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An Uncertain Future for a Population of Desert Tortoises Experiencing Human Impacts

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ABSTRACT: We evaluated the status of a population of Mojave Desert Tortoises (*Gopherus agassizii*), a threatened species, in the El Paso Mountains of the northwestern Mojave Desert in California, USA. The study area lies north of and adjacent to a designated critical habitat unit for the species, is adjacent to a state park, and is a short distance from the Desert Tortoise Research Natural Area. We randomly sampled 373 1-ha plots from a 239.1-km² area in the mountain range to determine demographic attributes of the population, vegetation associations, predator presence, and human uses. Live and dead *G. agassizii* and sign (burrows, scats, tracks) occurred on 35.7% of plots. Densities of adults were higher than in adjacent critical habitat, and threats (traumatic injuries, infectious and other diseases) were similar to those reported elsewhere in the geographic range. Signs of human use were evident on 98.4% of plots. We used a multimodel approach to determine distribution of *G. agassizii* in relation to vegetation, anthropogenic, and predator variables. Vegetation, predators, trash, mining activity, and vehicles were important factors affecting the distribution and intensity of tortoise sign. We concluded that this population is in a downward trend, like other populations in the western Mojave Desert. The high death rate of adults, low population density, high human visitor use, and ongoing decline in the adjacent critical habitat unit indicate that a viable population is unlikely to persist in the study area. The future for the population found in the El Paso Mountains might depend on survival in the adjacent roadless El Paso Mountains Wilderness Area.

Key words: Anthropogenic impacts; Climate warming; *Gopherus*; Models; Mojave Desert; Testudinidae

MANY tortoises and freshwater turtles throughout the world are threatened or endangered and face challenges to survive. Mojave Desert Tortoises (*Gopherus agassizii*; hereinafter tortoises) are listed as critically endangered by the international Turtle Conservation Coalition (2018) and as threatened by the US Fish and Wildlife Service (USFWS 1990, 1994). Historic and recent human activities imperil this species of the Mojave and western Sonoran deserts of the United States. Throughout most of the geographic range, populations in designated critical habitat (Tortoise Conservation Areas) have continued to decline (USFWS 2015; Allison and McLuckie 2018). In 2014, 74.0% of these populations were below viability levels needed to sustain them, with densities of <3.9 adults/km² (USFWS 2015). The Western Mojave Recovery Unit, one of five recovery units in the geographic range, and adjacent to our study population in the El Paso Mountains, experienced a 51% decline from 2004 to 2014, resulting in an adult density of 2.8 tortoises/km² in 2014. This desert species is particularly vulnerable because of the long period to sexual maturity (~12–21 yr), limited clutch size (1–10 eggs) and number (0–3), and low survival of juveniles (Berry and Murphy 2019).

One challenge to recovery efforts is the lack of knowledge about site-specific causes of declines and the importance of

each cause. The driver of loss to populations and habitats range-wide is human-related use (USFWS 1990, 1994). Examples of losses to populations include collection, vandalism, predation, and disease (Berry 1986; Jacobson et al. 1994, 2014; Kristan and Boarman 2003; Esque et al. 2010). Habitat was lost or degraded to urban, agriculture, mining, and renewable energy developments, transportation and utility corridors, military activities, and fires (USFWS 1990, 1994, 2010). Additional habitat deteriorated from grazing, military maneuvers, and vehicle-oriented recreation (Berry et al. 2006; Brooks et al. 2006; Egan et al. 2012). The sources and frequency of habitat disturbance contributed to invasion and establishment of nonnative annual grasses and forbs, species that compete effectively with the native flora of forbs and herbaceous perennial species that are essential forage for tortoises (Brooks and Berry 2006; Jennings and Berry 2015). Climate warming with increasing droughts is the most recent threat to survival, but it does not appear to be the primary or major cause of the current population declines and low numbers (Berry et al. 2002; Longshore et al. 2003; Allen et al. 2018; Sarhadi et al. 2018).

We conducted a study of tortoises in the El Paso Mountains to determine the status of the population and to evaluate the potential roles the population might play in recovery efforts for the species. The study area was adjacent to or close to areas receiving some protection from human uses: a designated critical habitat unit, a state park, a research natural area, and a wilderness area (Fig. 1). Specifically, our objectives were to (1) describe the distribution, demographic attributes, and health of the

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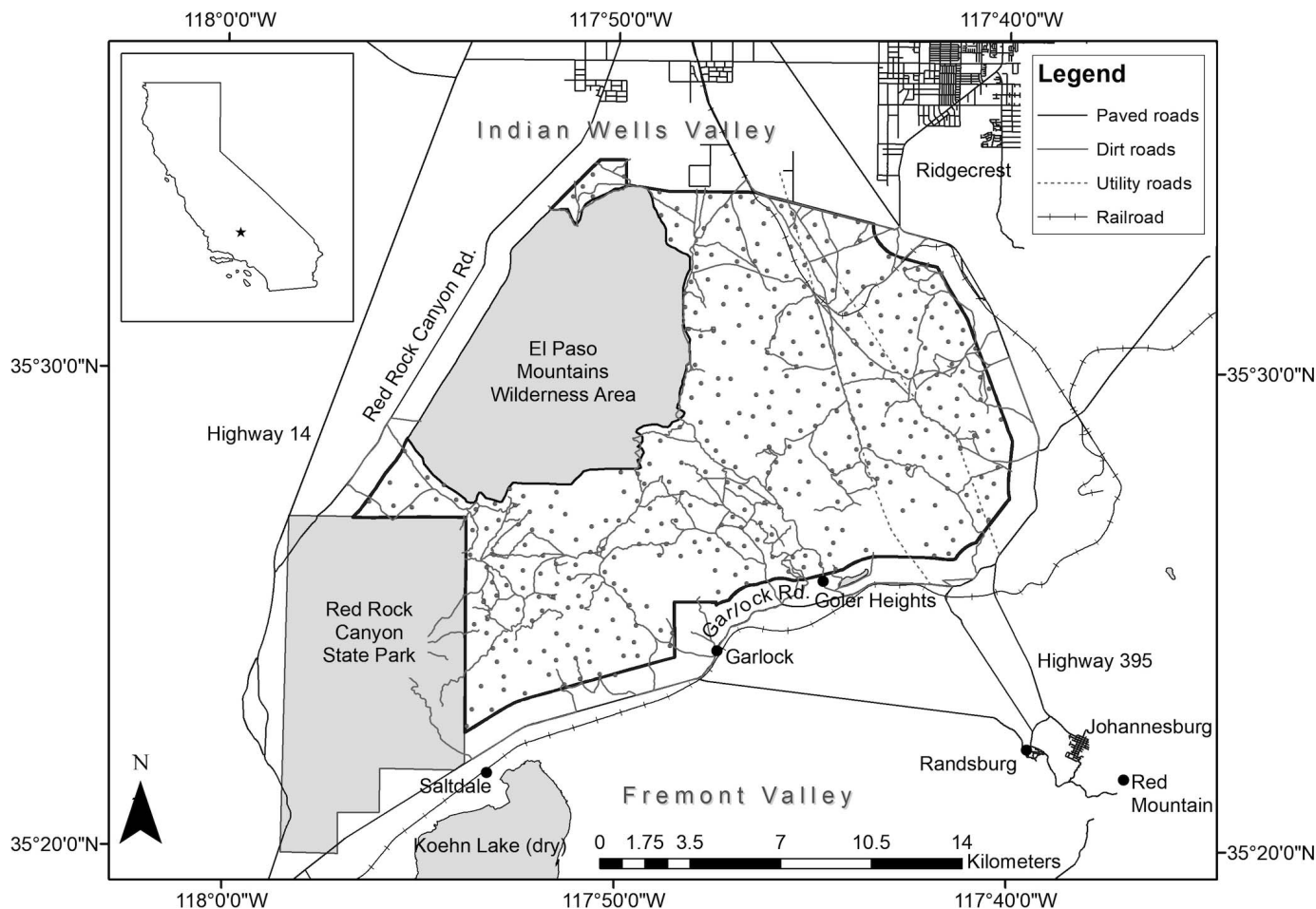


