be managed to improve growth in wild populations. Similarly, captive reptile populations have been studied to determine whether husbandry conditions can be manipulated to accelerate growth rates (Reiber et al. 1999; Jarvie et al. 2015; Daly et al. 2018).

Head-starting—the rearing of offspring in captivity until they are presumably more likely to survive in the wild once released (Burke 2015)—is gaining prominence among chelonian recovery efforts and is predicated on the assumption that juvenile size at release is positively correlated with postrelease survival (Haegen et al. 2009; Buhlmann et al. 2015; Quinn et al. 2018). In addition to attempting to increase postrelease survival by releasing larger individuals, head-starting can increase the number of juveniles recruited into the population at the release site. This is achieved by removing the threat of predation on the vulnerable hatchling size class while providing optimal conditions for growth during captivity. Although prioritizing habitat protection and high adult survivorship remains paramount in conserving populations, head-starting may help stabilize declining populations if implemented alongside other conservation measures (Tomillo et al. 2008; Crawford et al. 2014; Spencer et al. 2017). This multifaceted approach, where head-starting is used as a short-term augmentation tool together with broadly focused conservation initiatives, is being applied in the recovery of the Mojave desert tortoise *Gopherus agassizii* (USFWS 2011).

The Mojave desert tortoise (hereafter, desert tortoise; Figure 1), federally listed as threatened in 1990 (US Endangered Species Act [ESA 1973], as amended), has experienced severe population declines for the past half-century (USFWS 2011). Multiple factors have contributed to these declines, including habitat destruction, increased drought, road mortalities, and growing populations of subsidized predators (Berry 1986; Foreman et al. 1986; USFWS 2011; Peaden et al. 2015). In 1989, researchers began evaluating head-starting as a potential addition to the wide range of management strategies used to mitigate desert tortoise population declines (Morafka et al. 1997).

Early head-starting projects focused on evaluating the health and survival of head-started tortoises during

Figure 1. Juvenile Mojave desert tortoise *Gopherus agassizii* photographed on 31 July 2015 in the Mojave National Preserve, San Bernardino, California, United States. Photo credit: Jacob Daly

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captivity (Morafka et al. 1997; Nagy et al. 2015a), but researchers soon transitioned to assessing which factors most affected survival after release (Hazard et al. 2015; Nagy et al. 2015b). Based on 3 mo of monitoring postrelease survival, Hazard et al. (2015) recommended the release of head-starts measuring ≥84 mm midline carapace length (MCL). Subsequently, Nagy and colleagues (2015b) found that survivorship reached 100% during nondrought years at their study site for animals >100 mm MCL at time of release. Drought years induced prey-switching behavior in coyotes *Canis latrans,* resulting in losses of the larger individuals (>100 mm MCL) as well (Nagy et al. 2015b). Though these recommended release sizes may seem similar, a 16-mm difference in MCL represents ≥1 additional year of growth in captivity under conventional outdoor-rearing conditions (for growth rates see Nagy et al. 2015a; Daly et al. 2018; Tuberville et al. 2019). As a result, 5–9 y of outdoor rearing are required to reach previously recommended release sizes (Hazard et al. 2015; Nagy et al. 2015b). Therefore, refining the recommended release size has the potential to both increase postrelease success and maximize the efficiency of head-starting desert tortoises (Canessa et al. 2016).

In addition to the direct effects of size on survival, certain postrelease behaviors may affect survival of released head-starts, and these behaviors might be expected to vary depending on an individual's size or age. Long-distance dispersal from the release site has been identified as the primary driver of mortality risk in translocations of reptiles and amphibians (Germano and Bishop 2009). Dispersal increases risk of exposure to both thermal extremes and predation (Hazard and Morafka 2002; Stamps and Swaisgood 2007); thus, distance moved from release site may negatively correlate with survival probability. Regardless of dispersal distance, increased exposure and predation may also result from longer or more frequent bouts of surface activity. Daly et al. (2019) found that all surviving head-started desert tortoises released in their study were found out of their burrows on <30% of tracking events, and decreased surface activity was positively associated with survival probability. Desert tortoises spend a large proportion of their time inactive in their burrows (Zimmerman et al. 1994), but individuals vary in the number of burrows used in an active season (Harless et al. 2009). Moving between or relocating to different burrows requires tortoises to be surface active; therefore, the number of burrows used by an individual may be negatively associated with survival. Alternatively, burrow switching may be a form of predator avoidance (Henen et al. 2017), with greater survival probability associated with individuals that use this strategy. Thus, both the tendency to be surface active and variation in burrow switching behavior may be important predictors of postrelease survival.

Since 2011, our team has been evaluating the potential role of head-starting in contributing to the recovery of the desert tortoise. During this time, we conducted a series of experimental studies (Nafus et al. 2015; Todd et al. 2016; Daly et al. 2018, 2019; Tuberville et al. 2019) focused on identifying combinations of both pre- and postrelease conditions that maximize tortoise survival and the efficiency of head-starting. Herein, our primary objective was to evaluate the importance of size at release on survival of head-started desert tortoises during the first year following release. We also consider the potential influence of time spent in captivity, postrelease dispersal distance, surface activity, and burrow switching behavior on survival.

