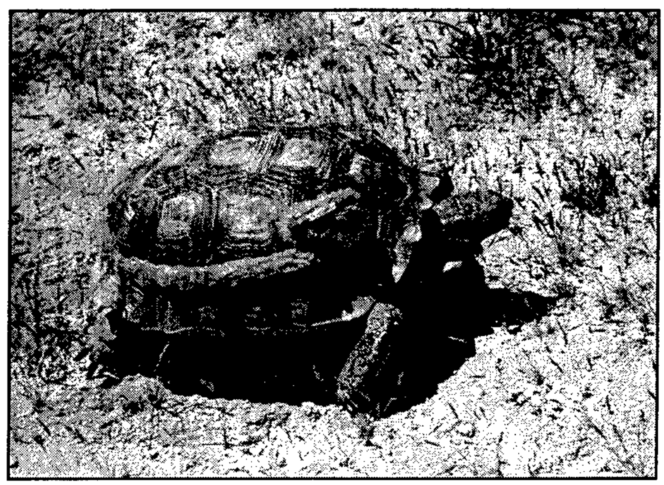
US Army Corps
of Engineers
Construction Engineering
Research Laboratories

USACERL Technical Report 98/39
May 1998

Radiotelemetry Study of a Desert Tortoise Population

Sand Hill Training Area, Marine Corps Air Ground Combat Center, Twentynine Palms, California

by
Jeffrey J. Duda and Anthony J. Krzysik



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Comparisons were made with a simultaneous study in a similar, but pristine, habitat at Pinto Basin in Joshua Tree National Park. Statistical comparisons were made for three parameters: home range size, number of burrows used, and distance traveled between successive recaptures. Each paired contrast: year (1995 vs. 1996), gender (male vs. female), and study site (Sand Hill vs. Pinto Basin); was analyzed using the other two contrasts as nested factor levels. Home range sizes, activity levels, and number of burrows used were greater in the productive year (1995) than in the drought year (1996). Both genders had similar home range sizes in the productive year, but in the drought year, males possessed larger home ranges. Both genders annually used similar numbers of different burrows, but in the productive year, Pinto Basin tortoises used a greater number of burrows annually than Sand Hill tortoises. General management guidelines were formulated.

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REPORT DOCUMENTATION PAGE

Form Approved
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1. AGENCY USE ONLY *(Leave Blank)*	2. REPORT DATE	3. REPORT TYPE AND DATES COVERED
	May 1998	Final

4. TITLE AND SUBTITLE
Radiotelemetry Study of a Desert Tortoise Population: Sand Hill Training Area, Marine Corps Air Ground Combat Center, Twentynine Palms, California

5. FUNDING NUMBERS
MIPR
M673999-4MPGR001,
M673999-4MPGR003,
M673999-5MPG1002, and
M673999-5MPG1003

6. AUTHOR(S)
Jeffrey J. Duda and Anthony J. Krzysik

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)
U.S. Army Construction Engineering Research Laboratories (USACERL)
P.O. Box 9005
Champaign, IL 61826-9005

8. PERFORMING ORGANIZATION REPORT NUMBER
TR 98/39

9. SPONSORING / MONITORING AGENCY NAME(S) AND ADDRESS(ES)
Commander, Sand Hill Training Range
ATTN: NREA
NREA Directorate, Bldg. 1451, Box 788110
McAgee, Twentynine Palms, CA 92278-5000

10. SPONSORING / MONITORING AGENCY REPORT NUMBER

11. SUPPLEMENTARY NOTES
Copies are available from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161.

12a. DISTRIBUTION / AVAILABILITY STATEMENT
Approved for public release; distribution is unlimited.

12b. DISTRIBUTION CODE

13. ABSTRACT (Maximum 200 words)
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14. SUBJECT TERMS
desert tortoise
threatened species
natural resource management
radiotelemetry

15. NUMBER OF PAGES
76

16. PRICE CODE

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
Unclassified	Unclassified	Unclassified	SAR

NSN 7540-01-280-5500

Standard Form 298 (Rev. 2-89)
Prescribed by ANSI Std 239-18
298-102

DTIC QUALITY INSPECTED 1

Foreword

This study was conducted for the Marine Corps Air Ground Combat Center (MCAGCC), Natural Resources and Environmental Affairs (NREA) Directorate and Range Control under Military Interdepartmental Purchase Request (MIPR) Nos. M6739994MPGR001 and M6739994MPG1003, Work Units 001BH3 and 001BMB in FY95; and MIPR Nos. M6739995MPGR002 and M6739995MPG1003, Work Units 001CV8 and 001CVZ in FY96, "Desert Tortoise Radiotelemetry Study." This project was also funded by the Department of Defense Legacy Program. The technical monitor was Sharon Jones, NREA.

The work was performed by the Natural Resource Assessment and Management Division (LL-N) of the Land Management Laboratory (LL), U.S. Army Construction Engineering Research Laboratories (USACERL). Jeffrey Duda was a graduate student in the Department of Biological Sciences, Wayne State University, Detroit, MI, whose contribution to this project also fulfilled his Masters Thesis requirement. The staff of Marine Corps Air Ground Combat Center (MCAGCC), Natural Resources and Environmental Affairs (NREA) Directorate and Range Control are acknowledged for their contributions. Ester Hutchinson provided the original funding for this project in 1995, and Sharon Jones funded the project in 1996. Rhys Evans helped with field work in 1996. Sharon Jones and Rhys Evans also provided a valuable review of the draft report. Roy Madden, Sharon Jones, Ken Kreklau, and Kip Otis-Diehl provided assistance with logistical support. Dr. Jerry Freilich, former ecologist of Joshua Tree National Park, provided valuable discussions, assistance, insight, and equipment, that benefitted all aspects of this study. Others at Joshua Tree that deserve thanks include Ann Garry and Chris Collins for their advice, support, and field work. The 2-year project would not have been possible without the help of many people at USACERL: Richard Stevens, Peg Gronemeyer, Jim Sechrest, and Joel Meloche contributed with fieldwork and database support. Jocelyn Aycrigg provided valuable GIS support. Barbara Kermeen (AVM Instrument Company) provided the radiotelemetry transmitters and receivers. The USACERL principal investigator was Dr. Anthony J. Krzysik. Dr. David J. Tazik is Acting Chief, CECER-LL-N; Dr. William D. Severinghaus is Operations Chief, CECER-LL; and William D. Goran is the responsible Technical Director, CECER-LL. The USACERL technical editor was William J. Wolfe, Technical Resources.

COL James A. Walter is Commander and Dr. Michael J. O'Connor is Director of USACERL.

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1 Introduction

Background

The desert tortoise radiotelemetry study was conducted at Sand Hill Training Area of the Marine Corps Air Ground Combat Center (MCAGCC), Twentynine Palms, CA, in the southcentral Mojave Desert. Detailed natural resources information dealing with this installation can be found in MCAGCC (1993), and in Krzysik and Trumbull (1996).

The Mojave population of the desert tortoise (*Gopherus agassizii*) was Federally listed as threatened on 2 April 1990 (USFWS 1990a), critical habitat was designated on 8 February 1994, and the recovery plan was approved and published on 28 June 1994 (USFWS 1994a). The "Mojave population" is an administrative and management designation for desert tortoise populations found west and north of the Colorado River. The petitioning for listing and the subsequent listing was motivated by perceived recent declines of the desert tortoise throughout much of its distribution in the Mojave Desert, but especially in the western portion of its range (reviewed by Krzysik 1994a). Many factors may have potentially caused its decline (Luckenbach 1982, Berry 1984, 1991, 1992; Berry et al. 1986a, 1986b, 1987, 1988, 1990; Knowles et al. 1990; Avery and Berry 1991; Jacobson 1994):

- urbanization and agricultural developments
- cattle and sheep grazing
- habitat degradation by off-road vehicles
- vandalism, including capture for pets or eating as well as casual shootings
- mining operations
- military training activities
- the southern California drought
- predation of ravens on hatchlings
- (possibly of paramount importance at this time) the occurrence of the usually fatal Upper Respiratory Disease Syndrome (URDS, also called Upper Respiratory Tract Disease [URTD]), in many populations, especially in the western Mojave Desert.

Although there is evidence of population declines at specific local scales, the widespread and large-scale decline in desert tortoise populations remains a controversial issue (USFWS 1990b; Bury and Corn 1995).

The Desert Tortoise Recovery Plan has identified 14 Desert Wildlife Management Areas (DWMAs), located in six "Recovery Units" in the Mojave and Colorado Deserts (USFWS 1994a, 1994b). The Colorado Desert is the northwestern portion of the Sonoran Desert that is located in California. MCAGCC is surrounded by three DWMAs in a landscape context. The northwest portion of the installation at the Sunshine Peak Training Area borders the Ord-Rodman DWMA. The other two DWMA boundaries are not located adjacent to MCAGCC boundaries. The Joshua Tree DWMA is located south of MCAGCC, and the Chemehuevi DWMA lies east of the installation. The extensive urban development in the municipalities of Twentynine Palms and Joshua Tree spatially isolates MCAGCC tortoises from Joshua Tree National Park and the Joshua Tree DWMA (Krzysik et al. 1995b). Nevertheless, relocations by well intentioned or careless humans are common in the Mojave Desert (Krzysik 1994a). Habitat destruction and its associated fragmentation of populations represent the greatest threat to the genetic integrity and ecological viability of native wildlife (see **Habitat Fragmentation**, p 18).

The Combat Center may represent a dispersal route for desert tortoise transients among the three DWMAs identified above. Although this potential for gene flow is low, only a single genetic transfer is required per generation for populations to be considered panmictic (population individuals freely interbreeding) (Wright 1931; Lewontin 1974; Lande and Barrowclough 1987). The generation time for desert tortoises is on the order of 15 to 30 years. U.S. Army Construction Engineering Research Laboratories (USACERL) researchers have observed desert tortoises or their signs (burrows and scats) throughout MCAGCC, but typically at very low densities. Tortoises and their signs were even observed in relatively rugged mountainous terrain. USACERL was tasked with determining home range sizes and associated parameters of adult desert tortoises in this military training landscape as compared with a similar but pristine habitat, to determine whether training activities adversely affect desert tortoise spatial ecology and to recommend management guidelines to maintain the integrity of tortoise populations at MCAGCC.

Objectives

The objectives of this study were to:

1. Determine gender-specific home range sizes of adult desert tortoises in a military training landscape at Sand Hill Training Area and compare these with home range sizes of tortoises living in a similar but pristine habitat, Pinto Basin, at Joshua Tree National Park (JTNP), located 64 km directly to the southeast.
2. Contrast interyear variation in home range sizes.
3. Determine the number of burrows that tortoises use, and the relationships between spatial and temporal patterns of burrow use and home range sizes.
4. Determine relative activity patterns of the desert tortoise.
5. Determine burrow characteristics: metrics (width, height, depth), relative condition, and association with perennial vegetation.
6. Make management recommendations.

Approach

Two square study plots were established at Sand Hill Training Area; each plot was 9.0 km^2 in area. A total of 36 adult tortoises, split approximately equally by gender, were fitted with radiotelemetry transmitters during the course of the study. Twenty-nine tortoises were available in each of the 2 years, 1995-1996, for data analysis. A 2.6 km^2 study plot at JTNP was simultaneously monitored by Dr. Jerry Freilich (Park Ecologist) and associates, and comparisons were made with the Sand Hill plots. Sample size at JTNP consisted of nine adult tortoises. Tortoises were monitored using AVM Instrument Company (Livermore, California) radiotelemetry transmitters and receivers, and Rockwell GPS (global positioning system) units. Home range estimates were calculated using the minimum convex polygon method. A number of parameters were evaluated for desert tortoises: home range size, activity levels, burrow use, annual weight changes, and burrow metrics (condition or age, association with perennial vegetation, width, height, and depth). Additional field data included tortoise morphological metrics and selected environmental variables. Statistical comparisons were made for three parameters: home range size, number of burrows used, and distance traveled between successive recaptures. Each paired contrast: year (1995 vs. 1996), gender (male vs. female), and study site (Sand Hill vs. Pinto Basin) was analyzed using the other two contrasts as nested factor levels. Results were analyzed and general management guidelines were formulated.

2 Desert Tortoise Ecology

The baseline ecosystem classification for MCAGCC suggests that the highest quality and most extensive habitat for the desert tortoise at MCAGCC is at the Sand Hill Training Area (Krzysik and Trumbull 1996). Tortoise populations, which may be of local significance, have also been reported at other training areas: Sunshine Peak, Gypsum Ridge, Emerson Lake, Cleghorn Pass, and Bullion (MCAGCC 1993; personal communications, Natural Resources and Environmental Affairs [NREA] and Range Control personnel; personal observations). While the current trend for natural resources and land management in the Department of Defense (DOD) is an ecosystem approach (e.g., Goodman 1994, 1996; Krzysik and Trumbull 1996), single-species management may represent an important strategy for addressing compliance mandates and protecting major "umbrella species," e.g., desert tortoise, spotted owl, and grizzly bear. These species possess extensive distributions or home ranges, and are therefore critical for landscape and biodiversity conservation. Chelonians (tortoises and turtles) may represent—worldwide—excellent examples of umbrella species and ecological indicators for landscape integrity. The wood turtle (*Clemmys insculpta*) would constitute an excellent umbrella species for the conservation of northeastern United States forested watersheds. Similarly, box turtles (*Terrapene carolina* and *T. ornata*) with six currently recognized subspecies, occupy most of the central and eastern United States and also represent excellent candidates for monitoring landscape integrity and ecological viability.

Desert Tortoise Ecology and Behavior

The desert tortoise is a herbivorous reptile occurring in suitable habitats throughout the Mojave and Sonoran Deserts of the southwestern United States. Mojave populations found west and north of the Colorado River include almost all tortoises found in the Mojave Desert, and those found in the Colorado Desert. A small strip of the Mojave Desert in northwest Arizona is not included in this designation, because this area lies east of the Colorado River. The preferred habitat or ecosystem of tortoises in the Mojave and Colorado Deserts (and possibly some populations just east of the Colorado River in Arizona's Sonoran Desert) is creosote/bursage (*Larrea tridentata / Ambrosia dumosa*) scrub found on gentle bajadas and valleys with sandy-loam soils, typically below 1000-1200 m of elevation. However, tortoises can also be found in a surprisingly wide variety of ecosystems including: yucca (*Yucca* sp.) woodlands, saltbush (*Atriplex* sp.) scrub, steep gravelly and rocky slopes, mountainous terrain, and even at elevations over 1200 m. Washes are a favored landscape element for foraging and for establishing winter caliche burrows. Caliche is a rocky layer resembling gravel embedded in concrete, and is chemically formed under natural conditions from calcium and magnesium carbonates, iron, and other minerals. Caliche in fluvial channels erodes through the action of flooding events forming caves. Locally, these caves may be occasionally very deep. Deep winter caliche burrows are important for desert tortoises in the northern extreme of their range (Woodbury and Hardy 1948). Researchers in this study report having observed MCAGCC tortoises in shallow caliche burrows.

Mojave populations differ genetically (Lamb et al. 1989), morphologically (Weinstein and Berry 1987), in burrow construction (authors' personal observation), and in habitat preferences (Barrett 1990) than desert tortoise populations that occupy the Sonoran Desert uplands of Arizona and Mexico. The Sonoran desert tortoise prefers rugged mountainous rocky habitats with dense perennial vegetation typified by foothills palo verde (*Cercidium microphyllum*). Burrowing behavior is not well developed in the Sonoran desert tortoise, and would be exceedingly difficult in the shallow rocky soils. Instead of well-constructed burrows, tortoises use shallow openings in rock or boulder outcrops and pallets in dense vegetation.

