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Attributes of desert tortoise populations at the National Training Center, Central Mojave Desert, California, USA

K.H. Berry[a,*], T.Y. Bailey[b], K.M. Anderson[c]

[a] *United States Department of the Interior, Geological Survey, Western Ecological Research Center, 22835 Calle San Juan de Los Lagos, Moreno Valley, CA 92553, USA*
[b] *619 Pinon Ct., Ridgecrest, CA 93555, USA*
[c] 324½ *15th Street, Seal Beach, CA 90740, USA*

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Abstract

We sampled 21 study plots for desert tortoises (*Gopherus agassizii*) at the National Training Center, Fort Irwin, California. Each plot was sampled once between 1997 and 2003 to obtain a snapshot of population attributes, status, and relationships between tortoise densities and human activities. Densities ranged from <1 to 28 tortoises km^{-2}; overall, tortoises were uncommon to rare at 16 of the 21 plots. Tortoise densities were negatively correlated with death rates, infectious disease (mycoplasmosis), surface disturbance and trash. Health status of tortoises was correlated with some anthropogenic uses. The presence of infectious disease in tortoises was negatively correlated with distances from offices, the Ft. Irwin cantonment, and paved roads. Also, significantly more tortoises with shell disease were found on plots with current and recent military use than on plots with no history of military use. Factors contributing to or causing deaths of tortoises included vehicles, vandalism, predation, mycoplasmosis and shell diseases. Annual death rates for subadult and adult tortoises ranged from 1.9% to 95.2% for the 4 years preceding surveys. Deaths from anthropogenic sources were significantly correlated with surface disturbances, trash, military ordnance, and proximity to offices and paved roads—typical characteristics of military training areas.
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Keywords: *Gopherus agassizii*; Military training; Disease; Roads; Trash; Chelonians

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[*] Corresponding author.
E-mail address: kristin_berry@usgs.gov (K.H. Berry).

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1. Introduction

The desert tortoise, *Gopherus agassizii*, occurs in the south-western United States (US) and adjacent Mexico. In the US, the tortoise is a federally listed, threatened species with a Recovery Plan and designated critical habitat (Fish and Wildlife Service (FWS), 1990, 1994). The tortoise is treated as an indicator, umbrella, and flagship species (definitions in Simberloff, 1997) for ecosystem health in large parts of the Mojave and Sonoran deserts by US government agencies. Several management plans have been developed with objectives of recovering tortoise populations and habitat (Berry, 1997).

The desert tortoise is a long-lived species and may require 12–25 years to reach reproductive maturity in the Mojave Desert (Woodbury and Hardy, 1948; Hardy, 1976; Turner et al., 1987). Females may lay from 0 to 3 clutches year^{-1}, with fecundity generally lower in younger and smaller females than in older, larger females (Turner et al., 1986; Mueller et al., 1998; Wallis et al., 1999; McLuckie and Fridell, 2002). The survivorship of juveniles to reproductive maturity is not well understood but must be sufficient to replace adults (Turner et al., 1987). Like some other species of turtles, the desert tortoise is vulnerable to environmental and anthropogenic stressors because of its combined life-history traits of longevity, delayed sexual maturity, low fecundity, and low survivorship of nests and juveniles (Congdon et al., 1993; Fish and Wildlife Service (FWS), 1994).

One region where the tortoise historically has experienced population declines and habitat loss is the West Mojave Recovery Unit (Fish and Wildlife Service (FWS), 1994; Berry and Medica, 1995; Brown et al., 1999). This Recovery Unit occupies the western, central, and southern parts of the Mojave Desert in California. In the central Mojave Desert, the National Training Center (NTC) at Fort Irwin encompasses $>2600\,\text{km}^2$ of land and contains habitat for the desert tortoise (Brussard et al., 1994; Krzysik, 1997). The NTC has been used for >60 years for military activities. It was first established as a military facility in 1940 and formally designated as the Department of the Army's NTC in 1979. In 1994, the FWS delineated $\sim 81\,\text{km}^2$ of critical habitat for the tortoise in the southern part of NTC (Fish and Wildlife Service (FWS), 1994; Fig. 1).

The first systematic surveys for desert tortoises on the NTC were conducted in 1983 and 1989 with the objectives of determining distribution and relative abundance in several management areas (Krzysik, 1997). The survey technique involved counting tortoise signs (live tortoises, scat, cover sites, shell-skeletal remains [scutes and bones], etc.) on strip transects. Surveys also were conducted within a $140\,\text{km}^2$ study area along the southern boundary of the NTC in 1995 to model desert tortoise habitat requirements (Andersen et al., 2000).

Our objectives were part of the Army's efforts to: determine population attributes (e.g. density, size class structure, sex ratios, causes of death, and death rates), and health status of tortoise populations within specific management areas of the NTC; compare population attributes in areas with different management histories; and identify anthropogenic factors which may affect health and well-being of the tortoises. We sampled tortoise populations during a single season when they were most likely to be above-ground and active, thus providing a "snapshot" of the population. The habitats were also sampled for anthropogenic disturbances. We hypothesized that tortoise populations would have higher population densities and lower death rates in undisturbed areas, remote from human contact, and higher death rates where human contacts with tortoises were common and land was chronically affected by anthropogenic activities. We also hypothesized that deaths from vehicles would be higher in military maneuver areas than in undisturbed areas.

2. Materials and methods

2.1. Selection of study plots

Between 1997 and 2003, we sampled 21 study plots at the NTC (Figs. 1–4) using two methods: (1) random sampling of a management unit or area and (2) non-random selection of four plots for specific purposes. A 135-km^2 management unit, the Goldstone Deep Space Communication Complex (Goldstone), was sampled randomly with fifteen 1-km^2 plots or 11% of the management unit. Similarly, the Eastgate 1 (3 km^2) and Eastgate 2 (9 km^2) management units were sampled randomly with 150 quadrats each, totaling 1.5 km^2 of each unit. Non-habitat areas (e.g. office buildings, dry lake beds, cliffs, steep slopes) were excluded from the samples. The remaining plots (Alvord Slope, Langford, Tiefort Mtns, Soda Mtns), chosen for management and scientific purposes, received a 100% survey.

The 21 plots represented a wide variety of landforms, including valleys, alluvial fans, piedmonts, low hills, steep slopes and boulder-strewn mesas (Table 1). Elevations ranged from 512 to 1223 m. The geology and soils represented numerous types (Cooke et al., 1993; Sobieraj, 1994; Yount et al., 1994; Schermer et al., 1996). Soils were of granitic, metamorphic, and volcanic origins. Sandy soils were common, but aeolian and rocky soils and gravels and rocks with silt were also represented.

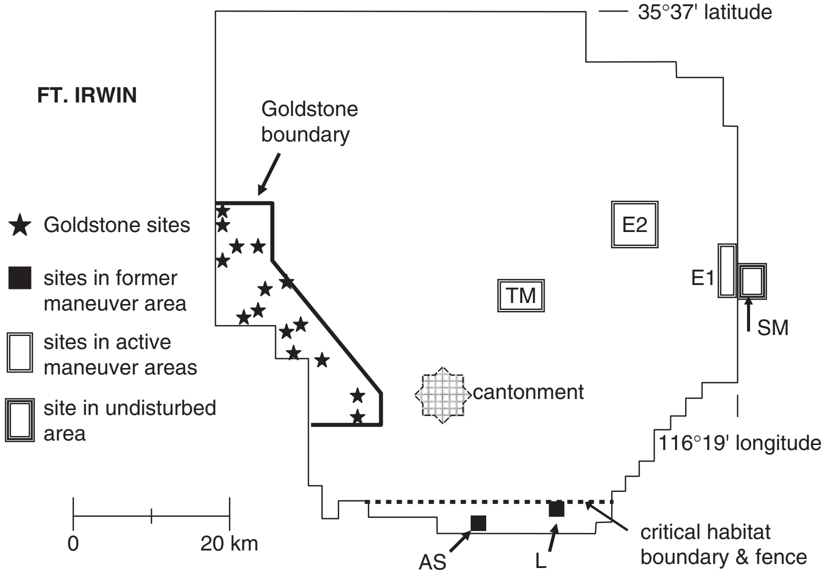

Fig. 1. Locations of 21 desert tortoise study plots at Goldstone, Fort Irwin, California. Fifteen plots are on Goldstone (G-1, etc.). Initials for plot names are: AS = Alvord Slope, L = Langford, TM = Tiefort Mountains, E2 = Eastgate 2, E1 = Eastgate 1, and SM = Soda Mountains.

