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POPULATION ECOLOGY - ORIGINAL RESEARCH

Spatial and temporal variation in survival of a rare reptile: a 22-year study of Sonoran desert tortoises

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Abstract Although many species may be vulnerable to changes in climate, forecasting species-level responses can be challenging given the array of physiological, behavioral, and demographic attributes that might be affected. One strategy to improve forecasts is to evaluate how species responded to climatic variation in the past. We used 22 years of capture-recapture data for Sonoran desert tortoises (*Gopherus morafkai*) collected from 15 locations across their geographic range in Arizona to evaluate how environmental factors affected spatial and temporal variation in survival. Although rates of annual survival were generally high ($\widehat{\Phi} = 0.92$), survival of adults decreased with drought severity, especially in portions of their range that were most arid and nearest to cities. In three locations where large numbers of carcasses from marked tortoises were recovered, survival of adults was markedly lower during periods of severe drought ($\widehat{\Phi} = 0.77$–0.81) compared to all other periods ($\widehat{\Phi} = 0.93$–0.98). Assuming continued levels of dependency of humans on fossil fuels, survival of adult tortoises is predicted to decrease by an average of 3 % during 2035–2060 relative to survival during 1987–2008 in 14 of the 15 populations we studied. This decrease could reduce persistence of tortoise populations, especially in arid portions of their range. Temporal and spatial variation in drought conditions are important determinants of survival in adult desert tortoises.

Keywords Capture-recapture · Climate change · Demography · Drought · *Gopherus morafkai*

Introduction

Across North America and worldwide, declines in many reptile populations have been attributed to multiple mechanisms, including habitat loss and degradation (Jenkins et al. 2003; Driscoll 2004), invasions by nonnative species (Towns et al. 2001; Jellinek et al. 2004), illegal collection (Webb et al. 2002), and climate change (Whitfield et al. 2007; Sinervo et al. 2010). Although each of these factors can affect reptile populations in complex ways, responses to climate change can be especially challenging to forecast because temperature and precipitation can affect species at multiple scales. For example, at the individual scale, changes in climate can affect behavior and physiology, and can increase susceptibility to disease (Pounds et al. 2006; Telemeco et al. 2009); at the population scale, climate change can alter sex ratios (Janzen 1994); and at the community scale, climate change can affect species composition (Sheldon et al. 2011). Further,

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species have the potential to moderate effects of climate change by shifting their geographic ranges or by altering behavior or activity periods to better meet the physiological requirements necessary for survival and reproduction (Sinervo et al. 2010; Moreno-Rueda et al. 2011). Understanding and forecasting effects of climate change on reptile populations is important because ectotherms are likely to be particularly vulnerable to these effects, given the influence of environmental conditions on many of their physiological functions (Deutsch et al. 2008).

One approach that can be used to better understand and forecast potential demographic responses to climate change is to evaluate retrospectively how populations changed in response to variation in climate. For long-lived species, this approach requires data collected over long time periods and over spatial scales that are sufficiently broad to capture meaningful variation in climate; these data are uncommon, especially when species are rare. Further, some aspects of demography, such as abundance, may be more difficult to estimate precisely for rare species relative to other aspects, such as survival, particularly over the long term (MacKenzie and Nichols 2004). Given the disproportionate influence of adult survival on the rate of population change in long-lived species (Doak et al. 1994; Heppell et al. 2000; Sæther and Bakke 2000), evaluating factors that influence survival may be especially important for developing recovery strategies for rare species.

One such long-lived species, the Sonoran desert tortoise (*Gopherus morafkai*), inhabits deserts south and east of the Colorado River in Arizona and northwestern Mexico, and thornscrub and deciduous forests of Sonora and Sinaloa, Mexico (Germano et al. 1994, U.S. Fish and Wildlife Service 2010). Until recently, *G. morafkai* was considered a distinct population segment of a single desert tortoise species, *G. agassizii*, but morphological, behavioral, and genetic evidence established that distinct lineages exist on either side of the Colorado River (Berry et al. 2002; Murphy et al. 2011; but see McLuckie et al. 1999). In 2010, the U.S. Fish and Wildlife Service determined that listing of the Sonoran desert tortoise under the Endangered Species Act was warranted but precluded by higher priority actions. Higher priority was not given to the Sonoran desert tortoise, in part because relatively little is known about long-term trends in their populations as well as their vulnerability to known and anticipated threats, including predicted changes in climate (U.S. Fish and Wildlife Service 2010).

