SAMPLING CONSIDERATIONS FOR IMPROVING HOME RANGE ESTIMATES OF DESERT TORTOISES: EFFECTS OF ESTIMATOR, SAMPLING REGIME, AND SEX

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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, the number of individuals, and other user-defined inputs differentially affect home range estimates using these two procedures. For the comparison of either MCP or FK estimates to be reliable, these variables need to be as similar as possible across studies. 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, and to identify factors important to space use by this species. 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 indicated that an increased sampling frequency inflates MCP estimates, while providing more use-specific detail and decreasing area for FK estimates. Analyses 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 for this and other species of herpetofauna. Both home range estimators provide valuable information on the biological needs of the Desert Tortoise and should be identified as a priority in land use investigations and conservation decisions for this species.

Key Words.—Desert Tortoise; *Gopherus agassizii*; home range; Mojave Desert; radio-telemetry; sampling

INTRODUCTION

An understanding of the land use and movement patterns of a species, in particular 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 (Kernohan 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*; Fig.1). However, the effectiveness of conservation efforts based on this information is likely hindered by the variety of methods and interpretations of how best to measure and identify spatial use by animals. Home range estimates may vary based on a number of factors, including method of estimation, number of locations, sampling frequency, study duration, distribution of locations, autocorrelation, software, and user-defined inputs (Seaman and Powell 1996; Lawson and Rodgers 1997; Mitchell, B.R. 2006. Comparison of programs for fixed kernel home range

analysis. Remotely Wild: Newsletter of The Wildlife Society's Geographic Information Systems, Remote Sensing, and Telemetry Working Group. Issue 21, June; Lever and Kelly 2008).

All home range estimation methods are not created equal, and each relies on different underlying assumptions with inherent positive and negative aspects. The two most widely used methods in studies on reptiles and amphibians are the minimum convex polygon (MCP; Mohr 1947) and the kernel density estimator (Silverman 1986). The MCP is formed by drawing a polygon using an individual's outermost capture locations such that no internal angle is greater than 180° (Hayne 1949). Thus, the MCP provides a crude measure of the total land area used by the focal animal during the year. Historically, the MCP was the most commonly used estimator because it is simple to use and is not constrained by underlying statistical assumptions.

The second most common home range estimation method, the kernel density estimator, provides an alternative measure of space use. The kernel method is

FIGURE 1. A Desert Tortoise (*Gopherus agassizii*) in its preferred habitat in the West Mojave Desert at Fort Irwin National Training Center, San Bernardino County, California, USA, in late March 2005. This was a very wet year with abundant winter annual plant production. (Photographed by Meagan Harless).

useful for identifying areas on the landscape that are of great importance to the individual. Kernel density estimators provide a utilization distribution 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).

These different estimators are uniquely constrained by factors related to study design and variables in calculation methods. 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 (Powell 2000; Taulman and Seaman 2000). The MCP also provides no measure of internal space use (Worton 1987) and tends to increase asymptotically with increasing number of locations (White and Garrott 1990; Seaman et al. 1999; Belant and Follmann 2002).

The kernel estimator, computed most often as the fixed kernel (FK; Seaman and Powell 1996), includes inherent statistical restrictions, such as the need for independent locations and the choice of smoothing parameters. For organisms that return to a specific location repeatedly throughout the year (e.g., burrows or dens), autocorrelation or non-independent locations are unavoidable. Numerous studies have addressed this issue (reviewed in Fieberg 2007). For understanding the space use of a species, Otis and White (1999) and De Solla et al. (1999) argued that random sampling in a stratified pattern over a long period of time is more important than constructing model-designed data sets that avoid autocorrelated data. Focusing on the avoidance of autocorrelated data may detract from the

main goal of home range estimation, namely understanding the space use of a species.

