Spatial Ecology of the Desert Tortoise: Sampling Frequency and Biological Influences

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Spatial Ecology of the Desert Tortoise: Sampling Frequency and Biological Influences

by

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Each person whose signature appears below certifies that this thesis in his/her opinion is adequate, in scope and quality, as a thesis for the degree Master of Science.

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Preface

The following thesis is presented in separate chapters, representing two manuscripts. A thorough literature review is presented in the first chapter, integrating the concepts discussed in each manuscript. The two manuscripts comprise chapters 2 and 3. Chapter 4 provides a summary reviewing the findings of both manuscripts.

This project was initiated prior to the involvement of the candidate and prior to her enrollment at Loma Linda University. However, she was the primary collector of the data utilized in this thesis. The two manuscripts will be co-authored by the candidate, the thesis supervisors, Dr. William K. Hayes and Andrew D. Walde, and Construction Engineering Research Laboratory (USACERL) employees David K. Delaney and Dr. Larry L. Pater. Furthermore, data analysis and the writing of the manuscripts contained within was the sole responsibility of the candidate.

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ABBREVIATIONS

AME Animal Movement Extension for ArcView
ANOVA Analysis of Variance
ANCOVA Analysis of Covariance
CDFG California Department of Fish and Game
CERL United States Army Construction and Engineering Research Laboratory
ERDC United States Army Engineer Research and Development Center
FK Fixed Kernel Density Estimator
IV Independent Variables
JT Jennrich and Turner Correction Factors
LDM Long-distance Movement
LSCV Least-squared Cross-validation
MCP Minimum Convex Polygon
MCL Midline Carapace Length
SE Standard Error
SR-A Parsed Sampling Regime A
SR-B Parsed Sampling Regime B
SR-C Parsed Sampling Regime C
SR-D Parsed Sampling Regime D
SR-O Sampling Regime O (all locations)
UD Utilization Distribution
USFWS United States Fish and Wildlife Service
UTM  Universal Transverse Mercator
Understanding the spatial ecology of an animal is crucial for making positive efforts to provide for its recovery. As a part of this understanding, home range estimates are used to answer a variety of questions in ecological studies. However, home range estimates based on a collection of radio-telemetry locations are sensitive to methodological variables, such as sample size, sampling frequency, and the choice of estimator. Further confounding these estimates are a number of physical, social, and ecological factors. Identifying the main determinants of space use patterns by a species may aid conservation efforts.

The Desert Tortoise (*Gopherus agassizii*) of the Mojave Desert inhabits an extreme environment where a number of factors likely influence its land use patterns. Prior home range estimates of the Desert Tortoise are wide ranging from different portions of the desert, due in part to the use of a variety of sampling methodologies. My goal was to determine how different facets of sampling methodology affect home range estimates of the Desert Tortoise using two widely-used home range estimators, the
minimum convex polygon and the fixed kernel density estimator. In addition, I investigated physical, social, and ecological variables to examine the dominant factor(s) influencing the spatial ecology of the Desert Tortoise.

Results suggested that previous home range estimates were highly influenced by the sampling regime utilized. Home range estimates in this study were much greater than those in the literature, possibly due to an intensive sampling regime. This suggests that tortoises may require more land than previously thought. Males and females demonstrated very different patterns of space and burrow use, suggesting these variables affect estimates for each sex differently. I conclude that a combination of these variables determines space use in tortoises. By adopting a uniform sampling methodology, researchers can better provide comparable data across studies in a holistic effort to understand the spatial ecology of a species.
CHAPTER 1

LITERATURE REVIEW

The Desert Tortoise

The Desert Tortoise (*Gopherus agassizii*) is a large, semi-fossorial reptile of the Southwestern United States and parts of Mexico occupying portions of the Mojave, Sonoran, and Great Basin Deserts. The range of this species extends from southern Nevada and extreme southwestern Utah southward through southeastern California, southwestern Arizona, and western Sonora to northwestern Sinaloa, Mexico (Ernst et al. 1994).

The behavior, morphology, and physiology of this species are vastly influenced by the characteristics of its extreme environment. These characteristics include limited food production, low water availability, and extreme daily and seasonal temperatures (Ernst et al. 1994). This thermal variation plays a key role in determining activity and movement patterns of Desert Tortoises, both daily and seasonally (Nagy and Medica 1986; Ruby and Niblick 1994). In spring, tortoises are most active when environmental temperatures are moderate and forage is in abundance. Activity then decreases in summer as daily temperatures exceed the thermal maxima for Desert Tortoise (Auffenberg and Iverson 1979; Ruby and Niblick 1994).

To escape the extreme temperatures of their environment, Desert Tortoises utilize underground burrows (McGinnis and Voigt 1971; Zimmerman et al. 1994; Rautenstrauch
et al. 2002). The burrow microhabitat provides a relatively constant temperature and increased humidity, thereby reducing water loss (Zimmerman et al. 1994; Bulova 2002). Burrows are also important in providing a staging area for social interactions, a refuge for predator avoidance, and a nest site for egg incubation (Woodbury and Hardy 1948; Patterson 1971; Bulova 1994). The number of burrows a Desert Tortoise utilizes has been found to vary between gender, location, season, and year (Burge 1978; Bulova 1994; Duda et al. 1999).

Studies and surveys on populations of the Desert Tortoise greatly increased in the 1970s and 1980s, but were unable to drastically increase the biological understanding of the species (Germano and Bury 1994). Reasons for this may be that the Desert Tortoise is a somewhat difficult species to study because of its cryptic nature, occurrence in low densities, utilization of underground burrows as a means of refuge, and inactivity for a large portion of the year (Ernst et al. 1994).

On 2 August 1989, *G. agassizii* was state-listed as threatened in California (California Fish and Game Commission 1989), with the Mojave population federally listed as threatened on 2 April 1990 (U.S. Fish and Wildlife Service 1990). Reasons cited for listing the Desert Tortoise included loss of individuals to disease, loss and degradation of habitat, increased levels of mortality associated with urban growth throughout the desert, and the inability of regulatory and management agencies to protect their habitat (U.S. Fish and Wildlife Service 1990).

The cryptic and fossorial nature of *G. agassizii*, combined with financial considerations, has often imposed temporal, spatial, and environmental constraints on the study designs of researchers. Thus, many previous investigators studied small numbers of
tortoises, often fewer than 10, and over a short time period, typically three to four months. Accordingly, data have seldom been collected throughout a complete biological cycle of *G. agassizii*, from early spring emergence to late fall dormancy, or across multiple years. The results and conclusions of these studies may be inaccurate estimations of various biological traits of the Desert Tortoise.

A more complete understanding of the home range, movements, and burrow use is critical in properly providing for the recovery of the Desert Tortoise. Identifying the requirements of this species should be a priority considering that much of the habitat of this species is located upon federal land managed by the Department of Defense, the Bureau of Land Management, and the National Park Service. These organizations are important in managing multi-use areas of land, and their conservation efforts will benefit from increased knowledge of these animals (Duda et al. 1999). In light of recent interest in tortoise relocation as an effective management procedure (e.g., Fort Irwin; Esque et al. 2005), increased understanding of the spatial ecology will help to more effectively evaluate this conservation strategy.

**Review of Home Range Estimation**

The biological definition of an animal's home range was first described by Burt (1943:351) as “the area usually around a home site, over which the animal normally travels in search of food.” To operationally define home range, Mohr (1947) utilized a polygonal home range calculation method by connecting outermost points of capture into a polygon representing the animal’s home range, termed the minimum convex polygon (MCP). This popular method is valuable for land management purposes in its ability to
estimate the total area of use for an animal, the implications of which may be important in habitat preservation and efforts to manage for travel corridors between disjunct metapopulations (Levins 1969). However, the MCP is flawed in that it may contain considerable areas never visited, geographically isolated from, or simply traversed by the focal animal (Worton 1987). In addition, criticisms of the MCP method emphasized that it provides no measure of internal space usage, is highly correlated to the number of observations, and is greatly affected by outermost locations in a given area (Worton 1987).

Later definitions of home range recognized that food resources might not be the primary determinants of home range size. Kaufmann (1983) improved upon Burt’s definition of home range to include indicators of multiple functions, such as energy balance, activity, resource availability, and opportunities for reproduction and social interaction. Furthermore, as with its conceptual definition, methods of home range estimation have also changed frequently over time (e.g., Powell 2000; Kernohan 2001).

In an effort to improve upon the reliability of home range estimates, a number of researchers developed novel methods of analysis. Alternate home range analysis methods focused on home range size relationships to the longest distance traveled (reviewed in Hayne 1949), trapping arrays (Stickel 1954; Schoener 1981; Worton 1987), and superimposed grid cells (Kaufmann 1995). The greatest distance method was proposed, which used the longest distance between two points as an axis of an ellipse, or the diameter of a circle (Hayne 1949). Although these distances were important factors of an animal’s home range, this method assumed home range shapes conformed specifically to a circular or elliptical pattern. These ellipses, or circles, included areas not utilized by the
animal. In addition, the application of the greatest distance method across species is
difficult considering the non-elliptical or non-circular movements of animals and their
heterogeneous habitat structure (Powell 2000).

Home range size analysis according to trap array also proved to be complex,
especially considering the different experimental designs and sampling methods between
studies (Stickel 1954). Grid cell methods, such as the quadrat summation area method,
attempted to limit the actual estimate of home range area to include only the suitable
habitat available to the animal, thereby improving upon MCP estimates by removing
unused space (Galbraith et al. 1987; Kaufmann 1995). The quadrat summation area
method divided suitable habitat into a grid system of a standardized area. Animal
locations within each cell were tallied and the home range was obtained by summing the
occupied grid cells. This method did relatively little to improve home range estimates and
was not widely adopted in space use investigations.

Research on a variety of species demonstrated that different areas within an
animal's home range are used more intensively than others (reviewed in Samuel et al.
1985). It is therefore important to examine the intensity with which an animal uses the
different areas within its home range, given the possibility of varying distribution of
limiting resources within an animal's habitat (Hayne 1949; Van Winkle 1975). Cluster
methods of home range estimation were then introduced in an effort to limit the amount
of unused space included in the home range. Cluster polygons were formed using a
nearest-neighbor linkage, effectively drawing a line around areas of increased use with
corridors linking these areas together (reviewed in Kenward 1987). This method was not
widely accepted due to the introduction of robust, parametric methods for home range analysis around the same time.

Hayne (1949) believed that a different understanding of the biological significance of an animal’s home range was then needed. He proposed a home range concept that emphasized the geographic center of all points of capture, which may not necessarily be a biologically relevant point. This point was considered the center of the home range, assuming the animal has an equal probability of being located throughout the distribution (Hayne 1949). Statistical analyses were then determined to be the most appropriate method for comparing ecological interactions as they relate to home range analysis (Koeppl et al. 1975; Worton 1987). Home range size was thus defined statistically as a probabilistic model, the utilization distribution (UD): the minimum area in which an animal has some specified probability of being located (Van Winkle 1975; Worton 1995).

Jennrich and Turner (1969) selected a bivariate normal distribution to best estimate the UD. This model, without the restrictions of an elliptical or circular distribution, provided a method for characterizing the home range of an animal inhabiting homogenous habitat (Van Winkle 1975). Similarly, the harmonic mean estimator was developed to estimate the distribution of locations, providing a visual interpretation of the areas used with greater frequency (Dixon and Chapman 1980; Worton 1987). Although the latter model improved upon previous models, inherent flaws in its complex methodology hindered comparability between studies.

In reviewing different UD estimation methods, Worton (1989) recommended the kernel method as a useful source of estimation due to the fact that it assumes no
constraints of normality on the UD. However, much like the MCP, the kernel density estimation method also contains inherent statistical restrictions relating to sampling size and frequency of data collection. Kernel estimates based on small samples will overestimate home range size (Seaman and Powell 1996), and will also be less able to detect fine structural changes within the home range (Hemson et al. 2005).

The kernel method was found to be effective in analyzing home range data with respect to spatial use patterns such as habitat usage (Worton 1995). Kernels produce an unbiased density estimate directly from the data, free from effects of grid cell size and placement (Silverman 1986). Common analyses include the use of the fixed kernel method and/or the adaptive kernel method. These methods differ largely in their inherent use of a “smoothing parameter,” or $h$, representing the bandwidth of each kernel cell (Worton 1989). The smoothing parameter works to control the amount of variation in each component of the density estimate. A lower value of the smoothing parameter demonstrates more detail in the density estimation than when high $h$ values are used (Worton 1989).

In the fixed kernel method (FK), the smoothing parameters are at a stable value over the plane of the utilization distribution (Worton 1989). This stable smoothing parameter is flawed in that it treats the distribution as a unimodal, normal distribution. Animal movements are generally multimodal, and thus violate the assumptions of normality. A stable smoothing parameter would be too large in a multimodal animal to effectively demonstrate detailed usage patterns (Seaman and Powell 1996). The adaptive kernel method alleviates this problem by varying the smoothing parameter so that area of
increased use will have a lower value of $h$ than areas with a lower concentration of capture points.

Worton (1989) determined that the choice of kernel method is not as important as selecting a proper smoothing parameter. The recommended method of determining the smoothing factor for either kernel model was to use a least-squares cross-validation approach (Worton 1989; Seaman and Powell 1996). This method examines various smoothing parameters and selects the one that provides the lowest mean integrated square error between the unknown density and the kernel density, thereby providing more-detailed area usage information (Worton 1989; Seaman and Powell 1996). A complete understanding of the relationships of the variables involved will improve the effectiveness and widespread use of the kernel method.

The choice of home range estimator ultimately depends on research objectives. Each estimate has both positive and negative aspects in terms of the effects of sampling methodology. In addition, each may provide different insight into the spatial ecology of an organism. At present, most home range studies use the MCP, the FK, or both methods.

**Burrow Use and Home Range Estimates of the Desert Tortoise**

Due to the importance of burrows to meeting the biological needs of the Desert Tortoise, a number of studies have quantified burrow use; however, most were either based on small sample sizes, penned animals, or limited duration (*reviewed in* Rautenstrauch et al. 2002). The relationship of burrow usage and home range is important to integrate into a successful model of estimating the home range of a Desert Tortoise. Duda et al. (2002) recognized this in their analysis of home range dynamics, citing
habitat selection and social factors as explanations of the observed aggregated spatial
patterns.

In a review of Testudinidae literature, Auffenberg and Weaver (1969) noted that a
thorough definition of home range was lacking. My review of the literature found that
little has changed since that review almost 40 years ago, and a concise definition of home
range and recommended estimators is still lacking. Many studies have utilized the MCP
to estimate the home range of Gopher Tortoises (Diemer 1992; Smith et al. 1997;
Eubanks et al. 2003), Desert Tortoises (Barrett 1990; O'Connor et al. 1994; Duda et al.
1999), and Texas Tortoises (Kazmaier et al. 2002), with varying results. To compensate
for low number of locations per tortoise, sample size correction factors (Jennrich and
Turner 1969) are sometimes utilized to adjust home range values (Burge 1977; Barrett
1990; O'Connor et al. 1994). Rautenstrauch and Holt (1995) found that use of these
correction factors may overestimate home range area of the Desert Tortoise by up to
200% when utilized on small data sets. In addition, Rautenstrauch and Holt (1995)
concluded the MCP method to be a reliable estimator of a Desert Tortoise's home range
if over 60 locations were observed. Aside from Rautenstrauch and Holt (1995), no other
past studies have collected over 60 location points for their analysis; thus, home range
estimates in the literature may not be reliable.

