

## MULTIPLE FACTORS AFFECT A POPULATION OF AGASSIZ'S DESERT TORTOISE (*GOPHERUS AGASSIZII*) IN THE NORTHWESTERN MOJAVE DESERT

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**ABSTRACT:** Numerous factors have contributed to declines in populations of the federally threatened Agassiz's Desert Tortoise (*Gopherus agassizii*) and continue to limit recovery. In 2010, we surveyed a low-density population on a military test facility in the northwestern Mojave Desert of California, USA, to evaluate population status and identify potential factors contributing to distribution and low densities. Estimated densities of live tortoises ranged spatially from 1.2/km<sup>2</sup> to 15.1/km<sup>2</sup>. Although only one death of a breeding-age tortoise was recorded for the 4-yr period prior to the survey, remains of 16 juvenile and immature tortoises were found, and most showed signs of predation by Common Ravens (*Corvus corax*) and mammals. Predation may have limited recruitment of young tortoises into the adult size classes. To evaluate the relative importance of different types of impacts to tortoises, we developed predictive models for spatially explicit densities of tortoise sign and live tortoises using topography (i.e., slope), predators (Common Raven, signs of mammalian predators), and anthropogenic impacts (distances from paved road and denuded areas, density of ordnance fragments) as covariates. Models suggest that densities of tortoise sign increased with slope and signs of mammalian predators and decreased with Common Ravens, while also varying based on interaction effects involving these predictors as well as distances from paved roads, denuded areas, and ordnance. Similarly, densities of live tortoises varied by interaction effects among distances to denuded areas and paved roads, density of ordnance fragments, and slope. Thus multiple factors predict the densities and distribution of this population.

*Key words:* Denuded areas; Ordnance; Predators; Roads

AGASSIZ'S Desert Tortoise (*Gopherus agassizii*, hereafter Desert Tortoise; Murphy et al., 2011), a species of the southwestern United States, was federally listed as threatened in 1990 because populations were declining and habitats were deteriorating or lost from multiple sources (US Fish and Wildlife Service [USFWS], 1990). One challenge to recovery of the tortoise is identification of critical drivers of population declines, both locally and regionally, and prioritization of recovery actions (USFWS, 2011; Averill-Murray et al., 2012; Darst et al., 2013). These drivers may be common on a landscape scale throughout the geographic range (e.g., roads, utility corridors) or specific to a particular land managing agency. Military installations, for example, contain 3.76% of designated critical habitat and 13.5% of habitat available within the geographic range (USFWS, 1994a,

2010; Berry, 1997). They can contribute to population and habitat losses from development of facilities, force-on-force military training with vehicles, testing of missiles and explosives, and other ground-disturbing activities (Tazik and Martin, 2002; USFWS, 2010). They also can be refuges where threatened and endangered species thrive in relatively undisturbed environments (Stein et al., 2008). Some recovery units and critical habitats for the Desert Tortoise are affected more than others by military use, e.g., military installations occupy 28% of habitat in the Western Mojave Recovery Unit (Fig. 1; USFWS, 2010).

The effects of military activities on the Desert Tortoise have been studied in the Western Mojave Recovery Unit at the National Training Center (NTC), Fort Irwin, California, USA (e.g., Krzysik, 1997; Berry et al., 2006), where troops are trained for ground maneuvers using tanks and other

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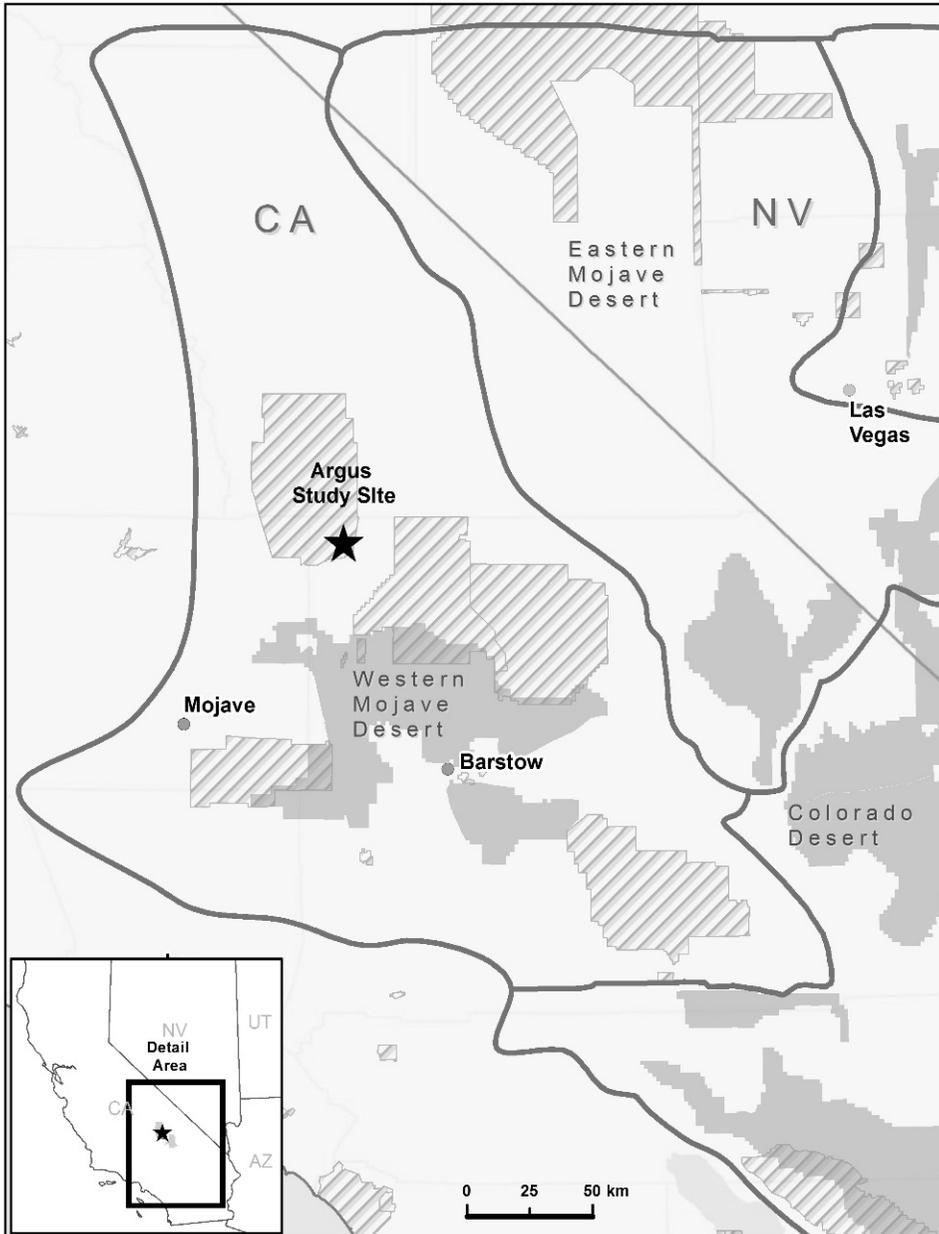


FIG. 1.—Location of the Argus study area for Desert Tortoises (star) with respect to the Western Mojave Desert Recovery Unit, boundaries of other Recovery Units, military installations (hatched), and the nearest Desert Tortoise critical habitats (solid grey polygons).

armored vehicles. Mortality of tortoises from vehicles was high (Berry et al., 2006). A recent expansion of NTC operations into critical habitat required off-site translocation of several hundred tortoises (Esque et al., 2005). At another military installation in Arizona, USA,

Grandmaison et al. (2010) examined the effects of multiple factors—live artillery fire and firing boxes, a network of gravel roads, livestock grazing, and recreation—on microhabitat use by the closely related Morafka's Tortoise (*Gopherus morafkai*). They reported

that a greater proportion of tortoise locations were found outside of firing box boundaries where shelter sites and vegetation showed little human impact than inside the firing boxes. They also noted that tortoises selected areas with a higher percentage of canopy cover of plants and where evidence of cattle activity was absent.

We analyzed the effects of multiple factors (munitions research, roads, predators, and topography) on an isolated population of the Desert Tortoise on the China Lake Naval Air Weapons Station (NAWS) in the northwestern part of the geographic range in California. The NAWS is a research-oriented facility with minimal ground-disturbing activities and with substantial areas that have been inaccessible to the public since 1942. Our objectives were to (1) evaluate the status of the Desert Tortoise population at a site inaccessible to the public; (2) model the effects of predators, topography, munition test areas, ordnance, and a paved road on distribution and density of Desert Tortoises; and (3) identify the variables with positive and negative relationships to the Desert Tortoise.

#### STUDY AREA

The 5.42-km<sup>2</sup> study area (35°41'33"N, 117°28'20"W; datum = WGS84) is in the southeastern portion of the China Lake NAWS (Fig. 2) in the foothills of the southern Argus Range and at the edge of Salt Wells Valley, San Bernardino County, California. Composed of low hills with scattered rock outcrops and small valleys at elevations of 597–732 m, the site is part of an estimated 130-km<sup>2</sup> fragment of habitat that is isolated from other tortoise populations by the steep topography of the Argus Range and anthropogenic activities. The 130 km<sup>2</sup> habitat fragment was in close proximity to high-density human populations 6.5 km to the east at Trona and Westend (1757 people; United States Census Bureau (USCB), 2010) and 15 km to the west, at NAWS, China Lake Acres, Ridgecrest, and Inyokern (30,591 people; USCB, 2010). To the south, Highway 178 parallels and is 3.2 km from the southern study area boundary, effectively isolating the fragment on NAWS from Desert Tortoise populations to the south. Populations to the

south also have been depleted from intensive recreational vehicle use in the US Department of the Interior, Bureau of Land Management's (BLM) Spangler Hills Off-Highway Vehicle Area (USBLM, 1973, 1980, 2006). The study area is in part of the NAWS with no public access since the mid-1940s. Between the late 1940s and 1973, the site received occasional use from NAWS scientists and engineers. In 1973, testing of ordnance began, generating unexploded ordnance (UXO), areas devoid of perennial vegetation, and vehicle traffic on roads.