In addition to autocorrelation, estimation using the kernel method is complicated by a number of parameters set by the user, such as the smoothing factor *h*, which can have a drastic impact on estimates of home range area (Worton 1987, 1995; Seaman and Powell 1996). Estimates decrease asymptotically as sample size increases (White and Garrott 1990; Seaman et al. 1999; Belant and Follmann 2002), which is opposite of the MCP. 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). For these reasons, comparison of either MCP or FK home ranges across studies is relatively useless unless sampling regime and user inputs are similar.

Investigations on space use and movements of the Desert Tortoise illustrate the limitations of sample size, sampling frequency, and project duration on research with long-lived herpetofauna. As with many other reptile and amphibian species, this organism is difficult to study because of its cryptic nature, occurrence in low densities, frequent use of underground burrows for refuge, and inactivity for a large portion of the year (Ernst et al. 1994). Its threatened status (California Fish and Game Commission 1989; U.S. Fish and Wildlife Service 1990) also necessitates special permits and permissions. In addition, Desert Tortoises are well known to make frequent long-distance movements during the active season that further complicate home range calculations (Berry 1986; Boarman et al. 1996; Freilich et al. 2000; Edwards et al. 2004). Moreover, the long-lived nature of the Desert Tortoise makes the home range difficult to define operationally, as home range size varies from year to year and becomes larger as more years are included in analysis (Holt and Rautenstrauch 1996; Harless et al. 2009).

Most studies involving conventional radio-telemetry on Desert Tortoises have used a small number of individuals, usually fewer than 20 (e.g., Burge 1977; O'Connor et al. 1994; Freilich et al. 2000). Furthermore, home ranges were typically calculated using few locations per tortoise, often less than 25 (e.g., Woodbury and Hardy 1948; Medica et al. 1985; Duda et al. 1999). In only a few studies did sampling occur throughout a complete biological cycle, from early spring emergence to late fall dormancy (e.g., Burge 1977; Medica et al. 1985; Freilich et al. 2000), or across multiple years (e.g., Medica et al. 1985; O'Connor et al. 1994; Holt and Rautenstrauch 1996). In addition, many researchers utilized Jennrich-Turner (JT) correction factors to alleviate sample size bias in calculations of MCP estimates (Jennrich and Turner 1969). To further confound inferences, home range estimates using the MCP method on different populations of Desert

Tortoises are often compared between studies in an effort to better understand the spatial needs of this organism, yet no attention is given to the different sampling methodologies (O'Connor et al. 1994; Rautenstrauch and Holt 1995; Freilich et al. 2000). The variations in methods of home range estimation as well as numerous confounding factors in previous studies on Desert Tortoises highlight the need for a comprehensive investigation into the space use by this species.

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 factors 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 Desert Tortoises, an important metric without which effective management decisions and recovery of the species will be hindered.

MATERIALS AND METHODS

Study site and field techniques.—Our study site consisted of a remote and undisturbed 3.74 km^2 area in federally designated Desert Tortoise critical habitat in the southwest corner of the National Training Center at Fort Irwin, California (35º14'N, 116º75'W; 59 FR 5820-5866, U. S. Fish and Wildlife Service 1994a, b). The site, survey effort, and general methodologies have previously been described in Walde et al. (2007) and Harless et al. (2009). We mounted low-duty, cycle-pulsed transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA; Holohil Systems Ltd., Carp, Ontario, Canada) directly onto the carapace of each tortoise using epoxy, 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.

