



Home range and movement of desert tortoises *Gopherus agassizii* in the Mojave Desert of California, USA

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ABSTRACT: Radio telemetry of 29 desert tortoises *Gopherus agassizii* in 2000 and 60 in 2001 at 4 sites in the Mojave Desert of California, USA, revealed that males had larger home ranges and moved greater distances than females, but that tortoises at sites with more rainfall did not always have larger home ranges or move greater distances. The Ivanpah Valley received more rainfall than the Fort Irwin area, Superior Valley, and Fremont, but differences between home range size and rainfall were not consistent. Within the Ivanpah Valley, the plot at the highest elevation received more rainfall than the lower plots. However, within the Ivanpah Valley, tortoises at the 3 locations did not differ in home range and movement. In the wetter year (2001), female tortoises moved greater distances each day at Ivanpah than female tortoises at Superior and Fremont, which were drier sites. Males moved farther per day than females in both years. In 2001, female tortoises in the Ivanpah Valley used more burrows than tortoises at Fremont and Superior, but similar numbers as tortoises at Fort Irwin. There was no mortality of tortoises in 2000 and a 5% mortality in 2001.

KEY WORDS: Desert tortoise · Radio telemetry · Rainfall · Ivanpah Valley · Fort Irwin · Minimum convex polygon · Climate change

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INTRODUCTION

The desert tortoise *Gopherus agassizii* inhabits the Mojave, Colorado, and Sonoran Deserts, USA, (Ernst et al. 1994) and is listed as a threatened species under the US Endangered Species Act in the western part of its range (US Fish & Wildlife Service 1990). Field data (Berry 1997) and demographic analyses by modeling (Doak et al. 1994) have indicated that many populations of desert tortoises are in decline. However, accuracy of historical density estimates have been challenged (Bury & Corn 1995) due to difficulties with desert tortoise surveys (Corn 1994, Freilich et al. 2000), large differences in local densities (Germano et al. 1994a), inter-observer bias (Freilich & LaRue 1998), and changes in tortoise activity due to changes in rainfall and plant productivity (Duda et al. 1999). In addition, tortoises may be undercounted in dry years (Freilich et al. 2000). Research is still needed to provide

more thorough and detailed knowledge of desert tortoise life history and ecology, including knowledge of desert tortoise movements, home range, and activity patterns, in order to establish a sound conservation or management strategy for the species (Berry 1986, Gibbons 1986, US Fish & Wildlife Service 1994, Freilich et al. 2000).

Home range (White & Garrott 1990) and movements are determined in part by the biotic resources and biophysical properties in an environment. The resource environment (e.g. water, energy, protein) and the social environment (e.g. mating strategies, territoriality) of an ectotherm influence its daily activity budget (Dunham et al. 1989). This daily activity budget in turn affects the movements and home range of that animal. Predator avoidance and demographics within a population also affect home range and movements.

Availability of water varies both temporally and spatially in the Mojave Desert (Shreve 1925, Beatley 1974,

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Germano et al. 1994b). This variation has a direct effect on the success of vegetation and the types of vegetation present in an area. From year to year, rainfall is highly variable, with years of drought followed by years of high rainfall. In the western Mojave Desert, rainfall primarily occurs in winter, with little or no summer rain. Historically, rainfall in the eastern Mojave Desert has been bimodal, with winter rains as well as a pulse of summer rain commonly seen in August and September (Shreve 1925). Since 1950, California has experienced increased effects of global warming, with warmer winter and spring temperatures and earlier spring flowering (Cayan et al. 2006). Climate models project that there will be an increase of 2.8 to 5.5°C in June to August temperatures in the Mojave Desert in 2070 to 2099 and a change of 5 to 20% in total precipitation during the 21st century due to an increase in CO₂ that will cause global warming (Cayan et al. 2008). We already know that seasonal, annual, and geographic differences in rainfall affect the physiology, behavior, and ecology of desert tortoises (Nagy & Medica 1986, Peterson 1996b, Henen et al. 1998). Therefore, it is important to determine how desert tortoises change behavior in response to differences in climate variables so that we can anticipate how tortoises will react to changes in climate over the next 50 to 100 yr.

Home range size, movements, and activity patterns of tortoises vary in time and space. Annual home range sizes of desert tortoises in the Mojave Desert are highly variable, ranging from 1 to 89 ha both between and within populations (Berry 1986, Duda et al. 1999, Field et al. 2007, Harless et al. 2009). Home range sizes and movements in 2 populations of desert tortoises differed between 1995 and 1996 in the south-central Mojave Desert (Duda et al. 1999). The first year was wet and had more plant productivity, and tortoises had larger home ranges and traveled higher average distances per day than in the subsequent drought year. Tortoises at 1 site had significantly smaller home range sizes than tortoises at the second site, correlated with plant productivity differences between sites (Duda et al. 1999).

The effect of sex on the home range and movements of tortoises varies. Home range size was the same for male and female tortoises in the Sonoran population in the Picacho Mountains (Barrett 1990) and in Saguaro National Park in Arizona (Stitt et al. 2003), and for the Mojave population near the Desert Tortoise Conservation Center in the Las Vegas Valley in Nevada (O'Connor et al. 1994). However, male desert tortoises had larger home ranges than females near Lake Mead, Nevada (Duda et al. 1999), in Joshua Tree National Park (Freilich et al. 2000), and in Fort Irwin, California (Harless et al. 2009), and translocated males had larger home ranges than females in southern Nevada (Field

et al. 2007). The reasons for these differences are unclear. Additional data are needed to determine whether differences in home range and movement at different locations represent a general phenomenon in desert tortoises and to determine the mechanisms that control home range size and movement of male and female tortoises at different sites in the Mojave Desert.