Study Site

Both the captive husbandry and field components took place in Ivanpah Valley in the northeastern most corner of the Mojave National Preserve, a 650,000-ha preserve in San Bernardino County, California. The primary habitat at our release site was *Yucca* woodland, dominated by creosote bush *Larrea tridentata,* white bursage *Ambrosia dumosa,* littleleaf ratany *Krameria erecta,* and heavily intermixed yucca *Yucca schidigera* and *Y. brevifolia* (Turner et al. 1984; Todd et al. 2016). Although habitat suitability remains relatively high in Ivanpah Valley (Nussear et al. 2009), the resident tortoise population has experienced considerable declines, largely mirroring range-wide declines of this threatened species (Allison and McLuckie 2018). The predominant causes of the declines in Ivanpah Valley have not been identified, but the synergistic effects of road mortalities, subsidized predators, drought, and disease are likely contributing factors (Berry 1984; Esque et al. 2010; USFWS 2011; Peaden et al. 2015). The captive-rearing portion of our study, carried out at the Ivanpah Desert Tortoise Research Facility, made use of indoor rearing facilities and outdoor predator-proof enclosures (further details below) located 15 km from our release site.

Methods

Obtaining hatchlings

In April 2011, we attached transmitters (RI-2B, Holohil Systems Ltd., Ontario, Canada) to 30 adult female desert tortoises from our field site in Ivanpah Valley. We tracked females monthly using a 3-element Yagi antenna (AF Antronics, Inc., Urbana, IL) and a R1000 receiver (Communications Specialists, Inc., Orange, CA). Each April, we brought all females to the Ivanpah Desert Tortoise Research Facility and radiographed them to check for the presence of calcified eggs (Diagnostic Imaging Systems, Poskam, CO; 60 kvp, 0.8 mAS, 74-cm focal length; Gibbons and Greene 1979). We placed gravid females in individual nesting enclosures (5 × 9 m) and allowed them to nest naturally. Nesting enclosures were constructed to deter both avian and mammalian predators and contained natural vegetation for shade and forage. We provided females with artificial burrows and supplemental water. Weekly, we monitored for egg deposition by radiographing each penned female tortoise. If nesting was confirmed, we immediately released the female at her point of capture. Accordant with our permits, we released any females that had not nested within 30 d at their last known burrow location.

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Eggs incubated naturally in the enclosures. After approximately 80 d, we began searching the pens daily for emerged hatchlings. We marked all hatchlings by notching unique combinations of marginal scutes using codes assigned by the U.S. Fish and Wildlife Service (USFWS) (Cagle 1939). We carefully excavated all nests that had unemerged hatchlings to recover any unhatched eggs or entombed hatchlings. We randomly assigned all healthy neonates to rearing enclosures at the end of the hatching season. This study includes juveniles from the 2011, 2012, and 2016 cohorts.

Prerelease husbandry

Each year we placed all (prior to 2015) or a subset (2015 and later) of the available hatchlings in predator-proof enclosures at the Ivanpah Desert Tortoise Research Facility to be reared exclusively outdoors. The enclosures contained natural substrate and vegetation (Alberts 2007) that we supplemented with rocks, downed *Yucca* logs, and artificial burrows as shelter sites. We also outfitted each enclosure with rotating garden sprinklers to provide artificial rain every 1–2 weeks during the tortoise active season (March–October) as described elsewhere (Nafus et al. 2017; Daly et al. 2018; Tuberville et al. 2019).

Initially, tortoises from the 2011–2015 cohorts received only supplemental rain and relied on natural vegetation growth in the pens for forage (Beatley 1974). Starting in March 2016, as a result of the depletion of native forage within the pens, we began providing supplemental food during each artificial watering event. Supplemental food, a measured mix of leafy greens and Mazuri® Tortoise Diet (Mazuri Exotic Animal Nutrition, St. Louis, MO; Daly et al. 2018), approximated the nutritional properties of the desert tortoise's natural diet (Jarchow et al. 2002). Thus, the 2011–2015 cohorts initially received only supplemental water, but starting in spring 2016, also received supplemental food, whereas the 2016 cohort received both supplemental water and food throughout their outdoor rearing. Animals reared in outdoor enclosures were allowed to undergo winter dormancy during which surface activity, feeding and, thus, growth are minimal.

Beginning in 2015, we started rearing a subset of each cohort indoors in an attempt to accelerate their growth while in captivity (Daly et al. 2018). Daly et al. (2018) compared indoor captive-rearing with conventional outdoor captive-rearing, finding that indoor-reared tortoises (7 mo) grew significantly faster (8×) than their outdoor-reared siblings but lacked the shell hardness of similar sized, yet older (3–4 y old) outdoor-reared individuals. To combine the increased growth of indoor rearing and the increased shell hardness of outdoor rearing, in autumn 2016 we initiated a novel method of combination rearing. Combination rearing consisted of 1 y of indoor rearing followed by 1 y of outdoor rearing in predator-proof enclosures, with the outdoor rearing portion including both supplemental water and food as described above.