Fig. 2. (a). Panoramic overview of Goldstone study plots, arrows from left to right: G-1, G-2, G-5, G-3, and G-4. Goldstone Lake (dry) is in the distance. (b,c) Study plots G-7 and G-9, respectively, at Goldstone, where tortoise densities were estimated at ~21 tortoises km^{-2} in the 1980s (Krzysik, 1997).

Human use varied throughout the NTC by plot and management unit (Fig. 1). The study plots were arranged in four classes in descending order of historic and recent anthropogenic impacts to habitat: (1) low levels of surface disturbance and rare human contact, on the edge of a military maneuver area (Soda Mtns); (2) historical and current use for research on deep space probes and satellite communications but generally not for military maneuvers (15 Goldstone plots); (3) historical use for military maneuvers until 1993 (Alvord Slope and Langford plots); and (4) historical and current use for military maneuvers (Tiefort Mtns, Eastgate 1, and Eastgate 2). The Soda Mtns plot has experienced little human contact since the 1940s and possibly earlier and was in a remote part of the NTC. The Goldstone management unit was highly fragmented by dirt and paved roads (density of 1.01 and 0.34 km km^{-2}, respectively) or other surfaces, contained five dispersed and actively used office facilities and two unused facilities. It had an estimated 35 km of boundaries with public lands where land was used for multiple purposes. (Human contact with tortoises was primarily by vehicles driven by government and contract workers on roads.) The Langford and Alvord Slope plots were near the southern edge of the NTC, were within designated critical habitat for the tortoise (Fish and Wildlife Service (FWS), 1994), and were protected from an adjacent military maneuver area by a three strand barbed-wire fence that was erected in 1993 (Fig. 1). The northern boundaries of both

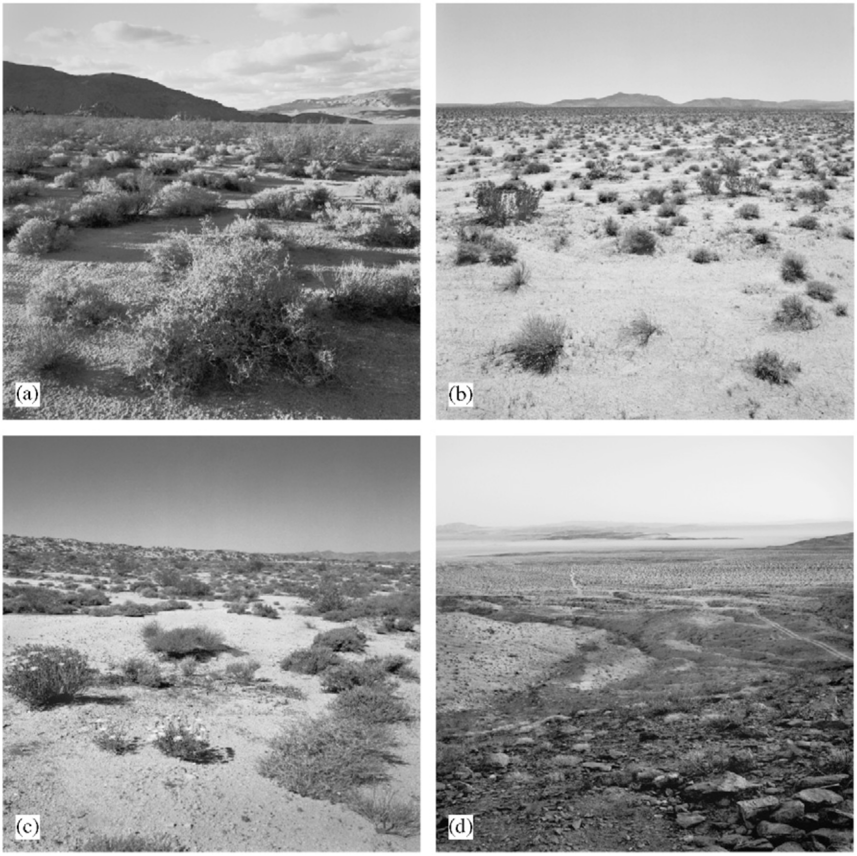

Fig. 3. (a) Study plot G-15 at Goldstone; G-14 is in the background. (b) The Langford study plot near the protective fence is in critical habitat for the desert tortoise. (c) The Alvord Slope study plot is in critical habitat for the desert tortoise. (d) The Tiefort Mountains plot is in a military training area.

Langford and Alvord Slope plots paralleled the protective fence. The Langford plot abutted the fence, whereas the northern boundary of the Alvord Slope plot was 1.4 km from the fence. The southern boundaries of the two plots were also close to the unfenced exterior, 28 km boundary of the NTC with public land, and were affected by adjacent non-military land uses. These two plots contained numerous dirt roads and old tracked areas from pre-1993 military activities, when lands were used for military maneuvers. The northern parts of plots historically experienced more extensive use and disturbance than did the southern parts. Past human contact and contact during the study was primarily by soldiers and unauthorized personnel entering the southern boundary. In contrast, plots in military maneuver areas (Tiefort Mtns, Eastgate 1, Eastgate 2) were in remote parts of the NTC inaccessible to the general public and isolated from other tortoise populations by military training activities. These three areas experienced force-on-force training by troops with tanks and other vehicles at intervals of approximately 2 weeks of use, followed by 2 weeks of non-use. Tortoises living here had direct encounters with soldiers and their vehicles.

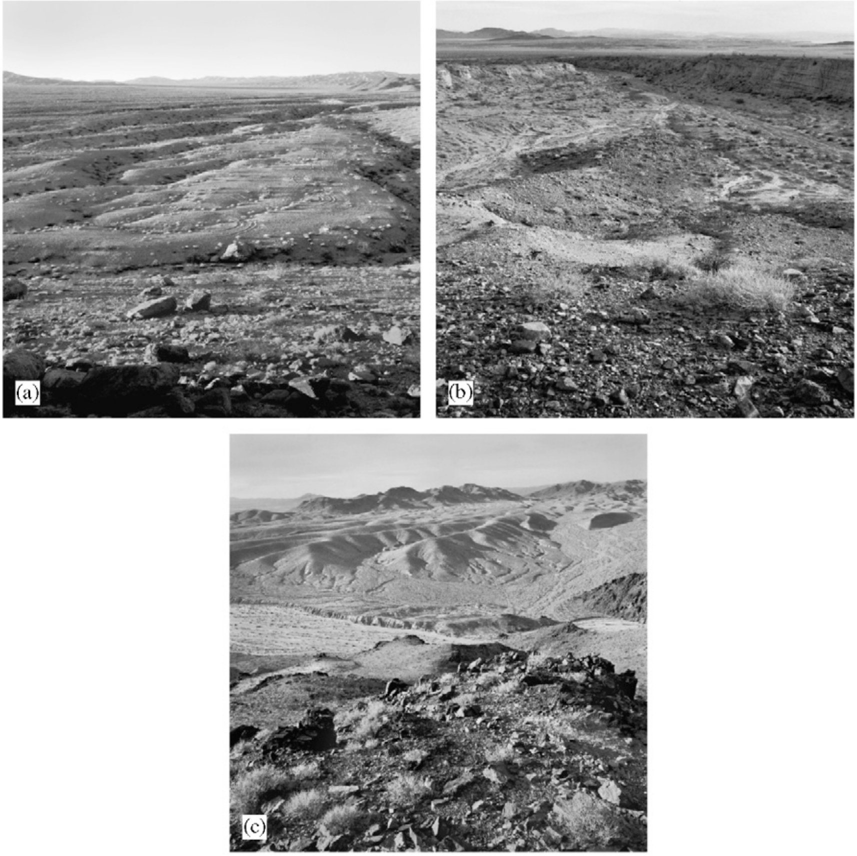

Fig. 4. (a) The Eastgate 1 study plot is in a military training area. (b) The Eastgate 2 study plot is in a military training area. (c) The Soda Mountains study plot is in a remote, undisturbed area.