We used radio telemetry to examine effects of year, sex, location, and rainfall on desert tortoise home range size, movement, and activity at 4 sites over a 2 yr period (2000 to 2001) in the California Mojave Desert. Radio telemetry continues to be a useful method to determine the home ranges of endangered species as varied as Mt. Graham red squirrels (Koprowski et al. 2008) and pangolins (Lim & Ng 2008). The objectives of the study were to: (1) determine whether rainfall affected home range size, movements, and activity, (2) determine whether home ranges, movements, and activity differed in male and female tortoises, and (3) determine whether home range size and location differed seasonally.

MATERIALS AND METHODS

We conducted this study at 4 locations in the California Mojave Desert (Fig. 1). We collected data from 2 sites in 2000 and from all 4 sites during 2001. Sites ranged from the western Mojave Desert near Helendale, California, to the eastern Mojave Desert near the Nevada–California border within the Mojave National Preserve (Fig. 1). Sites differed in human impact, ranging from heavy activity such as dumping and off-road vehicle (OHV) use (west Mojave) to little visible disturbance (east Mojave). Sites varied in elevation, rainfall amounts and frequency, and vegetation communities. We monitored tortoises of both sexes at 3 sites but only monitored female tortoises at 1 site due to logistical limitations. Sample sizes are given in Table 1. We were seriously limited in our ability to acquire equal sample sizes and times due to delays in permitting from United States Fish and Wildlife Service (USFWS) and the Mojave National Preserve of the National Parks Service.

Ivanpah Valley site. The Ivanpah Valley site was within the Mojave National Preserve approximately 10 km south and west of Nipton, California (Fig. 1). The Mojave National Preserve is a 650 000 ha protected area created in 1994. The valley is located between the Ivanpah and New York Mountains. Elevation ranges from 870 to 1100 m and increases from northeast to southwest. A creosote scrub-dominated community occurs at lower elevations, with Mojave yucca and Joshua trees occurring at higher elevations. Human impacts included a powerline corridor, cattle

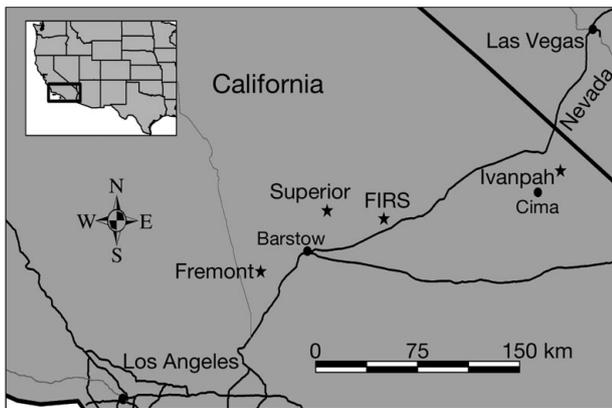


Fig. 1. Four study sites (stars) for desert tortoises in the California Mojave Desert (USA). FIRS: Fort Irwin Reference Site. Thick black lines show state borders, thin black lines are interstate highways, and thin gray lines are US highways

Table 1. *Gopherus agassizii*. Number of desert tortoises tracked with radio telemetry at 4 sites (FIRS, Ivanpah, Fremont and Superior) in the Mojave Desert (California, USA) in 2000 and 2001. FIRS: Fort Irwin Reference Site

Site	Sex	Year	Sample size	Months tracked
FIRS	Female	2000	7	May to Aug
FIRS	Female	2001	16 ^a	May to Oct
FIRS	Male	2001	5	Jul to Oct
Ivanpah	Female	2000	22	Mar to Jul
Powerline			6	
Water tank			4	
Cima			12	
Ivanpah	Female	2001	18 ^b	Jun to Oct
Powerline			3	
Water tank			4	
Cima			11	
Fremont	Female	2001	6	Aug to Oct
Fremont	Male	2001	5	Aug to Oct
Superior	Female	2001	4	Aug to Oct
Superior	Male	2001	4	Aug to Oct

^aFive of year 2000 tortoises were included in 2001
^bOne tortoise was new in 2001

grazing and water tanks, and a major railroad grade. In July 2001, the cattle were removed from the valley, but their impact on soils and vegetation was still clearly visible. Soil was more compacted, more non-native plants were present in grazed areas, and native grasses and bushes had not yet recovered, as documented earlier by Avery (1998).

Rainfall frequency was fairly consistent in the valley, but rainfall amounts during an event were highly variable. We collected rainfall data using a network of rain gauges spaced throughout the study area. Rainfall varied across a gradient with a 3- to 4-fold difference in rain-

fall amounts along a 10 km gradient. Areas at higher elevations in the valley received more rain than areas at lower elevations (Avery 1998, Avery et al. 2002).

We monitored tortoises from 3 study plots of 4 km² each within the valley. Plot 1 (Lower Powerline) was in the lower portion of the valley, with elevations ranging from 850 to 950 m. Plot 2 (Lower Water Tank) was in the middle to lower portion of the valley, with elevations ranging from 980 to 1050 m. Plot 3 (Cima) was in the upper portion of the valley, with elevations ranging from 1050 to 1100 m. The distance from Plot 1 to Plot 3 was approximately 8 km.

Fort Irwin Reference Site. The Fort Irwin Reference Site (FIRS) was an area used as a reference area to compare to areas of military training on Fort Irwin for a series of studies on desert tortoises by our group and others. The FIRS site was 4 km² and was located adjacent to the southeastern boundary of the US Army National Training Center at Fort Irwin, California, about 10 km northwest of Highway 15 (Fig. 1). It was a creosote-scrub dominated community with an elevation range of 450 to 900 m. Human impacts at this site included a major powerline corridor, a gas pipeline, and a fiber optic cable line. We measured rainfall monthly using a network of rain gauges spaced throughout the site.

