Herpetological Conservation and Biology 13(2):433–452.
Submitted: 19 February 2018; Accepted: 24 June 2018; Published: 31 August 2018.

Population Trends in Mojave Desert Tortoises (*Gopherus agassizii*)

Linda J. Allison[1,3] and Ann M. McLuckie[2]

[1]*Desert Tortoise Recovery Office, U.S. Fish and Wildlife Service, Reno, Nevada 89502, USA*
[2]*Utah Division of Wildlife Resources, Washington County Field Office, 451 N SR-318, Hurricane, Utah 84737, USA*
[3]*Corresponding author, email: linda_allison@fws.gov*

***Abstract.*—Populations of the Mojave Desert Tortoise (*Gopherus agassizii*) experienced severe declines in abundance in the decades leading up to 1990, when the species was listed as threatened under the U.S. Endangered Species Act. Population responses to recovery efforts have not been well documented because of the difficulties of studying this low-density, cryptic species over a time period appropriate to its long generation time. We used line distance sampling to estimate annual adult densities since 1999 in Utah and since 2004 elsewhere in the range of Mojave Desert Tortoises. We used generalized least squares regression on log-transformed adult tortoise densities to estimate annual percentage change through 2014 in each of 17 Tortoise Conservation Areas (TCAs) in the five recovery units. We report annual proportional increases in density of adults in the Northeastern Mojave Recovery Unit, but declines in the other four recovery units. Adjusting these densities and trends for the area of potential habitat in each recovery unit, we estimated that in 2004 there were 336,393 adult tortoises (standard error [SE] = 51,596), with an overall loss of 124,050 adult tortoises (SE = 36,062) by 2014. The proportion of juveniles in our surveys has been decreasing in all five recovery units since 2007. Prevailing declines in the abundance of adults overall and in four of the five recovery units indicate the need for more aggressive implementation of recovery actions and more critical evaluation of the suite of future activities and projects in tortoise habitat that may exacerbate ongoing population declines.**

Key Words.—Colorado Desert; distance sampling; information theory; long-term monitoring; Mojave Desert; species recovery

Introduction

Turtles around the world face the highest level of endangerment of any vertebrate lineage today (Stanford et al. 2018). Historical extinctions and recent crises have characterized species on islands or with relatively localized and easily exploitable populations (Stanford et al. 2018). However, turtles as a group are vulnerable in part due to their shared life histories based on high adult survival, delayed age at first reproduction, and low rates of juvenile recruitment (Congdon et al. 1993; Stanford et al. 2018). Even tortoises with relatively large historical ranges are susceptible to threats with relatively small effects, in combination and acting over long generation times, and this life-history strategy also diminishes their ability to recovery quickly from population losses.

Populations of the Desert Tortoise (*Gopherus agassizii*, *sensu stricto*) experienced severe declines in abundance in the decades leading up to 1990, when populations in the Mojave and Colorado deserts west and north of the Colorado River were listed as Threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service [USFWS]1990). Murphy et al. (2011) split the full species into two: the Mojave Desert Tortoise (*Gopherus agassizii*) occupying the range north and west of the Colorado River (the same area listed as Threatened above and retaining this listing) and the Sonoran Desert Tortoise (*G. morafkai*) south and east of the Colorado River. Population responses to recovery efforts for *G. agassizii* have not been well documented, in part, because of the difficulties of studying this low-density, long-lived species. The current recovery plan (USFWS 2011) designates five recovery units for *G. agassizii* that are intended to conserve genetic, behavioral, and morphological diversity necessary for the long-term recovery of the entire listed species (Fig. 1). The recovery plan also defines criteria that form the basis for decisions about continued listing status. For instance, rates of population change of *G. agassizii* should be increasing for at least one tortoise generation (25 y) in all recovery units to warrant delisting (USFWS 2011).

Whereas *G. agassizii* (*sensu stricto*) were initially protected on the basis of population declines estimated on a limited number of small, selectively located mark-recapture study plots, over the longer term, status descriptions should be based on more extensive and rigorous population estimates (Tracy, R.C., R. Averill-Murray, W.I. Boarman, D. Delehanty, J. Heaton, E. McCoy, D. Morafka, K. Nussear, B. Hagerty, and

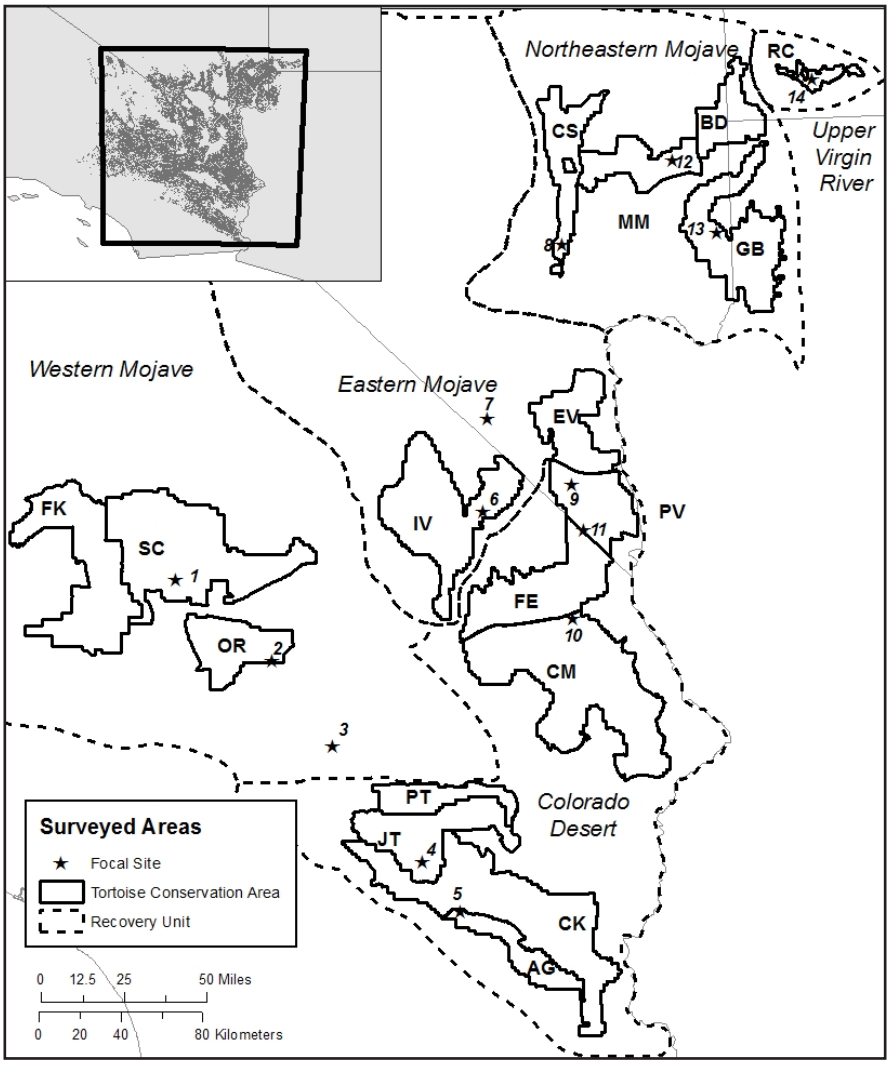

Figure 1. Tortoise Conservation Areas (TCAs, n = 17) for Mojave Desert Tortoises (*Gopherus agassizii*) that were monitored in the Mojave and Colorado deserts, USA. Sites were monitored through 2014 and began in 2004 except in the Red Cliffs Desert Reserve, where surveys started in 1999. TCAs and their codes are Chocolate Mountains Aerial Gunnery Range (AG), Beaver Dam Slope (BD), Chuckwalla (CK), Chemehuevi (CM), Coyote Springs Valley (CS), Eldorado Valley (EV), Fenner (FE), Fremont-Kramer (FK), Gold Butte-Pakoon (GB), Ivanpah (IV), Joshua Tree (JT), Mormon Mesa (MM), Ord-Rodman (OR), Pinto Mountains (PT), Piute Valley (PV), Red Cliffs (RC), Superior-Cronese (SC). Observations to estimate visibility were made of transmittered tortoises at the numbered focal sites: 1) Superior-Cronese, 2) Ord-Rodman, 3) Twentynine Palms, 4) Joshua Tree, 5) Chuckwalla, 6) Ivanpah, 7) Jean, 8) Indian Springs, 9) Piute Valley 1, 10) Chemehuevi, 11) Piute Valley 2, 12) Halfway Wash, 13) Gold Butte, 14) Red Cliffs. Potential habitat as defined in the text is overlain on the southwestern United States in the extent indicator.

P. Medica. 2004. Desert Tortoise Recovery Plan Assessment. Report to the U.S. Fish and Wildlife Service, Reno, Nevada. Available from http://www.fws.gov/nevada/desert_tortoise/documents/dtrpac/dtrpac_report.pdf [Accessed 15 August 2018]). In 1999, agencies cooperating on recovery of *G. agassizii* adopted distance sampling (Buckland et al. 2001) for estimating population density at large spatial scales. Surveyors use distance sampling to account for the proportion of the population that is not observed at increasing distances from the observers. We conducted distance sampling surveys for *G. agassizii* throughout Tortoise Conservation Areas (TCAs; Fig. 1), which include federally designated critical habitat for the species (USFWS 1994), as well as in contiguous areas with conservation designations and suitable tortoise habitat (Nussear et al. 2009). Most recovery units (USFWS 1994, 2011) contained more than one TCA (Fig. 1). Ongoing monitoring for *G. agassizii* based on distance sampling has been conducted since 1997 in the Upper

Virgin River Recovery Unit by the Utah Division of Wildlife Resources and by the USFWS in the remaining four recovery units starting in 2001.

In this paper, we start by developing annual density estimates for each TCA based on distance sampling. These efforts are typically collaboratively funded with each agency requiring annual reports that include annual population estimates. Our second and primary goal herein was to use these annual estimates to describe adult *G. agassizii* population trends for each TCA and recovery unit. These trends must account for precision of annual estimates that is often low, variable, and correlated between TCAs within years. Although we cannot fully evaluate the recovery criterion that requires increasing population numbers in each recovery unit until at least 25 y of surveys have been completed (USFWS 2011), this monitoring program is part of the adaptive management strategy for recovering *G. agassizii*. Our third goal was to use the interim regional population trends to evaluate the effectiveness of the recovery program. Our fourth goal was to characterize future trajectories for these populations based on changing patterns of relative abundance of juveniles.

Materials and Methods

Study areas.—*Gopherus agassizii* occur throughout large, continuous regions of the Mojave and Colorado deserts of North America (Fig. 1). They occupy a broad elevational range (sea level to 2,225 m) from valley bottoms and bajada slopes at lower elevations to upper alluvial and mountain slopes at higher elevations (Luckenbach 1982). Typical habitat for *G. agassizii* is Creosote Bush (*Larrea tridentata*) scrub in association with White Bursage (*Ambrosia dumosa*) but they are also found in Joshua Tree (*Yucca brevifolia*) woodland, Blackbrush (*Coleogyne ramosissima*) scrub, microphyll woodlands, Shadscale (*Atriplex confertifolia*) scrub, saltbush (*Atriplex* spp.) scrub, cactus scrub, and warm season grassland (Germano et al. 1994; Nussear et al. 2009). Throughout their range, tortoises inhabit areas that include deeply incised washes, sandstone outcrops, rugged rocky canyons, and basalt-capped ridges interspersed with sandy valleys (Bury et al. 1994). However, tortoises most commonly occur in areas with gentle slopes, sufficient shrub cover, and friable soils to allow burrow construction (Bury et al. 1994).