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

Sampling effort.—As part of a larger study on the behavior and ecology of the Desert Tortoise, we located transmittered animals using a systematic sampling scheme. In both 2004 and 2005, we completed tracking on a general schedule of one location per tortoise collected over Monday or Tuesday, with an additional location for each tortoise collected over Thursday or Friday of the same week. We located tortoises 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 (July and November). During December and January, we located tortoises once every one to two weeks. During the active season, we located tortoises in a random sequence. As Desert Tortoises were routinely observed in burrows, we standardized locations recorded at the same burrow number such 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) contained the largest number of locations as it 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. We did not locate some tortoises 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, we parsed the original data set for each year into four sampling regimes. 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. Sampling regime A (SR-A) included 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, we gave preference to locations collected on Monday and Tuesday of each week in an effort to ensure a consistent amount of time between locations. We gave preference in SR-C and SR-D 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.—We defined home range areas 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-squares cross-validation (LSCV) approach to standardize bandwidth in calculating the FK estimates, as recommended by Seaman and Powell (1996). We used the default smoothing factor (*h*) generated by the AME software in all kernel home range calculations. 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. In addition, we applied Jennrich-Turner correction factors (Jennrich and Turner 1969, Barrett 1990) to the MCP estimates from the four parsed datasets. We compared the resulting "adjusted" MCP estimates to estimates obtained from our SR-O sampling regime and from previous studies on the Desert Tortoise.

Effects of number of locations.—The home range literature lacks a standardized method to determine the number of locations needed when calculating home ranges using the MCP and FK estimators. The few researchers who 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, we used a bootstrap function to produce an area-observation curve for each tortoise using AME for ArcView 3.3 (Hooge et al. 1999). 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, we computed the MCP estimate 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. We then repeated calculations 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 defined forays as locations collected more than one km outside of the tortoise's normal polygon for 7–14 days (Freilich et al. 2000). We defined long-distance movements (LDMs) as a linear movement greater than 800 m (Boarman et al. 1996). 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 home range 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). We treated three of the four IVs – estimator (MCP, FK), year (2004, 2005), and sampling regime (five levels) – as within-subjects factors, and sex (two levels) as a between-subjects factor. The sample

TABLE 1. Number of radio-telemetry locations recorded for 35 Desert Tortoises (*Gopherus agassizii*) in the original and successive parsed sampling regimes in the West Mojave Desert, California, USA, 2004–2005.

	Sampling Regime				
	O	A	B	C	D
Total Expected	—	2730	1680	840	420
Observed 2004	3141	2492	1602	840	420
Observed 2005	3684	2726	1679	840	420
Expected Mean per Tortoise	—	78	48	24	12
Actual Mean Per Tortoise 2004	89	71	46	24	12
Actual Mean Per Tortoise 2005	105	78	48	24	12

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 did not include the variable body size (midline carapace length; MCL) in this model because supplemental analyses using MCL as a cofactor, with and without additional IVs, confirmed that it had a trivial influence on home range size (also see Harless et al. 2009). To examine the simple main effects of sampling regime on each estimator, we created additional ANOVA models for each home range estimator. We included the home range estimate (MCP or FK, depending on model) as the dependent variable in each model and three IVs: year (2004, 2005) and sampling regime (five levels) as within-subjects factors, and sex (two levels) as a between-subjects factor.

Home range estimates (both MCP and FK) failed to meet multivariate assumptions of normality and homoscedasticity; thus, we used log_{10}-transformed home range estimates in all statistical tests. We applied the Greenhouse-Geisser adjustment for degrees of freedom to all tests of hypotheses in the ANOVA models 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 η^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 greater than one, we divided each value by the sum of all values to obtain adjusted partial η^2 values. Using the MCP estimates from the bootstrap function, we compared the proportion of tortoises achieving the CV ≤ 0.10 criteria in each of the four sampling regimes using a Cochran's Q test (Conover 1999). We also compared Jennrich-Turner-corrected MCP estimates to SR-O estimates using a Wilcoxon test (Conover 1999). We performed all statistical analyses using SPSS v12.0 (2003, Statistical Package for the Social Sciences, Inc.,

Chicago, Illinois, USA). We set the alpha level for all analyses at 0.05. We report all means as the value ± 1 SE.