Fremont site. The Fremont site (4 km²) was located approximately 5 km north of Helendale, California, in the western Mojave Desert (Fig. 1). It is a creosote-scrub dominated community with an elevation range of 750 to 800 m. Human impacts included OHV use, presence of feral dogs, and large amounts of human refuse such as tin cans and discarded furniture. Rainfall patterns differed at this site, although most precipitation fell in winter, and it was rare for this site to have any rainfall during summer. We did not have rain gauges at this site but were able to obtain rainfall data from the El Mirage Air Field weather station, located approximately 20 km south.

Superior site. The Superior site (4 km²) was located approximately 5 km west of Fort Irwin Road in the Paradise Valley (Fig. 1). It was a creosote-scrub dominated community with an elevation range of 750 to 850 m. Human impacts were light with some OHV use and recreational camping areas. The Superior site was located approximately 35 to 40 km west of FIRS. Rainfall patterns and amounts were similar to those at FIRS. We measured rainfall monthly using a network of rain gauges spaced throughout the site.

Tortoise collection and transmitter attachment. We located tortoises by walking transects and searching active burrows. When we located an unmarked tortoise, we placed it in a sanitized plastic container and transported the tortoise to our staging area. We marked the location where we found the tortoise and took GPS

coordinates in order to return it to that exact location. Each animal was permanently marked by notching marginal scutes with a file and temporarily marked by using a small epoxy label (Avery 1998). We took measurements of each tortoise using calipers (± 0.5 mm) and weighed each tortoise (± 0.1 g) using a digital balance. We measured straight carapace length, straight carapace width, plastron length, and carapace height. During all handling of tortoises, we used disposable latex or nitril gloves and sanitized all equipment after each use with bleach and/or isopropyl alcohol.

We glued 2-stage radio transmitters (Advanced Telemetry Systems[®]) weighing less than 50 g to each tortoise. Each transmitter was set to turn on at 06:00 h Pacific Standard Time (PST) and turn off at 18:00 h PST in order to conserve battery power. Transmitter frequencies ranged from 164.000 to 168.999 MHz at the Ivanpah, FIRS, and Fremont sites. Frequencies at the Superior site ranged from 151.000 to 151.999 MHz and had been applied by other investigators for a different study. We received radio frequency approval for all of our transmitter frequencies from the US Fish & Wildlife Service, the US Geological Survey-Biological Resources Division, and the US Army.

We attached transmitters using a method consistent with Boarman et al. (1998) applying steel epoxy putty (Devcon[®] or Oatey[®]), which allowed for quick drying and easy removal. We anchored the transmitter to the 1st left costal scute and placed the antenna in a segment of aquarium tubing. The antenna was then attached to the 2nd, 3rd, and 4th costal scutes using epoxy. We attached the transmitters to the costal scutes in order to minimize the alteration of the shell profile. We released tortoises at the site of capture within 1 h of capture in order to minimize their disturbance. We changed transmitters after approximately 9 mo, as the transmitter batteries were only rated for that duration.

Radio-tracking. We monitored tortoises using ICOM[®] receivers with Telonics[®] 'H' antennas. We obtained a location for each tortoise weekly during 2001 and approximately every other week during 2000, usually during the morning activity period. We attempted to confirm a tortoise's location and behavior during each tracking. We recorded global position (GPS) coordinates using handheld GPS units (Magellan[®] Models MAP 410 and GPS 315 or Garmin[®] Model GPS 12) giving tortoise locations in universal transmercator (what datum?) coordinates with an error of ± 10 m.

Statistics, home range, and movement analyses. We used 2 methods to examine home ranges and 5 methods to examine movements and activity. We used the minimum convex polygon (MCP) method (Jennrich & Turner 1969, White & Garrott 1990) to estimate home ranges of tortoises monitored. The MCP method estimates home range by creating a polygon around the

outermost location points and calculating the area inside the polygon (White & Garrott 1990). This method was used in previous home range studies on desert tortoises (Barrett 1990, O'Connor et al. 1994, Duda et al. 1999). However, there are drawbacks to this method, such as a sample-size bias and overestimation of home range by inclusion of empty spaces not utilized by the animal (Jennrich & Turner 1969, O'Connor et al. 1994). Another problem with home range analysis is that of autocorrelation (Swihart & Slade 1985) when successive observations are not independent of each other (White & Garrott 1990). O'Connor et al. (1994) found substantial autocorrelation of desert tortoise location data where the mean interval between locations was 3.2 d. To minimize autocorrelation, we used a tracking interval of 7 to 10 d during 2001. To test for autocorrelation, we used Schoener's ratio (t^2/r^2), where t^2 is the mean squared distance between successive observations and r^2 is the mean squared distance from the center of activity (Schoener 1981). This ratio compares the mean distance moved in each location interval to the mean distance between all possible pairs of locations. Significant deviations from the expected value of 2.0 indicate that samples are not random (Schoener 1981). Even with these shortcomings, O'Connor et al. (1994) suggested that this method was sufficient when contrasting movement data between individuals, sexes, sites, and/or populations. As the present study compared home range and movements of tortoises of different sexes, at different sites, and between seasons, we chose the MCP method for these analyses.

We also used corrected MCP area to estimate home range, which was devised to correct for sample size bias. This method, derived by Turner (1969) and used by Barrett (1990), uses a logarithmic equation to standardize datasets with unequal numbers of sampling occasions. The resulting area is the animal's corrected MCP area. The formula used was:

$$(\text{MCP area}) / (0.257 \times \ln(n) - 0.31)$$

where n = number of location points (Barrett 1990). This method corrects for bias in sample size; however, it often overestimates and in some cases, grossly overestimates, home range sizes (Rautenstrauch & Holt 1994). We included this method because it was used in previous desert tortoise home range studies (Burge 1977, Barrett 1990, O'Connor et al. 1994).

