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PROTECTION BENEFITS DESERT TORTOISE (*GOPHERUS AGASSIZII*) ABUNDANCE: THE INFLUENCE OF THREE MANAGEMENT STRATEGIES ON A THREATENED SPECIES

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Abstract: We surveyed an area of ~260 km^2 in the western Mojave Desert to evaluate relationships between condition of Agassiz's Desert Tortoise populations (*Gopherus agassizii*) and habitat on lands that have experienced three different levels of management and protection. We established 240 1-ha plots using random sampling, with 80 plots on each of the three types of managed lands. We conducted surveys in spring 2011 and collected data on live tortoises, shell-skeletal remains, other signs of tortoises, perennial vegetation, predators, and evidence of human use. Throughout the study area and regardless of management area, tortoise abundance was positively associated with one of the more diverse associations of perennial vegetation. The management area with the longest history of protection, a fence, and legal exclusion of livestock and vehicles had significantly more live tortoises and lower death rates than the other two areas. Tortoise presence and abundance in this protected area had no significant positive or negative associations with predators or human-related impacts. In contrast, the management area with a more recent exclusion of livestock, limited vehicular traffic, and with a recent, partial fence had lower tortoise densities and high death rates. Tortoise abundance here was negatively associated with vehicle tracks and positively associated with mammalian predators and debris from firearms. The management area with the least protection—unfenced, with uncontrolled vehicle use, sheep grazing, and high trash counts—also had low tortoise densities and high death rates. Tortoise abundance was negatively associated with sheep grazing and positively associated with trash and mammalian predator scat.

Key words: Desert Tortoise Research Natural Area; Fence; Land use legacy; Mojave Desert; Protected areas; Sheep grazing; Vehicles

Agassiz's Desert Tortoise, *Gopherus agassizii* (hereafter called Desert Tortoise or tortoise), is both a federally and state-listed threatened species with designated critical habitat and recovery plans (US Fish and Wildlife Service [USFWS], 1990, 1994a, 1994b, 2011; California Department of Fish and Wildlife, 2013). Despite recovery efforts, populations have continued to decline and available habitat has been reduced largely because of human-related uses (USFWS, 2010). In 2011, *G. agassizii* was split into two species, *G. agassizii* and *G. morafkai*, and the geographic range of *G. agassizii* was reduced by ~66% (Murphy et al., 2011).

Few populations and places within the geographic range of *G. agassizii* are more threatened than the western Mojave Desert (USFWS, 1994a). Since the arrival of explorers and settlers in the mid-1800s, the desert ecosystem has experienced many uses and changes that have affected the tortoise. The historical patterns of land use have left a legacy that is important for understanding not only the decline of the tortoise and its habitat but also the potential effects of this legacy on current management strategies to recover the species (Foster et al., 2003; Leu et al., 2008). Briefly, in the mid- to late 1800s, early explorers and settlers engaged in dry-land farming and agriculture (Norris, 1982), livestock grazing and ranching (Wentworth, 1948; Powers, 1988, 2000), and mining (Vredenburg et al., 1981). The 1900s were characterized by growth and expansion of human populations, military bases and facilities, energy and transportation corridors, energy developments and facilities, and off-highway vehicle-oriented recreation (US Bureau of Land Management [USBLM], 1973, 1980, 2006; Hunter et al., 2003). With the exception of dry-land farming, these uses have continued and the

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total amount of land with surface disturbances has grown.

Livestock grazing, ranching, and other surface-disturbing activities have caused profound changes to the distribution and composition of annual and perennial vegetation once typical of the Mojave Desert (Minnich, 2008). The invasion and establishment of alien annual grasses, such as the fire-prone bromes (*Bromus madritensis* subsp. *rubens, B. tectorum*) and Arab grasses (*Schismus barbatus, S. arabicus*), have severely altered the biomass and composition of the annual flora in the region (Brooks and Berry, 2006; Brooks et al., 2006) and led to a fire-prone regime in some areas (Brooks and Matchett, 2006). Introduced forbs, such as *Erodium cicutarium* and members of the mustard family, also are highly successful and form a substantial part of the biomass in many areas (Brooks and Berry, 2006; Minnich, 2008). The alien annuals have altered the foods available to the tortoise; the alien grasses, in particular, are not preferred foods in this region (Jennings, 2002) and may be detrimental in diets of juvenile and adult tortoises (Nagy et al., 1998; Hazard et al., 2009, 2010).

Paved and dirt roads and recreational use of off-highway vehicles not only have created surface disturbances but also have provided access to previously remote wild lands (Brooks and Lair, 2009). Roads, whether paved or dirt, vehicle trails and routes, and tracks contribute to invasion and establishment of alien annual plants (Brooks and Berry, 2006). They can alter surface flow of water and nutrients, fragment the ecosystem, and reduce the surface available for food and shelter for the tortoises and other animals (Brooks and Lair, 2009). The increased access and recreational play areas also have created numerous areas denuded or partially denuded of vegetation (Busack and Bury, 1974; Bury and Luckenbach, 2002).

Another legacy associated with growth and expansion of human populations in the Mojave Desert is the concomitant growth of subsidized predator populations. Subsidized predators are predators with population sizes supported by anthropogenic sources of food, water, shelter, and perch sites. Subsidized predators have the potential to increase in numbers far beyond levels provided by the natural desert prey base by using food and water sources in nearby desert towns and settlements. They include the Common Ravens (*Corvus corax*), coyotes (*Canis latrans*), and domestic dogs (*Canis lupus familiaris*). These predators have used the subsidies to expand their populations and have engaged in hyperpredation of tortoises in some areas (Boarman, 1993; Boarman and Berry, 1995; Fedriani et al., 2001; Boyer and Boyer, 2006; Esque et al., 2010).

We designed this research project to evaluate how contiguous areas with three different land-use histories and types of management have affected Desert Tortoise populations and the habitats where they live. For comparisons, we selected the fenced Desert Tortoise Research Natural Area (Tortoise Natural Area) as most protected. The Tortoise Natural Area is internationally recognized as a protected area with an irreplaceability rank for threatened species in the top 6% of protected areas worldwide (Le Saout et al., 2013). We chose critical habitat for the tortoise in the Western Rand Area of Critical Environmental Concern as moderately protected. Critical habitat in this region is contained within three designated management areas: the Western Rand Area of Critical Environmental Concern, western parts of the Rand Mountains Management Area, and Fremont–Kramer Desert Wildlife Management Area and Area of Critical Environmental Concern (USBLM, 1980, 2006; USFWS, 1994b). The Fremont–Kramer Area of Critical Environmental Concern is also on the list of globally protected areas and has an irreplaceability rank for threatened species in the top 2% of protected areas worldwide (Le Saout et al., 2013). Private lands are least protected. Henceforth, we use the terms Tortoise Natural Area, critical habitat, and private lands to refer to the three management areas. These areas are interconnected and experienced similar land-use histories through the 1950s and 1960s, when nearby California City was established and off-highway vehicle-oriented recreation became a change agent in the region (USBLM, 1973). Throughout the interconnected areas, densities of tortoise populations were high in the late 1970s and early 1980s, ranging from 110 to 147

TABLE 1.—Historic density estimates of Desert Tortoise populations from long-term plots in the three management areas between 1979 and 1981, eastern Kern County, California. The density estimates are for all sizes of tortoises and are based on mark–recapture techniques and stratification of the tortoises into size classes for analysis.

Name of plot, size	Location in management area	Year of survey	Tortoise density/km^2 (95% interval)	Reference
Desert Tortoise Natural Area (interior), 1.1 km^2	Tortoise Natural Area	1979	147 (113–192)	Berry et al. (1986a), Berry and Medica (1995)
Desert Tortoise Natural Area Interpretive Center (inside fence), 4.53 km^2	Tortoise Natural Area	1979	131 (111–155)	Berry et al. (1986a)
Fremont Valley, 2.59 km^2	Critical habitat	1981	110 (83–144)	Turner and Berry (1984)
Desert Tortoise Natural Area Interpretive Center (outside fence), 3.24 km^2	Private lands	1979	114 (90–146)	Berry et al. (1986a)

tortoises/km^2, depending on location (Table 1; Turner and Berry, 1984; Berry et al., 1986a; Berry and Medica, 1995). For the three management areas, our objectives were to (1) describe the historical legacy and identify recent differences in management, (2) compare tortoise abundance and other population attributes in 2011, (3) identify natural and anthropogenic factors positively or negatively associated with tortoise abundance in 2011, (4) evaluate differences in mammalian and avian predators in 2011, and (5) discuss factors relevant to future recovery efforts for tortoises and their habitats.

STUDY AREA

General Description

The northern and northeast boundaries of the study area are the Red Rock–Randsburg, Garlock, and Goler paved roads; from these roads, the ~260-km^2 study area extends south through the Fremont Valley and Rand Mountains to the southern boundary of the Tortoise Natural Area (Figs. 1, 2). The only paved road within the study area is a ~8-km stretch of the Red Rock–Randsburg Road, which traverses the northern part of critical habitat. The nearest paved roads to study area boundaries are 1.6 km distant in the west (Neuralia Road), 3.2 km distant in the south (within California City), and 3.2 to 16.0 km in the east (US Highway 395). The settlements of Cantil and Goler Heights are within 4 km in the northwest and 0.8 km in the north, respectively; the towns of Randsburg and Johannesburg (populations 69 and 172, respectively) and the settlement of Red Mountain are within 2.9 km in the northeast; and urbanized California City (population of 14,327; US Census Bureau estimate for 2011) is 3.2 km to the south. More important, four high-use recreation areas are within 5 to 14 km of study area boundaries (Fig. 1): Red Rock Canyon State Park and three recreation areas with unrestricted access for off-highway vehicles (Jawbone Canyon, Dove Springs, and Spangler Hills).

Within the study area, elevations range from 590 m near the edge of Koehn Dry Lake to 1240 m at the crest of the Rand Mountains. Perennial vegetation is predominantly composed of white bur-sage (*Ambrosia dumosa*) and creosote bush (*Larrea tridentata*) alliances (California Department of Fish and Game, 2010), which change with elevation and surface disturbance. At the edge of Koehn Dry Lake in the north, allscale saltbush (*Atriplex polycarpa*) and other *Atriplex* species are common. On the floor of the Fremont Valley and the toeslope of the Rand Mountains, perennial vegetation grades into creosote bush scrub with white bur-sage and many different species of shrubs: cheesebush (*Ambrosia salsola*), goldenhead (*Acamptopappus sphaerocephalus*), spiny senna (*Senna armata*), silver cholla (*Cylindropuntia echinocarpa*), Nevada ephedra (*Ephedra nevadensis*), winter fat (*Krascheninnikovia lanata*), hop-sage (*Grayia spinosa*), Mojave indigo bush (*Psorothamnus arborescens*), Acton encelia (*Encelia actoni*), Mojave Desert California buckwheat (*Eriogonum fasciculatum*), Anderson box-thorn (*Lycium andersonii*), Cooper's box-thorn (*L. cooperi*), and wishbone bush (*Mirabilis laevis* var. *retrorsa*).

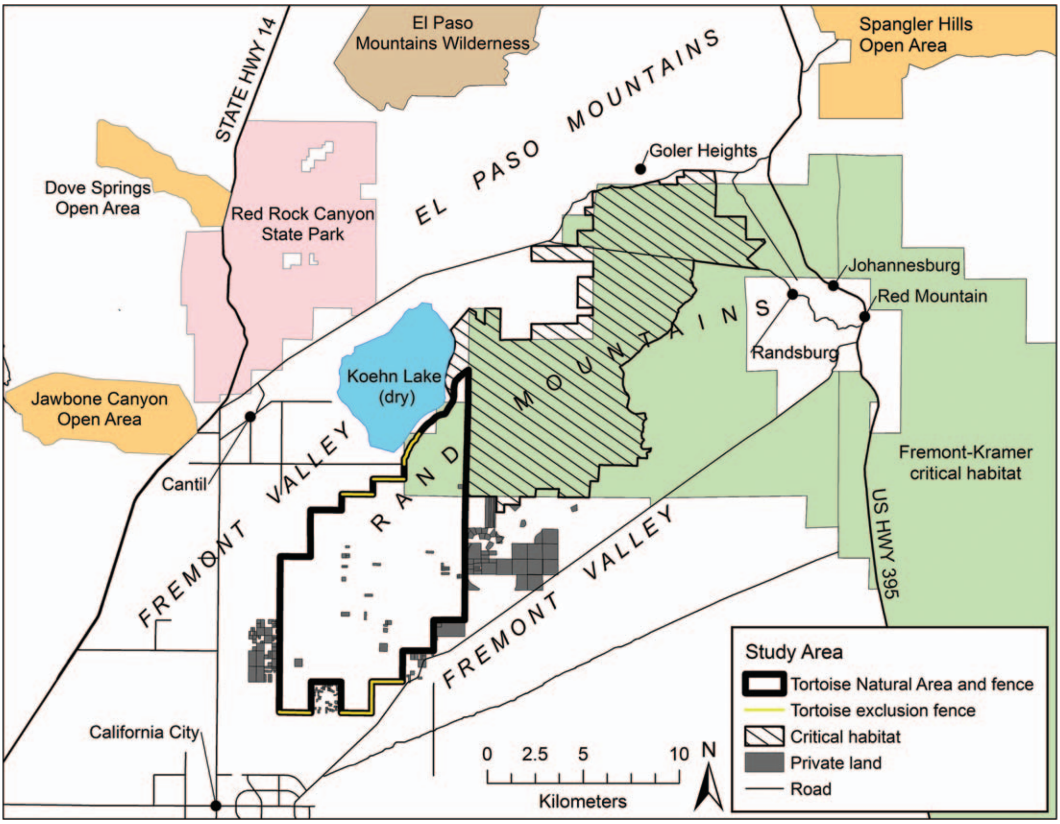

FIG. 1.—General location of the study area and the three interconnected management areas in the western Mojave Desert, eastern Kern County, California. In proximity to the study area are three areas designated for unrestricted recreational vehicle use (orange), a state park (pink), and wilderness (brown). Critical habitat in the western Mojave Desert is shown as green.