Over the course of their lifetime, desert tortoises probably spend over 95 percent of their time sheltered in underground burrows that they construct and maintain. These burrows serve as general shelters, hibernation and estivation dens, and often as nesting sites. Tortoise burrows also represent shelters for a wide variety of vertebrates and invertebrates (Woodbury and Hardy 1948; Burge 1978; Hohman et al. 1980; Luckenbach 1982; author's personal observations). Desert tortoise burrows are particularly important for snakes, lizards, burrowing owls, rodents, jackrabbits, and many specialized invertebrates. The burrows provide permanent homes, escape from predators, thermoregulation and maintenance of homeostasis, and hibernacula. An important purpose of burrow structures is to provide refuge from the extreme ranges of air and soil-surface temperatures, intense infra-red and ultraviolet sunlight, and strong desiccating winds, all typical of southwestern deserts. The ecological importance of thermal regulation in desert reptiles has long been appreciated (Cowles and Bogert 1944). The importance of burrow microclimates to desert vertebrates and invertebrates, and the exceedingly steep gradient of soil temperature with soil depth cannot be overstated (e.g., Louw and Seely 1982; Cloudsley-Thompson 1991). Burrows stabilize both daily and annual temperature extremes for desert inhabitants, providing both cooler and more humid environments during summer days, and warmer microclimates during summer nights and over the winter. Desert lizards are well-known for their thermoregulatory activities and burrow use (Bradshaw 1986; Pianka 1986). Snakes have not been researched to the same extent as lizards, but desert-adapted species that have been studied differ little in thermal preferences, maintaining homeostasis at approximately 30 °C. This is a relatively modest body temperature, considering the high ambient temperatures often encountered in their environments. Examples include: *Spalerosophis cliffordi* (ecologically and morphologically similar to our gopher snakes), from northern Africa, Arabian Desert, and Israel (Dmi'el and Borut 1972); and sidewinders (*Crotalus cerastes*) and speckled rattlesnakes (*C. mitchelli*) from southwestern United States (Moore 1978).

Burrows have been shown to be important for desert tortoise thermoregulation (Woodbury and Hardy 1948; McGinnis and Voigt 1971; Burge 1978; Nagy and Medica 1986; Auffenberg and Iverson 1989; Bulova 1994; Ruby et al. 1994). Tortoises spend prolonged periods in their burrows during winter hibernation (approximately November - March) and summer estivation (approximately June or July - August). During particularly hot and dry years inactivity may begin in June or mid-May, continue throughout the entire fall, and proceed into hibernation. Tortoises become active in late winter or early spring, usually late February through March. Activity patterns are directly and strongly dependent on temperature, precipitation, and the productivity of winter annuals (i.e., the biomass of annuals blooming during the spring months).

The Mojave Desert is characterized by gentle and relatively prolonged winter rains from Pacific storms that make their way across the western and southwestern mountains that outline the boundaries of the desert. Summer thunderstorms are highly unpredictable, patchy, violent, and short lived, arising from squall cells originating in tropical Mexico, the Gulf of California, or the Gulf of Mexico. The amount of annual precipitation in the Mojave Desert is spatially and temporally highly variable within and between years; in typical elevations it ranges locally from virtually no precipitation to 20 cm or more. Annual mean precipitation in typical Mojave Desert creosote scrub is approximately 5 to 10 cm. Precipitation is much higher than this in the highest mountain ranges of the desert. Bagdad (a town that no longer exists), located near the northeast corner of MCAGCC, has the distinction of recording the longest period without rainfall in the known history of North America — between February 1917 and January 1920, Bagdad received 0.25 mm of measured precipitation (Darlington 1996).

During years with adequate winter rainfall and a subsequent abundance of winter annuals (mainly forbs but also grasses), tortoises emerge from their burrows in the early spring and forage intensely. Although tortoises are known to forage on perennial forbs and rarely shrubs, they generally avoid them, probably because of plant toxins and high concentrations of potassium salts. Tortoises may also feed extensively on perennial grasses and cacti, especially when annuals are scarce or unavailable. Food habits are summarized in Krzysik (1994a).

Depending on both high and low temperatures, tortoises may forage all day long. As temperatures increase in mid-spring tortoises retreat to their burrows at mid-day, but continue to forage in the late afternoon. The vegetation desiccates in late spring and early summer as day temperatures increase. During these times, tortoises only observe an early morning period of activity, and eventually begin summer estivation. However, summer thunderstorms initiate a high activity level in tortoises as they actively seek drinking water, and many even initiate mating behavior (Krzysik et al. 1995c). Tortoises may dig shallow depressions in the soil to collect drinking water (Medica et al. 1980). Tortoises even display nocturnal activity levels during summer thunderstorms, but are not known to be nocturnal at other times (P. Medica, personal communication). Following a summer estivation period, tortoises may become active again in the fall depending on the availability of summer annuals (dependent on summer thunderstorms) and the biomass of perennial grasses, especially big galleta grass (*Pleuraphis [=Hilaria] rigida*). Tortoises may emerge as early as 0500 hrs, but sometime after 0700 hrs is more typical. Activity levels are summarized by Morafka (1995).

Tortoises use above-ground activity periods for foraging, thermoregulation, searching for mates, and constructing nests. Burge (1977) described single trip distances for 11 tortoises in southern Nevada. Seventy-five percent of these trips covered distances of 50-200 m, while only 18 percent covered distances greater than 200 m. Tortoises occasionally make long distance movements (1-7 km) outside of their home ranges for purposes of dispersal, mating opportunities, obtaining a limited resource (e.g., nutrients), or finding more suitable habitat (Marlow and Tollestrup 1982; Berry 1986; Boarman et al. 1996b).

During the spring period of high activity (March-June), a number of "summer" burrows are constructed or re-excavated. Morphologically, summer burrows have a single entrance slightly larger than the tortoise followed by a gently sloping (10-30 degrees, usually ~15) tunnel, whose length may vary from being only slightly longer than the tortoise, to burrows over 4 m in length. Over-wintering burrows (i.e., dens or hibernacula) are generally deeper and more complex, with lengths exceeding 10 m in the northern parts of the desert tortoise range (e.g., the Beaver Dam Slope in southwestern Utah, Woodbury and Hardy 1948). These are commonly found in washes associated with caliche layers. Often many tortoises can be found hibernating together in winter dens (Woodbury and Hardy 1948; personal observations), and it is common to find male and female tortoises together in the same burrow or in adjacent burrows, particularly in the spring and fall (personal observations). Cohabitation was obseved on eleven separate occasions with transmittered tortoises (five males, six females) in this study, and many additional times during routine burrow surveys.

Burrows are commonly associated with woody shrubs, and also perennial bunch grasses. The construction of burrows near perennial vegetation has a number of potentially valuable advantages: roots provide structural integrity to the burrow; shrubs provide shade and decreased wind velocities, and therefore aid in thermoregulation and resistance to desiccation; burrow openings and their potential nest sites are more effectively hidden from predators; and tortoises may find it easier to excavate soil that has already been conditioned by plant roots, or similarly, aeolian soils (wind deposited) at the base of shrubs may be easier to burrow in. Burrows are mostly found closely associated with common perennial vegetation, especially creosote bush (*Larrea tridentata*), burroweed (white bursage, *Ambrosia dumosa*), and big galleta grass. However, burrows can also occur on bare ground, completely exposed in the open (see Figure 9, p 39).

Radiotelemetry

Radiotelemetry or radio-tracking has become a popular and well-established technique for monitoring the movements of free-ranging animals, since its introduction in the early sixties (Cochran and Lord 1963). Major technological advances have increased the reliability, accuracy, precision, ease of use, and types of data that can be collected. Concurrently, costs have dramatically declined, making it economically feasible to extend the utility and applications of this important field technique. The most significant breakthrough came in the late 1980s and early 1990s when micro-processor technology was made available, and both transmitters and receivers became dramatically smaller and lighter with reduced power consumption. The small size and weight of modern mini-transmitters and their associated power supply appreciably extend the range of taxa that can be studied. Low power consumption enables appreciable field data to be collected before battery replacement. For example, the single AA lithium battery on AVM tortoise transmitters has an operating time of 12 to 15 months. It is currently possible to obtain physiological data (e.g., heart rate and body temperature) on free-ranging animals, which is stored in automated data logging units (Lund 1988). The integration of Geographic Information Systems (GIS) and satellite telemetry receivers has been another major stepping-stone, enabling wildlife researchers and resource managers to assess and monitor home range sizes, habitat use, behavior patterns, dispersal parameters, and migratory patterns of large wide-ranging vertebrates (Craighead et al. 1971; Amlaner and MacDonald 1980; Timko and Kolz 1982; Fancy et al. 1988, 1989; Tanaka et al. 1988; Marsh and Rathbun 1990; Keating et al. 1991). Associated global positioning systems (GPS) provide very accurate and completely reliable map coordinates in any desired cartographic coordinate or projection system. Modern high-speed, high-memory, gigabyte capacity, and most importantly–economical–microcomputers are currently available for storing, manipulating, analyzing, modeling, and outputting the large data sets that are typical of radiotelemetry studies.

The methods involved in radiotelemetry are relatively universal. Individual animals are equipped with a small (relative to the body size of the animal) transmitter, antenna, and battery unit that transmits a unique fixed-frequency pulsed signal. This signal allows researchers with a receiver/antenna to "home in" on the location of the transmitting individual. Location coordinates are collected with a GPS along with other parameters such as: air and soil surface temperature, weather conditions, time of day, specific behavioral activities, and habitat parameters. An excellent review and introduction to radiotelemetry is Samuel and Fuller (1996). The classic guides to radiotelemetry and its data analysis are Kenward (1987) and White and Garrott (1990).

Home Range

Home range is typically defined as the area in which an animal travels during its normal activities of feeding, mating, nesting, and caring for young (Burt 1943). As an ecological parameter, home range in its most general sense is simply a measure of the amount of space that an individual animal uses during a given time frame (e.g., day, season, or year). A more detailed analysis of the structure of home range includes: centers of activity, overlap with conspecifics, mating behavior, and details of habitat-use for specific activities such as foraging and mating behavior. These analyses provide valuable insight into spatial ecology, animal behavior, and social structure (Adams and Davis 1967; Horner and Powell 1990; Spencer et al. 1990). Home range sizes vary appreciably among animal species, of course, but even within a given species, home range sizes can vary significantly among individuals. Commonly studied parameters for assessing intraspecific differences include: gender, age class, social status, reproductive condition, population density, habitat condition or degradation, current or past weather, disturbance regimes, environmental impacts, or relevant biological parameters (e.g., predation, competition, parasites, pathogens). Many analytical techniques are available to convert radiotelemetry data into a quantitative measure of home range sizes. The choice of an appropriate method is determined by the objectives of the study and the nature of the data.

The minimum convex polygon (MCP) method provides an estimate of the maximum area used by an individual. It involves constructing a polygon, with no angle greater than 180 degrees, outlining the periphery of all relocation points. MCP is a fundamental and commonly used method for estimating home range sizes. Assumptions are reasonable and relative comparisons are easily made. However, the spatial extent of the area enclosed by the MCP may contain areas that are never visited by the experimental subject. MCP calculations are also sensitive to peripheral locations. Outlier points, represented by movements outside the region of normal activity, tend to produce inflated home range estimates. Desert tortoises have been observed to make long distance movements up to 7 km (Berry 1996; Boarmann et al. 1996b). While there are algorithms to correct for outlier points, no "atypical" long range movements were detected with the animals researched in this study, and MCP's were calculated without correction. Because this method is considered reliable (e.g., Samuel and Fuller 1996) and is frequently used for desert tortoise studies, the MCP method was selected for estimating home range sizes.

The harmonic mean estimate of home range size is a nonparametric approach that is based on the harmonic mean of the areal distribution of relocation points (White and Garrot 1990). The harmonic mean method calculates a center(s) of activity described by the harmonic mean of all animal locations. This mean more closely approximates the true center of an animal's activity, because it is insensitive to extreme locations or outlier points (Dixon and Chapman 1980). Contour lines can be calculated around the harmonic mean center(s), which relate to the frequency of data points within each contour. Other home range estimators that use an arithmetic mean to calculate centers of activity have been shown to be sensitive to outlier points. It is possible, for example, that the arithmetic mean approach may falsely calculate a center of activity in an area that an animal has never visited (Dixon and Chapman 1980; White and Garrot 1990).

The adaptive kernel estimator attempts to model contour lines of an animal's spatially explicit activity levels, and works well for active wide-ranging species such as ungulates. However, for sedentary species like the desert tortoise, this method overemphasizes the times that individuals are inactive (e.g., in their burrows).

The definition of home range implies that animals use the environment in a non-random manner, and suggests a degree of site fidelity. The desert tortoise fits this model very well. Desert tortoises exhibit strong site fidelity (Freilich 1997; Freilich et al. 1997), and rarely move more than 3.5 kilometers from the nest where they hatched (Auffenberg and Iverson 1989). An important observation in the natural history of desert tortoises is their construction of a burrow network throughout their home range. Tortoises use their burrow complexes in a single season and over many years (Bulova 1994). Although the physiological mechanism is unknown, tortoises have the ability to recognize parameters of habitat and terrain. They spatially perceive and are aware of the locations of their burrows and their home range, and exhibit an excellent ability to navigate among the spatial complex of their burrows. It is therefore unnecessary to empirically test for site fidelity (e.g., the existence of a home range) by the randomization methods described by Munger (1984) and Spenser et al. (1990).

Dispersal Barriers to Desert Tortoise Populations in the Mojave Desert

Anthropogenic disturbances are the predominant cause of the isolation of desert tortoise populations (demes) in the Mojave and Colorado Deserts. Barriers separating demes have many forms: outright habitat destruction, habitat degradation, roads/highways, urbanization and associated infrastructure, and agriculture. Tortoises may be killed or injured while trying to cross barriers (e.g., highways), or they can avoid barrier areas altogether (e.g., military training ranges with low cover of woody perennial vegetation).

Although desert tortoise populations were always to some extent discontinuous in the Mojave Desert, they are increasingly becoming more fragmented, often with considerable distance between suitable habitat patches. Mountain ranges and extensive playas represent natural barriers, but the recent addition of urbanization, agriculture, Interstate highways, and expansive military training areas (representing all four Services) represent cumulative serious threats to the maintenance of genetic integrity among increasingly isolated tortoise populations. The possible genetic isolation of the Sand Hill desert tortoise population was discussed in Krzysik et al. (1995b).

Habitat Fragmentation

The effect of habitat fragmentation on the desert tortoise is unknown, because very little is known about their population genetics, viable population sizes, and dispersal abilities across unfavorable habitats (Dodd 1986). Research is needed on desert tortoise metapopulation structure and dynamics (referring here to "metapopulation" in its more generalized terminology [Hanski and Simberloff 1997]). Does habitat fragmentation for desert tortoise populations produce the same problems that it does for other species? Fragmentation reduces the amount of habitat available for tortoises, and therefore, reduces total population size. Since tortoises possess relatively low dispersal abilities, fragmentation reduces or effectively prevents gene flow among demes (local populations), and prevents the recolonization of habitat patches subjected to local extinctions. Reduced gene flow reduces population fitness and increases the probability of local extinctions from inbreeding depression, loss of heterosis (decreased genetic variability), and genetic drift (the fixation of potentially ill-adapted gene complexes i.e., phenotypes). However, the genetic problems typically associated with small populations may be relaxed for tortoises (Larson et al. 1984; Bury et al. 1988). There are numerous examples of isolated tortoise and turtle populations worldwide (e.g., bog turtle, *Clemmys muhlenbergii*), apparently maintaining genetic viability despite very low population densities (e.g., 20–50 or fewer individuals) (A. Krzysik, personal observation). Indeed, 22 species (*not subspecies*) of chelonians, including 5 tortoises, of the 257 described species around the world are only known from a single geographic locality (A. Krzysik, data from Iverson 1992).

Reduced genetic variability also reduces a population's capacity to adapt to changing biological or environmental conditions. Beside genetic problems, isolated populations, especially small ones, are subjected to high extinction rates. The extinction process could be triggered by physical processes, such as drought, flooding, temperature extremes, or wildfire; biological processes, such as predation, competition, parasitism, and disease; or anthropogenic impacts, such as habitat destruction, pollution, or direct killing or collecting of specimens. These processes (with obvious exceptions) may not cause mortality directly, but usually affect food or shelter resources, reproduction, or some combination of these. Small isolated groups are also susceptible to extinction from stochastic (random) fluctuations in population numbers. Although the dynamics of population fluctuations are not completely understood, they have been observed for many species under natural conditions. Extinctions in local populations are undoubtedly a common occurrence in natural ecosystems, particularly in stressful environments such as deserts. However, in undisturbed ecosystems and intact landscapes, immigration from other populations fill the void—sometimes rapidly (Levins 1969; Gilpin and Hanski 1991; Hanski and Gilpin 1997) The realities of fragmentation and isolation of habitat patches are relative, and are dependent on many factors (Krzysik 1994a):

1. The nature and characteristics of the isolation barrier
2. Matrix characteristics - nature of the landscape between patches
3. The ecology and life history specifics of the species - primarily home range size, mobility, ecological and physiological needs and tolerances, reproductive needs
4. The distances between/among fragmented patches

5. Patch size and shape
6. Patch size relative to local disturbance regimes
7. Patch density in the landscape
8. Patch connectivity and characteristics of landscape corridors
9. Patch suitability, habitat quality, habitat degradation
10. Ecotone (transition zone) characteristics, structure, and dynamics.