Researchers have also pooled data from two or more years in an effort to increase
sample size (Burge 1977). Results of these and other studies show home range size and
number of observations to be directly related (Burge 1977; Freilich et al. 2000; O'Connor
et al. 1994). The overall area that a tortoise uses varies between years (Holt and
Rautenstrauch 1996). Multi-year comparisons within studies, as well as comparisons of
home range values between studies, is challenging due to differing methodologies and sampling regimes. The results of these studies indicate the need to further examine the relationship between sample size and home range estimates as applied to the Desert Tortoise.

O'Connor et al. (1994) recommended that home range methods that permit multiple activity centers may be better suited to Desert Tortoise home range analysis than methods that only permit one activity center. Home range estimators that only allow for one activity center are the MCP and bivariate normal ellipse. Rautenstrauch and Holt (1995) examined the bivariate normal ellipse (Jennrich and Turner 1969) and the weighted bivariate normal ellipse (Samuel and Garton 1985) and concluded that they are not appropriate methods in calculating the home range size for a Desert Tortoise. The kernel density estimator may be a good choice of home range estimation for the Desert Tortoise due to the tortoise's extensive use of localized burrows for survival. Multiple burrows would represent the activity centers utilized in the kernel density estimation. This method, when used along with the MCP method, may best represent the total land use patterns of the Desert Tortoise. The implications of this multi-faceted approach to examining the land use patterns of Desert Tortoises may greatly benefit the conservation of this species.

For other members of the genus Gopherus, researchers have struggled with the definition of home range. Aguirre et al. (1984) determined that, for the Bolson Tortoise (G. flavomarginatus), the mean distance and the maximum distance traveled per day were better indicators of tortoise motility than the calculated radius of activity. Alternatively, in studying a population of Gopher Tortoises (G. polyphemus), McRae et al. (1981)
identified two types of habitat usage that varied remarkably in size. The home range was defined as two distinct parts: 1) the daily feeding area or activity range, typically ca. 30 m around the burrow, and 2) an annual range, including areas used for mate searches, locating food sources, and winter burrows (McRae et al. 1981). This study recommended that the home range of a Gopher Tortoise is best described as the total area used annually for both feeding activity and important social interactions.

Desert Tortoises typically utilize a series of burrows throughout the year, which appears to be important in meeting its life history requirements (Bulova 1994). Studies of the Mojave Desert populations of this species view the home range as a circumscribed network of burrows (O’ Connor et al. 1994; Duda et al. 1999; Freilich et al. 2000). The number of different burrow sites and the distance between them has been shown to greatly affect home range size and shape (Duda et al. 1999). Two studies have examined between-year patterns in the home range of Desert Tortoises with differing conclusions (Holt and Rautenstrauch 1996; Duda et al. 1999).

Duda et al. (1999) noted an increase in home range size, number of burrows used, and distance traveled between locations in a year of higher precipitation compared to a year of decreased precipitation. They concluded that home range size and activity were directly proportional to forage biomass (Duda et al. 1999), as has been noted in studies of numerous species (McNab 1963). Holt and Rautenstrauch (1996) determined that tortoises moved less in a drier year, yet maintained a similar-sized home range between the dry and wet years. However, Holt and Rautenstrauch also concluded that tortoises used a smaller core area during the drought year when using the 95% cluster method.
Long-range movements comprise another factor complicating home range estimation in Desert Tortoises. Similar to the concept of home range, investigators have defined these movements differently, labeling them as long-distance movements (LDM; Boarman et al. 1996) or forays (Duda et al. 1999; Freilich et al. 2000). Boarman et al. (1996:36) defined an LDM as “any movement greater than or equal to the maximum linear size of the ‘normal’ home range”. Alternatively, a foray is considered “any movement that results in occupation of an area greater than or equal to 1 km outside of the ‘normal’ home range for 1-2 weeks” (Duda et al. 1999:1184; Freilich et al. 2000).

Home range estimates for *G. agassizii* are often calculated using only localized activity locations, disregarding these long-range movements (Burge 1977; Turner et al. 1984; Boarman et al. 1996). These movements are unknown in purpose and are therefore discarded (Berry 1986; Duda et al. 1999; Freilich et al. 2000). Researchers speculate these movements may be used to aid in dispersal (Gibbons 1986; Boarman et al. 1996) or to search for prospective mates, higher-quality food or shelter (McRae et al. 1981), nesting or hibernating sites (Burge 1977), or areas of limiting nutrients (Marlow and Tollestrup 1982). Thus, these long-range movements should be considered an important part of the life history of the Desert Tortoise (Burge 1977; Berry 1986; Boarman et al. 1996) and perhaps should not be removed from home range analyses. In the first description of home range, Burt (1943:351) specifically excluded these “occasional sallies outside the area, perhaps exploratory in nature.” However, Hayne (1949) felt that the longest observed movement of an animal is the most important clue to the home range, representing the farthest distance traveled by the animal during the period of investigation. Thus, the dilemma arises as to whether or not to include LDMs, or forays,
into home range calculations. Many researchers compute 100% MCP and/or 95% FK estimates, as it is the highest level of probability in available software packages. When considered together, these two estimates may best represent the area effectively utilized by an animal.

To date, no study has been conducted in the west Mojave Desert, completing the sampling regime of 60 locations per animal as recommended by Rautenstrauch and Holt (1995). Thus, an analysis is needed to explore the effect of sampling methodology on each of these home range estimators to better understand the home range requirements of the Desert Tortoise.

**Study Objectives**

In the following chapters, I detail a multi-faceted analysis of an intensive radio-telemetry study of a sample population of Desert Tortoises in the west Mojave Desert. In Chapter 2, I consider the effects of alternative sampling regimes on two widely-used home range estimators and simultaneously consider several other primary factors, including year, sex and body size. In Chapter 3, I examine patterns of spatial overlap and parameters of burrow use of this species. I considered how year, sex, body size, and home range area influenced spatial overlap and burrow use. In each chapter, I interpret the results in the context of improving the understanding of land use by *G. agassizii*, with a focus on providing information for effective management decisions. In Chapter 4, I summarize the main conclusions from the two primary studies.
CHAPTER 2

SAMPLING CONSIDERATIONS FOR IMPROVING HOME RANGE ESTIMATES FROM RADIO-TELEMETRY STUDIES

Abstract

Home range estimation as a measure of spatial utilization is an important tool in the management of wildlife. Operational methods of defining the spatial requirements of an animal differ in sampling regime and interpretation. The two most commonly used estimators, the minimum convex polygon (MCP) and the fixed kernel (FK), each provide a different measure of land use yet together allow for a better understanding of the spatial needs of a particular animal. Sampling frequency and number of individuals has been shown to differentially affect home range estimates using these two procedures. This presents a challenge to researchers in balancing financial, personnel, and temporal considerations. We conducted an intensive radio-telemetry study on a large number of Desert Tortoises (Gopherus agassizii) to determine an optimal sampling effort for home range estimation using both the MCP and FK estimates. Data were parsed into sampling regimes representative of previous home range studies in an effort to compare estimates across studies. Home range estimates using the MCP were over two times larger in this study when compared to previous studies on the Desert Tortoise in the Mojave Desert. Results indicate that an increased sampling frequency inflates MCP estimates, while providing more use-specific detail and
decreasing area for FK estimates. Analysis demonstrated home range area to be greatly affected by choice of estimator (MCP or FK), sampling regime, and sex. We recommend an intensive and systematic sampling effort to better define home range estimates, as well as to provide comparable data across studies. Minimum convex polygon and FK home range estimators both provide valuable information as to the biological needs of the Desert Tortoise and should be identified as a priority in land use investigations for conservation decisions.

Introduction

An understanding of the land use and movement patterns of a species, specifically home range area, has been the focus of numerous studies over the past few decades. The space use of a species or group is of great concern to biologists because it provides valuable insight into the specific needs of an organism (Kemohan et al. 2001). This information can be used in planning land conservation efforts to assist in the recovery of threatened and endangered species, such as the Desert Tortoise (Gopherus agassizii). A variety of methods and interpretations of how best to measure and identify spatial use by animals may limit the potential consensus within the scientific community, which could hinder the effectiveness of conservation management and recovery programs.

More than 60 years ago, Burt (1943:351) was among the first to describe the biological definition of an animal’s home range as “the area usually around a home site, over which the animal normally travels in search of food”. This definition was helpful in specifically defining the concept of a home range; however, it did not provide information on quantifying this area. Kaufmann (1983) later clarified this definition to
include indicators of multiple functions, including energy balance, activity, resource availability, and opportunities for reproduction and social interactions. This definition helped to specify important aspects of what a home range should represent, but failed to provide an operational method of quantification. These characteristics of an animal's home range may reflect important interspecific and intraspecific details of behavior and ecology, including habitat use, forage quality, population density, competition, and social systems (reviewed in Powell 2000).

To quantify home range area, the minimum convex polygon (MCP; Mohr 1947) is the most commonly used estimator because it is simple to use and is not constrained by underlying statistical assumptions (Powell 2000). Because of its historic use, the MCP is often used in studies on the same organism in an attempt to make results comparable. Due to the nature of the MCP method, estimated home range values may contain considerable areas never visited, geographically isolated from, or simply traversed by the focal animal. The MCP also provides no measure of internal space use and is highly correlated to the number of locations (Worton 1987) and tends to increase asymptotically with increasing number of locations (White and Garrott 1990; Seaman et al. 1999; Belant and Follmann 2002). MCP estimates are thus highly sensitive to outermost locations, as these determine the overall shape and area of the polygon.

Research on a variety of species demonstrates that different areas within an animal's home range are used more intensively than others (reviewed in Samuel and Garton 1985). Therefore, it is important to examine the intensity with which an animal uses different areas within its home range, given the possibility of varying distribution of limiting resources within an animal's habitat (Hayne 1949; Van Winkle 1975; Powell
The kernel density estimator is a non-parametric technique used to determine how an animal utilizes different portions of its habitat (Silverman 1986; Worton 1995). Kernel density estimators provide a utilization distribution (UD) of a specified probability that the animal will be located within a certain area (Powell 2000). The density of the kernel at any location in the home range is a function of how much time the animal spent in that location (Seaman and Powell 1996). The kernel estimator, computed most often as the fixed kernel (FK; Seaman and Powell 1996), also includes inherent statistical restrictions relating to the number of locations. The kernel estimator decreases asymptotically as sample size increases (White and Garrott 1990; Seaman et al. 1999; Belant and Follman 2002), which is opposite of the MCP. Thus, even though both MCP and FK are sensitive to sampling regime, the number of locations per animal and sampling interval are seldom reported or addressed in home range investigations (Powell 2000; Kernohan et al. 2001).

Studies of space use and movements of the Desert Tortoise illustrate the limitations of sample size, sampling frequency, and study duration. This species is difficult to study because of its cryptic nature, occurrence in low densities, use of underground burrows for refuge, and inactivity for a large portion of the year (Ernst et al. 1994), as well as its threatened status (California Fish and Game Commission 1989; U. S. Fish and Wildlife Service 1990), necessitating special permits and permissions. Most studies involving conventional radio-telemetry on G. agassizii used a small number of individuals, usually less than 20 (e.g., Burge 1977; O'Connor et al. 1994; Freilich et al. 2000). Home ranges were typically calculated using few locations per tortoise, often less than 25 (e.g., Woodbury and Hardy 1948; Medica et al. 1982; Duda et al. 1999). In only a few studies, sampling occurred throughout a complete biological cycle, from early spring...
emergence to late fall dormancy (e.g., Burge 1977; Medica et al. 1982; Freilich et al. 2000), or across multiple years (e.g., Medica et al. 1982; O’Connor et al. 1994; Holt and Rautenstrauch 1996).

Home range as a concept is also limited in its definition to the time interval of the study, such as yearly or seasonal use. This is an important consideration because researchers face constraints of time, funding, and personnel. In designing a study, home range should be quantified over a biologically meaningful period of time to adequately sample space use (Powell 2000).

Herein, we detail the results of an intensive two-year radio-telemetry study on a sample population of Desert Tortoises in the west Mojave Desert. We sought to: 1) determine the space use patterns of male and female Desert Tortoises using two popular home range estimation methods, the MCP and FK; 2) assess the relative sensitivity of each estimator to different sampling regimes; 3) determine the effect of long-range movements and the number of locations on each estimator; and 4) evaluate the primary factor(s) associated with home range estimates, including year, sex, and body size. We then interpret the results of the above analyses in the context of improving our understanding of land use by G. agassizii, with a focus on providing information for effective management decisions to provide for the recovery of this species.

Methods

STUDY SITE

The study was conducted in the southwest corner of the National Training Center at Fort Irwin, California (35°14’63”N, -116°75’17”W), on land federally designated as
Desert Tortoise critical habitat (59 FR 5820-5866, U. S. Fish and Wildlife Service 1994a,b). The study site was irregularly shaped, approximately 3.74 km², and comprised typical Mojave Desert vegetation: Creosote–White Bursage scrub (Larrea tridentata–Ambrosia dumosa; Turner 1982). This area of the military base is protected from public use, is located far from any regularly traveled roads, and is thus relatively undisturbed (Walde et al. 2007).

**DATA COLLECTION**

In 2003, the study site was extensively surveyed where Desert Tortoises encountered were captured and measured. Low-duty, cycle-pulsed transmitters (Advanced Telemetry Systems, Isanti, Minnesota; Holohil Systems Ltd., Carp, Ontario, Canada) were mounted directly onto the carapace of each tortoise, as is commonly done for this species (Bulova 1994; O’Connor et al. 1994; Boarman et al. 1998). Transmitters weighed < 5% of the tortoise’s mass and had an expected battery life of 18-36 months. Transmitter mounting varied by sex to ensure there was no constraint in tortoise movement, particularly during copulation attempts.

Portable radio receivers (Yaesu VR-500, Vertex Standard Inc., Cypress, California) and three-element hand-held directional Yagi antennas (Wildlife Materials International, Inc., Murphysboro, Illinois) were used to locate transmittered tortoises. The exact geographic location (universal transverse mercator, UTM) of each tortoise was obtained during each tracking event. Geographic locations were recorded using a global positioning unit (Garmin 12 Personal Navigator Unit, Garmin International, Olathe, Kansas) with an estimated probable error between 3-6 m. Geographic locations were
imported into ArcView 3.3 (Environmental Services Research Institute, Redlands, California) for mapping utilization functions.