Table 1
Summary of vegetation types and physical characteristics of 21 study plots at the National Training Center, Fort Irwin, California, USA

Plot name	Plant community (common perennial species)	% cover, perennial plants	Landforms, soils, surficial geology	Elevations (m)
G-1	*Larrea tridentata*, *Atriplex polycarpa*, *Ambrosia dumosa*	11.8	Steep rocky slopes, mountain top; rocky soils with silt; talus	968–1122
G-2	*L. tridentata*, *Ambrosia dumosa*	20.1	Valley, some aeolian sand and silt	938–1010
G-3	*Atriplex confertifolia*, *Artemisia spinescens*	4.6	Valley, adjacent to Goldstone playa	921–931
G-4	*Ericameria cooperi*, *Grayia spinosa*, *Lycium andersonii* (burned, formerly with *L. tridentata*)	4.0	Alluvial fan, valley	932–974
G-5	*L. tridentata*, *Atriplex polycarpa*	11.1	Small valley, rocky ground, interspersed colluvial slopes	931–976

Table 1 (*continued*)

Plot name	Plant community (common perennial species)	% cover, perennial plants	Landforms, soils, surficial geology	Elevations (m)
G-6	*L. tridentata*, *Ambrosia dumosa*	17.8	Low hills, rocky soils	956–1044
G-7	*L. tridentata*, *Atriplex confertifolia*, *Hymenoclea salsola*, *A. polycarpa*	14.7	Valley	930–946
G-8	*L. tridentata*, *Atriplex confertifolia*, *Ambrosia dumosa*, *Atriplex polycarpa*, *Lycium andersonii*	11.8	Mountain mesa, volcanic rocks, desert pavement	1121–1223
G-9	*L. tridentata*, *Krascheninnikovia lanata*, *Grayia spinosa, Ephedra nevadensis*	18.0	Rolling hills, low valley, silty soils	930–1001
G-10	*L. tridentata*, *Ambrosia dumosa*, *G. spinosa*	12.2	Valley, slope of low hills, soils basaltic in origin	1000–1067
G-11	*L. tridentata*, *A. dumosa*	18.0	Valley; sandy soils and silt beneath pebbles	966–1035
G-12	*L. tridentata*, *A. dumosa*, *G. spinosa*, *E. nevadensis*, *Eriogonum fasciculatum*	19.3	Valley, granitic soils	1035–1077
G-13	*L. tridentata*, *A. dumosa*, *Thamnosma montana*	31.2	Valley, granitic rock outcrop	957–1053
G-14	*A. dumosa*, *L. tridentata*	26.5	Dry wash, valley, rocky slope, talus	949–1069
G-15	*L. tridentata*, *Ericameria cooperi*, *Eriogonum fasciculatum*	28.0	Valley, granitic rock outcrops	990–1088
Alvord Slope	*A. dumosa*, *L. tridentata*, *Ephedra californica*, *Atriplex hymenelytra*, *Acamptopappus sphaerocephalus*	7.85	Primarily alluvial fan, rolling hills; rocky slopes, dry washes	760–840
Langford	*Ambrosia dumosa*, *L. tridentata*, *Lycium pallidum* var. *oligospermum*, *Menodora spinescens, Ephedra californica, Xylorhiza tortifolia*	8.74	Primarily alluvial fan, dry washes; rolling hills and badlands at southern end	720–800
Tiefort Mtn	*A. dumosa, Larrea tridentata, Senna armata, Krameria erecta, Encelia frutescens*	7.02	Mix of alluvial fan and piedmont cut with dry washes; rolling hills; steep, rocky slopes	640–800
Eastgate 1	*A. dumosa*, *L. tridentata*, *Krameria erecta*, *Stephanomeria pauciflora*	5.86	Piedmont cut by dry washes; rocky slopes	580–730
Eastgate 2	*L. tridentata*, *A. dumosa*, *Senna armata*, *H. salsola*	5.80	Piedmont cut by dry washes; rocky slopes, rolling hills, badlands	780–1000
Soda Mtns	*L. tridentata*, *H. salsola*, *A. dumosa*, *Ephedra californica*, *Bebbia juncea*	26.35	Piedmont cut by dry washes, rocky slopes	512–622

G = Goldstone.

2.2. Data collection

2.2.1. Precipitation

We used precipitation data from the weather station maintained by the National Oceanic and Atmospheric Administration (NOAA) (National Oceanic and Atmospheric Administration, 1976–2002) at Daggett Federal Aviation Administration Airport, California (34°52′N, 116°47′W, 585 m) which is 48.6–101.8 km from the plots. Weather stations established in 1995 at NTC provided additional information (Ruth Sparks, personal communication). Because timing and amounts of precipitation directly affect production of tortoise forage and above-ground activity (Henen et al., 1998; Jennings, 2002), we supplemented rainfall data with qualitative observations on biomass of winter and summer annual herbs, grasses and herbaceous perennial plants.

2.2.2. Perennial vegetation

On each plot, two to five $2 \times 100\,\mathrm{m}^2$ belt transects were randomly established within a habitat type. Each belt transect was subdivided into 50 $2 \times 2\,\mathrm{m}^2$ quadrats to measure species composition and cover of perennial plant species. The canopy cover (cm^2) of each perennial plant was measured using the equation for an ellipse (canopy area $= \pi r_1 r_2$, where $r_1 =$ minor radius and $r_2 =$ the major radius of the canopy). Plant nomenclature followed Baldwin et al. (2002).

2.2.3. Live tortoises

Sampling desert tortoises for population attributes presents many challenges because of limited activity above-ground (Nagy and Medica, 1986), difficulties in observing small tortoises (Morafka, 1994; but see Berry and Turner, 1986), and dependency of above-ground activity on precipitation (Henen et al., 1998; Duda et al., 1999). Where tortoises are scarce and densities are low, sampling is even more difficult. We chose the spring season, the key above-ground activity period for all sizes of tortoises in the Mojave Desert, to maximize captures of live tortoises and observance of tortoise sign (shell-skeletal remains, cover sites, tracks, scats, courtship rings, and drinking sites). Cover sites are defined as shelters used by tortoises and include burrows, caves, pallets, and rock shelters (Burge, 1978).

For ease of conducting surveys for tortoises, each plot was subdivided into either $100 \times 100\,\mathrm{m}^2$ or $150 \times 150\,\mathrm{m}^2$ quadrats. Quadrat size was dependent on terrain, landforms, and vegetation height. The corners of each quadrat were marked with reinforcing bar and a 3-m length of PVC pipe, which enabled field workers to keep track of their locations easily when walking transects to search for tortoises. Each plot was surveyed between late March and the first week of June of a single year during the multi-year study (Table 2). Field workers with experience in searching for tortoises thoroughly covered each plot twice, walking parallel belt transects at 10-m intervals in one direction (i.e. north–south) and then again in the other direction (east-west) for two complete coverages of each plot within 30–70 days. Because so few live tortoises were observed during the first coverage of each of the Goldstone plots, all tortoise sign was also counted and the locations were mapped during the second survey of the plots. At Alvord Slope, Langford and the Eastgate 1 and 2 plots, all cover sites were similarly counted and mapped but not locations of scats, tracks, courtship rings, and drinking sites. At Tiefort Mtns and Soda Mtns, only the cover sites observed to be used by the marked tortoises were counted and mapped.

Table 2
A summary of plot sizes, years of survey, precipitation levels, and relative forage quantities when surveys were undertaken on 21 study plots at the NTC, Fort Irwin, California

	Plot size (km^2)	Year of survey	Precipitation level at NOAA station	Relative forage quantity
Historic and current military use area at Goldstone Deep Space Communication Complex				
G-1–G-15	Each 1 km^2	1998	Above norm	Abundant
Former military training area (now critical habitat)				
Alvord Slope	2.25	1997	Above norm	Moderate
Langford	2.25	1997	Above norm	Moderate
Historic and current military training areas				
Tiefort Mtns	4.57	1997	Above norm	Moderate
Eastgate 1	1.51	2000	Below norm	Low
Eastgate 2	1.50	2000	Below norm	Low
Undisturbed area				
Soda Mtns	2.57	2003	Below norm	Abundant

The double coverage of each plot during a single spring was designed for estimating tortoise density and other population attributes using mark-recapture data. Each live tortoise was assigned a number, permanently marked with notches on marginal scutes of the carapace, measured for carapace length at the midline (MCL), weighed, assigned a sex for individuals $\geqslant 180$ mm MCL, and photographed (protocol in Berry and Christopher, 2001). Tortoise locations were recorded to within 1–5 m.

