
RECRUITMENT OF DESERT TORTOISES (*GOPHERUS AGASSIZII* AND *G. MORAFKAI*): A SYNTHESIS OF REPRODUCTION AND FIRST-YEAR SURVIVAL

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Abstract.—Recruitment is integral to population persistence, therefore characterizing this process is essential for evaluating recovery actions for species in decline. We gathered all data available and used Bayesian analyses to quantify annual recruitment of Mojave Desert (*Gopherus agassizii*) and Sonoran Desert (*G. morafkai*) tortoises as the product of four components: proportion of females that reproduced, number of eggs produced per reproducing female, hatching success, and hatchling survival. For Mojave Desert Tortoises, the estimated proportion of females that reproduced (0.81 [95% Credible Interval: 0.52–0.99]) and number of eggs produced per year (6.90 [5.51–8.16]) were higher than for Sonoran Desert Tortoises (0.52 [0.07–0.94] and 5.17 [3.05–7.60], respectively). For Mojave Desert Tortoises, hatching success averaged 0.61 (0.25–0.90). Data on hatchling success for Sonoran Desert Tortoises and hatchling survival for both species were sparse, therefore we represented these components with a range of plausible values. When we combined components, average recruitment for Mojave Desert Tortoises ranged from 0.51 females/female/y assuming that hatchling survival was 0.30 to 1.18 females/female/y with hatchling survival assumed to be 0.70. For Sonoran Desert Tortoises, average recruitment ranged from 0.25 to 0.57 females/female/y for the same values of hatchling survival. Differences in recruitment between species likely reflect the evolution of different life-history strategies for tortoises in Mojave and Sonoran Deserts, perhaps in response to variation in precipitation regimes. To better inform conservation and recovery of desert tortoises, more information is needed for all recruitment components, but especially for hatching success and hatchling survival.

Key Words.—Bayesian analysis; conservation; demography; Mojave Desert; Sonoran Desert

INTRODUCTION

Demography provides a foundation for exploring processes that govern population dynamics and for developing reliable strategies to recover species in decline. For many vulnerable species, however, demographic information is limited and often imprecise, which can make it difficult to determine an appropriate course of action for recovery (Tear et al. 1995; Beissinger and Westphal 1998; Morris et al. 2002). Nevertheless, delaying recovery actions in anticipation of additional information can prove detrimental for species whose populations are declining (Grantham et al. 2009). Therefore, it is often better to make weaker inference based on available data than to make no inference at all (Link and Barker 2010).

The need to develop and implement recovery actions based on limited demographic information is especially relevant for Mojave and Sonoran Desert Tortoises (*Gopherus agassizii* and *G. morafkai*, respectively). Across large portions of their geographic ranges, both species are thought to be declining in response to an array of threats that includes habitat loss, invasive

species, and disease (USFWS 1990, 2010, 2011; Darst et al. 2013; Gray and Steidl 2015), and they are likely vulnerable to a suite of emerging threats that includes climate change (Zylstra et al. 2013; Lovich et al. 2014). These declines have led the U. S. Fish and Wildlife Service to classify the Mojave Desert Tortoise as a threatened species and the Sonoran Desert Tortoise as a candidate for listing (USFWS 1990, 2010). Developing effective conservation strategies for these species will require understanding the nature and extent to which these threats affect different life stages and how life stages interact to affect demography and population dynamics. Although progress has been made toward this goal (Bury and Germano 1994; Van Devender 2002; USFWS 2011; Rostal et al. 2014), information is still lacking for key aspects of their life histories.

Information on recruitment, which we define as the number of offspring produced that survive their first year, is especially limited. There have been few attempts to estimate recruitment for Mojave Desert Tortoises (Turner et al. 1987; Doak et al. 1994; Karl 1998) and none for Sonoran Desert Tortoises, probably because different life-history events or components that comprise recruitment are challenging to study (Morafka

1994). For example, nests can be difficult to find because they are usually located inside burrows and are abandoned by female tortoises soon after they deposit eggs (Averill-Murray et al. 2014). Likewise, hatchlings can be difficult to find, mark, and track because they are cryptic and small. In addition, studies of recruitment may be considered lower priority because rates of population change for desert tortoises are thought to be governed primarily by rates of adult survival (Congdon et al. 1993; Doak et al. 1994; Heppell et al. 1996; Heppell 1998; but see Wisdom et al. 2000).