Starting in 1997 in Upper Virgin River Recovery Unit and in 2001 elsewhere, we surveyed 17 TCAs across the five recovery units (Fig. 1). We did not survey every TCA every year, but the total area of 29,127 km^2 comprises the long-term monitoring frame (Table 1). The TCAs named for Red Cliffs Desert Reserve (RC) and Joshua Tree National Park (JT) exclude portions of these jurisdictions that were not potential tortoise habitat (USFWS 1994); RC also excluded a portion that was used for translocations of wild tortoises displaced by development. Each year we made behavioral observations on tortoises at up to 11 of the 14 focal sites within the overall study area (Fig. 1) to estimate the proportion of tortoises that were potentially visible to transect surveyors.

Data collection.—Initially, we placed transects randomly within each TCA. In RC, these were permanent transect locations from the beginning of the program, and we surveyed the 153 transects annually between 1999 and 2001, then every other year. Between 2001 and 2003 in the rest of the range, there was restricted sampling based on various environmental criteria (USFWS 2006), so for comparability we only used data collected starting in 2004 when transects were sited at random throughout TCAs. Beginning in 2007 in these areas outside RC, we shifted from strictly random placement to random selection from a set of systematically placed transects that covered each TCA. Both of these methods result in transects that were located at random with respect to the location of tortoises, so the resulting annual density estimates are unbiased. Each year, available funding determined the number of transects assigned in each TCA.

Sampling methods we used adhered to study design considerations for distance sampling (Anderson, D.R., and K.P. Burnham. 1996. A monitoring program for the desert tortoise. Report to the Desert Tortoise Management Oversight Group. Available from https://www.fws.gov/nevada/desert_tortoise/documents/reports/Anderson-Burnham.1996.monitoringplan.pdf. [Accessed 15 August 2018]). We based initial transect and overall survey length on preliminary estimates of encounter rate and associated effort required to estimate density with a coefficient of variation (CV) of 0.10–0.15. We modified the number and length of transects as specified in Buckland et al. (2001) during earlier years of the surveys and based on updated information about encounter rates.

We completed surveys between mid-March and the end of May each year, when preferred food plants flower and *G. agassizii* are generally active outside of burrows. We started transects early enough so surveys would be completed before the hottest time of the day, scheduling survey dates in specific TCAs to correspond to peak daily tortoise activity based on past experience as well as observation of tortoises outfitted with radio-transmitters (see below). Surveys generally started around 0800 during March but started as early as sunrise by the beginning of May.

Generally, each two-person team walked one transect each day, using a compass and pre-specified bearings. Standard transects were 12 km long, walked in a

Table 1. Tortoise Conservation Areas within each Recovery Unit including total area (km²) and total effort (km) by year. Tortoise Conservation Areas (with acronym; Acr) are grouped under corresponding larger recovery units. Red Cliffs Desert Reserve was also surveyed in 1999 (307 km), 2000 (302 km), 2001 (314 km) and 2003 (309 km).

Tortoise Conservation Area	Acr	Area (km²)	2004	2005	2007	2008	2009	2010	2011	2012	2013	2014
Colorado Desert		13,530	3,319	3,984	2,007	1,348	1,375	2,383	1,316	1,403		
Chocolate Mtn Aerial												
Gunnery Range	AG	755	331	228	404	158	378	378		363	413	554
Chuckwalla	CK	3,509	1,083	866	747	112		613	280	213		
Chemehuevi	CM	4,038	836	1,129	180	84	119	458	354	176		
Fenner	FE	1,841	410	288	178	108	121	246	179	168		
Joshua Tree	JT	1,567	278	601	135	102	240	227	147	183		
Pinto Mountains	PT	751	56	155	131	72	162	213	118	140		
Piute Valley	PV	1,070	325	717	231	713	355	249	239	159		
Eastern Mojave		3,720	876	620	368	714	548	578	746	639		
Eldorado Valley	EV	1,153	361	452	188	594	427	212	331	320		
Ivanpah	IV	2,567	515	168	180	120	120	365	416	318		
Northeastern Mojave		4,889	1,037	1,489	2,304	1,485	4,154	4,265	3,984	4,184		
Beaver Dam Slope	BD	828		421	478	2578	631	662	751	819	683	
Coyote Springs Valley	CS	1,117	365	237	906	1,592	1,504	1,046	967	996		
Gold Butte-Pakoon	GB	1,977	361	432	300		733	1,258	1,039	1,116	923	
Mormon Mesa	MM	968	311	398	621	691	1,286	1,298	1,227	1,253		
Western Mojave		6,873	1,534	1,979	896	599	1,351	2,144	1,257	876		2,095
Fremont-Kramer	FK	2,417	463	661	300	216	361	566	264	193		815
Ord-Rodman	OR	1,124	381	310	141	102	197	270	174	158		472
Superior-Cronese	SC	3,332	690	1,009	456	281	793	1,307	820	525		808
Upper Virgin River		115		305	308		310		310		314	
Red Cliffs Desert Reserve	RC	115		305	308		310		310		314	

square that was 3 km on each side. Where relatively open creosote-bursage alluvial slopes dominated the landscape, we found that repeated searching near the centerline did not improve encounter rates or detection on the line (USFWS 2006), so we did not mark the transect centerline for additional search effort. Instead, the leader surveyed along a straight path with a 25-m cord trailing behind. The second observer followed at the end of the moving cord and searched independently. The cord served as the transect centerline when taking distance measurements, and we calculated the walked length of these transects as the straight-line distance between GPS point coordinates that were recorded approximately 500 m apart along the transect.

In RC, where terrain rendered tortoises less visible, surveyors used a three-pass survey to effectively search on and near the marked transect centerline. One crew member, Observer A, dragged the end of the 50-m surveyor tape, following the transect bearing to its intended location. Observer A then walked in a sinusoidal pattern back toward the beginning of the tape searching for tortoises on one side of the tape while the other crew member walked in a similar sinusoidal pattern on the opposite side. Observer A then searched directly along the tape back to the end. The process repeated itself, with the roles of the two surveyors reversing each time. This intensive searching and the rugged terrain limited transects to 2 km per team each day.

We measured the distance and bearing of the tortoise to the observer on the center line in order to calculate the perpendicular distance of the tortoise to the transect center line. We measured distances with 30-m fiberglass or 50-m surveyor tapes, and we measured bearings with compasses. We used all observations of tortoises > 180 mm carapace length (CL) to develop detection curves and density estimates, whether tortoises were in burrows, in the open, or under vegetation. When tortoises were on the surface or could be easily extracted from burrows, we recorded CL and sex. Without suggesting that there is a single size threshold for reproduction within or between populations (Germano 1994), we refer hereafter to tortoises that are at least 180 mm CL as adults and smaller tortoises as juveniles.

Because we placed transects at random with respect to terrain and human infrastructure, and because standard transects were 3 km on each side, it was not unusual for the surveyed path to cross through varied terrain or be blocked by an obstacle such as a highway.

The rules for modifying transects in these situations involved reflecting or elongating transects to avoid obstacles associated with human infrastructure (large roads, private inholdings, etc.), or shortening transects in rugged terrain. The sampling frame therefore represented the walkable area of each TCA. Transects that were partially outside TCA boundaries were initially completed without regard for these jurisdictional changes, but where the boundary was impassable, we reflected transect segments into TCAs as needed (Buckland et al. 2001) or pivoted shorter transects in RC on their northeastern corner to fit inside the TCA. By 2010 we reflected transects so that all paths were inside TCAs.

We used behavioral observations of tortoises carrying radio transmitters (Boarman et al. 1998) to estimate the proportion of individuals available to be seen above ground or in burrows during transect surveys, G_0 (Anderson and Burnham, *op. cit*.). Telemetry technicians used a VHF radio receiver and directional antenna to locate radio-equipped tortoises (n = 5–30) at each focal site (Fig. 1) during the same daily time period when field crews were walking transects in that region of the desert. Observers completed a survey circuit of all transmittered animals as many times as possible (range, 0–5 times per day) during the allotted time, recording each time whether the tortoise was visible.

Estimation of annual tortoise density in each TCA.—We used distance sampling (Buckland et al. 2001) to develop density estimates based on encounter rates in each TCA adjusted for imperfect detection of animals farther from the transect centerline. Estimates were developed each year separately for reporting to sponsoring agencies. We used Program DISTANCE, 6.2 (Thomas et al. 2010), to estimate P_a, the proportion of adult *G. agassizii* detected within w meters of the transect centerline. We truncated observations by distance from the centerline to improve model fit as judged by the simplicity of the resulting detection function (Buckland et al. 2001). Truncation typically reduced the number of observations overall by 5% or fewer, improving estimates of detection probability but reducing the number of observations to estimate encounter rate in each TCA. Sample size considerations also contributed to our decision to rely on pooling robustness (Buckland et al. 2001) rather than using covariates to model detection function estimates (Marques et al. 2007). Detection function estimation is robust in the face of pooling data from different observers, on different days, and in different areas (Buckland et al. 2001) as long as factors that cause variability in detection probability are represented proportionately (Marques et al. 2007). Such factors include vegetation that differentially obscures vision with distance and different detection patterns characteristic of individual crews (pairs). Crews on the same team walked the same number of transects although crews on different teams might not. For these reasons, we placed transects at random in each TCA and developed separate detection curves each year for each field team, pooling data from all TCAs surveyed by that team. Teams also correspond to regions of the desert, and years are correlated with precipitation conditions that affect spring vegetation height and cover, so detection curves that are created separately for teams and years also indirectly address additional factors that affect detection. In years when a team surveyed both in the Mojave and the Sonoran deserts, where the vegetation types may affect tortoise detection differentially, we used two separate detection curves if the sum of their AIC values was less than the AIC value for the single detection curve for the team. In RC, where the same transects were walked each year, we used a single detection curve for all years of the study. Although we pooled observations from multiple TCAs (or from multiple years in RC) for each detection curve, we estimated adult tortoise encounter rates (n/L) and the variance of n separately for each TCA each year.

The distance to which observations were truncated, w, determined the reported area searched in each TCA, $2wL$, where L is the total length in kilometers walked. We applied Akaike's Information Criterion (AIC) to select among detection-function models (uniform, half normal, and hazard-rate) and key function/series expansions recommended in Buckland et al. (2001). Where more than one model were strongly supported by the data, we selected on the basis of Chi-square goodness-of-fit statistics near the transect centerline.

If there is imperfect detection on the transect centerline, a further correction factor must be applied to estimate the true density of tortoises. Because transects in RC used a three-pass method to search the centerline, we assumed that all tortoises at the transect centerline were detected. Elsewhere, detections by two observers walking the centerline one after the other allowed estimation of the detection probability for tortoises within increasing distances from the transect centerline as for a two-pass removal estimator (White et al. 1982); this provides a test of the assumption that all tortoises on the transect centerline are recorded ($g(0) = 1$).

We used a final correction factor, G_0, to adjust the density estimate to account for tortoises hidden in burrows in addition to those that were visible. Each bootstrapped estimate of G_0 was based on one randomly selected visibility record for each tortoise outfitted with a radio transmitter on each day it was located. We generated 1,000 bootstrap samples in PASW Statistics (release 18.0.2, SPSS, Inc. Chicago, Illinois, USA) to estimate G_0 and its standard error by site.

