

Home Range and Dispersal of Texas Tortoises, *Gopherus berlandieri*, in a Managed Thornscrub Ecosystem

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ABSTRACT. – Southern Texas is dominated by *Prosopis-Acacia* mixed brush communities typical of the Tamaulipan Biotic Province, and the geographic range of the state-threatened Texas tortoise (*Gopherus berlandieri*) is nearly identical to the boundaries of this biotic province in Texas. In light of habitat fragmentation throughout southern Texas, we assessed home range use, movements, and natal dispersal of Texas tortoises at a managed site in the western Rio Grande Plains. Home ranges were larger for males (7–46 ha) than females (3–9 ha) regardless of method of home range calculation. Home range sizes determined by minimum convex polygon and bivariate normal methods were larger for individuals in ungrazed pastures (4–46 ha) relative to grazed pastures (3–15 ha), but home ranges derived from fixed and adaptive kernel estimators did not differ by treatment. Apparent treatment differences may be an artifact of an inability to adequately pair study areas given the scale of tortoise movement. Average distance between relocations indicated that males (74–153 m) moved more than females (31–41 m), but we did not detect differences in movement distances associated with grazing by cattle. Based on recapture distances of juveniles and adults, Texas tortoises appeared to exhibit male-biased natal dispersal. Our data suggest that Texas tortoises are highly mobile and may be capable of recolonizing across long distances following disturbance. Large home ranges suggest tortoises require large blocks of habitat to maintain stable populations. Populations of tortoises inhabiting small thornscrub fragments in the Lower Rio Grande Valley may be constrained by patch size of available habitat and have reduced recruitment because of dispersal losses.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus berlandieri*; tortoise; ecology; home range; dispersal; movement; cattle grazing; Texas; USA

The Texas tortoise (*Gopherus berlandieri*) is a conspicuous member of the Tamaulipan Biotic Province and the boundaries of the geographic range of this testudinid are nearly identical to the boundaries of this region (Blair, 1950; Iverson, 1992). All four North American tortoises (genus *Gopherus*) are of conservation interest (Bury and Germano, 1994). The Texas tortoise is considered threatened within the state of Texas, and the other three *Gopherus* receive some form of governmental protection because of declining populations (Bury and Germano, 1994; U.S. Fish and Wildlife Service, 1994). From ecological and conservation standpoints, home range use and dispersal are important characteristics of populations. Little information has been published on movements and home ranges of Texas tortoises (Rose and Judd, 1975, 1983) and knowledge of natal dispersal in reptiles is universally poor.

The Tamaulipan Biotic Province (Blair, 1950) of southern Texas is an ecologically diverse region composed of approximately 8 million ha of coastal prairies and inland shrublands. The western portion of the Tamaulipan Biotic Province or the Rio Grande Plains Ecoregion (Correll and Johnston, 1979) grades from *Prosopis-Acacia* savannas in the northwest to dense chaparral woodlands in the southeast. Landowners have

viewed brush invasion as a persistent problem within the western Rio Grande Plains (Archer, 1989, 1995), resulting in widespread application of range improvement techniques such as root-plowing, roller-chopping, chaining, and aeration to reduce woody vegetation and promote herbaceous vegetation for cattle (Archer, 1990; Kazmaier et al., 2001a). In southern and eastern portions of the region, habitat fragmentation has resulted from conversion of thornscrub communities for agriculture and urban development. These human-induced changes have resulted in extensive disturbance and fragmentation throughout the region, and only 1–5% of the original native brush remains in the Lower Rio Grande Valley (LRGV) (Jahrsdoerfer and Leslie, 1988).

In light of extensive human-induced modifications of thornscrub communities in southern Texas, we investigated the ecology of the Texas tortoise on a managed site in the western Rio Grande Plains. Our objectives were: 1) to assess home range size, movements, and dispersal of the Texas tortoise in contiguous habitat in the western portion of the Rio Grande Plains; 2) to use this information to discuss the potential effects of livestock grazing, brush manipulation, and habitat fragmentation on this protected species; and 3) make comparisons among various home range estimators.

METHODS

Study Area. — We conducted our work on the Chaparral Wildlife Management Area (WMA) in Dimmit and La Salle Counties, Texas. Chaparral WMA is a 6150 ha facility that has been managed as a research and demonstration area by the Wildlife Division of the Texas Parks and Wildlife Department (TPWD) since its acquisition in 1969. During our research, Chaparral WMA was composed of 15 pastures ranging from 258 to 750 ha. The area lies in the northern portion of the Tamaulipan Biotic Province (Blair, 1950) and the western portion of the Rio Grande Plains Ecoregion (Correl and Johnston, 1979).