Forman and Godron (1986) and Forman (1995) give a through discussion of patches and landscape ecology. Krzysik (1998) gives an introduction into landscape ecology.

A harmful effect of fragmentation, not always appreciated, is the creation of edges—ecotones between two different habitats. In the Mojave Desert, edges are created by urbanization and all its associated land-use, agricultural conversion, extensive off-road recreational vehicles (ORV) and recreational use, mining, and military training activities. Therefore, edges represent a source of additional mortality for desert tortoises. The desert tortoise is a K-selected species, characterized by low reproductive output, high adult survivorship, and long life expectancy. K-selected species are susceptible to even small increases in adult mortality rates.

Military Training Activities

Landscape-scale military training activities in desert regions, especially those employing armor and mechanized infantry elements, are physically destructive to woody perennial vegetation, soils, cryptogamic crusts, and dramatically alter the structure and function of vertebrate communities (Krzysik 1984, 1985, 1994a, 1994b, 1997a; Krzysik and Woodman 1991). Desert tortoise populations have shown significant declines at the U.S. Army's National Training Center, Fort Irwin, CA in training ranges subjected to high-use of tactical vehicles. However, populations have persisted in Fort Irwin landscapes where off-road vehicle use and subsequent loss of perennial vegetation cover was low (Krzysik and Woodman 1991; Krzysik 1994a, Krzysik 1997a). Military training lands that experience low off-road vehicle use include: borders of installations, live-fire ranges and their extensive buffer zones, and rugged high-bajadas where tactical vehicles are effectively funneled and constrained to traverse the landscape on roads that cross the steep-walled arroyos and canyons.

3 Methods

Study Plots

Two study plots of identical area, each 9 km^2 (North and South) were located at Sand Hill Training Area, MCAGCC (Table 1). These study plots are the same as two of the plots used to estimate desert tortoise densities in a companion project at MCAGCC. The North plot corresponds to the "CE plot" in the density study, while the South plot corresponds to the "SW plot." Sand Hill is a 11,053 ha (111 km^2) training range in the southwest corner of the installation. The training range boundaries are approximately 3 km east of the settlement of Landers, 13 km north of the village of Joshua Tree and 28 km west of the town of Twentynine Palms. Sand Hill lies in a broad valley, west of the Bullion Mountains. The terrain consists of low relief hills and gentle bajadas. Elevation ranges between 555 m at Deadman Lake at the eastern boundary to 883 m on a small hill on the western boundary. Most of the elevation contours of Sand Hill lie between 732-829 m. Elevation of the study plots varies from 762 m at the eastern boundary of the South Plot, to 817 m at the western boundary of the North Plot. Soils are finely sorted and consist of sandy-loams with some loose sands. The major plant community or series found throughout Sand Hill is creosote/bursage scrub. Patches of big galleta grass occur in both study plots, and scattered Joshua trees (*Yucca brevifolia*) are found in the southwestern portion of Sand Hill.

Four well-used dirt roads occur within the North and South study plots. A north-south road provides access to Sand Hill from the southern boundary and extends north into Emerson Lake Training Area. This road only traverses the North study plot at approximately 5,6470 easting. Two roads occur perpendicular to the north-south road and provide vehicle access to both study plots. Surprise Spring road diagonally traverses a small section of the southeast corner of the South study plot.

Table 1. UTM Coordinates (Zone 11) of corners of home range study plots at Sand Hill, MCAGCC.

	SW	NW	NE	SE
Study Plot	Northing - Easting	Northing - Easting	Northing - Easting	Northing - Easting
North	37 9400 - 5 6400	37 9700 - 5 6400	37 9700 - 5 6700	37 9400 - 5 6700
South	37 9100 - 5 6500	37 9400 - 5 6500	37 9400 - 5 6800	37 9100 - 5 6800

Off-road tactical vehicles have caused patchy and sometimes appreciable habitat damage adjacent to these roads. But at greater distances from the roads, off-road vehicle tracks are encountered less frequently. Table 1 shows the Universal Transverse Mercator (UTM) coordinates (WGS84) of the north and south study plots.

Military training activities at the Sand Hill Training Area have been relatively light, with most of the habitat damage occurring between 1942 and the present (Krzysik 1997a). There are recent scattered patches of moderate to heavy habitat damage by tactical vehicles, particularly in the vicinity of the unimproved dirt roads that traverse Sand Hill. A Tortoise Conservation Area (approximately 26 km^2) is located in the center of Sand Hill Training Area, where military training and off-road vehicles are not permitted. The study plots were selected on the basis of a preliminary survey conducted as part of this study in the early spring of 1995. Tortoise research data was available for this area from a previous study (Baxter and Stewart 1986; Baxter 1988).

A comparable desert tortoise radiotelemetry study was simultaneously being conducted in a similar, but pristine, habitat in Pinto Basin of Joshua Tree National Park (JTNP) (Freilich 1997). In this study, 4 male and 5 female adult tortoises were fitted with radiotelemetry transmitters and monitored in a 2.6 km^2 plot (Barrow Plot). The data used from JTNP was from Duda et al. (1997, and manuscript in preparation). Pinto Basin is located 64 km directly southeast of Sand Hill in the transition zone between the Mojave and Colorado Deserts. The Colorado Desert is the northwest arm of the Sonoran Desert. Perennial vegetation of Pinto Basin consists of typical Mojave creosote-bursage scrub, but with Sonoran influences exemplified by increases of white rhatany (*Krameria greyii*) and pencil cholla (*Opuntia ramossissima*), and the appearance of ocotillo (*Fouquieria splendens*) and jojoba (*Simmondsia californica*). The Barrow Plot has flat terrain with elevations ranging from 630 – 670 m.

The combination of Sand Hill lying on the periphery of the installation, the low level of military training activities, and the relatively high tortoise densities in high quality habitat may allow for genetic exchange with other neighboring tortoise populations. However, in an initial analysis the Sand Hill population appears to be isolated from other populations (Krzysik et al. 1995b). Concurrent with the radiotelemetry study in 1995, a field research project at Sand Hill and Joshua Tree National Park was initiated to develop an efficient and economic sampling protocol to estimate the distribution and density patterns of desert tortoises on landscape scales. The first year results of this research were summarized in Krzysik et al. (1995a).

Field Methods

The desert tortoise research conducted at MCAGCC and Joshua Tree National Park was conducted under U.S. Fish and Wildlife Service Endangered Species Permit #PRT-702631. The permit was issued to Joshua Tree National Park with research supervision by Dr. Jerry Freilich and Dr. Anthony Krzysik.

The desert tortoise radiotelemetry study was initiated in late March of 1995. Thirty-five adult tortoises were fitted with AVM transmitters in 1995 at the two Sand Hill study plots at MCAGCC. An additional tortoise was fitted with a transmitter in early March of 1996. Individual adult tortoises were located at random by two to four observers walking within the North and South study plots. Additional individuals were added to the study by serendipitous location while searching for or tracking a telemetered tortoise. The handling of tortoises required special precautions to minimize the potential spread of Upper Respiratory Disease Syndrome (URDS). This disease is usually fatal to desert tortoises, and its epidemiology is still under investigation. Sanitary steps were taken to reduce the chance of a researcher acting as a transmission vector between two tortoises. These included the use of disposable latex gloves whenever a researcher handled an animal, the washing of measuring equipment with full-strength laundry bleach and isopropyl alcohol, and the use of disposable plastic grocery bags for weight measurements. These steps were followed because of the regulations in U.S. Fish and Wildlife Service permits for handling desert tortoises. The tortoises in the current study consisted of a single population. Therefore, these precautions were probably unnecessary, because all individuals are potentially capable of direct contact. However, when simultaneously working on populations that are isolated or in different portions of their range, these specific precautions are mandatory to minimize the risk of spreading URDS.

The first time a tortoise was found, it was marked for permanent identification by filing notches on the edges of marginal scutes (Figure 1) with a small triangular file employing a standardized code (Table 2), and by cementing a small number tag in the center of a rear costal scute using fast-drying clear epoxy. The following parameters were then recorded:

1. *Gender.* Male or female. Juveniles and subadults were not used in this study.
2. *Maximum carapace length (MCL).* Measurements were made with outside calipers from the anterior nuchal scute to the posterior 5th vertebral scute.
3. *Maximum carapace width (MCW).* Measurements were taken at the junction of marginal scutes 5 and 6 on the left and right sides of the individual.

Table 2. Desert tortoise notch code for marking.

Marginal Scute Number		Field Number
Left	M1	1
	M2	2
	M3	4
Right	M1	10
	M2	20
	M3	40
Left	M9	7
	M10	70
	M11	700
Right	M9	400
	M10	200
	M11	100

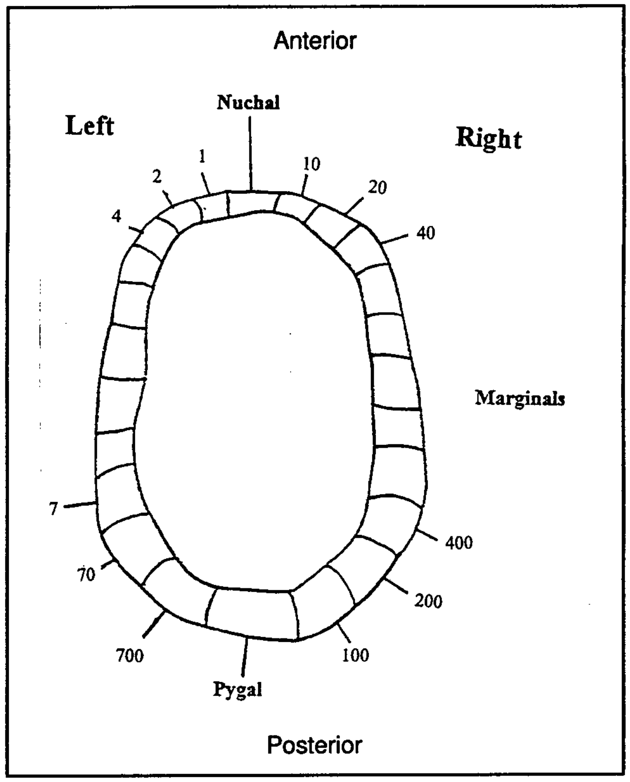

Figure 1. Location of marginal scute numbers.

4. *Weight.* Tortoises were weighed by placing individuals in a plastic grocery bag and using a Pesola 5 kg hanging portable scale. For individuals that exceeded 5 kg, two scales were used.
5. *Health profile of tortoise.* The general health of individual tortoises was primarily concerned with the detection of any signs of URDS. Acute symptoms of a diseased desert tortoise are: swollen eyes with abnormally high liquid discharge, irritated nasal openings with mucus discharge, weight loss, and severe wheezing. Nasal mucous discharges can easily be detected by observing the caking of soil around the nasal openings.
6. *Gross abnormalities,* such as scars, shell defects or shell necrosis, and deviations in normal carapace scute arrangements were recorded. Complete counts and micro-caliper measurements of selected costals and all marginal scutes were recorded. Identification markings from other Sand Hill studies were recorded. Many tortoises had chipped marginal scutes, broken gulars, or abrasions on front and rear legs which were probably caused by encounters with feral dogs or coyotes, or possibly but less likely, kit fox. Indeed, tortoise M95-5, a large male, was originally located by the barking of four feral dogs that were actively chewing on his carapace and plastron.

7. *GPS location coordinates* of tortoise and general notes on location, behavior, and activity. Important parameters included: in pallet, in shade under a shrub, out in the open, and foraging activities.
8. *Environmental parameters* were recorded:
   a. Air temperature taken in the shade 1 m above the ground.
   b. Substrate temperature taken in the sun, just below the soil surface.
   c. General weather conditions, including cloud cover.

Important considerations when designing an experimental field study using free-ranging animals are the potential effects that the experiment or experimenter may have on the behavior, physiology, reproduction, or even the survival of study animals. This is an important ethical and experimental consideration not often contemplated (Kenward 1987). Controlled experimental studies of radiotelemetry effects on tortoises/turtles is scarce (Boarman et al. 1996a). While Boarman et al. (1996a) report that tortoises with anterior mounted transmitters may become entangled in shrubby vegetation, the experience of USACERL and other researchers leads to the belief that this circumstance is not common with properly and carefully mounted transmitters, and that there are no significant effects to tortoise behavior, reproduction, or overall fitness. Potential interference with reproductive activities were minimized in this study by mounting transmitters on the anterior portion of the carapace, to allow for unobstructed male on female mounting during copulation.

Following the gathering of relevant morphological and environmental data, tortoises were fitted with AVM Side-Car radio-transmitters (AVM Instrument Company, Livermore, CA). This model has been specifically designed for carapace mounting on the desert tortoise, and is commonly used in tortoise radiotelemetry studies (Bulova 1994; O'Connor et al. 1994; Boarman et al. 1996a; Freilich 1997). The AVM two-stage SB2-M module consists of a small radio-transmitter (2 cm x 2 cm) and a lithium AA battery completely encased within a clear epoxy shell (Figure 2). A thin 28 cm long antenna exits the encased transmitter/battery package, and circles an edge of the carapace when fitted to the tortoise. The total weight of the entire module is approximately 100 g.

Attachment of the transmitter module was a two-step process. First, a brass module mounting plate was secured to the carapace of the animal with a fast drying, clear, strong, two-part epoxy cement. Most plates were placed anteriorly on the right first costal scute.

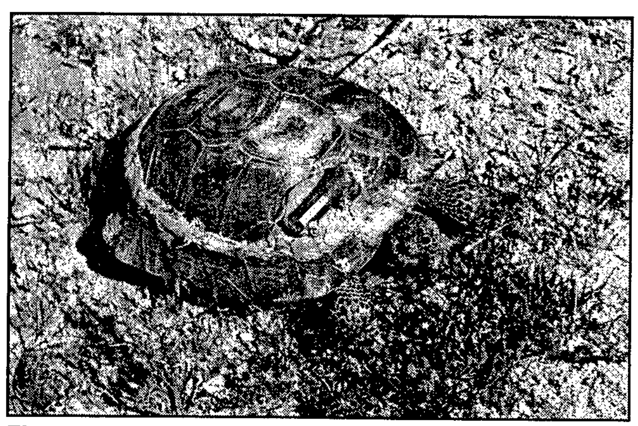

Figure 2. Tortoise with epoxied and siliconed hardware on shell.

On large males, it was found that placing the transmitter posteriorly on the right fourth costal scute was more effective in maintaining the integrity of the attached module when these large tortoises scraped their shells against burrow walls. Care was taken to place the plate in the center of the scute, avoiding the perimeter growth rings. When the plate was secure, the transmitter module was mounted on the threaded shaft attached to the plate and securely fastened with a small nylock nut. Next, the antenna was attached to the perimeter of the carapace with 2-3 drops of a tacky glue (Sportsman's Goop©). Finally, transmitter module edges and the antenna were encased with a thin layer of clear 100 percent silicone caulking compound. This served to protect the unit and antenna from physical abrasion, provided additional water- and dust-proofing, and provided integrity for a compact and somewhat streamlined fit between the transmitter module and the tortoise carapace. The silicone caulk has adequate plasticity to allow for normal scute and shell growth. The lithium AA battery has a field life of 12 to 15 months.