Annual density in each TCA was estimated as:

$$D = \frac{n}{2wLP_aG_0g(0)}.$$

Whereas n and L were estimated separately for each TCA, observations from multiple TCAs were used to generate a single estimate of P_a. We also applied estimates of G_0 to more than one TCA, and we based estimates of $g(0)$ on all observations from the two-pass surveys. This pooling of information can lead to covariance between TCA estimates in a given year (see below). Although two of the correction factors have similar symbols, when the parameter symbol involves a capital letter (G_0), we are referring to the proportion visible; the lower-case letter refers to the probability of detection of visible tortoises at the centerline.

Describing trends in adult tortoise densities.—We used R 3.4.1 (R Core Team 2017) to develop marginal models (Pinheiro et al. 2017) describing the natural log of tortoise density per km^2 as a function of year and location. Logarithmic transformations have a special interpretation when modelling trends; a modest linear trend in a logarithmic quantity represents a proportional change rather than a linear one (Keene 1995). A slope of 0.05 for ln(density) regressed on years, for instance, would be interpreted as a 5% increase per year. Our models included TCA, Year, and Year^2. Year was centered before modeling (Schielzeth 2010). Year^2 was included to capture any curvilinear population responses, and we anticipate modeling additional polynomial terms in the future when we are considering a longer time period. The full model also included two-way interactions between TCA and the linear and quadratic time factors. We used generalized least squares regression to also weight annual density estimates based on their variance and to add covariance structure to account for sets of density estimates that were inherently correlated because they shared correction factors of P_a or G_0 (Pekar and Brabec 2016). This second level of analysis therefore incorporated information about the first-level (annual density) variances and covariances.

We used a model based on the full suite of fixed effects to select among different variance weighting and covariance structures (Zuur et al. 2009). We used model selection procedures based on second-order AIC (AIC_c, Burnham and Anderson 2002; Mazerolle 2015) to decide whether to weight the analysis by the variance or CV of the annual density estimates. We also considered whether to model correlations among residuals for density estimates from the same Year, or due to use of pooled G_0 and P_a estimates for multiple TCA density estimates (see above). For all subsequent tests of potential fixed-effects models, we selected a covariance structure to account for within-Year correlation of residuals and weighted optimization procedures as a function of the CV of annual density estimates.

With the final variance weighting and correlation structures in place, we used AIC_c for selection among alternative models and examined the fit of the best model using marginal r^2 (Nagelkerke 1991). We used ANCOVA to examine whether slopes and intercepts of TCAs in each recovery unit described the same pattern (Zar 1996). To apply tortoise densities from the TCAs to entire recovery units, we estimated the area of potential habitat in each of the five recovery units based on Nussear et al. (2009). We only considered 1-km^2 grid cells assigned a probability of occupancy > 0.5 as potential habitat (Liu et al. 2005) after removing any area identified as an impervious surface (Fry et al. 2011).

Describing trends in representation of juvenile size class.—During surveys, we noted all observed tortoises of any size; however, smaller tortoises were less detectable than adults and there were too few observations of smaller tortoises to make density estimates based on distance sampling. Instead, to complement our analysis of changes in the abundance of adult tortoises, we used mixed effects logistic regression (Bates et al. 2015) to evaluate the relative proportion of juvenile tortoises detected in each recovery unit, fitting the observations to models including Year, Year^2, Recovery Unit, and two-way interactions between Recovery Unit and the time factors as predictors. We also included the categorical form of Year as a random factor to account for any enforced correlation across the recovery units in proportion of juveniles present due to annual conditions. Because we observed many fewer juvenile tortoises than adults, we report results at the larger spatial scale of the recovery unit rather than for each TCA. Tortoises that could not be extracted from burrows were often classified as unknown rather than as adults or juveniles, especially earlier in the study period. We conservatively assumed all unclassified tortoises were adults, so that estimates of the proportion of juvenile observations earlier in the time series were not inflated. Lacking information on detectability of juveniles to correct our raw data, the relative proportion of juveniles that we examined reflected their representation among detected animals, not the actual proportion of juveniles in the population. We used AIC for model selection, weighting, and averaging (Barton 2015). Note that because the continuous input variable Year was standardized to a mean of zero and divided by two standard deviations before model development (Schielzeth 2010), we could consider models with the quadratic form of this variable even if the linear form was not present in the model; this is equivalent to assuming opposing trends at the start and end of the study period

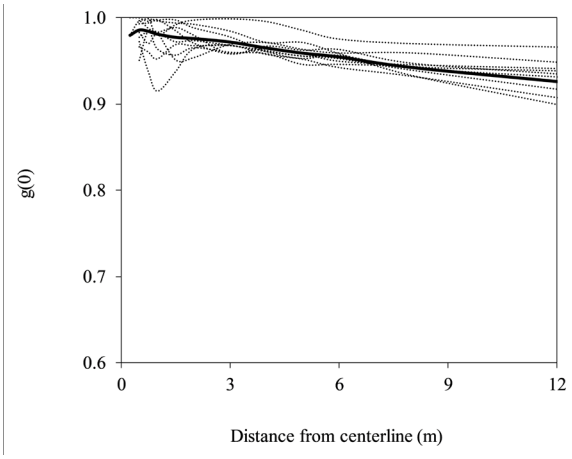

Figure 2. Detection of Mojave Desert Tortoises (*Gopherus agassizii*) at the transect centerline (*g(0)*) based on all two-pass survey observations as remote as x meters from the transect centerline. Dotted lines are annual curves; solid line is overall pattern across years from 2004 through 2014 (no surveys conducted in 2006). Note the convergence of *g(0)* on 1.0 as x goes to 0.

but no average trend overall. This standardization also allowed us to use model averaging on interaction terms (Schielzeth 2010). For models describing Year^2 effects, the inflection point at which trends shifted between increases and decreases in the odds of encountering juveniles on surveys was estimated as $-\beta_{Year}/2\beta_{Year}{}^2$.

Results

Adult densities and trends.—Annual probability of detection within 2 m of the transect centerline varied from 0.95 to 1.00, and converged on *g(0)* = 1.0 (Fig. 2), so we added no *g(0)* correction to annual density estimates. In contrast, although estimated tortoise visibility (G_0) was generally greater than 0.80, it was estimated as low as 0.35 at Chemehuevi in 2012 (Fig. 3, Appendix A), illustrating the degree of bias possible if tortoise density estimates do not include corrections for tortoises unavailable for detection. Some of our focal sites were consistently characterized by more above-ground activity than others (Fig. 3). The half-strip width, w, was generally between 12 and 22 m (Appendix B). Detection rate, P_a, was 0.64 in RC and averaged 0.45 in the other TCAs, where two-pass surveys were implemented; however, whether two- or three-pass sampling was used, the detection shoulder near the centerline consistently indicated nearly complete detection out to 2 m (10% of w) as recommended by Buckland et al. (2001).

Annual density estimates ranged from 0.2 adult tortoises/km^2 (SE = 0.2) in GB in 2005 to 28.0/ km^2 (SE = 4.0) in RC in 2000 (Table 2). During the first years reported here (2004 and 2005), TCAs in the Northeastern Mojave Recovery Unit had lower mean densities (< 5.0/

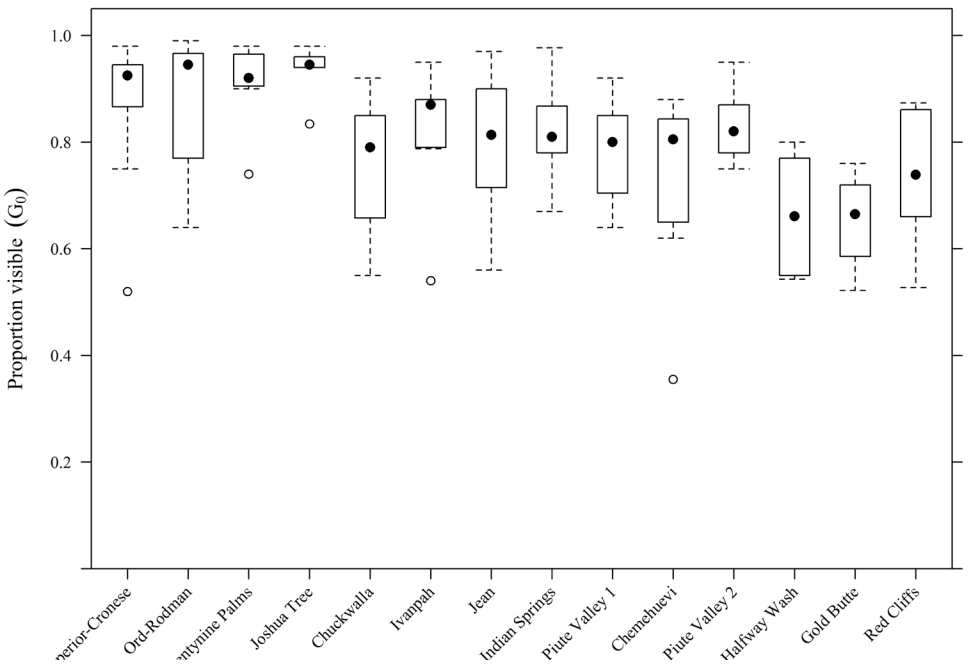

Figure 3. Box and whisker plots indicating the proportion of adult Mojave Desert Tortoises (*Gopherus agassizii*) visible (G_0) at each of 14 focal sites shown in Fig. 1 during transect surveys from 1999 through 2014. Boxes represent the interquartile range (values from the 25th – 75th percentile), crossed by a heavy bar at the median. Dotted-line whiskers indicate the extent of the 12.5–87.5 percentile, with any values outside this range shown as hollow dots below some whiskers. Sites are ordered from west on the left to east. Not all focal sites were used to correct density estimates each year. For instance, only Red Cliffs was monitored before 2004, and Jean was used in only one year of observation.

Table 2. Densities (n/km^2) of adult Mojave Desert Tortoises (*Gopherus agassizii*) and corresponding standard errors (SEs) in each Tortoise Conservation Area (TCA) from 2004 to 2014. Acronyms for TCAs are given in Table 1. RC was also surveyed earlier: 1999 (34.3, SE = 11.32), 2000 (25.7, SE = 5.61), 2001 (24.4, SE = 5.69), 2003 (14.0, SE = 2.79).