Joshua trees (*Yucca brevifolia*) are occasional on the slopes and crest of the Rand Mountains. Plant nomenclature follows Baldwin et al. (2012).

The climate is typical of the western Mojave Desert. The nearby Tehachapi Mountains to the west act as a rain shadow, influencing the amount of precipitation, frequency and velocity of winds, and temperatures. One long-term weather station (Randsburg station) has relevant precipitation data: average annual rainfall is estimated to be 174.24 mm (National Oceanic and Atmospheric Administration [NOAA], 2010–2011). More than 80% of precipitation occurs in fall and winter, between October and March. Overall, the study area is situated sufficiently close to the Tehachapi Mountains to receive more rain than many desert areas at similar elevations farther inland.

Management Areas, Land Uses, and Protections

The three management areas have had different histories of human uses for agriculture, mining, grazing, human settlements, and recreation during the last 40 yr, based in part on land ownership (Table 2; Fig. 2). In the late 1960s and early 1970s, most land within the study area was public and managed by the Bureau of Land Management; the rest was private. The Bureau of Land Management administers public lands for sheep grazing, mining, rights-of-way for transportation and utility corridors, leases, and sales; sheep grazing and mining were predominant uses

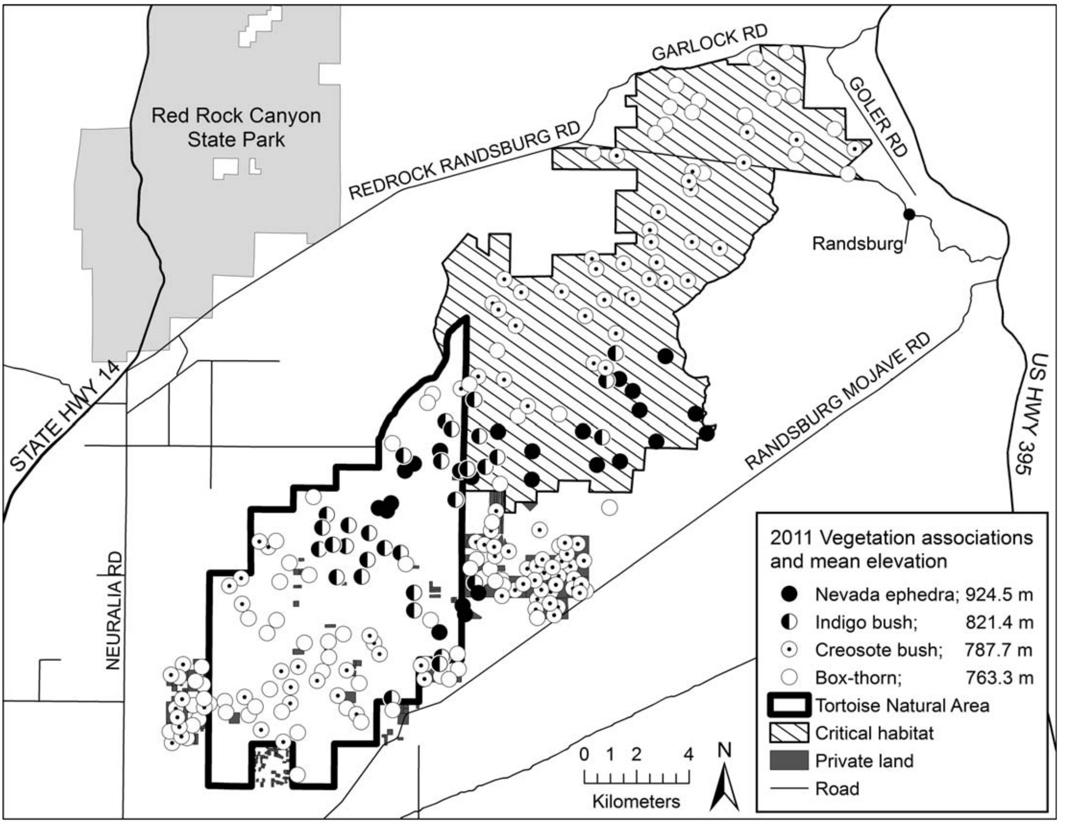

FIG. 2.—The locations of the 240 sampling points and the distribution of the four perennial vegetation associations determined by *k* clustering of means within the study area in the western Mojave Desert, eastern Kern County, California.

of public lands in the area. In the mid-1960s, off-highway vehicle-oriented recreation became a driving force and by the early 1970s, it was a major use in the region (USBLM, 1973). Private lands, mostly unfenced, undeveloped, and with absentee owners, were often in 5- to 10-acre parcels. Sheep also grazed on these properties under the open range provisions of the Kern County Estray Ordinance (established in 1942). Mining exploration occurred, as did uncontrolled, unauthorized off-road vehicle use.

In 1973, the Bureau of Land Management designated specific management areas on public lands as open or closed to recreational vehicle use under a California desert-wide recreation plan for off-highway vehicles (USBLM, 1973). The land that was to officially become the Tortoise Natural Area was closed to recreational vehicles and signs were erected along the boundaries. The land that was later to become critical habitat was designated as open to recreation vehicle use throughout, with no requirement to stay on trails or designated routes (Table 2).

Seven years later, in 1980, two of the three management areas received another, significant change toward protection, with publication of the Bureau of Land Management's *California Desert Conservation Area Plan, 1980* (USBLM, 1980; Table 2). The Tortoise Natural Area was designated as an Area of Critical Environmental Concern and Research Natural Area, and the US Congress formally withdrew these federal lands from the mining laws and livestock grazing. In the same year the Bureau of Land Management finished fencing the boundaries with hog-wire fencing (raised ~25 cm off the ground to permit movements of wild animals) and signed the area as closed to livestock grazing and recreational vehicles. Thus, the first Research Natural Area was created in the California deserts. Also as part of the same management plan, the land later to become critical habitat received two separate designations: the West Rand Area of Critical Environmental Concern and the Rand Mountain–Fremont Valley Recreation Area (USBLM, 1980). Under the 1980 plan, vehicles in both the West Rand Area of Critical Environmental Concern and Rand Mountains–Fremont Valley Recreation Area were restricted to existing routes.

Between 1980 and 2011, additional major changes occurred at the Tortoise Natural Area and on private lands. The Bureau of Land Management and California Department of Fish and Game, in conjunction with the Desert Tortoise Preserve Committee, Inc., a nonprofit corporation, developed a management plan for the Tortoise Natural Area (Bureau of Land Management and California Department of Fish and Game, 1988; Table 2). All three entities purchased small and large private inholdings within the Tortoise Natural Area boundaries for conservation purposes and for providing a wider connecting corridor to the adjacent critical habitat. From the 1990s to 2011, both the Desert Tortoise Preserve Committee and California Department of Fish and Game also began acquisition of private lands adjacent and to the west and east of the Tortoise Natural Area with the purpose of expanding the Tortoise Natural Area. At the time of our study in 2011, these private lands, recently acquired for conservation purposes, were in small and large blocks, had not been fenced, and were unprotected from sheep grazing, recreational vehicle use, shooting, and dumping of trash.

Between 1980 and 2011, the West Rand Area of Critical Concern and Rand Mountains–Fremont Valley Recreation Area experienced three significant protective actions (Table 2). When the Desert Tortoise was federally listed as threatened in 1990 (USFWS, 1990), the Bureau of Land Management closed the lands to livestock grazing to better protect the tortoise. In 1994, critical habitat was formally designated for the Desert Tortoise, and the West Rand Area of Critical Environmental Concern and Rand Mountains–Fremont Valley Recreation Area became part of critical habitat (USFWS, 1994b). However, during these three decades, unauthorized vehicle travel off existing routes was a significant and continuing issue (e.g., Goodlett and Goodlett, 1992; USBLM, 2002) and became the subject of legal action (US District Court, 2009, 2011). To protect the habitat, the Bureau of Land Management fenced parts of the West Rand Area of Critical Environmental Concern and closed the fenced portion to off-highway vehicle use from 2002 to 2008, and again in 2009 because of unauthorized use (details in Table 2).

Methods

Collection of Data on Vegetation, Desert Tortoises, Predators, and Human Impacts

We confined surveys within the study area to public land and to private lands that we had permission to access (lands held by the Desert Tortoise Preserve Committee, Inc.). We assumed, on the basis of 40 yr of experience within the region, that these private lands were representative of much larger areas to the east and west of the Tortoise Natural Area both within and outside our study area boundaries (Fig. 1). To randomly select the hectare plots for the study, we acquired geographic information system layers of land ownership from the Bureau of Land Management (USBLM, 2012) and Kern County (Kern County Engineering, Surveying and Permit Services Department, 2011). We established 80 1-ha plots using random sampling in each of the three types of managed lands for a total of 240 plots across the study area (Fig. 2). The 240 plots constituted a 0.92% sample of the study area. The 80 plots in the West Rand Area of Critical Environmental Concern were within or on the edge of critical habitat.

Field teams surveyed the plots in spring of 2011 (3 April–25 May) using methods similar to those described in Keith et al. (2008). Because detection of live and dead tortoises and other sign is imperfect, we designed field surveys to maximize detection of live tortoises, tortoise sign, predator sign, and anthropogenic impacts. We scheduled surveys to coincide with high aboveground activity levels for all sizes of tortoises, as well as for counting sign

TABLE 2.—Time line for management actions for the three management areas in the Fremont Valley and Rand Mountains, eastern Kern County, California.

Management area	Years	Land use and management action	References
All management areas	1950s–1970	Mix of public land managed by the Bureau of Land Management and private lands with absentee landowners; checkerboard of public and private land in southern part of study area.	Bureau of Land Management files, land-ownership maps; master title plats; Vredenburg et al. (1981),
		Sheep grazing: Cantil Common allotment with 15 operators and ~20,000–30,000 sheep.	Starry (1974); USBLM (1993)
		Mining exploration (bulldozed roads, exploration pits).	
	1960–1970	Growth of off-road vehicle recreation.	
Tortoise Natural Area	1973	Early boundaries of what was to become the Desert Tortoise Research Natural Area were established in a management plan; area posted with signs as closed to recreational vehicle use.	USBLM (1973)
	1974	Desert Tortoise Preserve Committee, Inc., formed to help establish a Tortoise Natural Area.	
	1979–1980	Desert Tortoise Preserve Committee begins land acquisition.	
	1980	US Congress withdraws Tortoise Natural Area from mining; Bureau of Land Management formally designated the Tortoise Natural Area as both a Research Natural Area and Area of Critical Environmental Concern; sheep grazing terminated; fencing of the Tortoise Natural Area completed, excluding recreational vehicles and sheep; interpretive kiosk constructed.	USBLM (1980)
	1988	Management plan for the Tortoise Natural Area published.	USBLM and California Department of Fish and Game (1988)
	1990s–2011	Ongoing land acquisition of inholdings by Bureau of Land Management, Desert Tortoise Preserve Committee, and California Department of Fish and Game, first inside Tortoise Natural Area boundaries then on adjacent private lands.	
	2006	Bureau of Land Management publishes West Mojave Plan; affirms expansion of Tortoise Natural Area through acquisition of private lands to west and east.	USBLM (2006)
	2010	Fence extended to ground in several areas (11.8 linear km) to prevent tortoises from leaving the Tortoise Natural Area and being hit by vehicles.	
Critical habitat	1973	Public lands in the Fremont Valley and Rand Mountains, not including Tortoise Natural Area, open to unrestricted recreational vehicle use (off-road vehicle racing, mass events). Between 1973 and 1987, from 3 to 34 competitive events occurred annually with numbers of participants (not including observers) ranging from 994 to 10,845. Other land uses continue (e.g., sheep grazing, mining).	USBLM (1973, 1993)
	1980	Bureau of Land Management modified the 1973 decision and designated the West Rand Area of Critical Environmental Concern (72.3 km^2) and the Rand Mountain–Fremont Valley Recreation Area. Recreational vehicle use limited to existing roads and routes but not enforced. Other land uses continued (e.g., sheep grazing, mining).	USBLM (1980)
	1980–2011	Unauthorized vehicle activities off existing routes continue.	USBLM (2002, 2006)
	1990	USFWS formally lists the Desert Tortoise as a threatened species; Bureau of Land Management closes potential critical habitat in the West Mojave to sheep grazing.	USFWS (1990)

TABLE 2.—Continued.