As part of the current study, we released 78 tortoises from three different cohorts, representing a wide range of release sizes (Data S1, *Supplemental Material*). We released 15 tortoises from each of our 2011 and 2012 cohorts. We released 48 tortoises from our 2016 cohort—half of which were reared outdoors only while the other half was combination reared. By releasing animals from these three cohorts (2011, 2012, 2016) reared under the protocols described above, we were able to release tortoises at sizes that bracketed the previously recommended release sizes (84 mm MCL, Hazard et al. 2015; 100 mm MCL, Nagy et al. 2015b). We did not consider husbandry treatment in analyzing individual fate because results from previous releases at our site have failed to detect differences in postrelease survival and behavior based on husbandry treatment groups (Daly et al. 2019; Tuberville et al. 2019), beyond those that could be attributed directly to effects of husbandry treatment on size at release (McGovern 2019).

Morphometrics and growth

We measured all hatchlings immediately after they emerged from nests. After these initial measurements, we measured animals each autumn (September), including immediately prior to release (25 September 2018). At each measuring period, we used vernier calipers to measure MCL as the straight-line distance (0.1-mm precision) from the anterior edge of the nuchal scute to the inside of the natural notch in the supracaudal scute. We compared mean MCL at hatching among cohorts using linear mixed-effects models ('nlme' package, 'lme' function in Program R) with hatchling mother as a random effect. Similarly, we compared mean MCL at release among cohorts. When a significant difference was detected ($\alpha = 0.05$ rate of Type I error), we used Tukey's post hoc comparisons ('glht' function in the 'multcomp' package) to investigate pairwise differences.

To calculate mean annual growth rates for each individual, we separated the captive-rearing period into three husbandry stages: 1) outdoor rearing with no supplemental food; 2) outdoor rearing with supplemental food; and 3) indoor rearing. Thus, for tortoises from our 2011 and 2012 cohorts, we calculated separate mean annual growth rates for their time spent in pens with no supplemental food and for their time spent in pens with supplemental food. Additionally, we calculated mean annual growth rates for their first 2 y of life, allowing us to compare growth of same-aged tortoises reared outdoors with (2016 cohort) and without (2011 and 2012 cohorts) supplemental food. For the combination-reared tortoises, we calculated separate annual growth rates for the indoor and outdoor rearing stages. To calculate annual growth rates, we divided the change in MCL between initial and last autumn measurements by the number of years reared under that husbandry stage. For the 2011 and 2012 cohorts, for which we modified

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outdoor husbandry protocols to include supplemental feeding during spring 2016, we used autumn 2015 measurements as final measurements for calculating growth for outdoor rearing with no supplemental feeding and used those same measurements as initial sizes to calculate growth resulting from outdoor rearing with supplemental food. We think it is appropriate to use autumn 2015 measurements despite the March 2016 change in husbandry because previous studies have found that desert tortoises exhibit relatively little growth before April and after July each year (Medica et al. 1975). Data are presented as means ± 1 standard error (SE).

Experimental releases

In autumn 2018, we released all juveniles into *Yucca* woodland habitat at our site. We chose the specific release site based on habitat quality, its accessible yet remote location, and previously published recommendations on minimum distance from potential perch sites for ravens *Corvus corax* (Nafus et al. 2015; Todd et al. 2016; Daly et al. 2019). Daly et al. (2019) reported that predicted survival of released head-started desert tortoises approached 100% when release sites were 1.6 km from a raven nest. Using ArcGIS (version 10.5; ESRI, Redlands, CA), we first delineated a 0.6-km^2 rectangular release plot (300 m × 2000 m) parallel to our lone sandy access road, with the nearest corner >1.9 km from a powerline near our site. We then used the 'Fishnet' function to generate release points throughout the plot at 50-m intervals. Next, we removed points to create three equally spaced blocks of release points within the rectangular plot. We then labeled points 1–78 to correspond with a release location for each juvenile tortoise. Each block, separated from each other by approximately 350 m, contained 26 points. We buffered release points 10 m to maximize our ability to select a release refugium for each juvenile that contained a large perennial shrub and an intact kangaroo rat *Dipodomys* spp. burrow (Nafus et al. 2015; Todd et al. 2016) at each generated release location. We released each juvenile tortoise head-first into a kangaroo rat burrow that we had previously enlarged as needed to safely conceal the released animal. Under this release protocol, taking into account the buffered limit of each release point, the minimum possible distance between release burrows was 30 m. We conducted bouts of tracking effort by replicate release block to most efficiently track the large number of released animals.