Chaparral WMA is surrounded by a 2.4 m high woven-wire fence that was erected in 1983. Thirteen interior pastures are separated by 5 strand barbed-wire cattle fences (see Kazmaier et al., 2001b). A span of 2.4 m high woven wire fence also divides the area down the center into east and west grazing units. Two outlying pastures, Baldy and Mare, have remained ungrazed since 1976 and 1984, respectively, and are completely surrounded by a 2.4 m woven-wire fence. Fences do not impede tortoise movement. After complete removal of all cattle on Chaparral WMA in 1984, cattle grazing was reinitiated in 1991 with a one-herd, dormant-season, short-duration, rotational grazing system on each side (east and west) of the area. Under this system, each herd was composed of 341–448 steers and grazed a pasture for 3–8 wks each year depending on pasture size and forage availability (Kazmaier et al., 2001b).

Rainfall on Chaparral WMA is typically bimodally distributed with a primary peak in May–June, a secondary peak in September, and an annual average rainfall of 66 cm (1969–97; TPWD, unpubl. data). Quantity and timing of rainfall, however, is extremely variable in this region, and droughts are common. Although woody vegetation on Chaparral WMA is dominated by *Prosopis-Acacia* thornscrub communities, habitats tend towards denser thornscrub in the east and more open savanna in the west (TPWD, unpubl. data).

Tortoise Telemetry. — We focused radiotelemetry effort on the 2 ungrazed pastures (Baldy and Mare) paired with 2 grazed pastures (East Blocker and South Jay; Kazmaier et al., 2001b) for movement and home range analyses. Grazed pastures were chosen for pairing with the ungrazed pastures based on similarity in vegetation types, as defined by canopy coverage and dominant species of woody plants (Kazmaier et al., 2001b). Soils in all study pastures were red sandy loams (Hatch et al., 1990). Because tortoises are relatively inactive from mid-October to mid-April, grazing in South Jay and East Blocker pastures occurred during the spring (April–May) when direct interactions between cattle and tortoises were most likely to be observed.

We attempted to monitor 6 female and 4 male tortoises using radiotelemetry in each of the 4 study pastures. Radiotransmitters (ca. 20 g; L.L. Electronics, Mahomet, IL) were attached to adults > 500 g by mounting transmitter bundles to the anterior portion of the carapace using silicon rubber. Radiotransmitters were coated with a layer of sand

from the area of collection before the silicon hardened to help camouflage the transmitter bundle. We relocated radiotransmitted tortoises using a 2-element, hand-held yagi antenna and a TR-4 receiver (Telonics, Mesa, AZ) at least once weekly during the active season (15 April – 15 October) and once monthly during the inactive season (16 October – 14 April). Tortoises were monitored by radiotelemetry from 15 June 1994 to 1 September 1997. All relocations were carried out by walking in and visually observing tortoises. Positions were established for each relocation by pacing in a cardinal direction from the tortoise to the nearest road and then pacing to a landmark along the road. Universal Transverse Mercator (UTM) coordinates were computed from pacing distances using a Geographical Information System (GIS) with layers for roads and landmarks.

Movement. — Average distance between locations of radiotransmitted individuals was calculated for each tortoise using the program CALHOME (Kie et al., 1996). This measure was used to index minimum weekly movement and was compared between sexes and treatment (grazed and ungrazed) using ANOVA with side (east or west) as a blocking variable. Randomness of movement was assessed using the site fidelity test of the Animal Movement Analysis Program (Hooge et al., 1999) within ArcView (Environmental Systems Research Institute, 1999). This method compares the movement patterns of an individual with pathways derived from actual distances between sequential locations at randomized angles in a Monte Carlo simulation. Conclusions regarding site fidelity were based upon 1000 iterations for each tortoise.

Dispersal. — From June 1990 to August 1999, Texas tortoises were also captured by road-cruising throughout the Chaparral WMA. Upon capture, location was recorded on a map and straight-line carapace length (CL) was measured using dial calipers. Tortoises < 120 mm CL were unsexable by external characters and were considered juveniles. All tortoises > 120 mm CL were considered adults (Hellgren et al., 2000). Adults with thickened anal scutes, concave plastrons, and/or enlarged sublingual glands were considered males; adults without these characters were considered females. Most Texas tortoises on Chaparral WMA reach adult size in 5 yrs (Hellgren et al., 2000). After measuring and sexing, individuals were given a unique identification number by notching the marginal scutes and released.