Each tortoise also was evaluated for health and disease status, including signs of starvation, dehydration, trauma and abnormalities, using field data sheets and 35-mm slides (Berry and Christopher, 2001; Berry et al., 2002). Clinical signs of upper respiratory tract diseases (URTD), which can be caused by mycoplasmosis, herpes virus, or other pathogens, were noted during examination of eyes, nares, beak and mouth (Jacobson et al., 1991; Brown et al., 1994, 1999, 2002; Origgi et al., 2001). Mycoplasmosis and herpes virus are caused by infectious pathogens and are considered to be serious threats to the desert tortoise. Clinical signs of shell lesions indicative of cutaneous dyskeratosis or necrosis and parasites are often evident on the shell, limbs, and other integument (Jacobson et al., 1994; Homer et al., 1998). We rated several variables on the eyes, nares, and beak for severity of clinical signs using four classes of severity: normal, mild, moderate, or severe (Berry and Christopher, 2001). We graded shell lesions and trauma on head, limbs, carapace, and plastron according to distribution, severity, and chronicity. Using sterile techniques, we collected blood from the brachial vein from a sample of tortoises with $\geqslant 180$ mm MCL (subadult and adult tortoises) for enzyme-linked immunoassay (ELISA) and polymerase chain reaction (PCR) tests for *Mycoplasma agassizii* and any new species of *Mycoplasma* (Schumacher et al., 1993; Brown et al., 1994, 2002). We also took nasal wash samples for cultures for *Mycoplasma* (for methods, see Brown et al., 1999, 2002). The Mycoplasma Laboratory (M. Brown), University of Florida, Gainesville, processed all blood and nasal samples.

2.2.4. Shell-skeletal remains and predators

Upon finding shell-skeletal remains or individual pieces of scute and bone, we examined the vicinity for other body parts and signs of potential cause(s) of death, e.g. trails or tracks of vehicles, evidence of predators, etc. We photographed remains in situ, recorded the locations, and collected them. We recorded locations of predator concentration areas (roosts, nests, perches, dens, scat concentration areas) and known avian predators: common raven, *Corvus corax*; golden eagle, *Aquila chrysaetos*; greater roadrunner, *Geococcyx californianus*; red-tailed hawk, *Buteo jamaicensis*; and loggerhead shrike, *Lanius ludovicianus* (Boarman, 1993; Berry, unpublished data). We also broke apart scats of coyotes (*Canis latrans*) and kit fox (*Vulpes macrotis*) to check for tortoise remains.

2.2.5. Anthropogenic impacts

Historical documents were reviewed to determine types and levels of past anthropogenic uses and the potential relevance to recent distribution, abundance, and status of desert tortoise populations. We established 10 m wide belt transects to quantitatively measure human impacts on each quadrat of each plot. Transects crossed the quadrats diagonally from NW to SW corners, except for the Soda Mountains plot where transects lines followed land contours because of steep terrain. For each transect, areas of surface disturbance were measured, e.g. lengths and widths of paved and dirt roads, vehicle trails and tracks, fences, excavation pits and bunkers, campsites, and areas partially and completely denuded of vegetation. We also counted trash (small and large items; balloons; spent military casings and shells [military ordnance], shooting targets, and shooting areas); excavations (foxholes) and bunkers; and posts.

2.3. Data analyses

2.3.1. Precipitation data

Using the NOAA records, we calculated 30-year means for winter rainfall (defined as October 1–March 31) and total annual rainfall (defined as the water or hydrologic year from October 1–September 30, see Manning, 1992). We compared the long-term means with precipitation from 1996 to 2003. We defined drought years as years when annual rainfall and winter rainfall fell below the long-term means.

2.3.2. Perennial vegetation

We calculated canopy cover (cm^2) per ha for each perennial species of plant by summing the cover values (cm^2) for each plant on a transect and multiplying by 50. Canopy cover for all perennial species was then summed, and % of total canopy cover ha^{-1} was calculated. The more common species were listed in order from highest to lowest values of canopy cover.

2.3.3. Live tortoises

Both live and dead tortoises were sorted by size-age class according to MCL: juvenile = <99 mm, immature = 100–179 mm, subadult/small adult = 180–207 mm, and adult ⩾208 mm. To determine if sex ratios of subadult and adult tortoises were significantly different than the expected 1:1 ratio at $p<0.05$, we used the Z statistic (Spiegel, 1961):

$$Z = (p - 0.5)/\surd(0.25/N), \tag{1}$$

where p is the proportion of males in the sample and N is the total sample size. The Z statistics were compared with the critical value of Z at $p<0.05$ (± 1.96).

We used two techniques to estimate density, with the type of technique dependent on number of tortoises found. Sixteen (Goldstone plots, Eastgate 1) of the 21 plots had few live tortoises. For the 15 Goldstone plots, we grouped the data and calculated density (group mean, 95% confidence intervals, CI) using the bootstrap method with 1000 simulations (Barreto and Howland, 2005), where each of the 15 plots was treated as a quadrat. For Eastgate 1, we used the same method for the 150 quadrats. Where mark-recapture data were sufficient on five plots (Alvord Slope, Langford, Teifort Mtn, Eastgate 2, Soda Mtns), we calculated densities using the Stratified Lincoln Index (Overton, 1971). We estimated densities separately for all tortoises and for the combined subadult and adult classes and reported results by the density estimate (numbers km^{-2}) and the 95% CI.

Clinical signs of disease rated as moderate to severe were considered to be important and potential indicators of ill-health (Jacobson et al., 1994; Berry and Christopher, 2001; Christopher et al., 2003). Tortoises with moderate to severe clinical signs of one or more diseases were noted. Tortoises testing positive for *Mycoplasma aggassizii* or other *Mycoplasma* species were considered to be chronically ill and potentially infectious. For this analysis, we grouped the 15 Goldstone plots as one unit and combined the two Eastgate plots as a second unit to achieve comparable sample sizes. Each of the remaining four plots was treated as its own unit for a total of six study units: Goldstone, Alvord Slope, Langford, Tiefort Mtns, Eastgate, and Soda Mtns. We used the Fisher's exact test to determine if statistically significant differences existed among the six units for laboratory test results for *Mycoplasma* and for clinical signs of mycoplasmosis, shell disease, and trauma (Mehta and Patel, 1983; Agresti, 1992; SAS Institute Inc., 1999, 2003). We also compared the relative use of cover sites (pallets, rock shelters, caves, and burrows) by tortoises among the six units using Chi-square (χ^2) analysis (SPSS Inc., 1998).

2.3.4. Shell-skeletal remains and predators

All shell-skeletal remains were evaluated in the laboratory to determine size-age category, sex, whether previously marked or captive, approximate time of death, and potential or probable cause of death. Carapace length was determined by one of three methods: direct measure of MCL if a sufficient amount of the shell remained; estimation of MCL using previously derived regression equations based on measurements of selected scutes, impressions of scutes on bone, or selected plastron measurements (Berry and Woodman, 1984); and estimation using fragments of bone or scute, drawing from the shell-skeletal collection. Time since death (time between collection and death) was estimated for each set of remains using keys in Berry and Woodman (1984). Estimates for time since death were placed in two classes: $\leqslant 4$ years and >4 years.

Tortoises were assigned one or more causes of or contributors to death, depending on general appearance, forensic evidence, and location. For example, a tortoise found crushed in a vehicle track was assigned a death due to vehicles, a tortoise found beneath a nest of *C. corax* nest with pecked shell (Boarman, 1993) was assigned a death due to *C. corax*, and a tortoise with a conchoidal fracture in scutes or bones was assigned a death due to gunshot (Berry, 1986). Some causes of death could be difficult to distinguish, i.e. between a mammalian predator kill and scavenging after a tortoise has just died of another cause, such as disease. A mammalian predator kill was distinguished from scavenging by puncture wounds and cracked bones accompanied by torsion and twisting of bones. Where data were ambiguous, the death was listed as unknown, or multiple potential sources were noted. Crude annual death rates were calculated for subadult and adult tortoises for the previous 4 years for the 15 Goldstone plots, which were grouped as a single unit, and for each of the other six plots as separate units. The formula for general death rates of subadult and adult tortoises was

$$d = D/N, \tag{2}$$

where D is mean number of subadult and adult tortoises dying/(year km^2), and N is the density estimate km^{-2} of subadult and adult tortoises. Annualized death rates were not calculated because the data sets for population densities were available for only one survey year for each plot. Death rates were considered to be high when $>2\%$ year^{-1} (Turner and Berry, 1984; Turner et al., 1987). The distances of avian predator nests from each plot were estimated, and the numbers of field hours/avian predator observed were calculated. Using Spearman rank correlation coefficients (r_s, SYSTAT 8.0 software: SPSS Inc., 1998), we tested for associations between mortalities caused by anthropogenic sources in general with seven other anthropogenic variables (% surface disturbances; distances [km] of plots from the cantonment, Ft. Irwin cantonment offices and paved roads; counts of trash and military ordnance; and numbers of field hours/avian predators observed). Likewise, we tested for associations between mortalities caused by vehicles and other anthropogenic variables. Probability values for r_s were computed with t values and referencing a t distribution (SAS Institute Inc., 1999, 2003).