The dominant perennial vegetation association was white bur-sage and creosote bush (*Ambrosia dumosa-Larrea tridentata*; California Department of Fish and Game (CADFG), 2010a). The long-term annual mean for precipitation was 104.4 mm for the hydrologic year (1 October–30 September) and 80.5 mm for winter rainfall (1 October–31 March; Trona weather station, 35°46'N, 117°23'W, 516.6 m; National Oceanic and Atmospheric Administration, 2009–2010). Prior to the survey, an estimated 116.84 mm of rain fell between 1 October 2009 and 31 March 2010, resulting in an abundance of winter annual plants, which were forage for tortoises during spring 2010.

#### MATERIALS AND METHODS

##### *Field Sampling*

We collected data on live and dead tortoises, tortoise sign (shelter sites, scats, tracks, egg shells, courtship rings, drinking sites), observations and signs of predators, and anthropogenic impacts. We recognize that detection of live and dead tortoises, other signs of tortoises and predators, and anthropogenic impacts is imperfect so we designed the field survey to maximize detection of live tortoises, tortoise sign, predator sign, and anthropogenic impacts. Since tortoises spend much of their lives underground, we selected spring, the time of greatest aboveground activity for all sizes of tortoises (Nagy and Medica, 1986). In addition, we chose a spring following a winter with above average precipitation when tortoise forage was abundant (Henen et al., 1998; Duda et al., 1999; Jennings, 2002). Based on previous research showing strong relationships between live

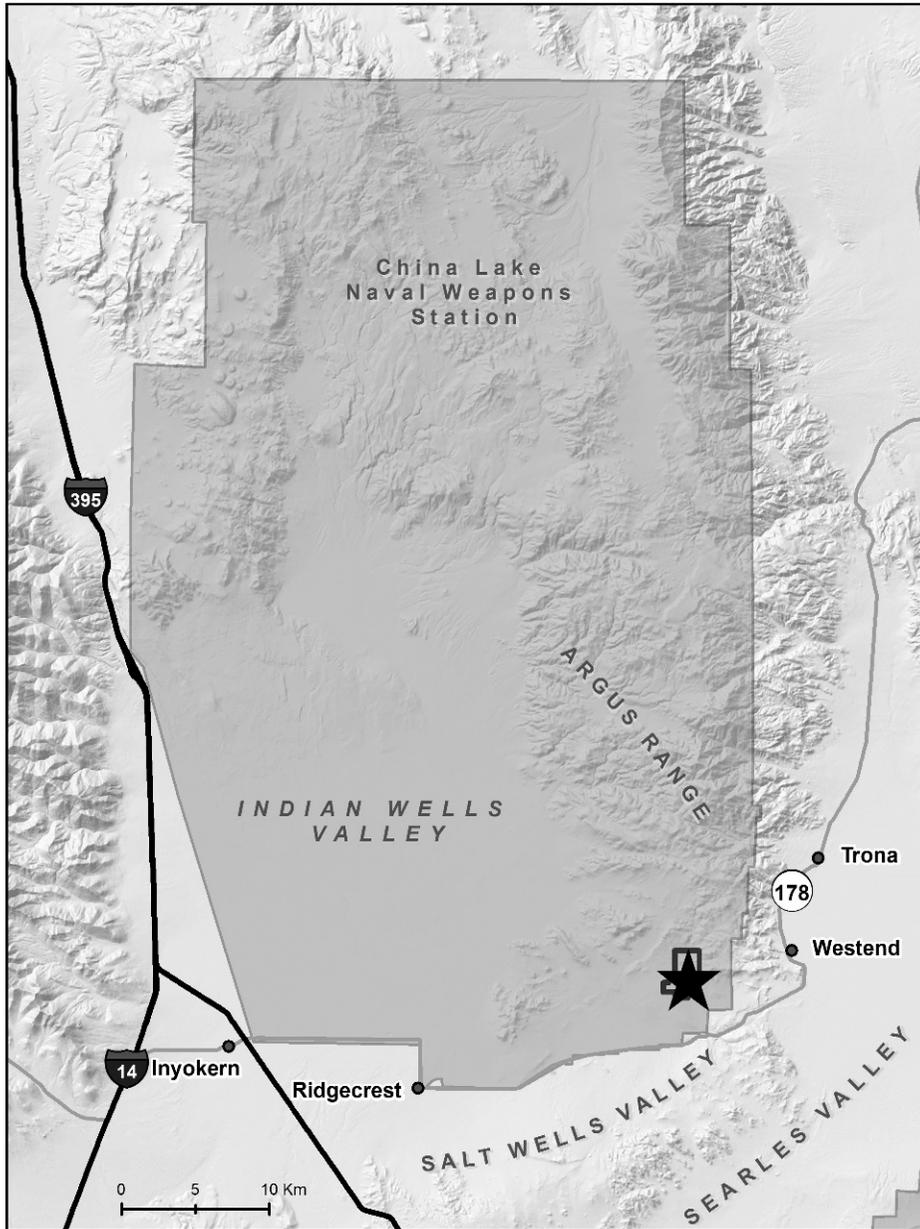


FIG. 2.—Location of the Argus study area for Desert Tortoises (star) within the Naval Air Weapons Station China Lake, San Bernardino County, California, and the proximity to local towns and highways.

tortoises and tortoise sign (e.g., burrows, scats, tracks, courtship rings), we assumed that tortoise sign at a location represented use for shelter, travel, feeding, and social interactions, and that we observed representative samples of each variable (Krzysik, 2002). We made similar assumptions for sign of mammalian

predators and anthropogenic impacts. The low cover of perennial shrubs, sandy soils, and areas denuded of vegetation by anthropogenic activities facilitated observations. We had an additional constraint and safety requirement: the field crew was to be in view of an NAWS UXO expert at all times.

A team of eight surveyed the area for a total of 583 h between 12 and 22 May searching for live tortoises, tortoise shell–skeletal remains, and other tortoise sign. The field team walked 10 m apart and covered the study area completely once, thus ensuring detection of most sign. In fall, the same field workers searched for tortoises for 86.5 h by revisiting shelters that were recently used or active during the previous May. The field team followed standard protocols to handle, mark, and evaluate health of and trauma on the tortoises (Berry and Christopher, 2001). They took digital images of carapace, plastron, eyes, beak, nares, and any lesions. They weighed the tortoises, measured carapace length at the midline (MCL), assigned a sex if  $\geq 180$  mm MCL, and noted locations in Universal Transverse Mercator coordinates. Field workers recorded clinical signs of health and disease, e.g., signs of lethargy, starvation and dehydration, trauma, or abnormalities (Berry and Christopher, 2001; Berry et al., 2002). Clinical signs of upper respiratory tract disease (Jacobson et al., 1991, 1995; Brown et al., 1994; Jacobson and Berry 2012), herpesvirus (Jacobson et al., 2012), shell disease (Jacobson et al., 1994; Homer et al., 1998), and trauma were rated as none, mild, moderate, severe, or unknown for each variable (e.g., palpebrae, periocular area, nares). Signs of severe trauma to the shell and limbs, such as vehicle hits or chewing by dogs and other predators were also noted (e.g., Boyer and Boyer, 2006). No blood samples were taken for laboratory tests for infectious diseases.

*Shell-skeletal remains.*—All shell-skeletal remains found within plot boundaries were collected and catalogued. When remains or parts of remains were discovered, the team examined the vicinity for signs of potential cause (or causes) of death. The team took digital images of remains in situ and recorded details of location, size and sex of the tortoise, condition, signs of predators and scavengers (e.g., predator scats), and human impacts (e.g., vehicle tracks) associated with the remains.

*Tortoise sign.*—We recorded all tortoise sign. We defined cover or shelter sites as burrows, pallets, rock shelters, and caves (after Burge, 1978).

*Potential predators of tortoises.*—We collected data on avian and mammalian predators

to determine predator pressure and to assess potential sources of mortality. We noted date, time, location, behavior, and species for all avian predators observed or heard (e.g., Common Raven, *Corvus corax*; Golden Eagle, *Aquila chrysaetos*; Greater Roadrunner, *Geococcyx californianus*; Red-tailed Hawk, *Buteo jamaicensis*; and Northern Shrike, *Lanius ludovicianus*; Boarman, 1993; K.H. Berry, personal observation). We examined areas with concentrations of predator sign (e.g., perches, nests, dens, marking sites, feeding posts, roosts) for evidence of tortoise remains. The field team broke apart scats of mammalian predators (coyote, *Canis latrans*; kit fox, *Vulpes macrotis*; badger, *Taxidea taxus*; bobcat, *Lynx rufus*) to look for remains of tortoises.

*Anthropogenic impacts.*—We used four methods to measure different aspects of anthropogenic impacts. First, to calculate surface disturbances from roads and areas partially or completely denuded of vegetation, we used aerial imagery from the National Agriculture Imagery Program with a summer natural color (ArcGIS Image Service from the CADFG, 2010b). We digitized disturbed areas (polygons) and road features (lines) on the screen and saved them as feature classes in a geo-database. To calculate disturbed surface areas for roads, we measured widths of the paved road with berm, several bulldozed dirt roads with berms, and old graded and ungraded dirt roads. For the second method, we used a geographic information system to generate 50 random points with a minimum distance of 200 m between points to sample anthropogenic impacts (ordnance from explosive testing, trash, vehicle tracks, mining excavations, utility lines, fences, and other miscellaneous types of human disturbances). Each of the 50 points was outside of denuded areas and was the starting point for 10 m  $\times$  100 m transects. We defined ordnance as metal shell casings, pieces and particles of explosives, wires, circuit boards, nuts, bolts, and rocket fins ranging in size from 1 cm<sup>3</sup> in volume to 0.5 m in length. Pieces of ordnance averaged 3 cm in diameter. For the third method, we established 40 additional 10 m  $\times$  100 m transects specifically for ordnance. These transects extended from the center of areas denuded by explosive

testing to 100–200 m beyond the boundaries of the denuded zone. For the fourth method, we counted all ordnance, trash, balloons, vehicle tracks off road, power poles and lines, fences, and burned areas (total counts only, no locational data recorded) while surveying the entire study area in May.

