EFFECTS OF SHORT-TERM, OUTDOOR HEAD-STARTING ON GROWTH AND SURVIVAL IN THE MOJAVE DESERT TORTOISE (GOPHERUS AGASSIZII)

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Abstract.—The combination of life-history traits that makes some turtle species vulnerable to population declines also limits their ability to recover even after threats have been addressed. Because juvenile turtle survival is typically lower than adult survival, head-starting, the process of rearing juveniles through one of their most vulnerable periods, may be a useful recovery tool. We evaluated short-term, outdoor head-starting in Mojave Desert Tortoises (*Gopherus agassizii*) by comparing growth and survival among three treatments: (1) juveniles reared in outdoor predator-resistant enclosures and receiving low (LOW) or (2) high levels of rain supplementation (HIGH); and (3) free-ranging animals released 0–18 mo after hatching (FIELD). Juveniles from the HIGH treatment had higher annual growth (12.7 mm midline carapace length [MCL] per year) than juveniles from the LOW or FIELD treatments (10.7 mm). Annual growth also varied among years, presumably due to variation in rainfall. Annual survival was high (0.94 ± 0.01) for both LOW and HIGH treatments; MCL at hatching had a weak positive effect on survival probability (effect size: 0.42 ± 0.35). Annual survival of FIELD animals averaged 0.48 ± 0.09. There was no effect of size at release (40.8–61.5 mm MCL) on post-release survival of FIELD animals, suggesting that the greatest benefit of short-term outdoor head-starting is increasing survival during the head-start period. Although releasing at larger sizes (100 mm MCL) has been recommended, slow growth in tortoises would require extended outdoor head-starting periods. Indoor rearing, which has been successfully implemented with other turtle species, may increase growth rates of juvenile Desert Tortoises and warrants future study as a conservation technique.

Key Words.— Mojave Desert; population manipulations; species recovery; Testudinidae

INTRODUCTION

Delayed sexual maturity, low reproductive output, and high adult survival, which are life-history characteristics of many turtle species, contribute to their vulnerability to environmental perturbations (Gibbons 1987; Congdon et al. 1993, 1994). These same traits can also inhibit population recovery once threats have been removed or mitigated. Documenting evidence of recovery may require decades (Hall et al. 1999; Balazs and Chaloupka 2004; Tuberville et al. 2014; Hamilton et al. 2015). Slow population responses, combined with often severely reduced population sizes, may limit recovery without additional management intervention.

Both long-term mark recapture studies and population models provide compelling evidence that, for many turtle species, adults are the most valuable members of the population for promoting population persistence and stability (Congdon et al. 1993, 1994; Doak et al. 1994; Heppell 1998). Thus, management aimed at maintaining high adult survival must remain a cornerstone of turtle conservation efforts; however, conservation approaches that positively affect multiple life stages may be most effective in achieving population recovery (Tomillo et al. 2008; Crawford et al. 2014; Spencer et al. 2017). Because efforts aimed solely at increasing recruitment and survival of juvenile turtles are unlikely to compensate for continued loss of adults (Doak et al. 1994; Heppell et al. 1996), such efforts have historically been perceived as detracting from, or even competing with, actions that target adult survival (Frazer 1992; Seigel and Dodd 2000). This perceived dichotomy, along with the failure of early, high-profile projects (Bowen et al. 1994; Heppell and Crowder 1998), made many scientists reluctant to consider head-starting, the process of rearing juvenile turtles in

captivity through their most vulnerable period (Burke 2015; Spencer et al. 2017), as a potentially worthwhile management tool.

Recently, there has been a resurgence of interest in head-starting (e.g., see Herpetological Conservation and Biology, Volume 10, Issue 3), with more explicit acknowledgment of head-starting as a viable component of a multi-faceted conservation program (Burke 2015; Spencer et al. 2017). In addition, management agencies are taking a measured approach, viewing head-starting as a short-term strategy to speed the recovery process, but not a long-term strategy to maintain declining populations (U.S. Fish and Wildlife Service [USFWS] 2011). Survival of juvenile turtles, particularly hatchlings, is suspected to be lower than that of adults, and highly variable (Wilbur and Morin 1988; Congdon and Gibbons 1990; but see Pike et al. 2008), likely resulting in only episodic recruitment (Morafka 1994; Reed et al. 2009). Perhaps infrequent bouts of high recruitment are sufficient to maintain stable, adult populations of these long-lived species. Alternatively, small but stable increases in annual juvenile recruitment may also support population persistence. Each of the prior patterns has two important implications for turtle recovery actions: the collection or use of a portion of the early life stages such as eggs or hatchlings for head-starting is unlikely to negatively affect donor populations (Ratnaswamy et al. 1997; Smith et al. 2013; Buhlmann et al. 2015; Quinn et al. 2016), and juvenile survival may be a life-history demographic that managers can reasonably manipulate (Heppell 1998; Tuberville et al. 2009). Indeed, population modeling efforts predict that, given scenarios of high adult survival, even small improvements in juvenile survival can transition population growth rates from declining to stable (Heppell et al. 1996; Heppell 1998; Tuberville et al. 2009).