2.3.5. *Anthropogenic disturbances*

Using the transect data from each plot on anthropogenic disturbances, we calculated the amounts (m^2) of surface disturbance on each transect from the following anthropogenic variables: vehicles (roads, trails, tracks), campsites, bunkers, and partially or completely denuded habitat. We then combined all transect data and extrapolated the % surface area affected for the entire plot. Counts of trash, military ordnance, excavations/bunkers, and fence posts were totaled separately. We calculated distances of each plot from the cantonment, NTC and Goldstone office facilities, and paved roads. We noted whether dirt roads were within or abutted on plot boundaries.

We tested hypotheses about effects of anthropogenic activities on tortoise densities and their habitats using r_s and associated probability values (SPSS Inc., 1998; SAS Institute Inc., 1999, 2003). We compared tortoise densities with seven impact variables: % surface disturbance; distances (km) to nearest offices, the Fort Irwin cantonment, or paved roads; counts of trash and military ordnance; and numbers of field hours/avian predators observed. All plots were treated separately, except for the Goldstone plots, which were grouped as a single unit. We used ANOVA to compare the % surface disturbance among plots grouped by four classes of historical and current military and other government uses (described in Section 2.1) (SPSS Inc., 1998). We also analysed the potential effects of historical military maneuvers and the protective fence on tortoise distribution for two plots (Alvord Slope and Langford) by using χ^2 to compare the numbers of tortoises and number of cover sites found on the north and south halves of the plots (SPSS Inc., 1998).

3. Results

3.1. Precipitation

The Daggett weather station receives ~60% of its annual rainfall during fall and winter (October 1–March 31). Precipitation exceeded the annual norm for the hydrologic years 1996–1997 and 1997–1998, the years of survey for Goldstone plots, Tiefort Mtn, Alvord Slope, and Langford. Winter rainfall, however, was below the norm for 1996–1997, the year of survey for Tiefort Mtn, Alvord Slope, and Langford. During the 1999–2000 hydrologic year when Eastgate 1 and Eastgate 2 were studied, both winter and annual rainfall were below the norms. Rainfall at the Soda Mtns plot also was below the norms for winter and the hydrologic year in 2002–2003. Our observations on the plots indicated that precipitation measured at Daggett was not necessarily reflective of precipitation occurring at the study plots or of annual plant production. We observed moderate production of winter annual plants in 1997, abundant crops in 1998 and 2003, and low production in 2000 (Table 2). Therefore, surveys on 16 plots were conducted when forage was abundant, on three plots when forage was moderate, and on two plots when forage was low.

3.2. Perennial vegetation and habitat types

The canopy cover of perennial vegetation ranged from 4.0% to 31.2%. Cover was lower on the burned plot (G-4), a plot adjacent to the Goldstone Lake playa (G-3), and on plots in recently and currently used military maneuver areas (Alvord Slope, Langford, Tiefort Mtns, and Eastgate 1 and 2) than elsewhere (Table 1). Vegetation on 20 of the 21 study plots was typical of creosote bush (*Larrea tridentata*) scrub communities, although more diverse vegetation was present on some plots than on others (Table 1, Figs. 2–4). The exception was a saltbush community on plot G-3 near the alkaline Goldstone Lake playa. This plot was dominated by *Artemisia spinescens* and species of *Atriplex* that typically occur in alkaline soils.

3.3. Live tortoises

Live tortoises, signs of recently live tortoises (shell-skeletal remains), or other tortoise sign were found on all but one plot (G-5) (Fig. 2a). A total of 182 live tortoises were found during 6072.6 search hours (Table 3). The numbers of live tortoises registered on each plot varied from 0 to 72 with the highest number found at Tiefort Mtns.

Sufficient sample sizes of tortoises were available from the Goldstone unit and the other plots to calculate two or more population variables: densities, size-class structure, sex ratios, and death rates. The Goldstone unit had 17 live tortoises and 135 remains of dead tortoises. The presence of live tortoises and other signs indicated that tortoises had used all Goldstone plots except for one (G-5) in the last few years (Tables 3 and 4). The majority of recent signs of tortoises were confined to five plots (G-6, G-7, G-9, G-12, and G-15). The density estimate was 1.146 tortoises km^{-2} (95% CI $= 0.333$–2.2 tortoises km^{-2}) (Table 5). Juvenile and immature tortoises were found live (29.4% of the sample) and dead (23.7% of the shell-skeletal remains), indicating that females were producing young that survived beyond the egg stage (Table 3). The sex ratio of subadults and adults was 7 males:

Table 3
Summary of size-age class data on live and dead desert tortoises from 21 study plots at the National Training Center, Fort Irwin, California

Plot name	*N*, live tortoises by size/age class					*N*, shell-skeletal remains found					Grand total
	Juvenile	Immature	Subadult	Adult	Total	Juvenile	Immature	Subadult	Adult	Total	Live and dead
G-1							2			2	2
G-2		1			1		1		1	2	3
G-3											
G-4				1	1						1
G-5											
G-6		1			1		3	1	3	7	8
G-7			1	1	2	6	5	1	54	66	68
G-8							1		4	5	5
G-9	1				1	3	4	3	23	33	34
G-10						1	2	1	5	9	9
G-11									2	2	2
G-12	1			5	6		3	1		4	10
G-13											
G-14							1		2	3	3
G-15		1		4	5				2	2	7
Goldstone subtotal	2	3	1	11	17	10	22	7	96	135	152
Alvord Slope	4	1	4	20	29	8	12	9	18	47	76
Langford		1	1	10	12	1	7		11	19	31
Tiefort Mtns	8	9	2	53	72	11	14	6	18	49	121
Eastgate 1				2	2		2	1	7	10	12
Eastgate 2	1		1	9	11	1	1	2	7	11	22
Soda Mtns	6	6	2	25	39	5	9	3	12	29	68
Total	21	20	11	130	182	36	67	28	169	300	482

Table 4
Summary of all tortoise sign found at the 15 Goldstone study plots and numbers of cover sites used by tortoises at other plots

Plot name	Tortoise sign: no. of cover sites				Subtotal:	Tortoise sign:	Total sign
	Caves	Burrows	Rock shelters	Pallets	Cover sites	No. of scats	
G-1							
G-2		2			2	1	3
G-3				1	1		1
G-4		5		3	8		8
G-5							
G-6		1		1	2	19	21
G-7		26		4	30	>25	>55
G-8		1			1	4	5
G-9		4		1	5	5	10
G-10				1	1		1
G-11		1		1	2		2
G-12		14	2	9	25	>75	>100
G-13		3			3		3
G-14						1	1
G-15		4		3	7	>25	>32
Goldstone subtotal		61	2	24	87	>155	>242
Langford		88			88		
Alvord Slope		129	6		135		
Tiefort Mtns	32	28	13	2	75		
Eastgate 1	16	1	2	1	20		
Eastgate 2	24	6	1	2	33		
Soda Mtns	26	14	2	4	46		

For the Tiefort Mtns and Soda Mtns plots, the numbers of cover sites shown are for marked desert tortoises only.

Table 5
A summary of densities and sex ratios for desert tortoises at the Goldstone unit and other 6 study units at the NTC, Fort Irwin, California

Plot name	Densities (number km^{-2}, 95% CI)		Sex ratios	
	All sizes	Subadults and adults	Male:female	Z-statistic
Goldstone unit	1.146 (0.333–2.20)	0.788 (0.133–1.6)	7:5	0.5773
Alvord Slope	17 (9–31)	14 (7–26)	15:9	1.2243
Langford	6 (2–16)	5(2–16)	9:2	2.1101[a]
Tiefort Mtns	28 (18–44)	15 (9–25)	28:27	0.1350
Eastgate 1	1.4 (0–3.3)	1.4 (0–3.3)	2:0	1.4140
Eastgate 2	13 (3–50)	12 (3–43)	8:4	1.1552
Soda Mtns	28 (17–45)	11 (7–19)	15:12	0.5780

[a] Sex ratios statistically significant at $p<0.05$.

5 females and was not significantly different from the expected 1:1 ratio (Table 5). The death rate for subadults and adults was very high, 95.2% year^{-1} (Table 6). Similarly, the density for the Eastgate 1 plot was low and the death rate was high: 1.4 tortoises km^{-2}

Table 6
Death rates for subadult and adult tortoises and causes of death for all sizes of tortoises on plots

Plot name	N, shell-skeletal remains	Death rates (%)	% shell-skeletal remains with signs of death from						
			Poaching, gunshot, vandalism	Predation		Predation/ disease or disease only	Military vehicle		Unknown
				Mammal	Bird		Only	Plus other signs	
Goldstone unit	135	95.2	1.2	53.1		12.3	2.5	1.2	29.6
Alvord Slope	47	4.7	8.5	46.8	2.1	6.4	2.1	8.5	25.5
Langford	19	13.3		15.8		15.8	15.8	26.3	26.3
Tiefort Mtns	49	1.9		30.6	6.1	16.3	22.4	14.3	10.2
Eastgate 1	10	23.8					30.0	20.0	50.0
Eastgate 2	11	5.5					45.5	27.2	27.3
Soda Mtns	29	9.7		20.6	3.5	3.5		6.9	65.5

A high death rate was defined as >2%. Some remains had signs of vehicular trauma, as well as signs of scavenging or predation. A few also showed signs of disease on the shells.