**SAMPLING EFFORT**

As part of a comprehensive study on the behavior and ecology of the Desert Tortoise, transmittered animals were located using a systematic sampling scheme (Table 2-1). In both 2004 and 2005, tracking events were completed in a general schedule of one location per tortoise collected over Monday and Tuesday, with an additional location for each tortoise collected over Thursday and Friday of the same week. Tortoises were located at least twice per week during peak activity periods, from February to the end of June and mid-August to late October, then once per week thereafter when daily activity decreased. During December and January, tortoises were located once every one to two weeks. During the active season, tortoises were located in a random sequence. As Desert Tortoises were routinely observed in burrows, locations recorded at the same burrow number were standardized so that the easting and northing UTMs were identical in an effort to reduce error in home range estimates. The original dataset (sampling regime SR-O) included all observations as described above, as well as opportunistic locations taken when performing other tasks of the research protocol, such as behavioral observations or transmitter maintenance. Consequently, the original dataset included the largest number of locations. Some tortoises were not located as frequently as dictated by the sampling regime due to logistic constraints resulting from long-distance movements by tortoises or military range-access conflicts. Male tortoises offered more opportunistic locations, as
they were part of an additional component of the project; therefore, some bias existed, with females having fewer locations than males in the original dataset.

To investigate the effect of sampling frequency on home range area, the original data set for each year was parsed into four sampling regimes (Table 2-1). The original dataset (SR-O) contained differing numbers of locations per individual, whereas each parsed sampling regime contained relatively equal numbers of locations per tortoise. The data were parsed into each sampling regime according to calendar week and month. As a consequence, the total number of locations per sampling regime may have exceeded those calculated using a strict number of weeks/months per year. Sampling regime A (SR-A) was composed of the following: two locations per week during the active months (March-June; August-October), one location per week during periods of low activity (February, July, and November), and twice per month during winter dormancy (November-December). Sampling regime B (SR-B) included locations taken once per week in February through November and twice per month in December and January. Sampling regime C (SR-C) included locations completed two times per month throughout the entire year. Finally, sampling regime D (SR-D) was comprised of locations completed once per month throughout the year.

Each sampling regime drew from locations from the original dataset so that successive sampling contained only locations of the previous regime. For example, SR-D was comprised of locations taken once per month, resulting from the removal of every other location throughout SR-C, for which locations were collected twice per month. In SR-A, preference was given to locations taken 1-2 days apart during the week in the active season. In SR-B and SR-D, preference was given to locations collected on Monday
and Tuesday of each week in an effort to ensure a consistent amount of time between locations. Preference in SR-C and SR-D was given to locations from the first and third weeks out of each month in a similar effort to standardize the time between successive locations.

**HOME RANGE ESTIMATES**

Home range areas were defined as 100% MCP and 95% FK estimates, calculated using the Animal Movement Extension (AME) for ArcView 3.3 (Hooge et al. 1999). We used the least-squared cross-validation (LSCV) approach to standardize bandwidth in calculating the FK estimates, as recommended by Seaman and Powell (1996). The AME software does not allow for calculations of a 100% kernel estimate; thus, the 95% isopleths were used to represent the home range area (Worton 1987). For one female tortoise, AME could not compute the FK estimate for SR-D; this reduced the sample size for some analyses to N = 34. In addition, Jennrich-Turner (JT) correction factors (Jennrich and Turner 1969; Barrett 1990) were applied to the MCP estimates from the four parsed datasets. The resulting “adjusted” MCP estimates were compared to estimates obtained from our SR-O sampling regime and from previous studies on the Desert Tortoise, but were not used in the following statistical analyses.

**EFFECTS OF NUMBER OF LOCATIONS**

A standardized method is lacking in the home range literature as to a sufficient number of locations needed when calculating home ranges using the MCP and FK estimators. The few researchers whom have dealt with this problem have chosen various
means by which to define a sufficient number of locations, such as regression analysis (Metzgar and Sheldon 1974), calculation of the approximate asymptote (Seaman et al. 1999), visual inspection of the area-observation curve for evidence of an asymptote (Pike 2006), and limitations on incremental increases in home range area as sample size increases (Odum and Kuenzler 1955, Belant and Follmann 2002, Girard et al. 2002).

To examine the effect of the number of locations on MCP values, a bootstrap function was used to produce an area-observation curve for each tortoise using AME for ArcView 3.3 (Hooge et al. 1999). Because MCP areas increase with number of locations, an area-observation curve illustrates when a sufficient number of locations produces an asymptotic, near-constant MCP value (Gese et al. 1988). Within each sampling regime, an MCP estimate was computed using 100 replicates of 15 randomly-selected locations for each tortoise. We excluded SR-D from this analysis because it lacked a sufficient number of locations. Calculations were then repeated after adding an additional five random locations, representing the sampling interval, until all locations were included. The resulting data set included up to 70 locations with 12 sampling intervals for SR-O, 65 locations with 11 intervals for SR-A, 40 locations with six intervals for SR-B, and 20 locations with two intervals for SR-C.

A more recent approach for evaluating a sufficient number of locations for MCP estimation is to determine the number of locations at which the coefficient of variation (CV) for individual bootstrapped MCP estimates reaches and sustains a value ≤ 10% (Boulanger and White 1990, Otis and White 1999). As the number of locations used for computing MCP increases, CV values decrease, with values ≤ 10% thought to indicate a high amount of precision in the estimate. The proportion of animals meeting the CV ≤
10% criterion (Belant and Follmann 2002; Girard et al. 2002) can be a useful means for assessing sampling regimes. Accordingly, we calculated the CV for each MCP estimate at all sample intervals from the bootstrap function.

**EFFECTS OF LONG-RANGE MOVEMENTS**

To determine how the inclusion of long-range movements affected home range estimates, we performed a post-hoc analysis. Using home range estimates from SR-O, we analyzed the location data set for evidence of either forays (Freilich et al. 2000) or long-distance movements (LDMs; Boarman et al. 1996), as defined by these authors. We removed these movements, separately for forays and LDMs, from SR-O and recalculated both the MCP and FK estimates to determine how each of these movement types affected each estimator.

**DATA ANALYSES**

We used a repeated-measures analysis of variance (ANOVA) model to determine how home range area was influenced by four independent variables (IVs). Of the four IVs, estimator (MCP, FK), year (2004, 2005), and sampling regime (five levels) were treated as within-subjects factors, and sex (two levels) was treated as a between-subjects factor. The sample size (N = 34 or 35; see below) was less than ideal for multivariate tests, with N ≥ 10 individuals for each IV in a model recommended; however, because the results were identical to models in which one or more IVs were removed, we gave preference to the omnibus model as described above. We removed the variable body size (MCL) from this model when supplemental analyses using MCL as a cofactor, with and without additional IVs, confirmed that it had trivial influence on home range size.
The simple main effects of sampling regime on each estimator were examined by creating two additional ANOVA models. Each model included the home range estimate (MCP or FK, depending on model) as the dependent variable and three IVs: year (2004, 2005) and sampling regime (five levels) as within-subjects factors, and sex (two levels) treated as a between-subjects factor.

Home range estimates (both MCP and FK) failed to meet multivariate assumptions of normality and homoscedasticity; thus, log_{10}-transformed home range estimates were used in all statistical tests. The Greenhouse-Geisser adjustment for degrees of freedom was applied to all tests of hypotheses in the ANOVA model due to the failure to meet Mauchly’s test of sphericity (Mertler and Vannatta 2004). We determined the effect size for each test as the partial $\eta^2$ value, indicating the approximate proportion of variance in the dependent variable explained by an independent variable or interaction (Mertler and Vannatta 2004). When the effect sizes for all IVs and interactions in a model summed to $> 1$, we divided each value by the sum of all values to obtain adjusted partial $\eta^2$ values.

Using the MCP estimates from the bootstrap function, we compared the proportion of tortoises achieving the CV $\leq 0.10$ criterion in each of the four sampling regimes using a Cochran’s Q test.

All statistical analyses were performed using SPSS v12.0 (2003; Statistical Package for the Social Sciences, Inc., Chicago, Illinois). The alpha level for all analyses was 0.05. All means are reported as mean $\pm$ 1 SE.
Results

**SAMPLING EFFORT**

Initially, 26 adult male and 15 adult female Desert Tortoises across the study site were fitted with radio transmitters. Tortoise were classified as adult if they had a midline carapace length (MCL) > 180 mm. We removed a total of six adult male tortoises from the following analyses for various reasons, including natural death (N = 3), long-term transmitter failure resulting in a lack of a sufficient number of locations as per the study objectives (N = 2), and movements followed by re-establishment to an area far outside of the designated study site boundary (N = 1). Thus, the resultant sample size for the following analyses is limited to 20 male and 15 female Desert Tortoises (N = 35).

During the 2004 season, a total of 3,141 locations were recorded on adult tortoises across the study site. The original data set resulted in a mean number of 89.7 locations per tortoise in 2004 (Table 2-2), with females (mean = 79.8) having 17.9% fewer locations than males (mean = 97.2). In 2005, a total of 3,684 locations were recorded for a mean of 105.3 per tortoise. As in 2004, female tortoises in 2005 were relocated less frequently (mean = 99.0; 9.1% fewer locations) than males (mean = 109.9). The parsed data sets comprising the four sampling regimes had fewer tortoise locations than the original dataset by definition (Tables 2-1, 2-2). Sampling regimes-A and B came close, but did not meet the total number of locations possible in either year. However, SR-C and D were fulfilled in both years with 24 and 12 locations recorded per tortoise, respectively.
FACTORS ASSOCIATED WITH HOME RANGE AREA

The ANOVA model for home range area identified a number of significant interactions and main effects. We detected a weak but significant interaction between year and sex ($F_{1,32} = 4.37, P = 0.045, \text{adj. partial } \eta^2 = 0.05$). The difference between sexes, with males having larger home ranges than females (see below), was greater in 2005 than 2004 (Fig. 2-1; Table 2-3). We found a much stronger interaction between estimator and sampling regime ($F_{2.9,95.1} = 186.96, P \leq 0.001, \text{adj. partial } \eta^2 = 0.35$). The MCP estimates decreased with each parsing of data in the five successive sampling regimes, whereas FK estimates increased. The main effect of sex was highly significant ($F_{1,32} = 23.11, P \leq 0.001, \text{adj. partial } \eta^2 = 0.17$), with males exhibiting much larger home ranges than females regardless of year (Fig. 2-2). The main effect of estimator was also significant ($F_{1,32} = 5.86, P = 0.021, \text{adj. partial } \eta^2 = 0.06$), with MCPs averaging larger than FKS regardless of sampling regime. Finally, the main effect of sampling regime was significant ($F_{1.6,51.1} = 36.35, P \leq 0.001, \text{adj. partial } \eta^2 = 0.22$), but differences among the sampling regimes depended largely on the estimator.

In looking at the effects of sampling regime on each estimator, we found the MCP was much more affected by sampling regime than the FK estimates. This difference in effect size was over six-fold on MCP area ($F_{1.7,56.3} = 180.92, P < 0.001, \text{partial } \eta^2 = 0.85$) than on FK area ($F_{1.9,63.2} = 5.16, P = 0.009, \text{partial } \eta^2 = 0.14$). When contrasting the area estimates for the MCP and FK for all tortoises over both years of study, we found the difference between the two estimators depended on sampling regime. In the most intensive, structured sampling regime, SR-A, the 95% fixed kernel estimate for all tortoises over both years was 33% smaller than the MCP area (Table 2-3). In comparing
the estimates of all tortoises from SR-D, the least frequent sampling regime, the FK area was more than two-fold greater than the MCP across both years.

**Adjusted Home Range Estimates**

Nearly all of the "adjusted" MCP areas calculated in the parsed sampling regimes for male, female, and all tortoises were larger than the MCP areas calculated using the SR-O in each year (Table 2-3). Adjusted MCP estimates for females in 2005 using SR-C were smaller by < 1%, whereas all other adjusted MCPs were larger than the raw estimates using SR-O. This increase was dependent on the JT correction factor used, calculated from the number of locations used in the estimate. SR-A required a JT factor of 0.78-0.80, whereas SR-B, C, and D required a JT factor of 0.66-0.68, 0.51, and 0.33, respectively. Compared to home range areas using SR-O, adjusted MCP values in each sampling regime were on average 16.8% larger in 2004 (mean = 13.0% for males, mean = 30.2% for females), and 24.1% larger in 2005 (mean = 26.9% for males, mean = 10.2% for females). Within each sampling regime, the mean adjusted values estimated on the parsed datasets were an average of 90% greater (25.3-203.9%) than the corresponding non-adjusted values, and this difference was greater as the sampling regime became less intensive (Table 2-3).

**Effects of Number of Locations**

The CV approach for determining a sufficient number of locations for MCP estimation resulted in substantial differences among the four sampling regimes (2004: Cochran's Q = 49.79, df = 3, P < 0.001; 2005: Q = 27.40, df = 3, P < 0.001; Table 2-4).
The proportion of tortoises reaching and maintaining CV values below the threshold of ≤ 10% was highest for SR-O and declined with each successively less-intensive sampling regime. The proportion of tortoises attaining threshold was also greater in 2004 than in 2005.

**EFFECTS OF LONG-RANGE MOVEMENTS**

We conducted post-hoc calculations of MCP and FK estimates after removal of either forays or LDMs from the SR-O sampling regime. Considering forays, we removed one movement from a male tortoise in 2004, reducing the mean MCP estimate for all tortoises in that year by 14% and the mean FK estimate by 8%. No forays were identified in 2005. For LDMs, no movements in 2004 met the definition. However, we removed locations representing movements from one male and one female tortoise in 2005, reducing the mean MCP and FK estimates for all tortoises that year by 3%.

**Discussion**

**SAMPLING EFFORT**

In examining the home range of the Desert Tortoise, we found great diversity among reported estimates and methodologies in the available literature (Table 2-5). Sampling regime is often not reported in Desert Tortoise literature, and varies greatly by study when available. In most studies, an opportunistic or unstructured sampling regime was used (Woodbury and Hardy 1948; Burge 1977; O’Connor et al. 1994), as well as a sampling frequency similar to SR-A (Duda et al. 1999; Freilich et al. 2000) and SR-B (Barrett 1990). Rautenstrauch and Holt (1995) concluded that the MCP method was a
reliable estimator of a Desert Tortoise's home range if over 60 locations were observed. To our knowledge, aside from Rautenstrauch and Holt (1995) and our study, no other studies have reported the use of over 60 tortoise locations within a yearly activity period.

The validity of home range estimates is greatly affected by the choice of estimator, as well as the chosen sampling frequency. As shown in this analysis, sampling frequency has a large effect on home range estimates using the MCP. While solving the problems of statistical and conceptual implications, FK estimates are also greatly affected by sampling frequency, but to a lesser extent. In parsing data into sampling regimes that are representative of telemetry data from previous studies, we have shown that sampling frequency significantly influences home range area. Using both the MCP and FK estimates, these data demonstrate that an increased sampling frequency, such as SR-A, will give a more realistic representation of land requirements of the focal animal in a single year of study.

**FACTORS ASSOCIATED WITH HOME RANGE AREA**

A low sampling frequency in home range investigations may mask statistically relevant differences, such as those between sexes. Duda et al. (1999) recommended that a large number of locations are required for home range analysis to reduce variability observed between individuals. Results from our analyses show a highly significant difference between sexes when using both 100% MCP and 95% FK area estimates on this larger data set.