Head-starting turtles may be one way to increase their survival as juveniles given the benefits of larger size. For example, size has been previously shown to be an important predictor of survival in some species of turtles; larger hatchlings have higher first-year survival than smaller hatchlings in Desert Tortoises (*Gopherus agassizii* [*sensu stricto*]; Nafus et al. 2015) and in Ploughshare Tortoises (*Geochelone yniphora*; O'Brien et al. 2005). Size at release influences post-release survival of head-started Desert Tortoises (Nagy et al. 2015b) and Redbelly Turtles (*Pseudemys rubriventris*; Haskell et al. 1996), with larger head-starts exhibiting higher survival. Size can even have consequences for survival of adult turtles in some scenarios (Tucker et al. 1999; Willemsen and Hailey 2001; Esque et al. 2010). Thus size, and, by extension, growth rates, have important implications for head-starting projects. Based on previous head-starting efforts, post-release survival

is expected to be affected by size at release and may help identify a minimum recommended release size. Growth during the head-starting period will dictate the duration of captivity required to produce juveniles of minimum release size, which will in turn determine the overall cost and feasibility of head-starting programs. Finally, accelerated growth during the captive period could potentially reduce the time to maturity for those turtle species in which maturity is size-dependent, further contributing to population recovery.

Biologists and managers have increasingly implemented head-starting as a recovery tool for the Mojave Desert Tortoise, *Gopherus agassizii* (USFWS 2011), a federally listed threatened species. Morafka et al. (1997) demonstrated that outdoor predator-proof enclosures could be used to successfully rear hatchling Desert Tortoises in semi-captive environments. Subsequently, pilot head-starting projects for Desert Tortoises were initiated at three military installations in the western and central Mojave Desert. Nagy et al. (2015a) showed that supplemental precipitation via irrigation sprinklers resulted in increased growth in hatchlings and older juveniles and was particularly important to survival of older juveniles during drought years. Although much was learned regarding the ecology and behavior of juvenile Desert Tortoises reared in outdoor enclosures (e.g., Spangenberg 1996; Nagy et al. 1997; Wilson et al. 1999), no study to date has evaluated the benefits of growth and survival of outdoor head-started animals compared to unmanipulated, free-ranging hatchlings.

Here, we compare growth and survival of head-started hatchling Mojave Desert Tortoises (hereafter Desert Tortoises) raised under two supplemental watering treatments to those of free-ranging animals released in the eastern Mojave Desert shortly after hatching to evaluate head-starting as a turtle recovery tool. We addressed the following questions: (1) To what extent does annual growth differ among free-ranging animals and those reared outdoors with varying levels of supplemental watering?; (2) To what extent does annual survival differ between free-ranging animals and those reared outdoors in enclosures?; and (3) To what extent does size at hatching or size at release affect post-release survival?

Materials and Methods

Study location.—We conducted our study in Ivanpah Valley in the Mojave National Preserve (MNP), San Bernardino County, California, USA, which lies in the eastern Mojave Desert and the Eastern Mojave recovery unit of the Desert Tortoise (USFWS 2011). The study area ranged from 800–1,050 m elevation and included both Creosote Scrub and Yucca Woodland habitats (Todd et al. 2016). The Creosote Scrub habitat was

composed primarily of Creosote (*Larrea tridentata*) and White Bursage (*Ambrosia dumosa*) intermixed with distinct patches of Galleta Grass (*Pleuraphis rigida*). The Yucca Woodland was also dominated by Creosote but intermixed heavily with Joshua Tree (*Yucca brevifolia*), Spanish Dagger (*Y. schidigera*), Boxthorn (*Lycium andersonii*), Littleleaf Ratany (*Krameria erecta*) and cholla (*Cylindropuntia* spp.). We conducted the majority of the work at the Ivanpah Desert Tortoise Research Facility (IDTRF), a head-starting facility at 826 m in the MNP, 20 km from our field site. The IDTRF included an outdoor female nesting enclosure and two outdoor juvenile rearing enclosures. Enclosures were 30 × 30 m and constructed of 1.8 m tall chain-link fence outer walls flanked by corrugated metal along the base to exclude mammalian predators. Each enclosure was covered with mesh netting over the top to exclude avian predators. Enclosures were partitioned with sheet metal into smaller pens and equipped with manually operated sprinkler systems fed by an underground aquifer. The female nesting enclosure was subdivided into 18 (5 × 9 m) pens and each of the two juvenile rearing enclosures was subdivided into nine (10 × 10 m) pens. Enclosures contained native vegetation and natural cover objects (e.g., rocks, downed yucca logs) and thus mimicked the natural environment of tortoises. Natural cover objects were supplemented with artificial burrows created from 53-cm long, 10-cm diameter perforated plastic pipes for hatchlings, or 1-m long, 30.5-cm diameter cardboard tubes for females. All pipes and tubes were cut in half longitudinally and placed at a 30° angle downward then buried underground to maximum depth of 0.5 m. Pens were seeded with edible, native annuals and perennials, including Desert Dandelion (*Malacothix glabrata*), Plantain (*Plantago ovata*), Desert Globemallow (*Sphaeralcea ambigua*), and Desert Marigold (*Baileya multiradiata*) in the fall or winter each year.

Hatchling production.—Beginning May 2011, we captured, marked, and radio-tracked up to 30 adult female Desert Tortoises (actual number varied among years). During 2011–2013, we radiographed females (Diagnostic Imaging Systems, Poskam, Colorado, USA; 60 kvp, 0.8 mAS, 74 cm focal length; Gibbons and Greene 1979) every 10–14 d during mid-April through early July. We brought females with calcified eggs into separate nesting pens at the IDTRF where they were left to nest. We returned females to their last burrow location immediately after nesting or within 30 d if they failed to nest.

We attempted to locate nests in pens and monitor their status. Beginning in mid-August (approximately 80 d after estimated nesting date), we searched pens daily for hatchlings. We removed hatchlings as they emerged from nests and immediately weighed them to the nearest 0.1 g and measured their midline carapace length (MCL) to the nearest 0.1 mm. We marked hatchlings with nail clippers by notching unique combinations of marginal scutes (modified from Cagle 1939). We searched nesting pens for any unhatched eggs or un-emerged hatchlings. In Spring 2012, we also received 14 hatchlings that emerged in Fall 2011 from females held at Ivanpah Solar Electric Generating Systems, located 20 km to the north.