Tortoises were recaptured (relocated) twice a week from mid-April until mid-June 1995 and from early-March through April 1996 using AVM receivers. After the peak spring activity began to wane, tortoises were recaptured weekly from mid-June until late-September 1995 and every 2 to 4 weeks from May until the end of October 1996. Additionally, tortoises were recaptured over a week-long period near the end of October and in early December in 1995. Typically, animals were tracked between 0700-1400 hours, but recaptures occurred throughout the entire day. Tortoise coordinate locations were recorded with a military Global Positioning System (GPS) unit, Rockwell International AN/PSN-11 PLGRs (Precision Lightweight GPS Receivers). PLGRs, initially intended for military use, were loaded with cryptographic keys issued by the National Security Agency (NSA). These devices allow the PLGR to receive true GPS satellite signals and thus override the effects of selective availability (SA), and avoid the need for a base-station and computer post-processing of a scrambled satellite signal. These proprietary units have an accuracy of 5-15 meters error radius, compared to approximately an accuracy of 100 m error radius for commercial units (using unprocessed GPS data). The accuracy of the PLGRs was usually estimated at 1-5 m by direct comparisons with Magellan Mark 10 computer post-processed data. To achieve similar precision with commercial GPS units, the collected GPS data must be corrected by computer processing with a differential correction algorithm (i.e., post-processing) and the use of a base station (a stationary permanent GPS unit), whose location has been accurately determined from a georeferenced USGS benchmark.

When a tortoise was recaptured, the following data were recorded in addition to GPS coordinates:

1. Environmental parameters as in the first capture.
2. Tortoise behavior and activity as in the first capture.
3. Burrow parameters: width, height, and depth of burrow; relative condition of burrow, based on a developed ordinal scale (see the following section on Burrow Survey); and location of burrow relative to perennial vegetation, including species identification of vegetation.
4. Burrow identification. Burrow locations were identified with high-visibility coded flagging, and a permanent aluminum nursery tag attached to the nearest shrub.

Burrow Survey

An intensive burrow inventory was conducted in the north and south study plots in 1996 in an attempt to locate all tortoise burrows. Each study plot was treated as a 30 m grid. Transects (each 3 km in length) were walked by two surveyors, 30 m apart, following north-south grid-lines. After a pair of transects were completed, the surveyors walked adjacent grid-lines in the opposite direction. This pattern was continued until each 9 km^2 plot was surveyed. The experimental design required that each surveyor was responsible for a 30 m band width (15 m on each side of the observer). This is less than optimal, since optimal band width for burrow detection is estimated to be 9 m by two independent analytical models (Krzysik, unpublished data; Krzysik et al. 1995d). However, a 30 m band width was determined to be more efficient for covering 18 km^2 by two surveyors for the desired sample size and sampling frame. Each surveyor stayed on the pre-defined transect line by using a GPS receiver in continuous signal mode, and using a Suunto® sighting-compass to maintain bearings of long-range topographic reference points.

When a burrow was located, the following parameters were recorded: width, height, depth, condition (a function of age and maintenance), position relative to perennial vegetation, and the species of proximate (<1 m) vegetation. Additionally, data on live tortoises and tortoise carcasses were collected.

Burrow metrics (width, height, depth) were measured with a flexible retractable steel tape measure. The condition (age and maintenance) of tortoise burrows were classified on an ordinal scale. A class 5 burrow (Active) is considered currently active and is defined as having the characteristic dome or crescent shape, disturbed soil and tailings near the entrance, recent foot prints, and lack of any vegetation litter or debris in the opening. A class 4 burrow (Excellent) is comparable in many respects to a class 5 burrow, and is in a condition that is readily habitable by a tortoise without any repairs, but does not possess signs of fresh soil disturbance and immediate occupancy. A class 3 burrow (Good) is still readily identified as a tortoise burrow, but has not been recently (possibly months) occupied or maintained. The class 3 burrow shows a little deterioration of its characteristic dome shape, may be partially collapsed, and some litter and debris may be in the opening. However, the interior tunnel is structurally sound and a tortoise, with minor repair and excavation, could readily use a class 3 burrow. A class 2 burrow (Fair) is in a general state of disrepair with some loss of the characteristic burrow shape, some caving-in is evident, and plant litter and debris is present in the opening. A class 1 burrow (Poor) can still be identified as a tortoise burrow, but it has collapsed and would require significant repair and excavation.

Burrow dimensions that were recorded are:
1. Maximum width at the base of the burrow.
2. Maximum height to the roof of burrow, but not to the surface of the soil. The height to the top of burrow refers to the actual opening of the burrow near its apex.
3. Maximum depth to the end of the burrow.

Data Analysis

Desert tortoise home range sizes were calculated using the Minimum Convex Polygon (MCP) method. This method was used for all comparisons among MCAGCC, JTNP, and published studies. Data were analyzed separately for males and females. Recapture loci were converted into home range estimates for 1995, 1996, and both years combined. Home range data were calculated using "Ranges V" software (Kenward 1996).

The data were tested for normality by the Kolmogorov-Smirnov goodness-of-fit test and for homogeneity of variances by Levine's statistic (Sokal and Rohlf 1995). The K-S test is a conservative (a smaller effective α) nonparametric test that has greater power for continuous frequency distributions than the more conventional chi-square or log-likelihood tests. A number of statistical comparisons in this study violated one or both of these parametric assumptions even when appropriate transformations were used with the raw data. Statistical inference and paired-comparisons for home range size, number of burrows used, and distance traveled between successive recaptures were conducted using the two-tailed Mann-Whitney U-Test (MWUT) (Siegel 1956). The reference to paired-comparisons refers to three statistical contrasts: years (1995 vs. 1996), gender (male vs. female), and study site (Sand Hill vs. Pinto Basin). The MWUT is a powerful nonparametric procedure and does not rely on parametric assumptions, including that test statistics follow the normal distribution (Siegel 1956). The MWUT is the nonparametric alternative to the t-test, and actually possesses greater statistical power than the t-test when the assumption of normality is violated (Conover 1980).

Analysis of variance (ANOVA) was used with natural logarithm transformed data (Sokal and Rohlf 1995) to statistically assess the weight change of male and female tortoises between 1995 and 1996. All statistical analyses were performed with "SPSS" software (SPSS 1996).

Four metrics are commonly used to describe dispersion around parameter means: standard deviation, variance, standard error, and confidence interval. Standard deviation represents the average difference between data points and the mean, and is useful to assess sample variation. The variance is the square of standard deviation. Standard error provides a measure of the reliability for estimating the mean. The confidence interval is simply the standard error weighed by the t-value at some chosen α. For example, $\alpha = 0.05$, a common Type I error rate, indicates a 95 percent confidence interval. Standard deviation, standard error, and 95 percent confidence interval of estimated means are provided in the appropriate tables. Standard error was used in the figures to emphasize the precision of estimated means when visual comparisons were made among the histograms.

4 Results

Data from 29 desert tortoises equipped with radiotelemetry units at Sand Hill comprised 1249 recaptures recorded bi-weekly (1995) and weekly (1996) during the season of peak tortoise activity, and bi-monthly during the summer of 1996. A total of 592 and 657 recaptures were recorded during 1995 and 1996 respectively (Table 3). The mean number of recaptures were similar between genders and years. Mean recaptures for males and females were respectively 20.2 and 20.6 in 1995, and 22.4 and 22.9 in 1996 (Table 3). These data are found in Appendix A.

Twenty-nine desert tortoises in each year provided home range data from the 35 in 1995 and one in 1996 that were fitted with radiotelemetry modules. Six animals were unavailable to the study in 1995, because of the following circumstances. Tortoise M95-16 (female) when recaptured on 8 June 1995 was found dead, lying on its carapace. Males in particular, but also females (author's personal observations, taken from field notes) are known to exhibit agonistic behavior and push each other around during territorial defense. Occasionally in these combats, tortoises are thrown on their backs. Tortoises are generally capable of righting themselves back into normal posture, but when they cannot, they rapidly succumb to strong sunlight and high ambient temperatures. The transmitter for M95-20 (female) was recaptured on 21 June 1995, and appeared to have been torn off by a feral dog or coyote. Packs of up to four feral dogs have occasionally been

Table 3. Home range sizes (hectares) of desert tortoises at Sand Hill, MCAGCC; based on the minimum convex polygon (MCP) method.

	1995	1996	1995/1996
Males	*N=13*	*N=14*	*N=14*
Mean MCP size	7.65	3.11	8.30
Standard Deviation	4.24	3.70	4.77
Standard Error	1.18	0.99	1.28
95% Confidence Interval	2.31	1.94	2.51
Range	3.68 - 16.88	0.0 - 14.41	2.19 - 19.79
Mean recaptures	20.2	22.4	41.1
Range of recaptures	14 - 25	19 - 25	22 - 50
Total recaptures	262	314	576
Females	*N=16*	*N=15*	*N=16*
Mean MCP size	7.26	0.93	9.56
Standard Deviation	5.15	0.97	8.27
Standard Error	1.34	0.25	2.07
95% Confidence Interval	2.63	0.49	4.06
Range	0.82 - 15.87	0.01 - 3.71	1.34 - 31.95
Mean recaptures	20.6	22.9	42.1
Range of recaptures	13 - 28	16 - 27	18 - 50
Total recaptures	330	343	673

seen in the southwestern portion of Sand Hill. Indeed, tortoise M95-5 was first located in response to the barking of four feral dogs that were attacking him (13 April 1995). Tortoise M95-5 (male) was crushed by a MLRS (Multiple Launch Rocket System) on 21 September 1995. This incident was reported to MCAGCC-NREA officials. Tortoises M95-3 (female), M95-6 (female), and M95-7 (male) have been recaptured fewer than five times, and their transmitted signals "disappeared" from the study plots early in the 1995 season. An additional tortoise (M95-19, female) was lost in the spring of 1996. Tortoise M95-4 (male) appeared to have its transmitter removed by a canid near the end of the 1996 season. Tortoise M95-6 (see above) was recovered on 31 October 1996, approximately 1 km from its last location in 1995 (R. Evans, NREA, personal communication). The entire transmitter unit was missing, but the silicone caulking residue was evident.

A physical separation between the transmitter and its antenna would effectively terminate the signal of the transmitter. The tortoise itself could have caused the separation by strong contact or rub against a rock or root, particularly in the confinement of a burrow; or as suspected in tortoises M95-20 and M95-4, feral dogs or coyotes could be responsible for a torn off transmitter. Coyotes (or possibly a kit fox) are suspected in removing transmitters from tortoises in the parallel research project at Joshua Tree National Park (K. Meyer, personal communication). Another possibility is the failure of the transmitter or battery. It is always possible, of course, that the tortoises dispersed a long distance, well beyond the range of the transmitters. This last possibility is unlikely, because individuals were relocated twice weekly, and JTNP's long-range receivers were used over a 1-km search radius around the tortoise's last known location, whenever a recapture of a given tortoise failed. Also, when relocating other tortoises, the frequency signature of a lost tortoise was routinely monitored, effectively expanding the search for missing tortoises over many square kilometers.

The winter (November through March) rainfall in 1994-1995 was 10.97 cm, resulting in a productive bloom of winter annuals in the spring. By contrast, the winter rainfall in 1995-1996 was 1.19 cm, making 1996 a drought year.

Home Range Size Estimates: Minimum Convex Polygon (MCP)

Table 3 shows mean MCP home range size estimates and associated descriptive statistics for Sand Hill. Table 4 lists estimates of home range span and associated descriptive statistics. The home range span is the metric that defines the maximum linear distance across a home range polygon. Appendix A (Tables A1-A6) list individual tortoise MCP home range size estimates for 1995, 1996, and for both

Table 4. Home range spans (meters) of desert tortoises at Sand Hill, MCAGCC. (Home range was based on the minimum convex polygon [MCP] method.)

	1995	1996	1995/1996
Males	*N=13*	*N=14*	*N=14*
Mean span	482	317	503
Standard Deviation	133	192	145
Standard Error	36.8	51.3	38.8
95% Confidence Interval	72.1	101	76.0
Range	291 - 719	0.0 - 745	251 - 745
Mean recaptures	20.2	22.4	41.1
Range of recaptures	14 - 25	19 - 25	22 - 50
Total recaptures	262	314	576
Females	*N=16*	*N=15*	*N=16*
Mean span	467	231	486
Standard Deviation	200	167	209
Standard Error	50.0	43.2	52.1
95% Confidence Interval	98.0	84.7	102
Range	149 - 854	93 - 765	163 - 854
Mean recaptures	20.6	22.9	42.1
Range of recaptures	13 - 28	16 - 27	18 - 50
Total recaptures	330	343	673

years. Figure 3 shows home range contrasts between Sand Hill and Pinto Basin, males and females, and productive (1995) and drought (1996) years. Table 5 lists all statistical contrasts and their significance.

Home range sizes were much larger in the productive year than in the drought year for both genders at Sand Hill and Pinto Basin. For example, the mean home range size for Sand Hill males in 1995 was 7.65 hectares, while in 1996 it dropped to 3.11 hectares (Table 3). Although this is visually apparent in Figure 3, note that the larger sample size (resulting in higher statistical power) at Sand Hill made statistical inference very clear ($P<0.001$, Table 5).

Males and females possessed similar home range sizes at both Sand Hill and Pinto Basin during the productive year. However, in the drought year, males had a significantly larger home range size than females at Sand Hill. Data shown in Figure 3 shows that Pinto Basin males appear to have a larger home range than females in the productive year. However, the small sample size and the high inherent variance in the data resulted in low statistical power, making statistical inference tenuous, i.e., $P=0.050$ (Table 5). Note the large standard error in the Pinto Basin data.

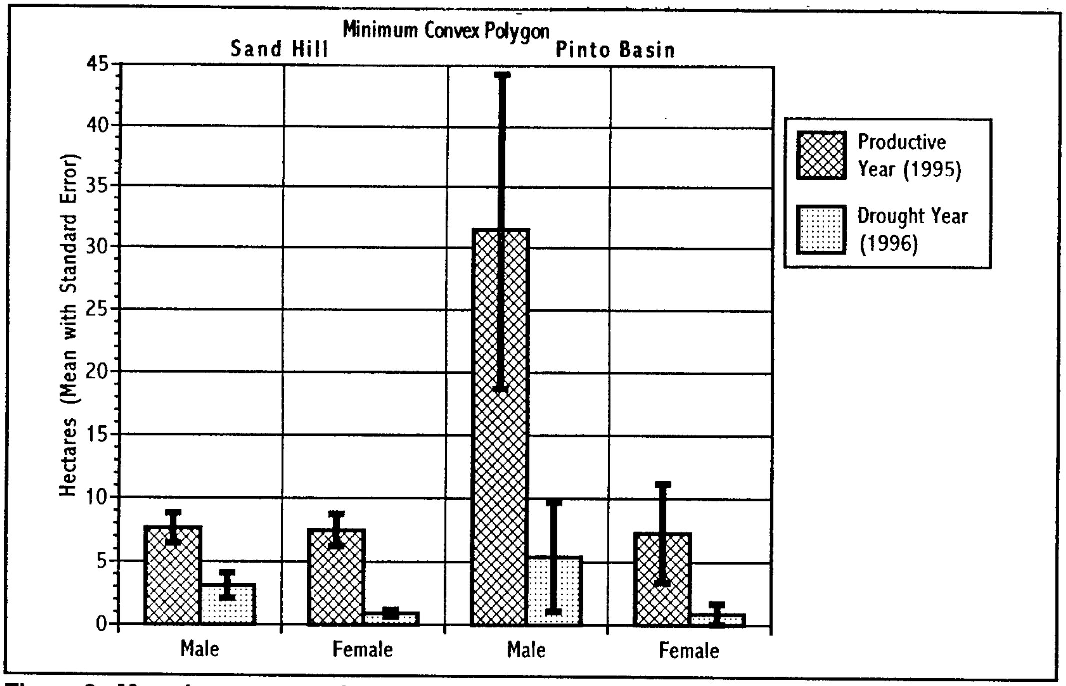

Figure 3. Mean home range size.

A comparison of Sand Hill to Pinto Basin shows that Pinto Basin males had a significantly larger home range size only during the productive year, but again, statistical power was low. There was no site difference for female tortoises when contrasts were made either between productive or drought years.