RESULTS

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

During the 2004 season, we recorded 3,141 locations from adult tortoises across the study site. The original data set resulted in a mean number of 89.7 ± 2.9 locations per tortoise in 2004, with females (mean = 79.8 ± 1.2) having 17.9% fewer locations than males (mean = 97.2 ± 4.4; Table 1). In 2005, we recorded 3,684 locations for a mean of 105.3 ± 1.9 per tortoise, with female tortoises relocated 9.1% less frequently (mean = 99.0 ± 1.6 locations) than males (mean = 109.9 ± 2.8). In addition to this sexual bias in SR-O, an artifact of not perfectly adhering to the sampling design, the methodology used in parsing the data resulted in some animals not exactly meeting the expectations of SR-A and SR-B in 2004 and 2005. For all animals, the numbers of observations were close to the number required by the sampling regime with more tortoises meeting the expectations of the sampling regime in 2005 than in 2004.

Factors associated with home range area.—The omnibus ANOVA model for home range area identified a number of significant interactions and main effects.
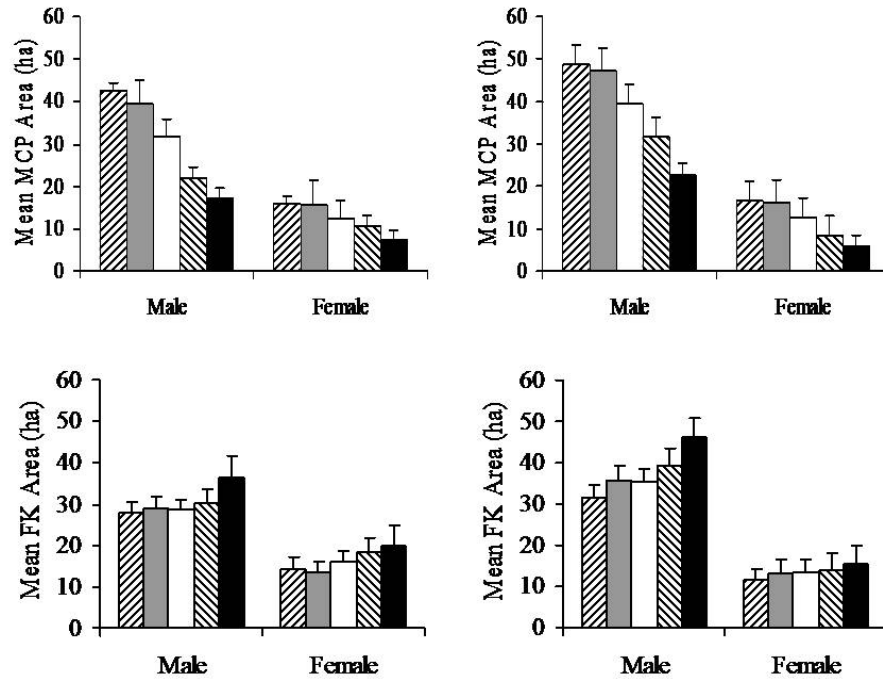
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FIGURE 2. Mean (+ 1 SE) home range estimates for 20 male and 15 female Desert Tortoises in the West Mojave Desert, California in 2004 (A, C) and 2005 (B, D). The 100% minimum convex polygon (MCP) estimates (A, B) and the 95% fixed kernel (FK) estimates (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 (■).

We detected a weak but significant interaction between year and sex ($F_{1, 32} = 4.37$, $P = 0.045$, 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; Table 2). We found a much stronger interaction between estimator and sampling regime ($F_{2.9, 95.1} = 186.96$, $P \leq 0.001$, 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 ($F_{1, 32} = 23.11$, $P \leq 0.001$, adj. partial $\eta^2 = 0.17$), with males exhibiting much larger home ranges than females regardless of year (Fig. 3). The main effect of estimator was also significant ($F_{1, 32} = 5.86$, $P = 0.021$, adj. partial $\eta^2 = 0.06$), with MCPs generally larger than FKs. Finally, the

TABLE 2. 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 West Mojave Desert, California, USA, 2004–2005.