Experimental treatments.—We compared growth and survival of hatchling Desert Tortoises reared under two frequencies of water supplementation (high rain and low rain; see below) to free-ranging hatchlings that emerged from the same nests. We elected to compare high rain treatments and low rain treatments rather than rain and no rain treatments to promote recovery of vegetation in pens following construction and to guard against possible unanticipated droughts during the study. For each annual cohort, we assigned hatchlings to one of three husbandry treatments in a stratified random design, with siblings from each clutch divided as evenly as possible among treatments. The three husbandry treatments included one group released into the field 0–18 mo after hatching (hereafter FIELD) and two groups that were not released, but instead were reared for the duration of the study in outdoor enclosures where they were provided different levels of supplemental water (LOW and HIGH). Hatchlings assigned to the LOW and HIGH treatments were distributed as evenly as possible among three pens within the corresponding treatment enclosure at a maximum density of approximately one individual per 10 m^2. We assigned no more than two siblings from each clutch to a specific pen. Of the 195 hatchlings produced (38 from 2011, 71 from 2012, 86 from 2013), we reared 77 exclusively in pens under LOW rain treatment and 72 exclusively under HIGH rain treatment.

We provided supplemental water from sprinkler systems inside the pens, with the HIGH enclosure watered every week and the LOW enclosure watered every other week, with approximately 3.7 mm applied to each pen per 30-min watering event. Supplemental water application was initiated in August 2011, but weak water pressure prevented us from initiating regimented treatments before April 2012. Supplemental water was applied twice as frequently in the HIGH treatment as in the LOW treatment throughout the year, except when precluded by low water pressure. Natural precipitation (PRISM Climate Group. 2018. PRISM Climate Data. Oregon State University, Corvallis, USA. Available from http://prism.oregonstate.edu. [Accessed 9 May 2018]) and amount of supplemental water applied to the HIGH and LOW enclosures varied during the study period (Table 1).

TABLE 1. Timing and amount (mm) of natural precipitation and supplemental water applied to the LOW and HIGH outdoor head-start enclosures at the Ivanpah Desert Tortoise Research Facility in Mojave National Preserve, California, USA. Supplemental water application did not start until August 2011.

Dates	Season	Natural rainfall	LOW supplement	HIGH supplement	Natural + LOW	Natural + HIGH
July - October 2011	Fall	36.7	44.27	88.55	80.97	125.25
November 2011 - March 2012	Winter	29.39	29.52	59.03	58.91	88.42
April - June 2012	Spring	8.71	29.52	59.03	38.23	67.74
July - October 2012	Fall	112.82	59.03	118.06	171.85	230.88
Annual (November 2011 - October 2012)		150.92	118.07	236.12	268.99	387.04
November 2012 - March 2013	Winter	39.31	44.24	88.55	83.55	127.86
April - June 2013	Spring	2.57	14.74	29.52	17.31	32.09
July - October 2013	Fall	88.22	29.48	59.03	117.70	147.25
Annual (November 2012 - October 2013)		130.1	88.46	177.1	218.56	307.20
November 2013 - March 2014	Winter	28.75	44.24	88.55	72.99	117.30
April - June 2014	Spring	0	22.11	44.27	22.11	44.27
July - October 2014	Fall	54.64	29.48	59.03	84.12	113.67
Annual (November 2013 - October 2014)		83.39	95.83	191.85	179.22	275.24

Monitoring of tortoises in pens.—We weighed and measured hatchlings reared in HIGH and LOW pens each spring and fall. We visually searched pens and burrows during these semi-annual periods to document all live juveniles. We recorded an animal as known alive during any sampling period, spring or fall, if it was either observed alive during that sampling period or if it was missed but observed alive in a subsequent sampling period. Each time we operated the sprinklers, we recorded which tortoises were active on the surface, with visual identification made possible by temporary color marks on the carapace while animals were captive. These additional visual observations provided more frequent information on fate of individuals (i.e., at least monthly), and we report these data through the Fall 2014 monitoring period.

Juvenile releases and post-release monitoring.— Of the 46 FIELD animals, we released 22 in the field immediately after hatching (age 0 mo), and 24 were initially reared in pens (split equally between LOW, HIGH treatments) for 6, 12, or 18 mo before release into the field (Table 2). We released FIELD animals in Fall 2012 (n = 18), Spring 2013 (n = 18), and Fall 2013 (n = 10). We attached small VHF transmitters (Holohil System Ltd., Carp, Ontario, Canada; type BD-2, 1.5 g; < 10% of tortoise body weight) to the 4th or 5th vertebral and weighed and measured each animal before release. We selected release areas 750 m away from dirt roads or powerline rights-of-way. For each individual, we located a Creosote shrub with multiple burrows made

by small mammals, such as kangaroo rats (*Dipodomys* sp.), to provide initial shelter.

We radio-tracked each tortoise within 24 h after their initial release. Thereafter, we tracked tortoises 1–2 times per week during their activity season (April-October) and every two weeks during their winter dormancy (November-March). We measured and weighed the released juveniles each time we changed transmitters (three to four times per year). When we encountered a dead tortoise, we recorded the date it was found dead and attempted to determine cause of death. Some tortoises were lost when radios failed, but in several cases, we later found them alive after intensive searching. At the end of each monthly tracking period, FIELD animals were documented as either Alive, Dead, or Fate Unknown (e.g., missing). We monitored tortoises through September 2014, representing monitoring periods of 12–24 mo.