Management area	Years	Land use and management action	References
	1993	Bureau of Land Management publishes Rand Mountains–Fremont Valley Plan, closing some off-highway vehicle routes, thereby reducing route density from 5.1 km/km^2 to 0.86 km/km^2 in the West Rand Area of Critical Environmental Concern and on lands scheduled to be designated as critical habitat in 1994. The boundaries of the West Rand Area of Critical Environmental Concern are proposed for expansion to the north and northeast by 53.1 km^2.	USBLM (1993)
	1994	Parts of the Fremont Valley and Rand Mountains were designated as critical habitat. Most of the West Rand Area of Critical Environmental Concern is in critical habitat.	USFWS (1994b)
	1995, 2002, 2005	Southern boundary of West Rand Area of Critical Environmental Concern fenced in 1995 to curtail unauthorized off-route use by recreational vehicles; northern and eastern boundaries fenced in 2002; two internal routes fenced in 2005 to protect tortoise habitat from off-highway vehicle use	
	2006	West Rand Area of Critical Environmental Concern is expanded north and northeast to include 53.1 km^2.	USBLM (2006)
	2002–2008, 2009–2011	Original West Rand Area of Critical Environmental Concern boundaries closed to off-highway vehicle travel to protect the tortoise and manage noncompliance of off-highway vehicle use; reopened temporarily to off-highway vehicle use between 2008 and 2009, then closed again.	USBLM (2002)
	2009	Center for Biological Diversity and other plaintiffs file suit in US District Court seeking protection from unauthorized off-highway vehicle use and reduction in route density.	US District Court (2009, 2011)
Private lands	1970–2011	Private land in a few large and many small parcels, not posted; absentee landowners, often unaware of location of parcels.	
		Private lands are open to sheep grazing under Estray Ordinance, unless fenced. Grazing often intensive, unregulated.	County of Kern, California (1942)
		Off-highway recreation intensive, unauthorized, without regard to land ownership.	
	1995–2011	Desert Tortoise Preserve Committee and California Department of Fish and Game acquire lands to east and west of the Tortoise Natural Area to add to the Tortoise Natural Area. In 2011 these private lands remain unfenced.	
	2011	Desert Tortoise Preserve Committee begins installation of protective signage on recently acquired private lands abutting the eastern boundary of the Tortoise Natural Area.	

(Zimmerman et al., 1994; Lance and Rostal, 2002). We selected a field team with demonstrated expertise in finding all sizes of live tortoises, shell-skeletal remains (including fragments), and other tortoise sign. Field team members also were experienced in finding predator sign and counting anthropogenic impacts. Each plot was surveyed twice and on the same day, with rare exceptions, by walking 10-m-wide transects: once in a N–S direction and then in an E–W direction to collect data on perennial vegetation, live tortoises, tortoise sign, shell-skeletal remains, predators, and human-related impacts. If sign was difficult to see with rough terrain or dense vegetation, the transect width was narrowed.

Vegetation.—Because tortoise distribution and abundance may differ among vegetation associations, we prepared a list of all perennial plant species likely to occur within the study area (shrubs, bunch grasses, cacti). For each plot, field-workers recorded data on these species by relative abundance: (0) absent from the plot, (1) one or two individuals, (2) rare, (3) sparse, (4) common, or (5) dominant or ubiquitous (for definitions, see Glossary in Baldwin et al., 2012). The surveyor finalized ratings for each plant species after covering the plot twice.

Live tortoises.—We processed live tortoises encountered on and off plots using protocols described by Berry and Christopher (2001). We recorded tortoise location, activity, and sex, and took measurements on carapace length at the midline, plastron length from notch to notch, and weight. We collected data on clinical signs of infectious disease, shell disease, and trauma. Observations for potential infectious diseases included general condition and behavior (e.g., active, listless, unresponsive); appearance of the nares (e.g., presence or absence of a nasal discharge; amount, color, and opacity of discharge; occlusion of nares); presence of a discharge from the chin glands during the nonbreeding seasons in adult males and at any time of year in adult females and juveniles; appearance of eyes (e.g., sunken, wet, or crusted); presence of caked dirt in, on, or near the beak or on the forelegs; and ulcers, plaques, or other lesions in the oral cavity. Of particular interest were signs of infectious disease, e.g., upper respiratory tract disease caused by mycoplasmosis (Jacobson et al., 1991; Brown et al., 1994, 2004; Johnson et al., 2006), lesions in the mouth typical of herpesvirus (Johnson et al., 2005; Jacobson, 2007), a shell disease described as cutaneous dyskeratosis (Jacobson et al., 1994; Homer et al., 1998), and trauma from dog attacks (Boyer and Boyer, 2006). We ranked the distribution, severity, and chronicity of clinical signs as none, mild, moderate, or severe on forms similar to those published in Berry and Christopher (2001).

We took digital photographs of the carapace, plastron, posterior left costal, right and left eyes and periocular areas, and a frontal view of the nares and beak. If the tortoise had ectoparasites, or unusual anomalies or injuries (e.g., missing limb), we took additional images.

Shell-skeletal remains.—Field-workers collected shell-skeletal remains encountered on and off plots. Before collecting the remains, they noted condition of the remains and signs of human activities or predators that may have caused or contributed to the death (e.g., trail or tracks of vehicles, human footprints, or predator scat). They took photographs of the remains in situ to document the setting where death may have occurred. In addition, they took at least three images of each shell-skeletal remains before handling: (1) a general picture showing the remains within the context of soils, vegetation, and land uses (if any); (2) a close-up image of the remains; and (3) a close-up image of the oldest and most deteriorated portion of the scutes and bones. Then they placed remains in a heavy-duty ziplock plastic bag for transfer to the US Geological Survey Field Station for further analysis.

Tortoise sign.—We primarily collected data on two types of tortoise sign: cover sites and scat. We measured and assigned shelters or cover sites (defined as burrows, caves, pallets, and rock shelters used by tortoises after Burge, 1978) to one of five classes on the basis of recency of use and condition (Berry et al., 2008; Keith et al., 2008). Similarly, we measured, aged, and recorded the number and sizes of tortoise scats using three age classes of recency and states of deterioration (Berry et al., 2008; Keith et al., 2008). Additionally, we identified and estimated recency of tortoise tracks by looking for impressions of scales and marks from toenails and tails. For courtship rings, we looked for depressions with freshly churned soil, tortoise tracks, drag marks from plastrons, and small areas of dried, clotted soil. At drinking sites, we looked for impressions of toenails in dried mud and scats.

Predators.—To evaluate geospatial relationships between predators and live and dead tortoises and other tortoise sign, the field team searched for perches, nests, roosts, burrows, dens, and scats of avian and mammalian predators. They recorded numbers and locations of these sites and also examined them for fragments of tortoise skin, scutes, and bones.

Human impacts.—To document historical and ongoing land uses, field-workers collected data on types and amounts of human disturbance.

Data Analysis

Vegetation.—We categorized plots by vegetation association by performing k-means clustering analysis on perennial plant data (Version 6.0; StatSoft, Inc., 2001) using the six ordinal categories of abundance. We specified $k = 4$ clusters for the analysis, and then verified that the four associations of perennial species were of biological significance by evaluating composition, relative abundance, and diversity within each of the vegetation associations and comparing each cluster to the Hierarchical List of Natural Communities with Holland Types (California Department of Fish and Game, 2010) to assign a vegetation community name. We used ANOVA to compare elevations among different vegetation associations and Tukey honestly significant difference (Tukey HSD) tests to conduct pair-wise comparisons. We considered those species with mean relative abundance values greater than the midpoint between the minimum and maximum relative abundance values (2.35) as "abundant species." We also used exact binomial tests to perform pair-wise comparisons among the numbers of plots associated with each vegetation association to identify differences both within and among management areas (binom.test function; R Development Core Team, 2013).

Underlying all statistical tests was the assumption that our plots were independently random in their representation of each management area. This assumption was met by the random process in which the plots were selected; however, we systematically excluded certain private lands not held by the Desert Tortoise Preserve Committee because of privacy considerations. We have no reason to expect that our sample plots differed substantially from the excluded private lands. The ANOVA tests further assume that data are normally distributed and homoscedastic. We did not need to check these assumptions, because our models are highly robust to nonnormal distributions due to the well-established asymptotic properties of the model test statistics (Arnold, 1981). For example, Jacqmin-Gadda et al. (2007) used sample sizes of 50 and 200 simulated nonnormal data to demonstrate that general linear mixed models, as a generalization of ANOVA models, had accuracy rates similar to those when performed on correctly specified normal data. We considered $P < 0.05$ as statistically significant for the ANOVA, Tukey HSD, and binomial exact tests.

Live and dead tortoises.—We assigned a size–age class to live tortoises by carapace length at the midline: juvenile $\leq$ 99 mm, immature = 100–179 mm, small adult/subadult = 180–207 mm, and adult $\geq$ 208 mm. To assess whether sex ratios of subadult and adult tortoises differed significantly from the expected 1:1 ratio, we used exact binomial tests to compare numbers of females and males. We used a 1000-simulation bootstrap to estimate densities (tortoises/km^2) and 95% confidence intervals of live subadult and adult tortoises and all sizes of tortoises for each of the three management areas, as well as for the entire study area (Barreto and Howland, 2006). To avoid cumbersome reporting, we presented the estimated densities/km^2 followed by the 95% interval in parentheses. We also estimated relative age of adults using age classes developed by Berry and Woodman (1984). For shell-skeletal remains, we measured or estimated carapace length, estimated time since death (dead $\leq$ 4 yr, $>$ 4 yr), and assigned causes of death (see details of methods in Berry et al., 2013). We calculated crude annual death rates for each management area, specifically for adult tortoises found dead on plots and with an estimated time since death of $\leq$ 4 yr; we used the equation $d = D/N$, where D is the number of dead adults/4 yr, and where N is the number of live and dead adult tortoises on plots.

Comparisons of predator activity and anthropogenic impacts among management areas.—We compared counts of Common Ravens (Ravens) and mammalian predator scat (Mammals) found on plots. We similarly compared surrogate variables for anthropogenic impacts, measured specifically as counts of sheep scat (Sheep); vehicle tracks (Vehicles); trash (Trash); shooting debris, including casings, shells, and targets (Firearms); and mines (Mines). We calculated amount of surface disturbance (m^2) for partially and completely denuded areas, dirt roads, and vehicle routes, trails, and tracks. For variables with abundant counts ($>$ 10 total per management area), we used generalized linear models (McCullagh and Nelder, 1989) with a log link function to analyze differences among management areas (glm function; R Development Core Team, 2013). We used quasi-Poisson distributions in our models when overdispersion was evident (i.e., variance $>$ mean μ). Thus, we corrected the SEs by modeling variance as $\mu \times \o$ (mean $\times$ overdispersion parameter; Zuur et al., 2009). For variables with low counts, we conducted exact binomial tests between pairs of areas to determine significant differences (binom.test function; R Development Core Team, 2013). We considered variables with $P < 0.10$ as statistically significant for the models and used 90% confidence intervals.

Models of tortoise presence across the study area.—We used generalized linear models with a logit link for binary outcomes of tortoise presence to examine the relationship between tortoise presence and the covariates for the three management areas combined and for each management area separately (R Development Core Team, 2013). Tortoise presence was indicated by the occurrence of live tortoises, shell-skeletal remains, and tortoise sign on each plot. Tortoise sign can be used as a surrogate for live tortoises, because a positive correlation has been demonstrated between tortoise sign and tortoise densities (Krzysik, 2002). Hereafter live tortoises, shell-skeletal remains, and tortoise sign collectively are called tortoise sign. We treated tortoise sign as a binary response variable where 0 = no live or dead tortoises or sign detected on the plot, and 1 = live, dead, or sign detected on the plot.

We evaluated all variables for indications of outliers that had >10% influence on correlations with tortoise sign using the Pearson r influence feature in Systat (Systat Software, Inc., 2007). We removed one plot on the Tortoise Natural Area that had large trash counts, apparently as a result of an old habitation or mining operation. All explanatory variables except Mines were log-transformed ($\log_{10}$) to normalize their distributions and reduce the influence of unusually large values. We conducted correlation analyses and calculated generalized variance inflation factors to assess multicollinearity (vif function; Fox and Weisberg, 2011). We omitted surface disturbance from models because of high correlations with other predictors ($r > 0.8$). Because multicollinearity can obscure the effects of predictors when used in combination, we used two complementing strategies to model Desert Tortoise presence. Our first approach was to model the relationship between Desert Tortoise presence with each individual predictor alone in a separate model, but including management area and vegetation association effects in every model to control for differences in plot types. Our second approach was to select a set of variables that best predict Desert Tortoise occurrence; we performed backward removal model selection by starting with a full model with all predictors, including interaction effects with management area, and sequentially dropping variables that were not significant according to chi-square tests at the 0.1 significance level (drop1 function; R Development Core Team, 2013). We arrived at a final model when no further variables could be dropped, and estimated the probability and odds of Desert Tortoise presence with respect to significant effects (lsmeans function; Lenth, 2013). For continuous predictors with model coefficients β, we estimated the percent change in the odds of Desert Tortoise presence as $(\exp[\beta] - 1) \times 100\%$.