		Home Range Estimate								
		MCP			Adjusted MCP[a]			95% FK		
		Male	Female	All	Male	Female	All	Male	Female	All
2004	SR-O	42.6 ± 1.5	15.8 ± 2.3	31.1 ± 1.9	—	—	—	27.9 ± 4.2	14.3 ± 2.6	22.1 ± 2.8
	SR-A	39.4 ± 9.4	15.6 ± 2.3	29.2 ± 5.8	50.3 ± 12.0	19.9 ± 2.9	37.2 ± 7.3	29.2 ± 3.3	13.5 ± 2.5	22.4 ± 2.5
	SR-B	31.7 ± 6.9	12.5 ± 1.9	23.5 ± 4.3	47.0 ± 10.3	18.6 ± 2.9	34.8 ± 6.4	28.3 ± 4.6	16.2 ± 3.3	23.3 ± 2.4
	SR-C	21.9 ± 3.5	10.7 ± 1.9	17.1 ± 2.4	43.4 ± 6.9	21.1 ± 3.8	33.9 ± 4.7	30.3 ± 4.6	18.5 ± 4.2	25.2 ± 3.3
	SR-D	17.0 ± 3.5	7.5 ± 1.8	13.0 ± 2.3	51.9 ± 10.7	22.7 ± 5.5	39.4 ± 6.9	36.4 ± 7.6	19.8[b] ± 5.8	29.3 ± 5.1
2005	SR-O	48.8 ± 7.7	16.6 ± 2.3	34.9 ± 5.5	—	—	—	31.7 ± 3.9	11.4 ± 2.0	23.0 ± 2.9
	SR-A	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
	SR-B	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
	SR-C	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
	SR-D	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
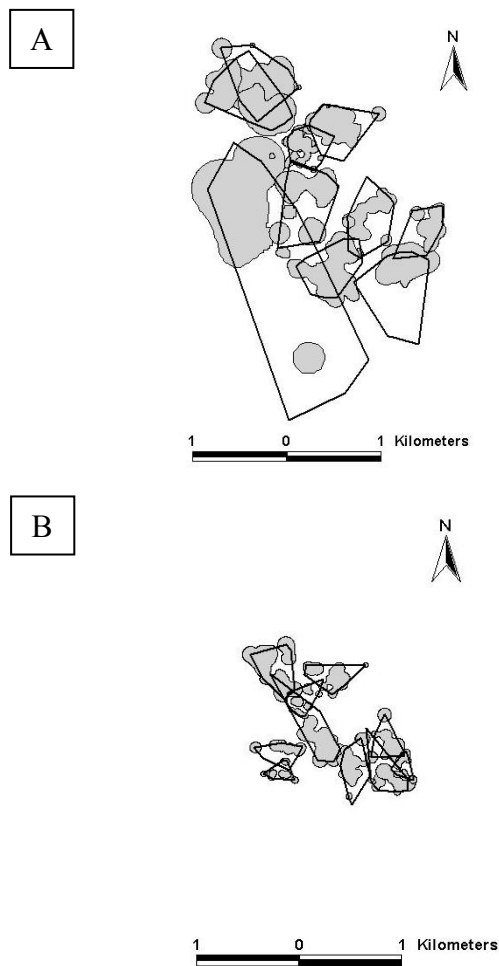
[b] N = 34 (see Results).

FIGURE 3. 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 individuals, A) male, and B) female Desert Tortoises (*Gopherus agassizii*) at Fort Irwin National Training center in the West Mojave Desert, California, USA in 2004. Map areas represent the same geographical position on the study site.

main effect of sampling regime was significant ($F_{1.6, 51.1}$ = 36.35, $P \leq 0.001$, adj. partial η^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 for MCP area ($F_{1.7, 56.3}$ = 180.92, $P < 0.001$, partial η^2 = 0.85) compared to FK area ($F_{1.9, 63.2}$ = 5.16, $P = 0.009$, partial η^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% FK estimate for all tortoises over both years was 33% smaller than the MCP area (Table 2). 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.