#### *Data Analysis*

*Live tortoises.*—We assigned live and dead tortoises to one of six size-age classes according to MCL: juvenile 1 = <60 mm, juvenile 2 = 60–99 mm; immature 1 = 100–139 mm; immature 2 = 140–179; subadult or small adult = 180–207 mm; adult =  $\geq$ 208 mm. We used the exact binomial proportion test and 90% confidence intervals (CIs) to determine if the sex ratio of subadult and adult tortoises was significantly different than the expected 1:1 ratio at  $P \leq 0.10$  (SAS Institute Inc., 2010). Tortoises with moderate to severe clinical signs of one or more diseases and trauma (e.g., upper respiratory tract disease, cutaneous dyskeratosis) were noted.

*Shell-skeletal remains.*—We evaluated shell-skeletal remains to determine size-age class, sex, whether previously marked or captive (e.g., painted numbers on shell), approximate time of death, and cause of death. We determined carapace length by one of three methods depending on the condition of remains in the following order of priority: direct measure of MCL; estimation of the MCL using scutes or impressions of scutes in the bony shell and previously derived regression equations based on measurements of selected scutes from the carapace and plastron (Berry and Woodman, 1984); or estimation of MCL by matching the fragments of scutes and bones to similarly sized whole tortoise shells from the US Geological Survey's (USGS's) collection of shell-skeletal remains. To estimate time since death (specifically, time elapsed between death and collection of remains), we used keys in Berry and Woodman (1984), and placed each tortoise in one of two classes: dead  $\leq$ 4 yr or >4 yr.

The general appearance, location, and forensic evidence associated with the remains provided information on cause of death, e.g., firearms or Common Ravens (Berry, 1986; Boarman, 1993). Tortoises hit by a vehicle have cracked and/or crushing injuries to the

shell. Tortoises killed by a mammalian predator are likely to have chew or gnaw marks, puncture wounds, and twisting of scute and bone. The twisting and deformation of scutes and bones occur when scutes and bones are pliable and the tortoise is alive or dying. In contrast, when remains are scavenged, scutes and bones are dry and tend to break and crack rather than showing signs of twisting and deformation. Some causes of death are ambiguous or unknown, e.g., a tortoise dying of disease and then scavenged by a predator or if only fragments of shell remain. Subadult and adult tortoises were used for a 4-yr retrospective calculation of crude death rate.

*Spatial data layers.*—In a preliminary evaluation of the data on anthropogenic impacts, we noted that the major surface disturbances were areas denuded of vegetation from testing, paved roads, and density of ordnance. We hypothesized that distance from denuded area, distance from the paved road, and density of ordnance would correlate with densities of live tortoises and tortoise sign. For the purposes of statistical modeling, we divided the study area into 31 sampling units based on a 500-m  $\times$  500-m grid snapped to major grid units using the Create Fishnet tool in ArcGIS Version 9.3.1 (ESRI, Inc., 2009a). Each grid was 0.25 km<sup>2</sup>, with the exception of grids truncated by the study area boundary. Those grids ranged in size from 0.024 km<sup>2</sup> to 0.216 km<sup>2</sup>.

We identified two response variables: density of live tortoises and density of tortoise sign. Density of live tortoises was measured as the count of live tortoises relative to the area surveyed within each grid square. For all statistical analyses the first known location of an individual tortoise was used. Tortoise sign density, the second response variable, was measured as the count of all tortoise sign relative to the area surveyed in each grid.

We evaluated three types of predictor variables: topography (slope), densities of predator sign, and densities of and distances to anthropogenic impacts. Degree of slope (hereafter, "Slope") was calculated from the 1/3-Arc Second (approximately 10 m) National Elevation Dataset (USGS, 2012) using the Slope tool in ArcGIS Version 9.3.1 (ESRI, Inc., 2009b). Predictive surfaces of predator

densities, Common Ravens and mammalian predator sign per km<sup>2</sup> (hereafter “Raven” and “Mammal,” respectively), were created using the Kernel Density tool in ArcGIS Version 9.3.1 (ESRI, Inc., 2009c). Slope and predator density surfaces were averaged across each grid square. Two predictor variables for anthropogenic impacts were distances from the center point of each grid square to the paved road and to nearest boundary of a denuded area (hereafter “Paved” and “Denuded,” respectively). Distances were determined using the Near tool (ESRI, Inc., 2009d). Density of ordnance was calculated for each of the 90 transects by dividing the number of ordnance pieces by the area of the transect (100 m × 10 m = 1000 m<sup>2</sup>). Transformed ordnance densities (using a fourth-root transformation and then back-transformed) were interpolated with ordinary kriging using a spherical model based on the nearest 20 neighbors with the Kriging tool in ArcGIS Version 9.3.1 (ESRI, Inc., 2009e). Based on kriging estimates, the density of ordnance at the center point of each grid square was identified (hereafter “Ordnance”).

*Models of live tortoises and tortoise sign vs. slope and anthropogenic and predator variables.*—We used generalized linear models (GLMs) to analyze the densities of live tortoises and densities of tortoise sign in relationship to Slope, Mammals, Ravens, Paved, Denuded, and Ordnance (Venables and Ripley, 2002; R Development Core Team, 2012). We modeled live tortoise counts and tortoise sign counts using GLMs based on the Poisson distribution and a log link function, which equates to density models when including an offset based on the log-transformed search area within each grid (McCullagh and Nelder, 1989).

Our use of GLMs carried implicit assumptions about the data, which we relaxed whenever possible or evaluated using second-order corrected Akaike’s information criteria (AIC<sub>c</sub>) based on 31 sampling units (Mazerolle, 2012). We assumed that counts followed a Poisson distribution, which holds many features that are compatible to the behavior of count data in natural systems. Poisson variables are integer-valued, nonnegative, and have a variance equal to its mean. The latter feature is

appropriate for data that exhibit increasing variance with increasing mean; however, it can also be overly restrictive when data are overdispersed, i.e., having variances that exceed the mean. We relaxed this constraint by incorporating an overdispersion factor in our models so that the variance was allowed to differ from the mean. Another conventional assumption of GLM is that the response data (i.e., tortoises) are independent among sampling units (i.e., grids). We relaxed this assumption by incorporating random effects into the model based on clusters of grids to account for spatial correlations between adjacent grids.

Prior to modeling the predictor effects, we assessed the data for overdispersion and spatial correlation based on grids grouped into two-by-two clusters (Dormann et al., 2007). We first accounted for any potential covariate effects by fitting a GLM to each response variable saturated with all covariates and their two-way interaction effects. We then extended the GLM to a generalized linear mixed model (GLMM; Bates et al., 2012) by including a random effect for grid cluster to model spatial correlation, a random effect for each unique grid identifier to model overdispersion, or both, and compared with a GLM based on ordinary dispersion and independence. We compared AIC<sub>c</sub> values among the GLM and the three GLMM (Mazerolle, 2012; AICcmodavg package). We identified the best model based on smallest AIC<sub>c</sub> to determine whether to include overdispersion or spatial correlation when analyzing predictors (Zuur et al., 2009).

Because of the small number of grids, we analyzed models with less than three predictors and one interaction. Prior to analysis we believed any of these predictor combinations could describe the variation in tortoise response. Therefore we examined all combinations equally to avoid biasing the results toward preselected combinations, except we excluded nearly all interaction terms involving Ordnance due to high correlations ( $r > 0.70$ ) between Ordnance terms, for a total of 96 predictor combinations. Models with the smallest AIC<sub>c</sub> best represented the data with the smallest loss of information, and additional models within two AIC<sub>c</sub> units were worthy of consideration (Burnham and Anderson, 2002).

We regarded the null model with no covariates as an uninformative model, and presented models only when they surpassed the null model by an  $AIC_c$  difference  $> 2$ .

Because the large number of models increases the potential for model selection uncertainty, we calculated the main effect of each covariate by model-averaging its coefficient ( $\beta$ ) across all models containing that covariate, excluding models in which that covariate has an interaction effect (Mazerolle, 2012). We standardized all covariates ( $[x - \bar{x}]/s$ ) so that model coefficients represent the effect on tortoises for every one standard deviation ( $s$ ) increase in the covariate. The coefficient  $\beta$  represents positive or negative effects on tortoise sign and live tortoise densities, on the log scale, per  $s$  increase for each covariate. We expressed these effects ( $\pm 1$  SE) as percentage changes by using the transformation  $(\exp[\beta] - 1) \times 100\%$ . We similarly calculated each interaction effect between two covariates by model-averaging the interaction coefficient across all models containing the interaction. Interaction coefficients cannot be interpreted independently from other coefficients; therefore we summarized the cumulative effects by calculating spatially explicit predictions of tortoise response by model-averaging predicted responses across all 96 models (Burnham and Anderson, 2002). We created predictive surfaces for tortoise sign and live tortoises to visualize the outputs of these model-averaged estimates using the Inverse Distance Weighted Spatial Analyst tool in ArcGIS Version 9.3.1 (ESRI, Inc., 2009f).

Our predictive surfaces for tortoise sign and live tortoise densities are based on the weight of evidence from multiple models, each of which assumes a log-linear relationship between tortoises and predictor variables. This assumption ensures that each model predicts positive densities; it can also produce misleading predictions if the predictor-response relationships are not actually log-linear. Our sample was too sparse to formally evaluate this assumption; however, our use of a multi-model framework accounts for some uncertainty in specifying a single correct model. We calculated standard errors to quantify the uncertainty around mean predictions. We calculated cor-

relations between predicted estimates and actual data, paired by grid, to describe the quality of the fit. Squared correlations are analogous to  $r^2$  values in regression analyses.

The unique conditions of the Argus study area precluded the availability of independent data from other sites that could be used to assess the robustness of our models. Instead, we used live tortoise sightings to corroborate our results based on the tortoise sign model. We tested the Pearson correlation between counts of live tortoises and model-predicted tortoise sign, paired by grid (R Development Core Team, 2012). We note that this correlation is positively biased because live tortoises were among the tortoise sign used to develop the predictive model; however, since the majority of tortoise sign were not live tortoises, we believe the correlation is only mildly biased. We similarly tested the correlations between counts of live tortoises and tortoise remains to determine similarities in the distributions of live and dead tortoises. We analyzed the correlation using remains aged  $< 4$  yr, as well as all remains.