TCA within Recovery Unit	Year									
	2004	2005	2007	2008	2009	2010	2011	2012	2013	2014
Colorado Desert										
AG	11.4 (3.55)	13.4 (4.31)	6.5 (1.50)	4.5 (2.56)	7.5 (2.74)	13.8 (3.52)		6.0 (1.84)	7.3 (1.96)	8.4 (2.09)
CK	4.9 (1.49)	6.0 (1.77)	4.3 (1.19)	4.2 (2.84)		3.7 (1.14)	3.9 (1.37)	3.9 (1.62)		
CM	6.7 (1.27)	10.3 (3.10)	3.9 (1.71)	4.8 (3.07)	9.4 (5.98)	4.2 (1.40)	4.0 (1.51)	0.8 (0.90)		
FE	8.2 (1.94)	13.5 (2.80)	6.2 (2.37)	6.6 (3.05)	8.3 (4.01)	6.9 (2.49)	6.8 (2.78)	0.9 (0.95)		
JT	1.9 (0.53)	2.7 (0.79)	3.0 (1.94)	2.3 (1.75)	2.3 (1.56)	2.8 (1.56)	3.5 (1.33)	3.4 (1.63)		
PT	2.2 (2.12)	9.9 (3.58)	1.9 (0.98)	3.3 (3.53)	4.3 (2.38)	3.4 (1.85)	3.3 (1.39)	3.7 (1.57)		
PV	2.9 (1.13)	3.7 (0.90)	4.1 (1.88)	4.1 (1.28)	3.6 (1.64)	3.8 (1.37)	6.6 (2.62)	1.9 (1.46)		
Eastern Mojave										
EV	2.6 (0.94)	5.0 (1.25)	4.1 (1.69)	1.8 (0.85)	3.8 (1.56)	1.0 (0.62)	2.8 (1.13)	0.9 (0.74)		
IV	4.4 (1.19)	4.4 (2.46)	5.6 (1.95)	5.1 (2.92)	4.1 (1.86)	1.0 (0.48)	4.5 (1.72)	2.8 (1.79)		
Northeastern Mojave										
BD		0.9 (0.49)	1.1 (0.57)	1.1 (0.59)	3.2 (1.61)	3.3 (0.93)	3.3 (1.22)	5.4 (1.60)	2.6 (1.06)	
CS	1.3 (0.54)	3.3 (1.23)	1.4 (0.47)	1.2 (0.37)	2.0 (0.74)	3.6 (0.87)	4.0 (0.88)	2.9 (0.66)		
GB	0.6 (0.34)	0.2 (0.18)	1.1 (0.58)		2.2 (1.14)	1.7 (0.61)	1.6 (0.58)	2.3 (0.74)	1.7 (0.68)	
MM	2.4 (0.88)	4.9 (1.37)	3.0 (0.93)	1.9 (0.73)	7.3 (2.83)	5.5 (1.15)	6.3 (2.10)	4.3 (1.30)		
Upper Virgin River										
RC		22.5 (4.59)	22.1 (10.76)		15.5 (3.74)		19.3 (4.14)		18.3 (5.58)	
Western Mojave										
FK	8.4 (2.31)	5.3 (1.28)	3.0 (1.46)	0.5 (0.51)	3.3 (1.13)	2.4 (0.60)	3.5 (1.11)	2.2 (1.07)		4.7 (1.05)
OR	7.3 (2.25)	7.7 (1.80)	7.1 (3.26)	5.0 (5.34)	7.2 (2.65)	7.5 (1.85)	3.2 (1.18)	4.6 (2.14)		3.5 (0.88)
SC	6.3 (1.84)	6.3 (1.32)	5.9 (2.28)	1.9 (1.19)	4.6 (1.12)	2.6 (0.49)	3.4 (0.79)	4.3 (1.41)		2.5 (0.60)

km^2) than TCAs in other recovery units. Each year we surveyed RC, it consistently had the highest densities of adult tortoises.

The best model to describe variation in adult tortoise densities supported the hypothesis that densities changed proportionally over time, with different linear trends in each TCA (Table 3). Models based on linear trends had strong support (cumulative model weights = $\sum w$ = 0.9996; Table 3), whereas those including quadratic effects of time had essentially no support ($\sum w < 0.0001$). We report tortoise trend estimates based only on the best-performing model, with $w > 0.999$ and describing a large amount of variation in $\log_e$(Density). Estimates of r^2 (marginal r^2 = 0.84, Nagelkerke's modified r^2 = 0.92) indicated that after weighting to address variance heterogeneity and building in covariance structure, there was considerable variance in adult densities that could be explained by the effects of Year, TCA, and their interaction. Covariance between TCA density estimates from the same year accounted for 17.0% of the total

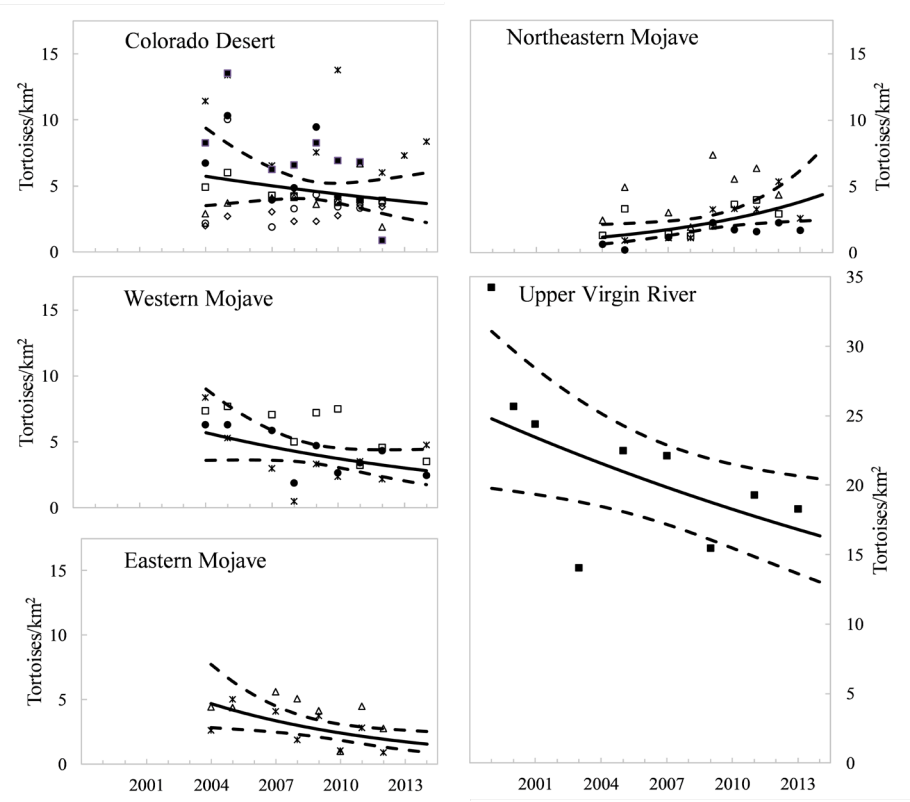

Figure 4. Trends in density (tortoises/km^2) of adult Mojave Desert Tortoises (*Gopherus agassizii*) in each recovery unit through 2014: since 1999 for Upper Virgin River Recovery Unit and for all others since 2004. Separate markers are used for annual density estimates for each tortoise conservation area within the recovery unit. The modeled change in density is the bold line and its 90% CI is shown with the dashed line, reflecting the Type I error specified in U.S. Fish and Wildlife Service (2011).

variance. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

Densities of adult *G. agassizii* were declining, on average, in every recovery unit except the Northeastern Mojave (Table 4, Fig. 4). Average density of adult tortoises increased in the Northeastern Mojave Recovery Unit at 13.1%/y (SE = 4.3%) since 2004, with especially large rates of increase (> 13%/y) estimated in BD and GB. Adult densities in the other four recovery units have declined at different annual rates: Colorado Desert (-4.5%, SE = 2.8%), Upper Virgin River (-3.2%, SE = 2.0%), Eastern Mojave (-11.2%, SE = 5.0%), and Western Mojave (-7.1%, SE = 3.3%). Based on analysis of covariance, three of the four recovery units with more than one TCA could be characterized by common regression slopes (Eastern Mojave: $F_{1,12} = 0.305$, $P = 0.591$; Western Mojave: $F_{2,21} = 0.094$, $P = 0.910$; Northeastern Mojave: $F_{3,24} = 1.206$, $P = 0.317$; Colorado Desert: $F_{6,43} = 2.391$, $P = 0.044$), but intercepts indicate different initial densities in two of the recovery units (Eastern Mojave: $F_{1,13} = 2.560$, $P = 0.134$; Western Mojave: $F_{2,23} = 3.326$, $P = 0.054$; Northeastern Mojave: $F_{3,27} = 11.073$, $P < 0.001$; Colorado Desert: $F_{6,49} = 5.090$, $P < 0.001$). The estimates we report above and in Table 4 are therefore total regression results for the Colorado Desert and Northeastern Mojave recovery units to characterize this greater within-recovery unit variation in slopes and/or intercepts, but common regression results for the other recovery units. Slopes differed between recovery units ($F_{4,119} = 9.422$, $P < 0.001$).

We applied estimated recovery unit densities based on TCAs to all potential habitat in each recovery unit, developing a high-end estimate of abundance for each recovery unit in 2004 and 2014 (Table 5). Despite the increasing population trend of adults in the Northeastern Mojave, its small area and low starting density resulted in a relatively small overall increase in the number of adult tortoises by 2014. In contrast, the much larger areas of the Eastern and Western Mojave and Colorado Desert recovery units, plus the higher estimated initial densities in these areas, explain much of the estimated total loss of adults since 2004. We estimate there were 124,050 fewer adult tortoises (SE = 36,062) range-wide in 2014 compared to the 336,393 tortoises (SE = 51,596) present in 2004.

Changes in representation of juvenile size class.— The full model of spatial and temporal effects describing the proportion of juveniles among observed tortoises

Table 3. Model selection table for all models fit to log-transformed annual densities of adult Mojave Desert Tortoises (*Gopherus agassizii*) through 2014 for all Tortoise Conservation Areas (TCAs), starting in 1999 for Red Cliffs Desert Reserve and in 2004 for the remaining 16 TCAs. Model weights (*w*) express the relative support for each model given the data and are based on relative scores for the second order Akaike's Information Criterion (AIC_c).

Model	Log likelihood	AIC_c	ΔAIC_c	*w*
TCA + Year + TCA×Year	-42.2	186.0	0.0	0.9996
TCA + Year	-76.7	203.2	17.2	0.0002
TCA	-78.4	203.9	17.9	0.0001
TCA + Year + Year^2	-76.0	204.7	18.7	0.0001
TCA + Year + Year^2 + TCA×Year + TCA×Year^2	-25.6	229.2	43.2	0.0000
Year + Year^2	-150.0	312.7	126.7	0.0000
Year	-155.3	321.1	135.1	0.0000
Random effects only	-160.3	329.0	143.0	0.0000

reduced the unexplained variance by 30.6% compared to the model of an overall average proportion, accounting for intra-year correlated proportions. Although the model with only Recovery Unit as a fixed effect had the lowest AIC, there was considerable support for models other than the top-ranking one (Table 6). The next five ranked models added Year or Year^2 effects and were within five AIC units of the best model; the cumulative weight of the top six models was > 0.95. As expected based on the ranked models, model-averaged parameter estimates indicated that the odds of finding a juvenile tortoise differed primarily between recovery units, with a weaker pattern of change over time (Table 7). This analysis approach does not allow us to estimate the true proportion of juveniles in the population, and indeed the higher proportion of juveniles found in the Upper Virgin River Recovery Unit is undoubtedly a product of the three-pass search technique used there in contrast to two-passes elsewhere. Of the four recovery units in which we used two-pass surveys, the probability of encountering a juvenile was consistently lowest in the Western Mojave Recovery Unit. The model-averaged Year parameter estimate indicated the average pattern over all years (1999 through 2014) because we standardized the input variable Year (mean = 2007.0, SD = 4.1). The model-averaged Year parameter for each recovery unit is close to zero, indicating similar proportions at the beginning and end of the survey period, with slightly fewer juveniles in the Northeastern and Western Mojave recovery units, and slightly more elsewhere. However, the negative sign of the Recovery Unit X Year^2 parameter estimates indicated that between the beginning and end of the survey period, there were increased odds of encountering juveniles (Schielzeth 2010); the proportion of juveniles was increasing when surveys began in 1999 but peaked in 2007 and have been declining in all recovery units since then.

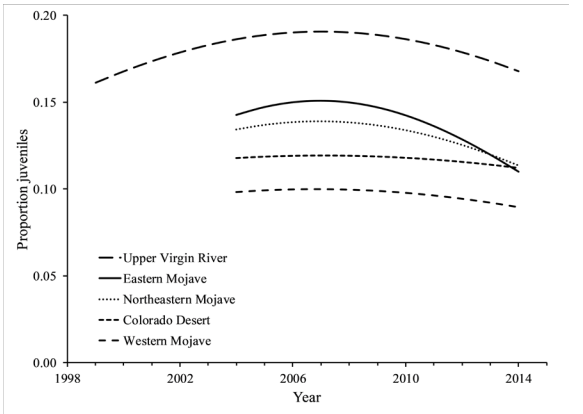

Figure 5. Relative proportion of juvenile Mojave Desert Tortoises (*Gopherus agassizii*) in each recovery unit through 2014: since 1999 for Upper Virgin River Recovery Unit and for all others since 2004.