Prior to release, we held all juveniles indoors for 3–5 d at the Ivanpah Desert Tortoise Research Facility, allowing us to soak and feed tortoises, visually assess their health, and attach transmitters. We randomly assigned each juvenile, irrespective of treatment, to 1 of the 78 release centers. We released all juveniles on 25 September 2018. We released animals in their preselected refugia between 0600 and 1000 hours to avoid extreme temperatures.

Postrelease monitoring

We attached VHF (very high frequency) radiotransmitters to juveniles prior to their release. We affixed transmitters (3.1 gram [g] R1670 on 2016 animals reared solely outdoors; 3.6-g R1680 transmitters on all others; Advanced Telemetry Systems, MN, USA) to the fifth vertebral scute with 5-minute epoxy (Devcon 5-minute epoxy gel, ITW Engineered Polymers, County Clare, Ireland). Transmitters weighed <5% of the body mass at time of release of the recipient tortoise (apart from the three smallest 2016 outdoor animals for which the transmitter weighed 6% of the preattachment body mass). To help camouflage the transmitter bundle, we coated all transmitters with a thin layer of sand before the epoxy hardened (Kazmaier et al. 2002).

We tracked each animal 24 h after initial release and then twice per week for the next 3 wk. We then tracked juveniles weekly until dormancy (31 October 2018), then every 10–14 d during dormancy (November 2018–February 2019). As tortoises became active in the spring (March 2019), we resumed weekly tracking for the remainder of the study (March 2019–September 2019). At each tracking occasion, we recorded the tortoise's location to the nearest ±3 m using a handheld global positioning system (GPS; Garmin model GPSMAP 76, Olathe, KS). We used these tracking occasions to monitor postrelease movement and behavior (surface activity, burrow switching), which were subsequently used as predictors in our survival models (details below).

We used an online calculator (Movable Type Ltd. 2015) to calculate, for each individual tortoise, the distance between its release burrow and its final location (total displacement). We set its final location as where it was found on the last day of the study (27 September 2019) for all individuals surviving the study or, for those that died, their last known live location. We calculated surface activity as the number of times a tortoise was found outside a burrow or pallet (short burrow with width longer than length) divided by the total number of tracking occasions. We considered a tortoise inside a burrow or pallet if any part of the animals' body was inside the refugium. We defined burrow switching as the number of unique burrows used by an individual divided by the total number of tracking occasions that individual was found in a burrow; the proportion thus accounted for differences in number of tracking occasions among individuals due to mortalities during the study. We did not include pallets when calculating the number of unique burrows used by each individual.

Survival rates

We estimated postrelease survival rates through the end of the 1-y monitoring period (September 2018–September 2019) using the Kaplan–Meier estimator in the R package 'survival' (R Core Team 2018). When a dead tortoise was found, we carefully inspected the surrounding area for any signs of what may have caused the death of the individual. Signs of predation included

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digging, tracks, scat, and teeth marks or beak punctures on the carcass. We photographed each carcass in situ and collected them for further analysis. We attributed mortalities to one of five classifications: mammal depredated, bird depredated, unidentified predator, exposure, or unknown fate. Clear digging activity or obvious tooth marks suggested mammal predation. We classified remains near perch sites with clear signs of being struck by a beak as bird depredated. If the carcass was damaged but remains showed no evidence of tooth marks or avian predation, we considered it to be depredated by an unidentified predator. We presumed dead tortoises found intact either on the surface or in their burrows to have been killed by exposure. We classified animals lost as a result of radio failure (faulty batteries or the unit fell off) as unknown fate, and we right-censored (no assumption of fate) these animals in our survival analysis.

We evaluated the effect of several factors on individual fate, using only the individuals with a known fate at the end of the study. We included time spent in captivity (TIC), MCL at release, total displacement (TDisp), surface activity (SA), and burrow switching (Burr) as potential predictors in a combination of generalized linear models with a binary response (alive = 1 and dead = 0). To construct the model set, we considered all combinations of predictors as main effects (32 models of main effects only, including intercept-only). We also considered 5 additional models containing two-way interactions that we believed to be biologically relevant (MCL × SA, MCL × TDisp, MCL × Burr, TIC × SA, TIC × TDisp). Models containing interactions also contained their constituent main effects. Coefficients of correlation (r) among predictor variables were all <0.65, with TIC and MCL at release being the most highly correlated ($r = 0.60$). We then used Akaike's information criterion (AIC) values to compare among the competing models and evaluate model fit. To account for uncertainty in model selection, we used multimodel averaging (R package 'AICcmodavg'). We generated model-averaged predictions and 95% confidence intervals (CIs) of survival across a range (60–150 mm) of MCL values, holding all other predictor variables to their average values. We kept predictor variables other than MCL constant because MCL at release is the only predictor under a manager's control.