FIG. 1.—Location of the El Paso Mountains study area in the northwestern Mojave Desert, California, USA (inset). The 373 1-ha sampling plots for Mojave Desert Tortoises (*Gopherus agassizii*) appear as dots. The proximity of roads and settlements bordering the study area indicates the potential for human use and access. Roads and designated routes (vehicle, railroad, utility) within the study area highlight amounts of fragmentation. A critical habitat unit for tortoises, Fremont-Kramer, lies south of and adjacent to the study area and connects with the Desert Tortoise Research Natural Area 5.6 km south of the southern boundary (not shown). Datum = WGS84.

tortoises; (2) determine the association between tortoise occurrence and vegetation; (3) develop predictive models of tortoise distribution and identify potential variables negatively affecting the species; and (4) project the probable future for the population.

MATERIALS AND METHODS

Study Area

The study area in the El Paso Mountains of eastern Kern County, California, USA, encompassed 239.1 km² of public land (Fig. 1). Interspersed private lands (11 km², 4.6% of the study area) were not included. Indian Wells Valley is adjacent to the north and west; Fremont Valley with part of the Fremont-Kramer critical habitat unit is adjacent to the south; the Desert Tortoise Research Natural Area is ~5.6 km south; and Red Rock Canyon State Park (RRCSP; 650–1100 m above sea level [a.s.l.], 102.5 km²) and the El Paso Mountains Wilderness Area (EPMWA; 850–1598 m a.s.l., 95.83 km²) form the western boundary. Topography is diverse with valleys, hills, and mountainous terrain (800–1520 m a.s.l.). Several canyons drain the southern slopes into Fremont Valley.

The type and distribution of perennial vegetation reflect elevation, soil type, slope, topography, precipitation, and human use. Vegetation ranged from predominantly creosote bush (*Larrea tridentata*) associations at lower elevations to mixed desert scrub with blackbrush (*Coleogyne ramosissima*) and Joshua trees (*Yucca brevifolia*) at higher elevations. The 30-yr average annual precipitation during the hydrologic year (October–September) was 174.1 mm, of which ~84% fell between 1 October and 30 March (Randsburg Station, ~6.4 km south of the southeastern study area boundary; National Oceanic and Atmospheric Association 2006–2008).

The study area has a history of human use dating from the 1860s with arrival of settlers, followed by the first military and mapping expeditions (Wheeler 1879). Settlers traveled to mining districts (Vredenburg et al. 1981; Pracchia 1995), often accompanied by livestock (Wentworth 1948; Powers 2000). Livestock grazed here from the late 1800s to the time of our study. In 1980, the rangeland was in poor condition from “unauthorized use and/or high historical use” and “off-road vehicles and/or recreationists” (US Department of the Interior, Bureau of Land Management [USBLM] 1980). Early documentation of water sources available to ranchers and miners (Mendenhall 1909) contributed to development

of mining communities and settlements. Homesteading began in the early 1900s and continued into the 20th century (JRP Historical Consulting Service 1997; Norris 1982). In the 21st century, human settlements and towns have bordered the study area, with the largest population of ~20,000 people within 1.4 km of the northern boundary of the study area. An estimated 11 exurban homes are situated within 1 km of the northern and eastern boundaries. Small communities border the southern boundary (Garlock, Goler Heights), and the mining towns of Randsburg, Johannesburg, and Red Mountain are a few kilometers to the south (Fig. 1). The study area is popular for vehicular recreation and visits to mines, springs, and other points of interest. In 2007 and 2008, the years of our study, the USBLM recorded 71,733 and 73,273 visits, respectively (USBLM 2019).

Collection of Data

We created a boundary around the study area and established a buffer of 1 km from the Garlock Road and Highway 395 (Fig. 1). We then developed a distribution of plots in a Geographic Information System (GIS) layer, using Hawth's Tools extension in ArcGIS v9.2 (Environmental Systems Research Institute [Esri], Redlands, California, USA) to establish locations of plots (Beyer 2004). Our objective was to survey ~370 plots; we expected to eliminate as many as 50 plots because of private inholdings or steep, unsafe terrain. We randomly placed 420 points to designate plot centers throughout the survey area, with a minimum distance of 400 m between points; a 1-ha plot was established around each center point, with a minimum distance of 300 m between plots. Ultimately, we sampled 373 plots, but three areas received little or no sampling: two steep areas on south-facing slopes and a 2.6-km² block of private land (Fig. 1).

We surveyed the plots in Summer and Fall 2007 (8 August–29 October) and 2008 (14 July–14 November) by using previously described methods (Keith et al. 2008; Berry et al. 2014). Summer and Fall are the courtship and mating seasons and are high-activity periods for adult tortoises (Zimmerman et al. 1994; Lance and Rostal 2002). Tortoise sign (e.g., burrows, tracks, scats) deposited earlier in the year was also visible. For each year of the study, one or two surveyors covered each plot twice on transects spaced at 10-m intervals, primarily on the same day: once in a north–south direction followed by an east–west direction. Surveyors were proficient in locating live and dead tortoises and had experience in recognizing and recording species of shrubs and anthropogenic evidence. They recorded data on vegetation, live individuals, sign, shell-skeletal remains, predators, and evidence of human-related activities. The open landscape, wide spacing of shrubs, and minimal ground cover during Summer and Autumn facilitated detections of tortoises and sign.

Vegetation.—Similar to methods reported in Berry et al. (2014), we categorized species of perennial shrubs and grasses by relative abundance on each plot and assigned ordinal numeric values: 0 = absent, 1 = one or two individuals, 2 = rare, 3 = sparse, 4 = common, or 5 = dominant or ubiquitous. Definitions were from the glossary in the Jepson eFlora manual (Jepson Flora Project 2017); nomenclature followed taxonomy at the same site.