To understand the influence of environmental factors on aspects of the demography of Sonoran desert tortoises, we used survey data collected over a 22-year period from 15 populations distributed across their geographic range in Arizona. We sought to identify biotic and abiotic factors associated with short-term variation in survival across time and space, and to distinguish those from long-term, persistent trajectories in survival that have implications for population persistence. Our findings are relevant to the conservation of this and perhaps other imperiled, long-lived species inhabiting the Sonoran Desert ecoregion, for which a comprehensive understanding of factors that drive population-level processes is necessary to predict anticipated effects of climatic change and to develop effective conservation strategies.

Materials and methods

Study area

Between 1987 and 1992, 15 plots were established on public lands across the range of the Sonoran desert tortoise in Arizona between elevations of 450 and 1,150 m, with the exception of extreme southwestern Arizona, where tortoise densities were too low to sample efficiently (Fig. 1). Most plots were in biotic communities dominated by Sonoran desertscrub, with a few plots also containing ecotonal elements of Mohave desertscrub (plot AM; two-letter codes for plots in Table 1), juniper woodland (HF), interior chaparral (LS), or desert grassland (SP); one plot (EB) was in Mohave desertscrub (Brown and Lowe 1982; Averill-Murray et al. 2002b). When established originally, plots ranged in size from 2.6 to 3.9 km^2, but between 2000

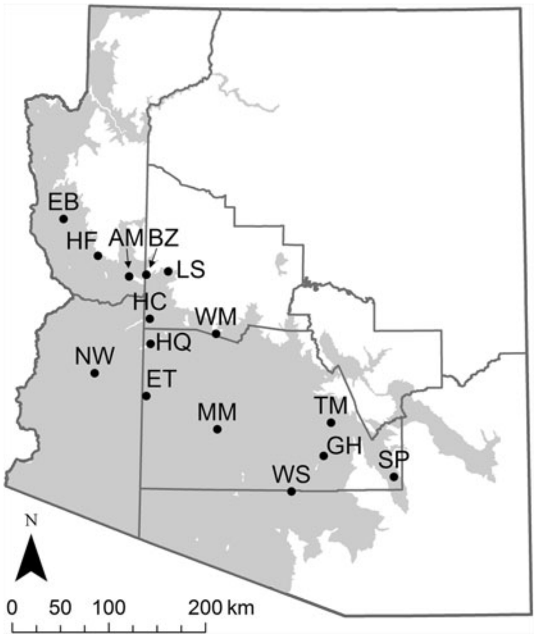

Fig. 1 Locations of 15 Sonoran desert tortoise populations surveyed between 1987 and 2008 and climate divisions in Arizona, USA. *Shading* indicates Sonoran desertscrub and Mojave desertscrub vegetation communities; *two-letter codes* are explained in Table 1

Table 1 Summary of capture-recapture data for 15 populations of adult Sonoran desert tortoises (MCL ≥ 180 mm) in Arizona, USA, surveyed between 1987 and 2008. Annual survival for adults of known sex ($\hat{\Phi}$) are based on estimates from the highest-ranking model (Table 3) averaged across years

Population	Code	Plot area (km^2)	No. annual surveys	Mean effort per annual survey[a]	No. adults marked	No. marked carcasses recovered	$\hat{\Phi}$	SE ($\hat{\Phi}$)
Arrastra Mtn	AM	2.74	4	37.8	23	1	0.92	0.01
Bonanza Wash	BZ	2.40[b]	4	37.8	25	1	0.95	0.01
Eagletail Mtns	ET	2.59	9	39.6	49	5	0.97	0.01
East Bajada	EB	2.59	5	55.4	77	28	0.87	0.02
Granite Hills	GH	2.63	8	57.8	107	16	0.93	0.01
Harcuvar Mtns	HC	2.59	5	59.4	102	8	0.93	0.01
Harquahala Mtns	HQ	3.88	4	47.6	26	3	0.94	0.01
Hualapai Foothills	HF	1.55[b]	4	53.8	57	14	0.89	0.01
Little Shipp Wash	LS	2.59	8	58.3	152	17	0.93	0.01
Maricopa Mtns	MM	2.25[b]	4	56.8	81	23	0.93	0.01
New Water Mtns	NW	2.59	4	29.5	40	1	0.95	0.01
San Pedro Valley	SP	2.59	5	53.8	125	23	0.90	0.01
Tortilla Mtns	TM	2.00[b]	4	56.0	110	8	0.91	0.01
West Silverbell Mtns	WS	2.59	5	53.8	176	20	0.93	0.01
Wickenburg Mtns	WM	1.30[b]	4	37.8	36	2	0.87	0.02
Total					1186	170	0.92	0.01

[a] Effort = number of 8-h person days spent surveying for tortoises during an annual survey