The linear and quadratic time effects indicate that in all recovery units the odds of encountering a juvenile have declined since 2007 (Table 7, Fig. 5), which is most of the period of surveys for four of the five recovery units. The magnitude of the Recovery Unit X Year^2 effects indicates this trend was strongest in the Eastern and Northeastern Mojave recovery units, so that in 2014 there were 23% fewer (Eastern Mojave) and 15% fewer (Northeastern Mojave) juveniles compared to 2004. In 2007, the year when the proportion of juveniles was estimated to be highest in all recovery units, $P(\text{juvenile}_{2007\text{UpperVirginRiver}}) = 0.189$, CV = 0.057 and, in contrast, $P(\text{juvenile}_{2007\text{Western Mojave}}) = 0.099$, CV = 0.067. The probability that an encountered tortoise was a juvenile was also consistently low in the Colorado Desert ($P[\text{juvenile}_{2007\text{Colorado Desert}}] = 0.119$, CV = 0.131) and lower than in the remaining two recovery units ($P[\text{juvenile}_{2007\text{Eastern Mojave}}] = 0.149$, CV = 0.187; $P[\text{juvenile}_{2007\text{Northeastern Mojave}}] = 0.140$, CV = 0.085).

Discussion

Our analyses provide the first estimates of regional and range-wide population trends for *G. agassizii*. Overall this threatened species is experiencing large, ongoing population declines, and adult tortoise numbers have decreased by over 50% in some recovery units since 2004. Although TCAs within the same recovery unit had very different initial densities, trends were more similar within recovery units than between them. Only one of the five recovery units (Northeastern Mojave) exhibited population increases across all TCAs; this recovery unit also had the lowest densities at the start of our study period in 2004.

Maximum annual population growth rate projected in the eastern Mojave Desert during optimum forage conditions on a 2.59-km^2 study plot was 2% (Turner et al. 1987, unpubl. report), while Nussear and Tracy (2007) simulated annual population growth rates as

Table 4. Parameter estimates and standard errors (SEs) from the best-fitting model describing $\log_e$ transformed density/km^2 of adult Mojave Desert Tortoises (*Gopherus agassizii*). The model applies for the period through 2014 for all recovery units, starting in 1999 in Upper Virgin River and in 2004 for the remaining four recovery units.

Recovery unit / Tortoise Conservation Area	Intercept (SE)	Slope (SE)
Western Mojave	-3.174(0.102)	-0.071(0.033)
Fremont-Kramer (FK)	-3.195(0.103)	-0.068(0.030)
Ord-Rodman (OR)	-2.801(0.104)	-0.082(0.031)
Superior-Cronese (SC)	-3.149(0.092)	-0.093(0.029)
Colorado Desert	-3.051(0.078)	-0.045(0.028)
Chocolate Mtn Aerial Gunnery Range (AG)	-2.395(0.115)	-0.033(0.033)
Chuckwalla (CK)	-3.093(0.119)	-0.041(0.042)
Chemehuevi (CM)	-2.966(0.131)	-0.108(0.047)
Fenner (FE)	-2.574(0.127)	-0.073(0.048)
Joshua Tree (JT)	-3.553(0.132)	0.062(0.044)
Pinto Mountains (PT)	-3.144(0.149)	-0.083(0.058)
Piute Valley (PV)	-3.193(0.120)	0.044(0.049)
Northeastern Mojave	-3.870(0.119)	0.131(0.043)
Beaver Dam Slope (BD)	-3.975(0.143)	0.222(0.052)
Coyote Springs Valley (CS)	-3.750(0.100)	0.102(0.041)
Gold Butte-Pakoon (GB)	-4.365(0.148)	0.144(0.048)
Mormon Mesa (MM)	-3.148(0.101)	0.082(0.041)
Eastern Mojave	-3.544(0.132)	-0.112(0.050)
Eldorado Valley (EV)	-3.589(0.131)	-0.092(0.051)
Ivanpah (IV)	-3.273(0.126)	-0.074(0.048)
Upper Virgin River	-1.654(0.093)	-0.032(0.021)
Red Cliffs Desert Reserve (RC)	-1.654(0.093)	-0.032(0.021)

high as 5%. We describe regional population increases in some TCAs much larger than this, possibly indicating that optimal environmental conditions alone do not explain these increases. Several unpaved roads in these TCAs have been closed by the BLM and legal protections since the early 1990s may have reduced the number of tortoises purposely killed or removed from the wild. Nonetheless, the 3.7-fold increase in adults since 2004 that is described here would be unexpected even under much more active management. The large variance associated with these estimates of population trend probably factors into the magnitude of the estimate. Large variances that describe the best estimates of trends in adult density indicate that more modest increases are almost as strongly supported by the data.

Encounter rates make the largest contribution to variance in the annual TCA density estimates, reflecting the non-random pattern of tortoises on the landscape. High between-transect variability in encounter rate means that within-year encounter rate variance will be high, as will between-year variance unless the same transects are surveyed each year. This is the case only in RC, the only TCA where encounter rate variance was never the primary contributor to the density variance (more about variance considerations below).

Based on the rapid increase in the number of adults, juveniles in the Northeastern Mojave Recovery Unit must also be increasing in absolute terms despite the -0.021 change in their relative number since 2004. Locally focused demographic studies are required to describe the roles of increasing adult survivorship and/or recruitment into adult size classes; these studies could also further our understanding of the survivorship of the more cryptic juveniles (USFWS 2011). Population trends of the future (over more than a generation) will provide a measure of reproduction and juvenile survivorship since 2004 in the Northeastern Mojave TCAs.

Declining adult densities through 2014 have left the Western Mojave adult numbers at 49% and in the Eastern Mojave at 33% of their 2004 levels. Such steep declines in the density of adults are only sustainable if there were suitably large improvements in reproduction and juvenile growth and survival. However, the proportion of juveniles has not increased anywhere since 2007, and in these two recovery units the proportion of juveniles in 2014 has declined to 91% and 77% of their representation in 2004, respectively. This may be a continuation of ongoing population declines for at least part of the Western Mojave (Berry et al. 2013).

Reductions in the number of juvenile tortoises may reflect reduced reproduction and/or increased mortality of smaller tortoises. Drought indices for the deserts of the southwestern United States have increased in recent decades (USFWS 2006, Guida et al. 2014), with speculation that female tortoises consequently reduce annual reproductive effort (Henen 1997, 2002) or that hatchlings may be at increased risk of emerging to find too little moisture and related forage (Morafka 1994; Nagy and Medica 1986; Nagy et al. 1997; Wilson et al. 2001). Many other sources of mortality to smaller desert tortoises have been identified (Darst et al. 2013), but recent attention has focused especially on increased predation risk in the Western Mojave, Eastern Mojave, and Colorado Desert recovery units due to prey-switching during droughts by Coyotes (*Canus latrans*; Esque et al. 2010) and especially by increasing abundance of Common Ravens (*Corvus corax*), which typically prey on smaller tortoises rather than on adults (Boarman and Berry 1995; Kristan and Boarman 2003).

Ultimately, trends in adult and juvenile densities reflect the impact of numerous unquantified threats to *G. agassizii* populations over the period of the study (Tracy et al., *op. cit*.; Darst et al. 2013). With few exceptions, the multitude of threats, acting over the long lives of these animals, prevents more rapid and direct identification of specific agents responsible for *G. agassizii* population

Table 5. Estimated change in abundance of adult Mojave Desert Tortoises (*Gopherus agassizii*) in each recovery unit between 2004 and 2014, including standard error (SE) of abundance estimates. Abundance estimates are based on recovery unit densities calculated from the model in Table 4 and applied to all areas of the associated recovery unit meeting criteria as modeled habitat, whether inside or outside TCAs.

Recovery Unit	Modeled Habitat (km^2)	2004 Abundance (SE)	2014 Abundance (SE)	Δ Abundance (SE)
Western Mojave	23,139	131,540 (35,415)	64,871 (17,465)	-66,668 (17,949)
Colorado Desert	18,024	103,675 (30,366)	66,097 (19,359)	-37,578 (11,006)
Northeastern Mojave	10,664	12,610 (4,304)	46,701 (15,940)	34,091 (11,636)
Eastern Mojave	16,061	75,342 (21,589)	24,664 (7,067)	-50,679 (14,522)
Upper Virgin River	613	13,226 (1,115)	10,010 (1,234)	-3,216 (340)
Total	68,501	336,393 (51,596)	212,343 (31,391)	-124,050 (36,062)

increases or declines. Local conditions in each TCA also determine whether the same threat will act with similar severity. For instance, although wildfires in 2005 in RC were associated with high tortoise mortality (McLuckie et al. 2014), similarly large fires that year in GB are believed to have impacted areas of poor tortoise habitat quality due to earlier overgrazing. These areas supported lower densities of tortoises at the time of the wildfire, so the impact of the fires was much less in GB than in RC (Tuma et al. 2016).

Techniques appropriate for describing survivorship and reproduction have characterized tortoise population dynamics in a handful of small, unrepresentative areas, while surveys in larger, more typical low-density areas are difficult to associate with specific local human activities. The trends we describe are consistent with published observations within some TCAs. As mentioned above in the Upper Virgin River Recovery Unit, RC experienced catastrophic wildfire as well as a drought-related die-off of tortoises during the period of this study (McLuckie et al. 2014). The vulnerability of this smaller recovery unit in the face of such large-scale impacts remains of paramount concern. In the Western Mojave Recovery Unit, decreasing population trends in the decades before 2004 were described based on multiple widespread but local mark-recapture plots (Doak et al. 1994; Berry and Medica 1995; Tracy et al., *op. cit.*); other evidence of population declines came from comparison of the frequency of live and dead tortoise sightings in the Western Mojave TCAs (Tracy et al., *op. cit.*). During the period covered by our study, Esque et al. (2010) also noted increased rates of predation by coyotes in the Western Mojave and linked this to decreases in their mammal prey base following drought.

In other parts of the desert, earlier research on local plots sometimes described population trajectories that differ from declines reported by us, such as static adult tortoise numbers on 2.59- km^2 plots in the IV TCA in the Eastern Mojave Recovery Unit, and in PV and FE in the Colorado Desert Recovery Unit (Berry and Medica 1995). The data in these cases were for earlier decades and describe patterns on single local plots that were not

Table 6. Model selection table for mixed model logistic regression describing the proportion of observations that were juvenile Mojave Desert Tortoises (*Gopherus agassizii*) from 2004 through 2014 for all recovery units (starting in 1999 for Upper Virgin River Recovery Unit). Year was also used as a categorical variable to capture the random effects of annual conditions. Model weights (*w*) express the relative support for each model given the data and are based on relative scores for Akaike's Information Criterion (AIC). Models with ΔAIC < 5 are shown (these model weights cumulatively account for > 0.95 of model support) as well as the top model for describing patterns in adult densities (Table 3) and the null model.