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, $P < 0.001$). The proportion of tortoises reaching and maintaining CV values below the threshold of $\leq 10\%$ was highest for SR-O (2004: 82.4, 2005: 51.4) and declined with each successively less-intensive sampling regime (SR-A 2004: 42.9, 2005: 31.4; SR-B 2004: 28.6, 2005: 20.0; SR-C 2004: 2.9, 2005: 5.7). The proportion of tortoises attaining the threshold value was greater in 2004 than in 2005 for each of the sampling regimes, except for SR-C.

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 for 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%.

Adjusted home range estimates.—Nearly all of the "adjusted" MCP areas calculated using Jennrich-Turner correction factors with the parsed sampling regimes were larger than the MCP areas calculated using the SR-O in each year. Adjusted MCP estimates for females in 2005 using SR-C were on average smaller by < 1%, whereas all other adjusted MCPs were on average larger than the raw estimates using SR-O (Table 2). 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–

TABLE 3. Minimum convex polygon (MCP) estimates (ha) and variable sampling methodology from current literature on Desert Tortoises (*Gopherus agassizii*) in the Mojave Desert, 1948–present.

100% MCP Home Range[a]			Number of Tortoises			Mean Number of Locations			Duration		
Male	Female	All (Range)	Male	Female	All	Male	Female	All	Months	Location	Source
—	—	20 (4–40)	—	—	182	—	—	4.5	99	NE Mojave	Woodbury and Hardy 1948
26	19	23 (11–38)[b]	3	3	6	138	220	179	8–15	NE Mojave	Burge 1977
23	11	(1–59)	—	—	—	—	—	—	—	NE Mojave	Hohman and Ohmart 1980*
—	—	22 (3–89)[c]	17	38	55	—	—	7	—	E Mojave	Turner et al.1984
—	—	19 (2–73)	25	52	77	—	—	14.5	9	E Mojave	Medica et al. 1985
53	21	(8–77)	—	—	—	—	—	—	—	E Mojave	Berry 1986[d]
21	9	15 (6–46)	8	7	15	31	25	28	5	E Mojave	O'Connor et al. 1994
53	18	33	16	22	38	—	—	>50	9	E Mojave	Holt and Rautenstrauch 1996
26	9	(3–44)	4	5	9	—	—	37	10[e]	W Mojave[f]	Duda et al. 1999
7	2	(0–14)	4	5	9	—	—	19	10[e]	W Mojave[f]	Duda et al. 1999
8	7	(1–17)	13	16	29	—	—	20	10[e]	W Mojave[g]	Duda et al. 1999
3	1	(0–14)	13	16	29	—	—	23	10[e]	W Mojave[g]	Duda et al. 1999
13	4	(2–24)	5	3	8	34	24	—	8	W Mojave[f]	Freilich et al. 2000
28	6	(3–35)	5	5	10	50	45	—	12		Freilich et al. 2000
32	7	(3–45)	4	5	9	48	47	—	12		Freilich et al. 2000
5	1	(0–12)	4	5	9	13	13	—	—		Freilich et al. 2000
43	16	31 (6–236)	20	15	35	97	80	90	12	W Mojave[h]	This study
49	17	35 (5–177)	20	15	35	109	99	105	12		This study

[a] Duda 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] Locations from January and February not included
[f] Joshua Tree National Park
[g] Marine Corp. Air Ground Combat Center
[h] National Training Center at Fort Irwin
* Hohman, J., and R.D. Ohmart. 1980. Ecology of the Desert Tortoise on the Beaver Dam Slope, Arizona. Arizona State University. Unpublished report for the Bureau of Land Management, Arizona Strip Office, St. George, Utah, USA.

203.9%) than the corresponding non-adjusted values, and this difference was greater as the sampling regime became less intensive (Table 2). Even when we compared only animals that reached the CV threshold (N = 33 and 15 for 2004 and 2005, respectively), the adjusted MCP estimates for SR-A were significantly larger than the SR-O estimates (averaging 15.8% and 21.3% larger in 2004 and 2005, respectively; Wilcoxon test, P ≤ 0.001 for both years).