## RESULTS

### *Population Attributes of Live Tortoises*

We found 28 live tortoises, of which 27 were captured in spring, and one, an immature 2, that was located for the first time in fall (Table 1). In the brief fall visit, 10 of the 27 were recaptured. The sample was almost equally composed of adults (46.5%) and immature and juvenile tortoises (53.6%). The immature 2 class was poorly represented and no subadults were observed. The sex ratio of subadult and adult tortoises was 10 females to 3 males, which differed from the expected 1:1 sex ratio (Exact binomial test,  $P = 0.0923$ , 90% CI = 0.51–0.93). The crude density of adult tortoises was 2.4 tortoises/km<sup>2</sup> (13 adults /5.42 km<sup>2</sup>). Densities of tortoises of all sizes, based on the predicted live tortoise density models, ranged from 1.2/km<sup>2</sup> to 15.1/km<sup>2</sup> depending on location (Fig. 3). The distribution of live tortoises differed throughout the study area, with lower predicted densities associated with the end of the paved road and near denuded areas where testing occurs and higher predicted densities to the northwest

TABLE 1.—Size–age class distributions of live Desert Tortoises and shell–skeletal remains, with estimated age of shell–skeletal remains collected in 2010 within the Argus study area at the Naval Air Weapons Station China Lake, San Bernardino County, California.

Size–age class structure (carapace length at the midline)	Live tortoise count	Dead tortoise count	
		≤4 yr since death	>4 yr since death
Juvenile 1 (<60 mm)	3	1	—
Juvenile 2 (60–99 mm)	5	7	1
Immature 1 (100–139 mm)	5	6	1
Immature 2 (140–179 mm)	2	2	1
Subadult (180–207 mm)	—	1	1
Adult (≥208 mm)	13	—	11
Totals	28	17	15

and northeast of the denuded areas (Fig. 3; see also models below).

The 28 tortoises appeared to be robust, active, and behaving normally. Juveniles had wide bands of new growth at the seams between the scutes, representing the ample forage available during the spring. No tortoises had wet nares or a purulent discharge, typical clinical signs of mycoplasmosis caused by the pathogens *Mycoplasma agassizii* (Jacobson et al., 1991; Brown et al., 1994; Homer et al., 1998) and *M. testudineum* (Brown et al., 2004; Jacobson and Berry, 2012). Some clinical signs suggestive of mycoplasmosis were evident, however. Eleven tortoises had mild and moderate occlusions of one or both nares. The occlusions appeared to be dirt or soil associated in most cases with layers of soil and plant sap from foraging, not mucus characteristic of mycoplasmosis. Twelve tortoises had moderate to severe edema of the palpebrae and/or periocular area, seven had dried or wet mucus crusts on the palpebrae or in the fornix, and the globes bulged in six tortoises. Such ocular signs are often observed in years of abundant forage and may be the result of sap and detritus from food plants or from disease (e.g., mycoplasmosis or cutaneous dyskeratosis). Twenty-four of the 28 tortoises had signs of active cutaneous dyskeratosis on and between the scales of the fore- and hind limbs covering 40% or less of the limbs. For all but one tortoise, severity of the lesions was rated as mild. Ten tortoises also had mild, active signs of cutaneous dyskeratosis on either plastron or carapace or both.

Signs of trauma were evident on 16 tortoises, all of which were ≥163 mm MCL.

The injuries were healing or had healed. One adult had severe healed injuries to the plastron and gular horn, which had been chewed away (injury typical of a domestic dog; A. Carlson and K. Berry, personal observation; Boyer and Boyer, 2006). Twelve juvenile and small immature tortoises (54–128 mm MCL) had no signs of past or recent injuries. Between the spring survey and early October of 2010, two tortoises were injured by predators: one was a 123-mm-MCL immature with bites and tears to the gular horn, plastron, and carapace and the other tortoise was an adult with injuries to the foreleg.

#### Death Rates and Causes of Death

We collected shell–skeletal remains of 32 tortoises, 17 of which represented tortoises estimated to have died between 2006 and 2010 (Table 1; Fig. 3). Sixteen juvenile and immature tortoises and one subadult female tortoise (MCL = 180 mm) died during that interval. No tortoises marked in spring were found dead during the fall visit; however, one juvenile hatched in summer of 2010 was found dead during the fall visit, killed by a raven. Most remains showed signs of traumatic deaths: broken scutes and bones, and signs of crushing, gnaws, or punctures. For these 17 dead tortoises, potential or probable causes of death included predation by mammalian carnivores (seven) and Common Ravens (two or three), trauma (which could include predation, two), and unknown (five). Remains of three tortoises (one juvenile in a coyote scat) were found at predator sign concentration areas: two sites were scat marking areas and the third was at a coyote rock shelter. Fifteen of the 32 tortoises died >4 yr previously; 12 of the 15 tortoises were subadult or adults. Several had signs of traumatic deaths or predation, but most could not be assigned a cause of death because of the deteriorated condition. The crude annual death rate based on 14 adults and subadult tortoises found to survive or die during 2006–2010 was 1.8% (1 dead out of 14, divided by 4 yr; Table 1).

#### Tortoise Sign

We located 285 tortoise sign: 140 shelter sites, 138 scats, 3 courtship rings, 2 sets of egg

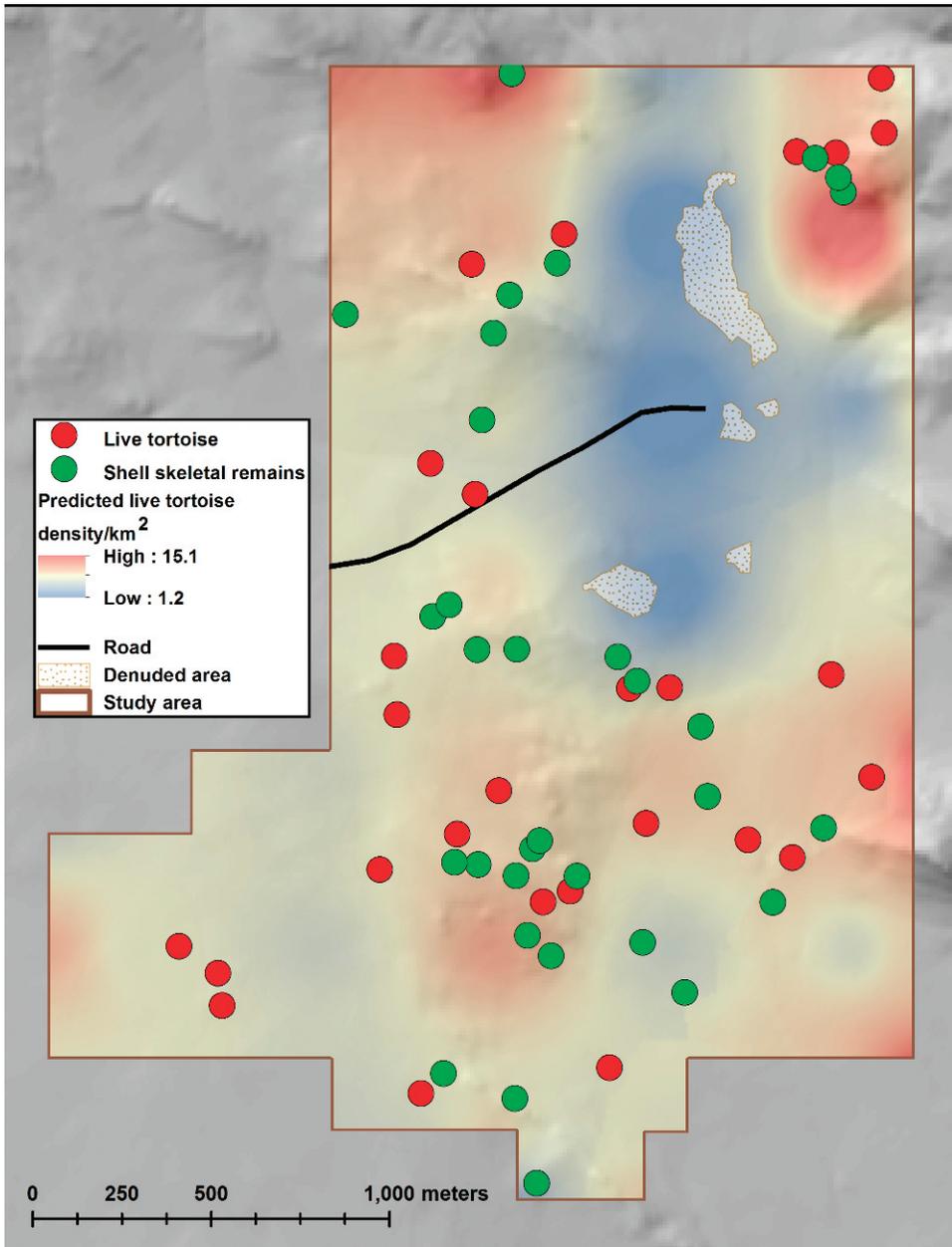


FIG. 3.—The locations of live and dead Desert Tortoises and the modeled predicted densities and distribution of live Desert Tortoises at the Argus study area, Naval Air Weapons Station China Lake, San Bernardino County, California, in 2010. The blue and red colors reflect low and high densities of Desert Tortoises, respectively.

shell fragments, and 2 sets of foot tracks (Fig. 4). Most shelters were burrows (132, 94.3%); only four rock shelters, two caves in calcic soils, and two pallets were observed.