Models of tortoise abundance for each management area.—Using a separate gener-

TABLE 3.—Vegetation associations found in the three management areas, eastern Kern County, California, in descending order by total plots assigned. Number of species includes perennial species (shrubs, herbaceous perennials, and bunch grasses). Bold values for creosote bush indicate that significantly more plots were assigned to this association than to other vegetation associations in the respective management areas. Elevation values sharing a superscript capital letter were not statistically different at $P < 0.05$.

Vegetation association name	Total plots assigned				No. of species	No. and % abundant species	Elevation range (m)	Elevation mean (m) ± SE
	Tortoise Natural Area	Critical habitat	Private lands	Total plots assigned				
Creosote bush	20	**37**	**49**	106	26	2 (7.7%)	590–960	788 ± 10.6^{BC}
Box-thorn	31	21	26	78	36	5 (13.9%)	613–1027	763 ± 10.6^{C}
Indigo bush	22	8	2	32	31	9 (29.0%)	682–1002	821 ± 13.3^{B}
Nevada ephedra	7	14	3	24	30	11 (36.7%)	753–1210	924 ± 26.2^{A}

alized linear model for each of the three management areas, based on a Poisson (or quasi-Poisson, if overdispersion was evident) distribution and log link function, we modeled tortoise sign counts to examine tortoise abundance in relationship to vegetation associations and anthropogenic and predator variables. As with our presence models, we performed backward removal starting with full models that included the same variables: Vegetation, Sheep (private lands only), Vehicles, Trash, Firearms, Mines (Tortoise Natural Area and critical habitat only), Ravens, and Mammals. Only one sheep scat was found in the Tortoise Natural Area and no sheep scat was found in critical habitat. No mines were found in the private lands. We dropped variables using F and chi-square tests, for quasi-Poisson and Poisson models respectively, until only variables significant at the 0.1 level remained. For continuous predictors with model coefficients β, we used β to calculate the percent change in mean tortoise sign.

RESULTS

Precipitation

Precipitation during the hydrologic year (1 October 2010–30 September 2011) was >218 mm for the fall–winter of 2010–2011 (1 October–30 March), and was above normal. The 2011 records from the National Climate Data Center were incomplete with missing values, and therefore precipitation could have been higher. Rainfall was recorded in every month between 1 October and 30 March. Wildflowers and therefore tortoise forage plants were abundant.

Perennial Vegetation

We identified 39 species of perennial shrubs and four species of perennial grasses on the plots. Creosote bushes and white bur-sage were common to dominant within all four associations. We assigned each plot to one of four vegetation associations (Table 3; Fig. 2): (1) creosote bush/white bur-sage (hereafter creosote bush) had only two abundant species among the 26 species found on these plots; (2) creosote bush/white bur-sage/Anderson box-thorn (hereafter box-thorn) had a total of five abundant species, including cheesebush and goldenhead; (3) creosote bush/white bur-sage/Mojave indigo bush (hereafter indigo bush) had nine dominant species (Anderson box-thorn, cheesebush, goldenhead, Nevada ephedra, Mojave California buckwheat, and desert trumpet, *Eriogonum inflatum*); and (4) creosote-bush/white bur-sage/Nevada ephedra (hereafter Nevada ephedra) was the most diverse, with 11 dominant species (goldenhead, Mojave indigo bush, Mojave California buckwheat, Anderson box-thorn, winter fat, hop-sage, and Mojave aster [*Xylorhiza tortifolia*]). The vegetation associations differed significantly in elevations ($F_{3,236} = 16.158$, $P = 0.001$), with Nevada ephedra occurring at higher elevations than the other three vegetation associations, and indigo bush occurring at a higher elevation than box-thorn (Tukey HSD, $P = 0.034$; Table 3). More plots in critical habitat and on private lands were assigned to the creosote bush association, the least diverse association with only two abundant species, than to the more diverse vegetation associations with more abundant species (exact binomial $P < 0.05$; Table 3).

TABLE 4.—Size–age classes of live Desert Tortoises and shell-skeletal remains occurring on and off plots on the Desert Tortoise Research Natural Area, critical habitat, and private lands in the study area in the western Mojave Desert, eastern Kern County, California.

Plot location	Tortoise Natural Area, on plot (off plot)			Critical habitat, on plot (off plot)			Private lands, on plot (off plot)		
		Dead			Dead			Dead	
Size–age class	Live	≤4 yr	>4 yr	Live	≤4 yr	>4 yr	Live	≤4 yr	>4 yr
Juvenile	2	2 (1)		(3)	1				
Immature	2 (1)	2		(1)	2 (1)			(1)	
Subadult	1		8 (1)	1 (1)	1	3 (2)			
Adult	7 (10)	1 (1)	9 (11)	1 (7)	8 (3)	8 (5)	3 (4)	1	1 (1)
Totals	12 (11)	5 (2)	17 (12)	2 (12)	12 (4)	11 (7)	3 (4)	1 (1)	1 (1)

Live Tortoises

The field team located 17 live tortoises on the 240 plots: 12 in the Tortoise Natural Area, 2 in critical habitat, and 3 on private lands. They observed an additional 27 tortoises off plots, when walking from one plot to another or to and from vehicles (Tortoise Natural Area, 11; critical habitat, 12; private lands, 4). In critical habitat, they observed a tortoise on a vehicle route, a juvenile on a motorcycle trail, and a third tortoise on a road.

The density and confidence intervals for adult tortoises on all 240 plots combined for the entire study area were 5.5 (5.4–5.6)/km^2. When we analyzed densities of adult tortoises separately for the three types of managed lands, the results differed significantly from one another by management area: for the Tortoise Natural Area, 10.2 (9.9–10.4) tortoises/km^2; for critical habitat, 2.4 (2.3–2.6) tortoises/km^2; and for private lands, 3.7 (3.6–3.8) tortoises/km^2. When we estimated densities and confidence intervals for all sizes of tortoises separately for the three types of managed lands, the results were 14.8 (14.6–15.1)/km^2 for the Tortoise Natural Area, 2.4 (2.3–2.6)/km^2 for critical habitat, and 3.7 (3.6–3.8)/km^2 for private lands.

Adults composed the majority of the samples for both on- and off-plot tortoises. For the 17 on-plot tortoises, the composition of the tortoises by size–age class was 11 adults ≥208 mm carapace length, 2 small adults, 2 large immature tortoises, and 2 juveniles (Table 4). The sex ratio of female-to-male subadult and adult tortoises was 9:4 and not statistically different from 1:1 (P = 0.27). Juvenile and immature tortoises were observed only on the Tortoise Natural Area plots. For the 27 off-plot tortoises, the size–age class composition was similar, with 21 adults, 1 small adult, 2 immature tortoises, and 3 juveniles, and the female-to-male sex ratio was 10:12, which was not statistically different from 1:1 (P = 0.83). Overall, for both on- and off-plot tortoises, the female-to-male sex ratio was 19:16 and also not significantly different from 1:1 (P = 0.74). Of the 34 adult tortoises that could be assigned an age class, 38% were young and growing, 24% were of middle age, and 38% were in the old-age classes.

Of the 44 tortoises observed during the surveys, 34 received comprehensive health evaluations. We could not handle the remaining tortoises because of federal permit constraints, but instead recorded some data for each individual on the basis of field observations. Two adult male tortoises, one on private lands and one in the Tortoise Natural Area management area, had moderate clinical signs of upper respiratory tract disease characteristic of mycoplasmosis (damp or wet beak from exudate or bubbles from the nares). Both tortoises also had other clinical signs, such as ocular discharge, crusts on the palpebrae and periocular area, mucus on the globe, and exposed conjunctiva. The nares of 19 other tortoises were partially or completely occluded, potentially from dried exudate or from plant sap or dirt and mud from drinking during rainstorms.

Without exception, signs of predator attacks were evident on all 25 adult tortoises that we handled. Twelve of the 25 had moderate to severe damage to the gular horn; for nine tortoises the gular horn was severely reduced or chewed away completely. Some signs of trauma (extensive chewing) appeared typical of domestic dog attacks. One adult tortoise had a healed injury from crushing, potentially by a vehicle. Two juvenile tortoises had ant heads attached to soft parts of the integument.

Shell-Skeletal Remains and Death Rates

We found shell-skeletal remains of 47 tortoises on plots, and observed 27 off plots (Table 4). We collected more remains from the Tortoise Natural Area and critical habitat plots than from private land plots. Eighteen of the 47 (38.3%) on-plot remains were from tortoises dead ≤ 4 yr: 11 adults, 4 immatures, and 3 juveniles. We assigned the 11 on-plot adult tortoises to two general categories: (1) unknown and found in desert woodrat (*Neotoma lepida*) middens (n = 5), and (2) traumatic deaths (n = 6). We separated traumatic deaths (fractured scutes, bones) by cause, where possible: three showed signs of mammalian predation (one, domestic dog), one had both pellet holes (gunshot death) and punctures, one was probably a vehicle kill, and one was killed by a predator at a site with a Common Raven perch and mammalian predator scats and prey remains. Three of the seven recent juvenile and immature remains showed signs of having been killed by Common Ravens or small mammals; we could not determine the causes of death for the other four. Causes of death for off-plot tortoises were similar and included predation by canids and Common Ravens, gunshot and vehicle kills, and unknown. Remains with evidence of gunshots occurred both within the Tortoise Natural Area and critical habitat; remains of tortoises likely to have been killed by vehicles were in the Tortoise Natural Area and on private lands.

Crude annual death rates for adults for the 4 yr preceding the survey differed by management area. The lowest rate was in the Tortoise Natural Area, with 2.8%/yr, followed in ascending order by private lands with 6.3%/yr and critical habitat with 20.4%/yr.

Tortoise Sign on Plots

We observed sign on 55.0% (44/80) of the Tortoise Natural Area plots, 47.5% (38/80) of critical habitat plots, and 12.5% (10/80) of private land plots (Fig. 3). Sign counts were highest (n = 190) on the Tortoise Natural Area plots, followed in descending order by critical habitat plots (n = 90) and private land plots (n = 20). Scats (n = 159) were the most common type of sign observed, followed by burrows and pallets (n = 77) and shell-skeletal remains (n = 47). The Tortoise Natural Area had ~2 × the total sign count of critical habitat and ~9 × the count of private lands. Shell-skeletal remains accounted for 25.6% of on-plot sign in critical habitat, compared with 11.6% at the Tortoise Natural Area and 10.0% on private lands.

Predators

We observed nine species of potential avian predators both on and off plots: the Common Raven (n = 193), Loggerhead Shrike (*Lanius ludovicianus*, n = 5), Red-tailed Hawk (*Buteo jamaicensis*, n = 4), Golden Eagle (*Aquila chrysaetos*, n = 4), Burrowing Owl (*Athene cunicularia*, n = 2), Greater Roadrunner (*Geococcyx californianus*, n = 1), Northern Harrier (*Circus cyaneus*, n = 1), American Kestrel (*Falco sparverius*, n = 1), and Prairie Falcon (*Falco mexicanus*, n = 1). Common Ravens composed 91.5% of the observations. We saw more avian predators on the Tortoise Natural Area (75 on plots, 13 off plots) compared with critical habitat (12 on plots, 20 off plots) and private lands (32 on plots, 41 off plots). We found remains of a juvenile tortoise below the perch of a Common Raven off plot at the Tortoise Natural Area. Sightings of Common Ravens were more common on plots in the Tortoise Natural Area and private lands than in critical habitat (Table 5; P = 0.002 and P = 0.018, respectively).