Capture locations were plotted from capture maps into a GIS. Distance and direction between recaptures were calculated using ArcView (Environmental Systems Research Institute, 1999). With this methodology, multiple recaptures allowed the calculation of multiple movement distances and directions for each individual. Use of multiple recaptures, however, results in data that is not necessarily statistically independent. Thus, when multiple recaptures occurred for an individual, we only used the initial capture and the last recapture for calculating distance and direction traveled. This procedure sacrificed sample size in favor of statistical independence.

Recaptures were classified into 5 categories: juveniles recaptured as juveniles (JJ), juveniles recaptured as adult females (JAF), juveniles recaptured as adult males (JAM), adult females recaptured as adults (AAF), and adult males recaptured as adults (AAM). To compare movement distances among recapture categories, we conducted ANOVA on ranks because of non-normality of the data (Conover and Iman, 1981; Hora and Conover, 1984) and used number of years between recaptures as a covariate.

Direction of movement was classified into 4 categories: north (316–45°), east (46–135°), south (136–225°), and west (226–315°). Within each of the 5 recapture categories, frequencies for direction categories were compared using Chi-Square to determine if movement was random. Frequencies for direction categories were compared across recapture categories using Chi-square to determine if direction of movement varied by recapture category. All statistical analyses were performed with the Statistical Analysis System (SAS) (SAS Institute Inc., 1989) and comparisons were considered significant when $p < 0.05$.

Home Range Analyses. — Home ranges were calculated at the 100% and 95% levels using the minimum convex polygon method (MCP) (Mohr, 1947) and the 95% level using the adaptive kernel method (Worton, 1989) with the program CALHOME (Kie et al., 1996). Bivariate normal (Jennrich and Turner, 1969) and fixed kernel (Worton, 1989) home ranges were calculated at the 95% level using the Animal Movement Analysis Program (Hooge et al., 1999) within ArcView (Environmental Systems Research Institute, 1999). Multiple methods were utilized to calculate home range because of inherent differences among methods and to maximize comparison with other studies (Harris et al., 1990). We only used locations collected during the active season for analyses and only calculated home ranges for tortoises that had > 20 locations. To reduce effects of variable durations of monitoring, home ranges were calculated over only 2 active seasons for each tortoise. Thus, home ranges used for analyses encompassed either 1994–95 or 1995–96. Home ranges were compared between treatments and sexes using ANOVA with side (east or west) as a blocking variable. Home ranges were compared among methods using a repeated-measures ANOVA. Analysis of variance was performed on ranks because of non-normality ($p = 0.0001$) in the home range data (Conover and Iman, 1981; Hora and Conover, 1984). All statistical analyses were performed with SAS and comparisons were considered significant when $p < 0.05$.

RESULTS

Movement. — Distances between relocations of adult radioed tortoises were normally distributed ($p = 0.07$) and were not different between grazed and ungrazed areas ($F_{1,31} = 1.86$, $p = 0.156$). Movements were greater for males, however, than females ($F_{1,31} = 24.79$, $p = 0.001$; Table 1). Site fidelity tests indicated that all radioed tortoises exhibited movements that were more constrained than random.

Table 1. Sample sizes (n), number of days of monitoring, number of points used in analysis, and average distances (m) moved between relocations for radiotelemetered male and female Texas tortoises in grazed and ungrazed areas on Chaparral WMA, Dimmit and La Salle Counties, Texas.

	Female				Male			
	Grazed		Ungrazed		Grazed		Ungrazed	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
n	13		9		7		7	
Days monitored	450	28	456	19	410	31	487	8
No. of locations	31.1	1.7	40.7	5.9	35.1	5.0	37.9	6.0
Distance	74.0	7.9	74.4	9.7	106.9	11.7	153.4	12.3

Dispersal. — Distance between recaptures from the 10-yr dataset varied by recapture category ($F_{5,347} = 2.73$, $p = 0.024$). Juvenile males recaptured as adults had larger recapture distances than the other 4 recapture groups ($p \leq 0.029$; Table 2). Median movement distance for the JAM group (511 m) was nearly twice as far as all other recapture classes (176–261 m; Table 2). The longest movement recorded for an individual was 11.3 km after 368 days for a JJ tortoise. This movement occurred when the tortoise was 3–4 yrs of age and only 1 mm shorter than the minimum adult CL upon recapture. The third longest movement was 8.0 km after 22 days for a 5-yr old male. Thirteen of 20 tortoises that had movement distances > 4.0 km were 3–5 yrs of age at some time during the time interval when movements were made. Comparison of frequency distributions across the 5 recapture classes indicated no differences between movement directions of the groups ($\chi^2_{12} = 4.75$, $p = 0.970$). Within each recapture class, movement directions were not different from random ($p > 0.72$, $n = 479$; Table 2).