Burrow Use

Table 6 shows the mean number of burrows used by desert tortoises and associated descriptive statistics for Sand Hill. Figure 4 shows how the number of burrows used contrasts between Sand Hill and Pinto Basin, males and females, and productive (1995) and drought (1996) years. Table 5 lists all statistical contrasts and their significance. The patterns presented here are visually (Figure 4) and statistically (Table 5) clear. Both genders at both sites used significantly more burrows during the productive year compared to the drought year, paralleling the results of the home range estimates. There was no difference in the number of burrows that males and females used at Sand Hill or at Pinto Basin for each year. However, both males and females used more burrows at Pinto Basin during the productive year. In the drought year, there was no difference between the two sites. The 28 tortoises from 1995 constructed 44 new burrows in 1996; 13 males constructed 18 burrows (1.4 burrows/tortoise), and 15 females constructed 26 burrows (1.7 burrows/tortoise).

Table 5. Statistical significance of paired contrasts based on the Mann-Whitney U-Test: Year (1995 vs 1996), Sex (male vs female), and Site (Sand Hill vs Pinto Basin) for two nested factor levels. Three parameters were tested: Home Range Size, Number of Burrows Used, and Distance Traveled Between Successive Recaptures.

	Factor 1	Factor 2	Home Range size	Number of Burrows	Distance Traveled
Contrast			P =	P =	P =
Year	Male	Sand Hill	0.001 **	0.0001 **	0.026 *
		Pinto Basin	0.043 *	0.019 *	0.083 NS
	Female	Sand Hill	0.0001 **	0.0001 **	0.005 **
		Pinto Basin	0.030 *	0.008 **	0.92 NS
Gender	Productive (1995)	Sand Hill	0.60 NS	0.62 NS	0.21 NS
		Pinto Basin	0.050 NS	0.13 NS	0.014 *
	Drought (1996)	Sand Hill	0.020 *	0.17 NS	0.029 *
		Pinto Basin	0.22 NS	0.38 NS	0.33 NS
Site	Productive (1995)	Male	0.007 **	0.003 **	0.024 *
		Female	0.74 NS	0.001 **	0.80 NS
	Drought (1996)	Male	0.40 NS	0.26 NS	0.042 *
		Female	0.49 NS	0.28 NS	0.08 NS

** Statistically Highly Significant: P < 0.010
* Statistically Significant: P < 0.050
NS Not Statistically Significant: P= / > 0.050

Activity Patterns

Figure 5 shows the mean distance individual tortoises moved between subsequent recaptures (relocations), and shows the contrasts between Sand Hill and Pinto Basin, males and females, and productive (1995) and drought (1996) years. Table 5 lists statistical contrasts and their significance. The analysis did not include cases when a specific tortoise individual did not move between two successive recaptures. Only nonzero movements between recaptures were used to calculate means and their associated metrics. One tortoise was stationary during the entire 1996 season (zero movements) and was not included in the analysis.

The data show three major trends: (1) tortoises move further in the productive year, (2) males tend to make larger moves than females, and (3) Pinto Basin males move

Table 6. Number of burrows used by desert tortoises at Sand Hill, MCAGCC.

	1995	1996	1995/1996
Males	*N=13*	*N=14*	*N=14*
Mean number	6.92	3.77	8.31
Standard Deviation	1.75	1.36	2.13
Standard Error	0.49	0.36	0.57
95% Confidence Interval	0.96	0.71	1.12
Range	5 - 11	1 - 5	6 - 13
Females	*N=16*	*N=15*	*N=16*
Mean number	6.21	3.08	7.80
Standard Deviation	2.21	1.50	2.46
Standard Error	0.55	0.41	0.62
95% Confidence Interval	1.08	0.80	1.22
Range	2 - 9	1 - 6	2 - 12

further than Sand Hill males (Fig ure 5). Still, only some of these trends were statistically significant (Table 5). Significant trends were that: (1) both male and female tortoises at Sand Hill moved further in the productive year than in the drought year; (2) male tortoises at Pinto Basin in the productive year, but Sand Hill males in the drought year moved further than females; and (3) Pinto Basin males move further than Sand Hill males in both productive and drought years. Comparable to the home range contrasts, the high inherent variability of the data complicated statistical inference.

The majority of recaptures found tortoises sheltered in their burrows. Even in the spring of a productive year (1995), a little more than half of recaptured tortoises were found in burrows. In the summer of a drought year (1996), 90 percent of recaptures were found in burrows (Figure 6). Genders were combined because they did not differ in surface activity levels. Note that surface activity of desert tortoises in the spring of a drought year is similar to, and even slightly less than, that of summer activity in a productive year. During these times, tortoises were found on the surface approximately 20 to 30 percent of the time.

Some of the tortoises located on the surface were found in pallets. Pallets are above-ground tortoise-sized cavities formed by tortoises in dense vegetation. In the productive year, 17 percent of tortoises recaptured on the surface at Sand Hill were in pallets, while during the drought year, 54 percent of the surfaced tortoise were in pallets. Pallets provide protection from sunlight and strong winds, and predator avoidance. Common plant species where pallets are constructed include: creosote bush stem/exposed root complexes, burroweed, big galleta grass, Mormon tea (*Ephedra* sp.), desert senna (*Senna armata*), bladder pod (*Salzaria mexicana*), cheese bush (*Hymenoclea salsola*), and desert thorn (*Lycium* sp.).

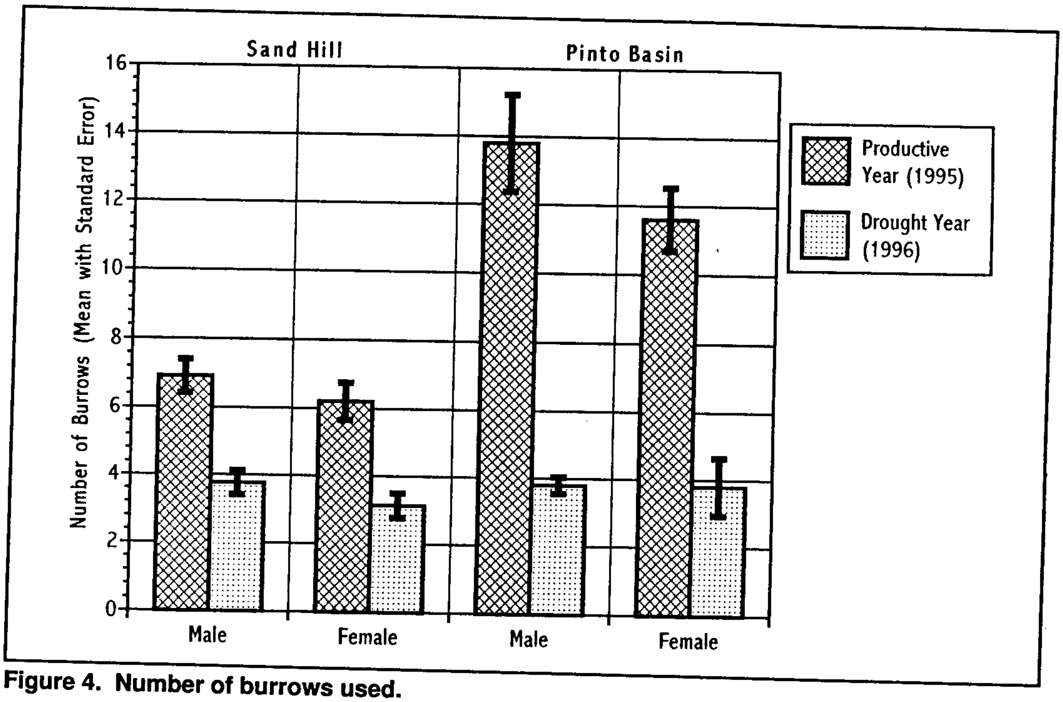

Figure 4. Number of burrows used.

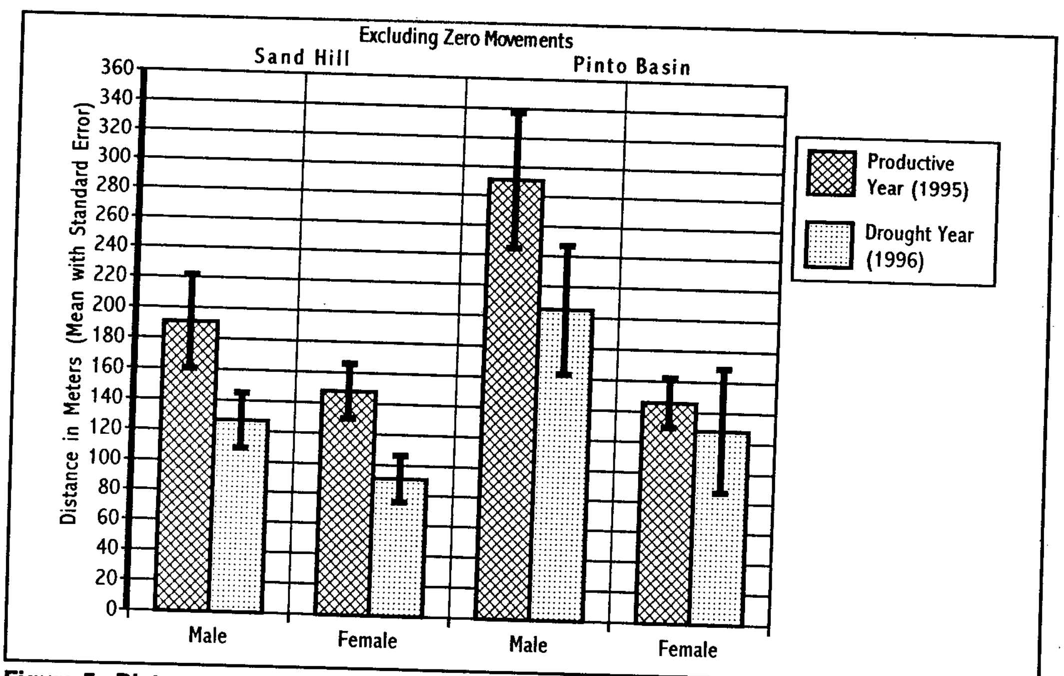

Figure 5. Distance moved between recaptures.

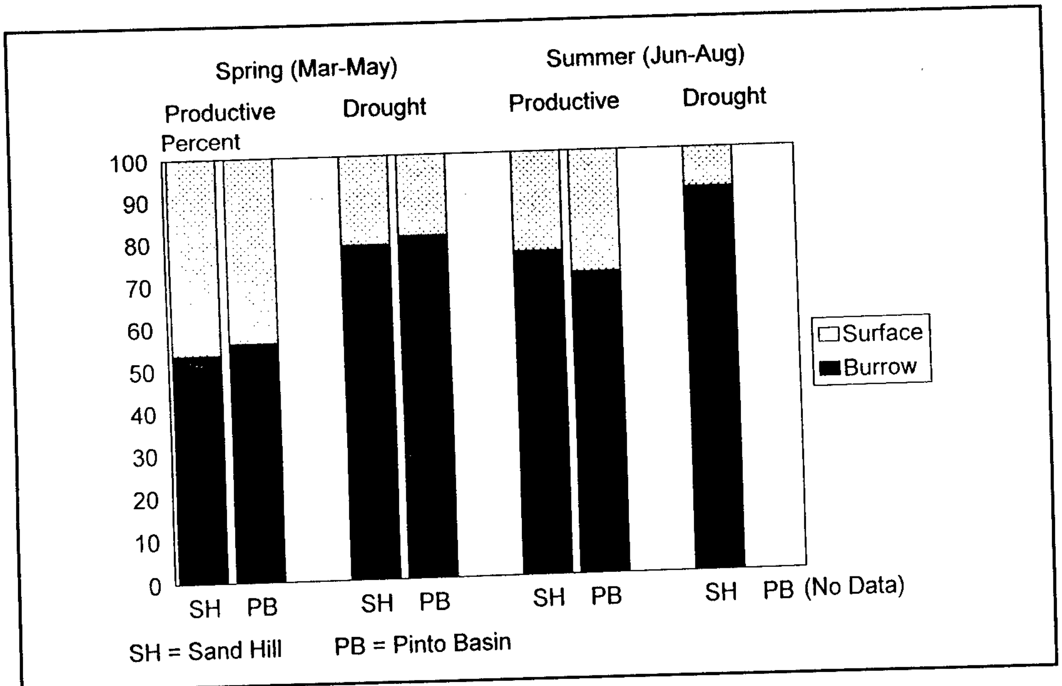

Figure 6. Surface vs. burrow activity by season.

Seventy-nine percent of the tortoises in 1996 revisited at least one burrow that they used in 1995, if revisiting their 1995-1996 hibernating burrow was included in the analysis. When hibernating burrows were excluded from the analysis, 48 percent of 1996 tortoises revisited 1995 burrows. In other words, 21 percent of the tortoises constructed new burrows in 1996 and never revisited a 1995 burrow. Some tortoises (e.g., M95-14 and M95-30) used a single burrow throughout most of the 1996 season. Tortoise M95-14 occupied the same burrow from 4 December 1995 to 27 June 1996, and was found in a different burrow on 12 July 1996. Tortoise M95-30 was always observed in the same burrow between 6 March 1996 and 1 August 1996, but was found on the surface on several occasions. Tortoise M95-27 was recaptured in the same burrow throughout 1996, and was never observed to be active on the surface. This tortoise was heard rustling around in the bottom of its burrow after gentle probing with a retractable steel tape measure.

Because of the drought in the winter of 1995-1996, it was suspected that tortoises would not be as active in 1996 as they were during the 1995 season. Initial field experience in late February and March verified this assumption. Therefore, in the 1996 season, once a tortoise was located in a burrow, several small thin sticks were placed vertically in the entrance of its burrow. These offered no barrier to a tortoise, and were used to document the movements of tortoises out of their burrows for brief periods of surface activity. On many occasions tortoises were consistently found in the same burrow, but the sticks would be displaced. This was a common pattern throughout the 1996 season, and taken as evidence that the tortoises were active on the surface, but not traveling far from their shelters.

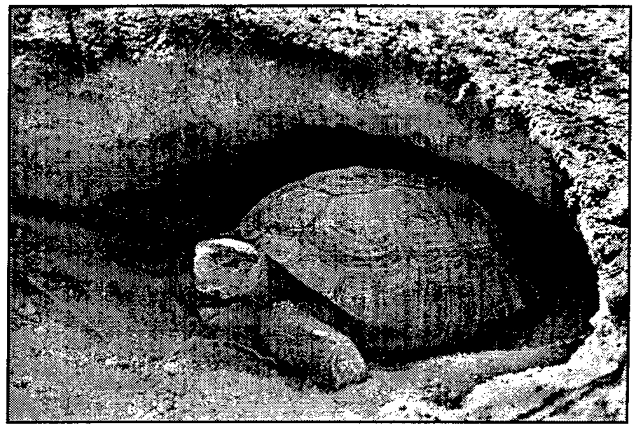

Figure 7. Tortoise at edge of burrow.

Burrow Metrics

Burrows that were ranked good, excellent, or active made up 64 percent of all tortoise burrows (Figure 7). Figure 8 shows the frequency distribution of the five burrow condition classes found at Sand Hill in 1996 during the 100 percent survey (see the "Burrow Survey," p 27). Only these three burrow condition classes were used to construct frequency histogram classes of burrow width, height, and depth.

Figure 9 shows the frequency distribution of burrows associated with perennial vegetation at Sand Hill. Approximately half of all tortoise burrows were closely associated with creosote bush, while a third were found out in the open between shrubs. Ten percent were associated with burroweed, a codominant with creosote bush whose cover varies from very high to very low on local scales. Tortoise burrows were associated with galleta grass 5 to 6 percent of the time. Galleta grass is a perennial that occurs in a patchy fashion on the landscape. Other species of shrubs were used for a combined total of only two percent, and included in order of number of individuals: *Krameria grayia*, *Hymenoclea salsola*, *Ephedra* sp., *Psorothamnus* sp.

Figure 10 shows the frequency distribution of tortoise burrow width classes at Sand Hill. Only burrows ranked active, excellent, or good were used in the analysis. Note that the distribution approximates a normal distribution, with 35 percent of the burrows (the mode of the distribution) being 30-35 cm in width. Burrows less than 15 cm and greater than 45 cm were rare. Importantly, note that the distribution is slightly skewed in favor of smaller burrow classes. In other words, the histograms lying on either side of the mode, and even those two histograms away (i.e., >20-25 and >40-45) consistently show higher frequencies for the smaller burrow widths. This is interpreted to mean that, once the population mode is reached, successively larger tortoise size classes are becoming rarer at a faster rate than smaller size classes. Juvenile tortoise burrows are very difficult to find and distinguish from rodent burrows (P. Woodman and T. Shields, personal communication).