Studies of varying duration have attempted to demonstrate sex differences literature for *G. agassizii*. Three studies, with more than two complete years of location
data found that males had significantly larger MCP areas than females (Holt and Rautenstrauch 1996; Duda et al. 1999; Freilich et al. 2000), whereas another study of similar duration did not detect this difference (Barrett 1990). In studies of less than one year, male and female MCP areas were not found to be significantly different (Burge 1977; O’Connor et al. 1994). Interestingly, O’Connor et al. (1994) pooled data from their study plus two others (Burge 1977; Barrett 1990) and found that males used a significantly greater MCP area based on locations collected from June to October of a single year. These results suggest that previous studies were too short in duration and/or had low numbers of locations with a small number of tortoises to accurately test for sex differences in Desert Tortoises.

Few researchers have identified significant yearly or size related differences in home range area among Desert Tortoises. In the west Mojave, Duda et al. (1999) noted significant differences between years in a two-year study. However, this difference was attributed to vastly different precipitation patterns in each year, with tortoises using smaller areas in the drought year. Freilich et al. (2000) report wide ranging home range values in their four-year study, but did not specifically test for yearly differences. O’Connor et al. (1994) did not find a significant effect of body size on home range area in a population of tortoises in the eastern Mojave. This suggests that the effect of year and body size on home range of G. agassizii warrants further analysis.

HOME RANGE ESTIMATES ACROSS STUDIES

A number of studies have utilized the MCP method to estimate a tortoise’s home range in different portions of the Mojave Desert, including the northeastern (Burge 1977;
Barrett 1990), eastern (Turner et al. 1984; Berry 1986; O'Connor et al. 1994) and the western Mojave (Duda et al. 1999; Freilich et al. 2000) with varying results (Table 2-5). In the west Mojave at Joshua Tree National Park, Duda et al. (1999) found mean MCP home ranges of males to be 26 ha and females 9 ha, while Freilich et al. (2000) estimated a mean of 19 ha per year for males and 4 ha for females. Further north at the Marine Corps Air Ground Combat Center, Freilich et al. (2000) reported small home range estimates per each of two years for both males (mean = 8 and 3 ha) and females (mean = 7 and 1 ha). Our estimates using SR-A were larger (mean = 39 and 47 ha for males in 2004 and 2005; mean = 16 ha for females in both years) and included over twice as many tortoise locations (mean = 74.5 for both years) compared with these studies. The MCP estimates we obtained using SR-D were similar to other MCP estimates from the western Mojave Desert that used less intensive sampling regimes (Table 2-5).

To compensate for a low number of locations in past studies on the Desert Tortoise, correction factors were often applied to MCP estimate home range estimates (Burge 1977; Barrett 1990; O'Connor et al. 1994). In one study, these correction factors were found to overestimate home range size of the Desert Tortoise by up to 200% (Rautenstrauch and Holt 1995). In our study, the correction factor overestimated the MCP area by as much as 25.3-203.9% within each successive sampling regime; however, adjusted areas were on averaged roughly 20% greater than the MCP values using SR-O in each year (Table 2-3). Similarly, in a study of less than two active seasons, Barrett (1990) used JT factors on five males and nine females and observed a 56% increase in MCP areas for males and 48% for females (mean number of locations = 45). We do not recommend the JT correction factors in place of a comprehensive sampling regime, as
this "correction factor" tends to overestimate the MCP home range area for Desert Tortoises.

Compared with passed sampling regimes, our analyses suggests that the larger MCPs we observed were most likely a result of sampling methodology, though numerous other factors such as habitat quality, nutrient resources, differences in climate, population density, social interactions among individuals, and/or locations of nesting sites, may also be at play.

**EFFECTS OF NUMBER OF LOCATIONS**

The CV criterion is biased favoring tortoises having sufficient number of locations at less-intense sampling regimes (Table 2-4). In SR-C, for example, only two sampling intervals were available—15 to 20 locations. If a tortoise simply met the criterion at 20 locations, it was deemed to have attained the criterion without having to sustain it over additional sampling intervals. In contrast, the more-intense sampling regimes had to both meet and sustain a CV < 10%. Despite this bias, very few tortoises met the criterion within the SR-B and SR-C sampling regimes.

**EFFECTS OF LONG-RANGE MOVEMENTS**

Tortoises are generally known to conduct forays or long-distance movements at various times throughout the active season (Berry 1986; Boarman et al. 1996; Duda et al. 1999). Researchers speculate these movements may be used to aid in dispersal (Gibbons 1986), search for prospective mates, locate higher quality food or shelter (Boarman et al. 1996), find nesting or hibernating sites (Burge 1977; McRae et al. 1981), or identify areas
of limiting nutrients (Marlow and Tollestrop 1982). Home range estimates for the Desert Tortoise are often calculated using only localized activity locations, disregarding these long-range movements as they are difficult to explain and complex to operationally define (Boarman et al. 1996; Duda et al. 1999; Freilich et al. 2000).

Long-range movements are often excluded from home range MCP estimates of Desert Tortoises in the West Mojave. Both Duda et al. (1999) and Freilich et al. (2000) reported the use of a sampling regime analogous to SR-A, which should have resulted in a mean of 78 locations per year. However, Duda et al. (1999) reported a mean of 19-37 locations per tortoise in each year of the two-year study, and Freilich et al. (2000) reported a mean range of 13-50 locations per tortoise. The difference may be partly due to the fact that short-term forays (Duda et al. 1999) were excluded from analyses, resulting in a low mean number of locations per the cited sampling regime. Freilich et al. (2000) reported removing five forays comprised of 14 locations from four animals, resulting in MCP areas that were 55% smaller. Similarly, Duda et al. (1999) reported removing one foray from each of two individuals, with no comments on the effect on MCP estimates.

In our study, the exclusion of forays reduced mean MCP estimates for all tortoises by a greater degree (14%) than FK estimates (8%), whereas the exclusion of LDMs reduced both estimators by 3%. Compared to Freilich et al. (2000), the inclusion of forays in our study demonstrated less impact on home range estimates using the MCP method. Because our home range estimates were more than two times larger than previous studies, it is unlikely that the inclusion of forays and LDMs was the sole
explanation for the larger home range values in our study (Table 2-5; Duda et al. 1999; Freilich et al. 2000).

Long-distance movements are frequently observed in numerous species and may be important in recolonizing depopulated areas and extending the species' range (Stickel 1954). Thus, long-distance movements should be considered an important part of the ecology of the Desert Tortoise (Burge 1977; Berry 1986; Boarman et al. 1996) and should not be removed from home range analyses. Furthermore, in considering sampling frequency between our study versus Duda et al. (1999) and Freilich et al. (2000), results suggest that with increasing time between locations, movements will more likely meet the definition of a foray or LDM (Garton et al. 2001). If researchers recognize this effect and design tracking methods appropriately, such as collecting locations using a systematic and evenly-spaced sampling regime, this bias may be reduced.

**Management Implications**

Despite statistical constraints, the FK method used in combination with the MCP method, may best represent the total land use patterns of an animal when utilized on a large number of individuals with frequent locations. Using these home range estimators in conjunction will provide a comprehensive understanding of land use patterns, as the MCP represents the total amount of area potentially used by the animal and the FK identifies specific areas of intensive use. In addition, an intensive sampling methodology will allow the researcher to avoid statistical complications and provide a more accurate understanding of land use patterns. Comparisons of home range estimates between
studies may also be facilitated when using the same sampling regime and this range wide knowledge should aid recovery efforts of threatened species, such as the Desert Tortoise.

We agree with O'Connor et al. (1994) in recommending that home range calculations that permit multiple activity centers may be better suited to Desert Tortoise home range analysis than methods that only permit one activity center. Fixed kernel estimates are well suited to address the land use of tortoises in respect to their heavy use of localized burrows to meet life history requirements (see Chapter 3). Due to the fact that kernel estimates sometimes demonstrate disjointed home range areas, the MCP method may be used to complement the interpretation of home range when planning land management activities. Examination of both home range estimates in conjunction will provide information on how animals travel across the landscape. Both estimates give valuable information and should be identified as a priority in land use investigations for conservation decisions. This knowledge is also crucial in understanding the relationship between land use and home range connectivity as travel corridors for metapopulations.

Radio-telemetry projects often must compromise the allocation of precious resources between the number of locations and relative independence of those locations. A statistically relevant number of locations may be impossible to achieve within a given activity season for sufficient home range analysis (Powell 2000). An intensive and regularly-spaced sampling regime is the most pragmatic method to obtain presumably unbiased home range calculations using both the MCP and FK estimators.

Does the Desert Tortoise have an "exclusive" home range in the west Mojave Desert? Despite our intensive efforts, these results suggest that this population may exhibit a fluid-like home range. We have identified how much area tortoises require
(MCP), and to what extent they use them (FK) without a concrete, delineated area per tortoise. The Desert Tortoises in the west Mojave Desert may modify their land use over the course of a year, or between years, through evaluation of immediate characteristics such as social interactions involving courtship and combat, areas of limiting resources containing water, minerals, and/or forage, or cognitive knowledge of burrow systems (Berry 1986). These results by no means suggest that home range estimates should be discounted as a measure of life history requirements; rather they need to be well defined in using the appropriate estimator(s) with a proper sampling regime. Even crudely estimated home range areas can increase the understanding of an animal but should be interpreted with caution, as the animal itself presumably does not recognize the exact boundaries of its "true" home range (Powell 2000). Research into the joint space use by Desert Tortoises has not been investigated and may shed light on this phenomenon and should be investigated in more detail in the future.

Considering the above analyses, it is our recommendation that SR-A provides the most robust data in association with the MCP and FK analyses. We therefore recommend it be used for home range estimation for Desert Tortoises. Advancements in radio-telemetry, such as GPS transmitters, may be helpful in allowing researchers to collect home range for all individuals and across multiple studies using the same sampling frequency. In addition, standardizing the sampling methodology in home range estimates will alleviate some of the difficulty in using these estimates for complementary investigations of land use such as joint-space use, resource selection, and/or social structure.
Implications of this multi-faceted approach to examining the land use patterns of Desert Tortoises may greatly benefit the conservation of this important species. In a review of Testudinidae literature, Auffenberg and Weaver (1969) suggested that a thorough, operational definition of home range is lacking for this family. We found, in reviewing more current literature that no such definition has yet been defined, and it is hoped that in the meantime the results of this study will suffice. A biologically relevant definition of the home range of a tortoise and the best method for estimation needs to be determined and agreed upon within the Desert Tortoise research community.

Understanding these aspects of the requirements of the *G. agassizii* should be a priority considering that much of the habitat for this species is located on federal land, i.e., Bureau of Land Management, Department of Defense, and the National Park Service (U. S. Fish and Wildlife Service 1994b) administered by agencies with very different management goals. These organizations manage multi-use areas of land that are important to sustaining this species throughout its range, and continued conservation efforts may improve from an increased understanding of the Desert Tortoise landscape needs. Basing land management activities on underrepresented home range estimates may hinder the ability of tortoises to cope with changing environmental conditions, as well as to provide for the long-term sustainability of metapopulations. In light of recent interest in tortoise relocation as an effective management procedure (Karl 2003; Esque et al. 2005), increased knowledge of space use by tortoises will help to more effectively evaluate this complex process.
Figure 2-1. Mean (+ 1 SE) home range estimates for 20 male and 15 female Desert Tortoises in the west Mojave Desert, California in 2004 (A, C) and 2005 (B, D). The 100% minimum convex polygon (MCP) estimate (A, B) and the 95% fixed kernel (FK) estimates (C, D) are presented for the original sampling regime, SR-O (■), and the successive parsed sampling regimes: SR-A (□), SR-B (○), SR-C (▲), and SR-D (■).
Figure 2-2. Graphical display of 100% minimum convex polygon (MCP; dark lines) and 95% fixed kernel (FK) home range estimates (gray contours) using the original dataset for ten individual A) male and B) female Desert Tortoises at Fort Irwin National Training center in the west Mojave Desert, California in 2004. Map areas represent the same geographical position on the study site.
Table 2-1. Frequency of radio-telemetry locations of Desert Tortoises throughout the calendar year for the original and successively parsed sampling regimes used for the analysis of home range area in the Mojave Desert, California, 2004-2005.

<table>
<thead>
<tr>
<th></th>
<th>O</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
<td>2 x month</td>
<td>2 x month</td>
<td>2 x month</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>Feb</td>
<td>Varied</td>
<td>1 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>Mar</td>
<td>Varied</td>
<td>2 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>April</td>
<td>Varied</td>
<td>2 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>May</td>
<td>Varied</td>
<td>2 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>June</td>
<td>Varied</td>
<td>2 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>July</td>
<td>Varied</td>
<td>1 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>Aug</td>
<td>Varied</td>
<td>2 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>Sept</td>
<td>Varied</td>
<td>2 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>Oct</td>
<td>Varied</td>
<td>2 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>Nov</td>
<td>Varied</td>
<td>1 x week</td>
<td>1 x week</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
<tr>
<td>Dec</td>
<td>2 x month</td>
<td>2 x month</td>
<td>2 x month</td>
<td>2 x month</td>
<td>1 x month</td>
</tr>
</tbody>
</table>
Table 2-2. Number of radio-telemetry locations recorded for 35 Desert Tortoises in the original and successive parsed sampling regimes in the Mojave Desert, California, 2004-2005.

<table>
<thead>
<tr>
<th>Sampling Regime</th>
<th>O</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Possible</td>
<td>—</td>
<td>2730</td>
<td>1680</td>
<td>840</td>
<td>420</td>
</tr>
<tr>
<td>Observed 2004</td>
<td>3141</td>
<td>2492</td>
<td>1602</td>
<td>840</td>
<td>420</td>
</tr>
<tr>
<td>Observed 2005</td>
<td>3684</td>
<td>2726</td>
<td>1679</td>
<td>840</td>
<td>420</td>
</tr>
<tr>
<td>Possible Mean per Tortoise</td>
<td>—</td>
<td>78</td>
<td>48</td>
<td>24</td>
<td>12</td>
</tr>
<tr>
<td>Actual Mean Per Tortoise 2004</td>
<td>89</td>
<td>71</td>
<td>46</td>
<td>24</td>
<td>12</td>
</tr>
<tr>
<td>Actual Mean Per Tortoise 2005</td>
<td>105</td>
<td>78</td>
<td>48</td>
<td>24</td>
<td>12</td>
</tr>
</tbody>
</table>
Table 2-3. Mean (± 1 SE) 100% minimum convex polygon (MCP), adjusted MCP, and 95% fixed kernel (FK) estimates of a sample of 35 Desert Tortoise home range areas (ha) for the original data set (SR-O) and four parsed sampling regimes (SR-A through D) in the Mojave Desert, California, 2004-2005.