Model	Log likel.	AIC	ΔAIC	*w*
RU	-1967.8	3947.5	0.0	0.324
RU + Year2	-1966.8	3947.6	0.1	0.309
RU + Year	-1967.7	3949.5	2.0	0.119
RU + Year + Year2	-1966.8	3949.6	2.1	0.114
RU + Year2 + RU×Year2	-1964.1	3950.2	2.7	0.084
RU + Year + Year2 + RU×Year2	-1964.0	3951.9	4.4	0.036
RU + Year + RU×Year	-1965.9	3953.8	6.3	0.014
Random factors only	-1982.0	3968.1	20.6	0.000

Table 7. Parameter estimates (standard errors) for changes in the relative proportion of juveniles observed on surveys for adult Mojave Desert Tortoises (*Gopherus agassizii*) from 2004 through 2014 in four of the five recovery units and since 1999 in Upper Virgin River Recovery Unit. Estimates are model-averaged with shrinkage across the top six models in Table 6. For interpreting inflection points, the input variable Year was standardized based on mean = 2007.0 and standard deviation = 4.1.

Recovery Unit	Intercept	Year	Year^2
Colorado Desert	-1.999 (0.133)	0.003 (0.088)	-0.097 (0.380)
Eastern Mojave	-1.729 (0.206)	0.003 (0.106)	-0.484 (1.262)
Northeastern Mojave	-1.822 (0.107)	-0.001 (0.095)	-0.307 (0.534)
Upper Virgin River	-1.445 (0.066)	0.003 (0.003)	-0.212 (0.045)
Western Mojave	-2.198 (0.071)	-0.005 (0.105)	-0.154 (0.330)

selected to be representative of the larger TCA (Corn 1994; Anderson et al. 2001; Tracy et al., *op. cit*.). For instance, ongoing and long-term declines on a 2.59-km^2 plot in the JT TCA of the Colorado Desert Recovery Unit (Lovich et al. 2014) may reflect drought impacts they describe, in addition to consequences from the unimproved road that bisects the plot, and predator impacts reported elsewhere in a low relief site (Berry et al. 2013). These characteristics of the plot differ from large areas of the TCA, which are in more rugged terrain and where we characterize populations as increasing.

Throughout our assessment, we describe tortoise status based on adult densities, which is useful for comparison of areas of different sizes. However, if the area available to tortoises is decreasing, then trends in tortoise density no longer capture the magnitude of decreases in abundance. Some of the area of potential habitat (68,501 km^2) has certainly been modified in a way that decreases the number of tortoises present. We used area estimates that removed impervious surfaces created by development as cities in the desert expanded. However, we did not address degradation and loss of habitat from recent expansion of military operations (753.4 km^2 so far on Fort Irwin and the Marine Corps Air Ground Command Center), from intense large scale fires such as those that burned 576.2 km^2 in critical habitat alone in 2005, or from development of utility-scale solar facilities in the desert that have been permitted on 194 km^2 to date (USFWS 2016). The impact of the many smaller land use conversions (habitat loss) have not been compiled, but this and the small scale of habitat restoration projects (habitat gain) have been dwarfed by the scale of habitat conversion from military exercises, renewable energy facilities, and catastrophic fire. Due to loss and degradation of potential habitat, the recovery unit abundance estimates in Table 5 are maximum estimates. Habitat loss would also disrupt the prevailing population structure of this widely distributed species with geographically limited dispersal (isolation by distance; Murphy et al. 2007; Hagerty and Tracy 2010). Demographic connection with nearby local populations has enabled repopulation of at least one area after a local die-off of tortoises (Germano and Joyner 1988). We therefore anticipate an additional impact of this habitat loss is decreasing resilience of local tortoise populations by reducing demographic connections to neighboring populations (Fahrig 2007). Military and commercial operations and infrastructure projects that reduce tortoise habitat in the desert are anticipated to continue.

The high variability of population estimates and the serious consequences of hypothesis testing that fails to detect a true population decline are ongoing topics in conservation biology (Johnson 1989; Taylor and Gerrodette 1993; Taylor et al. 2007; Gerrodette 2011). Conventional hypothesis testing involves comparison of observed trend estimates to a null model of static population size; this unnecessarily restricts the scope and usefulness of monitoring programs to acquiring enough information to rule out no-action (Wade 2000; Gerrodette 2011). Instead, we used an information-theoretic approach in which the data are applied to each competing model; we drew conclusions based on the relative support for each model given the data (Burnham and Anderson 2002). In this case, regional trend models best described the data in hand. Our current analysis strongly concludes that there are similar population trends within recovery units, with different trends between recovery units.

The range-wide scope of our analysis also uses the power of replication in space to underline regional trends rather than attempting to describe one local trend in isolation (see Freilich et al. 2005; Inman et al. 2009). We would have reached less definitive conclusions if the monitoring effort had continued exclusively in a few dozen 2.59-km^2 study plots that had been initiated in the 1970s or if fewer TCAs had been surveyed, perhaps in a less coordinated effort. Instead, the current range-wide distance sampling program provides fairly coarse but clear summaries of patterns in tortoise density and abundance, definitive because they sample regionally and range-wide.

Although our results demonstrate the power of this monitoring program to detect large positive and negative trends over a 10–15-y period, large SEs for density trends we found reflect two important sources of imprecision in the population growth estimates. First, long-term monitoring programs spread over a large area are describing multiple underlying local phenomena. This can be seen in the consistent but TCA-specific within-recovery-unit trends. The same phenomenon is expected within TCAs. For example, each end of a valley may be experiencing different population dynamics, or lowland habitat may offer different population growth potential from upland habitat. It is also to be expected that there is some variation in the degree of population growth supported by year-to-year environmental conditions. These sources of variability in TCA- or recovery-unit-level population dynamics are reflected in the SE of our population trend estimates. By modeling intra-year covariation in TCA density estimates, we accounted for some of the process variation due to annual conditions.

Sampling error of the density estimate is a composite of the errors from the encounter rate estimates as well as from both correction factors that are applied. Estimation of P_a consistently contributes about 10% to the variance in the annual density estimates (e.g., McLuckie et al. 2002), and many more observations are needed to develop a detection curve than to estimate encounter rate. Detection curves based on 60 observations might be minimally acceptable (Buckland et al. 2001), whereas

encounter rate estimates based on the same number of detections would be robust. This issue underlies the simulations by Freilich et al. (2005), which led them to reject distance sampling as a viable method for such sparsely distributed animals. The current monitoring program always applied much greater survey effort to estimate TCA-specific encounter rates than anticipated by Freilich et al. (2005); also, to avoid poor detection estimates, we pooled detection distances across all TCAs completed by a given team of surveyors. A certain amount of precision is also lost to the annual density estimates by correcting for G_0. However, this quantity can vary considerably between years, so failure to correct population estimates adequately would add bias to annual density estimates (Freilich et al. 2000).

Encounter rate estimation is consistently the largest variance component in all TCA density estimates (e.g., McLuckie et al. 2002). Most encounter rate variance is inherent to the distribution of tortoises on the landscape (Krzysik 2002), reflecting topographic and vegetation differences between transects with additional sampling variance reflecting relative survey effort. The planned and sustained effort in RC has resulted in much larger sample sizes than in other TCAs and more precision for annual population density estimates (CV = SE/density consistently between 0.12 and 0.15), contributing to lower between-year sampling error. Sampling error is also reduced because we survey the same transects in RC each year. The declining trend in abundance was therefore discernible even though RC was only monitored every other year, an approach that has not been pursued in the rest of the range where survey effort has fluctuated at a generally suboptimal level based on inconsistent funding.

Turtles and tortoises world-wide are as threatened with extinction as any other vertebrate lineage (Stanford et al. 2018). The crisis in turtle survival stems from ongoing direct exploitation that targets turtles for consumption or captivity as well as from indirect or untargeted harm such as mortality on roadways or non-lethal degradation of the habitat they need to survive. Most extinct turtle taxa in the past hundreds of years were extirpated from constrained areas (mostly giant tortoises endemic to islands), whereas the turtle species that are currently most endangered are primarily threatened by habitat alteration and collection for the pet trade or food market (Stanford et al. 2018). *Gopherus agassizii* is one of six North American species of *Gopherus*, part of all of which have protected status under U.S. or Mexican regulations or both. *Gopherus flavomarginatus* is listed among the top 25 threatened freshwater and terrestrial turtle species (Stanford et al. 2018), and populations have been decimated by habitat loss and ongoing collection for consumption. The remaining *Gopherus* species are widespread, which is not characteristic of turtles that have faced the first waves of extinction and local extirpation of the modern era. Population losses have nonetheless been documented in these *Gopherus* species (Bury et al. 1988; McCoy et al. 2006; Allison and McCoy 2014), and *G. agassizii* is now included in the list of the top 50 turtle and tortoise species at greatest risk (Stanford et al. 2018). Unlike earlier groups of turtle and tortoise species at risk of extinction, declines in *Gopherus* may instead reflect compounding impacts of threats that are not acutely lethal to individuals or populations (USFWS 2011). In common with other turtles and tortoises, their life history puts *G. agassizii* at greater risk from even slightly elevated adult mortality (Congdon et al. 1993; Doak et al. 1994) and recovery from population declines will require more than enhancing adult survivorship (Spencer et al. 2017). Currently, 60.8% of turtle species are designated Threatened on the International Union for Conservation of Nature (IUCN) Red List (IUCN 2017), including all *Gopherus* species except *G. berlandieri*. Although populations comprising *G. morafkai* and *G. evgoodei* were classified as conspecifics of *G. agassizii* at the time of the most recent IUCN status assessment, they are now recognized as distinct species, and are considered Vulnerable by the Tortoise and Freshwater Turtle Specialist Group, which officially consults to update the IUCN Red List (Rhodin et al. 2017).

The negative population trends in most of the TCAs for Mojave Desert Tortoises indicate that this species is on the path to extinction under current conditions. This may reflect inadequate recovery action implementation, slow response by tortoises and their habitat to implemented actions, or new and ongoing human activities in the desert that have not been mitigated appropriately. It may also be a result of stochastic or directional climatic events that impact large expanses of tortoise habitat (e.g., drought, fire, climate change) and are largely beyond the realm of local land management activities. Our results are a call to action to remove ongoing threats to tortoises from TCAs, and possibly to contemplate the role of human activities outside TCAs and their impact on tortoise populations inside them.

Long-term monitoring is an essential component of evidence-based management (Lindenmayer and Likens 2010). It determines whether the composite management efforts over ecologically meaningful time periods have been effective. For G. agassizii, the reinvigoration of the interagency management oversight group tasked with implementing recovery activities based on their predicted effectiveness has the potential to translate results from this monitoring program into decisions about maintaining or altering contemporary management activities. Monitoring of declining populations should be deeply integrated in conservation and recovery programs. Recovery plans under the U.S.

Endangered Species Act always stipulate population thresholds that would trigger removal of federal protection, but adaptive-management triggers based on monitoring results that show population declines are absent from most recovery planning (Lindenmayer et al. 2013) and have not yet been integrated into the management for *G. agassizii*.

Although these surveys were designed to provide a 25-y description of population growth, it is clear that this single purpose would be an underutilization of the program that can certainly address interim management questions (Nichols and Williams 2006). For long-lived *G. agassizii*, monitoring of the reproductive portion of the population also captures the effects of management on the population segment that must be the basis for recovery. Population recovery will necessitate accelerated, prioritized recovery activities (Darst et al. 2013). Targeted, local effectiveness monitoring (Lyons et al. 2008; Lindenmayer et al. 2011), where possible, would complement our larger population monitoring program. Both types of monitoring will be needed to characterize the effectiveness of recovery activities where the list of threats is so large and varied.