Live tortoises, shell-skeletal remains, and sign.—To maximize data on live and dead tortoises (because we expected low densities), we evaluated all live animals and shell-skeletal remains encountered, whether they were on plot or off plot. For live individuals, we used established protocols to record sex; carapace length at the midline (MCL; ± 1 mm) and mass (± 1 g); clinical signs of health, disease, or trauma; and behavior (Berry and Christopher 2001). We noted any clinical signs of upper respiratory tract disease caused by mycoplasmosis, shell lesions (i.e., cutaneous dyskeratosis), and trauma (Jacobson et al. 1994, 2014; Homer et al. 1998).

We processed shell-skeletal remains by using established protocols (Berry et al. 2006; Keith et al. 2008). We also examined scats, burrows, and dens of mammalian predators for skin, scutes, and bones of tortoises and similarly searched nest and perch sites of avian predators for remains. We also collected data on tortoise sign (only on plots): cover sites (burrows, caves, pallets, rock shelters), scats, and tracks by using established protocols (Berry et al. 2006, 2014; Keith et al. 2008).

Predators and anthropogenic impacts.—For each plot, the field team recorded observations of potential avian predators (nests, perches, roosts) and sign of mesocarnivores (tracks, dens, areas with concentrations of scats and canid sign posts). We noted counts and amounts of surface disturbance (m²) caused by past and present human activities: paved roads, dirt roads, vehicle trails, and individual tracks; trash, balloons, spent shells (firearms), shooting areas, and shooting targets; mining test pits and markers; campsites; sheep scat and tracks; fence lines, posts, and utility lines and towers; old buildings; and denuded or partially denuded habitats.

Data Analysis

We pooled data for 2007 and 2008 and, unless noted, restricted analyses to on-plot data of live and dead tortoises and their sign, predators, and evidence of human uses.

Vegetation.—To categorize plots by vegetation association, we performed a *k*-means clustering analysis on perennial shrubs and grasses by using the six ordinal categories of relative abundance treated as numeric values. We evaluated *k* = 3, 4, and 5 clusters for the analysis; verified the biological significance by evaluating composition, relative abundance, and diversity within groups of species; and selected *k* = 3 as the most meaningful biologically (see Data Set S1 in the Supplemental Material available online). To assign a vegetation association to each plot, we compared each cluster of species to the Natural Communities (California Department of Fish and Wildlife 2018). We considered a species as abundant when it occurred on >0.70 (70%) of plots within a vegetation association (Data Set S1).

Live and dead tortoises.—We assigned size-age classes to live and dead tortoises by MCL: juvenile, <99 mm; immature, 100–179 mm; and adult, ≥ 180 mm. To assess whether sex ratios of adults differed significantly from the expected 1:1 ratio, we used an exact binomial test. We used a 20,000-simulation bootstrap to estimate mean densities (tortoises/km²) and 95% confidence intervals (CIs) for live adult tortoises and estimated the total number for the entire study area (R Core Team 2017).

We evaluated remains of dead tortoises by using protocols for determining size, sex, and categorized time since death as ≤ 4 or > 4 yr (Berry and Woodman 1984). From the number of adults dying within the past 4 yr, we estimated an annualized crude death rate as $1 - (1 - D/N)^{(1/4)} \times 100\%$, where D was the number of adults dead ≤ 4 yr, and N was the sum of D and the number of live adults. We drew on location, forensic evidence, and general appearance to assign a cause of or contributors to death (Berry 1986; Berry et al. 2006).

Predators and anthropogenic impacts.—We grouped data into seven explanatory variables. We summed counts of Common Ravens and scats and burrows of mesocarnivores (Predators); trash and balloons combined (Trash); trash from spent shells and shooting targets (Shooting); and sheep scat (Sheep). We calculated areas of surface disturbance (m^2) from roads; routes, trails, vehicle tracks, and sites denuded by recreation vehicles (Vehicles); disturbances from mining, mining cairns, and markers (Mines); and other severe surface disturbances (OtherSurfDist).

Spatial patterning and correlations.—We initially analyzed spatial patterns in the data with ArcGIS v9.3 (Esri). We created point layers for vegetation associations, locations of live tortoises, shell-skeletal remains, and sign; evidence of predators; and the more common human disturbances (those occurring on $\geq 50\%$ of plots). We determined whether live and dead tortoises were clustered in the landscape with the Average Nearest Neighbor tool, part of the spatial statistics suite in ArcToolbox. We created a GIS layer of designated routes (roads and service routes) by overlaying a topographic coverage and manually tracing the routes within the survey area. Using Hawth's tools extension (Beyer 2004), we calculated distances between point layers and the nearest designated road or route (RoadDist).

To develop spatial models of distributions of tortoises, we used kriging in Geostatistical Analyst to interpolate spatial distributions based on raw, untransformed counts (ArcMap v10.5, Esri). We used the model-averaged predictions for each plot and selected ordinary kriging with a probability surface output and threshold value of 0 and allowed ArcMap to generate the layers by using the program defaults for semivariogram, nugget, and lag size/number. To develop spatial models describing the probability of distribution for selected anthropogenic uses, we selected standard kriging neighborhood analysis with two and five neighbors and four sectors with 45° offset.

We conducted Pearson correlation analyses to evaluate relationships between tortoise sign and pairs of seven anthropogenic variables, predators (Predators), and counts of perennial plant species (Vegetation). The anthropogenic variables were Trash, Vehicles, Shooting, Mines, Sheep, OtherSurfDist, and RoadDist (or distance from roads). We transformed anthropogenic variables into their ordered ranks before correlation analyses because of their zero-inflated and highly skewed distributions and conducted Spearman rank correlation analyses. We did not transform Vegetation, which had a bell-shaped distribution.

Modeling distribution of tortoises and live–dead status.—To assess possible spatial autocorrelation among plots, we divided the study area into 2- and 4- km^2 sampling blocks by overlaying a square grid of 2×2 - and 4×4 - km cells on a topographic map. These sampling blocks defined

spatial groupings of a minimum of five 1-ha plots at the 2-km spatial scale and 10 1-ha plots at the 4-km spatial scale. At the 2-km scale, 373 plots became 53 sampling blocks, with a mean (± 1 SD) of 7 ± 1.6 plots per sampling block. Similarly, at the 4-km scale, 373 plots became 21 sampling blocks, with a mean of 18 ± 3.3 plots per sampling block. We included block identifiers (2 km, 4 km) in our models as potential sources of spatial autocorrelation.

We used generalized linear mixed effects models with a Poisson distribution to evaluate tortoise distribution in relationship to six anthropogenic variables (RoadDist not included), Predators, and the three-category vegetation associations (Vegetation), including the 2- or 4-km random block effect as needed. For the response variables to tortoise distribution, we used the total number of live and dead tortoises, cover sites, scats, and tracks detected on each plot (LiveDeadSign). We evaluated spatial autocorrelation by using Akaike's Information Criterion corrected for small samples (AICc) to compare global models containing all predictors, including either 2 km, 4 km, or no random block effect, and selected the global model with the lowest AICc (Burnham and Anderson 2002). We used AICc to compare all possible subsets of predictor variables from the global model, resulting in 256 models, and then followed with model averaging, importance values, and the Wald test to identify the most important variables (Burnham and Anderson 2002, but see Cade 2015).