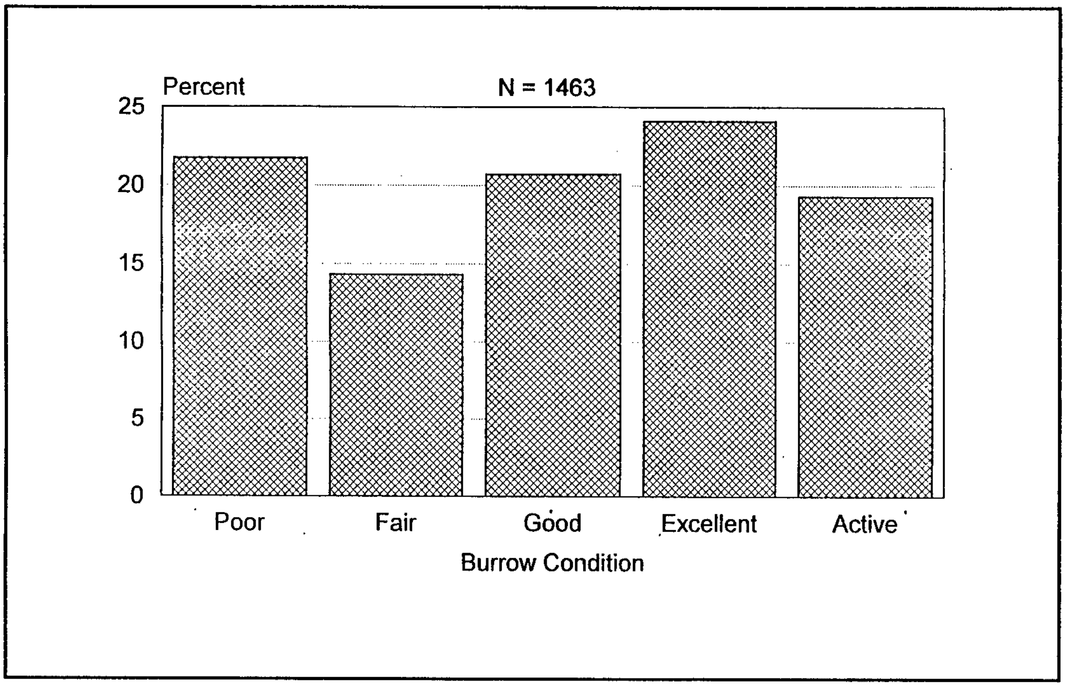

Figure 8. Frequency distribution of burrow condition classes at Sand Hill, MCAGCC (1996).

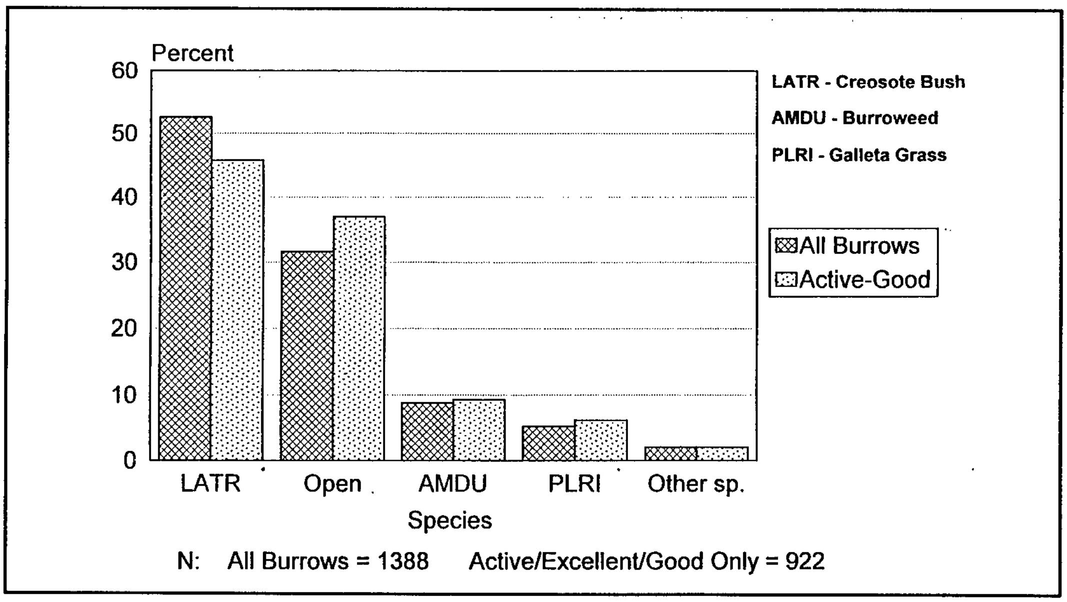

Figure 9. Frequency distribution of vegetation associated with burrows at Sand Hill, MCAGCC (1996).

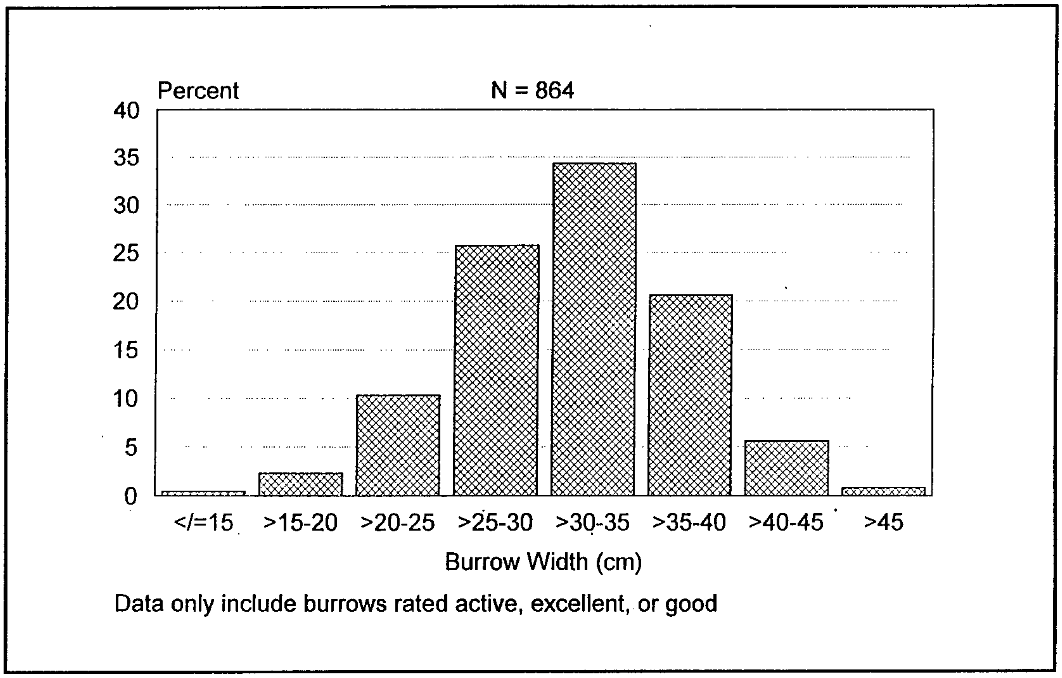

Figure 10. Frequency distribution of burrow width classes at Sand Hill, MCAGCC (1996).

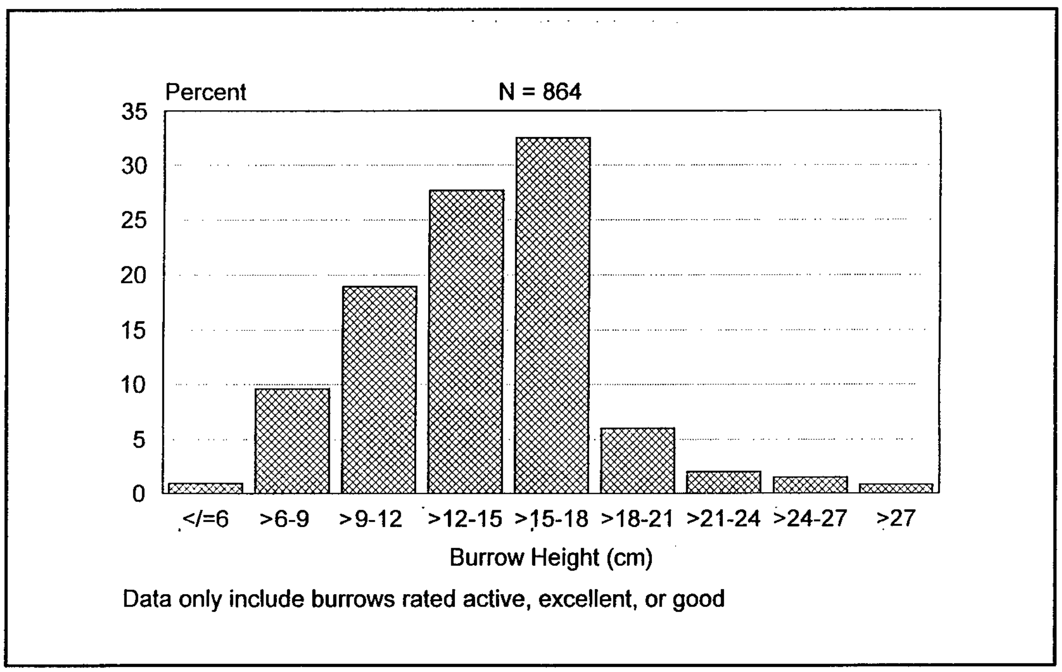

Figure 11. Frequency distribution of burrow height classes at Sand Hill, MCAGCC (1996).

Figure 11 shows the frequency distribution of tortoise burrow height classes at Sand Hill. Only burrows ranked active, excellent, or good were used in the analysis. Similar to the distribution in Figure 10, burrow height gradually increases to the mode giving the appearance of another normal distribution, and as in the case of burrow width, approximately 35 percent of burrow height samples were at the mode. However, after the mode is reached at 15 to 18 cm, the distribution rapidly becomes asymptotic, and burrow heights larger than 18 cm become increasingly rare. Apparently the width of a tortoise increases at a greater rate than its height once a given carapace size is reached (i.e., allometry changes). Another possibility is that tortoises within a given size class may behaviorally vary in the way individuals rest at burrow openings or rotate their bodies when they enter or exit burrows.

Figure 12 shows the frequency distribution of tortoise burrow depth classes at Sand Hill. Only burrows ranked active, excellent, or good were used in the analysis. Again, a completely different distribution is evident. There is a strong mode in the frequency, because half of all tortoise burrows range from 25 to 75 cm in depth, and almost three-quarters of burrows are a meter or less in depth. Typical summer burrow depths for desert tortoises have been reported as approximately a meter or less in the western Mojave (Marlow 1974), Nevada (Burge 1978), and California (Luckenbach 1982). Nevertheless, although most burrows are relatively shallow, the data from this study show that some burrows exceeded 3 m in depth. Deep burrows are important for winter hibernacula, and possibly for summer estivation in drought years. Woodbury and Hardy (1948) found winter burrows that were 10 m in depth on the Beaver Dam Slope in southwestern Utah, near the northern limit of desert tortoises distribution. These burrows were found in caliche layers at the bases of arroyo washes.

Figure 13 shows the same data as Figure 12, but presents the data as a cumulative frequency distribution. The figure clearly shows that 90 percent of the tortoise burrows found at the Sand Hill study plots were 1.5 m or less in depth. Burrows longer than 2.5 m were very rare.

Morphological Measurements and Weight loss

Appendix B presents the morphological measurements recorded for Sand Hill desert tortoises in 1995 and 1996. All recaptured desert tortoises that were reweighed in 1996 lost weight compared to their initial weight in 1995. These data are summarized in Table 7. Males lost an average of 0.93 kg, while females lost an average of 0.58 kg, and this was significant (ANOVA: $F = 5.575$, $P = 0.026$). However, because males are larger than females, both genders lost a similar proportion of their original body weights between the springs of 1995 and 1996, 21 and 19 percent, for males and females, respectively. These differences were not significant. Female tortoises exhibited a greater variability in weight loss among individuals by a factor of 2.5 when compared to males, based on respective standard deviations.

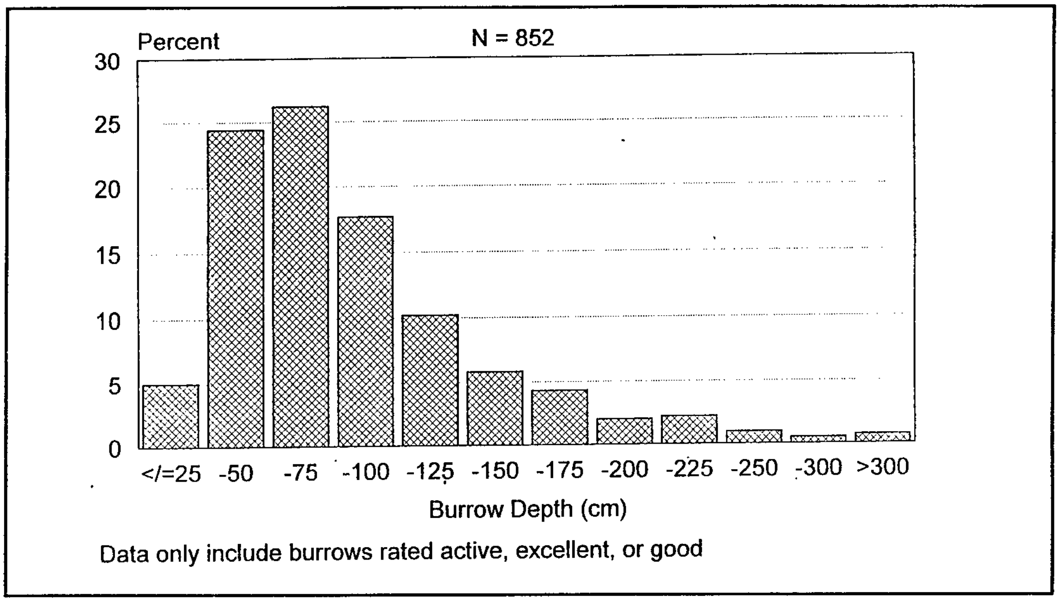

Figure 12. Frequency distribution of burrow depth classes at Sand Hill, MCAGCC (1996).

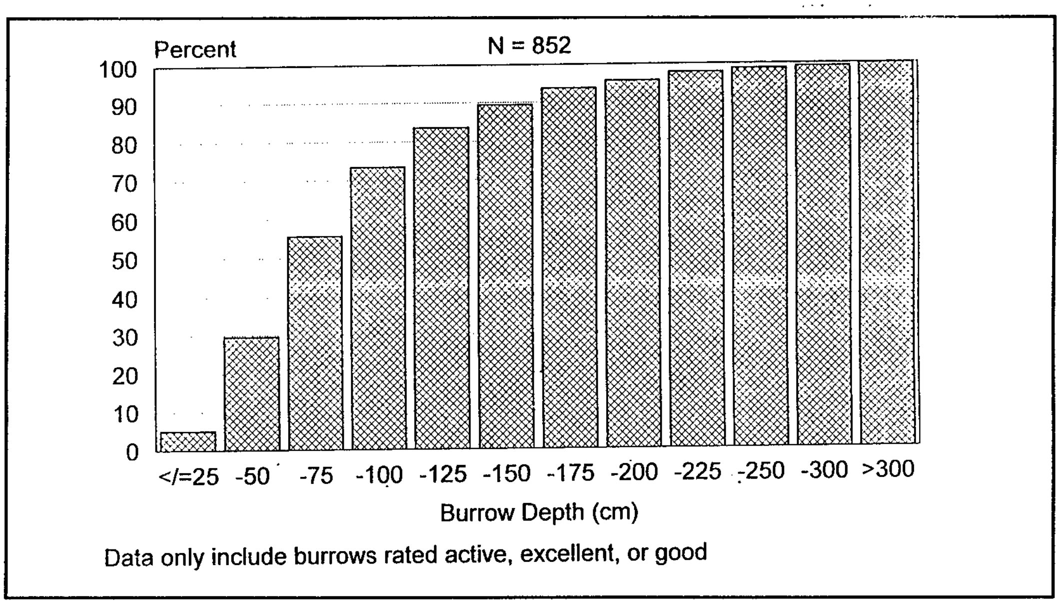

Figure 13. Cumulative frequency of burrow depth classes at Sand Hill, MCAGCC (1996).