The lack of reliable information on recruitment has made it difficult to evaluate the importance of this life-history stage on population dynamics. In particular, a lack of estimates of recruitment inhibits the use of stage- or age-structured population models, which integrate information from multiple life-history stages to evaluate rates of population change, gauge the relative importance of different life-history stages to population dynamics, predict population-level responses to threats or management, assess long-term population viability, and develop conservation strategies (Crouse et al. 1987; Caswell 2001; Morris et al. 2002; Morris and Doak 2002). The utility of single demographic rates for these purposes is limited to the extent that a specific rate reflects other demographic processes in a population (Radchuk et al. 2013). For example, recovery actions to increase adult survival might be misdirected if recruitment or juvenile survival is limiting population growth. Thus, recruitment estimates are necessary to understand population dynamics, and the lack of recruitment estimates currently impedes our ability to evaluate the relative efficacy of alternative recovery actions (USFWS 2010, 2011).

Given the importance of understanding the role of recruitment in recovery of Sonoran and Mojave desert tortoises, our primary objective was to estimate recruitment of tortoises by assembling and synthesizing data from studies across their geographic ranges in the United States. Despite limitations in the data available, we estimate recruitment because of its central importance in assessing the viability of these vulnerable species. Our secondary objectives were to summarize research on recruitment of desert tortoises, identify deficiencies in available data, and recommend directions for future research.

MATERIALS AND METHODS

Recruitment (R), which we defined as the number of females produced per female per year, is the product of four discrete components:

$$R = P_R \times E/2 \times P_H \times P_S$$

where P_R is the proportion of females in the population that reproduced, $E/2$ is the number of female eggs produced per reproducing female per year, P_H is the proportion of eggs that hatched successfully, and P_S is the proportion of hatchlings that survived to the end of their first year. In our analyses, we assumed that the sex ratio was 50:50 at laying, that rates of hatching success and hatchling survival were equal for males and females, and that tortoises were surveyed annually immediately prior to reproduction, such that recruitment equates to egg production offset by hatchling survival. Although recruitment could be subdivided into more components (e.g., P_H could be divided into the proportion of eggs that were fertile and the proportion of fertile eggs that hatched successfully), we used components that were studied most commonly.

Data.—We assembled data on recruitment components from journal articles, theses, and government reports (Table 1). In our analyses, we used point estimates of components from each site and year combination where data were available. Where raw data were available, we estimated recruitment components ourselves (73% of estimates), but otherwise we used estimates as reported (27%). Although there is uncertainty associated with all estimates, we did not include variance of estimates in our analyses because they were not provided for some reported estimates.

We considered the proportion of females reproducing (P_R) and annual egg production (E) as the reproductive portion of recruitment. For both components, we included only data from studies that used radiography to classify reproductive status and to quantify egg production because other methods are unreliable (Turner et al. 1984). We excluded estimates of egg production that were based on fewer than four tortoises (Table 1).

Hatching success (P_H) describes reductions in recruitment between egg laying and hatchling emergence from the nest due to egg breakage, infertility, incomplete development, and nest predation. We estimated this component as the number of hatchlings that emerged from all nests monitored at a site divided by the total number of eggs in all the nests. Although fates of eggs in the same clutch are probably not independent, we used eggs as sample units because most studies reported hatching success in this way. In two studies of Mojave Desert Tortoises, eggs were moved from nests to enclosures or eggs were protected *in situ* with fencing (Turner et al. 1986; McLuckie and Fridell 2002; Table 1); we included these studies because data for this component were sparse, protection measures did not prevent all predation, and estimates were within the range of values from studies that did not protect nests. The only study that examined this component for Sonoran Desert Tortoises reported data on eggs from only one nest (Stitt 2004; Table 1), which were

TABLE 1. Summary of studies with data relevant to recruitment in Mojave Desert (*Gopherus agassizii*) and Sonoran Desert (*G. morafkai*) tortoises. Components of recruitment are proportion of females reproducing (P_R), annual egg production of reproducing females (E), proportion of eggs hatching successfully (P_H), and proportion of hatchlings surviving the remainder of their first year (P_S). Units for sample sizes are numbers of females for P_R and E , number of eggs for P_H , and number of hatchlings for P_S .