TABLE 2. Timing and number of releases of captive-hatched juvenile Mojave Desert Tortoises (*Gopherus agassizii*) from the FIELD treatment in the Mojave National Preserve, San Bernardino County, California, USA. Juveniles ranged in age from 0–18 mo at time of release.

Release season	Cohort	Age at Release	No. animals	Release date
Fall 2012	2011	12 mo	6	25 Sept '12
Fall 2012	2012	0 mo	12	25 Sept '12
Spring 2013	2011	18 mo	6	7–8 Apr '13
Spring 2013	2012	6 mo	12	7–8 Apr '13
Fall 2013	2013	0 mo	10	24 Oct '13

TABLE 3. Model-averaged parameter estimates from Cormack-Jolly-Seber model for survival of juvenile Mojave Desert Tortoises (*Gopherus agassizii*) reared exclusively in outdoor enclosures at the Ivanpah Desert Tortoise Research Facility (Mojave National Preserve, California, USA); mean, standard deviation and 2.5 and 97.5 percentiles (corresponding to 95% Bayesian Credible Interval) of posterior distribution. Model averaging was based on indicator variable approach, where covariate coefficient $\beta = 0$ when the predictor is not in the model, and $\beta \neq 0$ when the predictor is in the model. One asterisk (*) is logit of survival at average MCL for LOW water supplementation treatment in November to March, and two asterisks (**) is annual survival probability derived from monthly estimates.

Model parameter	Mean	SD	2.50%	97.50%
Intercept*	5.352	0.339	4.738	6.086
β MCL	0.415	0.353	-0.440	0.885
β Water treatment = HIGH	-0.045	0.379	-0.890	0.620
β (Season = Apr-Jun)	0.047	0.411	-0.624	0.849
β (Season = Jul-Oct)	0.078	0.535	-0.602	1.304
Detection probability (p)	0.909	0.012	0.885	0.930
φ Treatment = LOW**	0.943	0.017	0.908	0.973
φ Treatment = HIGH**	0.941	0.017	0.903	0.969

Growth analysis.—We calculated growth rates for individuals using fall measurements and we present them as yearly change in MCL (mm per year). We calculated total growth rates for each individual for the entire time they were in the study by dividing the change in MCL between first fall and last fall captures by the number of years between measurements. For FIELD individuals that were held temporarily (0–18 months) in outdoor enclosures before being released, we analyzed their growth measurements for only the period after their release into the field to avoid pseudoreplication. We excluded tortoises that did not survive or were not detected (n = 46) during at least two fall measurements from analysis of growth because no growth rate could be calculated in such cases. We calculated total growth rates for 71 LOW, 64 HIGH, and 14 FIELD animals. We compared total growth rates among FIELD, LOW, and HIGH treatments using one-way ANOVA, followed by post-hoc comparisons using Tukey's HSD when significant differences were detected. We analyzed total growth in SPSS Statistics version 24 (IBM Corp., Armonk, New York, USA), with alpha set to 0.05. We square-root transformed growth data to meet the assumptions of normality (Shapiro-Wilks results, $P \geq 0.278$ for all treatment groups) and homogeneity of variances (Levene's test, $P = 0.463$). We performed all growth analyses on transformed data but reported and graphed as raw means ± 1 standard error (SE) to aid interpretation.

To account for both treatment effects and potential variation among years in growth due to interannual variability in precipitation, we also analyzed annual growth rates using linear mixed models in the R package lme4 (Bates et al. 2014; R Core Team 2016). We fit year and treatment as fixed effects in additive models. We also fit a model that included a treatment by year interaction term. In each model, we included tortoise identities as random intercepts. We selected top models using Akaike Information Criterion (AIC).

Survival analysis.—To estimate annual survival for the three treatment groups, we used open population capture-recapture models (Pollock et al. 1990; Lebreton et al. 1992). Specifically, we used a modified Cormack-Jolly-Seber (CJS) model (Cormack 1964; Lebreton et al. 1992), which conditions on the first capture of each individual in the data set and models recaptures only. Under this model, we considered each attempt to locate individual tortoises (monthly, for radio-telemetered FIELD animals and bi-annually for HIGH and LOW animals in the enclosures) a primary sampling period. Whether or not an individual tortoise was detected on a primary occasion was recorded and tortoise survival between these periods was estimated from the models. Because tortoises can go undetected at a given sampling occasion, there may be some individuals whose fate cannot be determined (for example, an individual known to be alive at time t, that is never observed again after time t, could be either alive or dead). The CJS model accounts for undetected individuals by estimating survival probability that is corrected for imperfect detection (detection probability $p < 1$). We implemented the CJS model in a Bayesian framework, following Kéry and Schaub (2012), to make use of dead encounters of study individuals. A Bayesian CJS model explicitly models the alive state of an individual i at time t, z_{it}. All individuals are known to be alive in primary occasion 1, when they enter the study (time of release for FIELD animals), hence $z_{i1} = 1$. The alive state at subsequent primary periods ($t > 1$) is modeled as a Bernoulli trial: $z_{it} \sim \text{Bernoulli}(\varphi\, z_{it-1})$, where φ is the survival probability, so that if the animal was alive at t-1, it can survive to time t. Alive states are partially observed (0 if known to be dead, 1 if known to be alive, non-applicable [NA] if state unknown), and unobserved alive states are estimated by the model. The Bayesian CJS model describes detections of animals, y_{it} for $t > 1$ (i.e., whether or not an individual is observed on a primary occasion, where 1 indicates an observation and 0 indicates no observation) as another Bernoulli trial: $y_{it} \sim \text{Bernoulli}(p)$, where p is the probability that an animal is detected, either dead or alive. Once we found a tortoise dead, it was no longer tracked, and we set p to 0 for those animals for each primary occasion after their known death. Effects of covariates on survival probability, φ, can be modeled on the logit scale (Lebreton et al. 1992): logit(φ)=$\alpha + \beta X$, where X is a covariate, α is the intercept, and β is the effect of X on logit(φ).