<table>
<thead>
<tr>
<th>Year</th>
<th>SR-O</th>
<th>SR-A</th>
<th>SR-B</th>
<th>SR-C</th>
<th>SR-D</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>MCP</td>
<td>Adjusted MCP</td>
<td>95% FK</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td>All</td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td></td>
<td>42.6 ± 1.5</td>
<td>15.8 ± 2.3</td>
<td>31.1 ± 1.9</td>
<td>50.3 ± 12.0</td>
<td>19.9 ± 2.9</td>
</tr>
<tr>
<td></td>
<td>39.4 ± 9.4</td>
<td>15.6 ± 2.3</td>
<td>29.2 ± 5.8</td>
<td>50.3 ± 12.0</td>
<td>19.9 ± 2.9</td>
</tr>
<tr>
<td></td>
<td>31.7 ± 6.9</td>
<td>12.5 ± 1.9</td>
<td>23.5 ± 4.3</td>
<td>47.0 ± 10.3</td>
<td>18.6 ± 2.9</td>
</tr>
<tr>
<td></td>
<td>21.9 ± 3.5</td>
<td>10.7 ± 1.9</td>
<td>17.1 ± 2.4</td>
<td>43.4 ± 6.9</td>
<td>21.1 ± 3.8</td>
</tr>
<tr>
<td></td>
<td>17.0 ± 3.5</td>
<td>7.5 ± 1.8</td>
<td>13.0 ± 2.3</td>
<td>51.9 ± 10.7</td>
<td>22.7 ± 5.5</td>
</tr>
</tbody>
</table>

2005 | MCP    | Adjusted MCP | 95% FK |        |        |
|      | Male   | Female | All    | Male   | Female | All    | Male   | Female | All    |
|      | 48.8 ± 7.7 | 16.6 ± 2.3 | 34.9 ± 5.5 | 58.5 ± 9.6 | 20.2 ± 2.8 | 42.1 ± 6.4 | 31.7 ± 3.9 | 11.4 ± 2.0 | 23.0 ± 2.9 |
|      | 47.4 ± 7.8 | 16.4 ± 2.3 | 34.1 ± 5.2 | 58.5 ± 9.6 | 20.2 ± 2.8 | 42.1 ± 6.4 | 35.8 ± 4.5 | 13.2 ± 2.2 | 26.1 ± 3.3 |
|      | 39.5 ± 6.9 | 12.6 ± 1.7 | 28.0 ± 4.6 | 57.8 ± 10.1 | 18.5 ± 2.6 | 41.0 ± 6.7 | 35.2 ± 4.7 | 13.3 ± 2.2 | 25.6 ± 3.4 |
|      | 31.8 ± 7.0 | 8.4 ± 1.3 | 21.8 ± 4.5 | 62.7 ± 12.4 | 16.5 ± 2.2 | 42.9 ± 7.9 | 39.3 ± 6.1 | 13.8 ± 2.3 | 28.4 ± 4.2 |
|      | 22.7 ± 3.7 | 5.9 ± 1.2 | 15.5 ± 2.6 | 68.7 ± 11.2 | 18.0 ± 3.6 | 47.2 ± 7.8 | 46.3 ± 6.3 | 15.3 ± 3.1 | 33.0 ± 4.6 |

a Standard correction factors acquired from Jennrich and Turner (1969) when N < 25; from Barrett (1990) when N > 25 using the formula: adjusted MCP = raw MCP + 0.257 ln (N) - 0.31

b N = 34 (see Methods)
Table 2-4. Percentage of individual Desert Tortoise minimum convex polygon (MCP) estimates from a bootstrap function reaching and attaining a confidence of variation (CV) value ≤ 10% per sampling regime in the Mojave Desert, California, 2004-2005.

<table>
<thead>
<tr>
<th>Year</th>
<th>Original</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>82.9</td>
<td>42.9</td>
<td>28.6</td>
<td>2.9</td>
</tr>
<tr>
<td>2005</td>
<td>51.4</td>
<td>31.4</td>
<td>20.0</td>
<td>5.7</td>
</tr>
</tbody>
</table>
Table 2-5. Minimum convex polygon (MCP) estimates (ha) and variable sampling methodology from current literature on Mojave Desert Tortoises 1948-present.

<table>
<thead>
<tr>
<th>100% MCP Home Rangea</th>
<th>Number of Tortoises</th>
<th>Mean Number of Locations</th>
<th>Duration</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>100% MCP Home Rangea</td>
<td>Number of Tortoises</td>
<td>Mean Number of Locations</td>
<td>Duration</td>
<td>Location</td>
<td>Source</td>
</tr>
<tr>
<td>Male</td>
<td>Female</td>
<td>All (Range)</td>
<td>Male</td>
<td>Female</td>
<td>All</td>
</tr>
<tr>
<td>26</td>
<td>19</td>
<td>23 (11-38)b</td>
<td>3</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>23</td>
<td>11</td>
<td>(1-59)</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>22 (3-89)c</td>
<td>17</td>
<td>38</td>
<td>55</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>19 (2-73)</td>
<td>25</td>
<td>52</td>
<td>77</td>
</tr>
<tr>
<td>53</td>
<td>21</td>
<td>(8-77)</td>
<td>8</td>
<td>7</td>
<td>15</td>
</tr>
<tr>
<td>16</td>
<td>11</td>
<td>13 (2-34)</td>
<td>5</td>
<td>9</td>
<td>14</td>
</tr>
<tr>
<td>21</td>
<td>9</td>
<td>15 (6-46)</td>
<td>8</td>
<td>7</td>
<td>15</td>
</tr>
<tr>
<td>53</td>
<td>18</td>
<td>33</td>
<td>16</td>
<td>22</td>
<td>38</td>
</tr>
<tr>
<td>26</td>
<td>9</td>
<td>(3-44)</td>
<td>4</td>
<td>5</td>
<td>9</td>
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<td>2</td>
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<td>9</td>
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<tr>
<td>8</td>
<td>7</td>
<td>(1-17)</td>
<td>13</td>
<td>16</td>
<td>29</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>(0-14)</td>
<td>13</td>
<td>16</td>
<td>29</td>
</tr>
<tr>
<td>13</td>
<td>4</td>
<td>(2-24)</td>
<td>5</td>
<td>3</td>
<td>8</td>
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<tr>
<td>32</td>
<td>7</td>
<td>(3-45)</td>
<td>4</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>(0-12)</td>
<td>4</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>43</td>
<td>16</td>
<td>31(6-236)</td>
<td>20</td>
<td>15</td>
<td>35</td>
</tr>
<tr>
<td>49</td>
<td>17</td>
<td>35 (5-177)</td>
<td>20</td>
<td>15</td>
<td>35</td>
</tr>
</tbody>
</table>

aDuda et al. 1999 and Freilich et al. 2000 excluded “forays” from home range analysis; resultant MCPs are not 100%, see text; b Data for some tortoises combined from two years to increase number of locations; values represent 95% MCP areas; c Only reported Jennrich-Turner adjusted home range values; mean values per four size classes; d Relocated tortoises; e Excluded locations from January and February; f Joshua Tree National Park; g Marine Corp. Air Ground Combat Center; h National Training Center at Fort Irwin
CHAPTER 3

HOME RANGE, SPATIAL OVERLAP, AND BURROW USE OF THE DESERT TORTOISE IN THE WEST MOJAVE DESERT

Abstract

Understanding the space use patterns of a population may provide crucial information regarding land management decisions. The space use patterns of organisms in extreme environments, such as the Desert Tortoise, are likely limited by one or more variables. Herein we provide a comprehensive analysis of factors affecting the space use of male and female tortoises, including physical, social, and environmental variables. In looking at spatial overlap our objectives were to determine how body size, as well as multiple parameters of burrow use, influence home range estimates of Desert Tortoises. Results show males were significantly larger than females, but this difference in size was independent of space use and burrow parameters. Home range estimates (100% MCP) were significantly greater than core areas (50% MCP), suggesting Desert Tortoises may be forced to limit their activity to a small portion of land. Males and females demonstrated very different patterns of space use in both home range and core area estimates. Females exhibited a strong male bias in overlap of both MCP estimates and burrow parameters. However, males overlapped and shared burrows with a similar number of tortoises of either sex. A lack of home range exclusivity in this population
suggests a lack of territoriality in this population, although this warrants further analysis. Burrow use played a predominant role in space use, suggesting that social factors are not the primary determinants of spatial patterns in the Desert Tortoise.

**Introduction**

Burt (1943:351) introduced the foundation for the concept of home range as “that area traversed by the individual in its normal activities such as food-gathering, mating, and caring for young.” This definition is heavily used in ecological studies across species to gain insight into the biological needs of an organism (Kernohan et al. 2001). Through knowledge of the location of resources within a home range, an animal may enhance its fitness by accessing limiting resources and avoiding or escaping predation (Peters 1978). Establishing a home range is thought to be a result of frequent travel along familiar routes (Stamps and Krishnan 1995).

Since Burt proposed the original concept of home range, ecologists have been interested in determining the factors that predict home range size. The benefits of maintaining a specific home range must outweigh the costs, in terms of resource acquisition, energy expenditure, and predator avoidance (Powell 2000). Site fidelity, or the tendency to return to a previously occupied location, is often used to designate the existence of a home range. In addition, fidelity by individuals to an area over the course of multiple years provides strong evidence of both stable resources and social systems (Powell 2000). Animals tend to focus space use around areas containing one or more limiting resources, most commonly food (e.g., Trivers 1976) and reproductive needs, such as nesting sites or access to reproductive females (e.g., Stamps 1983). Thus,
energetic needs are viewed as positively correlated with home range area (McNab 1963; Jetz et al. 2004; Borger et al. 2006), with demonstrated inter-specific variation in home range area (e.g., Schoener 1968; Rose 1982; Brown et al. 1993).

A number of variables may influence home range size. For example, diet presumably leads to space use differences between carnivores and herbivores (McNab 1963; Schoener 1968; Swihart et al. 1988), frugivorous and folivorous primates (Milton and May 1976), and browsing and grazing ungulates (Mysterud et al. 2001). Sex, age, activity pattern, habitat quality, season, and weather can all influence home range area (e.g., Stickel 1968; Mysterud et al. 2001), as can population density (Alberts 1993). Among reptiles, body size (Perry and Garland Jr. 2002), sex (Goodman et al. 2005; Roth 2005), and reproductive status (Graves and Duvall 1993; Litzgus and Mousseau 2004; Waldron et al. 2006) are important influences in determining home range size. Social interactions can also influence space use (Turchin 1998; Stamps and Krishnan 2001; Morales et al. 2004). Recent studies suggest that, aside from physical and phylogenetic factors, animal space use may be best understood through social factors, namely interactions between neighbors (Doncaster 1990; Sih and Mateo 2001; Stamps and Krishnan 2001).

Home range overlap may encompass a static interaction, as in the spatial overlap of two home ranges, or a dynamic interaction, as in the interdependent movements of animals whose home range’s overlap (Doncaster 1990). Dynamic interactions are rarely studied, as they are exceedingly difficult to quantify (Powell 2000). However, by comparing spatial overlap among individuals, static interactions can be informative. Spatial overlap can be examined to assess responses to environmental change, to assess
the degree of interaction among individuals within a population, or to infer territoriality when behaviors cannot be observed adequately (Powell 2000).

A more complete understanding of land use of a species can be gained by investigating different scales of land use. Analyses should also consider the portion of the area most important to the animal, such as the core area (Burt 1943; Kaufmann 1962; Samuel et al. 1985). Limiting resources are often patchy in a given environment, leading animals to focus land use around core areas containing precious resources (Powell 2000). Thus, interactions between individuals may be most important within core areas, and undoubtedly influence the spacing patterns of individuals (Borger et al. 2006).

The Desert Tortoise (*Gopherus agassizii*) represents a suitable model for exploring the spacing patterns of individuals at different levels of scale. The home range of this species is often described as a network of burrows separated by travel corridors of varying dimensions (O’Connor et al. 1994; Duda et al. 1999, 2002). Desert Tortoises depend heavily on burrows to meet various life history requirements, including thermoregulation, predator avoidance, and reproductive opportunities (Burge 1977; Bulova 1994; Duda et al. 1999). Due to a narrow temperature range of activity, tortoises are thought to spend upwards of 95% of their lives inactive either in burrows or shallow pallets (Nagy and Medica 1986; Duda et al. 2002). Burrows are often the only areas where males and females are located together, as males generally seek out females that remain within the burrow (Woodbury and Hardy 1948; Berry 1986). Burrows are known to be a limiting factor in the movements and space use of both the Gopher Tortoise (*Gopherus polyphemus*; McRae et al. 1981) and the Bolson Tortoise (*Gopherus flavomarginatus*; Aguirre et al. 1984). Thus, burrows presumably comprise core areas of
activity within a home range and their location likely influences the spatial distribution of individual tortoises.

A comprehensive model of the social structure of Desert Tortoises remains unclear, though a male-based dominance hierarchy is often cited from observations of antagonistic encounters and territorial displays (Berry 1986; Duda et al. 2002). In freshwater turtles, social behavior has been inferred from observations of home range overlap, agonistic encounters, stability of home ranges between years, and movement patterns (reviewed in Galbraith et al. 1987). Few studies have separately addressed these aspects of space use in a social context for *G. agassizii*, leaving a holistic understanding of the social structure of this species undefined. To our knowledge, only one previous study quantified yearly overlap of home ranges of Desert Tortoises (Holt and Rutenstrauch 1996), though two studies analyzed overlap in seasonal MCP areas (Burge 1977; O’Connor et al. 1994). The relationship between burrow use and space overlap has not been examined.

Previously published home range estimates for *G. agassizii* are wide ranging (reviewed in Chapter 2) and suggest more research is needed to understand space use patterns of this species. Our objective was to evaluate the relationships between home range area, core area, spatial overlap, and burrow use of Desert Tortoises in the west Mojave Desert. Understanding the factors affecting spatial ecology is important for land managers to consider in planning large-scale land conservation measures such as translocation projects (Karl 2003; Esque et al. 2005), and to protect and provide for the recovery of this species.
Methods

STUDY SITE

The study was conducted in the southwest corner of the National Training Center at Fort Irwin, California (35°14'63"N, -116°75'17"W) on land federally designated as Desert Tortoise critical habitat (59 FR 5820-5866, U. S. Fish and Wildlife Service 1994a,b). The study site was irregularly shaped, approximately 3.74 km², and comprised typical Mojave Desert vegetation: Creosote—White Bursage scrub (*Larrea tridentata—Ambrosia dumosa*; Turner 1982). This area of the military base is protected from public use, is located far from any regularly traveled roads, and is thus relatively undisturbed (Walde et al. 2007). Both years of the study, 2004 and 2005, experienced record high rainfall for the west Mojave Desert (National Climatic Data Center 2006).

RADIO-TRACKING

The study was initiated in 2003, when adult Desert Tortoises were captured during extensive surveys within the study boundary. Adult age was indicated by a midline carapace length (MCL) > 180 mm. Low-duty, cycle-pulsed transmitters (Advanced Telemetry Systems, Isanti, Minnesota; Holohil Systems Ltd., Carp, Ontario, Canada) were mounted directly onto the carapace of each tortoise, as is commonly done for this species (Bulova 1994; O’Connor et al. 1994; Boarman et al. 1998). Transmitters weighed < 5% of the tortoise’s mass and had an expected battery life of 18-36 months. Transmitter mounting varied by sex to ensure there was no constraint in tortoise movement, particularly during copulation attempts.
Portable radio receivers (Yaesu VR-500, Vertex Standard Inc., Cypress, California) and three-element hand-held directional Yagi antennas (Wildlife Materials International, Inc., Murphysboro, Illinois) were used to locate transmittered tortoises. The exact geographic location (universal transverse mercator, UTM), the assigned unique burrow number, and the identities of any nearby conspecifics were recorded during each tracking event. Geographic locations were recorded using a global positioning unit (Garmin 12 Personal Navigator Unit, Garmin International, Olathe, Kansas) with an estimated probable error between 3-6 m. Locations collected at the same burrow were standardized so as to limit possible error in home range and overlap calculations. Geographic locations were imported into ArcView 3.3 (Environmental Services Research Institute, Redlands, California) for mapping utilization functions.