Results

Morphometrics and growth

Mean MCL at hatching was 45.1 ± 0.2 mm ($n = 78$), though it differed among cohorts ($F_{2,48} = 9.022$; $P < 0.0001$; Data S1). For the 2011 and 2012 cohorts, growth during outdoor rearing averaged 10.9 ± 0.4 mm MCL/y with no supplemental food (2011–2015) and 16.3 ± 0.9 mm MCL/y with the addition of supplemental food (2016–2018). Juveniles from our 2016 cohort reared solely outdoors with supplemental food grew 19.1 ± 0.7 mm MCL/y (Data S1). Tortoises reared using combination rearing grew 57.2 ± 2.3 mm MCL/y while indoors (September 2016–September 2017) and 15.4 ± 1.3 mm MCL/y while outdoors with supplemental food (September 2017–September 2018; Data S1). The overall combination of rearing conditions and cohorts used in this study resulted in release sizes ranging from 68 to 145 mm MCL (Data S1). Mean time spent in captivity among released animals was 3.7 y and ranged from 2 to 7 y (Data S1).

Surface activity and burrow switching

Mean total displacement over the course of the 1-y postrelease monitoring period was 299 ± 55 m ($n = 73$; range = 10–3101 m; Data S1). Proportion of surface-active tracking events averaged 0.40 ± 0.02 ($n = 73$; range = 0.16–1.0; Data S1) among all released head-started tortoises with known fate at the end of the study. The mean number of unique burrows used by each individual over the monitoring period (25 September 2018–27 September 2019), or until the animal died, was 6.62 ± 0.31 (range = 0–12; Data S1). Mean burrow switching by all tortoises in our study was 0.34 ± 0.02 (range = 0.0–1.0; 1 animal was never found in a burrow before it was found depredated; Data S1).

Survival

Of the 78 tortoises released, 60 (76.9%) were confirmed alive at the end of the study (27 September 2019). Based on analysis of each dead animal in the field as well as the surroundings of each carcass, all mortalities were attributed to predation. Mammal predators were responsible for the largest percentage of mortality (12.8% of released tortoises). Three (3.8%) head-starts were predated by a bird and five (6.4%) were lost as a result of radio failure. Notably, all tortoises depredated by avian predators were 2016 solely outdoor-reared animals (tortoises in this husbandry group ranged 68–98 mm MCL at release). Based on the 78 tortoises released in this study, total 1-y postrelease survival was estimated at 0.83 (95% CI = 0.75–0.92; Figure 2).

No model for survival in the candidate set gathered >0.33 of AIC model weight, indicating high uncertainty in model selection (Table 1). In the four most competitive models in the set ($\triangle$AIC ≤ 2.0; accounting for 73% of AIC model weight collectively), MCL ($P \leq 0.009$) was the only significant predictor of fate appearing in all four models. Surface activity also appeared as a term in these four models, where it had a significant negative relationship with survival ($P \leq 0.022$) in the three models in which it did not interact with another term. The only model with an interaction in this most competitive set of models contained a negative interaction between MCL and surface activity; however, the effect was not significant ($P = 0.752$). Model-averaged predictions over the range of MCL (60–150 mm; with all other measured covariates held constant at their respective means) showed that survival probability increased with size at release (Table 2; Figure 3). Annual predicted survival probability ranged

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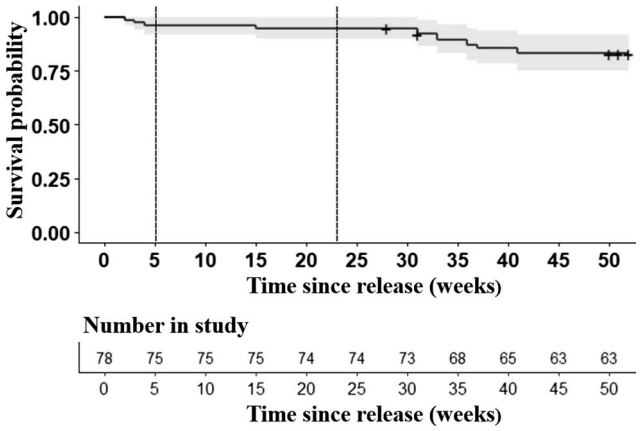

Figure 2. Kaplan–Meier survival curve for 78 head-started Mojave desert tortoises *Gopherus agassizii* released into the Mojave National Preserve, San Bernardino, California, United States. Estimates are based on monitoring from 25 September 2018 until 27 September 2019 (52 weeks). Dashed vertical lines represent the beginning and end of the dormancy period (31 October 2018–5 March 2019). Data were right-censored, in that no assumptions were made about the fate of lost or missing animals ($n = 5$). Shaded bands are 95% confidence intervals.

Table 1. Most parsimonious (Akaike weight $\geq$ 0.01) of 37 candidate models to evaluate which model terms best predict postrelease fate (1 = alive, 0 = dead) of head-started Mojave desert tortoises *Gopherus agassizii* released into the Mojave National Preserve, San Bernardino, California, United States, in order of descending Akaike Information Criteria (AIC) weight. All tortoises were released 25 September 2018 and monitored until 27 September 2019. Models containing an interaction term also contain the constituent terms of the interaction as main effects. Statistics for evaluating parsimony include model degrees of freedom (*K*), AIC, delta AIC (△AIC), and Akaike weight (AICwt); the last of these expresses the strength of evidence for the model relative to others in the candidate set.