We detected three species of mammalian predators by finding concentrated areas of marking sites, dens, and den complexes on plots: kit fox (*Vulpes macrotis*, n = 22), coyote (*Canis latrans*, n = 15), and badger (*Taxidea taxus*, n = 1); we assigned seven additional observations to canid sign, because it was unclear if the scat was from a coyote or kit fox. Signs of concentrated activity by mammalian predators (i.e., dens, marking sites) also were more common on plots within the Tortoise Natural Area (n = 25) than on plots within critical habitat (n = 11) or private lands (n = 9). By far the most common sign was scat or groups of scat deposited by coyotes and kit foxes (Table 5). We found no remains of

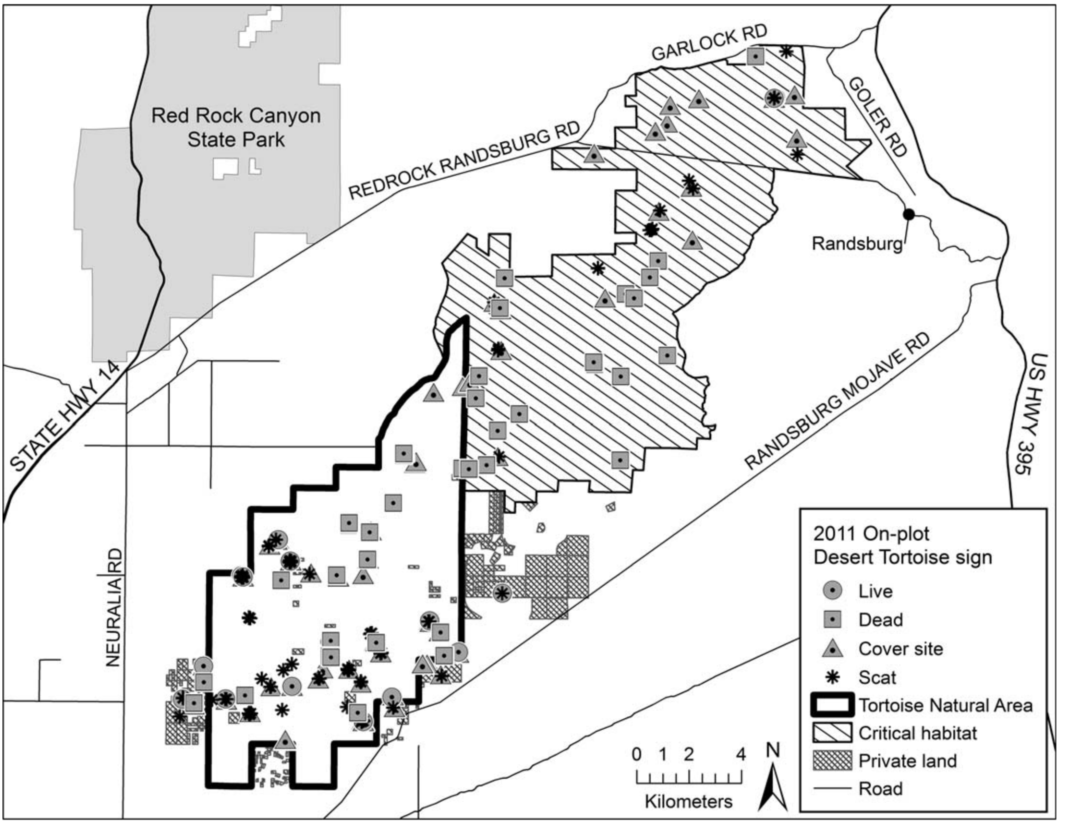

FIG. 3.—Locations of Desert Tortoise sign on the 240 1-ha plots, including live tortoises, remains of dead tortoises, cover sites (burrows and pallets), and scat in three management areas in the western Mojave Desert, eastern Kern County, California.

tortoises in 1222 predator scats or at 26 of the predator dens. We observed one kit fox on a plot and one coyote off plot within the Tortoise Natural Area during the surveys. Although we noted twice as many scat from mammalian predators in the Tortoise Natural Area compared with critical habitat and private lands (Table 5), the differences in scat counts between the three management areas were not significant ($P = 0.15$).

TABLE 5.—Total counts for observations of Common Ravens and mammalian predator scats and five anthropogenic variables in the three types of management areas for Desert Tortoises in the western Mojave Desert, California. Bold font emphasizes a management area with a variable that is significantly higher than the same variable in one or both of the other management areas ($P < 0.05$).

Type of disturbance on plots	Total counts from principal sources of anthropogenic impacts (no. plots affected)		
(Variable names)	Desert Tortoise Research Natural Area	Critical habitat	Private lands
Common Ravens (Ravens)	**88** (40)	32 (24)	**73** (36)
Mammalian predator scat (Mammals)	652 (55)	239 (47)	331 (30)
Sheep scat (Sheep)	1 (1)	0 (0)	**85,208** (77)
Vehicle tracks (Vehicles)	11 (6)	180 (42)	**1407** (73)
Trash, general (Trash)	362 (49)	370 (40)	**1324** (73)
Shooting debris: casings, shells, targets (Firearms)	191 (18)	108 (18)	209 (20)
Mining pits, excavations (Mines)	**6** (4)	**6** (6)	0 (0)

Human Uses

Counts of historic and recent anthropogenic impacts and amounts of area partially or completely denuded of vegetation differed by management area (Table 5). In general, plots on private lands had higher counts and more surface area disturbed by human uses than the other two areas. Total surface area disturbed was 8507 m^2 on the Tortoise Natural Area, 7082 m^2 on critical habitat, and 32,530 m^2 on private lands. Evidence of sheep grazing was almost nonexistent on plots in the Tortoise Natural Area and critical habitat but significantly more prevalent on private land plots ($P < 0.01$). Trash was a common occurrence on plots but counts were highest on private lands ($P = 0.01$), where 91% of plots had trash. On the Tortoise Natural Area, trash was generally old and associated with old homesteads and abandoned mines (broken bottles, rusted cans, old pieces of metal, wood). In critical habitat and on private lands, visitors commonly deposited trash at camp sites, in areas with recreation use, along roadsides, and at edges of urban areas. Counts of debris from shooting (Firearms), another form of trash, were similar on all three management areas ($P = 0.67$); some were very old. Mining was limited to six sites each at the Tortoise Natural Area and critical habitat and was minimal, yet statistically greater than the absence of mining on private lands ($P = 0.03$). With few exceptions, mining consisted of small, shallow pits and bulldozed areas <400 m^2. We considered one pit, covered with boards, as hazardous to tortoises.

Vehicle tracks were least common on the Tortoise Natural Area, although not statistically different from the critical habitat ($P = 0.10$), and significantly more common on private lands ($P < 0.01$; Table 5). The amount of surface area disturbed by vehicle tracks was lowest (467 m^2) on Tortoise Natural Area plots, higher on critical habitat plots (4109 m^2), and highest on private land plots (10,074 m^2). Counts of areas denuded or partially denuded of vegetation by vehicles were lowest in the Tortoise Natural Area and critical habitat ($n = 0$) and highest on private land plots ($n = 297$); total area disturbed was 18,820 m^2 on private lands. One partially denuded area, probably nonvehicle in origin, covered 400 m^2; 12 similar partially or completed denuded areas covering 1736 m^2 occurred on private land plots. Dirt road counts, whether graded or ungraded, were similar on the three management areas; total area disturbed was highest on the Tortoise Natural Area (7640 m^2) and lower on critical habitat and private lands (2863 m^2 and 2320 m^2, respectively). The important difference between the Tortoise Natural Area and other management areas is that dirt roads within Tortoise Natural Area boundaries have received little or no use since 1980. Only landowners with inholdings inside Tortoise Natural Area boundaries can drive to their parcels (a rare event). As a result, shrubs are in the process of colonizing most of these roads.

Models

We began by evaluating relationships between tortoise presence and single predictors. Anthropogenic and predator variables were generally negatively correlated with Desert Tortoise presence, except for Mammals, which was positively correlated; however, the relationships of these single predictors with Desert Tortoises were imprecise, and Sheep was the only predictor with a significant relationship when we considered only one predictor (Table 6). Although no other single predictor had a strong relationship with the Desert Tortoise, when we included all variables together in the full model, Sheep and management area were the only two predictors with a high variance inflation factor (6.9 and 10.7, respectively), which suggests multicollinearity between these variables. After we conducted backward removal model selection, Sheep remained as a significant predictor, with a 21% decrease in odds of occurrence of tortoise sign per twofold increase in Sheep ($P = 0.06$), whereas management area showed differences only with respect to the effects of Mammals within areas (Table 7; Appendix 1). The occurrence of tortoise sign also varied by vegetation association, with box-thorn having the highest probability of occurrence (0.46), about double that of Nevada ephedra and indigo bush (Table 7).

When we modeled the three management areas separately, we found differences in mean numbers of tortoise sign, with the

TABLE 6.—Estimated coefficients from a binomial logistic model on the presence of Desert Tortoise sign (live and dead tortoises and other tortoise sign) based on seven predictor variables (five anthropogenic uses and two types of predator sign). Each coefficient was estimated in isolation by separate models of presence and absence of Desert Tortoise sign, with only management area and vegetation factors included in all models to control for long-term categorical effects. Regression coefficients (β) are presented with SE, *z*-statistic (*z*), *P*-values (*P*), the 90% confidence interval, and the percent change in the odds of Desert Tortoise sign occurrence for a given change in predictor. * = significant at $P < 0.10$.

					Percent change in odds of Desert Tortoise sign		
Predictor variable	β	SE	*z*	*P*	% change	90% interval	Predictor change
Log(Ravens)	−1.056	0.675	−1.56	0.118	−27.2	(−48 to 2)	2× increment in Ravens
Log(Mammals)	0.196	0.332	0.59	0.556	6.1	(−10 to 25)	2× increment in Mammals
Log(Sheep)	−0.726	0.397	−1.83	0.068*	−19.6	(−34 to −2)	2× increment in Sheep scat
Log(Vehicles)	−0.231	0.431	−0.54	0.592	−6.7	(−25 to 15)	2× increment in Vehicle tracks
Log(Trash)	−0.284	0.321	−0.88	0.376	−8.2	(−22 to 8)	2× increment in Trash
Log(Firearms)	−0.017	0.432	−0.04	0.968	−0.5	(−20 to 23)	2× increment in Firearms
Mines	−0.384	0.533	−0.72	0.472	−31.9	(−72 to 64)	1 additional Mine

Tortoise Natural Area having the highest sign (2.2 per plot), followed by critical habitat (0.87) and private lands (0.09–0.43, depending on vegetation association; Table 8; Appendix 1). Desert Tortoises in the Tortoise Natural Area had no positive or negative associations with predators, livestock, or other human-related impacts. In critical habitat, tortoise sign was negatively associated with Vehicles (28% decrease per twofold increase in tracks); in private lands, tortoise sign was negatively associated with Sheep (14% decrease per twofold increase in Sheep). However, numbers of tortoise sign were also positively associated with certain anthropogenic impacts, including Firearms in critical habitat (52% increase per twofold increase in counts of Firearms) and Trash on private lands (26% increase per two-fold increase in Trash), and with Mammals in both critical habitat and private lands (41% and 46% increase, respectively, per twofold increase in mammalian predator sign). In private lands, we found more tortoise sign in the box-thorn vegetation association than in creosote bush ($P = 0.003$); however, we were unable to test the Nevada

TABLE 7.—Estimated probabilities of the presence of Desert Tortoise sign (live and dead tortoises and other sign) in eastern Kern County, California, including three management areas: Tortoise Natural Area, critical habitat, and private lands. Odds are the ratio of probability of presence divided by probability of absence, and change multiplicatively with incremental changes in predictors of binomial logistic models. These estimates and their chi-square tests were calculated by the final binomial logistic model of presence and absence of Desert Tortoise sign after backward removal of nonsignificant variables ($P > 0.10$) from a full model with all predictors. Significance levels: * = $P < 0.10$, ** = $P < 0.05$. Vegetation associations sharing a superscript capital letter were not significantly different ($P > 0.05$).

				Probability and odds of Desert Tortoise sign, or % change in odds of Desert Tortoise sign per increment in predictor	
Predictor variable	df	χ^2	*P*	Estimate (90% interval)	
Vegetation association	3	7.18	0.066*	0.46 (0.35 to 0.56)^{A}	Probability, box-thorn
				0.83 (0.54 to 1.30)	Odds
				0.35 (0.26 to 0.45)^{AB}	Probability, creosote bush
				0.53 (0.35 to 0.81)	Odds
				0.25 (0.14 to 0.39)^{B}	Probability, indigo bush
				0.33 (0.17 to 0.65)	Odds
				0.20 (0.10 to 0.36)^{B}	Probability, Nevada ephedra
				0.25 (0.11 to 0.56)	Odds
Log(Sheep)	1	3.53	0.06*	−21% (−3.5 to −36)	% change, per 2× increment in Sheep
Management area	2	0.539	0.764		
Log(Mammals)	1	0.35	0.554		
Management area × log(Mammals)	2	6.11	0.047**		

TABLE 8.—Estimated mean number of Desert Tortoise sign for each management area: Tortoise Natural Area, critical habitat, and private lands in eastern Kern County, California. These estimates and their chi-square tests were calculated for each management area separately by the final Poisson model (quasi-Poisson for the Tortoise Natural Area), after backward removal of nonsignificant variables ($P > 0.10$) from a full model with all predictors. Significance levels: * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.010$. Incr = increment; Na = not applicable.

Management area	Variable	df	χ^2	P	Mean Desert Tortoise sign, or % change per increment in predictor	
					Estimate (90% interval)	
Tortoise Natural Area	None				2.2 (1.6 to 2.9)	Mean
Critical habitat					0.87 (0.61 to 1.2)	Mean
	Log(Vehicles)	1	3.91	0.048**	−28% (−3.9 to −45)	% change, per 2× incr in vehicle tracks
	Log(Firearms)	1	5.81	0.016**	52% (17 to 97)	% change, per 2× incr in firearms
	Log(Mammals)	1	9.34	0.002***	41% (18 to 69)	% change, per 2× incr in predator sign
Private lands	Vegetation association	3	12.3	0.006***	Na	Mean, Nevada ephedra
					Na	Mean, indigo bush
					0.09 (0.04 to 0.20)	Mean, creosote bush
					0.43 (0.27 to 0.71)	Mean, boxthorn
	Log(Sheep)	1	3.56	0.059*	−14% (−3.2 to −24)	% change, per 2× incr in sheep
	Log(Trash)	1	3.65	0.056*	26% (3.6 to 53)	% change, per 2× incr in trash
	Log(Mammal)	1	5.27	0.022**	46% (15 to 85)	% change, per 2× incr in mammals

ephedra or the indigo bush vegetation associations for differences because the plots were few and no tortoise sign occurred on them (Tables 3 and 8).