Status of Desert Tortoises from Baxter and Stuart Study at MCAGCC

Appendix C gives the status of 28 tortoises originally marked in the 1984-1985 Baxter study (Baxter and Stuart 1986; Baxter 1988), and reidentified in this project. At least 41 tortoises were marked in the Baxter project. Twenty-one were found alive during the current study and two more were found in 1997. A total of 5 were identified from carcasses. Eleven of the 21 that were found were used in the radiotelemetry study, or 31 percent of all tortoises fitted with transmitters. These data indicate an estimated adult desert tortoise mortality rate of 18-48 tortoises per year per 1,000 tortoises in the 1985 - 1996 time frame at Sand Hill Training Area (Krzysik and Duda, in preparation). This mortality rate is much lower than reported for many other localities of the Mojave Desert, especially the western Mojave (see references on population declines in this report and in Krzysik 1994a).

Table 7. Weight changes in desert tortoises between spring 1995 and spring 1996 at Sand Hill, MCAGCC. (Data summarized from Appendix B.)

	Males	Females
Mean weight change (kg)	-0.93	-0.58
Range	-0.2 to -1.5	-0.1 to -1.7
Standard Deviation	0.39	0.41
Mean weight change (%)	-21.1	-19.3
Range	-14.3 to -27.8	-3.6 to -44.7
Standard Deviation	3.9	9.9
N	13	15

5 Discussion

The Mojave Desert is characterized by winter rainfall patterns, where precipitation falls predominantly from November through March. The 2 years of this field study, 1995 and 1996, provided a sharp contrast in winter precipitation, and subsequently the primary productivity (plant biomass) of winter annuals (forbs and grasses), which bloom in the following spring. The availability of succulent forage appreciably reflected significant differences in home range sizes and activity patterns of desert tortoises. Rainfall was appreciable in the winter of 1994-1995 (10.97 cm), and subsequently provided an abundance of annual vegetation in the spring of 1995. However, precipitation was sparse in the winter of 1995-1996 (1.19 cm), resulting in the virtual absence of annual plants in the spring of 1996. The 32 year annual mean (1960-1991) winter (November - March) rainfall for this region was 4.88 cm (data from NOAA, National Climate Data Center for Twentynine Palms, California). Therefore, the productive year of 1995 experienced an increase in precipitation that was 2¼ times the long-term mean, while the drought year of 1996 only received 24 percent of the region's average winter rainfall. Beatley (1974) reported that heavy precipitation (>2.5 cm in a single event) was required between late September and early December to initiate mass germination of annuals the following spring. During this study the total rainfall between October through December 1995 was 0.13 cm or only 3.6 percent of the 32 year mean.

Home range sizes for both male and female desert tortoises at Sand Hill were reduced 59 and 87 percent, respectively, in 1996 when compared to 1995 data (Table 3 and Figure 3). Paralleling their reduction in home range sizes, tortoises also reduced the number of burrows they used (Table 6 and Figure 4). One male was not observed outside his burrow in 1996 (M95-27, Appendix A, Table A3). It is hypothesized that the lack of preferred annual forage was the major factor responsible for the dramatic reduction in the home range sizes of desert tortoises in 1996. Tortoises simply did not shrink their 1995 home ranges, since their combined 1995-1996 home ranges usually increased. Ten of 13 males, and 12 of 16 females increased their combined 1995-1996 home range sizes when compared to their 1995 home range size (Appendix A, Tables A1 and A5 for males, Tables A2 and A6 for females). It can be hypothesized that, during a drought year, desert tortoises — while reducing their annual home ranges — select a high quality portion of their home range and even expand into an adjacent area to optimize the acquisition of required resources.

A comparable difference between desert tortoise home range sizes in 1995 and 1996 for both genders was verified at the Pinto Basin study plot in Joshua Tree National Park (Table 8 and Figure 3). Males decreased their home range by 75 percent and females by 78 percent. Although tortoise surface activity did not cover the same amount of area in 1996, tortoises did not completely restrict their above ground activity. Tortoises limited their surface activities by concentrating their surface forays locally around a single burrow instead of traveling among an extensive burrow network. The technique of placing small sticks vertically across burrow openings clearly demonstrated that tortoises were still active on the surface at Sand Hill and Pinto Basin. However, their consistent return to the same burrow strongly suggested that their surface forays were spatially limited, and they were concentrating their surface activities in the vicinity of a single burrow. This behavior was consistent for both male and female tortoises and resulted in the use of fewer burrows and a smaller range size during the drought year, 1996 (Table 6 and Figure 4). Both genders of tortoises annually used a similar number of burrows at a given site in a given year (Table 5).

Paralleling a reduction in home range sizes and the number of burrows used in 1996, Sand Hill tortoises were traveling shorter distances between successive recaptures in the drought year (Figure 5, Table 5). This was not the case at Pinto Basin, where interyear travel was not significantly different. This was probably due to the small sample size (low statistical power) available for Pinto Basin.

Tortoises were recaptured on the surface more frequently in the productive year than in the drought year, and tortoises were more active on the surface in the spring than in the summer for both productive and drought years (Figure 6). When they were recaptured on the surface, tortoises used pallets as cover more frequently in the drought year than they did in the productive year. Surface activity levels in

Table 8. Summary of mean and ranges of home range sizes (hectares) for desert tortoises at Sand Hill (MCAGCC) and Pinto Basin (JTNP) in 1995 and 1996 using minimum convex polygons (MCP); Sand Hill data from Table 3; Pinto Basin data from Freilich (1997). N = number of tortoises. R = number of recaptures.

	Productive Year (1995)		Drought Year (1996)	
Study Site	Males	Females	Males	Females
Sand Hill	7.7 (3.7-16.9) N=13 R=262	7.3 (0.8-15.9) N=16 R=330	3.1 (0-14.4) N=14 R=314	0.9 (0.01-3.7) N=15 R=343
Pinto Basin	26.4 (10.9-44.1) N=4 R=155	8.5 (2.5-13.6) N=5 R=184	6.7 (0.6-14.1) N=4 R=71	1.9 (0.2-4.9) N=5 R=88

tortoises closely paralleled the observations discussed above relating to home range size, number of burrows used, and distances moved between successive recaptures.

An important difference in tortoise activity between years when forage was abundant and when forage was scarce, was that tortoises foraged over a more extensive area in productive years, and subsequently used a larger number of burrows. This strategy avoided long return trips to previous burrows where they may have already depleted favored forage plants. During drought years, tortoises use a minimal foraging range, apparently to minimize energy expenditure. However, even in a lean year, tortoises were observed foraging on dry forbs and perennial grasses, possibly to obtain some minimal threshold of obligatory energy, nutrient, or mineral requirements. Nevertheless, in drought years, their overall strategy may be to minimize energy expenditures and rely on physiological adaptations to survive the absence of food and water.

All the desert tortoises that were weighed between 1995 and 1996 lost weight (Appendix B). Males and females each lost approximately a mean 20 percent of their body weight (Table 7). Weight loss among individual tortoises was much more variable with females than with males. This may be attributed to depositing or yolking eggs. For example, if a female was weighed in 1995 that was yolking eggs to be deposited in the summer, her weight loss the following drought year was attributable to both the effects of the drought and the loss of her egg mass. On the other hand, a female weighed in 1996 could have been actively yolking an egg clutch, and even though she demonstrated a weight loss from 1995, the developing egg mass would make the apparent weight loss smaller. Female desert tortoises are commonly known to nest in drought years, as has been demonstrated by Dr. David Morafka in his enclosure studies at Fort Irwin (D. Morafka, personnel communication). It was noted earlier that females reduced their home range sizes to a greater extent than males. This also may be an indication that females are conserving energy resources and yolking egg clutches.

Reducing home range size to conserve energy may be common in poikilotherms, but is in sharp contrast to birds and mammals, who must dramatically expand their home range sizes during food shortages to ensure meeting the mandatory high metabolic energy requirements of homeotherms.

Male and female tortoises possessed similar home range sizes in the productive (1995) year at both Sand Hill and Pinto Basin (Table 5), but in the drought year, Sand Hill males had a larger home range than females. During the productive year Sand Hill male tortoises possessed appreciably smaller home range sizes than Pinto Basin males (Table 5). The significance of this observation and that of other comparisons with Pinto Basin are difficult to interpret, because of the small sample size of JTNP experimental tortoises. Small sample size coupled with innate high natural variability resulted in low statistical power, making statistical inference (significance testing) tenuous.

Six published desert tortoise radiotelemetry home range studies were available in the literature (Table 9). The Barrett study must be interpreted with caution since it involves a population of the Sonoran Desert tortoise. Sonoran Desert tortoise populations exhibit characteristics quite different than Mojave Desert tortoise (see discussion in the Introduction). The other five studies summarized in Table 9 are with Mojave Desert populations. Note that for male desert tortoises, all published mean home range sizes, as well as the largest estimated home range size for individual male tortoise, are appreciably larger than those reported in this study (Table 3, 1995 or 1995/1996 data). Sand Hill male tortoises possessed home range sizes that were 63 to 76 percent smaller than estimates published in other Mojave studies. In all comparisons, the Minimum Convex Polygon (MCP) method was used. In contrast, published home range sizes for female tortoises are comparable to the values estimated in this study. An important comparison is with the Pinto Basin data (Duda et al. 1997 and manuscript in preparation; Freilich 1997). The JTNP study is both temporally and spatially comparable with this study, being conducted in Pinto Basin, 64 km directly southeast of the Sand Hill study plots.

Table 9. Home range size estimates from other desert tortoise studies.

Source	Location	♂ MCP (ha) (range)	♀ MCP (ha) (range)	Sexes Differ?
Hohman and Ohmart, 1980	Beaver Dam Slope, AZ	23(5-59) SD: n/a	11(1-29) SD: n/a	Not reported
O'Connor et al. 1994	DTCC Las Vegas, NV	20.92[a](7.7-46) SD:14.3	9.01[a](5.8-13.6) SD:3.01	Yes
Barrett 1990	Picacho Mtns, AZ	16.1[a](3.7-33) SD:11.1	10.7[a](1.9-34.2) SD:11.9	Yes[a]
Freilich 1997	Joshua Tree N.P. 1995	26.4(11-44) SD:16.2	8.5(2.5-13.6) SD:4.9	Yes
Freilich 1997	Joshua Tree N.P. 1996	6.7(0.6-14.1) SD:5.4	1.9(0.2-4.5) SD:1.5	Yes
Burge 1977	Arden, NV	32.3(11-65) ±6.0[b]	14.8(6-27) ± 2.6[b]	Yes

[a] O'Connor et al. (1994) and Barret (1990) used the Jennrich and Turner (1969) correction factor in calculating home range areas. They reported uncorrected values and these are used in the table above. Sexes differed for both studies using the uncorrected MCP values.
[b] Burge reported a standard error of the mean instead of the standard deviation.

The data of Table 9 also indicate that male tortoises possessed a significantly larger home range size than females. The Hohman and Ohmart study did not report that genders were different, but the data suggest that males had larger home range sizes. In the Barrett study, male and female tortoises possessed similar home range sizes only when the Jennrich and Turner (1969) sample size correction factor was applied to MCP estimates. Additionally, and more importantly, this was a population of the Sonoran Desert tortoise, who are quite different from Mojave Desert tortoises (see discussion in the Introduction).

The data of Table 9 contrast starkly to that of this study, which found that in a productive year (1995) or when both years were combined (1995-1996) both male and female tortoises possessed statistically similar home range sizes. As discussed above, this similarity is attributed to the relatively small home range sizes of male Sand Hill tortoises because home range sizes of female tortoises in this study were comparable to home range sizes reported in other studies. Only in the drought year of 1996, when home range sizes were appreciably retracted for both genders, did Sand Hill males exhibit significantly larger home range sizes than females.

The authors are currently evaluating hypotheses why the home range size of Sand Hill male desert tortoises was similar to females and significantly lower than reported in all the other published studies that were compared. This study differed appreciably from other published studies in three ways. First of all, a larger sample size (N = 29) of experimental subjects was used. Experimental subjects were located essentially at random, but there was some bias, since some tortoises were found when relocating already transmittered individuals. Additionally, this study was conducted over a much larger area than comparable studies. For example, the plots studied covered an area of 18 km^2, while the study plot at JTNP was 2.6 km^2 (comparable with other studies). Finally, this study was conducted on a military training installation. Sand Hill has been subjected to military training activities since 1942, but habitat degradation has been light, with some patchy recent to very old, moderate-to-high impacts in the vicinity of roads that traverse the training range. The large sample size and large study area used in this work lends confidence to the results, but the significant discrepancy of Sand Hill male tortoises possessing a smaller home than that reported in other studies remains a mystery, particularly because this study's data with female tortoises is comparable with a broad range of studies, and virtually identical with those at JTNP (Table 8).

Caution must be exercised when home range size comparisons are made with other studies. Analytical procedures calculating home range sizes may differ. Even the same analytical method may employ different mathematical formulas or computer algorithms for calculating the metrics. It can also be argued that studies are often not directly comparable because of the variability in habitat quality, geomorphological specifics, soil characteristics, and weather patterns or history. Barrett (1990) conducted her study in the Sonoran desert, within a palo verde mixed scrub habitat. O'Connor et al. (1994) and Burge (1977) conducted their studies in the eastern Mojave, which has a more bimodal rainfall regime, and therefore a good potential for a bloom of summer annuals. Freilich's (1997) study should be closely comparable to this one, because his study was conducted nearby at the same time in the Pinto Basin. Although the Pinto Basin represents a transition zone between the Mojave and Sonoran deserts, the habitat, soils, and species composition of the major vegetation is very similar.

Another factor that complicates comparisons among home range studies is differential land-use. This difference may have important management implications. All of the studies cited in Table 9 occurred in areas that are protected at some level from human disturbances. Sand Hill, on the other hand, has been subjected to locally severe off-road tactical vehicle use since 1942. Desert ecosystems are fragile and recover slowly from disturbance (reviewed in Krzysik 1994b). Cryptogamic (or microphytic) crusts represent important biological communities in many arid ecosystems (Belnap et al. 1994, Belnap 1995, Warren 1995). These crusts are responsible for nutrient uptake by plants and biogeochemical cycling in desert soils, especially nitrogen fixation. Cryptogamic crusts also are directly responsible for protecting the fragile desert soils from both wind and water erosion, because these crusts by their biological composition and chemical activities produce a surface armor of high stability and integrity by cementing and protecting soil surface particles. Once disturbed by off-road vehicles, cryptogamic crusts are slow to recover, taking 5 to 50 years to resume normal nitrogen fixation, and 40 to 100 years to resume their ability to stabilize soils (Belnap 1996). The disturbance of cryptogamic crusts may have important effects on desert tortoises, because impacts to the integrity of cryptogamic communities also reduce the diversity and abundance of annual and perennial plant species.

It is difficult to assess cause-effect relationship between habitat disturbance, including effects to vegetation and soils, and tortoise home range sizes. Detailed, long-term, and most importantly, carefully designed field experimental research would be required to unravel these cause-effect relationships in an ecologically and statistically valid context. Ideally, home range data prior to disturbance would produce the most robust comparisons. However, such data do not exist for Sand Hill, nor anywhere else.

Relevant research has reported the effects of human disturbance on home range and movement patterns of animals, especially large mammals. Gese et al. (1989)

examined the response of coyote home range size to the effects of miliary maneuvers in Colorado. Their results showed a significant difference in activity patterns between experimental and control groups. However, the trend was not directional, as some coyotes increased their home range size during military maneuvers, while others decreased their movements. The Department of Energy (DOE) conducted a study on the effects of anthropogenic disturbance to the home range sizes of desert tortoises at Yucca Mountain, Nevada Test Site. There was no significant difference between disturbed and undisturbed areas (K. Rautenstrauch, Science Applications International Corporation, personal communication).

Ecological parameters such as population densities, gender ratios, sample sizes (especially the number of tortoises used in a study), burrow distributions, and a detailed assessment of habitat metrics (including patchiness, and natural and a variety of anthropogenic disturbances) represent important elements and variables for comparative experimental studies. A more detailed analysis of home range sizes and their patterns and a GIS-based spatial analysis of movement patterns, including the ecological parameters discussed above, can generate testable hypotheses and through experimental field work eventually lead to an understanding of the activity and dispersal behaviors of the desert tortoise.