Species	State	Site	Code	Years	Sample Sizes				Source
					P_R	E	P_H	P_S	
Mojave	UT	Beaver Dam Slope	BEDS	1989	18	12	71 ^a		McLuckie and Fridell 2002
Mojave	CA	Desert Tortoise Natural Area	DTNA	1992–1993	24–32	18–29			Wallis et al. 1999
Mojave	CA	Fort Irwin	FOIR	1999				3 ^{b,c}	Hazard and Morafka 2002
Mojave	CA	Goffis	GOFF	1983–1986, 1988–1989, 1992–1993	9–36	9–28 ^d	57 ^{a,e}		Turner et al. 1986; Frederick Turner et al., unpubl. report; Wallis et al. 1999; Henen 1994; Henen 2002
Mojave	CA	Joshua Tree National Park	JTNP	1997–1998	7–8	1 ^{c,f}			Lovich et al. 1999
Mojave	CA	Mojave National Preserve	MONP	1997	18	12			Lovich et al. 1999
Mojave	CA	Palm Springs	PASP	1997–1998	10–13	9 ^f			Lovich et al. 1999
Mojave	CA	Sandhill Training Area	SATA	1998–1999			85–112	12–14 ^g	Bjurlin and Bissonette 2004
Mojave	CA	Upper Ward Valley	UPWV	1991–1995	20–31	16–27	152–193 ^h		Karl 1998
Mojave	NV	Yucca Mountain	YUMO	1993–1994		10–25			Mueller et al. 1998
Sonoran	AZ	Espanto Mountain	ESPA	1994	8	7			Elizabeth Wirt and Peter Holm, unpubl. report
Sonoran	AZ	Granite Hills	GRHI	1997	16	4			Averill-Murray 2002
Sonoran	AZ	Maricopa Mountain	MARI	1994	6	2 ^e			Elizabeth Wirt and Peter Holm, unpubl. report
Sonoran	AZ	Rincon Mountain	RINC	2001–2002	14–15	4–11	8 ⁱ		Stitt 2004
Sonoran	AZ	Sugarloaf Mountain	SUMO	1993, 1997–1999	10–19	4–13			Averill-Murray 2002

^a Data were from eggs that were moved from natural nests to enclosures or protected in natural nests with fencing.

^b Originally 12, 1–2 mo-old hatchlings were released in October 1999 but the status of only three were known by late August 2000.

^c Sample size was too small ($n < 4$) to yield reliable estimates.

^d Data for E only existed for 1983–1986 and 1992–1993.

^e Data for P_H only existed for 1984.

^f Data for E only existed for 1997.

^g P_S was only measured from emergence to hibernation and did not include mortality during and after hibernation.

^h Data for P_H only existed for 1991–1993.

ⁱ Data for P_H only existed for a single nest in 2001. Nest fate (success or failure) was reported for other nests without a count of eggs.

inadequate for estimating hatching success for Sonoran Desert Tortoises.

Hatchling survival (P_S) accounts for losses during the first year following emergence from the nest. There were only two studies that examined this component for Mojave Desert Tortoises (Table 1). In one study, the sample size was too small ($n = 3$) to provide a reliable estimate (Hazard and Morafka 2002). The other study only estimated hatchling survival from emergence to hibernation (Bjurlin and Bissonette 2004). Because this estimate did not include mortality during and after hibernation, it likely overestimated survival during the entire period, therefore we did not use this estimate. There were no studies about this component for Sonoran

Desert Tortoises. Consequently, we could find no usable estimates of this component for either species.

Data analysis.—We used a two-step process to estimate recruitment. First, we used Bayesian methods to estimate recruitment components where sufficient data were available. For components where data were not available, we specified uniform distributions with means that spanned a range of plausible values (described below). Second, we used Monte Carlo methods to combine components into estimates of recruitment according to our recruitment equation.

We used generalized linear-mixed models to estimate recruitment components P_R and E for Mojave and

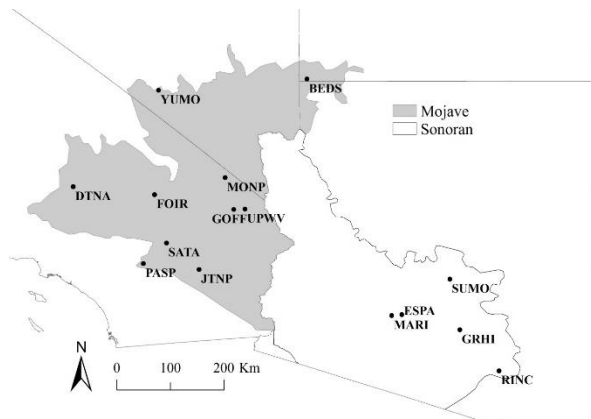


FIGURE 1. Locations of study sites where data were collected for one or more recruitment components of Mojave Desert (*Gopherus agassizii*) and Sonoran Desert (*G. morafkai*) tortoises. Site codes are in Table 1.

Sonoran desert tortoises and P_H for Mojave Desert Tortoises. In each model, we considered species as a fixed effect (α_i , i = Mojave or Sonoran) and site and year as random effects (β_s and β_y , respectively). We estimated variation in site (σ_s^2) and year (σ_y^2) as separate effects for each species because reproductive ecology and early life history differs between species (Germano 1994a; Averill-Murray 2002; Averill-Murray et al. 2014). Therefore, for each recruitment component (y_r), we included interactions between species and site and year effects ($y_r = \alpha_i + \beta_{i,s} + \beta_{i,y}$).