To develop a spatial model for the probability of tortoise presence (or intensity of tortoise sign), we conducted a kriging analysis in Geostatistical Analyst to interpolate estimates of the probability of presence derived from model averages for each plot (ArcMap v10.5, Esri). The same kriging interpolation techniques used for the raw data also were used for the model-estimated probabilities. We used the same kriging interpolation techniques described for the raw data for the model-estimated probabilities. We also created similar models for probability of roads, vehicle tracks, and trails and for all anthropogenic variables using counts.

We used a different approach for evaluating live and dead *G. agassizii* (Live:Dead ratio) because the sample size was small: 58 live and dead individuals (Live:Dead, Table 2) on 49 different plots. We used Fisher's exact test to determine whether proportions of live and dead tortoises varied with respect to Vegetation, Vehicles, Trash, Sheep, Shooting, Mines, OtherSurfDist, and Predators. We conducted most analyses with R v3.4.3 (R Core Team 2017).

RESULTS

Precipitation and Vegetation

During the field study, annual rainfall was below the long-term mean, and drought conditions prevailed. Precipitation was 29.7 and 111.3 mm in the 2006–2007 and 2007–2008 hydrologic year, respectively—17.1 and 63.9% of the long-term annual mean (174.1 mm).

We identified 51 species of perennial shrubs, 1 tree (Joshua tree), 1 nonnative genus of trees (*Tamarix* spp.), and 4 species of perennial grasses on plots. We documented a mean of 13.3 ± 4.2 species/plot. Three dominant species across all plots were creosote bush (352 plots), cheesebush (*Ambrosia salsola*, 330 plots), and white bursage (*A. dumosa*,

TABLE 1.—Vegetation associations in the El Paso Mountains study area for Mojave Desert Tortoises (*Gopherus agassizii*), northwestern Mojave Desert, California, USA. Each association was assigned a vegetation number (in parentheses) or cluster in the analyses.

Vegetation association (scrub)	No. of plots assigned	No. of species within	No. (%) of abundant species	Elevation: range (m)	Elevation: mean \pm 1 SE (m)
California buckwheat (3)	124	47	12 (25.5)	836–1500	1130 \pm 11.6
Cooper's goldenbush (2)	129	46	7 (15.2)	836–1360	1040 \pm 8.1
Creosote bush-white bursage (1)	120	44	3 (6.8)	690–1215	910 \pm 9.4

318 plots). Eleven other species were located on >50% of the plots.

We assigned each plot to one of three vegetation associations: (1) Creosote bush-white bursage scrub with cheesebush; (2) Cooper's goldenbush (*Ericameria cooperi*) with California buckwheat (*Eriogonum fasciculatum*), bladder-sage (*Scutellaria mexicana*), and Nevada Ephedra (*Ephedra nevadensis*); and (3) California buckwheat with bladder-sage, spiny hopsage (*Grayia spinosa*), Nevada Ephedra, Mojave indigo-bush (*Psoralea arborescens*), Mojave horsebrush (*Tetradymia stenolepis*), desert trumpet (*Eriogonum inflatum*), beavertail cactus (*Opuntia basilaris*), and Mojave aster (*Xylorhiza tortifolia*; Table 1; Data Set S1). Elevations varied among vegetation associations ($F_{2,370} = 125.1$, $P < 0.001$), with California buckwheat having the highest mean elevation followed in descending order by Cooper's goldenbush and creosote bush-white bursage. Similarly, California buckwheat was the most diverse, with a Shannon diversity index of 3.231, followed by Cooper's goldenbush (3.074) and creosote bush-white bursage (3.007).

Live and Dead Tortoises and Tortoise Sign

We observed 29 live *G. agassizii*: 18 on 16 plots (4.3% of the total plots) and 11 off plots (Table 2). The sex ratio of adults of 1.22:1 (0.47:1–3.35:1) was similar to the expected 1:1 ratio (exact binomial test, $P = 0.82$; see Berry and Murphy 2019 for sex ratios). Density of adults was 4.8/km² (95% CI = 2.7–7.5). Using these densities, we estimated 646–1793 adults were present in the study area. We detected no significant pattern in distribution (Average Nearest Neighbor, $z = -1.11$, $P = 0.10$). We observed live tortoises at a mean (\pm 1 SE) distance of 332.2 \pm 89.7 m from a designated road or service route, which is slightly greater than the 296.5-m distance at available plots (Fig. 1).

We evaluated 13 of the 29 tortoises for clinical signs of health and disease. None showed signs of dehydration or

starvation typical of prolonged droughts. Four adults (two males, two females) exhibited moderate-to-severe clinical signs of mycoplasmosis (damp or occluded nares and dried mucus on forelimbs). Twelve individuals showed signs of previous predator attacks (bites, punctures, chews, and gnashes to scutes and bones). Nine individuals had moderate-to-severe damage to the gular horn with exposed bone; the gular horn was chewed off on one adult. Most injuries were healed or healing. Five individuals had clinical signs of cutaneous dyskeratosis or another disease of the integument; lesions were moderate to severe and active in three cases. Blackened, necrotic areas were evident on the forelegs of an adult male. Only one small immature showed no clinical signs of disease or trauma.

We located 40 shell-skeletal remains on 35 plots (9.4% of all plots) and 27 off plots; most were adults (Table 3). Thirty-four had died within 4 yr of collection (Table 3). Deaths of most tortoises appeared traumatic (i.e., broken bones and scutes), and the causes included predators, vehicles, and shooting (Table 4). Remains often co-occurred on plots with human activity and predators: 23 were on 23 plots with shell casings and shooting targets, 12 were on plots with concentrations of predator sign, and 6 were on 6 of 60 plots with roads. When we combined data for shell-skeletal remains for on and off plots, the distribution was clustered in the northeastern portion of the study area (Average Nearest Neighbor, $z = -1.98$, $P < 0.05$). Conchoidal fractures typical of gunshots were evident on six tortoises; these remains were in the northeastern part of the study area. On average, the remains were 264.5 \pm 41.7 m from a designated road or service route, which was smaller than both the 332.2-m mean distance to live tortoises and the 296.5 distance to available plots, although these differences were not statistically significant because of relatively large errors in these averages (Fig. 1). The annualized death rate of adults for the previous 4–5 yr (~2003–2008) was 6.9%.

Tortoise sign occurred on 29.2% ($n = 109$) of plots; scat was the most abundant sign (376) followed by cover sites (156) and tracks (9) found on plots. When we combined data for plots where sign, live tortoises, and shell-skeletal remains

TABLE 2.—Size-age classes of live Mojave Desert Tortoises (*Gopherus agassizii*) and shell-skeletal remains found on and off 1-ha plots in the El Paso Mountains, northwestern Mojave Desert, California, USA, in 2007 and 2008.