We built separate models for FIELD animals and those reared exclusively in outdoor pens (LOW and HIGH treatments). For FIELD animals, covariates included carapace length at time of release (rMCL) to account for differing durations of rearing in pens, year of release, season of release (spring versus fall), and season of post-release monitoring (November-March: roughly corresponding to over-wintering when animals were inactive; April to June: roughly corresponding to spring period of heightened activity and foraging; July to October: roughly corresponding to summer and early fall period of variable activity depending on monsoonal rains and temperatures). Survival might be expected to vary seasonally due to differences in resource availability (Beatley 1974; Turner and Randall 1989) or tortoise movement and activity patterns (Esque et al. 2014; Spotila et al. 2014). We also included a random effect of the mothers because of potential maternal effects on survival (Nafus et al. 2015). For the animals reared only in pens for 12–36 mo depending on cohort (September 2011 to September 2014), covariates included MCL at hatching, water supplementation treatment (LOW or HIGH), and season of monitoring (defined as above). We attempted to include a random maternal effect and year as covariates, but models with these parameters did not converge, most likely due to sparse data. Continuous covariates (rMCL, MCL) were scaled so that they had a mean of 0 and a SD of 1. We scaled survival to monthly intervals (rather than annual) to make use of the monthly resolution in survey data for released animals and to account for variation in survival with season. We multiplied the resulting monthly survival estimates together to calculate estimates of annual survival.

Because of consistent survey effort and methodology, and because nearly all animals were detected in both spring and fall measurement surveys, we modeled detection probability for LOW and HIGH animals as constant. For FIELD animals, we set $p_{it} = 0$ when individual i was not searched for during survey t, but detection was constant (across individuals and surveys) otherwise. We did not allow for differences in detection probability for live and dead encounters, as both types of encounters were made using the same survey methods.

We applied an indicator variable model selection approach to determine which covariates were important predictors of survival (George and McCulloch 1993; Kuo and Mallick 1998), described as follows. Bayesian models are implemented using iterative Markov Chain Monte Carlo (MCMC) sampling to estimate model parameters and their standard errors. The indicator variable model selection approach allows a given covariate to be either included or excluded from the model at each MCMC iteration. Specifically, each covariate-coefficient β is multiplied by a binary indicator variable w that is updated at each iteration of the model. When $w = 1$, the predictor is included in the model; when $w = 0$, the respective coefficient is effectively fixed at 0 (equivalent to the covariate not being in the model; George and McCulloch 1993). The number of times, out of all iterations, that $w = 1$ provides a measure of how important the predictor is in the model, with predictors showing up in more iterations being deemed more important than those showing up in fewer iterations. As such, covariates are not retained or excluded before the model is fit; rather, the model is fit via MCMC including all covariates, and decisions about covariate importance (based on how often $w = 1$) are made based on model results. We present model-averaged estimates of covariate-coefficients β across all iterations when $w = 1$.

We implemented models in JAGS (Plummer 2003) version 4.2, using the package rjags version 4-6 (Plummer 2016) in R version 3.2.5 (R Core Team 2016). JAGS uses MCMC methods for parameter estimation, and for each model, we ran three parallel chains with 15,000 iterations each, thinned by five, after discarding the 500 initial iterations as burn-in. We checked all chains for convergence using the R-hat statistic (Gelman and Hill 2006). R-hat values were < 1.1 for all parameters in all models, indicating convergence. We present results as posterior mean, SE, and 95% Bayesian Credible Interval (BCI, Bayesian analog to 95% confidence interval). We consider a covariate effect to be strong when the 95% BCI of the model-averaged estimate of the covariate-coefficient does not include 0.

RESULTS

Growth.—Total growth rates for all individuals averaged 11.6 ± 0.3 mm MCL/y (range: 4.6–22.2) and varied significantly among treatments ($F_{2,146} = 6.196$, $P = 0.003$). Animals reared in the HIGH rain treatment had significantly higher growth (12.7 ± 0.4 mm MCL/y; range 6.7–22.2 mm) than those reared in the LOW rain treatment (10.7 ± 0.4mm MCL/y; Tukey HSD, $P = 0.003$; range 4.6–21.2 mm). Total growth rate in FIELD animals (10.7 ± 1.0 mm MCL/y; range 5.5–18.1 mm) did not differ significantly from either LOW (Tukey HSD, $P = 1.000$) or HIGH rain treatments (Tukey HSD, $P = 0.124$), although small sample size for FIELD animals may have limited the ability to compare the FIELD animals with the other two treatment groups.