(95% CI = 0–3.3, bootstrap simulation), and 23.8% year^{-1}, respectively (Tables 5 and 6). For the remaining five plots, density estimates and death rates ranged from 6 to 28 tortoises km^{-2} (Table 5) and from 1.9% to 13.3% (Table 6), respectively. Overall, for the Goldstone unit and other six plots, densities were negatively correlated with death rates ($r_s = -0.847$, $p = 0.008$). Juvenile and immature tortoises composed from 8.3% to 30.8% of captures (Table 3). When sex ratios were calculated for each of these plots, only the Langford plot (nine males: two females) was significantly different from the expected 1:1 sex ratio ($Z = 2.1101$, $p = 0.017$; Table 5).

The numbers of live tortoises and cover sites on the Alvord Slope plot differed between north and south halves of the plots. Both the numbers of live tortoise encounters and the numbers of sub-surface cover sites were significantly lower on the north-half of the plot, the area nearest to the protective fence and receiving the most historic disturbance ($\chi^2_{\text{tortoises}} = 17.28$, $p < 0.0001$, 1 df; $\chi^2_{\text{cover sites}} = 27.56$, $p < 0.0001$, 1 df). For the Langford plot, the north-half of the plot had fewer than half the number of tortoises compared with the south-half, but the difference was not statistically significant ($\chi^2_{\text{tortoises}} = 3.0$, $p = 0.083$, 1 df). Likewise, numbers of cover sites did not differ significantly between north and south halves ($\chi^2_{\text{cover sites}} = 1.1364$, $p = 0.286$, 1 df).

Tortoise use of subsurface cover sites differed significantly among study units ($\chi^2 = 362.281$, $p < 0.0001$, 15 df). Most tortoises at Goldstone used burrows (70.1%), followed by pallets and rock shelters. On Alvord Slope and Langford, tortoises used burrows (97.3%) and a few rock shelters. In contrast, tortoises at the other four plots (Eastgate 1, Eastgate 2, Tiefort Mtns, Soda Mountains; Table 4) used more caves than burrows or rock shelters. When the data sets for these four plots were combined, the figures were 56.3% for caves, 28.1% for burrows, and 10.3% for rock shelters. Caves did not exist at Goldstone, Alvord Slope, or Langford plots, because the landforms and surficial geology supporting this type of cover site were absent. At the other four plots, caves were common in the walls of dry washes in the piedmont, and the rock-strewn slopes provided opportunities for rock shelters.

Table 7
Health status for tortoises found on study plots

Plot name	No. of healthy tortoises and tortoises with moderate to severe clinical signs for					
	N	Healthy	URTD	Shell disease	Trauma	Other
G-2	1		1		1	
G-4	1	1				Abnormal scute depressions-malnutrition
G-6	1			1	1	
G-7	2	1		1	1	
G-9	1	1				
G-12	6	2	3	2		
G-15	5	1	5	3		Two tortoises tested positive for mycoplasmosis
Alvord Slope	29	21	7	2	7	
Langford	12	7	4	1	2	
Tiefort Mtns	72	36	34	7	11	Two tortoises with abnormal scute depressions
Eastgate 1	2	2				
Eastgate 2	11	8	2	1	4	
Soda Mtns	39	30	7	2	6	

Only tortoises with moderate to severe clinical signs of URTD, shell diseases, or significant signs of trauma are shown in the table. Several tortoises showed clinical signs of more than one disease or trauma and thus are represented in more than one column. Tortoises with trauma could also be considered healthy. Thus numbers of tortoises in columns for healthy and moderate to severe clinical signs of disease may exceed the sample size for each plot.

3.4. Health

Many tortoises (39.6%) showed moderate to severe clinical signs of disease or trauma (Table 7). The exception was for two plots, G-9 and Eastgate 1, where all three tortoises appeared healthy. Clinical signs of URTD were most common ($63/182 = 34.6\%$), followed by trauma ($33/182 = 18.1\%$), and shell diseases ($20/182 = 10.9\%$). Some tortoises exhibited clinical signs of both URTD and shell disease. More tortoises at Goldstone had moderate to severe signs of URTD than observed on other plots ($9/17 = 52.9\%$). Ninety-one of 182 tortoises (50%) on plots were tested for *M. agassizii* using the ELISA test, cultures, and PCR test. Most of the individuals tested were subadult or adult tortoises. With the exception of two tortoises at G-15, tests on all tortoises were negative. Both tortoises at G-15 tested positive with the ELISA test, and one also had a positive culture, indicating that the nares of the tortoise contained the pathogen. The differences among plots were significant for mycoplasmosis (Fisher's exact test, $p = 0.0330$) and for clinical signs of URTD (Fisher's exact test, $p = 0.0065$). Infectious disease (mycoplasmosis) and tortoise densities were negatively correlated ($r_s = -0.618$, $p = 0.070$), and mycoplasmosis and death rates were positively correlated ($r_s = 0.612$, $p = 0.072$). Mycoplasmosis was also negatively correlated with distances from Ft. Irwin offices, the cantonment, and paved roads ($r_s = -0.612$, $p = 0.072$ for each variable).

For shell disease (cutaneous dyskeratosis), differences between plots were significant (Fisher's exact test, $p = 0.0147$). Goldstone plots had higher numbers and the Soda Mtns plot had lower numbers of tortoises with moderate to severe signs of shell disease than the other plots. No significant differences existed in amounts of trauma among the plots (Fisher's exact test, $p = 0.7106$). No tortoises with moderate to severe signs of dehydration, starvation, lethargy or cachexia were observed.

3.5. Death rates, causes of and contributors to death

Overall, death rates were high for the four years prior to the surveys, with the exception of Tiefort Mtns (Table 6). Not all shell-skeletal remains (10.2–65.5%) could be assigned a cause of death. Where a cause or contributor to death could be assigned, vehicles and predators were often factors. Remains with signs of vehicle crushing occurred on all plots or management units (Goldstone) but were more common (10.7–72.7%) on the five plots with recent or on-going military maneuvers (Alvord Slope, Langford, Tiefort Mtns, Eastgate 1, Eastgate 2). Shell-skeletal remains are likely to be undercounted and death rates under-estimated on plots with military maneuvers, because remains are often crushed or buried with vehicular traffic. At the Tiefort Mtn plot, fragments of marked tortoises were found crushed on the surface as well as buried. Some remains had multiple signs of predation or scavenging, disease, and trauma from vehicles.

Deaths from vehicles were significantly correlated with surface disturbance ($r_s = 0.786$, $p = 0.018$); counts of trash ($r_s = 0.857$, $p = 0.007$) and military ordnance ($r_s = 0.821$, $p = 0.012$); and proximity to Ft. Irwin offices and paved roads ($r_s = 0.714$, $p = 0.036$ for both variables). Another important anthropogenic source of deaths was from shooting. Tortoise remains with gunshot evidence were observed at Goldstone and Alvord Slope, locations that were accessible to unauthorized personnel. When deaths from shooting and vehicles were combined, the r_s and p values were the same as for vehicles alone.

Predators may have played an important role in deaths of tortoises at some plots (Table 6). From 0% to 53.1% of shell-skeletal remains showed signs of trauma (tooth punctures, cracking of scute and bone, gnaws, chews) or possibly scavenging from *C. latrans*, *V. macrotis* and other mammals. Although some remains were found in mammalian scats, no concentrations of tortoise shells or bone/scute fragments were observed at sites frequented by mammalian carnivores (e.g. predator sign concentration areas). *C. latrans* was frequently observed when driving to and from plots within the NTC, but the sightings were not quantified off plots. In our experience, Ft. Irwin has a high concentration of this species.