We fit models using Bayesian methods because with small sample sizes, variance estimates for random effects were less likely to be biased than estimates from alternative methods (Kéry 2010). Bayesian methods generate posterior distributions of parameters based on a combination of data and prior information about parameters. For each species, we specified a uniform prior distribution for proportional components ($\alpha_i \sim \text{Unif}[0,1]$) and a normal prior distribution truncated between 1 and 18 for egg production ($\alpha_i \sim N[0, 1000]T[1,18]$), where 18 was the maximum number of eggs reported in the literature (two clutches of 8 and 10 eggs; McLuckie and Fridell 2002). For site and year effects, we specified normal prior distributions ($\beta_{i,s} \sim N[0, \sigma_{i,s}^2]$, $\beta_{i,y} \sim N[0, \sigma_{i,y}^2]$), with each standard deviation assigned its own uniform prior distribution ($\sigma_{i,s} \sim \text{Unif}[0,10]$, $\sigma_{i,y} \sim \text{Unif}[0,10]$). For each component, we based the posterior distribution on 15,000 samples from three independent Markov chains of 5,000 samples after discarding an initial 20,000 samples for each chain. We confirmed model convergence with the Gelman-Rubin statistic (Gelman et al. 2004) and by inspecting time-

series plots of the chains. We fit models with OpenBUGS version 3.2.1 (Thomas et al. 2006).

We incorporated P_H for Sonoran Desert Tortoises and P_S for both species in estimates of recruitment as a range of plausible values, each with their own distributions. We considered mean values of 0.2, 0.4, 0.61, and 0.8 for P_H of Sonoran Desert Tortoises and 0.3, 0.5, and 0.7 for P_S of both species. The distributions of all values except $P_H = 0.61$ were represented as uniform distributions with bounds that were established arbitrarily as the mean ± 0.2 (e.g., $\text{Unif}[0.2, 0.6]$ for $P_H = 0.4$). These prior uniform distributions also functioned as posterior distributions, because there were no data with which to update these distributions. The posterior distribution associated with $P_H = 0.61$ for Sonoran Desert Tortoises was the same as the empirical posterior distribution for Mojave Desert Tortoises.

To estimate recruitment (R) for each species, we used Monte Carlo methods to sample 10,000 values randomly from the posterior distributions of each component and combined the samples according to our recruitment equation to create 10,000 estimates of recruitment. For Sonoran Desert Tortoises, we combined samples from the empirically-based posterior distributions of P_R and E with samples from the posterior distributions of P_H and P_S corresponding with each combination of plausible values. Similarly, for Mojave Desert Tortoises, we combined samples from the empirically-based posterior distributions of P_R , E , and P_H with samples from the posterior distribution of P_S corresponding to each plausible value. We used the means and standard deviations of the resulting distributions to represent the means and standard errors of recruitment estimates for each species. To examine the magnitude of differences between Mojave and Sonoran Desert Tortoises for P_R , E , and R , we used 95% credible intervals of the posterior distribution of differences (95% CI_d) and the percentage of this distribution that exceeded zero (% $\text{PD}_d > 0$). We did not examine interspecific differences in P_H and P_S because of the lack of empirical data.

RESULTS

We identified 14 studies that reported at least one recruitment component for Desert Tortoises, 11 of which were studies of Mojave Desert Tortoises from 10 locations and three of which were studies of Sonoran Desert Tortoises from five locations (Table 1; Fig. 1). For both species, the proportion of females reproducing and annual egg production were measured at 70–100% of locations, hatching success was measured at 20–40% of locations, and hatchling survival was measured at 0–20% of locations (Table 1). In general, there was little temporal replication in estimates of components.

TABLE 2. Means, 95% credible intervals (95% CI), and variance components of recruitment components for Mojave Desert (*Gopherus agassizii*) and Sonoran Desert (*G. morafkai*) tortoises.

Recruitment component	Estimates				Variance components			
	Mojave		Sonoran		Mojave		Sonoran	
	Mean	95% CI	Mean	95% CI	Site	Year	Site	Year
Prop. females reproducing (P_R)	0.81	0.52–0.99	0.52	0.07–0.94	0.16	0.11	0.36	0.26
Total annual egg production (E)	6.90	5.51–8.16	5.17	3.05–7.60	1.06	0.71	1.21	1.24
Hatching success (P_H)	0.61	0.25–0.90	---	---	0.22	0.13	---	---
Hatchling survival (P_S)	---	---	---	---	---	---	---	---

Proportion of females reproducing and annual egg production were measured for 5–8 y at only two locations in the range of the Mojave Desert Tortoise and for 4 y at only one location in the range of the Sonoran Desert Tortoise. At most (71–100%) locations where a component was measured, temporal replication was limited to 1–2 y (Table 1).