Model[a]	*K*	AIC	△AIC	AICwt
MCL + SA	2	62.2	0.0	0.33
TIC + MCL + SA	3	63.7	1.5	0.15
MCL × SA	3	64.1	1.9	0.13
MCL + Burr + SA	3	64.2	2.0	0.12
TIC + MCL + Burr + SA	4	65.6	3.4	0.06
MCL + Burr + TDisp + SA	4	66	3.8	0.05
TIC × SA	3	66.5	4.3	0.04
TIC + MCL + Burr + TDisp + SA	5	67.3	5.1	0.03
MCL × Burr	3	67.7	5.5	0.02
MCL	1	67.9	5.7	0.02
MCL + Burr	2	68.9	6.7	0.01
MCL + TDisp	2	69.1	6.9	0.01

[a] Model terms included: TIC (Time in captivity in years; 2, 6, or 7), MCL (Midline carapace length in mm at release, September 2018), TDisp (Total displacement from release burrow until death or the end of the study on 27 September 2019), SA (surface activity, or the proportion of tracking events that an individual was on the surface), and Burr (Burrow switching, calculated as the number of unique burrows used divided by the total number of tracking events found in a burrow).

Table 2. Predictions of 1-y survival rates (25 September 2018–27 September 2019) and 95% confidence intervals (CI) for head-started juvenile Mojave desert tortoises *Gopherus agassizii* derived as model-weighted averages over a set of generalized linear models with fate as a binary response variable (1 = alive, 0 = dead) and MCL at release, time in captivity, total displacement, surface activity, and burrow switching as predictor variables. The latter four predictors were held constant at their overall means to generate predictions of survival over the range of MCL values (60–150 mm). MCL = midline carapace length in mm.

MCL	Survival probability	Lower 95% CI	Upper 95% CI
60	0.540	0.254	0.808
65	0.580	0.310	0.816
70	0.619	0.370	0.824
75	0.657	0.432	0.833
80	0.693	0.494	0.843
85	0.728	0.553	0.855
90	0.759	0.606	0.868
95	0.788	0.652	0.882
100	0.814	0.689	0.897
105	0.838	0.718	0.913
110	0.859	0.741	0.928
115	0.878	0.760	0.942
120	0.893	0.774	0.954
125	0.907	0.786	0.964
130	0.919	0.795	0.972
135	0.930	0.804	0.979
140	0.939	0.811	0.984
145	0.947	0.818	0.988
150	0.954	0.824	0.991

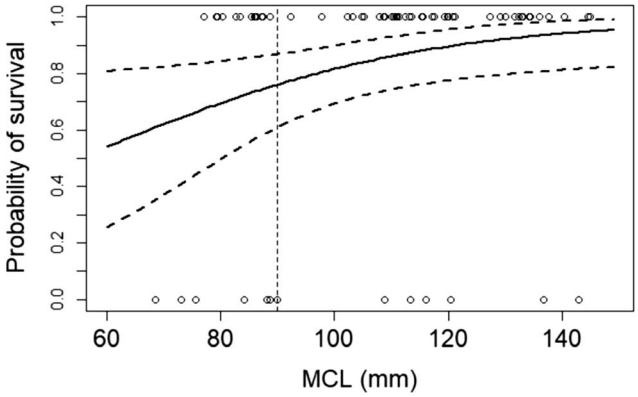

Figure 3. Observed survival fates (open circles) and predicted annual survival probabilities based on size (midline carapace length, MCL) at release for juvenile Mojave desert tortoises *Gopherus agassizii* released into the Mojave National Preserve, San Bernardino, California, United States, on 25 September 2018 and monitored until 27 September 2019. Predictions were generated as model-weighted averages over a set of generalized linear models in which the predictor variables, time in captivity (3.7 y), total displacement (299 m), surface activity (0.40), and burrow switching (0.34), were held at their respective means and MCL was varied over a range (60–150 mm). Solid lines are predicted model estimates and dashed lines are upper and lower limits of 95% confidence intervals. The vertical dashed line (MCL = 90 mm) represents the threshold size at release above which raven predation was not encountered in our study.

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from 0.54 (95% CI = 0.25–0.81) to 0.95 (0.82–0.99) at the MCL limits used in this study (60–150 mm MCL). Head-started tortoises released at our study site had predicted survival probabilities of 0.72 (0.54–0.85) and 0.81 (0.69–0.90) at the previously recommended release sizes of 84 mm MCL and 100 mm MCL (Hazard et al. 2015, Nagy et al. 2015b, respectively). Higher rates of surface activity decreased survival probability, with three of the four individuals found on the surface during >60% of tracking events having died in the first year postrelease. In the most parsimonious model, for each 1% increase in surface activity, survival probability over 1 y decreased by 5.62% ($\beta = -5.6178$; $z = -2.51$; $P = 0.012$). Time in captivity, total displacement, and burrow switching were not significant predictors of postrelease survival.