Five species of avian predators known or suspected to kill tortoises were observed: *A. chrysaetos*, *B. jamaicensis*, *L. ludovicianus*, *G. californianus*, and *C. corax*. *C. corax* was the most common avian predator sighted, and a few tortoise remains showed signs typical of a *C. corax* kill (Table 6). Most, if not all the plots, were within 1–2 km of known *C. corax* nesting sites, and the Soda Mtns plot supported an active nest. *C. corax* was seen more frequently at Goldstone ($\bar{x} = 5.63$ field h observation^{-1}, SD $= 2.10$, $N = 15$) and Soda Mtns (9.9 field h observation^{-1}, $N = 1$) than at plots in military maneuver areas ($\bar{x} = 28.28$ field h observation^{-1}, SD $= 11.156$, $N = 5$). The numbers of field h observation^{-1} of *C. corax* and other avian predators were positively but not significantly correlated with counts of trash and ordnance ($r_s = 0.500$, $p = 0.127$ for both variables) and for % surface disturbances and distances to paved roads and the Ft. Irwin offices ($r_s = 0.464$, $p = 0.147$ for all three variables).

Table 8
Anthropogenic impacts recorded on the 21 study plots

Plot name	% surface disturbance	No. trash items		No. of military ordnance	No. of excavations, pits, bunkers	No. of fence lines, posts	Field hours/avian predator observation
		Large	Small				
G-1	0.03	1	1	4			9.4
G-2	13.37	18	274	1			4.8
G-3	3.13	11	195		1		2.9
G-4	1.05	1	32		1		8.4
G-5	0.4	1	14		1		4.3
G-6	1.26	2	36	1			6.2
G-7	1.19	16	35	4			5.1
G-8	4.76	4	15			2	5.7
G-9	0.82	6	496	1			6.6
G-10	0.54		14		3		8.8
G-11	9.98	14	141	1			9.3
G-12	1.54	5	365				3.9
G-13	0.93	1	60	2	1	1	8.1
G-14	2.22		15	18			4.3
G-15	3.17		41	4			6.3
Alvord Slope	2.67		46	12			25.2
Langford	43.59	<1	260	20			28.6
Tiefort Mtns	9.82	<1	275	27	>1		32.9
Eastgate 1	13.01	4	382	15	2		42.6
Eastgate 2	15.61	16	>607	>615	4		12.1
Soda Mtns	1.46	7	2		1		9.9

Field hours = search plus processing hours. All countable items were normalized to per km^2.

3.6. Impacts in general

Tortoise density and % surface disturbance were negatively but not significantly correlated ($r_s = -0.414$, $p = 0.178$). All plots showed one or more signs of surface disturbance (Table 8), and the amount varied from 0.03% on G-1 to 43.59% on Langford ($\bar{x} = 6.22\%$, SD = 9.85%). Overall surface disturbance was lower at the Soda Mtns plot (1.46%) and the 15 Goldstone plots ($\bar{x} = 2.96\%$, SD = 3.81%) than at the five plots used for military maneuvers in the recent past or currently ($\bar{x} = 16.94\%$, SD = 15.67%). When the study plots were placed in four groups by historical and current land uses and disturbances, the % surface disturbance was significantly different (ANOVA, $F_{3,17} = 4.742$, $p = 0.014$).

The % surface disturbance was significantly correlated with counts of trash and military ordnance ($r_s = 0.786$, $p = 0.018$ for both variables). The counts of small trash followed a pattern similar to % surface disturbance: the lowest counts of trash ($x = 2$) occurred at the Soda Mtns plot, with higher counts on average at the Goldstone plots ($\bar{x} = 115.60$, SD = 151.53, $N = 15$) and the highest counts on the five plots recently or currently used for military maneuvers ($\bar{x} = 314.00$, SD = 204.17, $N = 5$). Similarly, the Soda Mtns plot had no debris from firearms or ordnance, followed by the Goldstone plots ($\bar{x} = 2.40$,

Table 9
Access to study plots: proximity to towns, offices, and paved roads

Plot name	Distance (km) from			Presence, location of dirt road (s) on plot
	FIC or towns*	FIC offices	Paved road	
G-1	25.0	2	2.1	Yes, NE corner
G-2	21.8	2.5	Abuts W plot edge	None
G-3	22.3	3.2	0.3	Yes, multiple
G-4	22.5	5.0	1.8	Yes, on NE corner
G-5	24.2	2.5	2.8	Yes, on plot
G-6	16.3	0.5	1.0	Yes, on plot
G-7	18.1	2.2	0.4	Yes, on edge
G-8	13.9	3.2	2.3	Yes, on plot
G-9	16.1	1.5	1.4	Yes, to edge
G-10	12.6	2.7	NW corner	Yes
G-11	15.0	2.5	Crosses SW	Yes
G-12	11.5	1.7	1.0	Yes
G-13	8.8	0.5	Abuts 1 boundary	Yes
G-14	6.3	1.0	Abuts two boundaries	Yes
G-15	6.0	1.0	0.1 km from two boundaries	Yes
Alvord Slope	12.6	10.0	12.6	Multiple-military, pre-1994
Langford	15.5	16.5	15.5	Multiple-military, pre-1994
Tiefort Mtns	18.2	18.2	18.2	Multiple-military
Eastgate 1	33 (FIC), 23*	33	20.7 from Hwy 127	Multiple-military
Eastgate 2	26.5	26.5	26.5	Multiple-military
Soda Mtns	19.9*	19.9	17.8 from Hwy 127	None, near boundary

FIC = cantonment at Ft. Irwin.

SD = 4.58, $N = 15$), and the five plots used recently or currently for military maneuvers ($\bar{x} = 137.80$, SD = 266.82, $N = 5$).

Proximity of dirt and paved roads, office facilities, and towns to the plots contributed to losses of tortoises through vehicle-related deaths (see above). All plots were accessible by dirt roads (Table 9). Dirt roads crossed, were on boundaries of, or otherwise contacted all of the plots. In contrast, paved roads were close to, crossed, or abutted on the Goldstone plots ($\bar{x} = 0.88$, SD = 0.98, $N = 15$) but were more distant ($\bar{x} = 18.70$ km, SD = 5.30, $N = 5$) from the recently or currently used military maneuver plots or the Soda Mtns plot (17.8 km). All Goldstone plots were close to office facilities ($\bar{x} = 2.13$ km, SD = 1.87, $N = 15$), whereas plots in current and recently used military maneuver areas were more distant ($\bar{x} = 20.84$ km, SD = 8.989, $N = 5$). The Soda Mtns plot was 19.9 km from offices. The distances of plots from human settlements such as the Fort Irwin cantonment or towns ranged from 6.0 to 26.5 km. Three plots (G-13, -14, -15) were within 8.8 km of the cantonment.

4. Discussion

4.1. Sampling for tortoises, precipitation, and habitats

With two exceptions, plots were sampled in years when precipitation and forage production were at or above the long-term norm, thereby ensuring that above-ground activity for tortoises would be high (Henen et al., 1998; Duda et al., 1999) and tortoises would be more easily observable for counts. Tortoise sign was evident on all but one plot, indicating that tortoises were using or had occupied the habitat in the recent past.

The 21 plots were representative and typical of many tortoise habitats in the Mojave Desert (Fish and Wildlife Service (FWS), 1994). The perennial vegetation, a desert scrub community with *L. tridentata* dominant by aspect, is widespread throughout the Mojave Desert. Likewise the varied topography of valleys and alluvial fans, piedmont, and rocky slopes of mountains strewn with boulders on the 21 plots is also characteristic of large parts of the Mojave Desert.

4.2. *Status of tortoise populations at the NTC*

All 21 plots exhibited one or more attributes indicative of recent, ongoing, or future declines in tortoise populations: low densities coupled with recent high death rates, deaths due to anthropogenic causes, presence of infectious and other diseases, multiple and chronic disturbances to habitat, fragmented habitat, and close proximity to human settlements. Populations with similar characteristics have experienced declines elsewhere in the Mojave and Colorado deserts in recent years (Fish and Wildlife Service (FWS), 1994; Berry and Medica, 1995; Berry, 1997; Brown et al., 1999; Christopher et al., 2003). Some moderate to high density (100–200 tortoises km^{-2}) populations of desert tortoises in the Mojave Desert declined 80–90% in <10 years (Berry and Medica, 1995; Brown et al., 1999; Christopher et al., 2003). Population densities were very low on 16 of the 21 plots and are probably no longer viable. The FWS estimated minimum density for genetic viability at >3.86 adult tortoises km^{-2} in the *Desert Tortoise* (*Mojave Population*) *Recovery Plan* (Fish and Wildlife Service (FWS), 1994); only tortoises on the Alvord Slope, Langford, Tiefort Mtns, Eastgate 2, and Soda Mtns plots equal or exceed this density.