Most shelter sites (110, 78.6%) were of sizes used by adults; 26 and 4 burrows were of sizes used by immature and juvenile tortoises, respectively. Tortoise sign counts (including

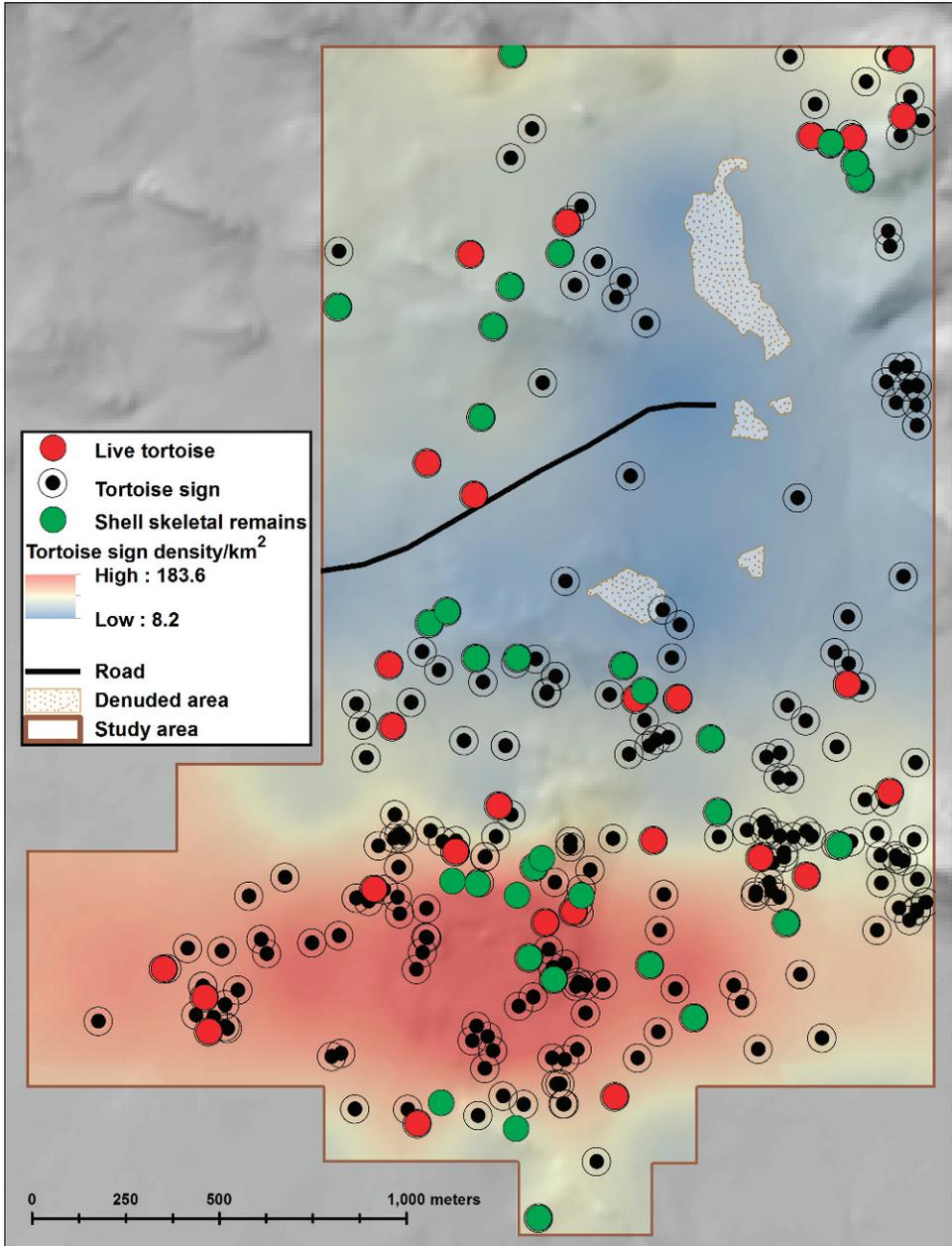


FIG. 4.—The locations of Desert Tortoise sign and the modeled-predicted distribution and density of tortoise sign at the Argus study area, Naval Air Weapons Station China Lake, San Bernardino County, California, in 2010. The blue and red colors reflect low and high densities of tortoise sign, respectively.

live tortoises and shell-skeletal remains) were lower in the northern two-thirds of the study area than in the south (Fig. 4). Predicted densities for sign counts ranged from 8.2/km<sup>2</sup> to 183.6/km<sup>2</sup> depending on location.

#### *Predators*

We recorded from one to three Common Ravens flying or perching on power poles for a total of 16 sightings in spring/583 person-h

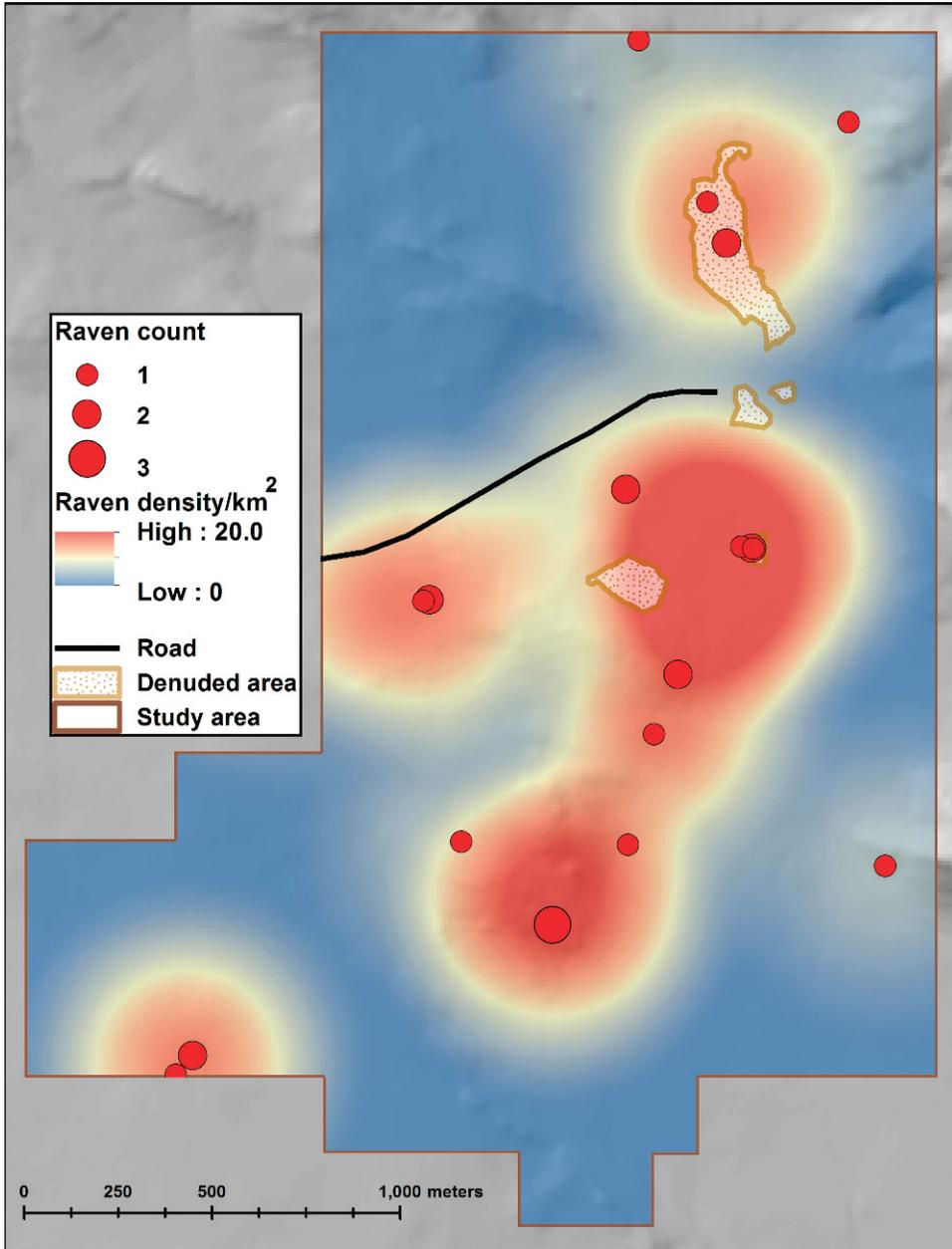


FIG. 5.—Observations of the Common Raven in May 2010 with predicted densities using a 500 m search radius at the Argus study area, Naval Air Weapons Station China Lake, San Bernardino County, California.

and 3 in fall/144 person-h with modeled estimates ranging from 0/km<sup>2</sup> to 20.0 Common Ravens/km<sup>2</sup> (Fig. 5). We also saw one each of three other avian predator species: Prairie Falcon (*Falco mexicanus*), Red-tailed Hawk,

and Northern Shrike. We identified 63 sign concentration areas (scat marking sites, dens, and other shelters) created by mammalian predators (Fig. 6) and of these, 46 were scat marking sites and 17 were dens, tunnels, or