[b] Area surveyed between 2000 and 2008; 2.59 km^2 surveyed before 2000

and 2002, 5 of 15 plots were reduced in size by 7–50 % to eliminate areas with few tortoises or little tortoise sign (shelters, scat, carcasses, or tracks; Table 1). Although plots were located in areas of natural vegetation, they were all influenced by human activities to some extent. Nearly all plots were bisected by ≥1 unimproved dirt road, many were occasionally grazed by livestock and used for recreation, and a few included power-distribution lines or hosted small-scale mining activities at some point during the 22-year study period. We considered populations of tortoises on each plot to be independent because the nearest-neighbor distance among plots averaged 44 km and tortoises in the Sonoran Desert infrequently traverse valley bottoms (Averill-Murray and Averill-Murray 2005).

Tortoise surveys

Between 1987 and 2008, each plot was surveyed in 4–9 different years (Table 1). Between 1987 and 1999, annual surveys consisted of experienced observers searching plots completely at the beginning of the season, then resurveying only those areas where they had observed tortoises or tortoise sign. Between 2000 and 2008, observers searched plots completely 2–5 times during each annual survey. Plots were surveyed between August and October, the period when Sonoran desert tortoises are most active (Averill-Murray et al. 2002a), with the exception of two plots (AM, MM) that were also surveyed in April and May of 1987. Observers surveyed for tortoises when ambient temperatures were generally <40 °C, during mornings and late afternoons early in the season, and occasionally throughout the day during late September and early October when temperatures were lower. Because topography and vegetation structure varied substantially within and among plots, the arrangement of survey routes across plots varied with local environmental features. However, survey routes were mapped to ensure that each plot was surveyed in its entirety. Observers searched for tortoises by scanning open ground, searching under vegetation, and using mirrors or flashlights to search inside holes and crevices. For each tortoise encountered, observers recorded its location, sex, mass, and straight-line midline carapace length (MCL). Observers marked each tortoise uniquely by filing notches into the marginal scutes (Cagle 1939) and released tortoises at the point of capture.

Environmental covariates

We characterized cover of perennial plants, proximity to human development, and water availability at each plot to evaluate their associations with survival and detectability of tortoises. Cover of perennial plants was estimated using line-intercept methods along four or five 100 m transects established permanently on each plot in areas where tortoise sign was common (Canfield 1941). Vegetation was sampled between 1 September and 31 October each year the plot was surveyed for tortoises between 1997 and 2006; cover of perennial plants on each plot was calculated as the average of all transects across all years. We calculated proximity to human development as the distance from the center of each plot to the boundary of the nearest incorporated city as identified by the Arizona Department of Revenue using data available from the Arizona State Land Department and spatial analysis tools in ArcGIS 9.3.

We characterized patterns of water availability for each plot with three measures. To characterize long-term water availability, we extracted the mean annual precipitation for each plot from a model that related average annual precipitation at known locations across a 30-year period (1971–2000) to a digital elevation model for Arizona (PRISM Climate Group 2010). To characterize annual fluctuations in water availability, we used both precipitation data from nearby weather stations and a derived measure of drought severity based on Palmer's drought severity index (PDSI), which measures the departure from normal moisture levels as a result of precipitation, evapotranspiration, and runoff (Palmer 1965). Because precipitation data were not available for specific plots, we obtained monthly precipitation totals from weather stations that (1) were near each plot (mean distance between plot and station = 25 km), (2) were below 1,200 m elevation, and (3) had data available for each year of the study. We standardized annual precipitation to a mean of zero and a standard deviation of 1 for each plot because we were interested in characterizing temporal variation in rainfall around long-term means rather than absolute differences in rainfall among plots. Annual precipitation values were highly correlated among proximate weather stations (slope from regression of correlation coefficients and geographic distances between all pairs of weather stations = -0.001, $t_{53} = -5.98$, $P < 0.001$), suggesting that temporal variation in annual precipitation at the weather stations reflected patterns of annual precipitation at each plot. To calculate drought severity, we obtained monthly PDSI values from the National Climatic Data Center for each of the five climate divisions in Arizona that encompassed plots (Fig. 1), and multiplied these values by -1, so that increasing values of drought severity corresponded to increasingly dry conditions, which facilitates interpretation. Because drought severity and standardized precipitation were correlated ($r = -0.80$; Fig. 2), we did not use both measures to explore variation in the same parameter. We assumed that annual precipitation affects growth of annual plants (Duda et al. 1999; Longshore et al. 2003) and consequently could affect the ability of observers to detect tortoises, whereas drought severity reflects ecosystem processes that govern overall water availability and could affect survival of tortoises.