DISCUSSION

Effects of sampling effort, number of locations, and long-range movements.—In examining the home range of the Desert Tortoise, we found great diversity among reported estimates and methodologies in the available literature (Table 3). 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 and the chosen sampling frequency. As shown in this analysis, sampling frequency has a large effect on home range estimates using the MCP. While solving some of the problems of statistical and conceptual implications, FK estimates are also affected by sampling frequency, and consequently autocorrelation, but to a lesser extent. For the sake of simplicity, we chose to compare only 100% MCP and 95% FK because these are the two most commonly reported estimators. We could have increased the scope and complexity of our study by

comparing other estimators (e.g., 95% MCP, 50% MCP, 50% FK); however, because FK and MCP measure different aspects of home range use, we expected sampling regime to differentially effect these more so than fine distinctions between different percentages of usage. For example, a 95% FK may yield a much larger estimate than 100% MCP depending on sample size or sampling regime (see Table 2) and the bandwidth used for computation of FK. Thus, in parsing data into sampling regimes that are representative of telemetry data from previous studies, we have demonstrated that sampling frequency significantly influences home range area using both the MCP and FK estimates.

The benefits of using a frequent and structured sampling regime in radio-telemetry studies on herpetofauna are important to consider when using such data for calculating home range estimates that are relied on heavily in making land conservation decisions (e.g., establishing protected areas). 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. For long-lived species, an increased sampling frequency will provide more detail in land use by the focal animal as far as both within- and between-year differences. More insight into the land use needs of the species throughout its life may be gained through this approach.

Although fewer than half of the tortoises in this study reached a stable MCP value according to the CV approach (with the exception of SR-O), we recommend the use of a structured sampling regime (such as SR-A) in future studies on Desert Tortoises. This sampling frequency represents a pragmatic schedule to adequately sample movement activities of the Desert Tortoise throughout the entire year (rather than weighting towards the active season) and will provide home range data that may be compared across studies on different populations. For long-lived species such as the Desert Tortoise, multiple years of data across environmentally variable conditions (e.g., wet and dry years) will be required to operationally define the species' home range and effectively model land use needs for the population. This sampling regime may also be applied in radio telemetry studies on other herpetofauna, with or without adjustments for differing activity levels.

The identification of occasional long distance movements in this population suggests that such movements are important to the survival of Desert Tortoise populations. Many researchers have speculated these movements may be used to aid in dispersal, search for prospective mates, locate higher quality food or shelter, find nesting or hibernating sites, or identify areas of limiting nutrients (Burge 1977; McRae et al. 1981; Marlow and Tollestrop 1982; Gibbons 1986; Boarman et al. 1996). 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). 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, suggesting that the SR-A sampling regime described in their methods was not followed. Alternatively, or in combination, the differences 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. Furthermore, in considering sampling frequency of 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.

Adjusted home range estimates.—For Desert Tortoises, JT correction factors possibly overestimate MCP home range areas. In our study, the correction factor increased the MCP area by as much as 25.3–203.9% within each successive sampling regime and averaged roughly 20% greater than the MCP values using SR-O in each year (Table 2). 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). Rautenstrauch and Holt (1995) also found these factors to increase home range size of the Desert Tortoise by up to 200%. Similarly, home range studies on other reptiles have demonstrated possible overestimation of MCP area when JT factors are applied (Rose 1982; Christian and Waldschmidt 1984; Perry and Garland 2002; Stone and Baird 2002). We do not recommend the JT correction factor in place of a comprehensive sampling regime, as this "correction factor" may overestimate the MCP home range area for Desert Tortoises.

Factors associated with home range area of Desert Tortoises.—Our analyses suggested that a number of factors may be more important in determining space use by Desert Tortoises than previously thought. We found a highly significant difference between sexes when using both 100% MCP and 95% FK area estimates. Studies of varying duration have attempted to demonstrate sex differences for *G. agassizii* in the Mojave Desert. 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 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. Similar analysis on Desert Tortoises from studies in different parts of the Sonoran Desert demonstrated males occupying significantly larger home range areas than females when data from multiple studies were combined (Averill-Murray et al. 2002). However, this difference was not significant within each of the six studies. These results suggest that these previous studies were too short in duration and/or had too few locations with a small number of tortoises to accurately test for sex differences in these populations of Desert Tortoises.