The proportion of females reproducing each year averaged 0.29 (56%) higher in Mojave Desert Tortoises than Sonoran Desert Tortoises (Table 2; 95% CI_d: -0.21–0.79, 85% PD_d > 0). For females that reproduced, Mojave Desert Tortoises produced 1.7 (33%) more eggs per year than Sonoran Desert Tortoises (95% CI_d: -1.02–4.17, 93% PD_d > 0). For Mojave Desert Tortoises, hatching success averaged 0.61. The uncertainty in estimates of components was relatively high for both species but tended to be greater for Sonoran Desert Tortoises (Table 2). Spatial variation was marginally greater than temporal variation for the proportion of females reproducing for both species and for annual egg production and hatching success of Mojave Desert Tortoises, whereas temporal variation was greater than spatial variation for egg production in Sonoran Desert Tortoises (Table 2).

For Mojave Desert Tortoises, overall estimates of recruitment ranged from 0.51 to 1.18 females/female/y across the range of plausible values for hatchling survival ($P_S = 0.3$ – 0.7 ; Table 3). For Sonoran Desert Tortoises, recruitment was estimated to be less than half that of Mojave Desert Tortoises when hatching success was assumed to be the same between the species ($P_H = 0.61$, Table 3, Fig. 2; 81–87% PD_d > 0). Even under the most optimistic plausible value of hatching success for Sonoran Desert Tortoises ($P_H = 0.8$), the range of recruitment estimates based on different values of hatchling survival (0.32–0.75 females/female/y) was still considerably lower than the range of estimates for Mojave Desert Tortoises (72–78% PD_d > 0). For Mojave Desert Tortoises, 66% of recruitment estimates exceeded 1 female/female/yr under the most optimistic plausible value for hatchling survival ($P_S = 0.7$). For Sonoran Desert Tortoises, only 12% of the recruitment estimates

exceeded 1 female/female/yr under the same combination of values ($P_H = 0.61$, $P_S = 0.7$) and 25% exceeded this value under the combination of the most optimistic values ($P_H = 0.8$, $P_S = 0.7$; Fig. 2).

DISCUSSION

Estimates of recruitment for Mojave Desert Tortoises for a given level of hatchling survival were always higher than those for Sonoran Desert Tortoises regardless of the value of hatching success for Sonoran Desert Tortoises. For example, when hatching success and hatchling survival were assumed to be the same for both species, recruitment in Mojave Desert Tortoises was estimated to be more than twice that of Sonoran Desert Tortoises. This disparity in recruitment resulted from differences between species in the proportion of females that reproduced and annual egg production, which may reflect reproductive strategies that diverged in response to differences in amount and seasonality of precipitation in the deserts they inhabit (Averill-Murray 2002). In the Mojave Desert, most precipitation occurs during winter, which governs production of spring annual plants that influences the number of clutches and annual egg production of female tortoises (Turner et al. 1986; Henen 1997; Karl 1998). Summer rains in the Mojave Desert tend to be inconsistent, however, so resources can be limited and unpredictable when tortoise hatchlings emerge in late summer (Henen 1997), particularly at the western extreme of their range where warm-season precipitation is rare (Germano 1994b; Hereford et al. 2006). To increase the probability that at least some hatchlings will emerge when conditions are favorable, Mojave Desert Tortoises may have evolved a bet-hedging strategy (Congdon et al. 1982; Henen 1997) wherein most females produce at least one clutch per year regardless of environmental conditions (Turner et al. 1986; Karl 1998; Mueller et al. 1998; Wallis et al. 1999). Similar to the Mojave Desert, winter rains in the Sonoran Desert govern the amount of forage available to female tortoises when eggs are developing (Averill-Murray 2002). Unlike Mojave Desert Tortoises,

TABLE 3. Mean recruitment estimates (95% credible intervals) for Mojave Desert (*Gopherus agassizii*) and Sonoran Desert (*G. morafkai*) tortoises based on a range of plausible values of hatching success (P_H) and hatchling survival (P_S).

Hatchling Survival	Hatching success				
	Mojave		Sonoran		
	0.61 ^a		0.2	0.4	0.61 ^a 0.8
0.3	0.51 (0.12–1.08)		0.08 (0.00–0.29)	0.16 (0.02–0.47)	0.25 (0.02–0.69) 0.32 (0.03–0.85)
0.5	0.85 (0.26–1.57)		0.13 (0.00–0.42)	0.27 (0.03–0.69)	0.41 (0.04–1.03) 0.54 (0.06–1.27)
0.7	1.18 (0.39–2.10)		0.19 (0.00–0.58)	0.38 (0.04–0.95)	0.57 (0.06–1.39) 0.75 (0.09–1.70)

^a Mean of the posterior distribution derived from empirical data for Mojave Desert Tortoises (see Table 2) was also included as a plausible value for Sonoran Desert Tortoises for comparison.