DISCUSSION

The topic of protected areas—their role in conserving biodiversity, maintaining populations of rare and endangered species and habitat integrity, and overall management effectiveness—has been a common theme in conservation science during the last decade (e.g., Leverington et al., 2010; Geldmann et al., 2013; Le Saout et al., 2013). Our study explores the effectiveness of three management strategies for two protected areas, the Tortoise Natural Area and adjacent critical habitat, as well as recently acquired private lands, in delivering positive conservation outcomes for the Desert Tortoise by evaluating the tortoise population, predators and predation, and habitat condition in the context of historic land uses and management plans. Our findings represent a spectrum based on land-use histories and protective measures.

Desert Tortoise Populations

Between the late 1970s and early 1990s, densities of all sizes of tortoises declined precipitously in the western Mojave Desert (Table 1; Berry et al., 1986a, 1986b; Berry and Medica, 1995; Brown et al., 1999). At the Tortoise Natural Area and in Fremont Valley, population declines of >90% were documented. The causes were numerous (USFWS, 1994a). Vandalism, vehicle kills on and off roads, and illegal collecting occurred (e.g., Berry, 1986; Berry et al., 1986a, 1986b). Mycoplasmosis contributed to population declines in the late 1980s and early 1990s (Jacobson et al., 1991; Brown et al., 1999). Hyperpredation by the Common Raven, described ~30 yr ago by Campbell (1983), has been and continues as a source of mortality to juvenile and immature tortoises (Berry et al., 1986a; Boarman, 1993; Boarman and Berry, 1995; Kristan and Boarman, 2003). The estimate of population density, 5.5 (5.4–5.6) subadult and adult tortoises/km^2 for the entire study area during spring of 2011, is similar to and within the densities reported by the USFWS using distance sampling, a technique of estimating densities at a landscape scale for critical habitat in the western Mojave Desert (USFWS, 2010). The USFWS reported annual density estimates for adult tortoises (≥180 mm carapace length, includes subadult tortoises) from 2001 through 2007 for the entire western Mojave Desert: mean figures ranged from 3.8 to 6.1 (3.0–8.5)/km^2. In 2011, in a survey of critical habitat in the Fremont–Kramer management area, the USFWS estimated a density of 3.5 adult tortoises/km^2 (USFWS, 2012). Therefore, densities have remained disturbingly low, compared with those reported for periods 26 to 32 yr earlier using mark–recapture studies in the region, e.g., from 40 to 92 subadult and adult tortoises/km^2 (Berry et al., 1986a, 1986b; Berry and Medica, 1995).

During our study, densities of live tortoises were significantly higher inside the Tortoise Natural Area fence than outside in critical habitat (~6×) or private lands (~4×), and sign counts further corroborate the finding. In contrast, critical habitat and private lands had significantly lower densities of adult tortoises and lower tortoise sign counts by >50%. Overall, in all three management areas, the tortoise population was composed primarily of adults in a relatively even sex ratio. The field team observed live juvenile and immature tortoises on plots inside the Tortoise Natural Area and off plots in critical habitat, indicating that some individuals in these age classes were present.

Crude annual death rates for adult tortoises were lowest in the Tortoise Natural Area (2.8%/yr), followed by private lands (6.3%/yr) and critical habitat (20.4%/yr). The high death rates in critical habitat were of particular concern: shell-skeletal remains composed 25.6% of on-plot tortoise sign, whereas in both the Tortoise Natural Area and private lands, shell-skeletal remains were <12% of the total tortoise sign. When causes of death could be determined, they included vehicles, gunshot, and predation by ravens and mammals. We have estimated that subadults and adults in stable populations of this long-lived species probably had annualized death rates of adult age classes of ~2%/yr in the past (Turner et al., 1987).

Subsidized Predators

Counts of Common Ravens and Mammals were highest in the Tortoise Natural Area, followed in descending order by private lands and critical habitat. The modeled relationships between tortoise abundance and predators didn't follow this pattern, however. The models showed no significant associations between tortoise abundance and Ravens in any management area, whereas the results of modeling effects of Mammals on tortoise abundance varied by management area. The most protected area, the Tortoise Natural Area, had no significant associations, positive or negative, with predators, in contrast to critical habitat and private lands, where the association between tortoise abundance and Mammals was positive. However, more than one-third of live tortoises in the study showed signs of predator attacks by mammals (coyotes, kit fox, and dogs), and many tortoise shell-skeletal remains showed signs of predation by mammals as well as Common Ravens. Of particular concern was the moderate to severe damage to shells of 12 of 34 live tortoises; predators severely reduced or chewed off the gular horn in nine cases. Severe injury to the gular horn is typical of dog attacks, which are more common within 5 km of settlements than in remote areas (Andrea Carlson and K.H. Berry, personal observations). A potential confounding factor is that dead tortoises, killed by predators, are included as part of the total tortoise sign used in the models. Furthermore, both the mammalian predators and Common Ravens have the potential to severely limit recovery of tortoise populations and potentially to drive local populations to extinction (Kristan and Boarman, 2003; Esque et al., 2010).

The explanations for the significant positive relationships between tortoise abundance and Mammals in two of the management areas (critical habitat, private lands) may be complex and involve other, unmeasured factors. Subsidies and attractants for mammals in the form of food, trash, and water may be important. Although standing water does not occur within the management areas, year-round food and water are available at one city, two towns, and two settlements within 4 km of the study area edge. The study area also is in proximity to heavily used recreation areas, each with tens of thousands of visitors per year: Jawbone Canyon and Dove Springs off-highway vehicle areas, Red Rock Canyon State Park, the Spangler Hills off-highway vehicle area, and the El Paso Mountains

(Fig. 1). Trash was available in all three management areas but generally was old in the Tortoise Natural Area.

The higher numbers of predator observations in the Tortoise Natural Area may be related to available prey of wild fauna and cover, as well as lack of human disturbances and interference. Studies by Brooks (1995, 1999) support these observations. Brooks reported a greater abundance and diversity of nocturnal rodents, biomass of seeds, and abundance and richness of bird and lizard species inside the fenced Tortoise Natural Area boundaries than outside. Other scientists have reported positive effects of fenced protected areas on birds and carnivores, e.g., populations of two species of foxes were higher inside a fenced protected area than outside (Lenain et al., 2004). The presence of humans may also be a factor, with protected areas offering an escape or greater physical distance from people (Ikuta and Blumstein, 2003; Gehrt et al., 2009).

Desert Tortoise Habitat and Anthropogenic Impacts

In the models, tortoise sign was negatively correlated with two anthropogenic predictor variables, each in a different management area: counts of livestock scat on private lands and vehicle tracks in critical habitat. Scientists have previously identified these predictor variables as contributing to deterioration of habitat and mortality of tortoises (Busack and Bury, 1974; Berry, 1978; Webb and Stielstra, 1979; Nicholson and Humphreys, 1981; USFWS, 1994a; Bury and Luckenbach, 2002; Berry et al., 2008; Keith et al., 2008). At the time of our survey in 2011, the Tortoise Natural Area had been protected from sheep grazing for 31 yr, since 1980, and from most vehicle use for 38 yr, since 1973. In contrast, sheep grazing ended in critical habitat in 1990, the year the Desert Tortoise was federally listed as threatened (USFWS, 1990). Recreation vehicle use was also intensive in critical habitat until the early 1990s, but unauthorized travel off existing routes has continued for decades. Private lands, unless fenced, have no protection from sheep grazing or vehicle use and thus receive heavy use.

Livestock, particularly sheep, have grazed western Mojave Desert lands for over a century (Wentworth, 1948). They have altered composition of perennial and annual vegetation by preferentially consuming edible forbs, perennial grasses, and shrubs (e.g., species of saltbush, hop-sage, white bur-sage, winter fat, Anderson and Cooper's box-thorn). Damage was most severe in the vicinity of watering sites, whether through stock tanks (e.g., Brooks et al., 2006) or watering trucks. In a study on effects of grazing on annual and perennial vegetation, Brooks et al. (2006) reported significant declines in cover, species richness, and density of perennial plants with increasing proximity to watering sites. The declines in cover were due primarily to declines of the small to mid-sized shrubs, e.g., box-thorn, hop-sage, cheesebush, and Nevada ephedra.

Vehicle use off-highway or off paved roads for recreation or other purposes similarly affects perennial vegetation (e.g., Busack and Bury, 1974; Lathrop, 1983; Bury and Luckenbach, 2002; Brooks and Lair, 2009). Where users concentrate camping and racing activities and where route and track densities are high, the result is partial or complete denudation of perennial shrubs, especially the several species of small shrubs occurring between the larger creosote bushes.

The long-term degradation and loss of perennial shrubs by grazing and vehicles probably account for significantly more plots in the creosote bush association on private lands and critical habitat than in the Tortoise Natural Area. The creosote bush association is the simplest and least diverse of the four vegetation associations in our study area, with only two abundant species compared with 5 to 11 abundant species in the other vegetation associations. In contrast, tortoise sign had the highest probability of occurrence in the box-thorn association, regardless of management area.

Both livestock grazing and vehicle use also have negative effects on availability of native annual forbs, important forage for the tortoise, through consumption, trampling, crushing, and compaction (Berry, 1978; Jennings, 1997, 2002; Oftedal, 2002). Grazing and vehicle travel additionally disturb soils, thereby enhancing opportunities for alien annual plants to thrive at the expense of the natives. For example, cover and richness of native annuals declined with increasing proximity to livestock watering sites (Brooks et al., 2006), and density of dirt roads was positively correlated with richness of alien annual species and biomass of the alien forb, filaree, *Erodium cicutarium* (Brooks and Berry, 2006).

Grazing and vehicle use more directly affect tortoises by damaging or destroying burrows, reducing canopies of shrubs used for shelter from predators and temperature extremes, and injuring or killing tortoises (Berry, 1978; Nicholson and Humphreys, 1981; Bury and Luckenbach, 2002). Paved and dirt roads, designated off-highway vehicle routes, and tracks also provide access to users who may shoot tortoises (Berry, 1986).

The significant effects of two other human activities were limited to private lands (Trash) and critical habitat (Firearms). The models showed a positive association between trash and Desert Tortoise abundance on private lands. The finding of a positive association differs from other, similar studies. Keith et al. (2008) reported that plots with tortoise sign had lower counts of trash than plots without tortoise sign, and Berry et al. (2006) noted that tortoise mortality was correlated with trash counts. Effects of trash on tortoises may have both positive and negative elements, and the relationship may change over time and location. Trash can be an indicator of heavy human use and habitat deterioration, as well as an attractant to subsidized predators. Trash also may attract tortoises, who may eat foreign objects out of hunger, accidental ingestion, or curiosity (Walde et al., 2007), or, if the object is sufficiently large, use it as cover. Consumption of trash as a cause of illness and death is well known to veterinarians who work with chelonians, whether tortoises, freshwater turtles, or sea turtles (Donoghue, 2006; Wyneken et al., 2006). Some trash, such as partially crushed cans, collects water during rain events, and can be a source of drinking water for wild tortoises. Debris from firearms may have similar positive and negative aspects. The positive association of debris from firearms with abundance of tortoise sign in critical habitat may have ominous implications: 25.6% of tortoise sign was composed of dead tortoises in this management area.

One surface-disturbing activity, mining, was minimal in the study area and held no significant associations with tortoise abundance in the models. Historically, mining was an important land use in the western Mojave Desert, especially in the Rand Mining District (eastern edge of our study area) and the nearby El Paso Mountains from the 1860s to recent times (Starry, 1974; Vredenburg et al., 1981; Chaffee and Berry, 2006). Mining has not been authorized in the Tortoise Natural Area since the Congressional withdrawal from the 1872 mining laws in 1980, but our surveys showed that some hazardous sites remain.

Overall, this study confirms that the Tortoise Natural Area, with higher densities of Desert Tortoises, has benefited from the protective fence and elimination of grazing and vehicle use. Despite the emergence and spread of a chronic, infectious disease (mycoplasmosis) throughout the western Mojave Desert (Jacobson et al., 1991; Homer et al., 1998; Brown et al., 1999), adult tortoise densities at the Tortoise Natural Area were significantly higher than in critical habitat not only in our study area but also throughout the West Mojave Recovery Unit (USFWS, 2010, 2012). The mammalian predators and avian predators also may have benefited from protection in the Tortoise Natural Area on the basis of our counts, as well as results from previous studies (Brooks, 1995, 1999). In our study, models of tortoise sign and presence suggest that relationships with these predator groups were neither positive nor negative. In other studies, vertebrate species have received benefits from fenced protected areas by reducing human disturbances and limiting transmission of wildlife-borne diseases (Ikuta and Blumstein, 2003; Lenain et al., 2004; Ferguson and Hanks, 2012). In a global analysis of the effectiveness of protected area management, Leverington et al. (2010) identified several factors related to overall success in maintaining biodiversity: legal establishment, design, legislation, and boundary marking. One critical question, addressed in the 1970s for the Tortoise Natural Area, was whether posting of signs alone was a sufficient and effective method for marking the boundary and eliminating unauthorized recreational vehicle use and sheep grazing. Because posting was ineffective, the Bureau of Land Management constructed the hog-wire fence in 1979–1980. Also ineffective was posting of signs to limit recreational vehicle use to existing routes and specific areas in the critical habitat portions of our study area, even after decades of effort by the Bureau of Land Management (e.g., Goodlett and Goodlett, 1992; USBLM, 2002, 2006; US District Court, 2009). As a result, the Bureau of Land Management closed and fenced a portion of the critical habitat in 2002, and this area remained closed with the exception of a year (2008–2009), when the area was reopened. Because of continued noncompliance by off-highway vehicle users, the area was again closed. The many years of sheep grazing and off-highway vehicle use degraded the habitat and therefore are likely contributors to the lower abundance and higher mortality of tortoises in critical habitat in 2011.