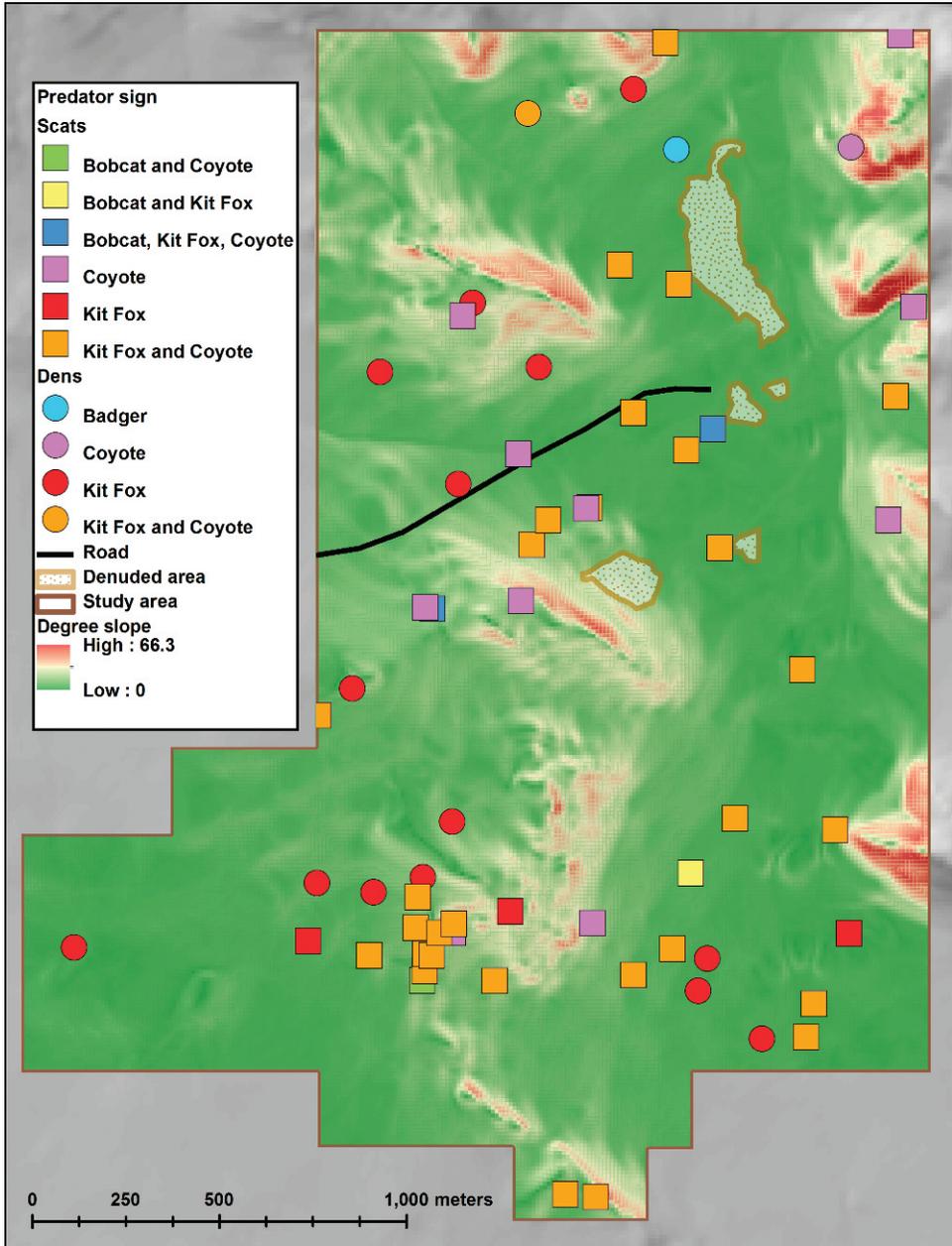


FIG. 6.—Slope and locations of mammalian predator sign at the Argus study area, Naval Air Weapons Station China Lake, San Bernardino County, California.

overhanging rocks used as shelters. These concentration areas were used by combinations of coyotes, kit foxes, and bobcats. Densities of mammalian predator signs ranged from a low of  $0/\text{km}^2$  to a high of  $70.3 \text{ signs}/\text{km}^2$  (Fig. 7).

#### *Anthropogenic Disturbances*

We estimated that areas denuded or partially denuded of perennial vegetation covered 34.52 ha or 6.38% of the area: 4.89 ha were totally denuded of vegetation in the test areas;

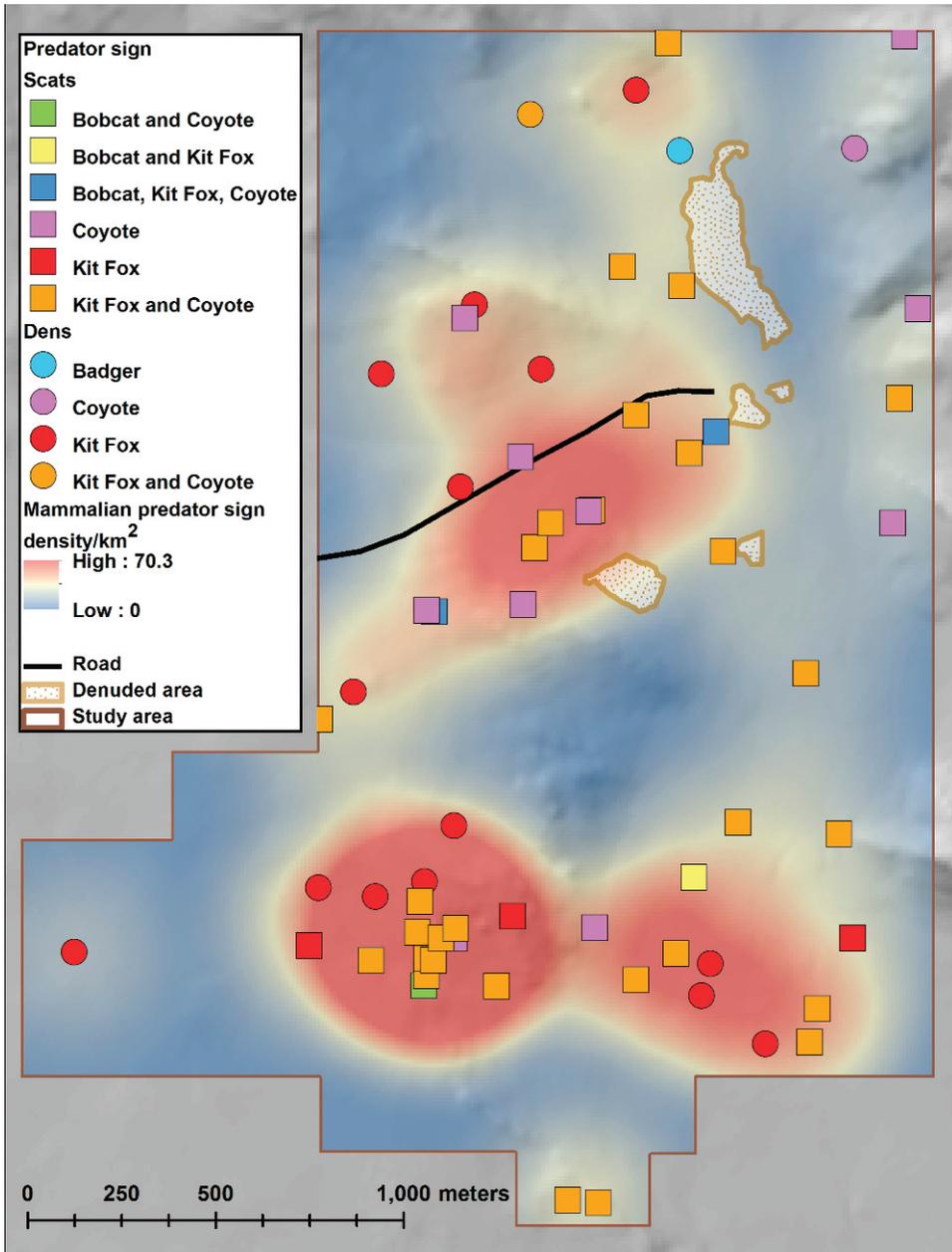


FIG. 7.—Modeled surfaces of mammalian predator sign density using a search radius of 400 m at the Argus study area, Naval Air Weapons Station China Lake, San Bernardino County, California, in 2010.

15.49 ha were partially denuded of vegetation in test areas and boundary trenches; 2.47 ha were composed of pavement, road shoulders, and adjacent denuded areas; and 11.67 ha were dirt roads. The field team counted 10,292 instances of ordnance, trash, balloons, burned

areas, utility lines, fences, and vehicle tracks. Ordnance accounted for 93.1%, followed in descending order by trash (5.4%), burned areas and balloons (each 0.5%), and vehicle tracks (0.4%). Counts of ordnance made on 50 randomly placed transects ranged from 0 to

TABLE 2—Models ranked according to corrected Akaike's Information Criterion ( $AIC_c$ ) using a generalized linear mixed effects model for three Desert Tortoise response variables at the Argus study area in San Bernardino County, California: density of tortoise sign and density of live tortoises. Models are based on one or more of the following covariates, except for the null model: distance from denuded areas (Denuded), distance from paved roads (Paved), density of ordnance (Ordnance), degree of slope (Slope), density of Common Ravens (Raven), and density of mammalian sign (Mammal). The symbol "+" denotes an additive effect and "×" denotes interaction effects. All models are ranked by second-order corrected  $AIC_c$  and listed from best to worst with the number of model parameters (K), log likelihood (LL), difference in corrected  $AIC_c$  relative to the best model ( $\Delta AIC_c$ ), Akaike weight ( $\omega AIC_c$ ), and cumulative weight (Cum wt). Only the models with Akaike weight  $>0.05$  and  $AIC_c$  at least 2 units better than the null model  $AIC_c$  are shown.

Model	K	LL	$AIC_c$	$\Delta AIC_c$	$\omega AIC_c$	Cum wt
Density of tortoise sign						
Denuded × Paved + Mammal	6	-44.05	103.59	0	0.72	0.72
Paved × Raven + Slope	6	-45.30	106.10	2.51	0.20	0.92
Density of live tortoises						
Ordnance × Slope	4	-30.90	71.33	0	0.20	0.20
Ordnance × Slope + Mammal	5	-30.56	73.51	2.18	0.07	0.26

1536 and averaged 40.8; whereas counts of ordnance made on 40 transects associated with the denuded areas ranged from 0 to 327 and averaged 87.3.

*Models of live tortoise density and tortoise sign density with predictor variables and interactions.*—The  $AIC_c$  statistics indicated no support for overdispersion, therefore our prediction models are based on conventional Poisson distributions. We found spatial correlations in the tortoise sign data and retained this spatial correlation structure in the remainder of those analyses. We did not find spatial correlations in the live tortoise data, however. Densities of tortoise sign were best predicted by distances from denuded areas and paved roads and densities of mammalian predator signs in a model supported by 72% of the total Akaike weight of evidence of all models combined (Table 2). A second model with 20% Akaike weight suggested that Common Ravens and slopes, which ranged from 0 to 66.3% (Fig. 6), were also important predictors. The two best models predicting live tortoise density included ordnance and slope and had a cumulative weight of 26% (Table 2). Certain individual covariates or interaction effects appeared repeatedly in supported models, indicating that specific covariates could be more important than specific models.