When we investigated the influence of both treatment (HIGH, LOW, and FIELD) and year on annual growth rates, the model that included fixed effects of year and treatment was best supported (AIC = 461.29), followed by the model that included year, treatment, and year by treatment interaction (AIC = 461.69, ΔAIC = 0.40). Within the top model, both year ($F_{2,224} = 4.62$, $P = 0.01$)
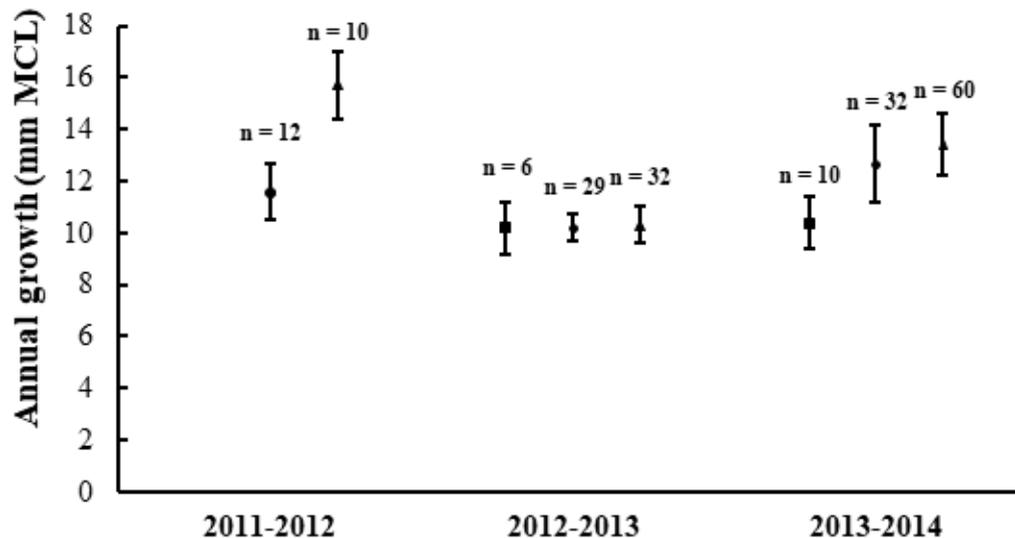
Figure 1. Average annual growth rate (mm MCL/y, where MCL is midline carapace length) of juvenile Mojave Desert Tortoises (*Gopherus agassizii*) released to the field at age 0, 6, 12 or 18 mo or reared exclusively in outdoor pens under either LOW (circles) or HIGH (triangles) rain supplementation treatments. Measurements for FIELD animals (squares) represent growth in the field following release. Growth is calculated from Fall measurements and is presented as means ± 1 standard error.

and treatment ($F_{2,224}$ = 4.35, P = 0.01) were significant, such that growth in years 2012–2013 and 2013–2014 were lower than 2011–2012 (-0.48 and -0.35, respectively), and tortoises within the HIGH treatment (+ 0.21) exhibited more growth than FIELD or LOW treatment tortoises (-0.05; Fig. 1). Models that included only year or treatment were not well-supported (ΔAIC ≥ 4 when compared to the top model).

Survival.—We observed 175 individuals in outdoor pens (90 in LOW treatment, 85 in HIGH treatment), including several animals that were held temporarily and later released as part of the FIELD treatment. Mean MCL at hatching was 44.2 ± 0.2 mm. We found nine tortoises dead during the study and 12 individuals had unknown fates (i.e, were not observed during the last survey). Detection probability was high, at 0.91 ± 0.01 (Table 3). For the animals in the pens, the model that included solely hatching MCL as a predictor of survival was the model most frequently selected by the indicator variable approach (63% of all iterations; Appendix 1), suggesting that MCL was the most important covariate on survival, out of those considered. The effect of hatching MCL on survival was positive (Table 3), but 95% BCIs widely overlapped 0, suggesting that the effect was weak. The second most frequently selected model was the null model (i.e., no predictors on survival, 26%; Appendix 1). Treatment was represented in models in just 9% of the iterations, and season in 4%. Coefficient estimates for these covariates also had 95% BCIs that widely overlapped 0, indicating that neither treatment nor season was an important predictor of survival for animals in the pens. Annual survival rate was high at

0.94 ± 0.02 for both the LOW and HIGH treatment groups (Table 3).

Of the 46 FIELD individuals, average release MCL was 49.5 ± 0.8 mm and ranged from 40.8–61.5 mm. Of the 19 tortoise we found dead, seven were found dead on the surface and appeared to have died from exposure, four showed evidence of predation by a mammal, and one showed evidence of predation by a bird. We found five tortoises dead in their burrows and the cause of two other mortalities was not recorded or could not be determined. Twelve animals had unknown fates despite intensive and protracted searching for several months, likely due to radio failures or the animals being carried away by predators or monsoonal floods. Fifteen animals were still alive in the field at the last primary observation at the end of September 2014.

The null model (no predictors and no random maternal effect) was the most frequently represented model (70%; Appendix 2), suggesting that none of the predictors we examined had strong effects on survival of FIELD animals. Maternal random effect (alone or in combination with other covariates) appeared in 25% of all iterations (Appendix 2). The covariates season and year were each in the model in fewer than 1% of all iterations (Appendix 2); release group (Fall or Spring) in 6%, and release MCL in fewer than 1% (Appendix 2). The 95% BCIs for all effect estimates widely overlapped zero. Detection probability for these radio-tracked animals was near 1.0. Estimates of annual post-release survival of the FIELD treatment group ranged from 0.48–0.49 ± 0.09 depending on the year and timing of release (Table 4), which was a survival rate roughly half that of HIGH and LOW individuals.

TABLE 4. Model averaged parameter estimates from Cormack-Jolly-Seber model for survival of juvenile Mojave Desert Tortoises (*Gopherus agassizii*) released into the field at age 0–18 mo; mean, standard deviation and 2.5 and 97.5 percentiles (corresponding to 95% Bayesian Credible Interval) of posterior distribution. Model averaging based on indicator variable approach, where covariate coefficient β = 0 when predictor is not in the model, β ≠0 when predictor is in the model. One asterisk (*) is logit of survival at average rMCL for fall release group in year 2012 in November to March, and two asterisks (**) is annual survival probability derived from monthly survival estimates.