Previous studies have failed to clarify the effect of year or body size on 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) reported wide-ranging home range values in their four-year study, but did not specifically test for yearly differences. Regarding the effect of body size, our results agreed with O'Connor et al. (1994) and indicated a lack of a significant effect of body size on home range area in a population of adult tortoises in the eastern Mojave. Previous analysis on our population suggests that tortoise body size within the range of adults examined (201–285 mm) has no influence on home range area (Harless et al. 2009). However, our study and that of O'Connor et al. (1994) focused on adult tortoises that were large enough to carry a radio transmitter (> 180 mm). The relationship between body size and home range area may be different when both juvenile and adult tortoises are examined simultaneously. In addition, body size may not be a primary determinant of home range area in this species with factors such as sex, number of burrows used, and number of overlapping individuals playing a larger role (Harless et al. 2009).

The results of our study and previous work suggest that effects of year and body size on home range of *G. agassizii* warrant further analysis.

Management implications.—Despite statistical constraints, the FK method used in combination with MCP may best represent the total land use patterns of a species when derived from 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. Row and Blouin-Demers (2006) recommended the use of both estimators for determining home range sizes of herpetofauna. 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. Compared to MCPs, FK estimates are less affected by variable sampling regimes, accommodate long-distance movements equally well, and seem well suited to address the reliance of tortoises on localized burrows to meet life history requirements. However, because 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 such as land conservation, habitat protection, and translocation. Moreover, because inherent statistical assumptions such as autocorrelation and choice of smoothing factor limit the comparison of FK estimates among studies (and these are compounded further by differences among software programs; Mitchell, 2006), MCP estimates based on similar sampling regimes may be more readily compared among studies (Kazmaier et al. 2002; Row and Blouin-Demers 2006).

Radio-telemetry projects often must compromise the allocation of 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), particularly when studying long-lived species where multiple years of data may be required to effectively define the home range. For these species, careful planning in study design is imperative to produce reliable and comparable home range estimates. Our results indicated that an intensive and regularly-spaced sampling regime is the most pragmatic method to obtain minimally biased home range calculations using both the MCP and FK estimators. We recommend that a structured sampling regime that covers both active and inactive periods be used to estimate home ranges of Desert Tortoises and perhaps other herpetofauna with

local areas of intense use. Advancements in radio-telemetry, such as GPS transmitters, may allow researchers to collect a large number of locations for all individuals and across multiple studies using similar sampling regimens over multiple years. Standardizing the sampling methodology will facilitate comparisons of home range estimates between studies and the use of home range estimates for complementary investigations of land use such as joint-space use, resource selection, and/or social structure.

Understanding the space requirements of threatened, endangered, and at-risk species of amphibians and reptiles should be a priority for planning conservation measures. This is particularly important for *G. agassizii*, as 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) and administered by agencies with very different management goals. Basing land management activities in these areas on underrepresented home range estimates may hinder the ability of tortoises to cope with changing environmental conditions and inadequately provide for long-term sustainability of metapopulations and connectivity (travel corridors) between them. In light of recent interest in tortoise relocation as a management tool (Karl, A. 2003. Hyundai motor America Mojave test track site: Desert Tortoise translocation program. Unpublished report to Hyundai Motor America. 24 pages plus appendices; Esque, T.C., K.E. Nussear, and P.A. Medica. 2005. Desert Tortoise translocation plan for Fort Irwin's land expansion program at the U.S. Army National Training Center (NTC) and Fort Irwin. Prepared for U.S. Army National Training Center, Directorate of Public Works. 129 pages), increased knowledge of space use by tortoises and appropriate measurements of it will help to more effectively evaluate its effectiveness.

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