Discussion

Among chelonians, smaller individuals often have higher rates of mortality than larger conspecifics (Haskell et al. 1996; O'Brien et al. 2005; Arsovski et al. 2018). The mortalities documented in our study followed this trend, with over half (7/13; 54%) occurring among animals smaller than 91 mm MCL and disproportionate to the number (21/78; 27%) of tortoises released below this size. Furthermore, the three smallest individuals released in this study were all depredated. Though we evaluated a suite of possible predictors on individual fate, size at release and surface activity were the only significant predictors among those we examined in our study.

A positive relationship between size at release and survival has been previously reported for desert tortoises (Hazard et al. 2015; Nagy et al. 2015b). Nagy et al. (2015b) found that survivorship reached 100% for tortoises released at sizes ≥100 mm MCL in their first year postrelease, adding that mortality was greatest amongst the smallest individuals (<80 mm MCL), none of which survived longer than 4 y postrelease. Another study at that same site in the western Mojave Desert found that no animal released at size >84 mm MCL died in the first 3 mo after release, the extent of their study (Hazard et al. 2015). Notably, tortoises in both studies were predominantly depredated by ravens. In fact, Hazard et al. (2015) reported ravens as the sole source of mortality, whereas only three (23% of mortalities) individuals in our study were found to have been killed by avian predators (presumably ravens). The size at release of our largest raven-depredated individual (90 mm MCL) was similar to that reported by both Nagy et al. (2015a; 80 mm MCL) and Hazard et al. (2015; 84 mm MCL) for raven predation at their site. Notably, Nagy et al. (2015a) found that raven predation was likely the cause for the near complete eradication of tortoises released at sizes <80 mm MCL from their study over 3 y. The three raven-depredated juveniles in our study ranged between 68 and 90 mm MCL at release, the two smallest of which showed clear signs of being punctured by a beak, whereas the largest of the three lacked puncture wounds. Similarly, in South Africa, pied crows *Corvus albus* selectively preyed on the smaller size classes of angulate tortoises *Chersina angulata*, with 227 carcasses ranging from 35 to 74 mm MCL found below several nests (Durà i Franch 2017). Our results, coupled with previous findings of release-size thresholds for avian predation (Hazard et al. 2015; Nagy et al. 2015a), suggest that risk of raven-related mortality is reduced as tortoises grow and their shells harden (Nagy et al. 2011).

Our results also corroborate previous findings that increased surface activity is a predictor of postrelease fate (Daly et al. 2019); however, in both Daly et al. (2019) and the present study, the negative relationship between surface activity and survival may have been an artifact of the numerous mortalities during the initial postrelease dispersal period when surface activity was unusually high. In addition to this possible negative relationship between surface activity and postrelease survival, our results also suggest a weak negative interaction between surface activity and MCL as they relate to survival. A negative interaction between these two predictors may suggest that juveniles on the larger end of our released size range are more easily seen and thus more at risk to certain predators (i.e., coyotes) while on the surface compared with their smaller counterparts.

Age and size are often too correlated to reliably differentiate their relative effects on survival. However, because of the overlapping sizes among cohorts due to differential husbandry practices used in this study, we were able to separately evaluate size and age at release (time spent in captivity) as predictors of postrelease fate. We found that size at release, rather than age, predicted individual fate at our site, with larger juveniles exhibiting greater survival than same-aged, smaller individuals. This finding suggests that accelerating growth of hatchling head-starts may maximize the success and efficiency of head-starting programs. For example, by incorporating both an indoor and outdoor component in the prerelease husbandry of head-started desert tortoises, our study shows that head-starting programs can rear tortoises equivalent in size to 6–8-y-old outdoor-reared animals in 2 y. This reduction in the captive period equates to 4 y of savings on husbandry- and personnel-related expenditures. These savings can increase the number of head-starts that can be reared each year or fund additional management efforts for the benefit of the species (i.e., restoration, habitat protection). Based on our releases to date, we have found no evidence that the accelerated growth rates associated with indoor rearing, at least under the husbandry practices we used, result in physiological impairment or differences in postrelease behavior or survival (Daly et al. 2018, 2019; Tuberville et al. 2019).

Reducing time spent in captivity may also hold physiological benefits, in addition to saving limited conservation dollars (Warkentin and West 1990; Hermes et al. 2004; de Assis et al. 2015). Prolonged captivity led to elevated stress hormone levels over the duration of the captive period as well as decreased immune response in the cururu toad *Rhinella icterica* (de Assis et al. 2015). Long-term captivity has also been implicated

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in increased basal metabolic rate and decreased antimicrobial fighting ability in birds (Warkentin and West 1990; Buehler et al. 2008). In reptiles specifically, time spent in captivity has been found to alter feeding behaviors and negatively affect postrelease survival in rat snakes *Pantherophis obsoletus* (DeGregorio et al. 2013, 2017). Our finding—that head-starting duration can be reduced by incorporating an indoor rearing component—limits the potential for manifestation of any negative consequences that might be associated with prolonged captivity.