Model parameter	Mean	SD	2.50%	97.50%
Intercept*	2.770	0.278	2.318	3.428
β MCL at release	-0.003	0.314	-0.622	0.603
β (Release group = Spring)	0.021	0.336	-0.618	0.704
β (Season = April-June)	-0.005	0.322	-0.634	0.624
β (Season = July-October)	-0.002	0.322	-0.642	0.615
β (Year = 2013)	-0.003	0.320	-0.619	0.610
β (Year = 2014)	0.005	0.323	-0.627	0.653
Detection probability (p)	0.978	0.008	0.961	0.990
σ (maternal random effect)	0.880	1.856	0.013	7.593
φ Year 1, (Release group = Spring)**	0.485	0.090	0.332	0.696
φ Year 2, (Release group = Spring)**	0.485	0.089	0.332	0.693
φ Year 3, (Release group = Spring)**	0.486	0.090	0.334	0.696
φ Year 1, (Release group = Fall)**	0.478	0.088	0.323	0.679
φ Year 2, (Release group = Fall)**	0.478	0.087	0.323	0.675
φ Year 3, (Release group = Fall)**	0.479	0.088	0.326	0.680

DISCUSSION

Supplemental watering increased growth rates in outdoor head-started Desert Tortoises, with juveniles in the HIGH rain treatment growing on average 2 mm more per year than either the LOW rain treatment or FIELD animals. The 12.7 mm annual growth in the HIGH treatment was similar to that reported for other free ranging juvenile tortoises in the eastern Mojave Desert under high precipitation years, in which mean annual growth over a 5-y period was 10.8 mm and ranged from 3.6 mm in a drought year to 14.7 mm in the highest rainfall year (Karl 1999). Similarly, juvenile Desert Tortoises in large (9 ha) outdoor enclosures in southern Nevada grew an average of 9 mm annually over a 5-y period, with greatest annual growth (12.3 mm) following winters of high precipitation (Medica et al. 1975). Thus, based on juvenile growth rates, our HIGH rain treatment simulated years with average to high precipitation over the course of our study. Collectively, these results suggest that provision of supplemental water when adequate native seeds and plants are available during outdoor head-starting is a prudent practice for buffering against drought conditions, particularly given that animals in enclosures are confined to a limited space within which to acquire resources.

Several mechanisms likely contributed to greater growth of juvenile Desert Tortoises, including greater water availability for the tortoises to drink and for the plants on which they forage. Rain supplementation should increase annual plant production and prolong its availability (Nagy et al. 1997). Additionally, tortoises can use water stored in their bladders to digest dry plant matter on which they might otherwise not feed, further extending their foraging opportunities (Nagy and Medica 1986; Peterson 1996). Lastly, higher levels of surface activity in both juvenile and adult Desert Tortoises have been reported in association with greater water availability or higher precipitation (Medica et al. 1980; Nagy and Medica 1986; Nafus et al. 2017b; Peaden et al. 2017). Collectively, these factors likely contributed to the higher growth rates of outdoor head-started juvenile tortoises that had greater access to water, comparable to results reported by Nagy et al. (2015a). Our supplemental watering study also corroborates field observations of increased growth following winters with high precipitation (Medica et al. 1975, 2012). Growth rates also varied among years, independent of watering treatment, likely reflecting variation in natural rainfall and associated forage availability.

Although the difference in growth between HIGH rain and both the LOW and FIELD animals was relatively modest (2 mm MCL/y), presumably the incremental improvement in growth would continue to accumulate over the captive rearing period. Even a 1 mm increase in MCL at hatching has been shown to significantly increase the probability of a hatchling surviving its first year in predator-proof enclosures (Nafus et al. 2015), where environmental exposure and digesting enough food are likely the greatest obstacles to survival. Thus, even such small differences in growth may have measurable effects on juvenile survival.

Annual survival of juveniles in pens was high, averaging 94%, and on par with levels documented for adult free-ranging Desert Tortoises during non-drought years (Freilich et al. 2000; Lovich et al. 2011, 2014). High juvenile survival is consistent with estimates from studies of outdoor-reared juveniles protected from predation in the central Mojave Desert, where survival averaged 90% (Spangenberg 1996; Nagy et al. 2015a). In the present study, survival in pens was positively, though weakly, influenced by size at hatching, as has been previously reported for Desert Tortoises (Nafus et al. 2015). Given that survival did not vary between rain treatments, perhaps only modest levels of rain supplementation are needed to maintain high juvenile survival, minimize desiccation risk, and buffer against weather-related mortality; however, small differences in survival may be difficult to detect when overall survival is very high under both watering treatments.

Average annual survival of released juvenile Desert Tortoises (FIELD treatment) was approximately 48%. None of the factors we explored appeared to exert a strong influence on survival probability in the field, suggesting that unmeasured parameters in the post-release environment may be more important than pre-release experience, at least for juveniles released at relatively small sizes. Habitat characteristics, such as the availability of rodent burrows, proximity to washes, and coverage by perennial shrubs, can drive habitat use, movement, and survival patterns in released juvenile Desert Tortoises (Todd et al. 2016; Nafus et al. 2017a). Environmental conditions and predator densities at the release site are also likely important factors influencing post-release survival (Esque et al. 2010).

We found no evidence for effects of size at release on post-release survival after animals were held for short periods of captivity. Similarly, release size was not shown to affect post-release survival of juveniles, aged 6 mo to 4 y, in nearby southern Nevada (Nafus et al. 2017a); however, juveniles in our study (≤ 62 mm MCL) and in the Nafus et al. (2017a) study (≤ 85 mm MCL) were smaller than the 100 mm MCL size threshold at which juvenile survival has been shown to markedly increase (Nagy et al. 2015b). Size likely plays a greater role in post-release survival when size at release is larger, spans a greater range of size classes, or when animals are subjected to greater pressure from subsidized predators such as Common Ravens (*Corvus corax*).