Size-age class	Live tortoises				% total	Shell-skeletal remains				% of total
	Male	Female	Unknown	Total		Male	Female	Unknown	Total	
On plot										
Juvenile				0				3	3	7.5
Immature			4	4	23.5			13	13	32.5
Adult	7	4	3	14	76.5	2	3	19	24	60.0
Total	7	4	7	18	100.0	2	3	35	40	100.0
Off plot				0						
Juvenile				0				2	2	7.4
Immature				0				3	3	11.1
Adult	4	5	2	11	100.0	7	10	5	22	81.5
Total	4	5	2	11	100.0	7	10	10	27	100.0

TABLE 3.—Estimated time since death of dead Mojave Desert Tortoises (*Gopherus agassizii*) and shell-skeletal remains found on and off 1-ha plots during 2007 and 2008 in the El Paso Mountains, northwestern Mojave Desert, California, USA, in 2007 and 2008.

Size-age class	On 1-ha plots				Off 1-ha plots			
	≤ 4 yr		> 4 yr		≤ 4 yr		> 4 yr	
	No.	% of total	No.	% of total	No.	% of total	No.	% of total
Juvenile	3	15.0	0	0.0	2	14.3	0	0.0
Immature	11	55.0	2	10.0	2	14.3	1	7.7
Adult	6	30.0	18	90.0	10	7.1	12	92.3
Total	20	100.0	20	100.0	14	64.3	13	100.0

TABLE 4.—Probable causes or contributors to death for shell-skeletal remains of Mojave Desert Tortoises (*Gopherus agassizii*) found on and off 1-ha plots during 2007 and 2008 in the El Paso Mountains, northwestern Mojave Desert, California, USA.

Cause of death	On plot		Off plot	
	No.	% of total	No.	% of total
Unknown	15	37.5	4	14.8
Traumatic: general	11	27.5	5	18.5
Predator-mammal	8	20.0	14	51.9
Predator-avian	1	2.5	1	3.7
Gunshot	3	7.5	3	11.1
Vehicle	2	5.0		
Total	40		27	

occurred, 35.7% of plots showed evidence of tortoise presence. More plots with sign occurred in Cooper's goldenbush vegetation association (41.86%), followed by California buckwheat (40.80%) and creosote bush (24.17%) associations. Mean counts for sign in all plots having a Cooper's goldenbush association was highest (2.24), followed by creosote bush (1.51) and California buckwheat (1.14). The highest values for the distributions of sign occurred

adjacent to the EPMWA and in the northeastern and eastern regions (Fig. 2).

Predators

We observed 317 avian predators on 107 plots. Common Ravens were the most frequent avian predator observed ($n = 299$, 94.3%), singly or in flocks of ≤ 31 birds; they were recorded on 99 or 25.5% of plots (99/373 plots). Other species were rarely observed (e.g., Red-tailed Hawks [*Buteo jamaicensis*]; $n = 4$, 1.26%) and Loggerhead Shrikes [*Lanius ludovicianus*]; $n = 3$, 0.63%). Several other known avian predators were rare, comprising 3.81% of observations.

Fifty-seven sign concentration areas of canids (coyote [*Canis latrans*], kit fox [*Vulpes macrotis*]), and American badger [*Taxidea taxus*] occurred on 40 plots. Dens and den complexes were the most common sign ($n = 32$, 64.0%), followed by concentrations of scats ($n = 18$, 36%). Three kit fox den complexes appeared to co-occur with tortoise burrows. Observations of both avian predators and mammalian predator sign were clustered in the northern part of the study area (Average Nearest Neighbor, $z_{\text{avian}} = -12.19$, $z_{\text{mammal}} = -4.09$, $P < 0.01$).

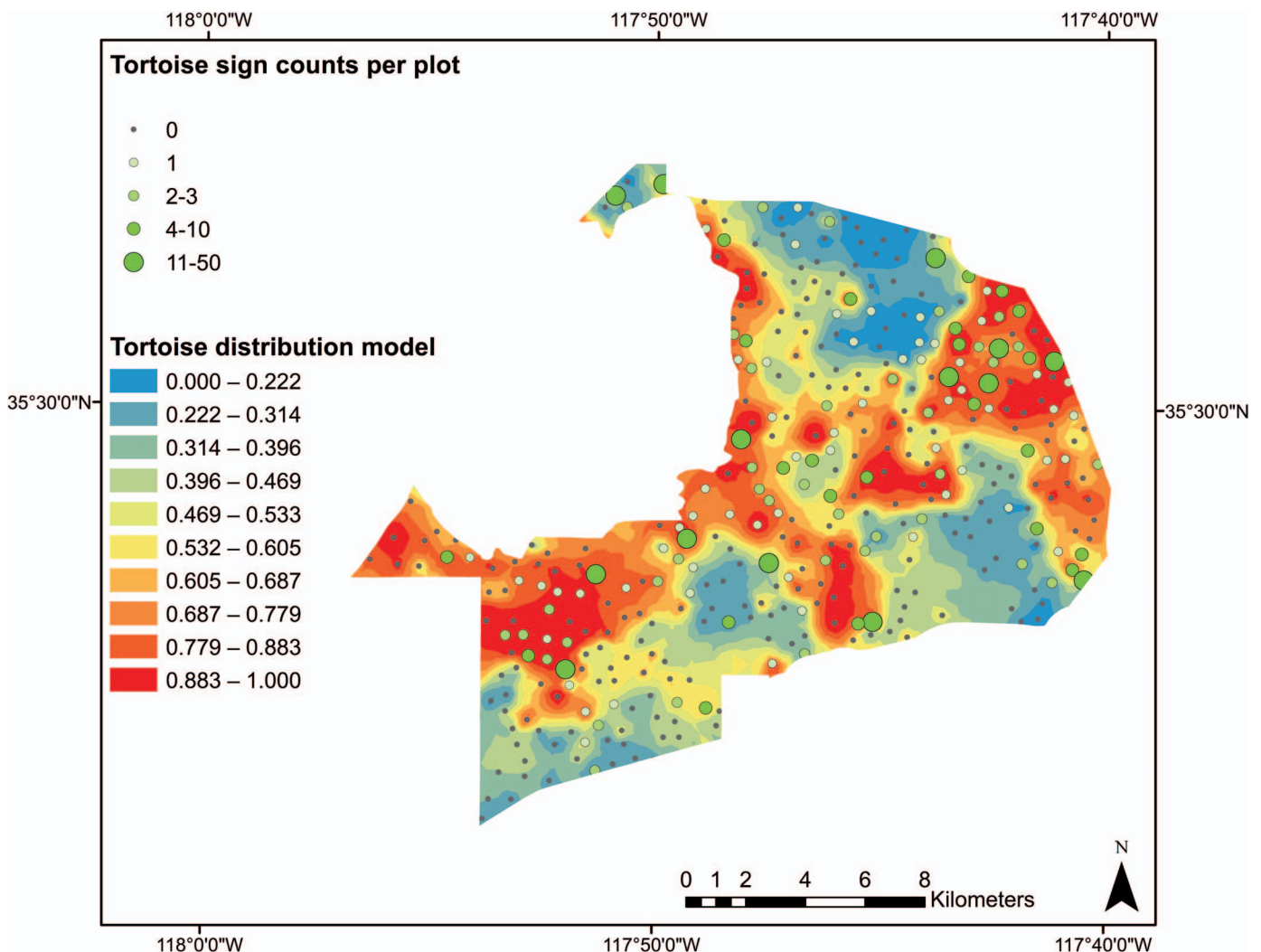


FIG. 2.—Model-averaged predictions for distributions of Mojave Desert Tortoises (*Gopherus agassizii*) in the El Paso Mountains, northwestern Mojave Desert, California, USA, by using counts of live and dead tortoises and tortoise sign on plots as an index of intensity of use.