Tortoise growth responds to husbandry manipulations, clearly shown by the variable growth rates of tortoises reared under the differing husbandry protocols implemented in this study. We observed greater growth when we used indoor rearing, during which head-starts grew nearly three times faster (57.5 mm MCL/y) than the fastest growing cohort of solely outdoor-reared juveniles (19.2 mm MCL/y) at our site. Alternatively, for programs focused on, or logistically constrained to, the rearing of tortoises exclusively outdoors, we found that growth was vastly improved by the addition of supplemental food, coupled with supplemental watering. While using indoor rearing is clearly the most efficient way to accelerate growth, outdoor rearing allows head-starts to acclimate to outdoor conditions and develop natural thermoregulatory behaviors. Given that we did not release solely indoor-reared tortoises as part of this study, we cannot ascertain how the lack of outdoor conditioning may affect postrelease survival relative to the tortoises released in our study. Solely indoor-reared tortoises released by Daly et al. (2019) at our study site exhibited survival rates similar to both outdoor-reared and direct-released siblings, although any potential differences may have been masked by high predation rates associated with a single brooding pair of ravens that became established shortly after the tortoises were released. We were able to minimize this source of mortality in our study by releasing animals in the autumn after raven nesting was completed and by releasing animals >1.6 km away from powerline pylons that serve as raven perch structures (Daly et al. 2019). The overall larger size of animals released in our study, coupled with our release protocols designed to reduce tortoise encounters with ravens (autumn release of tortoises ≥1.6 km from perch sites), may explain our minimal losses to avian predators as compared with previous studies (Nagy et al. 2015a; Daly et al. 2019). Our results suggest that as individuals surpass the threshold size for which tortoises are vulnerable to avian predation, mammal predation becomes the predominant source of juvenile desert tortoise mortalities at our study site.

In summary, our study lends further support for the positive relationship between size at release and postrelease survival in head-started juvenile desert tortoises, while highlighting how the higher growth rates associated with the indoor phase of combination rearing can improve the efficiency of head-starting programs. We found that size at release, not age, better predicts postrelease survival and corroborated that indoor rearing allows for significantly increased growth in comparison with conventional outdoor rearing (Daly et al. 2018). Our predictions of survival probability over a range of juvenile desert tortoise sizes provide managers with greater ability to predict outcomes of subsequent head-start releases based on release size. At our study site, raven predation only affected animals released at sizes ≤90 mm MCL, corroborating previous size-at-release thresholds for raven predation at a study site in the western Mojave Desert (Hazard et al. 2015; Nagy et al. 2015a). Though raven predation of tortoises released at sizes >90 mm MCL was not seen here, predicted survival continued to increase incrementally over the entire MCL range used in this study. We provide survival estimates over a wide range of potential release sizes because recommending a single specific size at release for future desert tortoise head-starting programs fails to recognize the complexity of variable release-site conditions and logistical constraints faced by individual projects. In producing our survival estimates, we acknowledge that survival will vary depending on habitat quality, predator abundance, climatic conditions, and other sources of variability. Site-specific conditions and program-specific objectives are factors to be considered when determining the ideal size at release and the most efficient, logistically feasible method of attaining that size.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Head-started Mojave desert tortoises *Gopherus agassizii* released into Mojave National Preserve, San Bernardino, California on 25 September 2018 and radio-tracked through 27 September 2019. Sheets within the data file (.xlsx) detail 1) husbandry, morphometric and postrelease movement, activity, and fate for all animals released; and 2) descriptions of data collected.

Found at DOI: https://doi.org/10.3996/JFWM-20-014.S1 (30 KB XLSX).

Reference S1. Morafka DJ, Berry KH, Spangenberg EK. 1997. Predator-proof field enclosures for enhancing hatchling success and survivorship of juvenile tortoises: a critical evaluation. Pages 147–165 in Van Abbema J, editor. Conservation, restoration, and management of tortoises and turtles—an international conference. Purchase: New York Turtle and Tortoise Society.

Found at DOI: https://doi.org/10.3996/JFWM-20-014.S2 (9.22 MB PDF).

Reference S2. Nussear KE, Esque TC, Inman RD, Gass L, Thomas KA, Wallace CSA, Blainey JB, Miller DM, Webb RH. 2009. Modeling habitat of the desert tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran Deserts

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of California, Nevada, Utah, and Arizona. U.S. Geological Survey Open-File Report 2009-1102.

Found at DOI: https://doi.org/10.3996/JFWM-20-014.S3 (1.56 MB PDF).

Reference S3. [USFWS] U.S. Fish and Wildlife Service. 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.

Found at DOI: https://doi.org/10.3996/JFWM-20-014.S4 (5.81 MB PDF); also available at https://www.fws.gov/nevada/desert_tortoise/documents/recovery_plan/RRP%20for%20the%20Mojave%20Desert%20Tortoise%20-%20May%202011.pdf.

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