Acknowledgments.—This monitoring program was developed and adapted around recommendations provided by David Anderson and Kenneth Burnham in 1996. P. Steven Corn, Clarence Everly, Richard Fridell, Jill Heaton, Ronald Marlow, Philip Medica, Kenneth Nussear, and C. Richard Tracy contributed to the early development of the program. Over the years, hundreds of surveyors collected field data, led over multiple years by Terry Christopher, Imogen Daly, Nathan Gregory, Deborah Harstad, and Peter Woodman. Melissa Brenneman, Rohit Patil, Clarence Everly, and Jill Heaton contributed to database development, quality control, and data management protocols. Reviews by Roy Averill-Murray, Catherine Darst, Kimberleigh Field, Katherine Ralls, J. Michael Reed, and Robert Steidl improved this manuscript considerably. Funding for various years of this study was provided by Arizona Strip Field Office, BLM; California Desert District, BLM; Clark County Desert Conservation Program; Edwards Air Force Base; Parashant National Monument, National Park Service; Joshua Tree National Park; Marine Corps Air Station, Yuma; Mojave National Preserve; National Training Center, Ft. Irwin; Southern Nevada Field Office, BLM; Washington County Habitat Conservation Plan; Utah Division of Wildlife Resources; and State of Utah Endangered Species Mitigation Fund. These and other government land managers provided access to surveyed areas. We conducted these minimal tortoise handling activities as well as all transmitter attachment, maintenance, and removal procedures in compliance with U.S. Fish and Wildlife Service recovery permits TE-108507 and TE-038224, which set out terms and conditions that were also requirements for our associated state permits. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

Literature Cited

Allison, L.J., and E.D. McCoy. 2014. North American tortoise abundance. Pp. 118–126 *In* Biology and Conservation of North American Tortoises. Rostal, D.C., E.D. McCoy, and H.R. Mushinsky (Eds.). Johns Hopkins University Press, Baltimore, Maryland, USA.

Anderson, D.R., K.P. Burnham, B.C. Lubow, L. Thomas, P.S. Corn, P.A. Medica, and R.W. Marlow. 2001. Field trials of line transect methods applied to estimation of desert tortoise abundance. Journal of Wildlife Management 65:583–597.

Barton, K. 2015. MuMIn: Multi-model Inference. R package version 1.15.1. R Foundation for Statistical Computing, Vienna, Austria. http://CRAN.R-project.org/package=MuMIn.

Bates D., M. Maechler, B. Bolker, and S. Walker. 2015. lme4: Linear Mixed-effects Models using Eigen and S4. R package version 1.1–8. R Foundation for Statistical Computing, Vienna, Austria. http://CRAN.R-project.org/package=lme4.

Berry, K.H., and P.A. Medica. 1995. Desert Tortoises in the Mojave and Colorado deserts. Pp. 135–137 *In* Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. LaRoe, E.T., G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac (Eds.). U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.

Berry, K.H., J.L. Yee, A.A. Coble, W.M. Perry, and T.A. Shields. 2013. Multiple factors affect a population of Agassiz's Desert Tortoise (*Gopherus agassizii*) in the northwestern Mojave Desert. Herpetological Monographs 27:87–109.

Boarman, W.I., and K.H. Berry. 1995. Common Ravens in the southwestern United States, 1968–92. Pages 73–75 *In* Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. LaRoe, E.T., G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac (Eds.). U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.

Boarman, W.I., T. Goodlett, G. Goodlett, and P. Hamilton. 1998. Review of radio transmitter attachment techniques for turtle research and recommendations for improvement. Herpetological Review 29:26–33.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001.

Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd Edition. Springer, New York, New York, USA.

Bury, R.B., T.C. Esque, L.A. DeFalco, and P.A. Medica. 1994. Distribution, habitat use, and protection of the desert tortoise in the Eastern Mojave Desert. Pp. 57–72 *In* Biology of North American Tortoises. Bury, R.B., and D.J. Germano (Eds). National Biological Survey, Fish and Wildlife Research 13, Washington, D.C., USA.

Bury, R.B., D.J. Morafka, and C.J. McCoy. 1988. Distribution, abundance and status of the Bolsón Tortoise. Pp. 5–30 *In* The Ecogeography of the Mexican Bolsón Tortoise (*Gopherus flavomarginatus*): Derivation of its Endangered Status and Recommendations for its Conservation. Morafka, D.J. and C.J. McCoy (Eds). Annuals of the Carnegie Museum 57.

Congdon, J.D., A.E. Dunham, and R.C. van Loeben 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.

Corn, P.S. 1994. Recent trends of Desert Tortoise populations in the Mojave Desert. Pp. 85–93 *In* Biology of North American Tortoises. Bury, R.B., and D.J. Germano (Eds). National Biological Survey, Fish and Wildlife Research 13, Washington, D.C., USA.

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. Karieva, and B. Klepetka.1994. Modeling population viability for the Desert Tortoise in the Western Mojave. Ecological Applications 4:446–460.

Esque, T.C., K.E. Nussear, K.K. Drake, A.D. Walde, K.H. Berry, R.C. Averill-Murray, A.P. Woodman, W.I. Boarman, P.A. Medica, J. Mack, and J.S. Heaton. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endangered Species Research 12:167–177.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003–1015.

Freilich, J.E., K.P. Burnham, C.M. Collins, and C.A. Garry. 2000. Factors affecting population assessments of Desert Tortoises. Conservation Biology 14:1479–1489.

Freilich, J.E., R.J. Camp, J.J. Duda, and A.E. Karl. 2005. Problems with sampling Desert Tortoises: a simulation analysis based on field data. Journal of Wildlife Management 69:45–56.

Fry, J., G. Xian, S. Jin, J. Dewitz, C. Homer, L. Yang, C. Barnes, N. Herold, and J. Wickham. 2011. Completion of the 2006 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 77:858–864.

Germano, D.J. 1994. Comparative life histories of North American tortoises. Pp. 175–185 *In* Biology of North American Tortoises. Bury, R.B., and D.J. Germano (Eds.). National Biological Survey, Fish and Wildlife Research 13, Washington, D.C., USA.

Germano, D.J., R.B. Bury, T.C. Esque, T.H. Fritts, and P.A. Medica. 1994. Range and habitat of the Desert Tortoise. Pp. 57–72 *In* Biology of North American Tortoises. Bury, R.B., and D.J. Germano (Eds.). National Biological Survey, Fish and Wildlife Research 13, Washington, D.C., USA.

Germano, D.J., and M.A. Joyner. 1988. Changes in a Desert Tortoise (*Gopherus agassizii*) population after a period of high mortality. Pp. 190–198 *In* Management of Amphibians, Reptiles, and Small Mammals in North America: Proceedings of the Symposium. Szaro, R.C., K.E. Severson, and D.R. Patton (Technical Coordinators). U.S. Department of Agriculture, Forest Service General Technical Report RM-166, Fort Collins, Colorado, USA.

Gerrodette, T. 2011. Inference without significance: measuring support for hypotheses rather than rejecting them. Marine Ecology 32:404–418.

Guida, R. J, S. R. Abella, W. J. Smith, Jr., H. Stephen, and C. L. Roberts. 2014. Climatic change and desert vegetation distribution: assessing thirty years of change in Southern Nevada's Mojave Desert. The Professional Geographer 66:311–322.

Hagerty, B.E., and C.R. Tracy. 2010. Defining population structure for the Mojave Desert Tortoise. Conservation Genetics 11:1795–1807.

Henen, B.T. 1997. Seasonal and annual energy budgets of female Desert Tortoises (*Gopherus agassizii*). Ecology 78:283–296.

Henen, B.T. 2002. Reproductive effort and reproductive nutrition of female Desert Tortoises: essential field methods. Integrative and Comparative Biology 42:43–50.

Inman, R.D, K.E. Nussear, and C.R. Tracy. 2009. Detecting trends in Desert Tortoise population growth: elusive behavior inflates variance in estimates of population density. Endangered Species Research 10:295–304.

International Union for Conservation of Nature (IUCN). 2017. IUCN Red List of Threatened Species. Version 2017–3. http://www.iucnredlist.org.

Johnson, D.H. 1989. An empirical Bayes approach to analyzing recurring animal surveys. Ecology 70:945–952.

Keene, O.N. 1995. The log transformation is special. Statistics in Medicine 14:811–819.

Kristan, W.B., and W.I. Boarman. 2003. Spatial pattern of risk of Common Raven predation on Desert Tortoises. Ecology 84:2432–2443.

Krzysik, A.J. 2002. A landscape sampling protocol for estimating distribution and density patterns of Desert Tortoises at multiple spatial scales. Chelonian Conservation and Biology 4:366–379.

Lindenmayer, D.B., and G.E. Likens. 2010. The science and application of ecological monitoring. Biological Conservation 143:1317–1328.

Lindenmayer, D.B., G.E. Likens, A. Haywood, and L. Miezis. 2011. Adaptive monitoring in the real world: proof of concept. Trends in Ecology and Evolution 26:641–646.

Lindenmayer, D.B., M.P. Piggott, and B.A. Wintle. 2013. Counting the books while the library burns: why conservation monitoring programs need a plan for action. Frontiers in Ecology and the Environment 11:549–555.

Liu, C., P.M. Berry, T.P. Dawson, and R.G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

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.

Luckenbach, R.A. 1982. Ecology and management of the Desert Tortoise (*Gopherus agassizii*) in California. Pp. 1–37 *In* North America Tortoises: Conservation and Ecology. Bury, R.B. (Ed.). National Biological Survey, U.S. Fish and Wildlife Service, Wildlife Research Report 12, Washington, D.C., USA.

Lyons, J.E., M.C. Runge, H.P. Laskowski, and W.L. Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management. Journal of Wildlife Management 72:1683–1692.

Marques, T.A., L. Thomas, S.G. Fancy, and S.T. Buckland. 2007. Improving estimates of bird density using multiple-covariate distance sampling. Auk 124:1229–1243.

Mazerolle, M.J. 2015. AICcmodavg: Model Selection and Multimodel Inference based on (Q)AIC(c). R package version 2.0-3. R Foundation for Statistical Computing, Vienna, Austria. http://CRAN.R-project.org/package=AICcmodavg.

McCoy, E.D., H.R. Mushinsky, and J. Lindzey. 2006. Declines of the Gopher Tortoise on protected lands. Biological Conservation 128:120–127.

McLuckie, A.M., D.L. Harstad, J.W. Marr, and R.A. Fridell. 2002. Regional Desert Tortoise monitoring in the Upper Virgin River Recovery Unit, Washington County, Utah. Chelonian Conservation and Biology 4:380–386.

McLuckie, A.M., E.T. Woodhouse, and R.A. Fridell. 2014. Regional Desert Tortoise monitoring in the Red Cliffs Desert Reserve, 2013. Utah Division of Wildlife Resources, Publication number 14-15. Salt Lake City, Utah, USA.

Morafka, D.J. 1994. Neonates: missing links in the life history of North American tortoises. Fish and Wildlife Service Research 13:161–173.

Murphy R.W., K.H. Berry, T. Edwards, A.E. Leviton, A. Lathrop, J.D. Riedle. 2011. The dazed and confused identity of Agassiz's land tortoise, *Gopherus agassizii* (Testudines, Testudinidae) with the description of a new species, and its consequences for conservation. ZooKeys 113:39–71.

Murphy, R.W., K.H. Berry, T. Edwards, and A.M. McLuckie. 2007. A genetic assessment of the recovery units for the Mojave population of the Desert Tortoise, *Gopherus agassizii*. Chelonian Conservation and Biology 6:229–251.

Nagelkerke, N.J.D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Nagy, K.A., and P.A. Medica. 1986. Physiological ecology of Desert Tortoises. Herpetologica 42:73–92.

Nagy, K. A., D. J. Morafka, and R. A. Yates. 1997. Young Desert Tortoise survival: energy, water, and food requirements in the field. Chelonian Conservation and Biology 2:396–404.