We entered GPS coordinates for each location into ArcView GIS, v.3.2a (Environmental Systems Research Institute, ESRI). We calculated MCP areas using ArcView GIS v.3.2a along with Spatial Analyst v.2.0 extension (ESRI) and the Animal Movements extension v.2.0-beta (Hooge & Eichenlaub 1997). Mean distance traveled (MDT) between locations was the average of the minimum linear distances between suc-

cessive captures. Maximum distance traveled (MaxDT) between locations was the greatest distance traveled between successive locations. Mean daily rate of movement (MDRM) was the total of minimum linear distances divided by number of days monitored. Maximum displacement mo^{-1} (MDM) was the greatest linear distance between 2 location points in a month. We also counted the number of burrows used by each tortoise.

We used analysis of covariance (ANCOVA) to compare home range areas of tortoises of each sex and at each site using the number of tortoise locations as the covariate (Zar 1998). We also used ANCOVA to compare movements and activity of tortoises of each sex and at each site, again using the number of tortoise locations as the covariate. We used a multivariate general linear model with post hoc Bonferroni comparisons for mean distance traveled and number of burrows. In order to stabilize all variances and normalize distributions, we transformed any data sets that were not normally distributed or homogenous by log transformation or square root transformation (Zar 1998). Homogeneity and normality were achieved using these transformations. We used a Mann-Whitney *U*-test for corrected MCPs because they violated normality rules. All statistical analyses were done using Stata version 6.0 and SPSS for Windows. All data are presented as means \pm SD.

RESULTS

Tortoise survival and locations

We tracked 29 tortoises in 2000 and 60 in 2001 (Table 1). No tortoises died or lost transmitters during 2000, whereas 3 of the 60 tortoises tracked in 2001 died (1 in Superior and 2 in Ivanpah) and 1 lost its transmitter (in Ivanpah). We could not calculate home ranges for the dead tortoise in Superior and one of the dead tortoises in Ivanpah due to insufficient data. Of the 3 dead tortoises, 1 was predated and the other 2 died of unknown causes. In 2000, there were 19.6 (\pm 5.3) location points per tortoise in FIRS with a time interval of 5.3 (\pm 1.4) d and 10.3 (\pm 2.5) points in Ivanpah, with a time interval of 11.3 (\pm 2.4) d. In 2001, there were 14.1 (\pm 4.6) location points with a time interval between locations of 7.5 d (6.6–9.0, \pm 0.9) across all sites.

Rainfall

Ivanpah Valley received more rain than FIRS, and 2001 was wetter than 2000 at both sites. There were 28.7 (\pm 1.6) mm of rain in FIRS and 122.3 (\pm 29.3) mm in Ivanpah in 2000, and 107.8 (\pm 12.6) mm of rain in FIRS

and 192.1 (\pm 33.2) mm in Ivanpah in 2001. In Ivanpah, we grouped the Lower Powerline and Lower Water Tank plots because these plots were within 3 km of each other. In those plots, rainfall for 2000 and 2001 was 116.9 (\pm 30.9) and 181.4 (\pm 31.4) mm, respectively. In the Cima plot, rainfall was 140.2 (\pm 19.5) mm in 2000 and 224.3 (\pm 3.9) mm in 2001. Most rain occurred during the first 5 mo of each year. In 2000, no rainfall occurred in FIRS after 27 March. In Ivanpah during both years and at FIRS in 2001, rainfall occurred mainly in late winter and early spring, with pulses of rainfall observed during July and August. In 2001, rainfall in Superior was 111.0 (\pm 7.2) mm. We did not collect rainfall data for the Fremont site, but rainfall in 2001 at El Mirage Air Field (20 km south) was 154.2 mm.

Home range

At Ivanpah in 2000, MCP areas for female tortoises were similar at the 3 plots and averaged 9.7 ha (1-way ANCOVA, $F = 0.48$, $df = 2, 1, 18$; $p = 0.63$; Table 2). Corrected MCP area was 34.7 ± 33.7 ha. The MCP at Ivanpah was larger than that for female tortoises at FIRS (5.3 ± 6.2 ha; 1-way ANCOVA, $F = 15.08$ $df = 1, 1, 25$; $p < 0.01$). Corrected MCP area for tortoises at FIRS was 10.8 ± 12.0 ha (Table 3). The home range of male and female tortoises increased with increased rainfall (Fig. 2)

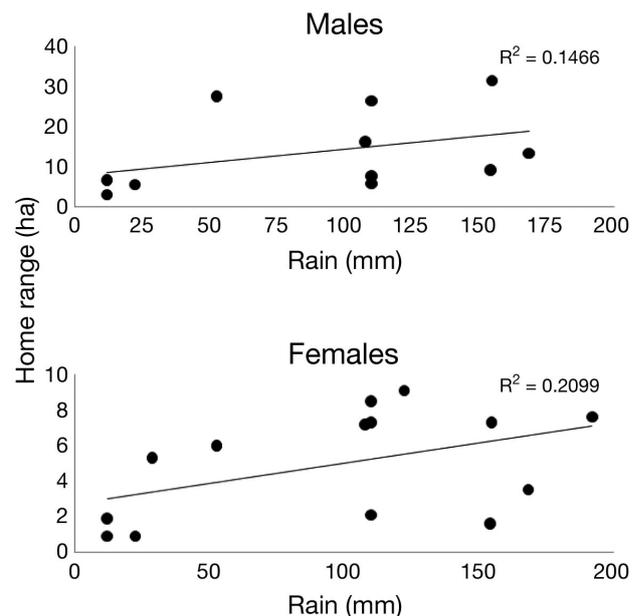


Fig. 2. Relationship between rainfall and home range of male and female desert tortoises in the Mojave Desert of California (USA). Note the different scales on the y-axes. Data are taken from this study and those of Freilich et al. (2000) and Duda et al. (1999). Linear regressions are significant at $p = 0.05$