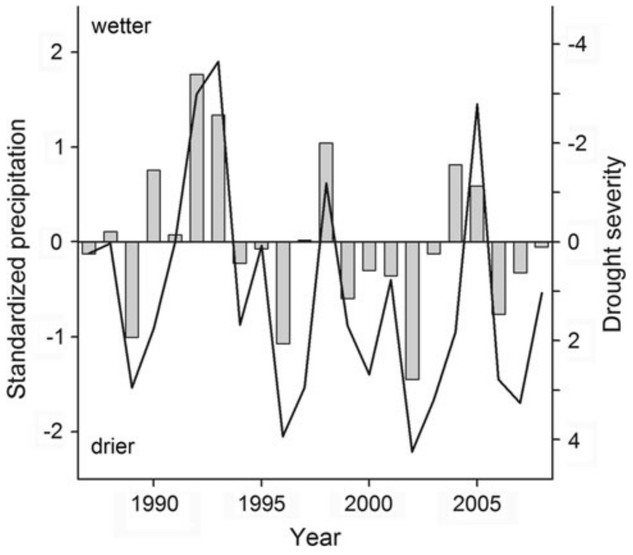

Fig. 2 Standardized annual precipitation (*gray bars*) averaged across weather stations nearest each tortoise population we studied, and mean annual drought severity (*black line*) averaged across five climate divisions in Arizona, USA. *Positive values* of drought severity indicate drier than normal conditions and *negative values* indicate wetter than normal conditions

Survival of adults

We estimated apparent annual survival (Φ, hereafter "survival") of adult tortoises (MCL ≥ 180 mm; Germano 1994) adjusted for recapture probability (*p*) with Cormack–Jolly–Seber (CJS) models in Program MARK 6.0 (Lebreton et al. 1992; White and Burnham 1999). For each tortoise captured, we created an encounter history to indicate whether or not the tortoise was observed at least once in a given year (1 or 0) or to indicate that the population was not surveyed in that year (.). We excluded individuals whose sex was unknown (<1 % of adults) and aggregated encounter histories across populations to increase the precision of estimates (Litt and Steidl 2010).

We modeled effects of environmental features, survey effort, and sex on survival and recapture probabilities of adult tortoises in three steps. In the first step, we identified factors that we thought could influence survival, including sex, distance to nearest city (city), mean annual precipitation (mean.precip), and drought severity (drought) while maintaining a fully parameterized model for recapture probability. Although grazing and other anthropogenic activities that occur far from urban areas could affect survival of tortoises, we did not include these covariates in models for survival because no information on the frequency and intensity of these activities at each plot over the 22-year period was available. We related annual survival of adult tortoises to mean drought severity for the 12-month survival period plus the 12 preceding months; for example, we related survival between August 1995 and July 1996 to mean drought severity between August 1994 and July 1996. Because we hypothesized that the effect of drought severity on survival might vary among areas with different rainfall regimes, we evaluated the interaction between these two factors (mean.precip × drought) whenever both factors were included in a model. We also evaluated whether survival varied over time by including a linear trend (T) in a subset of models. We did not include perennial plant cover in models for survival because it was correlated with mean annual precipitation ($r = 0.72$). We then created 40 models for survival based on combinations of these factors while maintaining a model for recapture probability that included sex, perennial plant cover (PPcover), the number of 8-h person-days per annual survey (effort), and standardized precipitation for the 12-month period from August to July immediately preceding each annual survey (ann.precip; Appendix 1 in the Electronic supplementary material, ESM). We compared summed Akaike model weights (Σw_i) to assess the influence of each factor on survival, and retained only those factors with $\Sigma w_i \geq 0.5$ (Burnham and Anderson 2002). In the second step, we evaluated the relative importance of sex, PPcover, effort, and ann.precip on recapture probability with 16 models that included combinations of these factors while maintaining a fully parameterized model for survival (Φ[mean.precip + city + T + drought + sex + mean.precip × drought]; Appendix 2 in the ESM). We retained only those factors with $\Sigma w_i \geq 0.5$. In the third step, we created a set of candidate models that included all combinations of factors retained in the first two steps. We used Akaike's information criterion for small sample sizes (AIC_c) to rank models.