Management Applications

Historic and recent human uses affect the functioning of ecosystems (Foster et al., 2003). The three management areas provide examples of how these legacies have become embedded in the sites and how Desert Tortoises, in turn, may have been affected. The legacies are persistent and need to be considered in framing expectations for recovery of the Desert Tortoise and in planning habitat restoration. Other important considerations are the types and levels of protection needed, enforcement of protective measures, and long-term monitoring.

In 1994, the USFWS outlined several activities that were incompatible with recovery of the Desert Tortoise and recommended that these activities be prohibited in recovery areas (USFWS, 1994a). Examples include all vehicle activity off designated roads, uncontrolled dogs out of vehicles, dumping and littering, domestic livestock grazing, and discharge of firearms (except for hunting of big game or upland game birds at specified times). The USFWS recommended emergency closures of dirt roads and routes where human-caused mortality of tortoises was a problem, as well as protective fencing and regular and frequent patrols of law enforcement personnel in areas with unauthorized vehicle use and vandalism. They made specific recommendations for the region where our study occurred, including reducing populations of Common Ravens to limit predation on juvenile Desert Tortoises. A few of these recommendations have been implemented; others remain to be accomplished. The results of our studies provide scientific support for implementing recommendations on livestock grazing, vehicle use off designated roads, and canid and raven predation. Areas such as the Tortoise Natural Area, fenced to prohibit entry of vehicles and livestock, appear to have benefited the Desert Tortoise compared with unfenced areas, if higher tortoise densities and lower mortality rates are used as measures. The recent fencing of parts of critical habitat to reduce unauthorized vehicle use may have similar benefits for Desert Tortoise recovery in the future. The high levels of trauma from canids on live tortoises are likely to inhibit recovery and demonstrate the need for better control of dogs and management of wild canids, at least on a local basis. Dog-proof fencing is an option to consider. Likewise, when Desert Tortoise densities are very low, predation by Common Ravens and mammals inhibits recovery. Government agencies have undertaken control of coyotes and Common Ravens to reduce hyperpredation of Desert Tortoises in limited areas of the Mojave and western Sonoran deserts but not at our study area or in the vicinity (USFWS, 2008a, 2008b). Other causes of death to tortoises, such as shooting and vehicle trauma, still remain to be addressed. The USFWS recovery recommendation on trash and litter has not been implemented on a landscape scale; volunteers collect litter in local areas, however.

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Literature Cited

Arnold, S.F. 1981. Asymptotic validity of procedures under nonnormal distributions. Pp. 141–158 *in* The Theory of Linear Models and Multivariate Analysis. John Wiley and Sons, Canada.

Baldwin, B.G., D.H. Goldman, D.J. Keil, R.W. Patterson, T.J. Rosatti, and D.H. Wilken (Eds.). 2012. The Jepson Manual: Vascular Plants of California. 2nd Ed. University of California Press, USA.

Barreto, H., and F.M. Howland. 2006. The Bootstrap Add-In. Pp. 718–721 in H. Barreto and F.M. Howland (Eds.), Introductory Econometrics: Using Monte Carlo Simulation and Microsoft Excel. Cambridge University Press, USA. Available at http://www3.wabash.edu/econometrics/EconometricsBook/Basic%20Tools/Excel AddIns/bootstrap.htm. Archived by WebCite at http://www.webcitation.org/6LZgPZ8Qs on 2 December 2013.

Berry, K.H. 1978. Livestock grazing and the desert tortoise. Pp. 505–519 in Transactions 43rd North American Wildlife and Natural Resources Conference. Wildlife Management Institute, USA.

Berry, K.H. 1986. Incidence of gunshot deaths in desert tortoises in California. Wildlife Society Bulletin 14:127–132.

Berry, K.H., and M.M. Christopher. 2001. Guidelines for the field evaluation of desert tortoise health and disease. Journal of Wildlife Diseases 37:427–450.

Berry, K.H., and P. Medica. 1995. Desert tortoises in the Mojave and Colorado deserts. Pp. 73–75 in E.L. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac (Eds.), Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. United States Department of the Interior, National Biological Service, USA.

Berry, K.H., and A.P. Woodman. 1984. Preliminary investigations of shell wear in determining adult age groups in desert tortoises. Appendix 4 in K.H. Berry (Ed.), The Status of the Desert Tortoise (*Gopherus agassizii*) in the United States. Desert Tortoise Council Report to US Fish and Wildlife Service, California, USA. Order No. 11310–0083–81.

Berry, K.H., T. Shields, A.P. Woodman, T. Campbell, J. Roberson, K. Bohuski, and A. Karl. 1986a. Changes in desert tortoise populations at the Desert Tortoise Research Natural Area between 1979 and 1985. Proceedings of the Desert Tortoise Council Symposium 1986:100–123.

Berry, K.H., L.L. Nicholson, S. Juarez, and A.P. Woodman. 1986b. Changes in desert tortoise populations at four study sites in California. Proceedings of the Desert Tortoise Council Symposium 1986:60–80.

Berry, K.H., K. Keith, and T. Bailey. 2008. Status of the desert tortoise in Red Rock Canyon State Park, California. California Fish and Game 94:98–118.

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

Boarman, W.I. 1993. When a native predator becomes a pest: a case study. Pp. 191–206 in S.K. Majumdar, E.W. Miller, D.E. Baker, E.K. Brown, J.R. Pratt, and R.F. Schmalz (Eds.), Conservation and Resource Management. Pennsylvania Academy of Sciences, USA.

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

Boyer, T.H., and D.M. Boyer. 2006. Turtles, tortoises, and terrapins. Pp. 78–99 in D.R. Mader (Ed.), Reptile Medicine and Surgery, 2nd Ed. Saunders Elsevier Inc., USA.

Brooks, M.L. 1995. Benefits of protective fencing to plant and rodent communities of the western Mojave Desert, California. Environmental Management 19:65–74.

Brooks, M.L. 1999. Effects of protective fencing on birds, lizards, and black-tailed hares in the western Mojave Desert. Environmental Management 23:387–400.

Brooks, M.L., and K.H. Berry. 2006. Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA. Journal of Arid Environments 67:100–124.

Brooks, M.L., and B.M. Lair. 2009. Ecological effects of vehicular routes in a desert ecosystem. Pp. 168–195 in R.H. Webb, L.F. Fenstermaker, J.S. Heaton, D.L. Hughson, E.V. McDonald, and D.M. Miller (Eds.), The Mojave Desert, Ecosystem Processes and Sustainability. University of Nevada Press, USA.

Brooks, M.L., and J.R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. Journal of Arid Environments 67:148–164.

Brooks, M.L., J.R. Matchett, and K.H. Berry. 2006. Effects of livestock watering sites on alien and native plants in the Mojave Desert, USA. Journal of Arid Environments 67:125–147.

Brown, D.R., J.L. Merritt, E.R. Jacobson, P.A. Klein, J.G. Tully, and M.B. Brown. 2004. *Mycoplasma testudineum* sp. nov., from a desert tortoise (*Gopherus agassizii*) with upper respiratory tract disease. International Journal of Systematic and Evolutionary Microbiology 43:1527–1529.

Brown, M.B., I.M. Schumacher, P.A. Klein, K. Harris, T. Correll, and E.R. Jacobson. 1994. *Mycoplasma agassizii* causes upper respiratory tract disease in the desert tortoise. Infection and Immunity 62:4580–4586.

Brown, M.B., K.H. Berry, I.M. Schumacher, K.A. Nagy, M.M. Christopher, and P.A. Klein. 1999. Seroepidemiology of upper respiratory tract disease in the desert tortoise in the western Mojave Desert of California. Journal of Wildlife Diseases 35:716–727.

Burge, B.L. 1978. Physical characteristics and patterns of utilization of cover sites used by *Gopherus agassizi* in southern Nevada. Proceedings of the Desert Tortoise Council Symposium 1978:80–111.

Bury, R.B., and R.A. Luckenbach. 2002. Comparison of desert tortoise (*Gopherus agassizii*) populations in an unused and off-road vehicle area in the Mojave Desert. Chelonian Conservation and Biology 4:457–463.

Busack, S.D., and R.B. Bury. 1974. Some effects of off-road vehicles and sheep grazing on lizard populations in the Mojave Desert. Biological Conservation 6:179–183.

California Department of Fish and Game. 2010. List of Vegetation Alliances and Associations. Vegetation Classification and Mapping Program. California Department of Fish and Game, USA. Available at http://www.dfg.ca.gov/biogeodata/vegcamp/natural_comm_list.asp. Archived by WebCite at http://www.webcitation.org/6LZggMgzq on 2 December 2013.

California Department of Fish and Wildlife. 2013. State and Federally Listed Endangered and Threatened Animals of California. California Department of Fish and Wildlife. Biogeographic Data Branch, California Natural Diversity Database, USA.

Campbell, T. 1983. Some natural history observations of desert tortoises and other species on and near the Desert Tortoise Natural Area, Kern County, California. Proceedings of the Desert Tortoise Council Symposium 1983:80–88.

Chaffee, M.A., and K.H. Berry. 2006. Abundance and distribution of selected elements in soils, stream sediments, and selected forage plants from desert tortoise habitats in the Mojave and Colorado deserts, USA. Journal of Arid Environments 67:35–87.

County of Kern, California. 1942. Code of Ordinances. Title 7—Animals. Chapter 7.16. Estrays-Grazing areas designated. Available at http://www.co.kern.ca.us/. Archived by WebCite at http://www.webcitation.org/6RHyU4fup on 23 July 2014.

Donoghue, S. 2006. Nutrition. Pp. 251–298 in D.R. Mader (Ed.), Reptile Medicine and Surgery. Saunders Elsevier, Inc., USA.

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

Fedriani, J.M., T.K. Fuller, and R.M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325–331.

Ferguson, K., and J. Hanks. 2012. The effects of protected area and veterinary fencing on wildlife conservation in southern Africa. Parks 18.1:49–60.

Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. BioScience 53:77–88.

Fox, J., and S. Weisberg. 2011. An {R} Companion to Applied Regression, 2nd Ed. Sage, USA. Available at http://socserv.socsci.mcmaster.ca/jfox/Books/Companion. Archived by WebCite at http://www.webcitation.org/6LZgkcXsR on 2 December 2013.

Gehrt, S.D., C. Anchor, and L.A. White. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90:1045–1057.

Geldmann, J., M. Barnes, L. Coad, I.D. Craigie, M. Hockings, and N.D. Burgess. 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biological Conservation 161:230–238.

Goodlett, G.O., and G.C. Goodlett. 1992. Studies of unauthorized off-highway vehicle activity in the Rand Mountains and Fremont Valley, Kern County, California. Proceedings of the Desert Tortoise Council Symposium 1992:163–187.

Hazard, L.C., D.R. Shemanski, and K.A. Nagy. 2009. Nutritional quality of natural foods of juvenile desert tortoises (*Gopherus agassizii*): Energy, nitrogen, and fiber digestibility. Journal of Herpetology 43:38–48.

Hazard, L.C., D.R. Shemanski, and K.A. Nagy. 2010. Nutritional quality of natural foods of juvenile desert tortoises (*Gopherus agassizii*): Calcium, phosphorus and magnesium digestibility. Journal of Herpetology 44:135–147.

Homer, B.L., K.H. Berry, M.B. Brown, G. Ellis, and E.R. Jacobson. 1998. Pathology of diseases in wild desert tortoises from California. Journal of Wildlife Diseases 34:508–523.

Hunter, L.M., M. De J. Gonzalez G., M. Stevenson, K.S. Karish, R. Toth, T.C. Edwards, R.J. Lileholm, and M. Cablk. 2003. Population and land use change in the California Mojave: Natural habitat implications of alternative futures. Population Research and Policy Review 22:373–397.

Ikuta, L.A., and D.T. Blumstein. 2003. Do fences protect birds from human disturbance? Biological Conservation 112:447–452.

Jacobson, E.R. 2007. Infectious Diseases and Pathology of Reptiles: Color Atlas and Text. CRC Press, USA.

Jacobson, E.R., J.M. Gaskin, M.B. Brown, R.K. Harris, C.H. Gardiner, J.L. LaPointe, H.P. Adams, and C. Reggiardo. 1991. Chronic upper respiratory tract disease of free-ranging desert tortoises (*Xerobates agassizii*). Journal of Wildlife Diseases 27:296–316.

Jacobson, E.R., T.J. Wronski, J. Schumacher, C. Reggiardo, and K.H. Berry. 1994. Cutaneous dyskeratosis in free-ranging desert tortoises, *Gopherus agassizii*, in the Colorado Desert of southern California. Journal of Zoo and Wildlife Medicine 25:68–81.

Jacqmin-Gadda, H., S. Sibillot, C. Proust, J.M. Molina, and R. Thiébaut. 2007. Robustness of the linear mixed model to misspecified error distribution. Computational Statistics and Data Analysis 51:5142–5154.