Tortoise sign density was positively related to degree of slope, increasing  $51 \pm 18\%$  per  $2.26^\circ$  increase in slope (Table 3). Tortoise sign density was also positively associated with

mammalian predator signs, increasing  $40 \pm 11\%$  per increase of 7.5 mammal signs/ $\text{km}^2$ . However, tortoise sign density was negatively related to Common Ravens, decreasing  $31 \pm 10\%$  for every 3.6 additional sightings/ $\text{km}^2$ . Model-averaged main effects based on anthropogenic predictors were not significant, based on CIs overlapping with zero; however, model-averaged interaction effects involving anthropogenic predictors were consistently significant whenever they appeared (Table 3).

No clear relationship emerged for live tortoises, which were observed in considerably lower numbers than tortoise sign (Tables 2 and 3). Only two models appeared to be better than the null model, and none of the main effects estimated in those models was significant. Although two of the model-averaged interaction terms were significant, the model-specific percentage changes associated with those interactions were not significant. Although all covariates seemed to play a role in predicting tortoise density, significant interactions suggest that the effect of covariates on prediction generally varied depending on other variables. We spatially mapped the cumulative effects of the covariates (Figs. 3 and 4). The quality of the regression models is modest but significant. Correlations between model-averaged predictions and observed data were 0.67 for tortoise sign and 0.70 for live tortoises ( $P < 0.0001$ ), analogous to  $r^2 = 0.45$  and  $r^2 = 0.49$ , respectively. While these models support general spatial patterns, the predicted values are subject to considerable error (Appendix I).

TABLE 3—Model-averaged effects and standard errors (SE) on estimated Desert Tortoise response (tortoise sign density, live tortoise density) in relationship to distances from denuded areas (Denuded) and paved roads (Paved), densities of ordnance (Ordnance), mammalian predator (Mammal) and Common Raven (Raven) densities, slope (Slope), and their interaction effects (denoted by ×). The model-averaged effects are for the Argus study area, Naval Air Weapons Station China Lake, San Bernardino County, California.

	Tortoise sign density		Live tortoise density	
	Estimate ± SE	90% CI	Estimate ± SE	90% CI
% change <sup>a</sup>				
Denuded	3 ± 22	-28, 46	22 ± 44	-40, 146
Paved	18 ± 18	-9, 52	-4 ± 24	-42, 58
Ordnance	-9 ± 21	-38, 33	-32 ± 25	-67, 39
Mammal	40 ± 11	22, 60 <sup>c</sup>	-16 ± 17	-43, 24
Raven	-31 ± 10	-46, -12 <sup>c</sup>	5 ± 26	-35, 69
Slope	51 ± 18	24, 84 <sup>c</sup>	54 ± 36	-3, 144
Interaction coefficient <sup>b</sup>				
Denuded × Paved	-0.60 ± 0.11	-0.78, -0.41 <sup>c</sup>	-0.80 ± 0.35	-1.49, -0.10 <sup>c</sup>
Denuded × Mammal	0.42 ± 0.11	0.24, 0.59 <sup>c</sup>	0.62 ± 0.40	-0.16, 1.41
Denuded × Raven	0.48 ± 0.10	0.32, 0.65 <sup>c</sup>	0.43 ± 0.27	-0.09, 0.96
Denuded × Slope	0.61 ± 0.15	0.36, 0.86 <sup>c</sup>	-0.27 ± 0.26	-0.79, 0.25
Paved × Mammal	0.44 ± 0.11	0.26, 0.63 <sup>c</sup>	0.17 ± 0.30	-0.43, 0.76
Paved × Raven	0.54 ± 0.11	0.37, 0.71 <sup>c</sup>	0.54 ± 0.32	-0.09, 1.17
Paved × Slope	0.54 ± 0.14	0.31, 0.77 <sup>c</sup>	0.24 ± 0.27	-0.29, 0.77
Ordnance × Slope	-0.37 ± 0.13	-0.58, -0.15 <sup>c</sup>	1.87 ± 1.17	0.37, 3.37 <sup>c</sup>
Mammal × Raven	0.07 ± 0.11	-0.11, 0.25	-0.11 ± 0.28	-0.66, 0.44
Mammal × Slope	-0.01 ± 0.08	-0.14, 0.13	0.32 ± 0.25	-0.17, 0.82
Raven × Slope	-0.42 ± 0.21	-0.77, -0.07 <sup>c</sup>	0.12 ± 0.33	-0.53, 0.77

<sup>a</sup> Main effects (a) are expressed as percent changes,  $(\exp[\beta]-1) \times 100\%$ , where  $\beta$  is the coefficient for tortoise response variables on the log scale, and

<sup>b</sup> Interaction effects (b) are expressed as  $\beta$ .

<sup>c</sup> Effects with 90% confidence interval (CI) not overlapping zero were significant at  $P < 0.10$ .

Live tortoise sightings corresponded significantly with model-predicted tortoise sign ( $r = 0.37$ ,  $P = 0.042$ , 90% CI = 0.07–0.60). Live tortoises also correlated positively with all tortoise remains ( $r = 0.39$ ,  $P = 0.028$ , 90% CI = 0.11–0.62), but not significantly for tortoise remains from within the previous 4 yr ( $r = 0.28$ ,  $P = 0.12$ , 90% CI = -0.02 to 0.54).

## DISCUSSION

Desert Tortoise populations were more widespread and higher in density in the western, central, and southern Mojave Desert regions during the 1970s and early 1980s (Berry et al., 1986a, 1986b; USFWS, 1994b; Berry and Medica, 1995) than they are today. The existing Argus population fragment (~130 km<sup>2</sup>) was part of this larger, higher-density, and interconnected population that extended from the Argus Range and Searles and Indian Wells valleys south to the southwest border of the geographic range (now the Western Mojave Recovery Unit; Figs. 1 and 2). By 2010, populations were

fragmented, tortoise densities were much lower than previously described, and recovery efforts were challenged by numerous anthropogenic impacts (USFWS, 2010). Although detection of tortoises is imperfect, our 2010 surveys were conducted under conditions that increase visibility, e.g., peak spring activity with abundant forage following above-average precipitation, and few concealment opportunities due to sandy soils and low cover of perennial shrubs. Despite favorable conditions for detection, our estimated densities at Argus for all sizes of tortoises were low; our estimates for densities of adult tortoises (2.4/km<sup>2</sup>) were similar to those reported by the USFWS for the nearest critical habitat 32 km to the south (Fremont-Kramer critical habitat, 2.5/km<sup>2</sup> in 2010; USFWS, 2012).

Low-density population fragments are potentially more vulnerable to loss and extirpation than are large, high-density, and robust populations (Simberloff and Abele, 1982; USFWS, 1994b). The Argus population

fragment has three positive demographic attributes favoring persistence and recovery: (1) the sex ratio favors female adults, (2) juvenile and small immature tortoises composed 53.6% of the sample, and (3) individual tortoises appeared robust and healthy. Other demographic attributes suggest vulnerability to stochastic events such as drought (Inter-governmental Panel on Climate Change, 2007; Seager et al., 2007) and hyperpredation (Kristan and Boarman, 2003; Esque et al., 2010). These attributes limit the potential for population growth and include (1) low population density; (2) small size of the fragment; (3) low survival of immature tortoises and low recruitment into the young, small-adult size class; and (4) frequent predator attacks on all sizes of tortoises, judging from signs of trauma on live tortoises, shell-skeletal remains, and tortoise parts in coyote scat.

The Argus area has several features in common with tortoise critical habitats managed by non-Defense Department agencies: subsidized predators, paved and dirt roads, areas with partially and completely denuded vegetation, patchy distribution of disturbances in the habitats, and close proximity to urban and exurban lands (USFWS, 1994b, 2011). Substantial differences exist too: only scientists and engineers use the site for research-related testing; the general public has had no access since 1942 or earlier; and shooting, hunting, mining, and livestock grazing are not permitted. Surface disturbances have been confined to specific areas, some of which have been in place for decades.

Although our sample was too small to model all covariates simultaneously, we found varying effects on tortoise sign density and live tortoise density in relationship to each of the anthropogenic, topographic, and predator variables across a variety of models. A large degree of evidence, based on Akaike weights, identified the best models for tortoise sign densities, while a lesser weight of evidence identified predictors for live tortoise densities. The significant effects on tortoise sign densities were positive with slope and mammal signs, negative for Common Ravens, and included interaction effects among these predictors as well as ordnance and distances to denuded areas and paved roads; for live

tortoise densities there were significant interaction effects between distances to denuded and paved areas, and between ordnance and slope. Our multi-model inferences allow the cumulative effects of these relationships to be mapped by averaging, weighted by Akaike evidence, all prediction surfaces for tortoise sign density and live tortoise density (Figs. 3 and 4).

#### *Predators and Their Role in Models*

Predators were prominent predictors in models of tortoise sign density, the population attribute with the most evidence. Although densities of tortoises were low at the study area in 2010, female tortoises were producing eggs as evidenced by egg shells, 14 live juvenile and immature tortoises, and remains of 16 dead juvenile and immature tortoises. However, no live subadult or young, small adult tortoises (180–220 mm MCL) were located during the study. Thus recruitment of immature tortoises into the adult population has been limited for several years. The probable cause of low survivorship was predation: the remains of most recently dead juvenile and immature tortoises showed signs of traumatic deaths (broken scutes/bones) typical of avian or canid predators. Further, pressure from subsidized mammalian predators was evident in new attacks on two tortoises between May and October field visits in 2010 and a fresh raven kill of a juvenile in early fall.