In three populations (EB, HF, MM), unusually high numbers of carcasses were found during one survey year, which varied among populations. To leverage the additional information provided by recovered carcasses, we estimated survival using joint live-encounter dead-recovery models (Burnham 1993). Unlike CJS models, joint live-dead models can separate mortality ($1 - S$, where $S =$ true survival) from emigration ($1 - F$, where $F =$ fidelity), while accounting for the probability of being recaptured alive (p) and the probability of being found dead (recovery probability, r). We were unable to aggregate encounter histories among populations because populations were surveyed in different years and could not include temporal covariates given added model complexity. Therefore, we modeled populations separately, assumed constant annual survival between successive survey years (i.e., within each survey interval), and evaluated a model that allowed annual survival, recapture probability, and recovery probability to vary among survey years (p, r) or survey intervals (S; S[t], p[t], r[t], F[.]).

Survival of subadults

Demographic studies of terrestrial turtles often exclude juvenile and subadult tortoises because recapture probabilities of young tortoises are typically much lower than those for adults (Averill-Murray and Averill-Murray 2005; Converse et al. 2005). Although data were not sufficient to explore survival of subadult tortoises as a function of environmental covariates as we did for adults, the number of tortoises encountered with MCL < 180 mm was sufficient to estimate survival reliably with less complex models in three populations surveyed in ≥8 years between 1987 and 2008 (ET, GH, LS). Similar to the approach we used to model survival of adults, we created encounter histories for all tortoises with MCL < 180 mm and aggregated histories among populations. We evaluated 16 CJS models where we allowed recapture probabilities and survival to be constant or to vary among populations, over time, or with a population × time interaction in all combinations, and model-averaged estimates from competing models (where $\text{AIC}_\text{c} < 4$).

Projected changes in survival and rate of population change in response to climate change

We used projections of mean annual precipitation and drought severity to predict annual survival of adult tortoises between 2035 and 2060 based on the highest ranking model in our candidate set that excluded a linear trend. We predicted drought severity across the 25-year period for each climate division in Arizona based on a model of projected PDSI for the western U.S. assuming a business-as-usual scenario for future carbon emissions (Hoerling and Eischeid 2007). We predicted mean precipitation for the same time period assuming continued dependency on fossil fuel consumption (A2 scenario) based on data obtained from the Bias Corrected and Downscaled World Climate Research Programme's CMIP3 Climate Projections archive (Bureau of Reclamation 2011).

We used current and projected estimates of survival to estimate rates of population change (λ). We estimated λ with a 2 × 2 stage-based Leslie matrix using estimates of adult and subadult survival (Φ_{adult} and Φ_{subadult}) from our CJS analyses. Although our estimates of Φ_{subadult} are likely biased high for small individuals that were captured infrequently (MCL < 90), we assumed that they reflected mean survival for all individuals with MCL < 180 mm because no other estimates were available. We calculated

Table 2 Cumulative weights (Σw_i) for variables included in 40 models for apparent survival (Φ) and 16 models for recapture probability (p) of Sonoran desert tortoises in Arizona, USA, 1987–2008

Factors	Σw_i	
	Φ	p
mean.precip	**1.00**	
PPcover		0.27
city	**1.00**	
sex	0.31	**1.00**
T	**0.98**	
drought	**1.00**	
effort		0.35
ann.precip		**0.94**
mean.precip × drought	**0.86**	

Bold values indicate factors included in a final set of candidate models

fecundity (F; number of female offspring female^{-1}, assuming a 1:1 sex ratio) based on published estimates of clutch frequency and clutch size for tortoises in central Arizona (Averill-Murray 2002). Because estimates of survival from hatching through the first year are unavailable for tortoises in the Sonoran Desert, we assumed that hatchling survival was the same as survival of subadults. We calculated transition rates (Ψ) between subadult and adult stage classes based on growth rates of 129 subadults that were recaptured at least once on the three plots that were used to estimate Φ_{subadult}. To estimate λ for the 22-year study period ($\lambda_{1987\text{–}2008}$), we used mean estimates of adult and subadult survival across all plots from our highest-ranking model. We used the predicted mean % change in adult survival between 1987–2008 and 2035–2060 to adjust estimates of both adult and subadult survival from the study period in calculations of λ for 2035–2060 ($\lambda_{2035\text{–}2060}$); we assumed no change in reproductive output under climate change scenarios. Finally, we generated 50,000 matrices for both $\lambda_{1987\text{–}2008}$ and $\lambda_{2035\text{–}2060}$, with matrix elements drawn at random from normal distributions for each parameter (Φ_{adult}, Φ_{subadult}, F, Ψ) based on calculated means and standard deviations. We determined the dominant eigenvalue for each matrix (λ), and calculated $\lambda_{1987\text{–}2008}$ and $\lambda_{2035\text{–}2060}$ as the means of their respective sampling distributions.