The Sand Hill Training Area probably contains the most contiguous and highest quality desert tortoise habitat at MCAGCC, and therefore, the highest density of tortoises. This assumption is based on three factors:

1. The ecosystem classification used here for the entire installation (Krzysik and Trumbull 1996).
2. Field experience gained and observations made throughout the entire installation (mainly in 1993-1994).
3. Both Sand Hill and Pinto Basin (a pristine wilderness area in JTNP) possessed similar estimates of high tortoise densities on local landscape patches (Krzysik 1997b).

This study of the desert tortoise at Sand Hill Training Area also concluded that the southwestern corner of the installation has been only lightly impacted by military training activities. Recent increases in military training maneuvers during the late summer of 1995 and in 1996 at Sand Hill may risk population viability of the desert tortoise in this area.

Tortoise populations, which may be of local significance, have also been reported at other training areas: Sunshine Peak, Gypsum Ridge, Emerson Lake, Cleghorn Pass, and Bullion (MCAGCC 1993; Natural Resources and Environmental Affairs [NREA] and Range Control personnel; personal observations).

6 Conclusions and Recommendations

Conclusions

A radiotelemetry study of the desert tortoise was conducted in 1995 and 1996 at Sand Hill Training Area of the Marine Corps Air Ground Combat Center (MCAGCC). Twenty-nine adult tortoises (divided approximately equally by gender) were equipped with radiotelemetry transmitters in two 9 km^2 study plots. A comparable study at Joshua Tree National Park (JTNP) monitored nine tortoises (four males, five females) in a 2.6 km^2 square plot. Productivity of annual vegetation was very high in 1995 because winter precipitation (November through March) was 2-¼ times higher than the 32-year mean. The second year of the study was a drought year, where winter rainfall was only 24 percent of the baseline long-term mean.

Home range sizes were estimated by the Minimum Convex Polygon algorithm. Both male and female tortoises dramatically reduced their home range sizes and the number of burrows they used during the drought year. Home range sizes were similar for both sexes at both sites in the productive year, but at Sand Hill in the drought year, males had a larger home range than females. Sand Hill males in the productive year possessed a smaller home range size than Pinto Basin males. The small sample size at JTNP reduced statistical power for paired comparisons, making statistical inference tenuous. Sand Hill male tortoises possessed smaller home range sizes than those reported in other studies. Although mean home range size for Sand Hill females was somewhat smaller than reported in other studies, an examination of the reported variability suggested that home range sizes for Sand Hill females were comparable to published studies.

All tortoise individuals that were weighed in 1995 and again in 1996 lost weight, with both genders similarly losing a mean 20 percent of their original weight. Females demonstrated a greater variability in weight loss among individuals, possibly attributable to depositing or yolking egg clutches.

Individual tortoises possess very small home range sizes on a landscape scale. Based on the 1995 data and assuming (unrealistically) a perfectly square home range, home range sizes varied from 26.5 to 400 m on a side. Freilich's (Freilich

1997; Freilich et al. 1997) data suggest that many tortoises remain faithful to their home ranges for 5 years or more. However, in the time frame of a generation, the temporal dynamics of desert tortoise home range requirements are unknown, and it would be premature to predict their spatial requirements for long-term population viability. Additionally, equally important details regarding viable population sizes, habitat needs, and required social structure are also unknown.

Sand Hill Training Area, in the southwestern corner of MCAGCC, has only been lightly impacted by military training activities. This area probably contains the largest contiguous expanse of high quality desert tortoise habitat on the installation, and therefore, the highest population of desert tortoises. Desert tortoise densities at Sand Hill were estimated to be higher south and east of the Desert Tortoise Conservation Zone than they were inside the zone itself (Krzysik et al. 1995a; Krzysik 1997b). Three Desert Wildlife Management Areas (DWMAs), designated by the U.S. Fish and Wildlife Service for tortoise recovery, are located near the installation, but the Sand Hill population is relatively isolated by urbanization, mountains, and Marine Corps heavily used training ranges.

Recommendations

The following desert tortoise management guidelines are presented for Sand Hill Training Area, based on extensive ecological and field experience at MCAGCC and the intensive desert tortoise studies at Sand Hill:

1. Desert tortoises and their habitat should be protected to the highest extent possible throughout Sand Hill Training Area. This requires that tactical vehicles stay on existing undeveloped roads or trails, and off-road training within the habitat consist of activities that will not crush tortoises or their burrows or destroy perennial vegetation and soil structure. Military personnel or contractors on roads or in the habitat should continue receiving briefings and training to be on the alert for tortoises and their burrows, to avoid handling or harassing tortoises, and not to disturb tortoise burrows. Tortoise burrows are easily crushed. Even when tortoises are hibernating or estivating in their burrows, their habitat remains sensitive to off-road vehicles. Tortoise burrows are relatively delicate and not very deep in their vertical aspect (usually less than half-meter along most of the burrow's length), and subsequently tortoises can easily be crushed or buried during winter hibernation or summer estivation. Tortoises overwinter in deeper burrows, often in caliche burrows located at the base of steep washes. Caliche burrows represent the securest dens for tortoises because of their location and the

strength of the parent material. Deep winter burrows can be over a meter in vertical aspect, and therefore not easy to crush. Tortoises readily excavate and escape from minor or even moderate natural burrow collapses. Dr. Jerry Freilich's field experience has been that in the winter and during droughts tortoises may occasionally be "buried" in natural burrow cave-ins with no apparent ill-affects. Nevertheless, field personnel should remain cautious near burrows, particularly when using vehicles. When it is necessary for vehicles to go off-road, extreme caution should be exercised to monitor tortoises and their burrows.

2. NREA land managers should use the home range size estimates and both the diurnal and seasonal activity patterns identified in this report to actively manage MCAGCC landscapes to avoid tortoise mortality and minimize tortoise-trainer conflicts. Field personnel should be particularly aware of the periods of both daily and annual peak activity levels for desert tortoises. Peak activity levels for desert tortoises are in the spring, approximately March-June at MCAGCC, and are highly dependent on winter precipitation and the subsequent biomass of winter annuals available in the spring. Tortoises also respond to current weather conditions, avoiding extremes of high or low temperatures. A good rule of thumb is, when the weather is comfortable for humans, it is also comfortable for desert tortoises. Tortoises usually become very active on the surface, even nocturnally, after summer thunderstorms. Tortoises enter hibernation in the southern Mojave Desert approximately November to early December, and emerge approximately mid-February to March. They estivate in the summer and even into the fall when the weather is hot and dry, particularly during periods of drought.

3. The landscape-scale desert tortoise distribution/density surface maps developed in a companion study and provided to NREA should be used illustratively to inform Marine Corps trainers and contractors on the relative distribution and density patterns of tortoises throughout Sand Hill Training Area (Krzysik et al. 1995a; Krzysik 1997b).

4. Direct field observations of feral dogs (with some individuals approaching and exceeding 40 kg), numerous scars observed on desert tortoises, the loss of six radio-transmitter modules from experimental animals, and the observation of four large dogs chewing and injuring a large male tortoise, provide compelling evidence that there is a feral dog problem at Sand Hill, and possibly at other periphery locations at the Combat Center. Feral dogs have probably been a persistent problem at Sand Hill, and were reported in 1985 (Baxter and Stewart 1986). It is possible that some of the lost transmitters and tortoise

scars could be attributed to coyotes, who have been implicated in comparable behavior, but the reality at Sand Hill is that feral dogs are probably the main culprit. These dogs are not truly feral, because they cannot independently survive in the desert environment. The dogs form loosely organized hunting-packs that originate in local rural communities. The communities (e.g., Landers) should be contacted and briefed concerning the wildlife damage that has and continues to occur. A community plan should be adopted to address the issue, monitor installation boundaries, and control feral dogs. Kit foxes could also contribute to tortoise harassment by canids, but observation does not suggest that this species causes any problems. One of the radiotelemetered tortoises hibernated peacefully within the confines of a large and very active kit fox den-complex, and emerged healthy and unscarred the following spring with its transmitter module completely intact.

5. MCAGCC-NREA has provided trainers and contractors with information regarding the protection of the desert tortoise and related compliance requirements. These have included: (a) briefing of training units prior to range-use, (b) information handouts, (c) a tortoise video, (d) the use of actual tortoise shells for visual familiarization, and (e) a pocket-size "Desert Tortoise Alert Card." The current tortoise awareness program is planned to continue indefinitely. This study recommends that this policy continue.

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Appendix A: Home Range Size Estimates for Adult Male and Female Desert Tortoises (1995, 1996, 1995/1996) Using the Minimum Convex Polygon Method at Sand Hill Training Area, MCAGCC

Table A1. Minimum convex polygon (MCP) home range sizes: males, 1995.

Tortoise #	MCP Size (ha)	Range Span (m)	N
2	10.83	881	24
4	16.88	719	20
11	10.34	660	20
15	3.97	291	25
17	6.61	576	19
18	7.71	531	20
21	13.97	598	23
23	3.82	397	19
24	4.08	341	22
27	6.46	617	17
28	3.68	406	20
29	7.25	393	19
33	3.87	402	14

Table A2. Minimum convex polygon (MCP) home range sizes: females, 1995.

Tortoise #	MCP Size (ha)	Range Span (m)	N
1	9.70	459	28
8	11.76	750	22
9	4.57	338	23
10	9.76	511	22
12	9.71	438	23
13	2.74	239	22
14	1.00	263	24
19	10.97	566	18
22	3.59	336	22
25	13.35	727	21
26	3.52	600	21
30	3.96	366	18
31	3.52	307	19
32	15.87	854	18
34	0.82	149	16
35	15.05	632	13

Table A3. Minimum convex polygon (MCP) home range sizes: males, 1996.

Tortoise #	MCP Size (ha)	Range Span (m)	N
2	0.23	69	24
4	14.41	745	19
11	0.44	144	24
15	1.72	241	25
17	1.11	429	25
18	6.41	457	25
21	2.84	281	23
23	2.67	360	20
24	0.98	193	22
27	0.0	0.0	22
28	2.75	289	22
29	3.00	293	20
33	4.76	394	21
36	2.19	251	22

Table A4. Minimum convex polygon (MCP) home range sizes: females, 1996.

Tortoise #	MCP Size (ha)	Range Span (m)	N
1	0.05	107	20
8	3.71	765	21
9	0.31	144	19
10	0.01	93	16
12	1.35	317	27
13	0.88	170	25
14	0.86	150	26
22	1.06	187	21
25	1.67	185	27
26	0.36	178	26
30	0.35	105	22
31	0.63	294	24
32	2.00	164	25
34	0.40	124	24
35	0.28	112	20

Table A5. Minimum convex polygon (MCP) home range sizes: males, 1995/1996 combined.

Tortoise #	MCP Size (ha)	Range Span (m)	N
2	11.21	536	48
4	19.79	745	39
11	11.08	670	44
15	4.24	291	50
17	7.55	576	44
18	11.34	561	45
21	13.97	598	46
23	4.27	397	39
24	4.08	341	44
27	6.46	617	39
28	4.93	434	42
29	8.57	410	39
33	6.48	504	35

Table A6. Minimum convex polygon (MCP) home range sizes: females, 1995/1996 combined.

Tortoise #	MCP Size (ha)	Range Span (m)	N
1	10.42	489	48
8*	31.95*	832*	43
9	5.25	338	42
10	9.76	511	38
12	10.93	458	50
13	2.80	239	47
14	1.89	294	50
22	3.59	336	43
25	13.35	727	48
26	4.10	636	47
30	4.87	386	40
31	3.70	307	43
32	21.68	854	43
34	1.34	163	40
35	16.33	632	33

* Removal of a single 700m move by tortoise #8 reduces MCP to 11.76 ha.

Appendix B: Morphological Measurements of Desert Tortoises Used in the Radiotelemetry Study (1995-1996) at Sand Hill Training Area, MCAGCC

Tortoise	Gen-der	Length (mm)	Width (mm)	1995 Weight (kg)	1996 Weight (kg)	Weight Change (kg, %)
M95-2	M	335	265	6.8	5.45	-1.35, 19.9
M95-4	M	246	187	2.95	2.4	-0.55, 18.6
M95-11	M	188	141	1.4	1.2	-0.2, 14.3
M95-15	M	303	224	5.4	3.9	-1.5, 27.8
M95-17	M	294	223	4.55	3.4	-1.15, 25.3
M95-18	M	278	216	4.1	3.15	-0.95, 23.2
M95-21	M	316	247	6.0	4.9	-1.1, 18.3
M95-23	M	263	196	3.2	2.7	-0.5, 15.6
M95-24	M	256	189	3.2	2.5	-0.7, 21.9
M95-27	M	284	223	4.7	3.8	-0.9, 19.1
M95-28	M	299	232	5.1	3.9	-1.2, 23.5
M95-29	M	254	191	3.2	2.5	-0.7, 21.9
M95-33	M	295	232	5.5	4.15	-1.35, 24.5
M96-36	M	287	224	3.3	NA	NA
M95-1	F	267	200	3.5	2.5	-1.0, 28.6
M95-8	F	251	185	2.85	2.0	-0.85, 29.8
M95-9	F	272	214	3.5	2.7	-0.8, 22.9
M95-10	F	230	184	2.55	2.0	-0.55, 21.6
M95-12	F	209	160	2.1	1.7	-0.4, 19.0
M95-13	F	250	188	3.0	2.6	-0.4, 13.3
M95-14	F	248	185	2.95	2.5	-0.45, 15.3
M95-19	F	232	167	2.3	NA	NA
M95-22	F	235	173	2.4	2.1	-0.3, 12.5
M95-25	F	241	186	2.8	2.7	-0.1, 3.6
M95-26	F	201	150	1.7	1.55	-0.15, 8.8
M95-30	F	265	198	3.7	2.85	-0.85, 23.0
M95-31	F	222	164	2.0	1.7	-0.3, 15.0
M95-32	F	246	186	3.8	2.1	-1.7, 44.7
M95-34	F	217	174	2.2	1.9	-0.3, 13.6
M95-35	F	245	186	2.8	2.3	-0.5, 17.9

Appendix C: Status of Desert Tortoises From Baxter and Stewart Study (1984-1985) at Sand Hill Training Area, MCAGCC

Baxter ID #	Gender	Location	Status
2	F	M95-1	M95-1
6	F	M95-10	M95-10
10	F	M95-34	M95-34
16 [a]	M	M95-33	M95-33
17 [a b]	F	66.75E, 94.96N	(M95-16)
25 [c]	F	65.78E, 95.12N	(M95-6)
26	M	M95-2	M95-2
28	M	M95-21	M95-21
63	M	M95-18	M95-18
R64	M	M95-36	M95-36
109	M	M95-23	M95-23
R24	M	66.961E, 96.366N	Alive 5-1-96
30	M	66.531E, 91.736N	Alive 9-16-97
34	F	66.632E, 92.634N	Alive 9-2-97
35	F	65.323E, 93.0232N	Alive 3-14-96
48		65.795E, 94.898N	Alive 6-7-96
52		65.536E, 93.304N	Alive 1995
64	M	66.115E, 93.020N	Alive 1995
66	M	66.579E, 92.382N	Alive 3-26-96
79		66.402E, 93.755N	Alive 1995
101	M	65.501E, 93.268N	Alive 3-14-96
103	M	66.803E, 94.967N	Alive 5-1-96
105	M	65.59E, 93.19N	Alive 1995
14	M	65.941E, 92.847N	Carcass 6-26-97
38	M	65.054E, 96.257N	Carcass 4-15-96
40	M	66.289E, 95.938N	Carcass 4-23-96
41 [d]	F	66.002E, 95.839N	Carcass 4-22-96
83	M	65.728E, 95.791N	Carcass 4-19-96

[a] The epoxy number from Baxter's study was faded and uncertain.
[b] Tortoise was found dead lying on its carapace when recaptured 8 June 1995.
[c] Tortoise was "missing" from the study, having fewer than five relocations in the 1995 season, but was found 31 October 1996 with its transmitter missing, less than 1 km from its last known location.
[d] Carcass was very recent, no more than 1 month old.

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