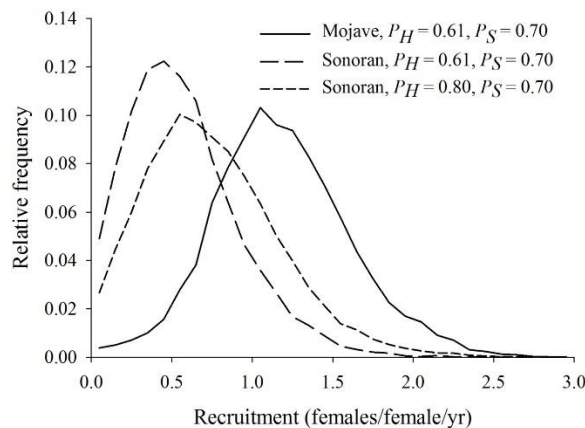
however, female Sonoran Desert Tortoises may forgo reproduction in years with little winter rainfall, which is reflected in the lower proportion of reproducing females in the Sonoran Desert (Table 2; Averill-Murray 2002). In summer, rainfall is both more reliable and 380% greater (about 85 mm) in the Sonoran than Mojave Desert (Germano 1994b). Therefore, if female Sonoran Desert Tortoises do reproduce, food resources are likely to be plentiful when hatchlings emerge in late summer, which may increase survival of hatchlings in their first year. Over evolutionary time, higher hatchling survival would tend to favor Sonoran Desert Tortoises that produce a single clutch with fewer eggs per year (i.e., tortoises that invest less resources into reproduction) than Mojave Desert Tortoises (Averill-Murray 2002).

Although data on hatchling survival were sparse, there are ecological reasons to expect that hatchling survival may be greater for Sonoran than Mojave Desert Tortoises. Hatchling survival may be greater in the Sonoran Desert because hatchlings emerge at the end of the rainy season when sufficient forage is available in most years (Averill-Murray et al. 2002). In contrast, hatchlings are likely to emerge in the Mojave Desert

when there is less forage available and must wait until the following spring to feed (Averill-Murray et al. 2002), which could increase mortality relative to hatchlings in the Sonoran Desert. Further, small tortoises may also be less conspicuous to predators in the rocky foothill areas of the Sonoran Desert than in the sandy valley bottoms of the Mojave Desert (Averill-Murray et al. 2002). Although greater rates of hatchling survival for Sonoran Desert Tortoises would reduce the estimated difference in recruitment between species, the differences would have to be large to compensate for differences in reproduction. Rates of hatching success also may differ between species, but not enough is known about the ecology of desert tortoises during this life stage to understand how these may differ between species.

There are at least three shortcomings inherent in the recruitment estimates we report. First, hatching success and hatchling survival were represented by a range of plausible values, which yielded a range of recruitment estimates for each species. Although a single, reliable estimate would be ideal, our estimates provide limits to the likely range of values for recruitment. Second, pooling data across broad spatial and temporal scales into range-wide estimates of recruitment can conflate spatial and temporal sources of variation (Wisdom et al. 2000). Range-wide estimates of recruitment are also probably of limited value if individual recruitment components vary considerably over space and time in response to local environmental conditions and threats. Third, recruitment components had high uncertainty due in part to low sampling effort, which in turn contributed to high uncertainty in overall recruitment estimates. Nevertheless, the uncertainty in recruitment may still have been underestimated because the uncertainty we included with values for components with no empirical data (i.e., hatching success and hatchling survival) may have been conservative.

Recommendations for future research.—We offer four recommendations for future research on desert tortoises. First, we suggest considering recruitment as a series of separate but inter-related life-history events or

**FIGURE 2.** Posterior distributions of recruitment for Mojave Desert (*Gopherus agassizii*) and Sonoran Desert (*G. morafkai*) tortoises under different plausible values for hatching success (P_H) and hatchling survival (P_S).

components. Although recruitment can be estimated as the ratio of female offspring to adult females in the previous season (Doak et al. 1994; Morris and Doak 2002), considering components individually promotes a more mechanistic understanding of the processes that influence recruitment and allows managers to target particular components for management. Second, studies that estimate hatching success and hatchling survival should be prioritized, because without these components, recruitment cannot be estimated reliably. Third, areas where no data exist should be prioritized for study and sites where there has been little or no temporal replication should be revisited. Understanding spatial and temporal patterns of variation can help determine if recruitment in some locations is less sensitive to environmental fluctuations and changes in threats than recruitment in other locations and can serve as a starting point for elucidating the mechanisms that govern recruitment. Finally, we suggest that whenever possible all recruitment components be measured during a study to avoid having to aggregate components across space and time, which could mask important patterns of variation in these components. Having spatially and temporally specific estimates of recruitment that can be combined with other similarly specific demographic rates (e.g., spatially-explicit estimates of juvenile and adult survival) will improve our understanding of population dynamics of Mojave and Sonoran Desert Tortoises across their range and advance the recovery of these declining species.