Results

Tortoise surveys

Between 1987 and 2008, 15 populations of Sonoran desert tortoises across Arizona were surveyed during a total of 77 survey years; on average, each population was surveyed during five different years (range = 4–9), with an average of four years between successive surveys (range = 1–11). Survey effort averaged 50 person days per population per survey year (95 % CI = 46–53; range = 11–86; Table 1). Across all populations, observers encountered 1,186 unique adult tortoises of known sex (Table 1); for the three populations surveyed $\geq$8 times each, observers encountered 245 subadult tortoises. On average, each adult tortoise was encountered in 2.34 survey years (95 % CI = 2.25–2.43; range = 1–9) and each subadult tortoise was encountered in 1.53 survey years (95 % CI = 1.42–1.63; range = 1–5).

Environmental covariates

Plots averaged 31.8 km from the nearest city (95 % CI = 20.0–43.7 km) in areas where cover of perennial plants averaged 27.0 % (23.0–30.9 %). Across all plots, 30-year mean annual precipitation averaged 303 mm year^{-1} (266–341 mm year^{-1}), but varied substantially among plots, with the most arid areas receiving <180 mm year^{-1} and the wettest areas receiving >430 mm year^{-1}. Precipitation and drought severity varied markedly over time and space, with annual rainfall ranging from 42 to 710 mm and annual drought severity ranging from −6.9 to 5.8. Although temporal variation in drought severity was similar across all five climate divisions (range of correlation coefficients = 0.57–0.92, all $P < 0.01$), drought conditions during the study period were consistently more severe in extreme northwestern Arizona (22-year mean = 3.06) than elsewhere (range = 0.24–1.30). Both annual precipitation and drought severity indicated that conditions were especially dry in the latter half of the study, particularly in 1996–1997 and 2002–2003 (Fig. 2).

Survival of adults

Five of the eight environmental, survey, and tortoise-related factors that we examined were associated with survival of adults and two with recapture rates (Table 2); these seven factors formed the basis for the set of 80 candidate models we developed to explore patterns in survival of tortoises (Appendix 3 in the ESM). A model that included all factors associated with survival and recapture probability (Φ [mean.precip + city + T + drought + mean.precip × drought], p [ann.precip + sex]) had considerably more support than the other candidate models (AIC$_c$ model weight = 0.80); we therefore based inferences on this model.

Between 1987 and 2008, annual survival of adult Sonoran desert tortoises was estimated to be 0.92 (SE = 0.01), with survival rates varying somewhat among populations (range = 0.87–0.97; Table 1). Survival was higher in populations farther from cities (Table 3); specifically, odds

Table 3 Estimates and 95 % confidence intervals on the logit scale for covariates from the highest-ranking model (Φ[mean.precip + city + T + drought + mean.precip × drought], p[ann.precip + sex]) describing variation in survival and recapture probability for adult Sonoran desert tortoises in Arizona, USA between 1987 and 2008

Parameter	Covariate	Estimate	95 % CI
Apparent survival (Φ)	mean.precip (mm)	−0.0050	−0.0074 to −0.0025
	city (km)	0.012	0.0066 to 0.0183
	T	0.043	0.0165 to 0.0698
	drought	−0.65	−0.989 to −0.319
	mean.precip × drought	0.0014	0.0003 to 0.0025
Recapture probability (p)	ann.precip (standardized)	−0.15	−0.265 to −0.044
	sex (male = 1)	0.49	0.236 to 0.749

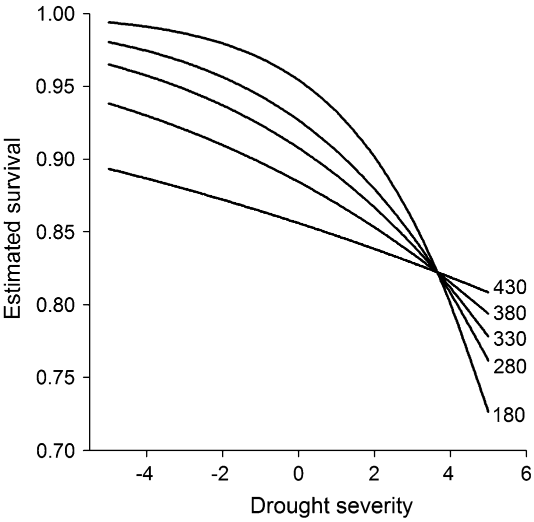

Fig. 3 Annual survival of Sonoran desert tortoises versus 24-month mean drought severity values for 15 populations in Arizona, USA, with mean annual precipitation ranging from 180 to 430 mm year^{-1}. Plotted values are based on predictions from the highest-ranking model used for inference (Table 3) after setting all other factors constant. *Positive values* of drought severity indicate drier than normal conditions, while *negative values* indicate wetter than normal conditions

of surviving one year increased 13 % (95 % CI = 7–20 %) for each 10 km increase in distance from a city. Mean annual precipitation and drought severity interacted to affect annual survival in a complex way. Although drought reduced survival of tortoises in all populations, effects were most severe for populations in the most arid regions (Fig. 3). When drought conditions were less than severe, however, survival was generally higher in more arid areas. After accounting for drought effects, there was a positive trend in annual survival of adult tortoises over the period of study, with odds of survival increasing by 4 % per year (95 % CI = 2–7 %; Table 3).