TABLE 5.—Frequency of occurrence of anthropogenic uses on 373 1-ha plots on the El Paso Mountains study area, northwestern Mojave Desert, California, USA.

Anthropogenic use	No. of plots	% of plots
Trash	304	81.5
Sheep	226	60.5
Shooting	213	57.1
Roads, vehicle tracks, and trails, areas denuded or partially denuded areas by vehicles	187	50.1
Mining	148	39.7
Campfire pits	11	2.9
Linear disturbances (utility lines, power lines, phone cables)	9	2.4
Old buildings	4	1.1

Access and Human Impacts

Evidence of human use occurred on 98.4% (367/373) of plots. Trash was the most common type, followed in descending order by evidence of Sheep, Shooting, Roads and Vehicles, Mining, and other uses (Table 5). Sheep scat was from grazing in previous year; no grazing occurred during 2007 and 2008 because of drought. Portions of roads occurred on 16.1% (60/373) of plots, with a total of 328.11

km of designated roads and service routes present at a density of 1.37 km/km² (Fig. 1). The study area was cut by roads and designated routes into 117 fragments; additional fragmentation occurred from unauthorized off-road travel, cross-country trails, and denuded areas. Vehicle-related surface disturbances ranged from 0 to 8137 m²/plot (mean = 222.5 m²/plot). Higher probabilities of observing vehicle use off-road or designated routes were close to urban and exurban developments, State Highway 395, dense road networks (Figs. 1, 3A), and old mining areas. Unauthorized vehicle use (distant from designated routes and roads) occurred on 45% (168) of plots. Counts of all signs of human use showed patterns with similarities to vehicle use (Fig. 3A,B). Evidence of surface disturbances from mining-related activities ranged from 0 to 2000 m²/plot, with a mean (± 1 SE) of 25.1 ± 7.7 m²/plot. Other uses on plots included campfire pits, linear disturbances (utility lines, power lines and roads, phone cables, berms, railroad grades, and water catchments), and remnants of old buildings. Burned habitats and remains of four dead dogs occurred on <1% of plots. The field team heard shooting during fieldwork on 50 plots (13.4%).

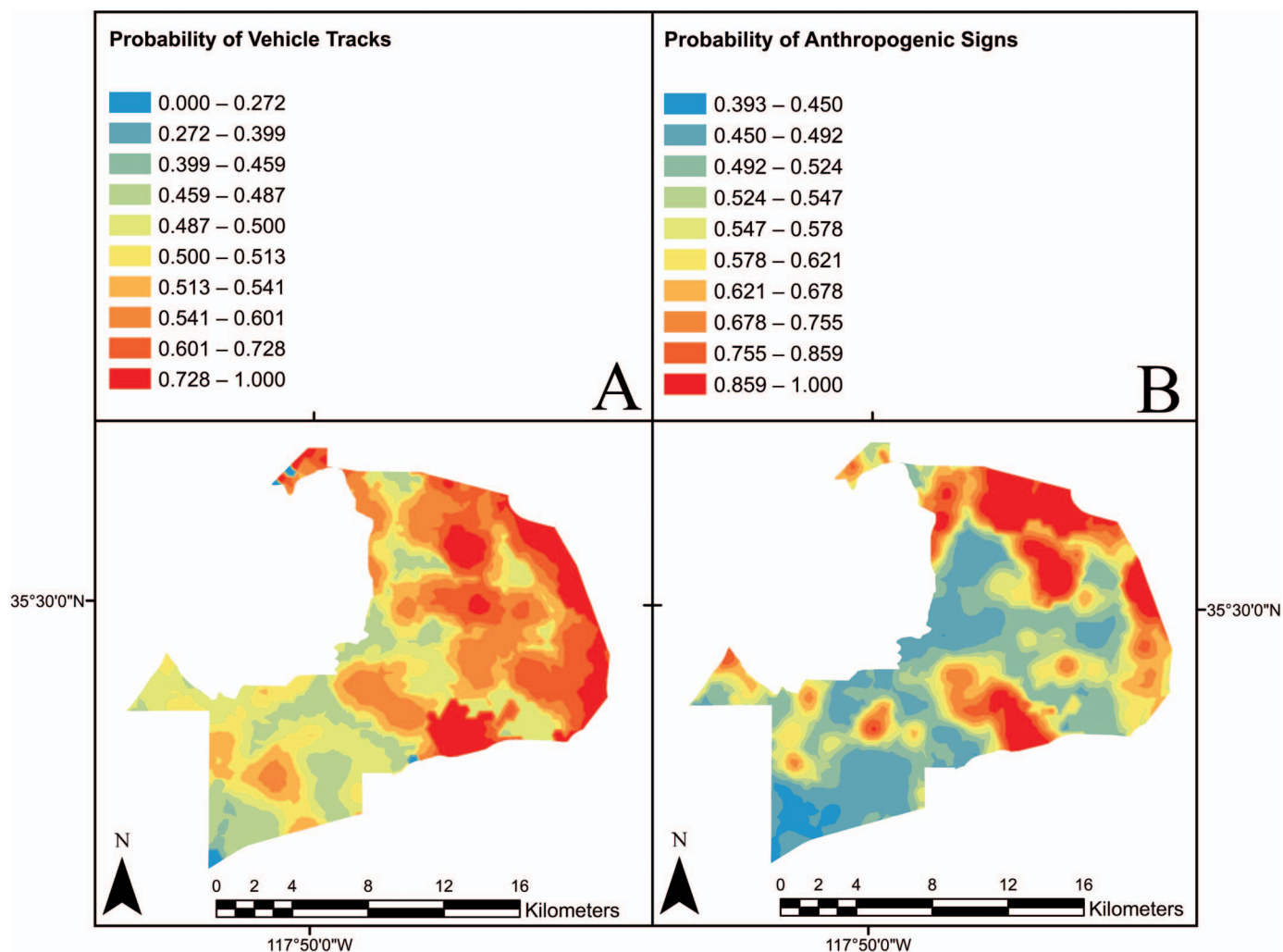


FIG. 3.—El Paso Mountains study area in the northwestern Mojave Desert, California, USA. (A) Probability of unauthorized vehicle use, based on data from vehicle use off designated routes of travel from 373 plots. (B) Probability of observing signs of human use. Note the change in legends from (A) to (B).