Table 2. *Gopherus agassizii*. Home ranges (minimum convex polygon, MCP), mean distances traveled (MDT), maximum distances traveled (MaxDT), mean daily rate of movement (MDRM), and number of burrows used by 40 female desert tortoises within the Ivanpah Valley (California, USA) during 2000 and 2001. See 'Materials and methods' for details of the study plot locations. n: no. of tortoises

Plot	Year	n	MCP area (ha)	±SD	MDT (m)	±SD	MaxDT (m)	±SD	MDRM (m d ⁻¹)	±SD	No. burrows	±SD
Lower Powerline	2000	6	10.6	11.2	195.4	106.3	527.5	356.2	14.4	4.8	4.0	1.1
Lower Water Tank	2000	4	10.5	2.8	207.8	22.0	589.4	159.0	17.6	2.1	5.5	1.0
Cima	2000	12	7.9	4.9	197.0	74.8	481.4	176.3	16.9	6.7	4.6	1.4
Lower Powerline	2001	3	6.5	3.9	114.2	32.8	353.7	72.3	13.7	3.8	6.3	0.6
Lower Water Tank	2001	4	8.2	4.7	137.2	34.1	416.4	137.4	16.9	4.2	4.3	1.3
Cima	2001	11	7.8	3.7	136.4	36.0	411.1	120.4	15.8	3.9	5.7	0.9

At Ivanpah in 2001, MCP areas for female tortoises were again similar at the 3 plots, 7.6 ± 3.7 ha. (1-way ANCOVA, $F = 0.01$, $df = 2, 1, 10$; $p = 0.99$). Corrected MCP area was 18.0 ± 8.8 ha. At FIRS, male tortoises had larger MCP areas than females (1-way ANCOVA, $F = 4.11$; $df = 1, 1, 18$; $p = 0.05$; Table 3). Corrected MCP area of FIRS male tortoises was significantly larger (46.3 ± 23.8 ha) than for female tortoises (16.8 ± 13.5 ha; Mann-Whitney U , $p = 0.008$). The MCP areas of female tortoises were similar in Ivanpah and FIRS (7.2 ± 5.7 ; 1-way ANCOVA, $F = 0.80$, $df = 1, 1, 29$; $p = 0.38$), as were the corrected MCP areas (Mann-Whitney U , $p > 0.05$).

At Fremont in 2001, male tortoises had larger MCP areas than females (1-way ANCOVA, $F = 5.95$ $df = 1, 1, 8$; $p = 0.04$; Table 3) and larger corrected MCP areas (29.0 ± 22.0 ha versus 5.0 ± 9.0 ha; Mann-Whitney U , $p = 0.017$) as well. At Superior in 2001, MCP areas were similar for male and female tortoises (1-way ANCOVA, $F = 2.24$, $df = 1, 1, 4$; $p = 0.19$). Corrected MCP area of male tortoises was 36.7 ± 48.0 ha and of female tortoises was 19.3 ± 34.5 ha. The MCP areas of tortoises were similar at Fremont and Superior, and the interaction of site and sex was not significant (2-way ANCOVA, $F = 0.05$, $df = 1, 1, 14$; Site: $p = 0.83$, Site \times Sex: $p = 0.80$). Females at Fremont had

smaller corrected MCPs than females at FIRS ($p = 0.01$) and Ivanpah ($p = 0.017$, Mann-Whitney U).

Autocorrelation

The mean of Schoener's ratio for female tortoises in Ivanpah Valley and FIRS in 2000 was $1.54 (\pm 0.4)$ and $1.12 (\pm 0.3)$, respectively. This was a significant deviation from the expected value of 2, suggesting autocorrelation in MCP areas (t -test, $df = 28$, $p < 0.01$). The mean of Schoener's ratio for tortoises monitored in 2001 was $1.2 (\pm 0.5)$. This was a significant deviation from expected, suggesting autocorrelation in the MCP areas (t -test, $df = 55$, $p < 0.01$). The problem of autocorrelation is dealt with in the 'Discussion'.

Mean distance traveled between locations and daily movements

MDT between telemetry locations by female tortoises in Ivanpah Valley in 2000 ranged from 81.0 to 354.0 m, with a mean of 198.0 m, and was similar at all 3 plots, as was the daily rate of movement (1-way

Table 3. *Gopherus agassizii*. Desert tortoise home ranges (minimum convex polygon, MCP), mean distances traveled (MDT), maximum distances traveled (MaxDT), mean daily rate of movement (MDRM), and number of burrows used for 87 tortoises at 4 sites in the Mojave Desert (California, USA) during 2000 and 2001. FIRS: Fort Irwin Reference Site; n: no. of tortoises