Recapture probability for adult tortoises averaged 0.77 (SE = 0.02) and was lower during years that followed 12-month periods of above-average precipitation. Odds of recapture decreased 14 % (95 % CI = 4–23 %) for every one standard deviation increase from average precipitation. Odds of recapturing male tortoises were 1.64 times greater (95 % CI = 1.27–2.12) than those of recapturing female tortoises in the same population.

In three populations, >24 % of marked tortoises were ultimately recovered dead, with ≥50 % of carcasses recovered during a single year. Annual survival varied with time in these populations, with substantially lower survival during one interval than all others. In two of these populations (EB, HF), periods of lowest survival (0.79, 0.81) coincided with periods of extreme drought, with drought severity during these periods plus the preceding 12 months equal to 4.09 and 4.08, respectively. With annual survival reduced to 0.77–0.81 for periods of 3–5 years, cumulative survival of adults during these periods was 0.30 (95 % CI = 0.05–0.56, EB), 0.34 (0.17–0.52, HF) and 0.46 (0.19–0.73, MM), indicating that abundance of adults was reduced by ≥50 % in each population.

Survival of subadults

Annual survival and recapture probabilities of subadult tortoises varied spatially ($\Sigma w_i = 0.80$ and 0.51 for models with variation in survival and recapture probabilities among populations, respectively; Appendix 4 in the ESM), but not temporally ($\Sigma w_i < 0.11$ for all models that included time or a population × time interaction for survival or recapture probability). Annual survival of subadults across all populations averaged 0.77 (SE = 0.05) and ranged from 0.73 (0.07) to 0.83 (0.03). Recapture probability across all populations averaged 0.41 (0.10) and ranged from 0.34 (0.12) to 0.45 (0.08).

Projected changes in survival and rate of population change in response to climate change

Drought severity during 2035–2060 (mean = 3.17, range = 2.50–4.50) is projected to be considerably higher than during 1987–2008 (mean = 1.11, range = 0.24–3.06), indicating increased drought frequency, severity, or both. In contrast, annual precipitation is projected to be similar to current levels. In 14 of 15 populations, annual survival of adult tortoises is projected to be 3 % lower on average (range = 1–5 %) during the period 2035–2060 (range = 0.83–0.93) relative to survival between 1987 and 2008 (0.87–0.97).

To assess the influence of reduced survival on the rate of population change, we decreased estimated rates of adult and subadult survival for the 22-year study period (0.92 and 0.77, respectively) by 3 % when calculating $\lambda_{2035\text{–}2060}$. We estimated average fecundity of tortoises to be 1.41 female offspring female^{-1} based on published estimates of clutch frequency and size, and estimated that an average of 7 % of subadult tortoises transition to the adult stage class each year, assuming a uniform size distribution across the entire subadult stage class (45 mm < MCL < 180 mm). Based on these values, we estimate that the rate of population change will decrease from 1.08 (95 % CI = 1.02–1.14) during 1987–2008 to 1.05 (95 % CI = 0.99–1.11) during 2035–2060.

Discussion

Demography of many reptile populations in arid environments is governed by short-term variation in rainfall, although the nature and strength of the relationship varies among taxa (Peterson 1994; Dickman et al. 1999; Longshore et al. 2003; Barrows 2006). For shorter-lived species, demographic parameters can fluctuate markedly among years, with populations recovering quickly after sharp declines when conditions are favorable (Barrows 2006). For longer-lived species, however, climatic events can have prolonged effects on populations because lower rates of reproduction and recruitment require longer periods to replace the loss of reproductive adults, even if survival of the remaining adults is high.

We found that survival of Sonoran desert tortoises was associated strongly and negatively with drought severity. Annual survival was generally high (mean = 0.92), as expected for a long-lived species, and was within the range of estimates reported for other populations in Arizona (0.89–0.97; Riedle et al. 2010) and populations of *G. agassizii* in the Mojave Desert (0.83–0.99; Berry 1986). The estimates we report likely reflect the prevalence of drought conditions in Arizona during the second half of the study, which, like much of the southwestern U.S., has been subject to moderate to extreme drought since the mid- to late-1990s (Cook et al. 2004; Fig. 2).