Common Ravens and coyotes present obstacles to recovery of low-density, fragmented Desert Tortoise populations through increased mortality. Common Ravens, for example, engage in hyperpredation of juveniles (Campbell, 1983; Boarman, 1993) and can also attack and kill adult tortoises (A.P. Woodman, A. Walde, W. Boarman, personal observations). Common Raven populations have grown substantially in the Mojave Desert, subsidized by resources available in cities, towns, and rural areas, including sewage ponds and landfills, road-killed animals, and perching opportunities from power poles (Boarman and Berry, 1995; Knight et al., 1995; Boarman et al., 2006). Common Ravens have the potential of driving local tortoise populations to extinction (Kristan and Boarman, 2003). Coyotes also are subsidized predators, and subsidies in the form of food and

water are readily available in the urban and exurban developments in Indian Wells and Searles valleys. They can move back and forth between sources of subsidies and adjacent wild lands, where tortoises are more common (Fedriani et al., 2001). During periods of drought, subsidized predators such as coyotes may turn to tortoises as food sources when other prey, such as rodents and rabbits, are in low numbers (Woodbury and Hardy, 1948; Esque et al., 2010). Domestic dogs, ranging from housing areas in the Indian Wells and Searles valleys, also may be responsible for attacks on tortoises, e.g., the tortoise with the severely damaged shell (Boyer and Boyer, 2006).

Tortoise sign density increased with increasing slope on the low hills and with mammalian predator sign (Table 3), a distribution pattern evident in Figs. 4 and 7. Based on sign, both tortoises and their mammalian predators appeared to spend more time in the hills and away from the low areas, where the denuded test areas and the paved road occurred. In contrast, observations of ravens were more concentrated at lower elevations, at the terminus of the road, and in denuded areas, sites with more human use but with fewer tortoise sign (Fig. 4). Thus tortoises are exposed to predator pressure whether in the hills or on flat terrain.

#### *Paved Roads and Denuded Areas*

Paved roads and denuded areas were important predictors of tortoise densities, as evidenced by the most successful model of tortoise sign. The locations and densities of tortoise sign and live tortoises were low near and including the terminus of the paved road and the denuded areas where testing occurs (Figs. 3 and 4). The areas with low tortoise densities extended for distances of 100–300 m beyond the denuded surfaces, thus encompassing about 15% to 25% of the study area. Spatial differences in detectability are unlikely to have contributed to lower tortoise counts in these locations, which tend to be more open than other parts of Argus and have fewer perennial shrubs where tortoises can hide. The effects of paved roads, especially roads with high traffic volume, on depleting adjacent tortoise populations are well known (e.g., von

Seckendorff Hoff and Marlow, 2002; Boarman and Sazaki, 2006). At the Argus site, habitat has been lost from the road, and regardless of the low traffic volume, the roadway itself serves as an attractant to the Common Raven (Knight and Kawashima, 1993; Knight et al., 1995). Areas partially or completely denuded of vegetation—whatever the source of damage—are unsuitable for tortoises: canopy cover of shrubs used for protection from extremes of temperature and predators is minimal or absent, compacted and denuded soils lack forage of annual wildflowers, burrows excavated in denuded areas are vulnerable to human disturbance, and deaths are likely to be higher than in intact habitats (e.g., Bury and Luckenbach, 2002; Berry et al., 2006; Grandmaison et al., 2010). Throughout the geographic range of the Desert Tortoise, roads and denuded areas are frequently coupled: roads terminate in disturbed areas e.g., campsites, off-highway vehicle recreation sites, livestock grazing piospheres, and mining operations. Where roads terminate in anthropogenic uses, we might expect to see more loss of habitat for tortoises than from the denuded surfaces alone, regardless of whether the surface is used for testing explosives and other ordnance or as a livestock watering area, mine, or recreational vehicle encampment.

Denuded areas may have served as a proxy for ordnance in some models. Although ordnance was not a major factor in the models, it may affect health and survival of individuals. Ordnance fragments, common in the denuded and partially denuded test areas, may be eaten by tortoises; chelonians in general are known to consume trash and foreign objects (Boyer and Boyer, 2006). Consumption of potentially toxic materials may contribute to limb and shell lesions, i.e., cutaneous dyskeratosis (Jacobson et al., 1994; Homer et al., 1998), which were common in the Argus tortoises. Static testing of explosives and other ordnance may have negative impacts on tortoises from noise and ground vibrations but we did not measure these impacts.

#### MANAGEMENT IMPLICATIONS

Many factors affect the well-being, distribution, survival, and ultimately the recovery

potential of Desert Tortoise populations. Suites of predictor variables and their interactions are likely to be complex and to vary over time and space. Separating the most from the least important variables can be challenging. The multiple impacts affecting the Argus tortoises are typical of anthropogenic uses occurring on lands managed by the Department of Defense and other government agencies throughout the geographic range of the species. Of the predictor variables we evaluated, only ordnance is primarily restricted to Department of Defense holdings.

Low-density population fragments with few adults and low recruitment of adults are especially susceptible to stochastic events. Networks of roads and denuded areas contribute to habitat loss, reduce the integrity of the fragments, and increase the likelihood of injury and death to the tortoises. Subsidized predators can also increase vulnerability of the population fragment by limiting recruitment of immature tortoises into the adult population and periodically reducing densities of adult tortoises. The close proximity of expanding towns and cities (Hunter et al., 2003) adds to potential predator subsidies. Unless impacts to Desert Tortoises from anthropogenic impacts are limited or mitigated effectively and unless predation from subsidized predators is reduced, the long-term persistence of this and other similar population fragments will be in doubt.

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## APPENDIX I

Predicted densities (counts/km<sup>2</sup> ± 1 SE) and predicted counts (per grid ± 1 SE) of tortoise signs and live tortoises at 31 grids (500 m × 500 m or smaller) comprising the Argus core study area, San Bernardino County, California. Predictions are averaged across all models, weighted by AIC<sub>c</sub> weight, and shown with observed counts. Coefficient of variations (CV = SE/prediction) represent accuracy of predictions.

Gridno	Grid area (km <sup>2</sup> )	Predicted tortoise sign density	Predicted live tortoise density	Observed tortoise sign	Predicted tortoise sign	CV	Observed live tortoises	Predicted live tortoises	CV
1	0.04	49 ± 20	8.0 ± 4.4	0	2.1 ± 0.8	0.41	0	0.34 ± 0.18	0.54
2	0.10	63 ± 31	9.4 ± 5.1	1	6.3 ± 3.1	0.48	0	0.94 ± 0.51	0.54
3	0.10	55 ± 20	3.2 ± 3.0	0	5.5 ± 2.0	0.36	0	0.32 ± 0.30	0.93
4	0.09	61 ± 28	7.2 ± 3.8	15	5.3 ± 2.5	0.46	2	0.63 ± 0.34	0.53
5	0.11	46 ± 15	6.2 ± 1.9	2	5.1 ± 1.7	0.33	0	0.69 ± 0.20	0.30
6	0.25	43 ± 27	6.4 ± 1.8	11	10.8 ± 6.7	0.62	3	1.61 ± 0.45	0.28
7	0.25	14 ± 6	1.2 ± 1.8	3	3.4 ± 1.5	0.44	0	0.30 ± 0.44	1.44
8	0.22	37 ± 30	10.0 ± 6.6	13	7.9 ± 6.6	0.83	2	2.15 ± 1.42	0.66
9	0.11	44 ± 18	5.3 ± 1.6	0	4.9 ± 2.0	0.40	0	0.59 ± 0.17	0.30
10	0.25	42 ± 28	5.3 ± 1.7	5	10.4 ± 7.1	0.68	2	1.33 ± 0.44	0.33
11	0.25	8 ± 5	1.5 ± 1.8	2	2.0 ± 1.3	0.64	0	0.37 ± 0.45	1.21
12	0.22	27 ± 28	3.1 ± 2.4	15	5.8 ± 6.1	1.06	0	0.68 ± 0.53	0.78
13	0.11	20 ± 11	5.3 ± 2.0	1	2.2 ± 1.3	0.57	1	0.58 ± 0.22	0.38
14	0.25	17 ± 7	5.8 ± 2.7	13	4.1 ± 1.8	0.42	0	1.46 ± 0.66	0.45
15	0.25	10 ± 5	2.0 ± 2.1	4	2.6 ± 1.3	0.52	0	0.51 ± 0.52	1.02
16	0.22	24 ± 11	5.4 ± 1.7	9	5.3 ± 2.4	0.45	1	1.18 ± 0.36	0.31
17	0.06	75 ± 41	5.6 ± 4.0	0	4.4 ± 2.4	0.54	0	0.33 ± 0.24	0.71
18	0.19	45 ± 17	4.9 ± 1.7	11	8.7 ± 3.3	0.38	1	0.95 ± 0.33	0.35
19	0.25	35 ± 12	6.1 ± 1.6	35	8.8 ± 2.9	0.33	2	1.53 ± 0.39	0.26
20	0.25	38 ± 14	6.2 ± 2.0	27	9.4 ± 3.4	0.36	4	1.56 ± 0.50	0.32
21	0.22	52 ± 17	6.2 ± 1.8	32	11.3 ± 3.8	0.33	2	1.35 ± 0.38	0.28
22	0.25	89 ± 61	5.3 ± 2.9	20	22.3 ± 15.2	0.68	3	1.33 ± 0.73	0.55
23	0.25	105 ± 62	4.7 ± 2.1	24	26.2 ± 15.4	0.59	1	1.17 ± 0.51	0.44
24	0.25	184 ± 112	7.0 ± 3.6	35	45.9 ± 27.9	0.61	2	1.74 ± 0.89	0.51
25	0.25	103 ± 57	4.6 ± 1.9	16	25.8 ± 14.3	0.55	0	1.15 ± 0.48	0.42
26	0.22	70 ± 37	4.9 ± 1.7	31	15.1 ± 8.1	0.53	0	1.07 ± 0.38	0.35
27	0.03	62 ± 41	5.5 ± 5.1	0	1.8 ± 1.2	0.67	0	0.16 ± 0.15	0.93
28	0.07	46 ± 25	4.7 ± 2.6	1	3.3 ± 1.8	0.54	0	0.33 ± 0.18	0.55
29	0.17	47 ± 22	5.7 ± 2.4	11	7.7 ± 3.7	0.47	1	0.95 ± 0.39	0.41
30	0.12	40 ± 24	5.1 ± 2.3	2	4.9 ± 2.9	0.59	1	0.63 ± 0.28	0.44
31	0.02	29 ± 23	4.1 ± 2.6	0	0.7 ± 0.6	0.80	0	0.10 ± 0.06	0.64
Correlation between observed and predicted					0.67			0.70	