Site	Sex	Year	n	MCP area (ha)	±SD	MDT (m)	±SD	MaxDT (m)	±SD	MDRM (m d ⁻¹)	±SD	No. burrows	±SD
FIRS	Female	2000	7	5.3	6.2	73.0	31.6	338.0	153.9	16.0	6.1	3.4	0.5
FIRS	Female	2001	16	7.2	5.7	101.0	42.3	341.9	172.2	12.0	4.8	4.3	1.3
FIRS	Male	2001	5	16.2	8.3	298.0	73.8	688.6	291.2	30.0	7.6	3.8	1.1
Ivanpah	Female	2000	22	9.1	6.7	198.0	75.6	514.0	227.7	16.0	5.6	4.5	1.2
Ivanpah	Female	2001	18	7.6	3.7	132.0	33.9	405.0	118.0	16.0	3.8	5.4	1.2
Fremont	Female	2001	6	1.6	2.7	48.0	44.2	200.2	130.2	6.0	5.9	3.6	1.1
Fremont	Male	2001	5	9.2	7.3	200.0	77.1	495.0	203.4	27.0	11.6	3.2	1.2
Superior	Female	2001	4	2.1	3.5	96.0	85.0	272.0	200.0	13.0	11.9	2.7	1.0
Superior	Male	2001	4	5.8	7.0	253.0	96.0	507.0	138.1	31.0	12.1	2.0	0.8

ANCOVA, $F = 0.21$, $df = 2, 1, 18$; $p = 0.81$; Table 2). The MDT by female tortoises in FIRS in 2000 ranged from 32.0 to 130.0 m, with a mean of 73.0 m (Table 3). However, female tortoises at the 2 locations had the same MDRM and traveled 16 m d^{-1} .

In 2001, MDT between telemetry locations by female tortoises in Ivanpah Valley ranged from 79.0 to 188.0 m, with a mean of 132.0 m (Table 2) and was similar at all 3 plots, as was the MDRM (1-way ANCOVA, $F = 0.03$, $df = 2, 1, 12$; $p = 0.97$). The MDT between telemetry locations was similar for females at all sites (post hoc Bonferroni comparison, $p = 1.0$; Table 3), although female tortoises at Fremont moved only 6.0 m d^{-1} as compared to 12.0 to 16.0 m d^{-1} at the other sites. Male tortoises traveled longer distances between locations than female tortoises at all sites (Mann-Whitney U , $p = 0.000$), but their MDT was similar at the different sites (Mann-Whitney U , $p = 0.587$; Table 3). Distance traveled d^{-1} by males in 2001 ranged from 27 m d^{-1} at Fremont to 31.0 m d^{-1} at Superior. Males had greater MDRM than female tortoises at FIRS (1-way ANCOVA, $F = 34.11$, $df = 1, 1, 33$; $p < 0.001$), Fremont (1-way ANCOVA, $F = 15.29$, $df = 1, 1, 8$; $p = 0.0004$) and Superior (1-way ANCOVA, $F = 6.16$, $df = 1, 1, 5$; $p = 0.05$). Female tortoises at Ivanpah had greater MDRM than female tortoises at the other sites (1-way ANCOVA, $F = 34.11$, $df = 1, 1, 33$; $p < 0.001$).

Maximum distance traveled

In 2000, MaxDT by female tortoises in Ivanpah Valley was $514.0 \pm 228.0 \text{ m}$ (Table 2) and was similar at the 3 plots (1-way ANCOVA, $F = 0.54$, $df = 2, 1, 18$; $p = 0.59$). The MaxDT by female tortoises in FIRS was $338.0 \pm 154.0 \text{ m}$. The MaxDT of female tortoises was similar at FIRS and Ivanpah (1-way ANCOVA, $F = 2.74$, $df = 1, 1, 25$; $p = 0.12$; Table 3).

In 2001, MaxDT by female tortoises in Ivanpah Valley was $405.0 (\pm 118.0) \text{ m}$ and again was similar at the 3 plots (1-way ANCOVA, $F = 0.06$, $df = 2, 1, 10$; $p = 0.94$; Table 2). There was no significant difference in MaxDT between FIRS females and Ivanpah females, but male tortoises traveled a greater MaxDT than female tortoises at FIRS (2-way ANCOVA, Site: $F = 2.55$ $df = 1, 1, 33$; $p = 0.12$; Sex: $F = 7.10$ $df = 1, 1, 33$; $p = 0.01$; Table 3). At Fremont, male tortoises traveled a greater MaxDT than female tortoises (1-way ANCOVA, $F = 6.46$ $df = 1, 1, 8$; $p = 0.03$; Table 3). There was no significant difference in MaxDT between tortoises at Fremont and Superior, and the interaction of Site and Sex was not significant (2-way ANCOVA, Site: $F = 0.00$, $df = 1, 1, 14$; $p = 0.99$; Site \times Sex: $F = 0.15$, $df = 1, 1, 14$; $p = 0.71$; Table 3).

Number of burrows used

In 2000, female tortoises used a similar number of burrows in the 3 plots at Ivanpah (4.5 , 1-way ANCOVA, $F = 1.72$, $df = 2, 1, 18$; $p = 0.21$; Table 2) and at FIRS (3.4 ; 1-way ANCOVA, $F = 7.12$, $df = 1, 25$; $p = 0.06$). In 2001, the multivariate general linear model with post hoc Bonferroni comparisons indicated that site had a significant effect ($p = 0.000$) on number of burrows used by tortoises, but that sex ($p = 0.606$) and the interaction of sex and site ($p = 0.425$) did not. Female tortoises in Ivanpah Valley used more burrows than tortoises at Fremont and Superior but similar numbers as tortoises at FIRS ($p = 0.05$). Tortoises at FIRS used more burrows than tortoises at Superior ($p = 0.05$), but similar numbers as tortoises at Ivanpah and Fremont (Table 3).

Maximum displacement

At FIRS and Ivanpah in 2000, MDM of females differed across months, but there was no significant difference in MDM between sites (repeated measures ANOVA, Month, $df = 1, 27, 2, 2, 36$; $p = 0.01$; Site, $df = 1, 27, 2, 2, 36$; $p = 0.17$; Month \times Site, $p = 0.47$). The longest displacements occurred in June and August and the shortest in July.