Jennings, W.B. 1997. Invasions of exotic plants: Implications for the desert tortoise, *Gopherus agassizii*, and its habitat in the western Mojave Desert. Pp. 10–12 in J. Van Abbema (Ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference. New York Turtle and Tortoise Society WCS Recovery Program, USA.

Jennings, W.B. 2002. Diet selection by the desert tortoise in relation to the flowering phenology of ephemeral plants. Chelonian Conservation and Biology 4:353–358.

Johnson, A.J., A.P. Pessier, J.F.X. Wellehan, and E.R. Jacobson. 2005. Identification of a novel herpesvirus from a California desert tortoise (*Gopherus agassizii*). Veterinary Microbiology 111:107–116.

Johnson, A.J., D.J. Morafka, and E.R. Jacobson. 2006. Seroprevalence of *Mycoplasma agassizii* and tortoise herpesvirus in captive desert tortoises (*Gopherus agassizii*) from the Greater Barstow Area, Mojave

Desert, California. Journal of Arid Environments 67:192–201.

Keith, K., K.H. Berry, and J.F. Weigand. 2008. When desert tortoises are rare: Testing a new protocol for assessing status. California Fish and Game 94:75–97.

Kern County Engineering, Surveying and Permit Services Department. 2011. Kern Parcels. Available at http://www.co.kern.ca.us/gis/downloads.asp. Archived by WebCite at http://www.webcitation.org/6LZgqmojW on 2 December 2013.

Kristan, W.B. III, and W.I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology 84:2432–2443.

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

Lance, V.A., and D.C. Rostal. 2002. The annual reproductive cycle of the male and female desert tortoise: Physiology and endocrinology. Chelonian Conservation and Biology 4:302–312.

Lathrop, E. 1983. The effect of vehicle use on desert vegetation. Pp. 153–166 in R.H. Webb and H.G. Wilshire (Eds.), Environmental Effects of Off-Road Vehicles. Impacts and Management in Arid Regions. Springer-Verlag, USA.

Lenain, D.M., E. Olfermann, and S. Warrington. 2004. Ecology, diet and behavior of two fox species in a large, fenced protected area in central Saudi Arabia. Journal of Arid Environments 57:45–60.

Lenth, R.V. 2013. lsmeans: Least-squares means. R package Version 1.10-01. Available at http://CRAN.R-project.org/package=lsmeans. Archived by WebCite at http://www.webcitation.org/6LZh1fMtU on 2 December 2013.

Le Saout, S., M. Hoffmann, Y. Shi, A. Hughes, C. Bernard, T.M. Brooks, B. Bertzky, S.H.M. Butchart, S.N. Stuart, T. Badman, and A.S.L. Rodrigues. 2013. Protected areas and effective biodiversity conservation. Science 342:803–805.

Leu, M., S.E. Hanser, and S.T. Knick. 2008. The human footprint in the West: A large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Leverington, F., K. Lemos Costa, H. Pavese, A. Lisle, and M. Hockings. 2010. A global analysis of protected area management effectiveness. Environmental Management 46:685–698.

McCullagh, P., and J.A. Nelder. 1989. Generalized Linear Models, 2nd Ed. Chapman and Hall, UK.

Minnich, R.A. 2008. California's Fading Wildflowers: Lost Legacy and Biological Invasions. University of California Press, USA.

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

Nagy, K.A., B.T. Henen, and D.B. Vyas. 1998. Nutritional quality of native and introduced food plants of wild desert tortoises. Journal of Herpetology 32:260–267.

NOAA (National Oceanic and Atmospheric Administration). 2010–2011. Climatological Data for California. National Climatic Data Center, Asheville, North Carolina. Randsburg Station, Kern County, USA.

Nicholson, L., and K. Humphreys. 1981. Sheep grazing at the Kramer study plot, San Bernardino County, California. Proceedings of the Desert Tortoise Council Symposium 1981:163–194.

Norris, F. 1982. On beyond reason: homesteading in the California Desert, 1885–1940. Southern California Quarterly—Historical Society of Southern California 64:297–312.

Oftedal, O.T. 2002. Nutritional ecology of the desert tortoise in the Mohave and Sonoran deserts. Pp. in 194–241 in T.R. Van Devender (Ed.), The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. University of Arizona Press and the Arizona–Sonora Desert Museum, USA.

Powers, R.L. 1988. South Fork Country. The Arthur H. Clark Company. Fifth printing by Westernlore Press, USA.

Powers, R.L. 2000. Kern River Country. Fourth printing, The Arthur H. Clark Company, USA.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051–07–0. Available at http://www.R-project.org/ Archived by WebCite at http://www.webcitation.org/6MVfpiCBW on 10 January 2014.

Starry, R.M. 1974. Gold Gamble. Maturango Museum Publication 7. Maturango Museum of Indian Wells Valley, USA.

StatSoft, Inc. 2001. STATISTICA (data analysis software system), Version 6. Available at www.statsoft.com. StatSoft, Inc., USA.

Systat Software, Inc. 2007. SYSTAT 12. Available at http://www.systat.com. Systat Software, Inc., USA.

Turner, F.B., and K.H. Berry. 1984. Methods used in analyzing desert tortoise populations. Appendix in K.H. Berry (Ed.), The Status of the Desert Tortoise (*Gopherus agassizii*) in the United States. Order No. 11310–0083–81. Desert Tortoise Council Report to US Fish and Wildlife Service, California, USA.

Turner, F.B., K.H. Berry, D.C. Randall, and G.C. White. 1987. Population ecology of the desert tortoise at Goffs, California, 1983–1986. Report to Southern California Edison Company, USA.

USBLM (US Department of the Interior, Bureau of Land Management). 1973. Interim Critical Management Plan for Recreational Vehicle Use in the California Desert. United States Department of the Interior, Bureau of Land Management, California Desert Program, USA.

USBLM (US Department of the Interior, Bureau of Land Management). 1980. The California Desert Conservation Area Plan, 1980. United States Department of the Interior, Bureau of Land Management, Desert District, California, USA.

USBLM (US Department of the Interior, Bureau of Land Management). 1993. Final Rand Mountains–Fremont Valley Management Plan. A Sikes Act Plan. United States Department of the Interior, Bureau of Land Management, Ridgecrest Resource Area, California, USA.

USBLM (US Department of the Interior, Bureau of Land Management). 2002. Decision Record and Finding of No Significant Impact for the Interim Closure to

Motorized Vehicle Use of Selected Routes within the Western Rand Mountains Area of Critical Environmental Concern. United States Department of the Interior, Bureau of Land Management, Ridgecrest Field Office, California, USA.

USBLM (US Department of the Interior, Bureau of Land Management). 2006. Record of Decision, West Mojave Plan, Amendment to the California Desert Conservation Area Plan. March 2006. United States Department of the Interior, Bureau of Land Management, California Desert District, USA.

USBLM (US Department of the Interior, Bureau of Land Management). 2012. Geospatial Data Downloads. Available at http://www.blm.gov/ca/gis/. Archived by WebCite at http://www.webcitation.org/6LZhCi1u0 on 2 December 2013.

USBLM (US Department of the Interior, Bureau of Land Management) and California Department of Fish and Game. 1988. A Sikes Act Management Plan for the Desert Tortoise Research Natural Area and Area of Critical Environmental Concern. United States Department of the Interior, Bureau of Land Management, Ridgecrest Office, California, USA.

US District Court. 2009. Order summary judgment motions. Case 3:06-cv-04884-SI. Center for Biological Diversity, et al., Plaintiffs v. BLM. United States District Court for the Northern District of California, California, USA. Available at http://www.biologicaldiversity.org/programs/public_lands/deserts/california_desert_conservation_area/pdfs/WEMO_NECO_case_order_9-28-09.pdf. Archived by WebCite at http://www.webcitation.org/6MVf7ZZHO on 10 January 2014.

US District Court. 2011. Order re: remedy. Case 3:06-cv-04884-SI. Center for Biological Diversity, et al., Plaintiffs v. BLM. United States District Court for the Northern District of California, USA.

USFWS (US Fish and Wildlife Service). 1990. Endangered and threatened wildlife and plants; determination of threatened status for the Mojave population of the desert tortoise. Federal Register 55:12178–12191.

USFWS (US Fish and Wildlife Service). 1994*a*. Desert Tortoise (Mojave Population) Recovery Plan. US Fish and Wildlife Service, Oregon, USA.

USFWS (US Fish and Wildlife Service). 1994*b*. Endangered and threatened wildlife and plants; determination of critical habitat for the Mojave population of the desert tortoise. Federal Register 59:5820–5866.

USFWS (US Fish and Wildlife Service). 2008*a*. Environmental Assessment to Implement a Desert Tortoise Recovery Plan Task: Reduce Common Raven Predation on the Desert Tortoise. Final. United States Fish and Wildlife Service, California, USA.

USFWS (US Fish and Wildlife Service). 2008*b*. Letter dated April 15 (2008-I-00365) from Carl T. Benz to M.A. Bari, National Training Center, Fort Irwin concurring on proposed predator removal program. United States Fish and Wildlife Service, California, USA.

USFWS (US Fish and Wildlife Service). 2010. Mojave Population of the Desert Tortoise (*Gopherus agassizii*), 5-Year Review: Summary and Evaluation. United States Fish and Wildlife Service, Desert Tortoise Recovery Office, Nevada, USA.

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

USFWS (US Fish and Wildlife Service). 2012. Range-wide Monitoring of the Mojave Desert Tortoise (*Gopherus agassizii*): 2011 Annual Report (Draft). United States Fish and Wildlife Service, Desert Tortoise Recovery Office, Nevada, USA.

Vredenburg, L.M., G.L. Shumway, and R.D. Hartill. 1981. Desert Fever: An Overview of Mining in the California Desert. Living West Press, USA.

Walde, A.D., M.L. Harless, D.K. Delaney, and L.L. Pater. 2007. Anthropogenic threat to the desert tortoise (*Gopherus agassizii*): Litter in the Mojave Desert. Western North American Naturalist 67:147–149.

Webb, R.H., and S.S. Stielstra. 1979. Sheep grazing effects on Mojave Desert vegetation and soils. Environmental Management 3:517–529.

Wentworth, E.N. 1948. America's Sheep Trails. Iowa State College Press, USA.

Wyneken, J., D.R. Mader, E.S. Weber, III, and C. Merigo. 2006. Medical care of sea turtles. Pp. 972–1007 in D.R. Mader (Ed.), Reptile Medicine and Surgery. Saunders Elsevier, Inc., USA.

Zimmerman, L.C., M.P. O'Connor, S.J. Bulova, J.R. Spotila, S.J. Kemp, and C.J. Salice. 1994. Thermal ecology of desert tortoises in the eastern Mojave Desert: Seasonal patterns of operative and body temperatures, and microhabitat utilization. Herpetological Monographs 8:45–59.

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

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Appendix I

Coefficients for generalized linear models for Desert Tortoise presence—in all three management areas and for abundance in three separate areas. Colons in the predictor variable represent an interaction effect between two predictors. Coefficients for presence and private lands models were tested using *z*-statistics. Coefficients for the Tortoise Natural Area and critical habitat models were analyzed with quasi-Poisson models and were tested using *t*-statistics based on 78 and 76 df respectively. Regression coefficients (β) are presented with SE, *z*-statistic (*z*), and *P*-values (*P*). Levels of significance: * $P < 0.10$, ** $P < 0.05$, *** $P < 0.010$.

Response variable	Predictor variable	β	SE	*z*, *t*	*P*	
Presence in three areas	Intercept (box thorn and Tortoise Natural Area)	0.934	0.400	2.33	0.020	
	Veg. (creosote bush)	−0.456	0.365	−1.25	0.211	**
	Veg. (indigo bush)	−0.926	0.465	−1.99	0.046	**
	Veg. (Nevada ephedra)	−1.195	0.544	−2.20	0.028	**
	Log(Sheep)	−0.795	0.411	−1.93	0.053	*
	Management area (critical habitat)	−0.888	0.471	−1.88	0.059	*
	Management area (private lands)	−1.043	1.043	−1.00	0.317	
	Log(Mammals)	−0.509	0.442	−1.15	0.250	
	Management area (critical habitat): log(Mammals)	1.504	0.737	2.04	0.041	**
	Management area (private): log(Mammals)	1.644	0.860	1.91	0.056	*
Abundance in TortoiseNatural Area	Intercept	0.772	0.177	4.36	<0.001	***
Abundance in critical habitat	Intercept	−0.396	0.308	−1.29	0.202	
	Log(Vehicles)	−1.075	0.572	−1.88	0.064	*
	Log(Firearms)	1.387	0.526	2.64	0.010	**
	Log(Mammals)	1.152	0.361	3.19	0.002	***
Abundance in private lands	Intercept (box thorn)	−0.491	0.760	−0.65	0.518	*
	Veg. (creosote bush)	−1.567	0.529	−2.96	0.003	
	Veg. (indigo bush)	−17.108	3168	−0.01	0.996	**
	Veg. (Nevada ephedra)	−16.789	2282	−0.01	0.994	
	Log(Sheep)	−0.516	0.248	−2.08	0.037	**
	Log(Trash)	0.764	0.393	1.94	0.052	*
	Log(Mammals)	1.248	0.485	2.57	0.010	**