Home Range. — We monitored 36 tortoises (13F:7M on grazed sites; 9F:7M on ungrazed sites) for sufficient time to calculate home ranges. Although the number of locations used to calculate home ranges varied from 20–64, regressions within each sex and treatment indicated no relationship between number of locations and home range size ($p \geq 0.061$ for 100% MCP, $p \geq 0.061$ for 95% MCP, $p \geq 0.112$ for bivariate normal, $p \geq 0.204$ for fixed kernel, $p \geq 0.074$ for adaptive kernel). Number of locations used to calculate home ranges was not different between sexes ($F_{1,31} = 0.05$, $p = 0.817$) or treatment ($F_{1,31} = 0.64$, $p = 0.431$; Table 1).

Table 2. Comparison of movements between recaptures for non-telemetered Texas tortoises on Chaparral WMA, Dimmit and La Salle Counties, Texas, from 1990–99. Recapture history relates to the status (J = juvenile, A = adult; F = female, M = Male) of the individual at its initial capture and at its final recapture.

Recapture history	n	Distance between first and last capture (m)			Test for randomness of direction	
		median	\bar{x}	SE	χ^2	p
JJ	106	176	673	146	1.340	0.72
JAF	58	210	870	184	0.316	0.96
AAF	133	239	555	81	0.854	0.84
JAM	27	511	1478	347	0.356	0.95
AAM	155	261	759	108	0.922	0.82

Table 3. Home range size (ha) calculated by minimum convex polygon (MCP), bivariate normal (BV), adaptive kernel (ADK), and fixed kernel (FK) methods for radiotelemetered female and male Texas tortoises in grazed and ungrazed areas on Chaparral WMA, Dimmit and La Salle Counties, Texas. Home ranges are cumulative over 2 years, either 1994–95 or 1995–96.

Sex	Method	Grazed				Ungrazed			
		\bar{x}	SE	Median	Range	\bar{x}	SE	Median	Range
Female	100% MCP	5.0	1.4	3.3	1.0–19.8	6.8	2.1	4.9	1.5–21.6
	95% MCP	3.1	0.6	1.9	0.8–6.8	4.2	2.4	4.1	1.5–8.2
	95% BV	7.0	1.5	3.7	2.4–19.6	9.4	2.4	7.2	3.1–25.9
	95% ADK	6.4	1.4	4.4	1.9–19.0	7.8	1.7	6.2	2.5–15.0
	95% FK	4.0	0.5	2.7	1.1–8.8	4.8	1.1	4.7	1.9–12.8
Male	100% MCP	9.5	2.4	7.7	4.8–23.2	31.8	16.6	14.4	9.2–130.7
	95% MCP	7.6	1.9	5.3	4.0–19.0	20.6	9.4	10.4	5.8–75.8
	95% BV	15.0	3.4	14.7	7.7–33.6	46.0	21.2	23.5	15.7–170.2
	95% ADK	14.0	3.4	10.3	8.2–33.8	36.0	16.2	20.2	8.9–131.5
	95% FK	7.0	1.9	5.7	2.0–16.0	20.4	8.6	11.0	6.7–69.4

Home range sizes differed depending on method of calculation, with adaptive kernel and bivariate normal methods producing the largest home ranges and fixed kernel and 95% MCP methods producing the smallest home ranges (Table 3; Fig. 1). Comparisons between methods indicated differences in home range size based on methodology ($F = 5.0$, $p < 0.001$). Fixed kernel areas were not different from

95% MCP ($p = 0.694$) or 100% MCP ($p = 0.246$) areas, and adaptive kernel areas were not different from bivariate normal areas ($p = 0.627$) and 100% MCP ($p = 0.130$). All other pairwise comparisons revealed differences between methods ($p < 0.008$).

Home ranges were larger for males than females for all methods of calculation ($p < 0.001$ for 95% adaptive kernel, 95% fixed kernel, and both MCP methods, $p = 0.030$ for bivariate normals; Table 3). Tortoises in ungrazed pastures had larger home ranges than tortoises in grazed pastures when using the MCP ($p = 0.027$ for 100%, $p = 0.018$ for 95%) and bivariate normal ($p = 0.029$) methods, but this relationship was weaker for home ranges calculated by adaptive ($p = 0.103$) and fixed ($p = 0.077$) kernel methods (Table 3). Overlap between home ranges from different individuals was variable (Figs. 2–3). Interactions between treatment and sex were not significant ($p > 0.20$) for any home range method.