In 2001, tortoises in Ivanpah moved more in August (MDM) than in other months (repeated measures ANOVA, $df = 16, 4, 52$; $p < 0.01$). Ivanpah females moved greater distances than FIRS females in June through August, but in September and October, FIRS females moved farther (repeated measures ANOVA, Site $df = 1, 31, 4, 112$; $p < 0.01$; Month $df = 1, 31, 4, 112$; $p = 0.05$). Males at FIRS moved farther than females in July through October (repeated measures ANOVA, Sex $df = 1, 19, 4, 3, 69$; $p = 0.01$; Month $df = 1, 19, 4, 3, 69$; $p = 0.03$). Males at the Fremont site moved farther than females (repeated measures ANOVA, Sex $df = 1, 9, 1, 1, 9$; $p = 0.00$; Month $df = 1, 9, 1, 1, 9$; $p = 0.13$; Sex \times Month $p = 0.25$). Insufficient data precluded MDM calculations for the Superior site.

DISCUSSION

In 2000, female tortoises in Ivanpah Valley had significantly larger MCP areas and greater MDT between telemetry locations than females at FIRS. The MDT between telemetry locations was affected by time between locations, so that was not a useful measure of tortoise movement. There was no difference between sites in MaxDT, MDRM, number of burrows used, and MDM. In 2001, sex had a significant effect on all vari-

ables, except number of burrows used, with males having larger home ranges and moving greater distances than females. MDRM, number of burrows used, and MDM differed between sites. MDM also differed by month. Differences between sites and years were not consistently related to differences in rainfall.

Tortoise mortality

The mortality rate of adult tortoises monitored in 2001 was 5.0% for 60 tortoises. Luckenbach (1982) suggested that annual adult mortality rate is about 5%. Woodbury & Hardy (1948) found a 1% annual mortality rate over a 10 yr period. The mortality rate in 2001 was similar to that of desert tortoises studied in the Ivanpah Valley during 1980 to 1981 (4.4%; Turner et al. 1984). However, during 1981 to 1982, Turner et al. (1984) found a mortality rate of 18.4%. Similarly, Peterson (1994) found a 0% mortality rate for desert tortoises at Ivanpah Valley during 1988 and 1989 but a 41% mortality rate in 1990. Turner et al. (1984) and Peterson (1994) suggested that mortality rates might increase during drought years due to increased physiological stresses placed on the tortoises. Longshore et al. (2003) found that short-term drought caused severe reductions in desert tortoise survival near Lake Mead, Nevada, with a 0.218 survival probability for females and 0.319 for males over 7 yr at a site affected by drought. Field et al. (2007) reported that drought was correlated with a 21.4% mortality rate in 1 yr during a translocation study of desert tortoises in southern Nevada. Only female tortoises died during our study. They were probably more physiologically stressed due to reproductive costs. Wirt & Holm (1998) found that adult female desert tortoises suffered the highest relative mortality rate in a population of desert tortoises in Arizona over an 8 yr period.

Autocorrelation

Because O'Connor et al. (1994) found substantial autocorrelation of desert tortoise location data where the mean interval between locations was 3.2 d, we used a tracking interval of 7 to 10 d during 2001. However, Schoener's ratios of the MCP home range areas in our study were still autocorrelated. Spatial observations for these animals were not independent of each other. This is not unexpected, since the location of an animal on one day is related to its location on a previous day. Swihart & Slade (1985), among others, suggested that autocorrelated spatial data should be analyzed to determine at what sampling interval autocorrelation is eliminated. The data can then be

adjusted to only include independent locations for home range estimations. However, O'Connor et al. (1994) suggested that autocorrelation of tracking data was not a problem when comparing 'movement data between individuals, sexes, sites, and/or populations.' In addition, recent studies indicate that eliminating data points to achieve independence of observations reduces accuracy and precision of home range estimates (De Solla et al. 1999). Finally, altering sampling intervals typically causes an underestimation in home range sizes and rates of movements (Rooney et al. 1998). Therefore, while we recognized that autocorrelation occurred in our data, we chose not to eliminate any locations, since to do so would underestimate home range size.

Effects of sex on home range and movements

In this study, male tortoises had significantly larger home ranges than female tortoises at 2 of the 3 sites where we studied both males and females (FIRS and Fremont). The lack of difference at the Superior site was probably due to greater variability relative to mean MCP at that site. Males also had larger MDT and MDRM in 2001, but again MDT was not a good measure because it depended upon time between telemetry locations. These results are similar to those of Duda et al. (1999), Freilich et al. (2000), and Harless et al. (2009), who found that male desert tortoises had larger home ranges and moved greater distances than female tortoises. Male desert tortoises also had larger home range sizes than female tortoises in a translocation study in southern Nevada (Field et al. 2007). Home ranges in that study were similar to those of tortoises in Ivanpah and FIRS. At most locations in the Sonoran Desert, male tortoises have larger home ranges than female tortoises (Averill-Murray et al. 2002). In Texas tortoises *Gopherus berlandieri*, males also have larger home ranges than females (Rose & Judd 1975). The same is true of freshwater turtles (Morreale et al. 1984, Schubauer et al. 1990, Saba & Spotila 2003).

Burge (1977), Barrett (1990), O'Connor et al. (1994), and Stitt et al. (2003) found no sex differences in home range size in their studies on desert tortoise movements in the Mojave and Sonoran Deserts. However, when O'Connor et al. (1994) pooled the data from their study with those of Burge (1977) in the Mojave Desert in southern Nevada and with those of Barrett (1990) in the Picacho Mountains of the Sonoran Desert of Arizona, they found significant differences in home ranges between sexes. This indicates the need for large sample sizes in home range and movement studies. Geffen & Mendelssohn (1988) found that home ranges of a total of 18 male and female Egyptian tor-

toises did not differ. They suggested that the lack of significant difference was due to low sample size.