Nichols, J.D., and B.K. Williams. 2006. Monitoring for conservation. Trends in Ecology and Evolution 21:668–673.

Nussear, K.E., and C.R. Tracy. 2007. Can modeling improve estimation of Desert Tortoise population densities? Ecological Applications 17:579–586.

Nussear, K.E., T.C. Esque, R.D. Inman, L. Gass, K.A. Thomas, C.S.A. Wallace, J.B. Blainey, D.M. Miller, and R.H. Webb. 2009. Modeling habitat of the Desert Tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran deserts of California, Nevada, Utah, and Arizona. Open-file Report 2009–1102, U.S. Geological Survey, Reston, Virginia, USA.

Pekár, S., and M. Brabec 2016. Marginal models via GLS: a convenient yet neglected tool for the analysis of correlated data in the behavioural sciences. Ethology 122:621–631.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131. R Foundation for Statistical Computing, Vienna, Austria. http://CRAN.R-project.org/package=nlme.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rhodin, A.G.J., J.B. Iverson, R. Bour, U. Fritz, A. Georges, H.B. Shaffer, and P.P. van Dijk (Turtle Taxonomy Working Group). 2017. Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status. Pp. 1–292 *In* Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the International Union for Conservation of Nature (SSC Tortoise and Freshwater Turtle Specialist Group). Rhodin, A.G.J., J.B. Iverson, P.P. van Dijk, R.A. Saumure, K.A. Buhlmann, P.C.H. Pritchard, and R.A. Mittermeier (Eds.). Chelonian Research Monographs 7, Lunenburg, Massachusetts, USA.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Spencer, R.-J., J.U. Van Dyke, and M.B. Thompson. 2017. Critically evaluating best management practices for preventing freshwater turtle extinctions. Conservation Biology 31:1340–1349.

Stanford, C.B., A.G.J. Rhodin, P.P. van Dijk, B. D. Horne, T. Blanck, E.V. Goode, R. Hudson, R. A. Mittermeier, A. Currylow, C. Eisemberg, et al. (Turtle Conservation Coalition). 2018. Turtles in Trouble: The World's 25+ Most Endangered Tortoises and Freshwater Turtles–2018. International Union for Conservation of Nature Tortoise and Freshwater Turtle Specialist Group, Turtle Conservancy, Turtle Survival Alliance, Turtle Conservation Fund, Conservation International, Chelonian Research Foundation, Wildlife Conservation Society, and Global Wildlife Conservation, Ojai, California, USA.

Taylor, B.L., and T. Gerrodette. 1993. The uses of statistical power in conservation biology: the Vaquita and Northern Spotted Owl. Conservation Biology 7:489–500.

Taylor, B.L., M. Martinez, T. Gerrodette, J. Barlow, and Y.N. Hrovat. 2007. Lessons from monitoring trends in abundance of marine mammals. Marine Mammal Science 23:157–175.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques, and K.P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Tuma, M.W., C. Millington, N. Schumaker, and P. Burnett. 2016. Modeling Agassizi's Desert Tortoise population response to anthropogenic stressors. Journal of Wildlife Management 80:414–429.

U.S. Fish and Wildlife Service. 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. 1994. Desert Tortoise (Mojave Population) Recovery Plan. U.S. Fish and Wildlife Service, Portland, Oregon, USA.

U.S. Fish and Wildlife Service 2006. Range-wide Monitoring of the Mojave Population of the Desert Tortoise: 2001–2005 Summary Report. Report by the Desert Tortoise Recovery Office, U.S. Fish and Wildlife Service, Reno, Nevada, USA. 85 pp.

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

U.S. Fish and Wildlife Service. 2016. Biological Opinion on the Proposed Land Use Plan Amendment under the Desert Renewable Energy Plan. Memorandum to Deputy State Director, Bureau of Land Management, Sacramento, California. Dated August 16. From Field Supervisor, Carlsbad Fish and Wildlife Office. Carlsbad, California. 203 pp.

Wade, P.R. 2000. Bayesian methods in conservation biology. Conservation Biology 14:1308–1316.

White, G.C., D.R. Anderson, K.P. Burnham, and D.L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Publication LA-87-87-NERP. Los Alamos National Laboratory, Los Alamos, New Mexico, USA.

Wilson, D.S., K.A. Nagy, C.R. Tracy, D.J. Morafka, and R.A. Yates. 2001. Water balance in neonate and juvenile desert tortoises, *Gopherus agassizii*. Herpetological Monographs 15:158–170.

Zar, J.H. 1996. Biostatistical Analysis. 3rd Edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Zuur, A.R., E.N. Ieno, N.J. Walker, A.A. Saveliev, G.M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, New York, USA.

Linda J. Allison is an Ecologist with the Desert Tortoise Recovery Office of the U.S. Fish and Wildlife Service in Reno, Nevada, USA. One of her roles is coordination of a four-state line distance sampling effort to describe Mojave Desert Tortoise status and trends. Linda has degrees in Biology with an emphasis in ecology and evolution from the University of California, Berkeley, USA (B.S.), and from Arizona State University, Tempe, USA (M.S.). (Photographed by Rebecca Palush).

Ann M. McLuckie received her M.S. from University of Arizona, Tucson, USA, studying the genetics, morphology, and ecology of the Desert Tortoise in the Black Mountains in Mojave County, Arizona. Since 1997, she has worked as a Wildlife Biologist with the Utah Division of Wildlife Resources, USA, designing and implementing a Desert Tortoise monitoring program for the Red Cliffs Desert Reserve and Red Cliffs National Conservation Area, USA. (Photographed by Brian Bock).

Appendix A. Annual proportion visible, G_0 (standard error), at each focal site where we monitored transmittered adult Mojave Desert Tortoises (*Gopherus agassizii*). Sites are listed in order from the western-most to the eastern-most and their locations are indicated in Fig. 1. Red Cliffs was also surveyed earlier: 1999 (0.63, SE = 0.185), 2000 (0.86, SE = 0. 144), 2001 (0.86, SE = 0.167), 2003 (0.87, SE = 0. 135).

Site	2004	2005	2007	2008	2009	2010	2011	2012	2013	2014
Superior-Cronese	0.95 (0.081)	0.92 (0.094)	0.96 (0.050)	0.75 (0.197)	0.90 (0.120)	0.98 (0.056)	0.94 (0.073)	0.94 (0.073)		0.91 (0.101)
Ord-Rodman	0.98 (0.035)	0.92 (0.083)	0.64 (0.213)	0.74 (0.130)	0.96 (0.054)	0.94 (0.072)	0.95 (0.062)	0.79 (0.156)		0.99 (0.030)
Twentynine Palms	0.98 (0.028)	0.90 (0.110)	0.97 (0.047)	0.74 (0.113)						
Chuckwalla	0.70 (0.183)	0.74 (0.153)	0.87 (0.060)	0.55 (0.105)	0.73 (0.175)	0.84 (0.125)	0.85 (0.108)	0.82 (0.075)	0.84 (0.058)	0.59 (0.087)
Ivanpah	0.95 (0.071)	0.87 (0.102)	0.94 (0.091)	0.79 (0.107)	0.79 (0.120)	0.88 (0.157)	0.87 (0.149)	0.54 (0.098)		
Jean	0.86 (0.142)									
Indian Springs			0.79 (0.140)	0.83 (0.153)	0.88 (0.118)	0.86 (0.130)	0.79 (0.093)	0.98 (0.049)		
Piute Valley 1	0.84 (0.148)	0.91 (0.118)	0.81 (0.178)	0.73 (0.127)		0.79 (0.218)	0.86 (0.141)	0.65 (0.148)		
Chemehuevi	0.88 (0.104)	0.65 (0.174)	0.62 (0.118)	0.80 (0.120)	0.84 (0.130)	0.81 (0.144)	0.80 (0.162)	0.35 (0.077)		
Piute Valley 2	0.80 (0.191)	0.87 (0.166)								
Halfway Wash					0.64 (0.167)	0.77 (0.200)	0.55 (0.152)	0.54 (0.116)	0.68 (0.136)	
Gold Butte						0.76 (0.141)	0.65 (0.155)	0.52 (0.118)	0.68 (0.123)	
Red Cliffs		0.86 (0.140)	0.53 (0.247)		0.68 (0.131)		0.74 (0.134)		0.66 (0.180)	

Appendix B. Detection statistics for field teams surveying separate Tortoise Conservation Areas (TCAs) each year. Teams walked *L* total km over *k* transects and detected n adult Mojave Desert Tortoises, which was P_a proportion of those available within *w* meters of the transect centerline. The coefficient of variation (CV) for P_a is also listed. Separate detection curves were built for each team each year, except in Red Cliffs Desert Reserve (RC), for which we report on the single composite detection curve. Other TCAs are abbreviated as Chocolate Mountains Aerial Gunnery Range (AG), Beaver Dam Slope (BD), Chuckwalla (CK), Chemehuevi (CM), Coyote Springs Valley (CS), Eldorado Valley (EV), Fenner (FE), Fremont-Kramer (FK), Gold Butte-Pakoon (GB), Ivanpah (IV), Joshua Tree (JT), Mormon Mesa (MM), Ord-Rodman (OR), Pinto Mountains (PT), Piute Valley (PV), and Superior-Cronese (SC).

Year	TCAs	*k*	*L*	*w*	n	P_a	CV(P_a)
1999 to 2013	RC	1,417	2,778	20	1,141	0.64	0.02
2004	AG, CK, CM, FE, IV, JT, PT	316	3,509	15	292	0.57	0.03
2004	FK, OR, SC	138	1,534	15	134	0.42	0.19
2004	BD, CS, EV, GB, MM, PV	175	1,723	22	57	0.47	0.10
2005	AG, CK, CM, FE, FK, IV, JT, OR, PT, SC	451	5,414	13	394	0.47	0.06
2005	BD, CS, EV, GB, MM, PV	267	2,852	18	108	0.40	0.10
2007	BD, CS, EV, GB, MM, PV	282	2,723	13	67	0.57	0.10
2007	AG, CK, CM, FE, FK, IV, JT, OR, PT, SC	271	3,174	16	155	0.39	0.09
2008	BD, CS, EV, MM, PM	566	5,705	18	127	0.41	0.10
2008	AG, CK, CM, FE, FK, IV, JT, OR, PT, SC	118	1,354	14	42	0.47	0.33
2009	BD, CS, EV, GB, MM, PV	568	5,525	15	109	0.25	0.23
2009	AG, CM, FE, FK, IV, JT, OR, PT, SC	225	2,492	14	103	0.35	0.10
2010	BD, CS, GB, MM	425	4,265	16	164	0.41	0.08
2010	CM, EV, FE, IV, PV	368	2,465	14	109	0.59	0.06
2010	FK, OR, SC	187	2,144	12	91	0.58	0.07
2010	AG, CK, JT, PT	140	1,431	8	85	0.67	0.10
2011	BD, CS, GB, MM	380	3,984	20	166	0.43	0.10
2011	CM, EV, FE, IV, PV	312	2,548	20	133	0.32	0.19
2011	CK, FK, JT, OR, PT, SC	160	1,802	16	100	0.53	0.08
2012	BD, CS, GB, MM	369	4,184	21	151	0.38	0.12
2012	CM, EV, FE, IV, PV	201	1,695	15	28	0.43	0.26
2012	AG, CK, FK, JT, OR, PT, SC	162	1,776	14	73	0.40	0.15
2013	AG, BD, GB	173	2,019	16	68	0.45	0.20
2014	AG, FK, OR, SC	230	2,649	10	118	0.61	0.06