DISCUSSION

Movement and Dispersal. — We interpret the large movements between recaptures from juvenile to adult classes for males as evidence that Texas tortoises on Chaparral WMA exhibit male-biased juvenile dispersal. In general, mammals tend to utilize male-biased dispersal whereas birds have a tendency toward female-biased dispersal (Greenwood, 1980). Dispersal has been poorly addressed for reptiles, and we can find no references to juvenile dispersal for tortoises. Differential dispersal based on sex can be a mechanism to encourage outbreeding (Pusey, 1987). Much of the long-distance movement was tied to individuals that were 3–5 yrs of age. Female Texas tortoises on Chaparral WMA typically become sexually mature at age 5 yrs (Hellgren et al., 2000). Although we do not have data on male sexual maturity, male tortoises on Chaparral WMA begin to develop plastral concavities, thickened anal scutes, and enlarged chin glands at 4–5 yrs of age (RTK, unpubl. data). The appearance of these hormone-induced, secondary sexual characteristics coincides with the timing of long-distance movements by young males. The timing of natal dispersal at the onset of sexual maturity is

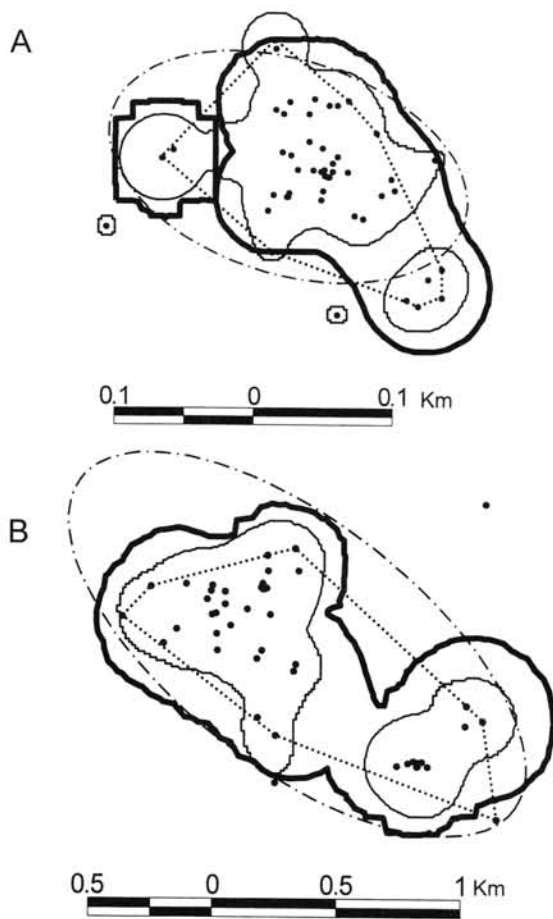


Figure 1. Comparison of home ranges (95%) derived from minimum convex polygon (dotted line), bivariate normal (dash-dotted line), adaptive kernel (thick solid line), and fixed kernel (thin solid line) methods for a representative female (A; 60 locations) and male (B; 64 locations) Texas tortoise from Baldy Pasture on Chaparral WMA, Dimmit and La Salle Counties, Texas (1994–95). Black points represent individual locations.

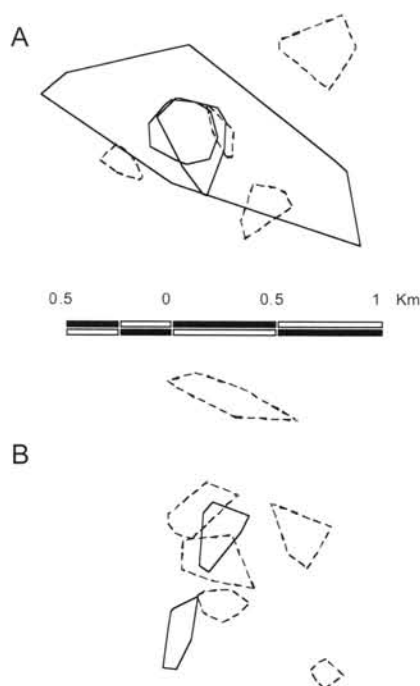


Figure 2. Minimum convex polygon (95%) home ranges for Texas tortoises from Baldy (A; ungrazed) and East Blocker (B; grazed) pastures on Chaparral WMA, Dimmit County, Texas (1994–96). Solid lines represent male home ranges and dashed lines represent female home ranges.

consistent with dispersal patterns exhibited by many birds and mammals (Greenwood, 1980).

Dispersal data derived from mark-recapture data suffer from constraints imposed by the size of the study area. We recorded a movement distance of 8 km in 22 days by a young male tortoise, yet the maximum possible distance between recaptures on Chaparral WMA is only 14.5 km on the east-west and 6 km on the north-south axes. Clearly, tortoises are capable of moving beyond the boundaries of the study area and our measurement of dispersal distance should not be considered to include maximum movement distances.