Site, rainfall, and season

Home range size and movement of tortoises at the 3 study plots at Ivanpah were similar, as was rainfall. In 2001, rainfall at all sites was greater but still similar, and there were no differences in home range size between sites.

A comparison of MCP versus rainfall between sites and years from this study and those of Duda et al. (1999) and Freilich et al. (2000) indicated that MCP generally increased with increased rainfall but that the relationship was confounded by differences in site characteristics that went beyond rainfall (Fig. 2). The linear regressions of home range size on rainfall were significant ($p = 0.05$), but the r^2 was only 0.2090 and 0.1466 for female and male tortoises, respectively, so the relationship did not explain very much of the variation in the data. For example, an annual rainfall of about 110 mm at the '29 Palms' site of Duda et al. (1999) and our FIRS, Ivanpah, and Superior sites gave MCPs of 2.1 to 9.1 ha for female tortoises and 5.8 to 26.4 ha for male tortoises. An annual rainfall of about 15 cm at the Joshua Tree National Park site of Freilich et al. (2000) and our Fremont site gave MCPs of 7.3 and 1.6 ha for female and 31.5 and 9.2 ha for male tortoises, respectively. Male tortoises had consistently greater MCPs than females, but the absolute results from 1 site would not predict the results from another site. Thus, there are other factors that are affecting this relationship. The productivity of annual vegetation is very important (Duda et al. 1999, Freilich et al. 2000, Longshore et al. 2003), and in addition to rainfall, edaphic factors can affect plant productivity. These factors may differ from site to site. Biotic factors such as intraspecific competition and danger of predation are also important.

Desert tortoises show many sex-based differences in energy budgets, behavior, and reproductive strategies (Turner et al. 1984, Peterson 1996a, Hemen et al. 1998). In turtles and tortoises, these sexual differences have been attributed to functional differences in habitat usage. Males roam more because they must actively search for mates (Schubauer et al. 1990). They also must defend territories, which requires them to traverse large areas to locate potential intruders (Morreale et al. 1984). Males also have more energy to support movements as they do not have to allocate resources for egg development. Detailed studies of the biophysical constraints imposed by different sites on male and female tortoises would help to clarify the mechanisms involved in determining the differences in home range sizes observed in this and other studies.

In June, July, and August of 2001, female tortoises in Ivanpah moved farther than female tortoises in FIRS. In October, females from FIRS moved farther than females at Ivanpah. These differences appeared to be related to differences in rainfall and associated plant productivity. Ivanpah received more rainfall than FIRS in both 2000 and 2001, although FIRS received much more rain in 2001 than in 2000. MDM of Ivanpah females peaked in August and then decreased through October. However, MDM of FIRS females increased throughout the season. Female tortoises at FIRS may have been forced to forage later in the season to balance energy budgets after egg laying and before hibernation because of the lower overall plant productivity at that site.

CONCLUSIONS

Desert tortoises, along with other reptiles living in highly variable, xeric environments, alter their behavior to minimize energy loss during drought years and maximize energy gain during productive years. During productive years, they increase movements and expand home ranges to exploit available resources. During drought years they restrict activity and spend most of their time in their burrows. This has serious implications for our ability to manage and recover this species and to prevent its extinction, because it is difficult to accurately assess the sizes and trends of populations affected by droughts (Freilich et al. 2000).

Desert tortoises are long-lived animals, with adults attaining 50 yr (Curtin et al. 2008). They are subject to many anthropogenically-mediated factors such as death on highways (Boarman & Sasaki 2006), disease (Jacobson et al. 1991), and raven predation on hatchlings and juveniles (Kristan & Boarman 2003). Ravens are subsidized by the increase in human habitation of the Mojave Desert (Boarman 2003), which also leads to an increase in tortoise deaths from gunshots, vandalism, surface disturbance, and trash (Berry et al. 2006). Desert tortoises are difficult to count accurately (Freilich et al. 2000), so we do not know how many animals are actually alive in the desert. Finally, global warming will cause an increase in variability of precipitation in the deserts of the southwestern US along with an increase in temperature (Cayan et al. 2006, 2008). This may lead to more drought years and greater periods of stress (i.e. lack of germinating plants and water) for the tortoise.

Therefore, to understand the biology of the desert tortoise and its response to climate change, it is necessary to expand studies such as this one to include biophysical measurements, measurements of foraging

availability, and use of telemetry to monitor tortoise home ranges and movements over multiple years at multiple sites. Surveys, counts, and line distance sampling are inadequate to assess populations and to understand the mechanisms controlling tortoise populations. While more habitat needs to be protected, more research is needed to better manage tortoise populations on land that is already protected.

Acknowledgements. We thank the US Army National Training Center at Fort Irwin for financial support through the Charis Corporation, the Earthwatch Institute for a grant, and the Betz Chair endowment of Drexel University for financial support for this research. We are indebted to the late D. Morafka for his assistance and advice during this research. He is sorely missed by all those studying the desert tortoise. We thank M. Ciferri, E. Flossic, L. Jarusewic, J. Fekete, C. Johnson, J. Behm, M. Griffin, M. Thyng, A. Curtin, A. Sieg, B. Wallace, S. Clusella, V. Izzo, and all other students and volunteers who assisted in the field. M. O'Connor, S. Kilham, and W. Bien provided valuable help in the analysis and writing of this manuscript. This research was approved by the Drexel University Animal Care and Use Committee and was carried out under permits from the US Fish and Wildlife Service, the Mojave National Preserve, and the State of California.

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Editorial responsibility: Jeffrey Seminoff,
La Jolla, California, USA

Submitted: September 30, 2009; Accepted: September 13, 2010
Proofs received from author(s): February 20, 2011