As part of a comprehensive study on the behavior and ecology of the Desert Tortoise, transmittered animals were located using a systematic sampling scheme from January 2004-December 2005. We collected locations following a systematic schedule to standardize the amount of time between tracking events (i.e., sampling regime SR-A; see Methods, Chapter 2). Locations were collected at staggered times throughout the day. During the active season (March-June, August-October), locations were collected twice per week, with locations collected once per week during the less active periods (February, July, and November). During the winter period of decreased activity (December-January), locations were limited to twice per month.
HOME RANGE, CORE AREA, AND OVERLAP CALCULATIONS

The minimum convex polygon (MCP) is thought to be ideal for home range estimates of the Desert Tortoise (O’Connor et al. 1994; Rautenstrauch and Holt 1995), despite implications of serial autocorrelation and problems in sampling methodology (White and Garrott 1990; see also Chapter 2). This method of home range estimation is ideal for animals such as the Desert Tortoise because they are relatively slow moving, they generally do not travel long-distances, and use the same areas, such as burrows, many times during a season (Row and Blouin-Demers 2006).

We calculated both 100% (home range) and 50% (core area) MCP areas for each tortoise during 2004 and 2005 using the Animal Movement Extension for ArcView (AME; Hooge et al. 1999). We designated the core area as the 50% MCP resulting from the algorhythmic removal of half of the locations furthest from the geographic center (Samuel et al. 1985; White and Garrott 1990). We used MCP instead of kernel estimates for home range overlap assessments because kernel estimates are known to buffer actual data points, inherently inflating overlap estimates (Millspaugh et al. 2006). Moreover, multiple centers of activity are often combined by the fixed kernel approach, thereby removing area between the centers of activity and further obscuring areas of overlap (Kernohan et al. 2001).

We calculated overlap in MCP areas using AME in conjunction with the XTools application extension for ArcView (DeLaune 2003). We used two measures to calculate overlap between neighboring tortoises. First, we counted the number of overlapping males and females that shared a portion of an individual’s home range or core area. Individual tortoises were counted as overlapping in home range where any portion of
each MCP covered the same area. Second, using the polygon shapes of the home range and core areas separately, the percentage of MCP overlap between two given individuals was calculated. This was done with XTools by overlaying the two polygons and determining the percentage of an individual’s home range that was shared with another tortoise (Kemohan et al. 2001; Bernstein et al. 2006).

We also quantified site fidelity, the percentage of overlap between years of an individual’s MCP area, using a similar method with AME and XTools. Each polygon MCP area for the 100% and 50% MCP was overlaid to determine the shared area of overlap between years. We report site fidelity here as the proportion of the 2004 MCP that was contained in the MCP from 2005; in other words, overlap was relative to the 2004 MCP area.

BURROW USE

We examined numerous aspects of burrow use by tortoises to better understand its relationship to home range estimates and spatial overlap. We quantified burrow use for each tortoise at five levels, including: 1) number of burrows used each year; 2) burrow fidelity, i.e., the number of burrows used during both years of study; 3) number of unique burrows, i.e., burrows used only by a single individual; 4) number of shared burrows, defined as non-simultaneous use of the same burrow by more than one individual; and 5) frequency of cohabitation, defined as two or more tortoises simultaneously occupying the same burrow.
DATA ANALYSES

For statistical analyses, we relied primarily on general linear models, specifically analyses of variance (ANOVA) and analyses of covariance (ANCOVA). Parametric assumptions were met in most cases, although some variables had to be log_{10}- or rank-transformed. One dependent variable, log_{10}-transformed core area, failed to meet parametric assumptions; however, we decided to report the ANCOVA results because supplemental non-parametric tests, with alpha levels adjusted for multiple tests, confirmed that results from the general linear models involving this variable were robust.

For all ANOVA and ANCOVA models, we began with an omnibus model that incorporated all relevant variables, including body size as a covariate. Because body size consistently showed no correspondence with home range estimates (Chapter 2), overlap, or burrow use, we omitted it from all final models. We calculated the effect size of independent variables and interactions using partial η^2 values (Mertler and Vannatta 2004). When the partial η^2 values for main effects and interactions summed to >1.0, we adjusted these by dividing each partial η^2 by the sum of all partial η^2 values.

In addition to the general linear models, we used Pearson correlation analyses when parametric assumptions were met, and either independent t-tests or nonparametric Mann-Whitney U tests for pairwise comparisons. We performed all statistical analyses using SPSS v14.0 (2006, Statistical Package for the Social Sciences, Inc., Chicago, Illinois). The critical alpha level was set for all analyses at 0.05. All means are reported as mean ± 1 SE.
Results

**RADIO-TRACKING**

Initially, we attached radio transmitters to 26 male and 15 female adult Desert Tortoises across the study site. We removed a total of seven adult tortoises from the following analyses for various reasons, including natural death (N = 3), long-term transmitter failure resulting in a lack of a sufficient number of locations as per the study objectives (N = 2), and movements followed by home range re-establishment to an area far outside of the designated study site boundary (N = 2). Thus, the resultant sample size for the following analyses is limited to 20 male and 14 female Desert Tortoises (N = 34). Although males were significantly larger than females based on an independent samples t-test ($t = 3.22, P = 0.003$; Table 3-1), body size demonstrated no effect in any of the statistical analyses (see below; Chapter 2).

We conducted several analyses to evaluate possible bias associated with the number of locations and body size. A $2 \times 2$ mixed ANOVA using year (within-subjects) and sex (between-subjects) as independent variables revealed that the mean number of locations per tortoise in 2004 (2,426 total locations; $71.4 \pm 0.4$ per tortoise) was significantly less than in 2005 (2,645 locations; $77.8 \pm 0.0$ per tortoise; $F_{1,32} = 231.98, P < 0.001$, partial $\eta^2 = 0.88$; Table 3-1); in the second year, we adhered more closely to the sampling regime. The number of locations did not vary by sex ($F_{1,32} = 0.50, P = 0.48$, partial $\eta^2 = 0.02$), nor was there a significant interaction between year and sex ($F_{1,32} = 0.47, P = 0.50$, partial $\eta^2 = 0.02$).
HOME RANGE AND CORE AREA ESTIMATES

We used a $2 \times 2 \times 2$ mixed ANOVA to identify the variables influencing home range estimates. This model included the MCP estimate ($\log_{10}$-transformed) as the dependent variable and three independent variables: estimator (100% and 50% MCP, within-subjects), year (within-subjects), and sex (between-subjects).

Each of the three independent variables demonstrated a significant effect on the MCP estimate (Table 3-2; Fig. 3-1). Home range estimates were significantly larger than core area estimates ($F_{1,32} = 407.35, P < 0.001$, adj. partial $\eta^2 = 0.52$). Both MCP estimates for all tortoises were on average 20% and 24% larger in 2005 than in 2004 respectively ($F_{1,32} = 6.72, P = 0.014$, adj. partial $\eta^2 = 0.10$). Male home range and core area estimates were on average 65% and 73% larger than females, respectively ($F_{1,32} = 35.67, P < 0.001$, adj. partial $\eta^2 = 0.29$). There were no interactions among these three variables, indicating that both MCP estimates were similarly affected by year and sex. Core areas represented a small fraction of the total home range area. Male core areas represented 13.7% of the home range area in both years, whereas female core areas represented only 9.4% of the home range in 2004 and 11.2% in 2005. Because of the importance of year and sex to analyses of spatial use, we included these variables in the following analyses of overlap and burrow use.

Pearson correlation analyses were conducted to determine whether home range and core area estimates ($\log_{10}$-transformed) were positively correlated with each other in each of the two years. Indeed, there was a positive correlation when all tortoises were pooled (2004: $r^2 = 0.49, P < 0.001$; 2005: $r^2 = 0.55, P < 0.001$). The correlations, though positive in each case, were not significant when males (2004: $r^2 = 0.06, P = 0.29$; 2005: $r^2$
Similar analyses confirmed that both the home range and core area estimates \((\log_{10}\text{-transformed})\) from individual tortoises in 2004 were positively correlated with the 2005 estimates. In other words, tortoises having relatively small or large MCP estimates in 2004 had correspondingly small or large estimates in 2005. This was evident when all tortoises were pooled (home range: \(r^2 = 0.79, P < 0.001\); core area: \(r^2 = 0.59, P < 0.001\)) and when males and females were considered separately \((r^2 = 0.22-0.85; \text{all } P \leq 0.037)\). Thus, when including home range or core area as a cofactor in subsequent models, we used the 2-year mean.

**Overlap Between Years (Site Fidelity)**

We examined home range overlap between 2004 and 2005 as a measure of site fidelity using a \(2 \times 2\) mixed ANOVA model. We used percent overlap between years as the dependent measure, with estimator (rank-transformed overlap of home range and core areas, a within-subjects factor) and sex (between-subjects factor) as the independent variables. Site fidelity differed significantly for the two estimators \((F_{1,32} = 11.71, P = 0.002, \text{partial } \eta^2 = 0.27; \text{Table 3-2})\), with a two-fold or greater percentage of overlap in home ranges compared to core areas. There was no difference between the sexes \((F_{1,32} = 0.15, P = 0.70, \text{partial } \eta^2 = 0.01)\), nor an interaction between estimator and sex \((F_{1,32} = 1.75, P = 0.20, \text{partial } \eta^2 = 0.05)\).
OVERLAP OF INDIVIDUAL HOME RANGES

We used two ANCOVA models to examine factors associated with home range overlap. The first model treated number of overlapping individuals as the dependent variable, whereas the second used percent of home range overlap. Each model included three independent variables: year (within-subjects factor), sex of overlapping tortoise (within-subjects factor), and sex of individual (between-subjects factor). The two-year mean home range (logio-transformed) was used as the covariate.

There was a significant effect of year on the number of overlapping individuals, with fewer overlapping individuals in 2004 than in 2005 ($F_{1,31} = 6.70, \ P = 0.015$, partial $\eta^2 = 0.18$; Table 3-2). Males and females overlapped with a similar number of individuals ($F_{1,31} = 0.08, \ P = 0.784$, partial $\eta^2 = 0.00$), whereas tortoises with larger home ranges overlapped with significantly more individuals each year ($F_{1,31} = 4.34, \ P = 0.046$, partial $\eta^2 = 0.12$). The significant interaction between year and home range ($F_{1,31} = 11.91, \ P = 0.002$, partial $\eta^2 = 0.28$) indicated that home range had a larger effect on overlap in 2005. In addition, the significant interaction between sex of tortoise and sex of overlapping individuals ($F_{1,31} = 4.40, \ P = 0.044$, partial $\eta^2 = 0.12$) resulted from female home ranges overlapping with more males than females, whereas males overlapped with a similar number of tortoises of either sex (Table 3-2).

The percentage of home range overlap between individuals (Table 3-2; Fig 3-2) was similar for both sexes ($F_{1,31} = 0.66, \ P = 0.42$, partial $\eta^2 = 0.02$) and did not differ between years ($F_{1,31} = 2.10, \ P = 0.16$, partial $\eta^2 = 0.06$). However, percent overlap was significantly affected by sex of overlapping tortoise ($F_{1,31} = 7.07, \ P = 0.012$, partial $\eta^2 = 0.19$), with tortoises of both sexes overlapping to a greater extent with males compared to
females (Fig. 3-2). Also, tortoises with larger home ranges demonstrated a higher percentage of overlap with adjacent tortoises ($F_{1,31} = 8.69, P = 0.006, \text{partial } \eta^2 = 0.22$). There were no significant interactions among the variables in this model.

**OVERLAP OF INDIVIDUAL CORE AREAS**

We used the same two ANCOVA models described above for home range overlap, except that the dependent variables applied to core area overlap and the two-year mean core area ($\log_{10}$-transformed) was the covariate. In the first model for number of overlapping individuals (Table 3-2), a significant interaction was observed between sex of the individual and sex of overlapping tortoise ($F_{1,31} = 8.48, P = 0.007, \text{partial } \eta^2 = 0.22$). The core areas for males overlapped with a similar number of tortoises of either sex, whereas females demonstrated a male bias in core area overlap. No female core areas overlapped in 2004, whereas one pair overlapped in 2005. The number of overlapping individuals was similar between years ($F_{1,31} = 0.25, P = 0.620, \text{partial } \eta^2 = 0.01$) and independent of core area ($F_{1,31} = 2.75, P = 0.107, \text{partial } \eta^2 = 0.08$). No other interactions or main effects were significant.

For the percentage of core area overlap (Table 3-2; Fig 3-2), we observed a three-way interaction between sex of the individual, sex of overlapping tortoise, and year ($F_{1,31} = 9.13, P = 0.005, \text{adj. partial } \eta^2 = 0.19$). This interaction resulted in part from three two-way interactions. As with the first model, sex of the individual and sex of overlapping tortoise affected core area overlap ($F_{1,31} = 5.38, P = 0.027, \text{adj. partial } \eta^2 = 0.12$), with females again demonstrating a significant male bias in percentage of core area overlap with males. The interaction between year and sex of the individual ($F_{1,31} = 5.91, P = \ldots$)
0.021, adj. partial $\eta^2 = 0.13$) confirmed that male overlap was similar for both years, whereas females overlapped with more individuals in 2005 compared to 2004. The interaction between year and core area ($F_{1,31} = 5.67, P = 0.024$, adj. partial $\eta^2 = 0.13$) resulted from core area estimates being larger in 2005 than in 2004.

**Burrow Use and Fidelity**

Burrow occupation was clearly important to tortoises (Table 3-1). The majority of tortoises were found at or within 1 m of a burrow in 2004 (94.6% of $N = 2,426$ locations) and 2005 (96.2% of $N = 2,645$ locations). The total number of burrows used by all tortoises was similar for the two years, with 412 recorded in 2004 and 418 in 2005. The majority of burrows were used only by a single tortoise, though a large number of burrows were used by multiple tortoises (see Unique Burrow Use below). All tortoises used one or more of the same burrows in each of the two years (range = 1-10). Roughly one-third of burrows used by individuals in 2004 were used again in 2005 (Table 3-1). Relative burrow fidelity, the number of burrows used in both years divided by the mean number of burrows used in each year, was similar for both sexes (males: $34.3 \pm 5.5$, females: $33.8 \pm 3.6$; Mann-Whitney $U = 95.0$, asymptotic $P = 0.115$).

**Burrow Use and Home Range Estimates**

We used a mixed ANCOVA model to examine how the mean number of burrows used per year varied with year (within-subjects), sex of the individual (between-subjects), and home range area ($\log_{10}$-transformed mean 100% MCP over both years as the covariate). The number of burrows used (Table 3-1) was independent of home range size.
(F_{1,31} = 0.80, P = 0.38, partial \eta^2 = 0.03) and was similar for the two years (F_{1,31} = 0.52, P = 0.478, partial \eta^2 = 0.02). However, differential burrow use was observed between the sexes (F_{1,31} = 5.26, P = 0.029, partial \eta^2 = 0.15), with males utilizing a significantly greater number of burrows per year than females. No significant interactions existed among these variables.