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LITERATURE CITED

- Averill-Murray, R.C. 2002. Reproduction of *Gopherus agassizii* in the Sonoran Desert, Arizona. *Chelonian Conservation and Biology* 4:295–301.
- Averill-Murray, R.C., A.P. Woodman, and J.M. Howland. 2002. Population ecology of the Sonoran Desert Tortoise in Arizona. Pp. 109–134 *In* The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. Van Devender, T.R. (Ed.). University of Arizona Press, Tucson, Arizona, USA.
- Averill-Murray, R.C., L.J. Allison, and L.L. Smith. 2014. Nesting and reproductive output among North American tortoises. Pp. 110–117 *In* Biology and Conservation of North American Tortoises. Rostal, D.C., E.D. McCoy, and H.R. Mushinsky (Eds.). John Hopkins University Press, Baltimore, Maryland, USA.
- Beissinger, S.R., and M.I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–844.
- Bjurlin, C.D., and J.A. Bissonette. 2004. Survival during early life stages of the Desert Tortoise (*Gopherus agassizii*) in the south-central Mojave Desert. *Journal of Herpetology* 38:527–535.
- Bury, R.B., and D.J. Germano (Eds.). 1994. Biology of North American Tortoises. Fish and Wildlife Research, No. 13. U.S. Department of Interior, National Biological Survey, Washington, D.C., USA.
- Caswell, H. 2001. Matrix Population Models. 2nd Edition. Sinauer Associates Inc., Sunderland Massachusetts, USA.
- Congdon, J. D., A.E. Dunham, and D.W. Tinkle. 1982. Energy budgets and life histories of reptiles. Pp. 233–271 *In* Biology of the Reptilia, Vol.13 (Physiology D). Gans, C., and F. H. Pough (Eds.). Academic Press, New York, New York, USA.
- Congdon, J.D., A.E. Dunham, and R.C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's Turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7:826–833.
- Crouse, D.T., L.B. Crowder, H. Caswell. 1987. A stage-based population model for Loggerhead Sea Turtles and implications for conservation. *Ecology* 68:1412–1423.
- Darst, C.R., P.J. Murphy, N.W. Strout, S.P. Campbell, K.J. Field, L. Allison, and R.C. Averill-Murray. 2013. A strategy for prioritizing threats and recovery actions for at-risk species. *Environmental Management* 51:786–800.
- Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the Desert Tortoise in the western Mojave Desert. *Ecological Applications* 4:446–460.
- Gelman, A., J.B. Carlin, H.S. Stern, and D.B. Rubin. 2004. Bayesian Data Analysis. 2nd Edition. Chapman and Hall / CRC, Boca Raton, Florida, USA.
- Germano, D.J. 1994a. Comparative life histories of North American tortoises. Pp. 175–185 *In* Biology of North American Tortoises. Bury, R.B., and D.J. Germano (Eds.). Fish and Wildlife Research, No. 13. U.S. Department of Interior, National Biological Survey, Washington, D.C., USA.
- Germano, D.J. 1994b. Growth and age at maturity of North American tortoises in relation to regional climates. *Canadian Journal of Zoology* 72:918–931.
- Grantham, H.S., K.A. Wilson, A. Moilanen, T. Rebelo, and H.P. Possingham. 2009. Delaying conservation actions for improved knowledge: how long should we wait? *Ecology Letters* 12:293–301.