Home Range.—Home range size differed considerably depending on method of home range calculation. The MCP method has been criticized because it can include considerable unused space in home range estimates (Harris et al., 1990; Powell, 2000). Thus, various utilization distribution tests (i.e., kernel methods) are increasingly being used to describe home range (Worton, 1989; Harris et al., 1990). The 95% MCP method consistently produced smaller home ranges than bivariate normal or adaptive kernel methods, however. In some cases, the bivariate normal and both kernel methods produced home ranges that were so large that they incorporated portions of adjacent pastures that were not used by tortoises. Because development of kernel home ranges is dependent upon designation of a smoothing parameter (Worton, 1989), kernel estimates derived from the same data set can vary tremendously depending on the method used to obtain that parameter. The MCP method, however, consistently produces the same value from a given data set. Although kernel methods may be more desirable for

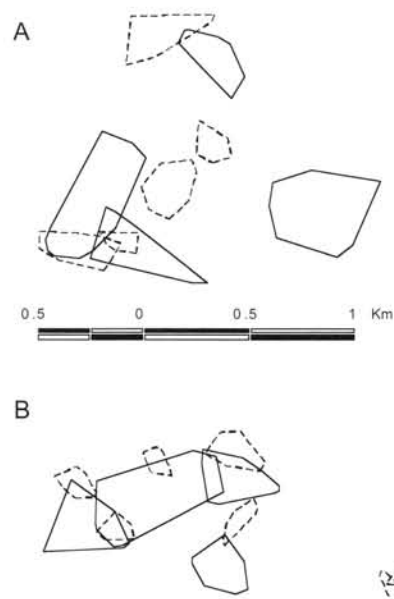


Figure 3. Minimum convex polygon (95%) home ranges for Texas tortoises from Mare (A; ungrazed) and South Jay (B; grazed) pastures on Chaparral WMA, La Salle County, Texas (1994–96). Solid lines represent male home ranges and dashed lines represent female home ranges. One disjunct male home range from South Jay pasture is not depicted for ease of presentation of the different pastures at the same scale.

delineating core areas within home ranges, we believe that MCPs provide the most useful estimate of the areal extent of home range size. Use of kernel home range estimators is potentially problematic when comparisons with other studies are desirable, because differences in the designation of a smoothing parameter and variable sample sizes between studies could cloud interpretations of the home ranges produced.

Texas tortoises on Chaparral WMA had much larger home ranges and movement distances than was reported previously. Judd and Rose (1983) reported home ranges (100% MCPs) for Texas tortoises as 0.47 ha for males and 0.34 ha for females for a coastal population in Cameron County, Texas, after a 5-yr study. In the same population, distances between recaptures averaged 57 m for males and 42 m for females (Judd and Rose, 1983). Judd and Rose (1983) also suggested that neither home range size nor movement distances varied by sex for tortoises in Cameron County.

Differences in range size and movements between Cameron County and Chaparral WMA might be linked to differences in plant productivity, area constraints of available habitat, low densities or skewed sex ratios leading to mate searching, or research methods. Because of higher primary productivity in the more equitable, mesic, coastal climate, foraging movements to meet nutritional demands may be reduced in coastal areas relative to more xeric inland sites. Additionally, the population studied in Cameron County existed on a loma (coastal clay hill). It is suspected that tortoises do not voluntarily leave lomas because of unsuit-

able surrounding habitat (Auffenberg and Weaver, 1969; Bury and Smith, 1986). Thus, home range size might be restricted to the areal extent of the study loma in Cameron County as compared to the large area of contiguous habitat on Chaparral WMA. Judd and Rose (1983) reported densities of 8–22 tortoises/ha for their Cameron County site, whereas densities on Chaparral WMA were < 1 tortoises/ha (Hellgren et al., 2000). Increased densities might decrease search effort to find mates and, thus, decrease home range size.

Some of the difference in ranging behavior between previous work and the present study might be methodological. Texas tortoises on Chaparral WMA were monitored by radiotelemetry, whereas tortoises in Cameron County were relocated using grid searches (Rose and Judd, 1975; Judd and Rose, 1983). Because grid searches by definition are conducted over a specified area, maximum possible size of home ranges was predetermined by the areal extent of the search area. The Cameron County study grid was only 3.3 ha (Judd and Rose, 1983). In addition, number of locations used to calculate tortoise home ranges in Cameron County were small (\bar{x} = 4.1 captures for males, \bar{x} = 8.7 captures for females; Judd and Rose, 1983). The degree to which these differences affect our ability to compare home ranges between studies is unknown. More comparative information between inland and coastal populations is needed to elucidate factors causing regional differences in home range size.