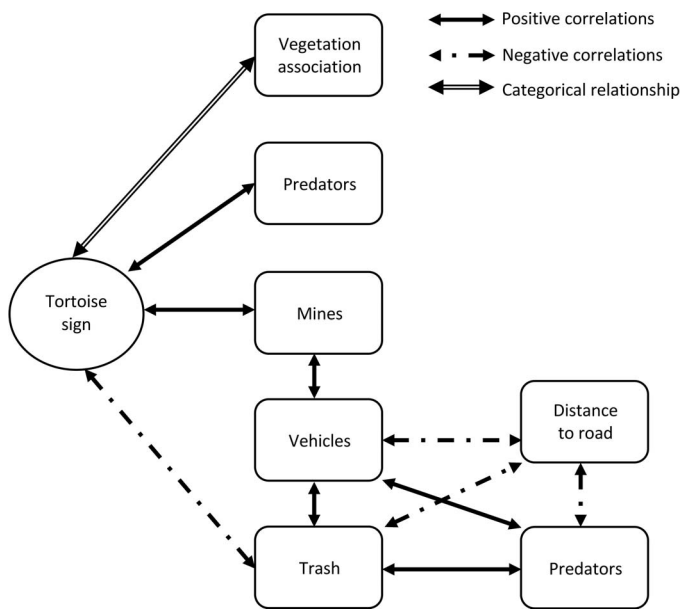


FIG. 4.—Path diagram for relationships among predictors and predicted abundance of sign (live, dead, or other signs) for Mojave Desert Tortoises (*Gopherus agassizii*) at the El Paso Mountains study area in the northwestern Mojave Desert, California, USA. Arrows connected to tortoise sign indicate predictors with variable importance weights >0.86 ; solid arrows additionally represent positive rank correlations and dashed arrows represent negative correlations ($r > 0.2$, $P < 0.0001$). Vegetation association held a high importance value as a categorical predictor of tortoise sign, with Cooper's goldenbush having the most tortoise sign.

The path diagram of relationships between the predicted abundance of all tortoise sign (LiveDeadSign), an index of intensity of sign, and anthropogenic predictors and predators revealed both positive and negative values (Fig. 4). Positive predictors for all tortoise sign were Predators and Mines (variable importance weights, ≥ 0.992); the negative predictor was Trash (variable importance weight = 0.862; Fig. 4; Table 6). In addition, anthropogenic variables were positively or negatively correlated with each other: mines were positively correlated with Vehicles and Vehicles, Trash, and Shootings were positively correlated. Distance to roads (RoadDist) was negatively correlated with Trash, Vehicles, and Shooting (Fig. 4). That is, counts of Trash, Vehicles, and Shooting were in higher numbers closer to roads than more

distant. With one exception (Trash), the rank correlations between variables were either positive or negative ($r > 0.2$, $P < 0.001$).

Models of Distribution and Live–Dead Status of Tortoises

Models based on random spatial factors at the 2-km scale represented the presence and distribution of tortoises and sign better than models based on the larger (4-km) scale or without spatial effects ($\Delta AIC_{\text{none}} = 800.6$, $\Delta AIC_{4 \text{ km}} = 182.0$). Therefore, we evaluated distribution using the 2-km variable (see Data Set S2 in the Supplemental Material available online for the 256 models). Cooper's goldenbush vegetation association was the most important predictor of tortoises and sign counts (Table 6).

Distribution of *G. agassizii* was positively associated with Cooper's goldenbush, Predators, and Mines but negatively associated with Trash ($P < 0.001$). The other variable with an importance value of >0.60 was Vehicles. No significant relationships existed between variables for the ratio of Live:Dead and vegetation associations, anthropogenic uses, and predators (Fisher's exact tests, $P > 0.20$).

DISCUSSION

The status and trends in the tortoise population in the El Paso Mountains reflected local and regional human activities occurring over the last century and were typical of activities in the geographic range of the species and in the American West (Leu et al. 2008; Berry et al. 2013, 2014). Several human uses directly and indirectly influenced distribution, causes of death, and condition of habitats. The frequency of anthropogenic sign (98.4% of plots) is evidence of the ubiquitous human use and degraded habitat. Those signs of human use were facilitated by the network of roads and routes to access areas of interest for mining, livestock grazing, shooting, and vehicle-oriented recreation. Models of tortoise distribution revealed the importance, in descending order, of Cooper's goldenbush vegetation association, Predators, Mines, Trash, and Vehicles in shaping distribution in the years before and during the study. The correlation analyses provided similar results with additional relationships between some variables. Cooper's goldenbush association was the most important vegetation association; it was midway in elevation and numbers of predominant species of shrubs

TABLE 6.—Importance values, model-averaged coefficients, and probability values for testing variables affecting distribution of tortoises and tortoise sign for the population of Mojave Desert Tortoises (*Gopherus agassizii*) in the El Paso Mountains, northwestern Mojave Desert, California, USA.

Variable	Importance value	Model average coefficient	Model average coefficient (SE)	Wald test	P
Intercept (creosote bush-white bursage) ^a	1.000	-0.158	0.234	-0.680	0.496
Cooper's goldenbush ^b	1.000	0.732	0.154	4.766	0.001
California buckwheat ^c	1.000	0.015	0.158	0.095	0.924
Log(Predator)	0.999	0.138	0.031	4.385	0.001
Log(Mines)	0.992	0.059	0.018	3.331	0.001
Log(Trash)	0.862	-0.066	0.040	-1.675	0.094
Log(Vehicles)	0.629	0.012	0.013	0.954	0.342
Log(RoadDistance)	0.345	0.006	0.017	0.391	0.696
Log(Sheep)	0.328	0.004	0.011	0.391	0.696
Log(OtherSurfDist) ^d	0.301	-0.009	-0.029	-0.310	0.757
Log(Shooting)	0.271	0.001	0.015	0.040	0.968

^a Intercept represents mean log (count of tortoises on 1-ha plots with creosote bush-white bursage vegetation association when all other predictors are 0).

^b Difference in mean log(count) of tortoise sign on 1-ha plots with Cooper's goldenbush vegetation association compared to plots with creosote bush-white bursage.

^c Difference in mean log (count) of tortoise sign on 1-ha plots with California buckwheat vegetation association compared to plots with creosote bush-white bursage.

^d OtherSurfDist = severe surface disturbances other than vehicles and mines.

compared with the other two vegetation associations but also shared similar counts of plots with tortoise sign with California buckwheat. By contrast, the creosote bush-white bursage association had only three abundant species, and one was a short-lived shrub species, cheesebush, typical of disturbed land (Vasek 1979/1980). Predators, Mines, Trash, and Vehicles were associated with human presence, a result, in part, of access via the network of designated roads and routes. Additional support for the models came from causes of death for the tortoises, specifically predators, shooting, and vehicle kills associated with roads or routes.