To determine whether number of overlapping individuals influenced burrow use, we added both number of overlapping males and number of overlapping females as covariates to the preceding model. We again found just one significant relationship, the difference between the sexes (F_{1,29} = 6.46, P = 0.017, partial \eta^2 = 0.18). We obtained similar results when using percent home range overlap of males and of females instead of number of overlapping individuals as covariates (for sex: F_{1,29} = 6.49, P = 0.016, partial \eta^2 = 0.18). Thus, in models including 100% MCP, the number of burrows used depended on sex but otherwise was independent of home range size, year, number of overlapping tortoises, and percent of home range overlap with other individuals.

**Burrow Use and Core Area Estimates**

We used another mixed ANCOVA model to examine how the mean number of burrows used for the season varied by year (within-subjects), sex of the individual (between-subjects), and core area (log_{10}-transformed mean core area over both years as the covariate). We obtained very different results when using core area, compared with home range as a covariate (preceding section). There was no difference between years (F_{1,31} = 0.22, P = 0.646, partial \eta^2 = 0.01) and sexes (F_{1,32} = 1.63, P = 0.211, partial \eta^2 = 0.05), but there was a significant positive association between number of burrows used
and core area ($F_{1,31} = 6.64, P = 0.015, \text{partial } \eta^2 = 0.18$). In two additional models, core area was again the only significant main effect when we added either number of overlapping males and females as covariates (core area: $F_{1,29} = 4.51, P = 0.040, \text{partial } \eta^2 = 0.14$) or the percentage of overlap by males and females as covariates (core area: $F_{1,29} = 6.25, P = 0.018, \text{partial } \eta^2 = 0.18$). Thus, in contrast to models involving home range area, these analyses suggest a close relationship between burrow use and core area that is independent of sex, year, and overlap with other tortoises.

**Unique Burrow Use**

More than three-quarters of burrows used each year were only utilized by a single tortoise (2004: 77.6% of 412 total burrows; 2005: 78.5% of 418 total burrows). A $2 \times 2$ (year $\times$ sex) ANOVA for number of unique burrows used per year per individual (Table 3-1) revealed that males and females used a similar number of unique burrows ($F_{1,32} = 3.61, P = 0.066, \text{partial } \eta^2 = 0.10$). The proportion of unique burrow use per year relative to burrow use over both years was similar for males (2004: 71.4% total burrows; 2005: 67.4% of total burrows) and females (2004: 67.8% of total burrows; 2005: 61.2% total burrows). There was no difference between years ($F_{1,32} = 2.75, P = 0.107, \text{partial } \eta^2 = 0.08$) and no interaction between year and sex ($F_{1,32} = 0.13, P = 0.720, \text{partial } \eta^2 = 0.004$).

Using the same model with the percentage of total burrow use represented by unique burrows, we observed similar results for each main effect (sex: $F_{1,32} = 0.11, P = 0.743, \text{partial } \eta^2 = 0.003$; year: $F_{1,32} = 3.95, P = 0.056, \text{partial } \eta^2 = 0.11$) and the interaction (year $\times$ sex: $F_{1,32} = 1.56, P = 0.220, \text{partial } \eta^2 = 0.05$).
SHARED BURROW USE

Due to home range overlap, each tortoise used burrows that were occupied at some point in time (not simultaneously; see next section) by another tortoise. To examine selectivity in shared burrow use, we applied a $2 \times 2 \times 2$ (year $\times$ sex $\times$ sex of other burrow user) ANOVA to the number of shared burrows per tortoise.

We observed a three-way interaction between the variables year, sex, and sex of other burrow user ($F_{1,32} = 4.63$, $P = 0.039$, adj. partial $\eta^2 = 0.13$). This resulted in part from a significant two-way interaction and two significant main effects. The two-way interaction between sex and sex of other burrow user ($F_{1,32} = 920.65$, $P < 0.001$, adj. partial $\eta^2 = 0.43$) indicated that males more often shared burrows used by other males, whereas females more often shared burrows used by other females (Fig. 3-3; Table 3-3). The main effect of year ($F_{1,32} = 20.68$, $P < 0.001$, adj. partial $\eta^2 = 0.18$) indicated a greater frequency of shared burrow use in 2005 than 2004. The main effect of sex of other burrow user ($F_{1,32} = 54.95$, $P < 0.001$, partial $\eta^2 = 0.28$) resulted from a greater number of males sharing burrows than females.

BURROW COHABITATION

Tortoises were occasionally found cohabitating the same burrow. To examine selectivity in cohabitation, we examined the number of cohabited burrows using a $2 \times 2 \times 2$ (year $\times$ sex $\times$ sex of cohabitant) ANOVA. Parametric assumptions were not met in this model, but the results were highly robust. In additional models, we added one of three covariates: two-year mean home range, core area, or number of burrows to examine how cohabitation might be affected by other measures of space and burrow use.
The main effect of year was not significant ($F_{1,32} = 0.06$, $P = 0.811$, adj. partial $\eta^2 < 0.01$); however, there was a significant interaction between sex and sex of the cohabitant ($F_{1,33} = 29.51$, $P < 0.001$, adj. partial $\eta^2 = 0.46$; Fig.3-4; Table 3-3). Males were equally likely to cohabit with individuals of either sex, whereas females demonstrated a significant male bias in cohabitation. None of the three covariates were significant when added independently to the model, and in each case the sex $\times$ sex of cohabitant interaction remained significant.

**FACTORS AFFECTING HOME RANGE AND CORE AREAS**

The above analyses suggested that home range area and core area are subject to different influences. Sex appeared to be a primary determinant for both measures of space use. In addition, the number of overlapping individuals, as a social variable, seemed independent of both area measures. However, the number of burrows used, a behavioral variable, appeared to be closely associated only with core area use. To confirm the relative importance of these factors to each MCP estimator, we used two more ANCOVA models, one for home range area ($\log_{10}$-transformed, two-year mean home range) and one for core area ($\log_{10}$-transformed, two-year mean core area). The independent variables in each model were mean number of burrows used per year, sex, mean number of overlapping males, and mean number of overlapping females.

For home range area, sex was the only significant variable, with males having larger home ranges than females ($F_{1,29} = 11.67$, $P = 0.002$, partial $\eta^2 = 0.29$). Home range area was independent of mean number of burrows used per year ($F_{1,29} = 0.23$, $P = 0.633$, partial $\eta^2 = 0.01$) and the mean number of overlapping individuals of either sex (males:
For core area, sex had a similar effect ($F_{1,29} = 10.54, P = 0.003$, partial $\eta^2 = 0.27$), but there was also a significantly positive relationship between core area and mean number of burrows per year ($F_{1,29} = 4.59, P = 0.041$, partial $\eta^2 = 0.14$). As with the home range estimates (above), the mean number of overlapping males and females did not significantly affect core area estimates (males: $F_{1,29} = 1.60, P = 0.22$, partial $\eta^2 = 0.05$; females: $F_{1,29} = 0.05, P = 0.83$, partial $\eta^2 = 0.002$). The difference between the two models suggests that core areas are more dependent upon a network of burrows than are home ranges areas.

Discussion

SEXUAL DIFFERENCES IN SPACE USE

Both home range and core area estimates were larger for male than female tortoises. Male Desert Tortoises elsewhere have exhibited larger home ranges than females (Holt and Rautenstrauch 1996; Duda et al. 1999; Freilich et al. 2000), though in some studies the difference was not statistically significant (Burge 1977; Barrett 1990; O’Connor et al. 1994). To our knowledge, no prior studies of Desert Tortoises have reported measures of core area.

Differences between sexes in land use could arise from a number of physiological or behavioral differences. First, the disparity could simply be an artifact of body size, as males are generally larger than females and, thus, need more resources (Sandell 1989; Jetz et al. 2004). The effect of body size on home range area has been shown for
numerous lizards (Turner et al. 1969; Rose 1982; Perry and Garland 2002) and terrestrial and aquatic turtles (Auffenberg and Weaver 1969; Auffenberg and Iverson 1979; Bury 1979), including the Texas Tortoise, *Gopherus berlandieri* (Auffenberg and Weaver 1969). Results indicate a significant difference in body size (MCL) between the sexes; however, we found that home range area, overlap variables, and burrow use were independent of adult body size within the range of body sizes examined (201-285 mm; see Chapter 2). O'Connor et al. (1994) similarly found no relationship between body size and home range area for Desert Tortoises using a smaller number of individuals with a more narrow range of body size (N = 15 adults; MCL range = 220-276 mm).

Second, reproductive condition could affect space use. In some reptiles, gravid females undertake long-distance migrations to nesting areas and exhibit larger home range areas than males (e.g., Grand Cayman Blue Iguana, *Cyclura lewisi*, Goodman et al. 2005; Spotted Turtle, *Clemmys guattata*, Litzgus and Mousseau 2005). In other reptiles, gravid females move substantially less than non-gravid females and males, whereas non-gravid females and males exhibit similar home range size and movements (e.g., Common Adder, *Vipera berus*, Viitanen 1967; reviewed in Marshall et al. 2006). Desert Tortoises are known to exhibit a bet-hedging life history strategy, where females modify metabolic rates and food requirements to reflect resource availability, producing eggs through periods of ample rain and drought (Henen 1997). In our study, we lacked information on the reproductive condition of females. Although environmental conditions were presumably favorable (i.e., ample rain; National Climatic Data Center 2006) for reproduction during the years of our study (cf., Lovich et al. 1999), we did not x-ray females to neither identify enlarged follicles or eggs nor observe nesting activities.
Finally, reproductive behaviors could influence space use. Sexual differences could arise, for example, from males patrolling larger areas in search of mates (e.g., Duvall et al. 1992; Walker 2000), which has been proposed for Desert Tortoises (Berry 1986). The different pattern of space use by males and females suggests management decisions should consider each sex separately. Clearly, the causal basis for sexual differences warrants further study.

**Variation in Space Use**

Tortoises in 2005 exhibited larger home range (17%) and core (20%) areas than in 2004. Although the differences could be related to precipitation and/or temperature variation (Duda et al. 1999; Freilich et al. 2000), we suspect the difference resulted from a sample size bias. That is, we adhered better to the intensive sampling regime in 2005, resulting in more locations than in 2004. The number of locations is positively associated with MCP area (White and Garrott 1990; Powell 2000; Chapter 2).

Individuals were consistent between years in their relative use of space. Tortoises having relatively small or large MCP estimates in 2004 had correspondingly small or large estimates in 2005 (100% MCP: \( r^2 = 0.89 \); 50% MCP: \( r^2 = 0.77 \)). This suggests a strong individual component to space use by Desert Tortoises.

**Home Range Versus Core Area Estimates**

As expected from their definition and computation, home range estimates were significantly larger than core area estimates in both years. Core areas represented a small fraction of the total home range area (males: 13.7% for each year; females: 9.4% in 2004,
and 11.2% in 2005). This suggests that, although tortoises may be familiar with a large area of land, they selectively concentrate most of their use to a small portion of that area. Core area estimates in most studies are derived from kernel densities (Worton 1989; Gorman et al. 2006), and have not been applied in studies on the Desert Tortoise. Because our focus here was on overlap, for which kernel estimates should not be used (e.g., Kernohan et al. 2001), we cannot make comparisons to other studies.

The ANCOVA models allowed us to examine the relative influence of sexual, social, and environmental variables on home range and core area estimates. For both home range and core area, sexual differences were very important, though social influences such as the number of overlapping individuals of either sex were negligible. The one environmental influence considered was number of burrows, which was independent of home range area, but was significantly associated with core area. The difference between the two models suggests that core areas are more dependent upon a network of burrows than are home ranges. In contrast to our findings, Duda et al. (1999) found a correlation at each study site between home range area and number of burrows used during the year by Desert Tortoises at a different location in the west Mojave. Differences in methodology in study design and home range estimates may complicate this comparison between studies, though a real difference in habitat use may exist.

Home range area in a number of lizards appears to have a strong social component. For most lizard species, home range is primarily determined by energetics, yet social factors also play an important role (e.g., Perry and Garland 2002; Haenel et al. 2003). In iguanids, differences in the spatial ecology of males and females are related to mate search polygyny (Goodman et al. 2005). Males typically travel to court and defend
several females, whereas females do not travel outside their normal areas to seek males
for mating. Although we failed to detect a social component in home range and core areas
of Desert Tortoises, we feel that investigators should pay closer attention to social
variables. A long-term study may be needed to detect these important social influences on
space use within tortoise populations.

Population density may also play an important role in the spatial ecology of
Desert Tortoises. For a number of species of lizards, population density is negatively
associated with home range area (e.g., Schoener and Schoener 1982; Alberts 1993). Albe…
degree of home range overlap (100% MCPs) between successive years (mean = 78%) and across the three years (65%) of their study. In the western Mojave, Freilich et al. (2000) refound over 77% of tortoises within 300 m of the original capture site 1-4 year later.

Site fidelity may also have a seasonal component. O’Connor et al. (1994) showed that Desert Tortoises in the eastern Mojave use different parts of their home range at different times of the year, with a mean of 18% overlap between “early” and “late” portions of their tracking period (June-October 1992). In a study done in the same region of the Mojave, Burge (1977) noted a similar pattern of use of the activity areas. O’Connor et al. (1994) then concluded that tortoises in the Las Vegas area sequentially use small portions of their home range throughout the year. Although we did not delineate home range estimates per season in this study, site fidelity is best measured using the entire area used over a full year. From a management perspective, total use areas are more informative regarding land management decisions.

The high degree of annual site fidelity suggests that Desert Tortoises in the Mojave Desert concentrate their land use to areas they are familiar with. This may reflect the extreme environment, where knowledge of the locations of limited resources such as food, reproductive females, water, and/or nutrients can have a great impact on fitness (Stamps and Krishnan 1995; Powell 2000). Duda et al. (2002) cite energetic demands of living in an extreme environment as the cause for site fidelity in Desert Tortoises, though there may be other contributing factors.
OVERLAP OF INDIVIDUAL HOME RANGES

The two measures of home range overlap, the number of overlapping individuals and percentage of area overlap, yielded similar results in that both home range size and sex of overlapping individual were important. Overlap with other individuals was positively associated with home range area, apparently to a greater extent in 2005 than in 2004, though the difference between years could be a result of sample size bias. For percentage of area overlap, both sexes exhibited greater overlap with other males than females. For number of overlapping individuals, females exhibited this bias to a greater extent than males.

This male bias in overlap may be the result of a number of factors. First, males demonstrated significantly larger home range estimates and core areas. As such, a higher degree of male overlap in both MCP measures would be expected. Second, if female home ranges are relatively evenly spaced across the landscape (see core area overlap below), then they would be expected to overlap more with males than other females. Third, social interactions may determine the degree of home range overlap. This social component of space use has been demonstrated in lizards, with females exhibiting a strong male bias in home range overlap for both the number of individuals and the percentage of shared area (Haenel et al. 2003).