Texas tortoises from Chaparral WMA have large home ranges relative to their body size (< 180 mm CL) compared to gopher (*G. polyphemus*) and desert (*G. agassizii*) tortoises. Gopher tortoise home ranges have been reported as 0.04–1.44 ha in Georgia (McRae et al., 1981) and 0.002–1.4 ha in Florida (Diemer, 1992; Smith, 1992). The largest home range reported for a gopher tortoise is 3.1 ha (Gourley, 1969 in Ernst et al., 1994). Desert tortoises exhibited home ranges of 4.0–40.5 ha in Utah (Woodbury and Hardy, 1948), 1.0–53.0 ha in Arizona (Vaughan, 1984; Barrett, 1990; Averill-Murray et al., 2002), 5.9–46.0 ha in Nevada (Burge, 1977; O'Connor et al., 1994), and 0.4–34.0 ha in California (Vaughan, 1983).

Mechanisms causing variation in range use patterns among and within the four *Gopherus* spp. are not understood and deserve further attention. *Gopherus polyphemus* presumably have small home ranges because of their obligatory reliance on burrow systems and the relatively high primary productivity in the southeastern United States. Although *G. agassizii* also use burrows, they rely on them to a lesser extent than *G. polyphemus*, and the less productive deserts of the southwestern United States probably necessitate larger foraging movements and, thus, larger home ranges. Texas tortoises on Chaparral WMA have large home ranges relative to other *Gopherus*, do not normally use burrows (Rose and Judd, 1982; Kazmaier, 2000) and exist in a region intermediate in primary productivity between the other North American tortoises (Germano, 1994).

Male Texas tortoises on Chaparral WMA had larger home ranges and exhibited greater activity than female tortoises. Behavioral analyses have indicated that males tend to be more active than females (Kazmaier et al., 2001c), and they frequently made long, linear forays for distances up to 1.7 km. These forays were common in July–September and often ended in close association to a female (RTK, *pers. obs.*). Female tortoises also made occasional long forays for distances of up to 0.8 km in May–June. Because of their timing and/or interactions with other tortoises during these movements, we interpret the long-distance male movements as mate seeking and female movements as nesting movements. Whereas females typically returned to their previous center of activity following such movements, males frequently resided in the new area for several weeks. Long forays for mate searching and nesting appear to be rather common across turtle taxa (Gibbons, 1986), and such movements may be responsible for the differences in home range size and activity between the sexes observed here. Our interpretations are also consistent with observations made on *G. agassizii* in the Sonoran Desert (Averill-Murray et al., 2002).

Male *G. polyphemus* tend to have larger home ranges than females (McRae et al., 1981; Diemer, 1992). Similarly, a tendency exists for male *G. agassizii* to have larger home ranges than females (Berry, 1986; Averill-Murray et al., 2002), but Vaughan (1983) reported larger home ranges for females (\bar{x} = 7.0 ha) than males (\bar{x} = 5.5 ha). In addition, both Barrett (1990) and O'Connor et al. (1994) found no differences in home range size between the sexes in the populations they studied.

The home ranges we observed demonstrated little overlap between adjacent tortoises and this could be interpreted as territoriality. Texas tortoises are known to be extremely aggressive towards conspecifics (Weaver, 1970), and this aggression could influence spacing patterns. However, we argue against the interpretation that Texas tortoises are territorial on Chaparral WMA using our radiotelemetry data, because we only monitored a few of the adult tortoises present in each study pasture. Examination of all tortoise captures in these study areas from fortuitous captures and road-cruising over a larger time frame (1990–96) suggests a great deal of overlap in range use (TPWD, unpubl. data), and we have never observed aggression between Texas tortoises on Chaparral WMA. Exploration of territoriality would require more intensive monitoring than was possible during our study, but our perception of overlapping home ranges of *G. berlandieri* is consistent with observations made on *G. agassizii* in the Sonoran Desert (Averill-Murray et al., 2002).

The apparent effects of grazing on home range size of Texas tortoises varied depending on method of calculation. Measurement of home range by MCP and bivariate normal methods produced larger home ranges for individuals on ungrazed areas compared to grazed areas. Calculation of home ranges using fixed or adaptive kernel methods suggested no relationship between grazing and range size.