The probability of tortoise distribution (index of intensity of sign) was higher adjacent to EPMWA and in the northeastern and eastern parts of the study area than elsewhere (Fig. 2). The low end of the confidence interval for the density of adults ($4.8/\text{km}^2$, 95% CI = $2.7\text{--}7.5/\text{km}^2$) was the same as the density reported for the adjacent critical habitat unit during 2007 ($2.7/\text{km}^2$), but not in 2008 ($0.4/\text{km}^2$; USFWS 2009, 2012). The midpoint of adult densities in the study area, however, was marginally above the estimated minimum viable density of adults ($3.9\text{ adults}/\text{km}^2$) necessary to maintain viable populations (USFWS 2015; Allison and McLuckie 2018).

Size-age structure of live and dead on-plot individuals included juvenile and immature tortoises, indicating that females were producing young. However, the numbers of young individuals surviving to maturity were insufficient to offset deaths of adults (Turner et al. 1987). The population structure was comparable to the population in RRCSP and in the adjacent critical habitat unit (Fig. 1; Berry et al. 2008).

Human activities influenced causes of death and the death rate of adults. The annualized death rate (6.9%) of adults was too high to sustain a population requiring up to 2 decades to reach sexual maturity and with low recruitment and survival of juveniles (Turner et al. 1987; Allison and McLuckie 2018; Berry and Murphy 2019). Small tortoises were vulnerable to predation (Berry and Murphy 2019). Signs of predator attacks on most live tortoises and shell-skeletal remains supported the importance of predators. Although predators have a negative effect on tortoises, the positive association in models and the correlation analyses between Predators and tortoises was a result of a co-occurrence of sign of mammalian predators and observations of Common Ravens on most plots. Predator scat was observed in association with tortoise remains, and tortoises occasionally had a burrow in a mound of kit fox dens. The incidence of extensive chewing typical of domestic dogs was comparable to, or higher than, that observed at some other sites (Berry et al. 2013, 2014). Predators, such as dogs, Common Ravens and coyotes—subsidized by human resources—thrive in proximity to areas with human activities. Populations of Common Ravens, the majority of observed avian predators, have increased multifold in the Mojave Desert (Boarman and Berry 1995), and excessive predation rates can lead to local extirpations of tortoises (Kristan and Boarman 2003). Similarly, coyote populations have grown in conjunction with urbanized landscapes (Fedriani et al. 2001). Esque et al. (2010) described increased rates of coyote predation on *G. agassizii* populations at several locations throughout the Mojave Desert during drought conditions. Factors influencing higher predation rates included proximity to human

populations and road density (Esque et al. 2010). In our study, the highest levels of predator observations and sign were close to populated areas north and northeast of the study area and where road networks and a state highway occurred.

High mortality and clinical signs of disease in adult tortoises were limiting factors for long-term survival of the population. The proportion of shell-skeletal remains with evidence of crushing by vehicles and gunshots (12.5% of plots) reflected high levels of human use and access via the network of roads, routes, and unauthorized trails (Berry 1986; Nafus et al. 2013). The positive relationship between Vehicles and tortoise sign in the models resulted from co-occurrence of evidence on plots. Tortoises are vulnerable to death from vehicle traffic on roads and routes that bisect or cross their large home ranges (cf. Harless et al. 2009). Population of tortoises are depleted within several hundred meters of dirt and paved roads as a result of deaths or collection, or a road impact zone or road-effect zone (von Seckendorff Hoff and Marlow 2002; Nafus et al. 2013). In our study, dead tortoises were found nearer to roads and routes than live tortoises. The correlation between Vehicles and Shooting also was positive. Berry (1986) reported associations between deaths of tortoises caused by gunshots on plots and proximity to vehicle-oriented, concentrated recreational use zones and high visitor counts per year. The relationships between Vehicles and Trash were positive, but between Trash and tortoise sign were negative. Tortoises are known to consume trash and balloons, which can lead to death (Donoghue 2006; Walde et al. 2007).

Roads also led to mining activity, and the model and correlations showed positive relationships between tortoise sign and Mines. Yet, this relationship is both positive and negative: horizontal tunnels provide escape from extremes of temperature, spoil piles are construction sites for burrows, but vertical shafts and pits are sources of deaths. The existing network of roads also created opportunities for illegal collecting (not observed) and unauthorized off-road travel (Figs. 1, 3).

Implications for Recovery

The El Paso Mountains support tortoise populations, but high levels of visitor use ($>70,000/\text{yr}$) contribute to excessive mortality of adults (and other size classes) and degradation of habitat. These findings align with results from studies in RRCSP, the adjacent critical habitat unit in Fremont Valley, and elsewhere in the geographic range (Berry et al. 2008, 2014; Berry and Murphy 2019). We expect that the El Paso population tracked the reported 51% decline in the Western Mojave Recovery Unit and Fremont-Kramer critical habitat unit between 2004 and 2014 (USFWS 2015; Allison and McLuckie 2018). The future for a viable population in the study area is doubtful. Range-wide, Allison and McLuckie (2018) concluded that the species was on the path to extinction in critical habitat under current conditions.

The anthropogenic activities affecting the El Paso Mountains and other populations are well known. In the first recovery plan, the USFWS recommended management actions to implement in recovery areas, including several associated with closure and limitations to vehicular access (USFWS 1994). A partial list of prohibited activities included vehicle activity off designated routes, habitat-destructive

activities that diminish the capacity of the land, livestock grazing, littering, dogs, and firearms use. All these activities occurred in the El Paso Mountains study area. Importantly, the study area is a popular, high visitation site for vehicle-oriented recreation. The route network was reaffirmed in a government plan (USBLM 2019). The El Paso Mountains are not part of critical habitat or recovery efforts for the tortoise (USFWS 2015).

At the Desert Tortoise Research Natural Area ~5.6 km to the south in the Fremont Valley, fencing to exclude recreational vehicles and grazing successfully protected tortoise populations from two sources of mortality and habitat degradation, but not from infectious diseases and predation by Common Ravens (Berry et al. 2014). This natural area had higher densities of tortoises (10.2 adults/km²) than on private land (3.7 adults/km²) or the critical habitat unit in Fremont Valley (2.4 adults/km²).

Regardless of management decisions for the study area, the adjacent EPMWA with elevations of 850–1598 m has potential as a refuge from high visitation, vehicles, and habitat degradation as well as potential climate change (Cook et al. 2015; Allen et al. 2018; Sarhadi et al. 2018). The intensity of tortoise sign was higher along the EPMWA boundary, indicating that populations might be larger in EPMWA. Models have demonstrated that tortoises are likely to occur at higher elevations in warmer climates (Barrows 2011; Barrows et al. 2016). Future survival in EPMWA will be dependent on population viability, minimizing human-caused sources of mortality and habitat degradation, and the severity of future droughts. Although *G. agassizii* has physiological and behavioral adaptations for survival in deserts, prolonged periods of drought without water or forage and extreme temperatures will challenge the persistence of populations in otherwise suitable habitat areas (Turner et al. 1984; Henen et al. 1998; Berry et al. 2002; Longshore et al. 2003).

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/Herpetologica-D-18-00033.S1>; <https://doi.org/10.1655/Herpetologica-D-18-00033.S2>

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