- Gray, K.M., and R.J. Steidl. 2015. A plant invasion affects condition but not density or population structure of a vulnerable reptile. *Biological Invasions* 17:1979–1988.
- Hazard, L.C., and D.J. Morafka. 2002. Comparative dispersion of neonate and headstarted juvenile Desert Tortoises (*Gopherus agassizii*): a preliminary assessment of age effects. *Chelonian Conservation and Biology* 4: 406–409.
- Henen, B.T. 1994. Seasonal and annual energy and water budgets of female Desert Tortoises (*Xerobates agassizii*) at Goffs, California. Ph.D. Dissertation, University of California, Los Angeles, California, USA. 185 pp.
- Henen, B.T. 1997. Seasonal and annual energy budgets of female Desert Tortoises (*Gopherus agassizii*). *Ecology* 78:283–296.
- Henen, B.T. 2002. Energy and water balance, diet, and reproduction of female Desert Tortoises (*Gopherus agassizii*). *Chelonian Conservation and Biology* 4:319–329.
- Heppell, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998:367–375.
- Heppell, S.S., L.B. Crowder, and D.T. Crouse. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications* 6:556–565.
- Hereford, R., R.H. Webb, and C.I. Longpré. 2006. Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893–2001. *Journal of Arid Environments* 67:13–34.
- Karl, A.E. 1998. Reproductive strategies, growth patterns, and survivorship of a long-lived herbivore inhabiting a temporally variable environment. Ph.D. Dissertation, University of California, Davis, California, USA. 178 pp.
- Kéry, M. 2010. Introduction to WinBUGS for Ecologists: A Bayesian Approach to Regression, ANOVA, Mixed Models, and Related Analyses. Academic Press, Burlington, Massachusetts, USA.
- Link, W.A., and R.J. Barker. 2010. Bayesian Inference with Ecological Applications. Elsevier/Academic Press, London, UK.
- Lovich, J., P. Medica, H. Avery, K. Meyer, G. Bowser, and A. Brown. 1999. Studies of reproductive output of the Desert Tortoise at Joshua Tree National Park, the Mojave National Preserve, and comparative sites. *Park Science* 19:22–24.
- Lovich, J.E., C.B. Yackulic, J. Freilich, M. Agha, M. Austin, K.P. Meyer, T.R. Arundel, J. Hansen, M.S. Vamstad, and S.A. Root. 2014. Climatic variation and tortoise survival: has a desert species met its match? *Biological Conservation* 169:214–224.
- Morafka, D.J. 1994. Neonates: missing links in the life histories of North American tortoises. Pp. 161–173 *In* Biology of North American Tortoises. Bury, R.B., and D.J. Germano (Eds.). Fish and Wildlife Research, No. 13. National Biological Survey, Washington, D.C., USA.
- McLuckie, A.M., and R.A. Fridell. 2002. Reproduction in a Desert Tortoise (*Gopherus agassizii*) population on the Beaver Dam Slope, Washington County, Utah. *Chelonian Conservation and Biology* 4:288–294.
- Morris, W.F., P.L. Bloch, B.R. Hudgens, L.C. Moyle, and J.R. Stinchcombe. 2002. Population viability analysis in endangered species recovery plans: past use and future improvements. *Ecological Applications* 12:708–712.
- Morris, W.F., and D.F. Doak. 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- Mueller, J.M., K.R. Sharp, K.K. Zander, D.L. Rakestraw, K.R. Rautenstrauch, and P.E. Lederle. 1998. Size-specific fecundity of the Desert Tortoise (*Gopherus agassizii*). *Journal of Herpetology* 32:313–319.
- Radchuk, V., C. Turlure, and N. Schtickzelle. 2013. Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology* 82:275–285.
- Rostal, D.C., and E.D. McCoy, and H.R. Mushinsky (Eds.). 2014. Biology and Conservation of North American Tortoises. John Hopkins University Press, Baltimore, MD, USA.
- Stitt, E.W. 2004. Demography, reproduction, and movements of Desert Tortoises (*Gopherus agassizii*) in the Rincon Mountains, Arizona. M.Sc. Thesis, University of Arizona, Tucson, Arizona, USA. 70 pp.
- Tear, T.H., J.M. Scott, P.H. Hayward, and B. Griffith. 1995. Recovery plans and the Endangered Species Act: are criticisms supported by data? *Conservation Biology* 9:182–195.
- Thomas, A., B. O'Hara, U. Ligges, and S. Sturtz. 2006. Making BUGS open. *R News* 6:12–17.
- Turner, F.B., P.A. Medica, and C.L. Lyons. 1984. Reproduction and survival of the Desert Tortoise (*Scaptochelys agassizii*) in Ivanpah Valley, California. *Copeia* 1984:811–820.
- Turner, F.B., P. Hayden, B.L. Burge, and J.B. Roberson. 1986. Egg production by the Desert Tortoise (*Gopherus agassizii*) in California. *Herpetologica* 42:93–104.
- U.S. Fish and Wildlife Service (USFWS). 1990. Endangered and threatened wildlife and plants; determination of threatened status for the Mojave population of the Desert Tortoise. *Federal Register* 55:12178–12191.
- U.S. Fish and Wildlife Service (USFWS). 2010.

Herpetological Conservation and Biology

Endangered and threatened wildlife and plants; 12-month finding on a petition to list the Sonoran population of the Desert Tortoise as endangered or threatened. Federal Register 75:78094–78146.

U.S. Fish and Wildlife Service (USFWS). 2011. Revised Recovery Plan for the Mojave Population of the Desert Tortoise (*Gopherus agassizii*). U.S. Fish and Wildlife Service, Sacramento, California, USA.

Van Devender, T.R. (Ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. University of Arizona Press, Tucson, Arizona, USA.

Wallis, I.R., B.T. Henen, and K.A. Nagy. 1999. Egg size and annual egg production by female Desert Tortoises

(*Gopherus agassizii*): the importance of food abundance, body size, and date of egg shelling. Journal of Herpetology 33:394–408.

Wisdom, M.J., L.S. Mills, and D.F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628–641.

Zylstra, E.R., R.J. Steidl, C.A. Jones, and R.C. Averill-Murray. 2013. Spatial and temporal variation in survival of a rare reptile: a 22-year study of Sonoran Desert Tortoises. Oecologia 173:107–116.

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