Decreased home range size in grazed pastures could be a response to increased resource (*i.e.*, forage) availability as a response to disturbance from cattle. Increased vegetation diversities and abundances of certain species are common under intermediate levels of disturbance (Collins and Barber, 1985; Gibson, 1989), and total forb cover does increase with grazing on Chaparral WMA (Ruthven et al., 2000). If disturbance by cattle increases the availability of food plants important to tortoises, then home range size might decrease. Unfortunately, the diet of the Texas tortoise is poorly characterized and it is not known how important food items, such as *Commelina erecta* and *Evolvulus* spp., respond to disturbance.

Alternatively, differences in home range size between treatments might be an artifact of inadequate pairing of sites. This study was designed with the assumption that Texas tortoises on Chaparral WMA would behave similarly to those that had been previously observed in Cameron County, Texas (Rose and Judd, 1975; Judd and Rose, 1983). However, Chaparral WMA tortoises had much larger home ranges. As a result, as tortoises made longer than expected movements, they incorporated habitats that differed between the paired sites. This effect was notable on the west side where an exposed sandstone escarpment and an adjacent blackbrush acacia (*Acacia rigidula*) zone were frequently utilized in Baldy Pasture (ungrazed), but were unavailable in East Blocker Pasture, the paired grazed pasture. A similar problem occurred on the east side where a region dominated by hogplum (*Colubrina texensis*) was used by radioed tortoises in Mare Pasture (ungrazed), but was absent from South Jay Pasture, the paired grazed pasture.

Rose and Judd (1982) suggested that the presence of cactus is essential to Texas tortoises. Baldy pasture had lower cactus density relative to the other study sites and this may have influenced home range size in that pasture. However, some robust tortoise populations exist in the Lower Rio Grande Valley (LRGV) on areas with very low cactus densities (RTK, unpubl. data). Texas tortoises on Chaparral WMA, however, seem to use habitats in proportion to their availability at the macro-scale, except for selective avoidance of old field and dense riparian habitats that represent extremes in canopy coverage (Kazmaier et al., 2001a). Thus, Texas tortoises do not seem to select either for or against the hogplum and blackbrush acacia habitats that seemed to disrupt our pairing of pastures. These observations suggest that if differences in home range size are an artifact of differential availability of habitats instead of an effect of grazing, Texas tortoises were responding to habitat variables that we did not measure or to different spatial scales.

Because of the difficulty in decoupling effects of cattle grazing from differences in habitat availability on home range size of Texas tortoises in our study, we need more information to determine if the grazing regime utilized by Chaparral WMA has an effect on home range size for this tortoise population. However, the lack of compelling evidence for effects of cattle grazing on demography, growth,

or behavior of the Texas tortoise on Chaparral WMA (Kazmaier et al., 2001b,c) lead us to believe that any differences in home range size attributable to grazing are minor. Ultimately, the effects of grazing are tied to the intensity and duration of grazing and potential exists for other grazing systems utilized in southern Texas to affect tortoises. Thus, examination of Texas tortoise populations exposed to different grazing regimes is certainly warranted.

Range use and dispersal by Texas tortoises have important implications for the sustainability of this protected species in Texas in the context of increased fragmentation and habitat manipulation throughout much of the Rio Grande Plains. Widespread use of range management techniques that convert woodland and savanna habitats into old-field areas to benefit cattle may directly kill tortoises and produce habitats that are not readily utilized by tortoises (Kazmaier et al., 2001a). However, if these communities are allowed to recover and source populations exist, Texas tortoises, particularly juveniles, are capable of moving considerable distances for recolonization.

The potential effects on tortoises of conversion of land to agriculture and the resulting habitat fragmentation needs further exploration, particularly in the LRGV. Assuming that tortoise dispersal in the LRGV is similar to Chaparral WMA, agriculture has become so extensive in some regions that tortoises dispersing from remaining habitat islands cannot move sufficient distances to locate other suitable habitat. Some populations in the LRGV appear to have age distributions much more skewed to older age classes than tortoises on Chaparral WMA (RTK, unpubl. data), and this difference could be partially the result of losses from juvenile dispersal. Home ranges exhibited by tortoises on Chaparral WMA were often larger than some of the habitat fragments remaining in the LRGV. Although it has been reported that tortoises in the LRGV have small home ranges (Rose and Judd, 1975; Judd and Rose, 1983), this could be an artifact of methodology. If tortoises in the LRGV actually require larger than these reported home ranges to obtain resources, then they may be constrained by the small size of the remaining habitat patches. Further evaluation of regional variation in range use by Texas tortoises is necessary to address these issues. Comparisons of Texas tortoises at both the population and genetic level between natural habitat islands (*i.e.*, lomas) and nearby man-made fragments in the LRGV would aid in understanding the implications of increased fragmentation on this threatened taxa.

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