During the 4 years preceding the surveys, death rates were high on all but the Tiefort Mtn plot, exceeding the 2% annualized adult mortality figure estimated for stable populations (Turner et al., 1984). No indications of drought-associated deaths from dehydration or starvation were evident on plots, although deaths from drought have been documented elsewhere in the Mojave Desert in the 1980s and early 1990s (Turner et al., 1984; Berry et al., 2002). The elevated death rates at the NTC were due in part to anthropogenic causes. Known causes or contributors to mortality included vehicles, vandalism, disease, and predators. Deaths from vehicles contributed to a substantial portion of deaths on plots with recent and current military maneuvers. Vehicular travel on or off paved or dirt roads can have negative effects on tortoises, other species of wildlife, and the ecosystem (Forman et al., 2003). Loss of habitat, fugitive dust, and contaminants from vehicles and the roadbed are a few potential problems. Roads can deplete adjacent desert tortoise populations for distances >4000 m from the roadway, depending on traffic volume (von Seckendorff Hoff and Marlow, 2002; Boarman and Sazaki, 2006). A protected area adjacent to a military maneuver area probably experiences a similar depletion or source-sink effect (e.g. Jonzén et al., 2005). The Langford and Alvord Slope plots, in critical habitat and protected from a maneuver area by a fence, had fewer tortoises on the parts of the plots close to the maneuver area. Dirt roads may function in a manner similar to paved roads, albeit to a lesser extent. Every Goldstone plot contained dirt roads or abutted on dirt roads. Plots with recent and current military maneuvers were crossed by numerous dirt roads and vehicle tracks, but were distant from paved roads.

Tortoises with signs of gunshot deaths were found on the Alvord Slope and Goldstone plots, which are in close proximity to the NTC boundaries with public land. Public lands have multiple uses and are accessible to the general public. In a study of gunshot deaths of wild tortoises in the California deserts during the mid-1970s and early 1980s, the highest incidences (14.6–28.9%) occurred in the western and southern Mojave Desert (Berry, 1986). Although the NTC was not included in the study, it is adjacent to the sampled areas. The frequency of gunshot deaths was linked to numbers of human visitors, concentrated recreational use areas, vehicular access, and proximity to urban centers.

Infectious disease is a potentially important and critical factor near the Fort Irwin cantonment, office facilities, and roads. The presence of mycoplasmosis was confirmed in two tortoises at southern Goldstone plots, and tortoises with moderate to severe clinical signs typical of URTD were observed at Goldstone as well as on the Alvord Slope. In addition, NTC personnel have observed escaped, ill, captive tortoises and wild tortoises with clinical signs of URTD near Goldstone office facilities and the cantonment (Mark Massar, personal communication). Mycoplasmosis and other infectious diseases are more likely to occur in captive tortoises living in towns or cities, in wild tortoises living at the desert-urban interface, and in desert areas where captive tortoises have been released or escaped (Jacobson et al., 1995; Johnson et al., 2006) than in remote desert areas. Mycoplasmosis may have contributed to the recent population declines at the Goldstone plots. Mycoplasmosis has been implicated in catastrophic declines of tortoise populations at the Desert Tortoise Research Natural Area and elsewhere in the Mojave Desert (Jacobson et al., 1991; Brown et al., 1999; Christopher et al., 2003). No tortoises with positive tests for mycoplasmosis occurred at remote plots.

In contrast to the findings for mycoplasmosis, significantly more shell disease occurred on plots in currently and recently used military maneuver areas than on the plot with no history of military use. The higher amounts of surface disturbance, vehicle use, trash, debris from firearms and ordnance, and possibly dust in the military maneuver areas may be sources of potential toxicants or other stressors that contribute to shell disease (Jacobson et al., 1994; Homer et al., 1998; Seltzer and Berry, 2005; Chaffee and Berry, 2006).

Populations of the avian predator, *C. corax*, have increased dramatically in recent years (Boarman and Berry, 1995; Boarman and Coe, 2002). Population increases are due to anthropogenic subsidies in the form of food (trash at landfills, road kills on dirt and paved roads, and food sources in and near towns) and perches (power towers and poles) (Boarman, 1993, 2003; Kristan and Boarman, 2003; Kristan et al., 2004). *C. corax* is similarly subsidized at the NTC (Boarman et al., 2006) and is a very successful predator of juvenile tortoises. Kills by *C. corax* formed a small portion of tortoise deaths at our NTC plots, unlike the high mortality experienced by juvenile tortoises at another NTC study site where a head-starting programme was underway (Morafka et al., 1997). This predator has the potential for hyperpredation, which can lead to declines in local tortoise populations (Kristan and Boarman, 2003; Kristan et al., 2004). *C. latrans* is also likely to be similarly subsidized in terms of food sources, however, no studies have been undertaken in the Mojave Desert to address the subject.

4.3. Anthropogenic impacts to habitat; cumulative impacts

Human activities are an important consideration in the well-being of tortoises at local, regional, and landscape scales (Fish and Wildlife Service (FWS), 1994). Anthropogenic impacts can operate cumulatively and synergistically to have negative effects on tortoises and their habitats. In this case, the anthropogenic impacts were typical of military installations or intensively used recreation areas. The percent of surface disturbance and amounts of trash, firearms and ordnance were lowest at the Soda Mtns plot, increased at Goldstone plots, and reached highest levels on plots currently or recently used for military maneuvers. Much of the surface disturbance was caused by vehicles, troop movements, and bivouac areas. A pattern similar to surface disturbance existed for paved and dirt roads. The Soda Mtns plot was distant from paved roads and had no dirt roads, whereas Goldstone plots were, on average, 0.88 km from paved roads. Deaths of tortoises from anthropogenic sources were significantly correlated with % surface disturbance, counts of trash and ordnance, and proximity to Ft. Irwin offices and paved roads.

Military maneuvers and training activities have negative effects on tortoise habitat. Shrub cover is reduced and soils are compacted (e.g. Lathrop 1983; Prose, 1985; Prose et al., 1987). Such disturbances contribute to invasions and establishment of alien annual plants (Brooks and Berry, 2006). Impacts on soils and vegetation may persist for decades, if not centuries, and have a cascade of effects on the tortoises, e.g. reduced cover of shrubs can expose the tortoises to predators, burrows are crushed, biomass and composition of forage is altered (Jennings, 1997), and trash and contaminated soil may be consumed. In a degraded habitat, tortoise populations are likely to be stressed and more susceptible to disease and mortality.

5. Conclusions

We hypothesized that tortoise populations would have higher densities and lower death rates in undisturbed areas, remote from human contact, and higher death rates where human contacts with tortoises were common and land was chronically affected by anthropogenic activities. Our survey of 21 plots at the NTC in the central Mojave Desert revealed low densities and high death rates of desert tortoises on most plots. Tortoises had died from multiple anthropogenic causes (vehicles, gunshot, subsidized predators), and many showed moderate to severe signs of disease. Our data were insufficient to test the first part of the hypothesis, that tortoises would have higher densities and lower death rates at undisturbed sites, remote from human contact, because only one plot, Soda Mtns, was "undisturbed." Densities at Soda Mtns were modest, and only a few tortoises showed moderate to severe clinical signs of disease, but death rates were high, primarily from predation. The Soda Mtns plot was not an ideal example of an undisturbed, remote plot because it was adjacent to Eastgate 1, a plot with heavy military use, a low tortoise density and high death rate. As such, Soda Mtns may have experienced a source-sink or edge effect relationship with the adjacent military use area in Eastgate 1. Additional challenges to testing this part of the hypothesis are a lack of undisturbed tortoise populations and habitat to use as a control, no historical data base for tortoise population attributes for the NTC and nearby areas, and numerous and multi-layered historical and recent anthropogenic uses in the central Mojave Desert.

Our data sets supported the second part of the hypothesis. Tortoise densities were significantly and inversely correlated with death rates, and a substantial portion of the deaths were caused by vehicles and to a lesser extent shooting. Vehicle-related deaths were significantly correlated with other anthropogenic activities (% surface disturbances, ordnance, trash, and proximity to Ft. Irwin offices and paved roads), all of which were related to the military uses. Densities were also negatively correlated with infectious diseases, but not significantly so ($p = 0.070$). In turn, infectious disease was negatively correlated with distances from Ft. Irwin offices and paved roads—a relationship observed elsewhere at the urban–desert interface. Tortoises with infectious diseases are more likely to occur near human habitations and where people are than in remote areas. While similar causes of death and cumulative disturbances of habitat occur elsewhere in the geographic range of the tortoise (Fish and Wildlife Service (FWS), 1994), military bases such as the NTC have a unique set of disturbances typical of training areas. Populations of tortoises are unlikely to persist where death rates remain high.

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