Effects of drought on survival of tortoises varied geographically, with more severe effects manifesting in the most arid regions. This pattern suggests that tortoises in these areas might be closer to their limits of drought tolerance. Despite numerous morphological, physiological, and behavioral characteristics that enable them to cope with arid environments, such as water storage in large bladders, tortoises require periodic rainfall to provide free-standing water to drink and to spur growth of the annual plants and grasses on which they forage (Nagy and Medica 1986; Duda et al. 1999). If tortoises are near their tolerance limits in these areas, prolonged drought could have adverse consequences for health, reproduction, and survival, because even in more mesic conditions tortoises carry negative water and energy balances for considerable portions of the year (Nagy and Medica 1986; Henen 1997). Drought can reduce survival of tortoises directly through dehydration or starvation when forage availability declines with reduced precipitation (Peterson 1994; Longshore et al. 2003). Alternatively, drought could reduce survival of tortoises indirectly by triggering physiological and behavioral stress responses that increase their susceptibility to disease or predation (Peterson 1994; Esque et al. 2010). Survival of tortoises could be reduced further if predators, such as coyotes *Canis latrans* or mountain lions *Puma concolor*, rely more on alternative prey such as tortoises when drought conditions reduce abundance of their preferred prey (Prugh 2005; Esque et al. 2010).

In three populations, annual survival of adult tortoises dropped by 10–20 % during 3–5 year periods. Although the proximate cause of death could not be determined for the majority of the carcasses, these increases in mortality were associated with regional drought severity in two of the populations and with a severe, localized drought that persisted for an eight-year period in the third population (Averill-Murray et al. 2002b). Given that precipitation is often localized and spatially stochastic in many desert areas (Noy-Meir 1973), episodic mortality in response to drought is not unexpected, and has been documented in previous studies of *G. agassizii* (Peterson 1994; Longshore et al. 2003) and other reptiles (Barrows 2006). In the populations we studied, survival rebounded within a few years after drought and remained high for the remainder of the study (4–15 years). If drought frequency or severity increases in the region, however, as predicted by several climate-change models (Cook et al. 2004; Hoerling and Eischeid 2007; Seager et al. 2007), recovery and persistence of tortoise populations could be affected adversely, especially in arid areas where populations are most vulnerable to drought effects.

Annual rates of adult survival and population change projected under likely climate-change scenarios averaged 3 % lower than rates observed during 1987–2008. If temporal variation in drought severity remains similar to what we observed (Fig. 2), we would expect survival to drop well below projected means during short periods of extreme drought. Projected declines in the rate of population change mirrored predicted declines in adult survival, reflecting the influence of adult survival on rates of population change for long-lived species. A 3 % decline in λ in response to increased drought severity associated with climate change could affect the persistence of some tortoise populations, particularly those in the most arid parts of their range.

Although rates of population change for long-lived chelonians are often most sensitive to changes in adult survival (Congdon et al. 1993; Doak et al. 1994), estimates of fecundity, juvenile survival, and recruitment are necessary to reliably gauge the long-term viability of these populations. Estimates of these vital rates are notoriously difficult to obtain for Sonoran desert tortoises because their nests are challenging to locate and juveniles are especially cryptic. The estimates of fecundity and transition rates we used to calculate λ in this study were based on relatively few data from 1–3 locations across the entire range of the Sonoran desert tortoise. Although borrowing estimates from similar species is common in population viability analyses (Beissinger and Westphal 1998), this would be problematic for desert tortoises because reproductive strategies of North American tortoises vary considerably among species (Germano 1994; Averill-Murray 2002). Therefore, to thoroughly understand population dynamics and provide the information required to inform future management and listing decisions (U.S. Fish and Wildlife Service 2010), reliable estimates of fecundity and juvenile survival need to be obtained for populations of Sonoran desert tortoises across their range, regardless of the inherent logistical difficulties.

In addition to variations in response to drought and annual rainfall, survival of adult tortoises varied geographically, with lower survival in populations closer to cities. Distance to cities is a proxy for an array of factors that are likely to be associated with intensity of human impact, including use of off-highway vehicles and recreational activities. Because Arizona is one of the fastest growing states in the U.S. (U.S. Census Bureau 2011), expansion of urban and suburban areas will continue to affect tortoise populations by reducing the quantity or quality of habitat for tortoises and other sensitive species. Despite some limitations, the results of this study can be used to gauge the effects of future changes in land use and environmental conditions, including climate, on tortoises and similar reptiles in arid environments.

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