Few survival estimates are available for free-ranging juvenile Desert Tortoises due to their secretive behavior and low detectability (Morafka 1994; Karl 1998). Survival of wild hatchlings to their first dormancy can vary widely, ranging from 30–91% among studies and years (Goodwin et al. 1995; Bjurlin and Bissonette 2004). Recent radio-telemetry studies of released captive-reared juveniles have provided much-needed insight into survival rates of juvenile tortoises in the wild. Nafus et al. (2017a) reported an overall first year post-release survival of 68% of juveniles age 0.5–4 y, while Nagy et al. (2015b) documented annual survival of 76–79% of 2–15 y-old juveniles during the first two years after release.

The relative importance of predation on survival has varied greatly among studies. Predation was attributed to 91% of mortality in the Nagy et al. (2015b) study, with Common Ravens being the primary predator; just 9% of mortalities were suspected from exposure. Nafus et al. (2017a) reported that mortalities were more evenly split among predation (44%) and a combination of desiccation, starvation, or exposure (56%). In our study, most mortalities were attributed to exposure (36.8%), followed by predation (26.3%). The differences in mortality sources among studies may be due to the smaller size of juveniles in our study and in Nafus et al. (2017a) relative to the Nagy et al. (2015b) study in which predation played a larger role. Smaller juveniles have smaller bladders for storing water and larger surface-to-volume ratios, which can increase evaporative water loss, factors that place them at greater risk of desiccation; however, sources of mortality can change over time, as illustrated by subsequent releases at our study site in which juveniles released in later years sustained greater predation by Common Ravens (Daly 2017). Altogether, these studies highlight the degree to which survival of juvenile Desert Tortoises in the wild can vary and be influenced by extrinsic factors, such as presence or abundance of particular predators, habitat features, and environmental conditions.

Conclusions and recommendations.—Our findings, in combination with prior efforts, show the effectiveness of outdoor enclosures in increasing juvenile survivorship relative to animals from the same cohorts released into the field. In addition, allowing females to nest in predator-resistant enclosures also increases hatchling production by virtually eliminating nest predation, which can limit recruitment in wild tortoise populations (Bjurlin and Bissonette 2004; Smith et al. 2013). Supplemental rain treatments appeared to primarily affect growth rates rather than survival. Because exposure was one of the primary sources of mortality in field-monitored animals in our study, and because previous studies have demonstrated that drought can negatively affect body condition and survival of both juvenile and adult desert tortoises (Longshore et al. 2003; Lovich et al. 2014; Nagy et al. 1997, 2002, 2015a), we suspect that providing water in addition to natural rainfall contributed to high survival of juveniles in the pens.

Given that neither supplemental water treatment (HIGH, LOW) nor size at release (at least over the range of sizes we tested; 40.8–61.5 mm MCL) influenced post-release survival, the greatest benefit of short-term outdoor head-starting appears to be in increasing survival during the head-start period, at least when animals are released at less than two years of age. Studies that have released a wider size range of head-started juveniles suggest that waiting to release juvenile tortoises until they reach at least 100–110 mm MCL will likely confer survival benefits to free-ranging juvenile tortoises (Nagy et al. 2011, 2015b). The estimated 5–9 y of outdoor head-starting needed to produce animals of sufficient size (Nagy et al. 2015a), however, limits the number of animals that a head-starting facility can produce, suggesting additional head-starting techniques should be explored. In other turtle species, rearing animals indoors during at least their first year of life, where they can remain active and feeding during the

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APPENDICES

Appendix 1. Relative support for different combinations of covariates on survival in a Cormack-Jolly-Seber model for juvenile Mojave Desert Tortoises (*Gopherus agassizii*) reared exclusively in outdoor enclosures at the Ivanpah Desert Tortoise Research Facility (Mojave National Preserve, California, USA) under either HIGH or LOW levels of rain supplementation. Support is estimated using the indicator variable approach as the proportion of all Markov Chain Monte Carlo iterations in which a combination of covariates is included in the model (see main text for description of the indicator variable approach). A covariate occurring in a higher proportion of iterations is deemed a more important predictor of survival. The abbreviation MCL = midline carapace length. Treatments are HIGH or LOW water supplementation and seasons are April-June, July-October, and November-March.

Model	Relative support
MCL	0.629
Null	0.257
MCL+Treatment	0.060
Treatment	0.022
MCL+Season	0.018
Season	0.012
MCL+Treatment+Season	0.002

Appendix 2. Relative support for different combinations of covariates on survival in a Cormack-Jolly-Seber model for juvenile Mojave Desert Tortoises (*Gopherus agassizii*) released into the field at age 0, 6, 12, and 18 mo. Support is estimated using the indicator variable approach as the proportion of all Markov Chain Monte Carlo iterations in which a combination of covariates is included in the model (see main text for description of the indicator variable approach). A covariate occurring in a higher proportion of iterations is deemed a more important predictor of survival. Seasons are April-June, July-October, and November-March; Mother = random ('ran') effect accounting for hatchling mother; Group = release group (Spring or Fall); Year = year of study; and rMCL = midline carapace length at time of release.

Model	Relative model weight
Null	0.698
Mother(ran)	0.227
Group	0.041
Group+Mother(ran)	0.016
Year	0.004
Season	0.003
Season+Mother(ran)	0.003
rMCL	0.003
Year+Mother	0.002
rMCL+Mother(ran)	0.002