OVERLAP OF INDIVIDUAL CORE AREAS

As with home range overlap, females exhibited greater core overlap with males than females, and this bias was again greater in 2005 than in 2004. Having comparatively small core areas, females rarely overlapped with each other, suggesting avoidance of
overlap with other females and/or homogenous distribution across the landscape. Males differed significantly from females, as they overlapped with a similar number of individuals of either sex. The presence of females within a male’s core area suggests that males actively included one or more females within their core areas. Indeed, we observed burrow sharing between sexes (see below) and frequent sexual activities (unpubl. obs.). In contrast to home range overlap, overlap in core areas was independent of the size of the core area.

**BURROW USE, HOME RANGES, AND CORE AREAS**

Results show that males, with larger home ranges, use significantly more burrows throughout the year than females. However, the statistical analyses determined that the number of burrows used by a tortoise was independent of home range area, yet it significantly affected core area estimates. This is interesting given that, in this study, tortoises were located in burrows for upwards of 94% of all locations. This suggests that the movements by tortoises, whether exploratory or site-specific, are more important in determining home range area. Burrows, as a main source of social interaction for tortoises, did not influence the number of overlapping individuals or the percentage of shared home range.

Desert Tortoises are known to utilize a series of burrows, switching between a few choice burrows throughout year. The frequency of shifting burrow use pattern varies seasonally (Duda et al. 1999) and between males and females (Bulova 1994), possibly due to changing climatic conditions (Rostal et al. 1994). These sex differences may also arise from the observation that peak burrow shifts in females occurred in the spring.
possibly through searching for nest sites (Bulova 1994). However, male burrow shifts peak in the fall, due to courtship and mating patterns as a strategy to increase the number of encounters with females (Duda et al. 2002).

Burrow sharing among the population depended heavily on the sex of the individual and the sex of the other burrow user, with a same sex preference by both males and females. This bias is interesting given that males used a significantly higher number of burrows than females in each year. Females demonstrated a preference for a few choice burrows that were previously used by other females.

Burrow location is of primary importance to the reproductive opportunities of male and female tortoises. Neither home range, core area, nor the number of burrows used per year was dependent on the frequency of burrow cohabitation. However, home range area was independent of the number of observations of cohabitation by either sex or measurements of spatial overlap, suggesting that reproductive opportunities are not a primary determinant of home range area in Desert Tortoises (e.g., O’Connor et al. 1994).

**Burrow Use and Fidelity**

As noted in other studies, burrows are extremely important to Desert Tortoises for a number of reasons, such as of thermoregulation, protection from predators, and nesting sites (Burge 1977; Bulova 1994; O’Connor et al. 1994). We recorded a large proportion of tortoise locations in burrows (94-96%). In the Mojave Desert, the number of burrows used by a tortoise varies by gender, location, season, and year, ranging anywhere from 1-20 (Burge 1978; Bulova 1994; Duda et al. 1999). Tortoises in this study used a similar number of burrows (5-24 burrows per year; Table 3-1), with a third of those burrows used
again in the second year. Although males used a significantly greater number of burrows in both years, which corresponded to their larger core area, burrow fidelity was similar between the sexes.

**FACTORS AFFECTING HOME RANGE AND CORE AREAS**

In our final statistical models, home range and core areas were dependent on sex and independent of social interactions, measured by the number of overlapping individuals. Core areas, however, were dependent on the number of burrows used, whereas home ranges were not, suggesting that core areas are more dependent on a network of burrows. Accordingly, the home range of the Desert Tortoise appears to be the result of multiple functions, not solely social interactions.

If the social structure of the Desert Tortoise were a male-based territorial system, we would expect to see certain patterns in home range overlap and burrow use within the population (Brown and Orians 1970; Powell 2000). For example, the home ranges of male tortoises would be expected to overlap little with that of other male tortoises, and more so with female home ranges. Also, we would expect to see a higher degree of site fidelity in male home ranges between years (Brown and Orians 1970; Powell 2000). In this study, males and females demonstrated a similar degree of site fidelity, but males had larger home range areas and a greater number of burrows used between years. Male home ranges also included a significant portion of female home ranges, with few male home ranges entirely encompassing those of one or more females (Fig. 3-2), common to polygamous species (Stamps 1977). O'Connor et al. (1994) also noted this lack of home range exclusivity, suggesting a lack of territoriality in Desert Tortoises.
Flexibility in territorial behavior is observed in a number of species, ultimately related to the degree to which the resource is economically defensible (Brown and Orians 1970; Kaufmann 1983). This high degree of overlap between the home ranges suggests that territories, as far Desert Tortoises are concerned, are not economically defensible (Powell 2000). Tortoises may occupy non-exclusive home ranges while exhibiting territorial behavior, as demonstrated in lizards (Haenel et al. 2003; Kerr and Bull 2006). Depending on the nature of the limiting resource(s), the benefit and cost of maintaining a territory may change temporally and/or spatially (Kerr and Bull 2006). Particularly in long-lived species with individual recognition, passive avoidance is used as a means to refrain from engaging in costly antagonistic encounters (Stamps 1977).

Precipitation may also determine home range area in the Desert Tortoise. Holt and Rautenstrauch (1996) attempted to correlate home range area with annual precipitation during their three-year study. They noted that, in a drier year, tortoises exhibited smaller home range areas using the cluster method of analysis. However, home range areas using the 100% MCP method failed to differ between years in their study. Due to the nature of these two estimators, Holt and Rautenstrauch’s (1996) interpretation was that Desert Tortoises spent more time in smaller areas in the drier year as compared to the wet years. Using the MCP method, both Duda et al. (1999) and Freilich et al. (2000) found tortoises in the west Mojave had significantly larger home ranges during wet years when compared to dry years. In contrast, Esque et al. (in prep, cited in U. S. Fish and Wildlife Service 1994) found that tortoises had larger MCP home ranges in dry years.

In 2004 and 2005, record high rainfall was reported for the west Mojave (National Climatic Data Center 2006). This may help to explain the large home range estimates.
from our study. It is not known if these conflicting results across studies on Desert Tortoises are an artifact of study design, methodology of home range estimates, or geographic location. A long-term study may provide greater insight into this phenomenon for this species, encompassing years of variable resources.
Figure 3-1. Graphical display of minimum convex polygon (MCP) estimates for male and female Desert Tortoises in the west Mojave Desert over two years of study. The core area is presented for A) 2004 and C) 2005 while home is presented for B) 2004 and D) 2005 respectively. Map areas represent the same position on the study site.
Figure 3-2. Mean (+ 1 SE) percentage of overlap of individual minimum convex polygon (MCP) areas with other male and female Desert Tortoises, computed from core area (A, B) and home range (C, D) estimates in 2004 and 2005, respectively. Filled bars represent overlap values for males, with unfilled bars representing values for females.
Figure 3. The frequency of button sharing (non-simultaneous use; mean ± 1 SE) in a population of desert tortoises for 2004 (A) and 2005 (B) separated by sex. Filled bars represent the number of males sharing buttons of another individual, and unfilled bars represent the number of males sharing buttons of females.
Figure 3.4. The mean number of observations of burrow combination between male and female Desert Torosios in the West Mojave Desert in 2004 (A) and 2005 (B). Values represent the mean number of observations of a burrow occupying a burrow with another. Females are filled bars for each sex, males are open bars. Combustion males are represented as filled bars, and combustion females are filled bars.
Table 3-1. Average measurements (mean ± 1 SE, range) from Desert Tortoises (*Gopherus agassizii*; 20 males, 14 females) in the west Mojave Desert, including midline carapace length (MCL, mm), number of radio-telemetry locations, and burrow use statistics for 2004 and 2005.

<table>
<thead>
<tr>
<th></th>
<th>2004</th>
<th>2005</th>
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<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Body size (MCL)</td>
<td>256.1 ± 4.3</td>
<td>235.4 ± 4.6</td>
</tr>
<tr>
<td>Number of Locations</td>
<td>71.6 ± 0.6</td>
<td>71.0 ± 0.5</td>
</tr>
<tr>
<td>Number of Burrows Used per Year</td>
<td>15.4 ± 0.7</td>
<td>11.4 ± 0.9</td>
</tr>
<tr>
<td>Number of Burrows Used Over Both Years</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Number of Unique Burrows</td>
<td>11.0 ± 0.9</td>
<td>6.8 ± 1.0</td>
</tr>
</tbody>
</table>
Table 3-2. Measurements (mean ± 1 SE, range) of site fidelity, number of overlapping tortoises, and percentage of home range and core area overlap of minimum convex polygon (MCP) estimates for 34 Desert Tortoises (*Gopherus agassizii*; 20 males, 14 females) in the west Mojave Desert for 2004 and 2005.

<table>
<thead>
<tr>
<th></th>
<th>2004</th>
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<th>2005</th>
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<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td>All (Range)</td>
<td>Male</td>
<td>Female</td>
<td>All (Range)</td>
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<tr>
<td><strong>Home Range</strong></td>
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</tr>
<tr>
<td>100% MCP</td>
<td>39.4 ± 9.4</td>
<td>13.8 ± 1.6</td>
<td>28.9 ± 5.9 (6-210)</td>
<td>47.4 ± 7.8</td>
<td>16.9 ± 2.4</td>
<td>34.8 ± 4.5 (5-177)</td>
</tr>
<tr>
<td>Percent Yearly</td>
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</tr>
<tr>
<td>Overlap Number</td>
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<tr>
<td>Males</td>
<td>4.9 ± 0.5</td>
<td>5.0 ± 0.4</td>
<td>4.9 ± 0.3 (1-9)</td>
<td>7.1 ± 0.8</td>
<td>6.5 ± 0.7</td>
<td>6.9 ± 0.5 (2-14)</td>
</tr>
<tr>
<td>Number of Overlapping</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>3.5 ± 0.4</td>
<td>2.6 ± 0.4</td>
<td>3.1 ± 0.3 (1-6)</td>
<td>4.6 ± 0.4</td>
<td>2.4 ± 0.4</td>
<td>3.7 ± 0.3 (0-7)</td>
</tr>
<tr>
<td>Percent Male Overlap</td>
<td>27.3 ± 3.2</td>
<td>43.1 ± 3.5</td>
<td>33.8 ± 2.7 (3-75)</td>
<td>25.0 ± 2.3</td>
<td>37.2 ± 2.8</td>
<td>30.0 ± 2.0 (1-62)</td>
</tr>
<tr>
<td>Percent Female</td>
<td></td>
<td></td>
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<tr>
<td>Overlap</td>
<td>22.5 ± 3.7</td>
<td>15.8 ± 3.6</td>
<td>19.7 ± 2.6 (0.5-75)</td>
<td>17.4 ± 2.1</td>
<td>17.4 ± 3.6</td>
<td>17.4 ± 1.9 (0-41)</td>
</tr>
<tr>
<td><strong>Core Area</strong></td>
<td></td>
<td></td>
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<tr>
<td>50% MCP</td>
<td>5.4 ± 0.8</td>
<td>1.3 ± 0.3</td>
<td>3.7 ± 0.6 (0.2-13)</td>
<td>6.5 ± 1.0</td>
<td>1.9 ± 0.5</td>
<td>4.6 ± 0.7 (0.3-15)</td>
</tr>
<tr>
<td>Percent Yearly</td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Overlap Number</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>0.7 ± 0.2</td>
<td>0.9 ± 0.3</td>
<td>0.8 ± 0.2 (0-3)</td>
<td>1.0 ± 0.2</td>
<td>0.9 ± 0.3</td>
<td>0.9 ± 0.2 (0-4)</td>
</tr>
<tr>
<td>Number of Overlapping</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>0.7 ± 0.2</td>
<td>0</td>
<td>0.4 ± 0.1 (0-3)</td>
<td>0.6 ± 0.1</td>
<td>0.1 ± 0.1</td>
<td>0.4 ± 0.1 (0-2)</td>
</tr>
<tr>
<td>Percent Male Overlap</td>
<td>13.6 ± 4.6</td>
<td>17.6 ± 6.4</td>
<td>15.2 ± 3.8 (0-80)</td>
<td>8.6 ± 3.7</td>
<td>32.1 ± 10.7</td>
<td>18.3 ± 5.2 (0-100)</td>
</tr>
<tr>
<td>Percent Female</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overlap</td>
<td>3.7 ± 1.7</td>
<td>0</td>
<td>2.2 ± 1.0 (0-32)</td>
<td>12.2 ± 4.8</td>
<td>0.9 ± 0.8</td>
<td>7.6 ± 2.9 (0-72)</td>
</tr>
</tbody>
</table>
Table 3-3. Burrow use measurements (mean ± 1 SE, range) from Desert Tortoises (*Gopherus agassizii*; 20 males, 14 females) in the west Mojave Desert, including burrow sharing (non-simultaneous use of a single burrow) and observations of cohabitation (simultaneous use of a single burrow) for 2004 and 2005.

<table>
<thead>
<tr>
<th></th>
<th>2004</th>
<th>2005</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Number of Males Sharing</td>
<td>1.2 ± 0.5</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td>Burrows</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of Females Sharing</td>
<td>0.1 ± 0.0</td>
<td>1.0 ± 0.0</td>
</tr>
<tr>
<td>Burrows</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Number of Tortoises</td>
<td>1.3 ± 0.1</td>
<td>1.3 ± 0.1</td>
</tr>
<tr>
<td>Sharing Burrows</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of Cohabitating</td>
<td>1.6 ± 0.3</td>
<td>2.9 ± 0.6</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of Cohabitating</td>
<td>1.4 ± 0.3</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Number of Cohabitating</td>
<td>2.9 ± 0.5</td>
<td>3.0 ± 0.5</td>
</tr>
<tr>
<td>Individuals</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER 4

CONCLUSIONS

In this thesis, we present an analysis of space use by *Gopherus agassizii* in the hopes that home range analysis will be more carefully considered in future studies. Particularly for sensitive and endangered species such as this, careful foresight in land management practices will have a significant positive impact on the sustainability of the species.

In the analysis of sampling methodology on the home range estimates of Desert Tortoises in Chapter 2, we demonstrated that home range estimates are poorly understood. Methodology is a factor in all analyses, and considering it carefully in planning research projects will only improve comparisons between studies. With a more intensive sampling regime of longer duration, investigators will be better able to understand exactly what an animal requires as far as land use is concerned. Both estimators, the MCP and FK are important tools for understanding space use, and we recommend that they both be used. Our analysis demonstrates that *Gopherus agassizii* may require larger areas of land for sustainability than previously thought. Certainly, this warrants further study across additional populations.

Identifying the important factors regarding space use by *Gopherus agassizii* in Chapter 3 revealed that space use corresponds to a number of factors. Desert Tortoises focus their space use based largely on environmental constraints, though social factors
may play a lesser role. Males and females demonstrated very different patterns in space use and burrow parameters, suggesting that future investigations should separate the sexes in their analyses. Home ranges and core areas were each affected by different variables. And finally, the analysis of burrow use within and between individuals identified distinct patterns of use by males and females.

Although we analyzed a small portion of the myriad of factors influencing space use by Desert Tortoises, this study provides insight into what the animal requires for sustainability. We hope that in providing this analysis, land managers carefully consider all aspects of space use when making important decisions. Future studies will only build on this knowledge, no doubt improving the mitigation and land management practices for this and other species.


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